Ajith H. Perera · Brian R. Sturtevant
Lisa J. Buse *Editors*

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Preface

Simulation models of landscape disturbances have proliferated and matured. They are now applied to an extent that would have not been conceivable a few decades ago, when we began to perceive the processes that "disturb" or disrupt ecosystems as integral mechanisms that shape the spatial patterns of forest landscapes. A large proportion of the scientific papers on landscape ecology are dedicated to this topic, as are many graduate theses and dissertations. In this context, it is timely that we explore efforts to model forest landscape disturbances so that we can capture the current state of knowledge and ponder future directions. In this book, we have sought the insights of a group of ecologists who focus on a range of forest landscape disturbances and develop simulation models to study those disturbances. The topics they address include a wide variety of disturbance processes: physical disturbances such as drought, wind, and fire; biological disturbances such as defoliating insects, bark beetles, and tree pathogens; anthropogenic influences; the interactions among disturbances and climate change; and the recovery of forest landscapes from disturbances—all from a simulation modeling perspective. Their discussions and examples offer a broad synopsis of the state of this rapidly evolving subject.

This book will be relevant to those who develop and apply models or who are interested in understanding and exploring forest landscape disturbances using simulation models. As such, it will appeal to academics, researchers, and graduate students, as well as to advanced users of models in applications related to managing forest landscapes. We hope that readers will benefit from the authors' explorations of the current state of modeling of forest landscape disturbances and their insights into where these efforts should be heading. Readers should not expect this compilation to be a comprehensive treatise on specific models, an enumeration of the available models, or an exhaustive review of the literature. Nor will they find a user manual that defines when or how to use individual models. Rather, our intent is to provide general insights into current approaches and, in doing so, highlight the gaps in knowledge to help focus future efforts to advance the modeling of forest landscape disturbances in natural ecosystems as well as in increasingly anthropogenically influenced ecosystems.

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Chapter 1
Simulation Modeling of Forest Landscape Disturbances: An Overview

Ajith H. Perera, Brian R. Sturtevant and Lisa J. Buse

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1.1 Background

Quantification of ecological processes and formulation of the mathematical expressions that describe those processes in computer models has been a cornerstone of landscape ecology research and its application. Consequently, the body of publications on simulation models in landscape ecology has grown rapidly in recent decades. This trend is also evident in the subfield of forest landscape ecology, particularly in relation to the topic of disturbance.

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Broad-scale disturbances are prevalent in forest landscapes, and sometimes they are inherent to the evolution of those systems: disturbances create patterns and heterogeneity, which in turn influence ecological processes and flows (Turner 2010). The broad spatial and temporal scales of disturbance processes substantially limit our ability to perform the kinds of manipulative experiments necessary to understand the underlying mechanisms of these processes and the spatial patterns they create in forest landscapes. Instead, we can use simulation models as a fundamental vehicle to explore and understand disturbance processes, impacts, and patterns.

As with all ecological models, the simulation models developed for forest landscape disturbances are approximations of nature; that is, they are a simplified portrayal of vastly complex biological, physical, and chemical processes that interact with each other and among scales. Such models are founded on scientific knowledge, logic, and assumptions, and typically require large arrays of spatially explicit input data. The expanding knowledge base and data available to support these models also necessitate their continuous testing, study, and improvement. Simulation modeling of some disturbance types in forest landscapes is relatively mature, whereas for others it remains in the very early stages. Still other disturbances have not yet even begun to be formulated as simulation models.

Simulation modeling of forest landscape disturbances is not only a burgeoning field of research and academic pursuit. This research effort has also led to widespread application of the resulting understanding of forest landscape disturbances in management efforts: It is becoming increasingly common to consider applications of forest landscape disturbance models in exploring and devising land management policies and strategies.

It is in this context that we explore simulation modeling of forest landscape disturbances in this book. Specifically, we examine the present state of knowledge and explore future possibilities for quantifying forest landscape disturbances at broad spatial and temporal scales. This first chapter provides an overview of the topic and a general guide to the scope and contents of the book.

1.2 The Topic

To frame the topic, it is necessary to describe, if not define, what is meant by the three major terms that form the book's title: (a) forest landscapes, (b) disturbances, and (c) simulation modeling. However, we do not intend to embark on an exhaustive review and a critique of the very large body of literature on these topics or to compare and contrast the range of terms and views therein. Such a task is beyond the scope of this chapter. Therefore, while acknowledging that there will be a diversity of views and preferences about these terms, we briefly describe them in the context of the contents of this volume.

1.2.1 Forest Landscapes

By *forest landscapes*, we mean large areas of land dominated by forest cover. From an academic viewpoint, the scale of a "landscape" is best defined from the perspective of the organisms that interact with that landscape (Allen and Hoekstra 1992). More pragmatically, landscape can be defined from the human perspective to provide insights into the processes that affect the system's dynamics at scales relevant to human decision-making. As a working definition, we adopt the description by Perera et al. (2000): a forest landscape is a large geographical unit dominated by a mosaic of forest cover types, sometimes interspersed with non-forest cover types, including those that have been altered by anthropogenic activities. In North America, the source of most of the examples in this book, such milieus include expanses of forest in boreal plains, forests in both western and eastern mountain ranges, and pine-dominated southern forests. In practice, a forest landscape is a unit of land demarcated by a specific research question and method or by a specific management goal—an ecological system that is dominated by spatially interspersed tree communities of different ages and species, and that encompasses other vegetation communities and bodies of water.

1.2.2 Disturbances

By *disturbances*, we propose a description based on those of Rykiel (1985) and Pickett and White (1985): events that cause drastic changes in the state of an ecological system (for our purposes, a forest landscape) in response to a physical or biological cause. Often, the causal agent originates outside the boundaries of the ecological system of interest and results in a *perturbation* of the minimal structure, and therefore the function, of the system (Pickett et al. 1989).

Most such disturbances are considered to be discrete events (Rykiel 1985). Given the short duration of these events, some authors describe them as "pulse" disturbances (Bender et al. 1984). In contrast, continuous and slow disruptive forces can also result in perturbations that create a stress on the system (Rykiel 1985). These have been referred to as "press" disturbances (Bender et al. 1984). Descriptions and definitions of these terms are summarized in Table 1.1. A continuous period of stress can also eventually result in perturbation of the forest landscape's state and of its minimal structure. Perturbations are also scale-related: a disturbance can cause perturbation of an individual system's subcomponents or of the whole system (Pickett et al. 1989). Extreme but rare disturbances represent a distinct category, as they destroy an entire forest landscape system and its structure. These catastrophes are termed "LIDS"—large and infrequent disturbances (Foster et al. 1998).

Regardless of the temporal aspects of a disturbance event, perturbations caused by external disturbance agents markedly exceed the ranges of fluctuations in

Table 1.1 Common terms used to define, describe, and categorize ecological disturbances

Term		Definition and descriptions	Source
Event		Any relatively temporally discrete occurrence that disrupts an ecosystem, community, or population structure and changes the resources, substrate availability, or physical environment	White and Pickett (1985)
		A physical force, agent, or process, either abiotic or biotic, which causes a perturbation (an effect or change in the system's state) of an ecological component or system	Rykiel (1985)
		A change in the minimal structure caused by a factor external to the level of interest	Pickett et al. (1989)
		The cause of a perturbation	Glasby and Underwood (1996)
		An initiating cause (a physical force, process, or event) that produces an effect (a consequence) that is greater than average, normal, or expected	Coulson and Tchakerian (2010)
Type	Abiotic	Events in the physical environment that cause an abrupt change. (White does not use the term "abiotic", but separates physical from biotic effects)	White (1979)
	Biotic	The effects of biological agents such as insect and disease outbreaks	
Origin	Autogenic	The change is driven by biological properties of the system	White and Pickett (1985)
	Allogenic	The change is driven by an external environmental "forcing" function	
Duration	Pulse	A relatively instantaneous alteration of some aspect of the system, such as the number of species (i.e., a sudden and short-term event)	Bender et al. (1984)
		A short-term, high-magnitude change in the ecological environment	Glasby and Underwood (1996)
	Press	A sustained alteration of some aspect of the system, such as species densities (ongoing or long-term)	Bender et al. (1984)
		A long-term, low-magnitude, change in the ecological environment	Glasby and Underwood (1996)

structure and function that are characteristic of the ecological system (Coulson and Tchakerian 2010). Disturbances inherent to ecological systems are termed *autogenic*, whereas those that arise outside the system are referred to as *allogenic*, even though such classifications, as is the case with the terms *endogenous* or *exogenous*, are arbitrary because disturbances are a continuum (Pickett and White 1985) and are highly dependent on the spatial and temporal scales that define the system. Given the ever-increasing extent, intensity, and variety of anthropogenic impacts on forest landscapes, it has become common to separate them from non-anthropogenic disturbances, and refer to the latter category as “natural”. Not only is that distinction sometimes arbitrary, the term natural could also mean *typical* (as opposed to *atypical*), *normal* (vs. *abnormal*), and *inherent* (vs. *exogenous*), and may therefore be misleading (Suffling and Perera 2004). Forest landscape systems may be perturbed by a single disturbance agent or by several agents acting independently or interactively. Multiple serial disturbances could result in cumulative effects in forest landscapes, leading to nonlinear or unanticipated responses. Furthermore, with respect to disturbance, the line between “anthropogenic” and “natural” is inherently fuzzy, since humans modify disturbances both directly and indirectly through their actions. However, human actions are also strongly affected by social, political, and economic forces operating at scales much larger than landscapes. Within the context of this book, we acknowledge that these forces shape nearly all forest landscapes, but we do not examine these dimensions in any meaningful way (i.e., from the perspective of disturbance modeling). For this reason, we distinguish between *ecological* disturbances that occur with or without human influence, and *anthropogenic* disturbances that are the direct result of human actions.

All ecological disturbances in forest landscapes can be categorized in the context of the terms described in Table 1.1. Some examples of abiotic and biotic disturbances (White 1979) distinguished by the duration of the disturbance event (Bender et al. 1984) are provided in Table 1.2. Anthropogenic disturbances can be viewed as a third type, with their own duration: pulse (e.g., clearing of land, clear-cut harvesting) or press (e.g., pollution, recreational use).

When aggregated in space and time, various aspects of disturbance events, such as their intensity, extent, and spatial and temporal probability of occurrence, can be characteristic of certain ecological systems. These synoptic properties are termed a *disturbance regime,* which has been variously described and defined (Table 1.3) and which has been assigned a range of attributes (Table 1.4). Some reserve this term for the population characteristics of one disturbance type, whereas others include a suite of different types within a disturbance regime (Suffling and Perera 2004; Coulson and Tchakerian 2010). Individual disturbance

Table 1.2 Examples of forest landscape disturbances based on their type (*sensu* White 1979) and duration (*sensu* Bender et al. 1984)

Forest landscape disturbance trait		Duration	
		Pulse	Press
Type	Abiotic	Earthquake, lava flow, landslide, flood, windstorm, ice storm, wildfire	Drought, water table fluctuation, temperature fluctuation, soil freeze–thaw cycles, soil erosion and deposition
	Biotic	Pest outbreaks, clearing of land, flooding by beavers	Disease, low-intensity harvesting, grazing

Table 1.3 Common terms used to describe and define disturbance regimes

Descriptions and definitions	Source
Disturbance regime depends on the particular disruptive force and responses being studied; descriptors include the spatial extent, magnitude (intensity or severity), frequency, predictability, turnover rate, and rotation period	Sousa (1984)
Disturbance regime is described by distribution, frequency, return interval, rotation period, predictability, magnitude (intensity or severity), and synergistic effects	White and Pickett (1985)
Disturbance regimes are characterized by all natural and human-caused disturbance drivers that are present, their stochastic and regular spatial and temporal distributions, their intensities, and the severities of their effects on the landscape's component ecosystems, including interactions between different disturbance agents	Suffling and Perera (2004)
Disturbance regime represents the ensemble of disturbance types associated with a specific landscape environment	Coulson and Tchakerian (2010)

events that exceed the expected characteristics of a disturbance regime are termed *extreme events* (Alvarado et al. 1998).

Figure 1.1 illustrates the concept of ecological disturbance and the associated terms as they are applied within the context of this book. We identify three major components associated with the entire sequence, which we call the *disturbance process*: the cause(s), effect(s), and result(s) of a disturbance event. These components comprise the intrinsic characteristics of the disturbance agent(s), the interactions among disturbance agents and the forest landscape in time and space, and the resulting altered state of the forest landscape. These are the main domains of study in disturbance ecology, and are the focus of efforts to simulate forest landscape disturbances.

Perturbed forest landscapes recover over time, with changes occurring in landscape composition, patterns, and processes. The landscape will eventually reach a state similar to its pre-disturbance condition or, in some cases, achieve an entirely different state. The nature of the recovery process is the focus of forest succession research, whether the system characteristic being tracked is a process, a pattern, or landscape composition.

1.2.3 Simulation Modeling

By a *simulation model*, we mean (*sensu* Hall and Day 1977; Rosen 1991; Oreskes 2003) a mathematical simplification of an ecological system and its processes (here, a forest landscape and the associated disturbance processes) for the purposes of exploration, scenario-building, projection, prediction, and forecasting. By s*imulation modeling*, we mean the acts of developing or applying a simulation model. Developing a simulation model involves describing the system from a

Table 1.4 Major components of a forest landscape disturbance regime (adapted from Suffling and Perera 2004)

Aspect	Component	Description	Example
How often the disturbance occurs (refers to single disturbance agents)	Frequency	Number of events caused by a given disturbance agent per time period at a given point in a forest landscape	Five blowdown events in 250 years at a given location
The magnitude of the disturbance (refers to single disturbance agents)	Intensity	Amount of energy released by a disturbance event per unit area per unit time	Frontal intensity of a fast-moving boreal wildfire could exceed 50,000 kW m^{-1}
	Severity	Effect of the disturbance on a forest landscape	An average of 55 % of the soil's O horizon burned in one fire versus 5 % in another
	Patch size	Sizes of individual disturbance patches as well as the size distribution of all patches	In a management unit, the average wildfire size is 5000 ha and the modal size is 50 ha
Variability of disturbance (refers to single or multiple agents)	Spatial	How the disturbance varies across the landscape	Some parts of a forest landscape will have a higher incidence of wildfires than others
	Temporal	How the disturbance varies in time	In some years, insect defoliation will be more intense than in others
	Stochastic	Effects of nondeterminism in a disturbance	The characteristics of recurring windstorms will be different, even if they occur at the same place
Diversity of disturbance (refers to multiple agents)	Causal agent	Types of disturbance that occur in a forest landscape	Fires, windstorms, and floods
	Interactions: synergism and antagonism between agents	Influence of disturbance agents on one another	Synergism: a windstorm increases the intensity of a fire Antagonism: a fire decreases the severity of a subsequent insect outbreak

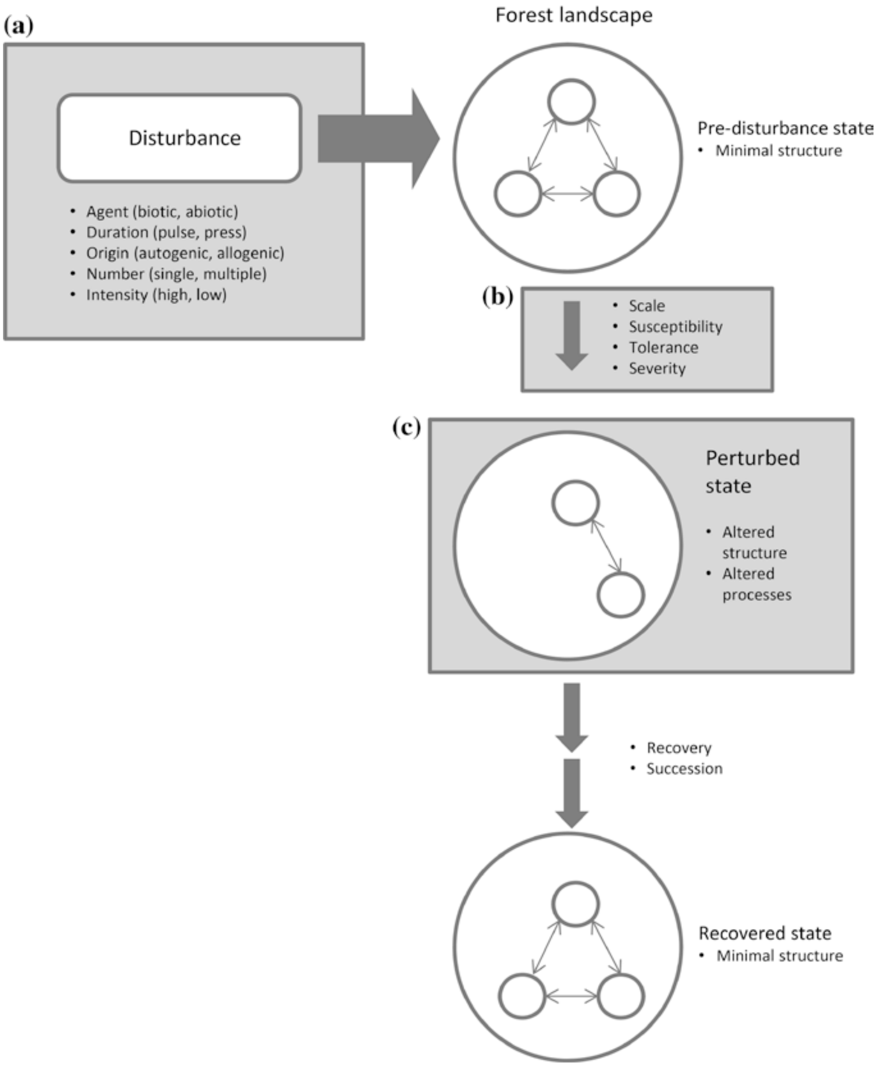

Fig. 1.1 A conceptual illustration of the major components and steps in a forest landscape disturbance process. **a** characteristics of the disturbance agent (the cause), **b** interactions between the forest landscape and the disturbance agent (the effect), and **c** characteristics of the perturbed forest landscape (the result)

reductionist perspective and including only those processes we can readily investigate and quantify. Equations that describe these processes are then encoded in computer algorithms to facilitate efficient computation, graphical visualization, and analyses of the simulated results. The degree of simplification that needs to be attained, and how and what processes are reduced to mathematical expressions, are points that are strongly debated among ecologists: some prefer simple

$$Z = f(XY) + \varepsilon$$

$$Z_{ij} = f(XY_{ij}) + g(XY_{kl}) + \varepsilon_{ij}$$

Fig. 1.2 Basic components of a forest landscape disturbance simulation model: Z = the perturbed forest landscape state, X = pre-disturbance forest landscape state, Y = characteristics of the disturbance, f = interaction between the forest landscape and disturbance, and ε = the sources of variability. A spatially explicit expression includes spatial interactions (g), a two-dimensional index of spatial variability in model components (ij), and the influence of spatial proximity (kl). Modified from King and Perera (2006)

and parsimonious models, whereas others argue for complex and detailed ones (e.g., Logan 1994; Canham et al. 2003; Evans et al. 2013). Landscape simulation models not only address broader-scale phenomena (i.e., at scales above those of individual trees and communities), they are also spatially explicit (i.e., location-specific and account for neighborhood effects). Simulating forest landscape disturbance with a model entails quantifying the characteristics and behavior of the disturbance agents, their interactions with the forest landscape (the perturbation), and the characteristics (perturbed state) of the resulting forest landscape (i.e., a, b, and c in Fig. 1.1).

Such a model expression will include the characteristics of the perturbed forest landscape as variables that are not directly measured (Z), the pre-disturbance state of the forest landscape (X) and the characteristics of the disturbance (Y) that are directly measured, their interaction as an estimated relationship (f), and sources of variability (ε). Because all forest landscape simulation models are expected to be spatially explicit, a spatial interaction term (g) is also included (Fig. 1.2).

There are two major approaches to development of a simulation model, which differ both in concept and in intent and produce models that differ in their applications: the *mechanistic* and *empirical* approaches (Korzukhin et al. 1996; Suffling and Perera 2004; Gustafson 2013). The *mechanistic* approach leads to process-based simulation models, commonly termed mechanistic models, a term we will use in this volume. This approach requires a thorough understanding of the fundamental mechanisms of disturbance and response processes, as suggested by Running and Coughlin (1988), who simulated primary physiological and hydrological processes at a landscape scale more than 25 years ago. In the context of this book, the mechanistic approach describes the physics, chemistry, and biology of disturbance agents, as well as their interactions with the forest landscape (the terms Y and f, respectively, in Fig. 1.2). Therefore, mechanistic models draw heavily on scientific knowledge developed through observations and experiments, and this knowledge forms the foundation for reducing disturbance processes to equations that include spatial interactions and temporal trajectories.

Ideally, all such equations would be based on first principles (Gustafson 2013). In practice, when we lack, or have only partial knowledge, of some aspects of the biological, physical, or chemical properties, various model assumptions are used to replace more definitive descriptions of the interaction term *f* and the sources-of-variability term ε (Fig. 1.2). Even though the individual steps, namely the disturbance (*Y*) and its interactions with the forest landscape (*f*), are known or assumed, the overall outcome of the model (*Z*) cannot be readily known given the numerous factors that influence the interactions (*Y* and *X*) and the myriad interacting steps. Thus, the outcomes of process-based simulation models are an emergent property that cannot be predicted a priori from the individual components of that model (Hall and Day 1977). When such simulations are conducted repeatedly under different conditions, with varying values for the disturbance processes (*Y*) and forest landscape characteristics (*X*), a range of outcome states (*Z*) may emerge. Thus, the modeled characteristics of a perturbed state of a forest landscape will be a probability distribution instead of a single value. This insight into the emergent stochasticity of the disturbance outcome helps modelers to understand the natural heterogeneity associated with disturbance regimes in forest landscapes, and to isolate three key aspects of that variability: its temporal, spatial, and stochastic characteristics (Lertzman et al. 1998).

The other simulation modeling method is the *empirical* approach, which leads to phenomenological models, commonly termed empirical models, a term we will use in this volume. This approach involves generalizing ecological phenomena, as illustrated by Usher's (1992) pioneering demonstration of modeling vegetation succession across a landscape. In the context of this book, empirical modeling involves quantitative descriptions of forest landscape disturbance events and regimes through empirical observations. These models draw heavily on statistical analyses of data from past disturbance events to define their effects on the processes and (mostly) on the outcomes. Here, the interaction between the forest landscape and disturbance (*f*), and the sources of variability (ε), are derived statistically from past empirical observations of *Z*, *Y*, and *X*. Here too, the simulated characteristics of a perturbed state of a forest landscape will be a probability distribution instead of a single value. However, unlike their mechanistic counterparts, empirical models do not have emergent properties with respect to model outcomes or associated heterogeneity.

Despite the conceptual dichotomy between mechanistic and empirical models, almost all mechanistic models of forest landscape disturbances are, in practice, hybrids. They contain many empirical assumptions and modules that fill gaps in the scientific knowledge of ecological processes. Another important point is that all models are provisional in their logic, structure, and components. Over time, models should change to incorporate advances in scientific knowledge. With advances in understanding, model development and applications should evolve toward mechanistic ecological models that are based on first principles of biology, physics, and chemistry (Gustafson 2013). In addition, because models are but hypotheses of numerical implications for ecological systems, continuous testing with data should lead to rejection or modification of some assumptions and model functions, and the development of new ones (Hilborn and Mangel 1997; Evans et al. 2014).

Models also differ in their applications. For example, they differ with respect to why and how they are used for varying purposes such as exploring and understanding ecological systems, developing and testing hypotheses about system behavior, and supporting strategies for ecosystem management and decision-making. During the early stages of the evolution of a subfield in ecology, models are typically developed and used for *descriptive* purposes to increase knowledge of ecological phenomena, to support hypothesis development, and to discover a system's behavior. Later, as the knowledge advances and understanding matures, models become useful for *predictive* purposes (Korzukhin et al. 1996).

Even with advances in knowledge, expecting a high predictive ability from forest landscape disturbance models is perhaps not realistic. To elucidate this point, and following Bugmann (2003), we further divide "predictive" applications of forest landscape disturbance models into four broad categories (Table 1.5). The differences among these categories extend beyond semantics; they are important distinctions that both model developers and model users must understand. The degree of certainty required for the predictive and forecast categories to support tactical applications may not be realistic for models of ecological systems (Bugmann 2003), and may be almost impossible to achieve with forest landscape disturbance models. Conversely, examining synoptic possibilities for future states of forest landscapes under what-if disturbance scenarios to support strategic applications is a more relevant and plausible pursuit (Perera and Cui 2010). Fortunately,

Table 1.5 Possible applications of forest landscape ecological disturbance models, based on the categories and definitions of Bugmann (2003)

Application category	Definition	Goal of application	Example
Prediction	Commonly denotes inference from facts or accepted laws of nature, and implies *certainty*	Tactical: to precisely know the occurrence and characteristics of a disturbance event	Spatially or temporally precise prediction of a wildfire event; that is, of the ignition, extinguishment, extent, duration, intensity, and severity
Forecast	Adds the implication of anticipating eventualities and differs from prediction in being concerned with *probabilities*		Spatially and temporally precise prediction of the likelihood of a wildfire event and of its characteristics
Projection	An estimate of future *possibilities*	Strategic: to discover what is possible and the probabilities of disturbance events and their characteristics	Spatially and temporally explicit portrayal of a single probability distribution for future wildfire events and their characteristics under one set of assumptions
Scenario	An account or synopsis of a *possible* course of action or events		Spatially and temporally explicit scenarios of multiple probability distributions for future wildfire events and their characteristics under varying sets of assumptions

it is this goal of *discovery* (i.e., simulation of scenarios for the possible future states of ecological systems) that appears to be gaining momentum in applications in forest landscape disturbance modeling, with an emphasis on mechanistic models (Gustafson 2013).

1.3 The Contents of the Book

Included in this book are efforts to model an array of forest landscape disturbance types, ranging from physical to biological and from single to multiple. Also included are attempts to model interactions among disturbances by natural agents and anthropogenic effects, and the simulation of forest landscape recovery from disturbance (Table 1.6). The intent of these discourses is to illustrate the diversity of forest disturbance types that occur on landscapes, and approaches to their modeling. As well, these reviews of the various modeling approaches show

Table 1.6 An overview of the chapter contents: intent, disturbance attributes, and the modeling focus and approach

Chapter number and lead author	Intent	Disturbance	Disturbance type	Disturbance duration	Modeling focus	Modeling approach[a]
2. Mitchell	Review	Windthrow	Abiotic	Pulse	Response	Empirical and hybrid-mechanistic
3. Gustafson	Case study and review	Drought		Press	Disturbance and response	Empirical, mechanistic
4. McKenzie	Synthesis	Wildfire regimes		Pulse		Process, empirical, and hybrid
5. Sturtevant	Review and synthesis	Spruce budworm	Biotic			Empirical, mechanistic
6. Regnière	Case study	Mountain pine beetle			Disturbance	Mechanistic individual-based
7. Birt	Review	Southern pine beetle			Disturbance and response	Mechanistic
8. Keane	Case study	Disturbance interactions	Integrated	Pulse/press		
9. Wimberly	Review	Coupled human and natural systems		Press		
10. Scheller	Case study and review	Forest recovery	–	–	Recovery	Moving to mechanistic

[a] Based on the terminology used by the chapter author

the different stages of maturity in model development. Given the authors' backgrounds, the implicit bias is toward North American forest landscapes, although the many case studies capture the geographical diversity within this continent. The chapters written specifically on simulation modeling topics provide a literature review that is not exhaustive, but that is sufficient to summarize the state of knowledge on that topic. They also address topics related to disturbance modeling as syntheses and provide a visionary perspective for conceptual advances. When

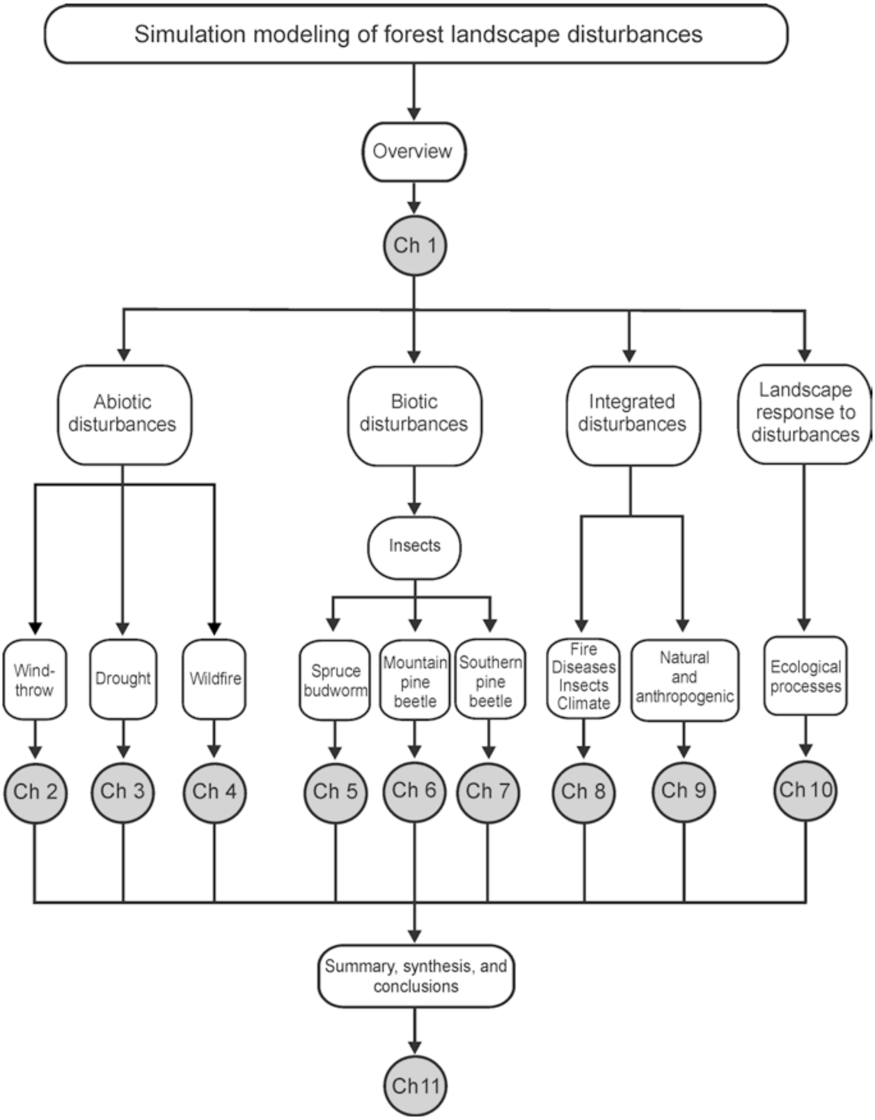

Fig. 1.3 The organizational structure of the chapters

a specific example of model use is described, it is meant only as a case study to illustrate and support a broader argument. Thus, we expect the relevance of the points made in this book to last well beyond the lifespan of typical research papers on model development and applications.

The book begins with the present overview chapter, followed by a series of chapters that focus on modeling of a specific disturbance type. We have organized these into broad groups (abiotic, biotic, and integrated disturbances), with the final chapter addressing the recovery of forest landscapes (Fig. 1.3). The chapters on modeling abiotic disturbance include windthrow in forest landscapes (Chap. 2: Mitchell and Ruel), drought-induced forest mortality (Chap. 3: Gustafson and Shinneman), and wildfire regimes (Chap. 4: McKenzie and Perera). The group of chapters on biotic disturbances addresses forest-dwelling insects that periodically create epidemic-level disturbances: spruce budworm defoliation (Chap. 5: Sturtevant et al.), the response of the mountain pine beetle to climate change (Chap. 6: Regnière et al.), and disturbance by the southern pine beetle (Chap. 7: Birt and Coulson). The two chapters on integrated disturbances focus on interactions between biotic and abiotic disturbance agents under climate change (Chap. 8: Keane et al.) and under coupled natural and anthropogenic disturbance in forest landscapes (Chap. 9: Wimberly et al.). The next chapter, on simulating the recovery of a forest landscape, addresses the dynamics of vegetation and biogeochemistry soon after disturbance (Chap. 10: Scheller and Swanson). We conclude with a summary and a synthesis of the book's contents, as well as insights into future simulation modeling of forest landscape disturbances and their application (Chap. 11: Perera et al.).

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Chapter 2
Modeling Windthrow at Stand and Landscape Scales

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2.1 Introduction

Wind damage to trees and stands has ecological and management implications. The spectrum of damage can range from creation of canopy gaps and development of multi-cohort (uneven-aged) stands, to whole-stand replacement and initiation of single-cohort (even-aged) stands (e.g., Kramer et al. 2001; Busby et al. 2008; Bouchard et al. 2009). Individual trees can be broken or uprooted. Soil inversion by overturned rootwads leads to complex microtopography, improves soil fertility (Schaetzl et al. 1989; Kramer et al. 2004), and creates a regeneration niche for many tree and understory plant species (Ulanova 2000). On steep slopes, the disturbance contributes to downslope movement of soil (Gallaway et al. 2009). In managed forests, as well as rural and urban landscapes, windthrow damages crop and amenity trees, affects conservation and recreation values, and poses a threat to human life and built structures (Fig. 2.1a; Schmidlin 2009). Rather than being viewed as individual catastrophic events, windthrow is more realistically viewed as a recurrent disturbance process, with an inverse relationship between event frequency and severity. At a given location, the likelihood and severity result from

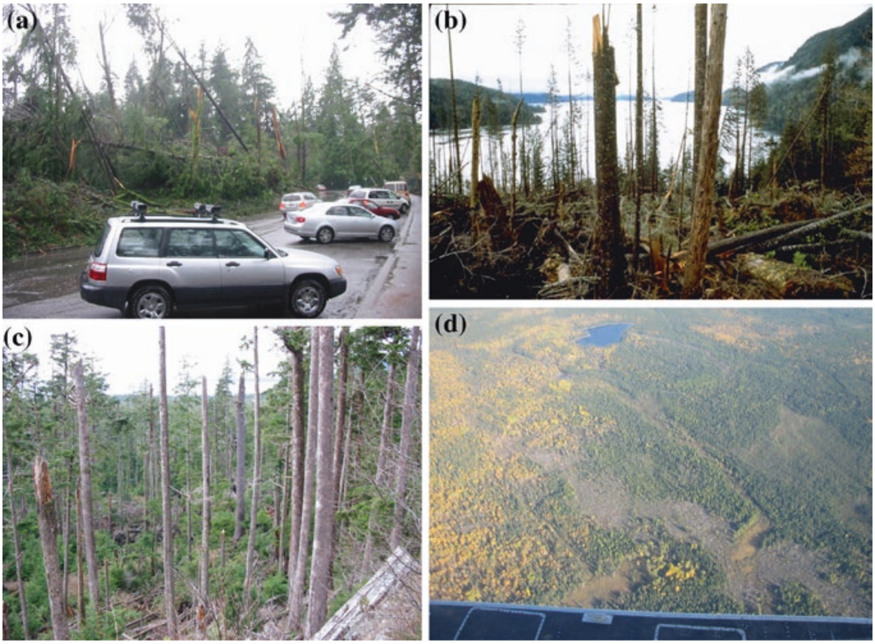

Fig. 2.1 **a** Aftermath of the December 15, 2006 windstorm in Stanley Park, Vancouver, British Columbia, Canada (photo credit S.J. Mitchell). **b** Stand-replacing windthrow from an extra-tropical cyclone in coastal British Columbia, Canada (photo credit S.J. Mitchell). **c** Partial-windthrow from an extra-tropical cyclone, coastal British Columbia, Canada (photo credit S.J. Mitchell). **d** Stand-replacing windthrow from a convective downburst—boreal forest in Ontario, Canada (photo credit A. Perera)

interactions among regional wind climate and local terrain, vegetation, and management regime (Mitchell 2013). Scientists use models to improve their understanding of the processes underlying forest disturbances and to integrate results of empirical, biomechanical, and numerical investigations. Ideally, the models or the results of modeling are presented in the form of decision support tools (e.g., Hanewinkel et al. 2011) that can be used by resource and conservation managers as well as those responsible for public utilities to evaluate windthrow risk and develop mitigative responses in a wide range of forest conditions.

In this chapter, we review the factors that contribute to windthrow frequency and severity within stands and across landscapes, summarize current approaches used to model windthrow, identify and discuss the gaps in existing modeling approaches, and outline strategies to improve modeling and application of windthrow models for decision support.

2.2 Overview of Factors that Contribute to Windthrow

A turning moment is the tendency of a force to rotate an object around its axis, and is calculated by multiplying the force by the length of the lever arm. Windthrow results when wind-induced turning moments exceed root anchorage or stem strength and trees uproot or break. The level of damage in forest stands ranges from partial to stand-replacing, depending on wind speed and the susceptibility of trees that make up the stand (Fig. 2.1 b, c). In temperate climates, most windthrow occurs during extreme weather associated with extra-tropical cyclones or remnant tropical cyclones. These systems produce sustained high winds over wide areas and are often accompanied by heavy rainfall that reduces anchorage. Regional-scale airflow is modified by local terrain, leading to areas of higher or lower topographic exposure to wind (Ruel et al. 2002). Downbursts or tornados associated with convective storms cause severe, localized windthrow along the track of the storm (Fig. 2.1d; Peterson 2007). In tropical climates, windthrow is caused by cyclones (e.g., Lugo 2008) and convective downbursts (Garstang et al. 1998).

The mechanical stability of individual trees reflects their long-term exposure to wind and the effects of inter-tree competition. Open-grown trees maintain long live crowns, and acclimate to local wind regimes by developing thick stems and structural roots. In locations with prevailing winds, their crowns are often wind-shaped or flagged, and stems and roots thicken asymmetrically (Telewski 1995; Fig. 2.2). Stand-grown trees are partially sheltered by neighboring trees, and compete with them for light and soil resources. Here, height growth, maintenance of sun exposed foliage, and fine root production take priority over stem and root thickening, leading to slender trees with lower mechanical stability (Mitchell 2000). Dense, uniform stands can grow into a condition where the whole stand becomes unstable as it reaches some critical height. This phenomenon has been reported for single-cohort stands in temperate forests around the world, and

Fig. 2.2 Wind shaped tree crowns in an area of strong prevailing winds (photo credit J.-C. Ruel)

motivated the original windthrow hazard classification system developed for the United Kingdom (Miller 1985). Management activities such as patch cutting, heavy thinning, or retaining isolated stems within harvested areas, which produce sudden increases in wind exposure, can lead to windthrow during routine winds. In contrast, planting trees at wide spacing, or gradually thinning stands, can lead to trees that are well acclimated to the local wind climate and therefore less susceptible to windthrow (Albrecht et al. 2012).

The influence of soils on tree and stand stability is complex. Open-grown trees may form stable anchorage on a wide variety of soils. Shallow or poorly drained soils can restrict anchorage; however, landscape-scale studies of windthrow often reveal that stands on deep soils are more susceptible (Dobbertin 2002; Bouchard et al. 2009). This apparent paradox may be explained by the fact that stands grow taller and trees compete more for light on sites with deeper, more fertile soils, making them more susceptible to windthrow.

Observations of the recurrent nature of wind damage and the role of component factors, have informed the development of classification schemes based on local expert knowledge (e.g., Miller 1985; Mitchell 1998; Wood et al. 2008), and have led to two broad approaches to windthrow modeling: empirical and hybrid empirical-mechanistic.

2.3 Empirical Modeling

2.3.1 Approaches to Empirical Modeling

The aims of empirical windthrow modeling are diagnostic, i.e., to identify the factors associated with windthrow, and predictive, i.e., to improve our capacity to predict where and how much damage is likely within forested landscapes.

Empirical modeling can be undertaken at spatial scales ranging from national through regional to local, and incorporate landscape-, stand-, and tree-scale data. Temporally, models can address damage from a single event or class of similar events, or cumulative damage that occurs over a fixed time interval. Wind damage estimates can be obtained via classification of aerial or satellite images (Ruel and Benoit 1999; Mitchell et al. 2001), establishment of temporary plots (Scott and Mitchell 2005), or from periodic re-measurement of permanent sample plots (Valinger and Fridman 1999). Predictor variables can be obtained via field measurement or from spatial data layers (e.g., topography, vegetation, soils, and management history maps). Wind exposure is often represented using topographic exposure indices but potential sources of wind data are many, including local climate stations, broad-scale regional wind atlases, and mesoscale modeling (Ruel et al. 1997, 2002).

In empirical modeling, local outcomes can be examined at the stand (plot) or individual tree scale. At stand scale, the response variable can be the percentage of stems or canopy area affected, but since it is common for the majority of plots or trees in a given study area not to be affected, the outcome is often represented as binary, i.e., above or below some damage threshold. Classification and Regression Trees (CART) can be used to identify damage thresholds and predictor variables (e.g., Kamimura et al. 2008). Tree-scale outcomes are dichotomous (trees fail, meaning they break or uproot, or remain standing), so logistic regression models are typically used to predict the probability of individual tree failure, and can also be used to determine the probability of damage within plots exceeding some threshold level of damage severity (Table 2.1).

Table 2.1 Examples of empirical windthrow models

Author	Location	Temporal scale	Spatial scale	Sample point	Other information sources	Analytical approach
Albrecht et al. (2012)	Germany	Multiple events	Tree and stand	Permanent sample plots	Tree, stand, site, management	GLMM
Dobbertin (2002)	Europe	Two events	Stand	Permanent sample plots	Stand, site	CART
Kamimura et al. (2008)	Japan	Multiple events	Stand	Temporary sample plots	Site, management	CART
Lavoie et al. (2012)	Canada (Québec)	Multiple events	Tree and stand	Temporary sample plots	Site, management	Logistic regression, mixed models
Mitchell and Lanquaye-Opoku (2005)	Canada (British Columbia)	Multiple events	Stand	Cutblock edge segments	Stand, site, management	Logistic regression
Moore et al. (2013)	New Zealand	Multiple events	National and regional	Regional summaries of area damaged	Wind speed	Generalized Pareto distribution
Scott and Mitchell (2005)	Canada (British Columbia)	Multiple events	Tree	Temporary sample plots	Tree, stand, site, management	Logistic regression
Valinger and Fridman (2011)	Sweden	Single event	Stand	Permanent sample plots	Stand, management	Logistic regression

One of the considerations in the use of logistic regression for developing windthrow prediction models is the potential for lack of spatial independence between observations used for model fitting. Spatial independence will differ among tree-, stand-, and landscape-scale variables, and will depend on the extent of the study area. Spatial independence can be tested using semivariance techniques (Carr 1995). The spatial independence of topographic and wind variables will depend on topographic heterogeneity and the grid resolution at which these variables are characterized. Another way to account for the lack of spatial independence at different scales is through the use of mixed models. For instance, random effects can be associated with plots and with harvest blocks to account for the fact that trees within a given plot and plots within the same harvest block are not independent (e.g., Lavoie et al. 2012).

In addition to ensuring adequate distances between sample points to reduce spatial correlation, it is good practice to reserve a portion of the data set for model testing. The portability of empirical models in space or time can be examined by testing their goodness-of-fit for observations collected in different locations, and over different time periods. Mitchell and Lanquaye-Opoku (2005) found consistency in variables among models fit for coastal and continental regions in British Columbia, Canada, and that models from one region gave good predictions of relative windthrow likelihood in other regions.

In their review of natural hazards modeling, Hanewinkel et al. (2011) identify as problematic the relatively high rates of misclassification for individual cases when the number of observations differs substantially between categories, as is often the case for wind damaged versus undamaged trees and stands. They provide examples of some alternative approaches including the generalized additive mixed model (GAMM) used by Schmidt et al. (2010) to explore damage caused by Storm Lothar, which affected Europe in 1999. Albrecht et al. (2012) used generalized linear mixed modeling (GLMM) to explore factors contributing to winter storm damage in southwest Germany. Described as very powerful tools, GLMMs are challenging to use even for statisticians, which can lead to inappropriate applications (Bolker et al. 2008). For nonspatial national or regional analyses of area damaged, extreme value approaches are useful. Moore et al. (2013) used generalized Pareto distributions to (i) examine the probability that the total area wind damaged in any year exceeded a threshold level, and (ii) predict the level of damage associated with a given return period, both for forested areas of New Zealand.

The results of empirical modeling have been incorporated into decision support tools. Kamimura et al. (2008) used the CART approach to create a decision support tool for windthrow in sugi (*Cryptomeria japonica*) forests in Japan. Regional stand-level logistic regression models have been incorporated into the growth and yield model TIPSY in British Columbia, Canada (Di Lucca et al. 2006). Where attributes such as stand, soil, topographic, or wind variables derived from existing spatial inventories are used for model fitting, the data sets can be compiled using geographic information system (GIS) software, with custom scripts for characterizing topographic exposure, drainage, and land management variables. The resulting predictive models can be entered into map-calculators (tools with a

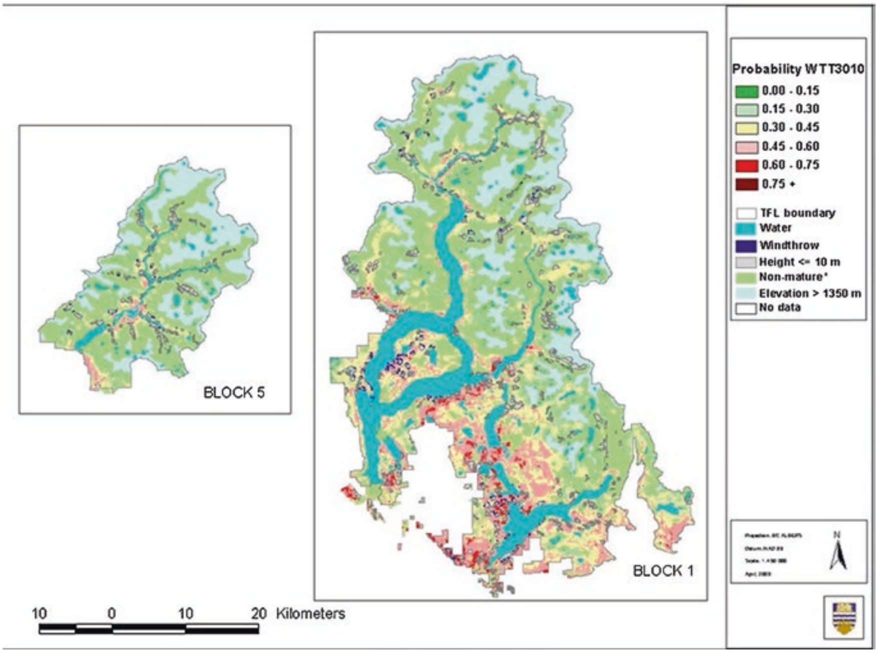

Fig. 2.3 Local windthrow probability maps produced using an empirical model with stand-level data, coastal British Columbia, Canada. *Shading* indicates probability of wind damage to forested edges of new, windward-facing clearcut boundaries due to routine winter winds (photo credit S.J. Mitchell)

GIS that enable users to combine values from different map layers via algebraic or logical expressions) to produce maps of stand vulnerability across the landscape (Fig. 2.3). These maps promote understanding of wind disturbance regimes and assist with the location and design of harvesting/thinning areas in order to reduce windthrow losses, or to better emulate natural disturbance patterns (e.g., Mitchell et al. 2001).

2.3.2 Advantages and Disadvantages of Empirical Models

Although they may have some shortcomings, empirical windthrow models have several advantages over existing mechanistic models. The full range of current ecological and management complexity can be accounted for in the data sets used for model fitting, including representation of multi-species, multi-aged stands with senescing and partially decayed trees. Harvest designs ranging from simple geometric clear-cuts to complex selection or variable retention harvests can be sampled and represented. While empirical models may not provide direct evidence of the mechanisms that lead to windthrow, they can be used to identify key factors to be evaluated in field-level diagnosis of its likelihood (e.g., Mitchell 1998). They also provide insights into how to represent climatic, geographic, and stand variables in mechanistic models. Furthermore, the data sets needed for empirical models can be assembled rapidly, particularly when windthrow is mapped via remote sensing, and are useful for testing and validating mechanistic models.

Regardless of the analytical framework or model form, empirical models are based on past or current outcomes. Changes in storm, temperature, or precipitation regimes, whether due to short-term climate cycles or longer-term climate change, and changes in the composition and arrangement of stands as land use and management practices change will influence the validity of these models. Other disadvantages of empirical models of windthrow include the typically coarse resolution of topographic (spatial) and wind (spatial and temporal) variables, and the difficulty in identifying the underlying biological or mechanical processes from the resulting models.

2.4 Hybrid-Mechanistic-Empirical Models

2.4.1 Windthrow Mechanics as Represented in Hybrid-Mechanistic Models

Windthrow mechanics are reviewed by Mayer (1989) and Wood (1995), both of whom identify static and dynamic aspects of wind loading and tree response. Windthrow occurs when the turning moments produced by wind acting on the crown of a tree exceed the capacity of the stem to resist the bending stresses—leading to stem breakage, or the capacity of the root-soil system to resist overturning. In purely mechanistic windthrow modeling, it would be possible to link a series of calculations of the applied and resistive moments for an individual tree at a given above-canopy wind speed, estimate the critical above-canopy wind speed at which the tree will fail, and apply these calculations to all of the trees that make up a given stand, while accounting for the dynamic aspects of tree motion and wind turbulence (e.g., Wood 1995). In reality, trees and stands are mechanically and architecturally complex and heterogeneous, as are wind patterns during wind storms, terrain and soil properties. In developing windthrow process models, researchers make several conceptual simplifications, including applying expert judgement about the value or range of key parameters and incorporating empirically-derived equations to simplify model construction (Fig. 2.4). The resulting products are best described as hybrid mechanistic–empirical models. The ultimate motivation for developing these models is to improve prediction of potential damage, and allow users to explore how different ecological and management scenarios would affect the likelihood and severity of damage. Development and validation of these models also focuses attention on the key component processes and relationships that drive this complex natural phenomenon. The following summary introduces key terminology, approaches, and information sources used in the major windthrow models, wherein windthrow is treated primarily as a static problem (e.g., Peltola 2006).

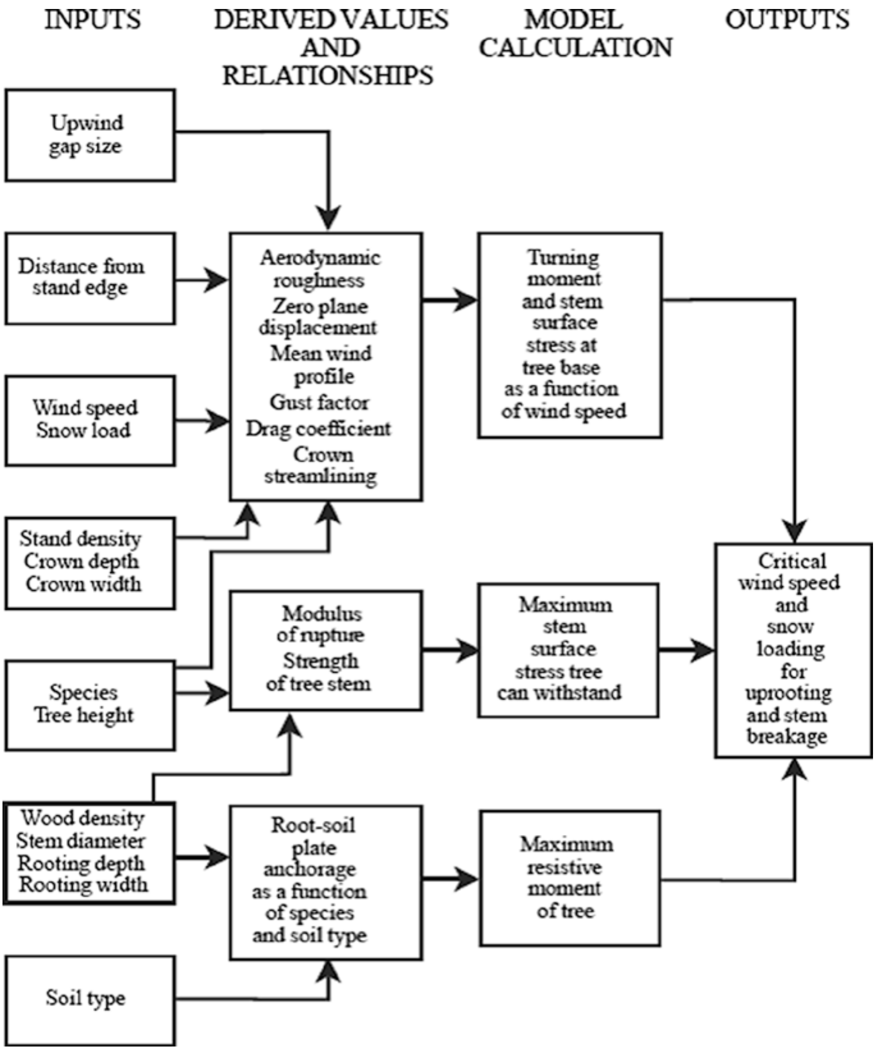

Fig. 2.4 The key inputs, relationships, calculations and outputs of the hybrid-mechanistic windthrow risk model HWIND (from Peltola et al. 1999)

In the simplest models, the stand is assumed to comprise identical trees, and when the representative tree fails, so does the entire stand. With this simplification, it is possible to estimate wind loading on trees within the stand using the "roughness" approach. In this approach, the shear stress that develops across the forest canopy as a function of the above-canopy wind speed and the canopy surface roughness is evenly distributed among the trees within a given area and is assumed to act at approximately two-thirds of the stand height (Gardiner et al. 2000, 2008).

The resulting equations for critical above-canopy wind speed that would lead to breakage (Uh_{break}) or uprooting (Uh_{over}) become (Table 2.2):

$$Uh_{\text{break}} = \frac{1}{kD}\left[\frac{\pi \text{MOR} \times \text{d.b.h.}^3}{32\rho\, G(d-1.3)}\right]^{\frac{1}{2}}\left[\frac{f_{\text{knot}}}{f_{\text{edge}} f_{\text{CW}}}\right]^{\frac{1}{2}} \ln\left(\frac{h-d}{z_0}\right) \tag{2.1}$$

$$Uh_{\text{over}} = \frac{1}{kD}\left[\frac{C_{\text{reg}}\text{SW}}{\rho\, Gd}\right]^{\frac{1}{2}}\left[\frac{1}{f_{\text{edge}} f_{\text{CW}}}\right]^{\frac{1}{2}} \ln\left(\frac{h-d}{z_0}\right) \tag{2.2}$$

The modulus of rupture (MOR) for sound green wood obtained from standard wood properties tables (e.g., Alden 1997) is modified to represent living tree stems by including a reduction in strength due to knots (f_{knot}) obtained from three-point bending tests with recently harvested logs. Ruel et al. (2010) demonstrated this process for balsam fir (*Abies balsamea* (L) Mill.) and expanded it by estimating the decay factor for logs with heart rot (Fig. 2.5).

Trees may be windthrown as a result of stem or root system failure. Critical resistance to uprooting is tested experimentally via tree-pulling (Fig. 2.6). This technique has been standardized, and very strong linear relationships are typically found between critical turning moment and stem mass (C_{reg}, SW) in conifers (Nicoll et al. 2006). These regressions are applicable across fairly large geographic regions (Bergeron et al. 2009). However, when wind climate varies across a region, regressions may need to be adjusted to reflect acclimation to the local climate (Nicoll et al. 2008). Stem and crown attributes are typically estimated from tree diameter and height via dendrometric (or biomass) equations developed via destructive analysis of felled or pulled trees. During tree-pulling studies, most

Table 2.2 Description of terms used in Eqs. 2.1 and 2.2

Symbol	Description	Units
k	von Karman's constant	Dimensionless
d	Zero plane displacement	m
$z0$	Aerodynamic roughness	m
D	Average spacing between trees	m
G	Gust factor	Dimensionless
h	Mean tree height	m
ρ	Air density	kg/m^3
d.b.h.	Diameter at breast height (1.3 m above ground)	m
f_{knot}	Knot factor—reduction of wood strength due to knots	Dimensionless
f_{edge}	Increase in load due to proximity of tree to forest edge	Dimensionless
f_{cw}	Increase in load due to stem and crown displacement under wind load	Dimensionless
MOR	Modulus of rupture for sound green wood	Pa
SW	Stem mass	kg
C_{reg}	Regression constant that relates critical turning moment to stem mass	Dimensionless

Fig. 2.5 Three-point bending tests of stem with heart rot (photo credit J.-C. Ruel)

Fig. 2.6 Static tree-pulling with motorized winch to determine critical turning moment (photo credit J.-C. Ruel)

trees uproot, but a proportion of sound trees experience stem failure. In some studies, critical moments for stem-failed trees were comparable to those of uprooted trees of similar size (e.g., Achim et al. 2005; Byrne and Mitchell 2007), while in other studies stem failure occurred at higher bending moments than uprooting (e.g., Moore 2000; Bergeron et al. 2009).

While it is the standard approach for measuring tree resistance to wind loads, tree-pulling has limitations. Any structure is most likely to fail at the weakest point, and while trees may not universally do so, they can theoretically maintain optimum stability while remaining competitive with other trees by allocating photosynthate in the most structurally efficient manner. This is known as the uniform stress hypothesis (e.g., Morgan and Cannell 1994). In the standard tree-pulling technique, cables are often attached below the crown for practical and safety reasons, and this is lower than would be required to generate a uniform stress in the outer stem fibers (e.g., Wood 1995). Furthermore, pulling is “static”, i.e., is a straight pull with gradually increasing cable tension) and does not emulate tree motion during storms and the potential for gradual loss of root-soil cohesion.

The roughness method of calculating critical wind speed applies to conditions well downwind of any gaps or stand edges. The effect of the width of an opening on wind loading at the stand edge and with distance into the downwind stand has been tested empirically in wind tunnel studies with turbulent airflow and model stands made up of flexible "trees" (Gardiner et al. 1997). The ratio of peak to mean applied moments at the base of individual trees is referred to as the gust factor (G), while the effect of upwind gaps, referred to as fetch, is accounted for with a gap factor and distance from stand edge. An alternate method of estimating wind loading, which is better suited to stand edges, is the "profile" method (e.g., Smith et al. 1987; Peltola et al. 1999). The latter method is also more suitable for evaluating loads on individual trees in nonuniform and mixed species stands. In the profile method, the wind load on an individual tree is calculated from the within-canopy wind speed profile, the crown frontal area, and the drag coefficient, using the classical drag equation (Eq. 2.3):

$$F_d = 0.5\,\rho * C_d * A * U^2 \tag{2.3}$$

where F_d is the drag force acting on the tree crown, ρ is air density, C_d is the drag coefficient, A is the frontal area of the tree crown in still air and U is the horizontal wind speed. In reality, tree branches and foliage are not rigid. Branches taper toward the tip, similar to fishing rods, leading to increasing flexibility at the periphery of the crown. Branches and foliage reconfigure and realign as wind speeds increase (Fig. 2.7), streamlining drag elements and reducing frontal area. Where the classical drag equation is used with a fixed drag coefficient, it is necessary to adjust the crown frontal area measured in still air (A_s) using a streamlining coefficient (S):

$$S = c * U^{-n} \tag{2.4}$$

where the parameters c and n are species specific and represent the rate of crown frontal area reduction with increasing wind speed. Drag and streamlining coefficients have been determined experimentally for several conifer and broadleaf species, by placing the crowns of small trees in wind tunnels (Mayhead 1973;

Fig. 2.7 Side view of western redcedar (*Thuja plicata* Donn ex D. Don) tree crown in a wind tunnel in horizontal airflow (photo credit S.J. Mitchell)

Rudnicki et al. 2004; Vollsinger et al. 2005) or by mounting them on vehicles that are driven at a succession of higher wind speeds through calm air (e.g., Kane et al. 2008). However, experimentally determined drag coefficients are not available for many species, and whether the behavior of small crowns is representative of large tree crowns remains an open question.

Combining Eqs. 2.3 and 2.4 leads to:

$$F_d = 0.5\,\rho * S * C_d * A_s * U^2 \tag{2.5}$$

Drag can be calculated for whole crowns and applied at the height of center of pressure to calculate applied turning moment, or it can be calculated for successive vertical segments of the crown. When vertical segmenting is used, differing vertical wind profiles can be applied at stand edges and within the stand. The attenuation of the wind profile within forest canopies depends on canopy density (e.g., Cionco 1972; Shaw et al. 1988).

Horizontal wind loads deflect the tree stem from vertical, and an additional applied moment is created from the displaced stem and crown mass. This additional bending moment is estimated by assuming that the tree stem behaves like a tapered cantilever beam, anchored at the base, and is normally calculated iteratively since the displaced mass leads to further displacement until the resistive moment balances the applied and self-loading moments.

Once the critical wind speed has been estimated using either the roughness or profile methods, the probability of a wind of this speed occurring at a given site can be estimated. Since long-term weather stations tend to be concentrated near urbanized areas rather than distributed through forested landscapes, a variety of approaches are used. The UK Forestry Commission used tatter flags located across open moorland as a direct measure of wind exposure, and related this to a variety of indices of topographic exposure to wind and to regional windiness (Hannah et al. 1995). The underlying assumption in these approaches is that a relationship exists between general windiness at a location and the recurrence of extreme winds. Physical airflow models and numerical weather prediction models can be used to represent the effect of complex terrain on local wind speed and direction (Ruel et al. 1997). Numerical weather prediction models have the advantage of allowing for reconstruction of specific weather events, and can be used to predict wind, temperature, and precipitation. As well, they can be used to produce gridded maps of mean and extreme wind and precipitation conditions (e.g., Guthrie et al. 2010). Goodrick and Stanturf (2010) refer to this as “event risk”, and describe a process for producing gridded maps from climatological models.

2.4.2 *Overview of Hybrid-Mechanistic Models*

Several hybrid-mechanistic windthrow models incorporate some or all of the components described above (Table 2.3). The most broadly applied model, ForestGALES, was initially developed by the UK Forestry Commission to predict

Table 2.3 Examples of hybrid-mechanistic models for predicting windthrow

Author	Origin	Base model	Adaptations
Gardiner et al. (2000, 2006)	United Kingdom	ForestGALES	France Cucchi et al. (2005), New Zealand Moore and Quine (2000), Japan Kamimura et al. (2008), Canada—Québec Ruel et al. (2000), British Columbia Byrne and Mitchell (2013)
Peltola et al. (1999)	Finland	HWIND	Sweden Blennow and Sallnäs (2004), The Netherlands Schelhaas et al. (2007)
Ancelin et al. (2004)	France	FOREOLE	–

failure of Sitka spruce (*Picea sitchensis*) plantations in Britain (Gardiner et al. 2006). It can be run using either the roughness or profile method to calculate critical wind speeds (however, the profile method is not included in the public version), and can be used to simulate outcomes for even-aged plantations of major commercial conifer species for uniform thinning or strip cutting scenarios. Regional windiness is modified via a topographic exposure score to estimate the probability of a critical wind speed occurring at the target location. Topographic exposure accounts for elevation, local topography, the direction of prevailing winds, and the funneling effect of valleys (Quine and White 1993). In the public version, the stand is treated as completely uniform and if the critical wind speed for the representative tree is exceeded the entire stand will fail. The effects of upwind gaps and uniform thinning can be evaluated. Soil type and drainage are used to modify critical turning moments using adjustment factors derived from tree-pulling studies on a range of soil types. The model has been coupled with data from growth and yield tables to project the age at which stands will reach critical height. The ForestGALES model has been adapted by research groups in New Zealand (Moore and Quine 2000), France (Cucchi et al. 2005), Japan (Kamimura et al. 2008), and Canada (Québec—Ruel et al. 2000; British Columbia—Byrne and Mitchell 2013) by adding tree-pulling and dendrometric data for local species (primarily conifers), use of local wind climate data, and local stand growth models.

The model HWIND was developed in Finland to predict the risk of wind or snow damage via uprooting or stem breakage along recently exposed stand edges (Peltola et al. 1999), and incorporates the profile method to calculate critical wind speed. Stands are assumed to be uniform and edge trees will fail if the critical wind speed is reached at a newly exposed edge. The model includes the effect of distance from the stand edge and it is possible to calculate critical wind speeds separately at one, two, or more tree heights from the edge. Wind loading, deflection, and resistance are calculated for representative trees for successive vertical stem/crown sections. The other major difference between HWIND and ForestGALES is that the critical moment for uprooting is calculated from root system dimensions (root system mass) rather than estimated based on stem mass using empirical relationships from tree-pulling studies. Schelhaas et al. (2007) have adapted HWIND in their model ForGEM-W to include spatial mapping of trees and tree-to-tree shelter and collision effects.

Ancelin et al. (2004) developed FOREOLE, an individual tree model in which the profile method is used to calculate wind loading and resistance for successive vertical stem/crown sections. Loads are calculated assuming static loading and are adjusted for turbulent wind effects using a gust factor. The principle departure from ForestGALES in the wind loading and resistance calculations is in the improved representation of stem taper and the use of the transfer matrix method for stepwise calculation of loads, displacement, and resistance within stem segments. This model has been linked with an individual-tree-based growth and yield model (Courbaud et al. 2001) within the Computer Aided Projection of Strategies in Silviculture (CAPSIS) platform (e.g., Dufour-Kowalski et al. 2012) and allows windthrow to be simulated for populations of trees at any point in the growth of uniform or nonuniform stands. While CAPSIS allows for the spatial representation of modeled trees, Ancelin et al. (2004) did not incorporate iterative processing in FOREOLE to account for the effect of damage propagation during a given wind event.

ForestGALES_BC/WindFIRM extends the capacity of ForestGALES to model damage propagation in nonuniform, mixed species stands under complex partial harvesting scenarios (Byrne and Mitchell 2013). The model has two modules. The first, WindFIRM, assembles spatial information from input GIS layers and spatially explicit tree lists, calculates stand attributes for 25 m × 25 m grid cells, and passes the stand- and tree-scale data to the second, ForestGALES_BC, for calculation of the critical and applied wind speeds for each tree in the area under investigation. Rather than using a representative tree, the model uses an input table that lists each tree in the stand, with its species, diameter at breast height, height, and location (x, y coordinate). These "tree lists" can be derived from field measurements, growth and yield models, or other sources, including LIDAR. Using the spatially explicit tree list, the critical wind speed for each tree in the stand is calculated using the profile method. The within-canopy wind profile acting on each tree is calculated by modifying the user-specified above-canopy wind speed based on the canopy density in upwind grid cells. To better represent damage propagation, any trees that would fail for the user-specified above-canopy wind speed are deleted from the tree list. The resulting tree list is passed from the ForestGALES_BC module back to the WindFIRM module for recalculation of stand attributes within each 25 m × 25 m grid cell, and then passed back to ForestGALES_BC to recalculate tree-level wind loading for the remaining trees. These calculations are repeated until no additional trees in the stand would fail for the user-specified above-canopy wind speed (Fig. 2.8).

2.4.3 Integration of Hybrid-Mechanistic Models into Spatial Decision Support Models

Both ForestGALES and HWIND have been integrated with other models and information layers within GIS to expand their capacity for decision support at stand and landscape scales. For example, HWIND has been integrated with the European Wind Atlas Analysis and Application Program (WASP) within a GIS

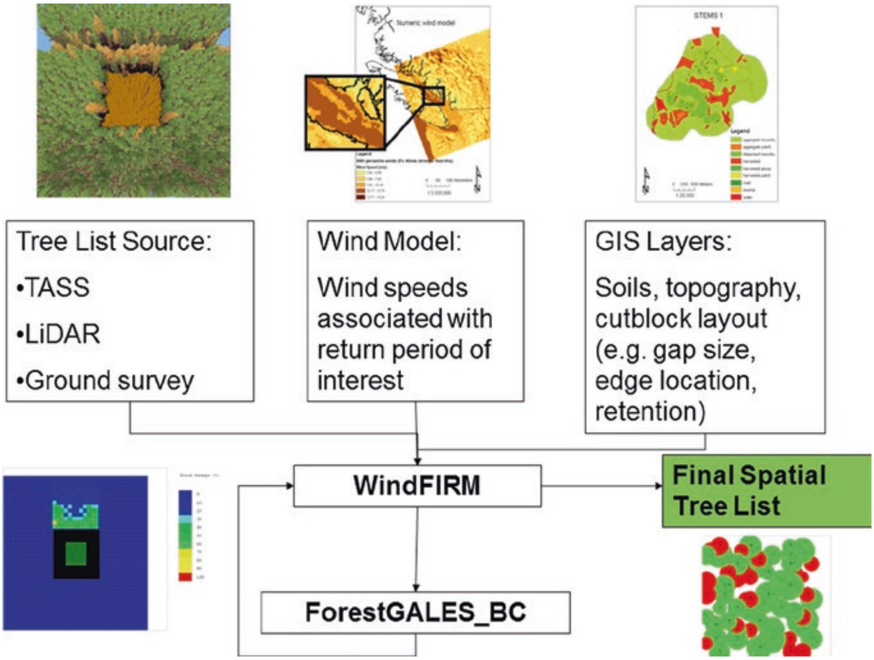

Fig. 2.8 Integration of ForestGALES_BC and WindFIRM, spatial decision support system for windthrow likelihood modeling (from Gardiner et al. 2008)

in the predictive framework WINDA to examine the probability of wind damage across landscapes where stand edges are exposed following forest harvesting (Blennow and Sallnäs 2004). It has also been integrated with forest growth models and forest cover data to examine windthrow potential across landscapes under various growth and management regimes (Zeng et al. 2007a, b), and with current and future wind climate simulations to explore the implications of climate change (Blennow et al. 2010; Peltola et al. 2010).

2.4.4 Advantages and Disadvantages of Hybrid-Mechanistic Modeling

Researchers have examined and characterized several of the biological, ecological, and physical processes that contribute to windthrow at individual tree to landscape scales (Mitchell 2013). Hybrid-mechanistic windthrow models provide conceptual and computational vehicles to link knowledge on component processes, allow input information to be scaled appropriately, and produce tabular or graphical outputs. Representing the process of windthrow via a series of linked algorithms helps researchers to generate hypotheses and identify knowledge gaps. Model predictions can be tested for individual components or the whole model, using independent data. As forest management decision support tools, hybrid mechanistic models are useful for examining and contrasting management scenarios, albeit with full regard for the inherent limitations in how these models represent reality. Ideally, prior to their application in a new location, models are adapted to include parameters for local conditions, and model outputs are compared to local observations. In contrast to empirical models, hybrid-mechanistic models allow exploration of management or climate scenarios that have not yet occurred or are not documented in observational data sets of wind damage. In these simulations however, it is important to keep in mind that these models contain empirical components.

The empirical equations included in the calculation of applied and resistive moments are based on a limited number of tree-pulling and wind tunnel studies. For example, in the base ForestGALES, FOREOLE, and HWIND models, the drag coefficients are estimated based on the work of Mayhead (1973) who tested small numbers of sapling-sized specimens of commercial conifers in the United Kingdom, at speeds under 30 m s^{-1}. Additional studies have been conducted in recent years (e.g., Rudnicki et al. 2004; Vollsinger et al. 2005; Kane et al. 2008) and new parameters could easily be added to the models. Similarly, in each of these models, the gust factors are derived from the wind tunnel work of Gardiner et al. (1997, 2000) with model trees, but could be updated with results from field studies and numerical simulations. The representation of stands by an average or typical tree is clearly a simplification, even for the most uniform plantations. Using the profile method to calculate wind loading provides the potential to incorporate tree lists and simulate outcomes for mixed species, multi-storied, and partially harvested stands. However, to properly represent the windthrow process for stands in which tree stability varies, it is necessary to represent the process of damage propagation during storm events. At this point, only ForestGALES_BC/WindFIRM is designed to account for progressive loss of upwind trees and damage propagation (Byrne and Mitchell 2013). The iterative approach used in this model is computationally intensive, which limits the speed at which a user can compare scenarios if the area under study extends beyond a few tens of hectares. However, since computational speed is constantly increasing, this problem will resolve itself in time.

The veracity of the major models and decision support systems has been examined using sensitivity analysis and by comparing results with observational data sets of stand- or landscape-scale windthrow outcomes (Gardiner et al. 2008; Byrne and Mitchell 2013). The tendency in these validation exercises, however, is to find real-world situations where the simplicity of stand, landform, and management matches the level of sophistication of the model. Plenty of opportunity remains to improve representation of the windthrow process and the heterogeneity of tree, stand, landscape, and climatological conditions.

2.5 Discussion of Modeling Gaps and Potential Approaches

2.5.1 Representation of Spatial Variability in Factors Contributing to Windthrow

Hybrid-mechanistic windthrow models can be broadly viewed as stand-scale models such as ForestGALES (UK model, roughness-approach), and tree-scale models such as FOREOLE, ForestGALES_BC, and ForGEM-W. For stand-scale models, the outcome is total damage or no damage for a given above-canopy wind speed. Tree-scale models can be used to identify which trees in the stand are vulnerable at a given above-canopy wind speed. Outcomes for individual trees can be aggregated to outcomes for cells or polygons, giving stand-scale outcomes as the number or percentage of tree loss. In ForestGALES_BC/WindFIRM, the individual tree outcomes are aggregated into 25 m × 25 m cells and the tree loss in one cell affects wind exposure of downwind cells. Where tree- and stand-scale models are incorporated in a decision support system that is integrated with a GIS, outcomes can be examined and represented across the landscape (e.g., Zeng et al. 2007a; Blennow et al. 2010).

The cellular approach used in ForestGALES_BC/WindFIRM suggests how the resolution of stand-level prediction models could be improved by better representing the variability in above-canopy wind speed, stand, or soil attributes across landscapes. Improving the resolution of wind loading and resistance components of tree-scale models depends on the resolution of the input spatial layers. With spatial tree lists, it is easy to represent loss of upwind trees via clear-cut, partial harvesting, or wind damage, by removing trees from the tree-list. Where upwind stand density is variable due to irregular thinning or variable retention harvesting, empirically derived fetch indices such as VRFetch (Scott and Mitchell 2005) can be used, but these only crudely represent the effects of canopy heterogeneity on wind flow. Schelhaas et al. (2007) used the height and crown dimensions of upwind trees to calculate their sheltering effect on the subject tree and used this to modify the gust factor. Hale et al. (2012) have found a relationship between the applied turning moment experienced by individual trees and competition indices that represent their immediate growing environments, suggesting an alternative way to represent wind loading in heterogeneous stands. Computational techniques such as large eddy simulation (LES) allow for the three-dimensional simulation of airflow over and through canopies with varying porosity and gaps (e.g., Clark and Mitchell 2007; Dupont and Brunet 2008). Although LES is computationally intensive, as processors improve it may be possible to couple LES simulation directly with windthrow prediction models to evaluate partial harvesting and thinning scenarios. Landscape-scale variability in wind speed can be represented via gridded data sets derived from numerical weather prediction or climatological modeling (e.g., Goodrick and Stanturf 2010; Guthrie et al. 2010).

Soil conditions affect windfirmness, and vary in space and time. Peltola et al. (2000) have examined the effects of soil freezing on tree resistance to uprooting, and trees have been pulled on sites across a gradient of soil drainage (Nicoll et al. 2006). Kamimura et al. (2012) have explored the effect of intense precipitation and soil saturation on critical turning moments, but these ephemeral effects have not been incorporated into windthrow models. Some sites are more prone to soil moisture accumulation during storms. Information on soil drainage is usually coarsely mapped, and representation of spatial and temporal patterns of soil moisture could be improved using higher resolution ground surface maps derived from field mapping or LIDAR, integrated with water flow models (e.g., Murphy et al. 2009).

Rudnicki et al. (2001) have documented tree collisions, and their effect on tree motion at sub-lethal wind speeds. Schelhaas et al. (2007) have taken the first steps to integrate tree collisions into ForGEM-W. They use the overlap in crown area between the subject tree and downwind neighbors to reduce the applied turning moment. They partially account for tree collisions once critical wind speeds are exceeded by adding a moment derived from the mass and contact height of failed trees to the self-loading moments of downwind neighbors that they contact as they fall. However, ForGEM-W does not simulate damage propagation via iterative calculations, momentum transfer during multiple tree cascades, nor directional effects. Alternative approaches to modeling wind damage propagation within and between stands include cellular automata models used in slope failure or wildfire modeling (e.g., Malamud and Turcotte 2000).

2.5.2 Representation of Temporal Variability in Factors Contributing to Windthrow

Each of the major windthrow models has been coupled with stand growth models, including ForestGALES with the UK Forestry Commission Yield Models (Gardiner et al. 2006), ForestGALES and FOREOLE within CAPSIS (Ancelin et al. 2004; Cucchi et al. 2005), and HWIND with SIMA (Zeng et al. 2007b). With this coupling, information on stand growth over time is used in windthrow models to estimate the age and height at which the stand will reach the point where annually recurring peak winds exceed critical wind speeds (critical height) for a site with a particular wind exposure and soil type. Tree-scale windthrow models can be linked with spatially explicit stand growth models. For example, ForestGALES_BC uses tree lists from, and can be directly coupled with, the Tree and Stand Simulator (TASS) growth model (Byrne 2011). At a given time step, TASS provides a tree list to ForestGALES_BC for calculation of whether the tree would fail for a given above-canopy wind speed. Once a high wind event has been simulated, the resulting list of surviving trees can be re-entered into TASS for further growth simulation. In this way, the short- and long-term growth and yield implications of a given harvesting or thinning prescription can be represented, with windthrow losses accounted for.

Stand growth models account for the effect of growing space on tree size, height, and diameter for the average tree, or for spatially explicit tree lists, depending on the sophistication of the model. Growing space depends on the number of stems per ha at the time of regeneration (initial stand density), and changes through the life of a stand as the number of stems decreases due to competition-induced mortality or planned thinning treatments. Reduced growing space typically leads to greater stem slenderness for a given height and shorter live-crown length. When coupled with stand growth models, windthrow models can be used to explore the implications of initial spacing for stand stability—in particular, the trade-off between reduced stem slenderness (and therefore stem and root resistance) and increased wind loading due to increased wind penetration into the canopy and larger crown sizes. In general, model simulations reveal that stands planted at wider initial spacings are more stable for a given tree or stand height, and this is consistent with field observations (e.g., Schelhaas et al. 2007). Thinning leads to more growing space for individual trees, but also increases canopy porosity and wind loading. Healthy, vigorous trees gradually respond to increased growing space by a general increase in crown volume and diameter increment, but also acclimate via preferential thickening of the lower stem and temporary reduction in height increment, leading to rapid reductions in stem slenderness (Mitchell 2000; Ruel et al. 2003). The representation of stand and tree growth following thinning varies among growth models. Stand-scale models can represent immediate changes in average tree diameter due to the removal of smaller trees during thinning. They can also represent the increase in radial growth due to increased growing space in the years following thinning. Post-thinning acclimative growth patterns are not represented, even in spatially explicit tree-scale models such as TASS. Such growth pattern changes could be represented in growth and yield and windthrow prediction models by linking with functional-structural plant growth models (e.g., Fourcaud et al. 2008).

In addition to projected changes due to stand growth, natural and human-caused disturbances will occur. These can be tracked via change-detection techniques using high or moderate resolution satellite imagery (e.g., Rossi et al. 2013). Climate change is expected to affect the frequency, intensity, and timing of severe weather events, as well as forest growth (Dale et al. 2001). Hybrid-mechanistic windthrow risk models have been used to explore the implications of climate change scenarios in storm-prone landscapes (e.g., Blennow et al. 2010; Peltola et al. 2010).

2.5.3 Improving Windthrow Modeling at the Landscape-Scale

Empirical windthrow models have been fit for landscape-scale data sets, and can be used to predict damage from routine winds to stand edges recently exposed by harvesting (“endemic damage”, e.g., Mitchell and Lanquaye-Opoku 2005) and to examine risk factors for stand-replacing damage from infrequently occurring extreme winds ("catastrophic damage"; Ruel and Benoit 1999). However, empirical models have been fit for only a few forest types or regions. Representation of gap or stand-replacing windthrow across landscapes via hybrid-mechanistic models remains simplistic, particularly for the effects of upwind canopy properties and propagation of damage. Many of the required elements are in place for rapid expansion of coverage by empirical windthrow models to more forest types and regions, and refinement of hybrid-mechanistic models to support landscape-scale prediction of windthrow.

Using successive moderate to high-resolution satellite images (e.g., MODUS, IKONOS) enables detection and mapping of gap or stand-replacing damage across landscapes shortly after damage occurs. The same data sets could be used to detect thinning or harvesting activities that expose trees or stand edges to higher within-canopy wind loads (e.g., Coops et al. 2009). Change-detection results could be linked with gridded wind and precipitation climatologies derived from weather data or from numerical weather predictions (e.g., Goodrick and Stanturf 2010; Guthrie et al. 2010), and with spatial data sets of terrain, soil, and stand attributes. Regional LiDAR data sets are becoming available, and LiDAR has improved the resolution of terrain mapping, the evaluation of soil drainage, and the characterization of stand structure (e.g., White et al. 2012; Wulder et al. 2012). Significant computational capacity would be needed to iteratively run tree-scale damage propagation calculations for large landscapes, but computational efficiency of hybrid-mechanistic models could be improved by aggregating trees into cells and examining cell-to-cell interactions.

2.5.3.1 Integrating Model Predictions with Consequences and Responses

An ideal decision support tool for windthrow management would provide forest managers with the capacity to predict the probability of wind damage in a particular site and stand, and explore how alternate growing, tending, and harvesting regimes, and climate change scenarios, would affect this probability. Ideally, the results could be represented spatially within a GIS so that both stand- and landscape-scale outcomes could be examined relative to other resource values and management objectives. Hanewinkel et al. (2011) identify the following sequential steps for integrating risk of natural hazards into forest management decision-making, in the context of changing climates: (i) create analysis framework, which includes choosing climate scenarios, downscaling a global climate model to a regional climate model, and determining storm recurrence intervals; (ii) evaluate probabilities of hazards; (iii) estimate costs of acting versus not acting to reduce hazards; and (iv) choose action. Steps (iii) and (iv) of Hanewinkel et al.'s framework link the likelihood of a damaging event to its consequences and choice of action. The consequences of windthrow extend from benign ecological impacts, such as soil turnover and acceleration of stand development in natural stands (e.g., Schaetzl et al. 1989), to human injury or death (Schmidlin 2009). In locations with recurrent wind storms, it makes sense to consider the potential consequences, determine the acceptable level of loss and impact, and act when predicted losses and impacts exceed acceptable levels. Actions can include acceptance of loss, insurance to minimize severe financial losses, and modification of management regimes to reduce loss (Gardiner and Quine 2000; Fig. 2.9). Mickovski et al. (2005) demonstrate how windthrow susceptibility can be incorporated into a

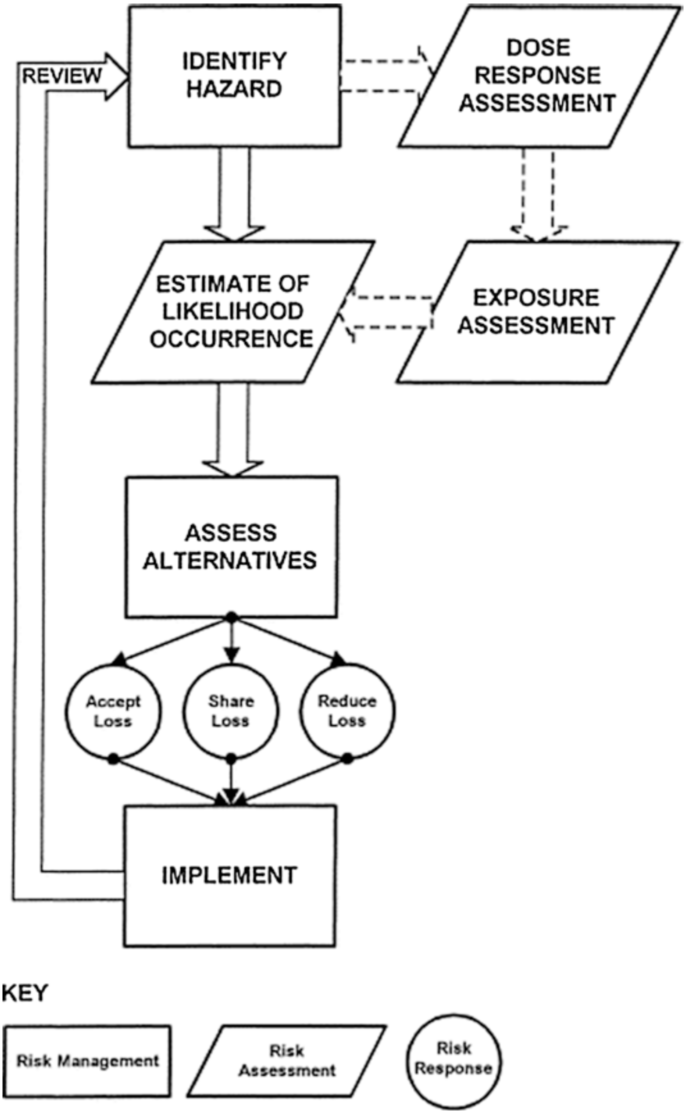

Fig. 2.9 Elements of a risk management framework (from Gardiner and Quine 2000)

generic tree- and stand-scale decision support system. von Gadow (2000) suggests an approach to integrating risk from windthrow and other hazards into forest-level planning, via examination of alternate management scenarios using age dependent cumulative survival rates at the stand scale, and optimizing harvest scheduling at the forest scale. At this point no windthrow risk decision support systems integrate all of these components. Only ForestGALES version 2.1 (Gardiner et al. 2006), which enables users to examine stand-scale outcomes, nonspatially, using the roughness method, is available in a format and with supporting documentation that allow practitioners to easily input data and examine their own scenarios using a stand-alone computer or the internet.

2.6 Conclusions

Empirical windthrow models capture the range of variability in natural and managed stands. The relative portability of empirical models points to consistency in underlying processes over large geographic areas, but provides only limited insights into the biomechanics of windthrow. Hybrid-mechanistic windthrow models have allowed for the integration of expert knowledge and research results from forestry, atmospheric sciences, engineering, biology, and ecology, but many functions remain empirical surrogates for, or simplified versions of, component processes and some key processes (soil saturation during storms, for example) are not represented in any current models. New techniques and information sources are available to improve representation of many of these processes. Both empirical and hybrid-mechanistic models are useful in decision support, and have been used by researchers to explore stand- and landscape-scale implications of climate change. GISs-based decision support systems that integrate tree-based windthrow modeling with stand- and landscape-scale scenario analysis and optimization have been developed by researchers, but are not yet available in formats and with supporting documentation that enable easy use by practitioners.

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Chapter 3
Approaches to Modeling Landscape-Scale Drought-Induced Forest Mortality

Eric J. Gustafson and Douglas J. Shinneman

Contents

3.1 Introduction

Global changes, including climate change, are rapidly creating new environmental conditions and stressors for forests around the world. Climate change may have modest direct effects, at least initially, but indirect effects and interactions with disturbances can produce important changes in forest composition and landscape

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pattern (Dale et al. 2001; Gustafson et al. 2010), with consequences for ecological function and ecosystem services. Global Circulation Models generate varied predictions of future climate in any given part of the globe, and precipitation projections are usually much more uncertain than those for temperature (IPCC 2007). Nevertheless, almost all forested regions are expected to be subject to warming trends throughout the current century, with warming already pronounced at high latitudes (IPCC 2007). While precipitation projections are variable and less certain, in very few locations do confidence intervals indicate that precipitation will increase sufficiently to compensate higher evapotranspiration rates caused by increased temperature and, in some locations, precipitation may actually decrease (IPCC 2007). Consequently, drought stress of vegetation is expected to become more common in many parts of the world and this will have consequences for tree establishment, survival, and growth. Because species differ in their ability to tolerate moisture deficits, long-term consequences will be significant for forest composition and landscape pattern through the processes of competition, succession, and altered disturbance regimes. In this chapter, we review how drought affects forest ecosystems and the different ways these effects have been modeled (both spatially and aspatially). Building on those efforts, we describe several approaches to modeling drought effects in Landscape Disturbance and Succession Models (LDSMs), discuss advantages and shortcomings of each, and include two case studies for illustration.

Researchers and forest managers often use LDSMs to project the interacting effects of succession and disturbance at broad spatial and temporal scales and to compare the outcomes of alternative scenarios or management options. These models are unique in that they explicitly account for spatial relationships and processes, and provide answers about ecosystem dynamics and function at ecological time scales. They provide exceptional power to explore the efficacy of proposed management actions to mitigate the negative consequences of global change on biodiversity and ecosystem services. Not surprisingly, they are becoming widely used to project the impacts of multiple global changes and their interactions with natural and anthropogenic disturbances.

Although in some LDSMs variability in precipitation is used to affect fire regimes and tree growth rates, surprisingly few include this approach to simulate drought as a disturbance that kills trees. Gustafson and Sturtevant (2013) developed a drought disturbance extension for the LANDIS-II LDSM, and their results suggested that drought-induced mortality alone can indeed change forest composition and affect carbon storage. However, in most LDSMs direct interactions between drought and other disturbance and succession processes (establishment, growth, and competition) are not yet explicitly simulated, although exploratory modeling exercises and other research suggest that such effects should be accounted for in studies of global change effects on forest ecosystems. For example, because tree species thrive in different climate envelopes a persistent change in climate should result in altered establishment and competitive relationships (Allen et al. 2010). Additionally, drought-induced changes in vegetation composition can lead to changes in disturbance regimes (e.g., fire), which in turn are also directly modified by climate. The generally weak capability of LDSMs to include these types of drought effects and their interactions is a significant gap that reduces our ability to accurately project forest dynamics under future climate conditions.

3.2 Effects of Drought on Forest Landscapes

The physiological mechanisms behind drought-associated tree mortality are generally attributed either to direct water stress or to contributing factors that are exacerbated by drought, such as insects and pathogens (Mattson and Haack 1987; Manion 1991). McDowell et al. (2008) described three primary interacting mechanisms that can lead to tree mortality under drought conditions: hydraulic failure, carbon starvation, and biological agents. Hydraulic failure results when soil water decreases and evaporative demand increases, leading to cavitation (formation of air pockets) in xylem conduits that prevents movement of water to plant tissue. Carbon starvation occurs when plants use stomatal closure to avoid hydraulic failure, and respiration subsequently depletes carbohydrate reserves. Biological disturbance agents (e.g., insects, fungal pathogens) often respond positively to the physiological stress of drought-affected trees through population irruptions and enhanced rates of attack, leading to further stress and damage to trees, and higher rates of mortality (Mattson and Haack 1987). The relative contribution of each mechanism depends on species physiological traits, environmental conditions, and the duration and magnitude of water stress (McDowell 2011).

Drought can affect forest ecosystems at multiple spatial scales. At the individual tree level, vulnerability to drought varies with factors such as age, species, environmental setting, and interactions with other disturbance agents. Isohydric tree species are more likely to maintain xylem water potential during drought via stomatal closure, avoiding hydraulic failure but risking eventual carbon starvation, while anisohydric species better tolerate drought by maintaining continued gas exchange, but risk hydraulic failure (Adams et al. 2009). Tree age is also a factor, with older individuals often more vulnerable to drought-induced disturbance agents (Mueller et al. 2005; Ganey and Vojta 2011), and younger trees susceptible to direct mortality due to moisture stress (Ogle et al. 2000; Suarez et al. 2004). Environmental settings that affect climatic water deficits also play a role, including influence of soil texture and depth on hydraulic conductivity and water storage, and influence of topographic position on incident solar radiation and air temperature (Stephenson 1998). However, the precise physiological mechanism behind drought-related mortality or survival of trees is not always clear (Sala et al. 2010; McDowell 2011). For instance, knowledge of the differential role of non-structural carbon reserves required to maintain hydraulic conductivity during periods of stress is lacking for many species (Sala et al. 2012).

Drought-induced mortality events can substantially change forest composition within stands, across landscapes, and at regional-scales. For instance, in forests of the Great Lakes region, historic declines in beech (*Fagus grandifolia*) populations were likely caused by multi-decadal droughts during the Medieval Climate Anomaly (Booth et al. 2012). In northern Patagonia, massive drought-induced overstory and sapling mortality in southern beech (*Nothofagus* spp.*)* forests during 1998–1999 favored advanced regeneration of Chilean cedar (*Austrocedrus chilensis*) over coigüe (*Nothofagus dombeyi*), potentially leading to long-term shifts in forest composition (Suarez et al. 2004). Severe and persistent droughts over the last several hundred years in the southwestern United States contributed to intermittent dominance of junipers (*Juniperus* spp.) over less drought-tolerant piñon pines (*Pinus* spp.), while periods of above-average moisture, including during the early A.D. 1900s, contributed to increased piñon pine populations (Shinneman and Baker 2009). The severe drought of the A.D. late 1990s to mid-2000s in the US southwest, and associated wildfire activity and bark beetle outbreaks, have since caused massive piñon pine die-off events (Mueller et al. 2005; Breshears et al. 2005).

Drought also alters forest structure across broad scales, including the distributions and densities of forest patches, tree size and age classes, and live and dead biomass (Hogg et al. 2008; Anderegg et al. 2013). Drought-induced changes in forest composition and structure in turn influence forest function, including nutrient cycling and carbon, water, and energy fluxes (Dale et al. 2001; McDowell et al. 2008; Anderegg et al. 2013). In the short-term, drought-induced losses of leaf area decrease gross primary productivity in a forest stand and recent droughts have been shown to reduce terrestrial net primary production at a global scale (Zhao and Running 2010). Drought-associated mortality can also potentially result in bioregional forest carbon sinks becoming carbon sources (Ma et al. 2012). Drought is a key driver of the occurrence and magnitude of other natural disturbance events such as wildfire. Drought increases fire weather indices, decreases fuel moisture, and increases fuel loads (through mortality), and in many forest landscapes the area burned by wildfire is highly correlated with spatial and temporal patterns of dry versus wet periods (Westerling and Swetnam 2003; Girardin et al. 2006; Heyerdahl et al. 2008). Depending on ecosystem resilience, extreme drought and associated disturbance may alter succession and as result convert ecosystems from one type to another, especially under climate regime shifts (Burkett et al. 2005).

3.2.1 Drought Dynamics

Drought has long been a significant source of natural disturbance in forest ecosystems worldwide (Allen et al. 2010) and in many regions drought events of the last 150 years far exceed the severity and duration of earlier droughts. In North America, reconstructions of the Palmer Drought Severity Index (PDSI), derived from tree rings as proxies for climate variability, reveal that severe droughts of the twentieth century, such as the 1930s Dust Bowl drought, were relatively minor compared to several, multi-decadal "mega-droughts" that occurred over the past 1200 years, typically centered over western North America (Cook et al. 2004;

Stahle et al. 2007). These extreme climate events likely caused substantial mortality of some tree species and altered forest composition (Grissino-Mayer and Swetnam 2000).

The frequency, extent, duration, and intensity of drought are primarily driven by global-scale interactions (teleconnections) between anomalous sea surface temperatures (SSTs) and atmospheric conditions, further modified by land surface conditions. The SST anomalies in the eastern tropical Pacific Ocean drive the El Nino-Southern Oscillation (ENSO), of which the cool (La Niña) phase has been recognized as a primary driver of severe droughts in southwestern and southeastern North America (Cook et al. 2011). Other SST anomalies, such as the warm phase of the Atlantic Multi-decadal Oscillation (AMO) and the cool phase of the Pacific Decadal Oscillation (PDO), may enhance ENSO events and are also considered major contributors of drought and pluvial events throughout North America (McCabe et al. 2004). Although drought events are less frequent in mesic forest regions compared to more arid regions, oceanic–atmospheric fluctuations have been linked to severe droughts that have occurred in eastern temperate forests (Seager et al. 2009), forests of the Pacific Northwest (Nelson et al. 2011), boreal forests (Fauria and Johnson 2008), and other forest regions worldwide (e.g., Hendon et al. 2007).

Anthropogenic global climate change will likely substantially alter the intensity, frequency, location, spatial extent, timing, and duration of future droughts, as well as associated effects on forest ecosystems. Recent assessments indicate that overall aridity, as well as the area affected by droughts, has increased during the twentieth century, at regional to global scales (Dai 2011). Based on projections from global climate models (GCMs), researchers predict that in the twenty-first century droughts will intensify in some regions, including southwestern North America (Seager et al. 2007) and southern Europe (Beniston 2009). A key challenge to forecasting drought under climate change is to reliably transform projected changes in atmospheric conditions into dynamic physical processes that account for interactions with ecological processes. Generating robust predictions of future drought trends and effects will therefore not only require downscaling GCM-projected climate variables to generate indices of drought (e.g., PDSI) applicable across temporal and spatial scales (Wehner et al. 2011), but also developing more effective models of the dynamic role of tropical SSTs to shape future regional drought patterns and behavior (Dai 2010). Moreover, to project future effects of drought, researchers must consider how climate variability affects vegetation conditions (e.g., mortality, fuel moisture) that drive drought-induced disturbance events such as wildfire (Westerling and Swetnam 2003) or that induce feedbacks to temperature and precipitation (Wang et al. 2012; Anderegg et al. 2013).

3.3 Approaches to Modeling Drought

Models that simulate forest landscape ecosystem processes can provide a comprehensive understanding of the many complex relationships among climate, vegetation, and biogeochemical dynamics, including how forest diversity, productivity, and mortality respond to drought under different environmental settings. In this section, we provide a brief overview of drought applications within four broadly defined ecosystem model categories: forest gap models, ecosystem process models, LDSMs, and dynamic global vegetation models (DGVMs). This is not an exhaustive review of such models and their functionality, nor do we attempt to address all varieties, hybrids, or similar models. Detailed classifications and assessments of forest ecosystem models and their uses have been provided in numerous comprehensive reviews (e.g., Mladenoff and Baker 1999; Bugmann 2001; Keane et al. 2004; Scheller and Mladenoff 2007; He et al. 2008; Medlyn et al. 2011). Here we provide a brief overview of the functionality of basic forest ecosystem models that can be used to simulate the effects of drought and associated disturbances, and how such models simulate spatial interactions among these dynamics at broad scales.

3.3.1 Past and Developing Approaches

Early forest gap models, such as JABOWA, were developed to simulate the effects of physiological drivers on the rates of establishment, growth, and mortality among competing species of trees within a relatively homogenous forest stand or patch (Botkin et al. 1972; Shugart 1984). Early gap models were not spatially explicit, but some later gap models were developed to simulate spatial interactions among trees at fine scales (Pacala et al. 1993: SORTIE; Miller and Urban 2000: FM), and to specifically address the influence of environmental gradients (e.g., Bugmann et al. 1996: FORCLIM). Gap models typically require input parameters for mean precipitation rates, temperature, soil attributes, and species tolerance to drought stress to calculate the effect of soil moisture deficits on tree productivity (e.g., Pastor and Post 1986: LINKAGES). Despite this, most early gap models did not simulate realistic disturbance-induced tree mortality (Keane et al. 2001), prompting researchers to design alternatives that could be used to simulate the effects of specific disturbance types, including drought, on forest ecosystems across a range of environmental conditions (Prentice et al. 1993: FORSKA; Bugmann and Cramer 1998: FORCLIM). These advancements have further evolved into spatially explicit applications of gap-based models that simulate mortality events and project forest composition, structure, and productivity at landscape scales (e.g., Busing et al. 2007: FORCLIM), though such models still do not account for interactions among landscape-scale processes.

Ecosystem process models are similar to forest gap models in that they simulate the effects of biogeochemical processes (e.g., fluxes of energy and mass) on ecological dynamics (e.g., forest growth rate, carbon accumulation). Unlike gap models, ecosystem process models emphasize biogeochemical dynamics for potential vegetation types rather than individual trees or species (Cushman et al. 2007). Ecosystem process models generally incorporate water availability, plant water use, and evapotranspiration at forest sites to calculate water balance and determine water stress, permitting investigations of drought influence on forest ecosystem productivity (Aber and Federer 1992: PnET; Running and Gower 1991: Forest-BGC). However, only a few such models have specifically included the effects of drought-induced mortality (e.g., Grant et al. 2006: Ecosys). Ecosystem process models have been applied at broad scales, typically using land cover data sets from remotely sensed imagery, with each pixel representing a site. For instance, Aber et al. (1995: PnET-II) estimated the effects of water stress on ecosystem productivity in the northeastern U.S., and Turner et al. (2007: BIOME-BGC) examined the influence of wildfire and logging disturbance on carbon dynamics in Oregon. However, similar to forest gap models, spatially explicit interactions among landscape-scale processes are not generally simulated in such models (Scheller and Mladenoff 2007).

Here, LDSMs are distinguished from gap and ecosystem process models in that they are primarily intended to simulate forest disturbance and successional processes, as well as their interactions, across broad spatial and temporal scales (He et al. 2008). These models also generally provide spatially continuous projections of disturbance and vegetation dynamics (Cushman et al. 2007) that are valuable for determining key drivers of landscape-level forest composition or structure (e.g., Shinneman et al. 2010: LANDIS-II) or disturbance behavior (e.g., Keane et al. 2011: Fire-BGCv2). Within this framework, the diverse LDSM family of models can be further classified based on whether they can be used to simulate multiple processes or operate at fine temporal resolutions (He et al. 2008), and whether community change is static or dynamic, with the former determined by a priori successional stages and the latter by the life history attributes, behavior (e.g., seed dispersal), and physiological requirements of individual species (Scheller and Mladenoff 2007). Some LDSMs directly or indirectly incorporate the influence of biogeochemical process on forest productivity (Scheller and Mladenoff 2004: LANDIS-II; Keane et al. 2011: Fire-BGCv2), and can be coupled with gap or ecosystem process models to derive inputs representing climate effects on species establishment probabilities or productivity (e.g., Xu et al. 2009: LANDIS-II and PnET-II). Unlike DGVMs (discussed below), LDSMs do not incorporate feedback loops with GCMs and they cannot yet be applied at continental to global scales.

Dynamic global vegetation models are similar to terrestrial biogeochemical models, but additionally simulate competition among vegetation types (but not individual species) and are coupled to GCMs, allowing feedbacks to climate at regional to global scales (Medlyn et al. 2011). Thus, DGVMs can be used to simulate climate change effects on tree establishment and mortality via mechanistic plant responses to biogeochemical and hydrological dynamics (e.g., Sato et al. 2007: SEIB–DGVM). Moreover, DGVMs are useful for simulating interactions among disturbance, vegetation conditions, and climatological processes. For instance, Lenihan et al. (2008: MC1) simulated interactions between climate, vegetation, and wildfire to predict altered patterns of plant community and biomass distribution due to increased area burned under warmer and drier climate projected for California, USA. However, specific drought mortality mechanisms for different vegetation types or species have generally not been incorporated in DVGMs (Wang et al. 2012).

The focus of this chapter is LDSMs. Though direct simulation of drought dynamics using LDSMs is reported in remarkably few published studies, these models have tremendous potential for effectively projecting drought impacts on forest composition, structure, and function at landscape scales, in part by including spatially and temporally explicit interactions with other disturbance agents, such as wildfire (Cushman et al. 2007). For example, LDSMs that include individual species response to climate variability are also well-suited for projecting the effects of future climate change (including increasing aridity) on forest ecosystem composition and productivity (Scheller and Mladenoff 2007; Gustafson 2013). Moreover, drought effects in process-based LDSMs can be derived using either empirical or mechanistic approaches. An empirical approach assumes that historical relationships between measures of drought and tree mortality of the past can be used to predict drought effects in the future. A mechanistic approach directly links climate drivers to mechanistic tree responses; for instance, projecting tree growth and productivity under variable soil water conditions. Alternatively, drought events and their effects can be simulated using relatively stochastic or deterministic modeling approaches. Below, we present case studies to illustrate how these various general approaches to ecosystem modeling can be incorporated in LDSMs, often in combination, to simulate drought effects through development of new model extensions, coupling of complimentary models, and integration of empirically derived relationships.

3.3.2 Empirical Approach

The empirical approach involves estimating statistical models to predict drought-induced tree mortality as a function of a measure of drought using long-term tree inventory records, which are then applied within an LDSM to simulate mortality at each time step. A recent example of this approach used the extensive US Forest Service Forest Inventory and Analysis (FIA) database to estimate empirical models for the upper Midwest (Gustafson and Sturtevant 2013) and northeast United States (Gustafson 2014). The major difficulty of this approach is detecting the drought-induced mortality signal in a data set amidst the mortality caused by all other factors. Drought is seldom noted as the cause of death in inventory records, yet drought stress often increases the susceptibility of trees to death by other factors. The approach also requires observations from a variety of wet and dry periods to provide a useful range of values of the predictor (drought) variable, which means that a fairly long (>40 years) inventory record may be required. The large number of observations in the FIA data set allows the drought signal to be detected.

Gustafson and Sturtevant (2013) implemented this empirical approach as an extension to LANDIS-II (Scheller et al. 2007), which is a grid-cell forest LDSM that simulates the forest development processes of establishment, growth, and competition, and the forest degenerative processes of senescence and disturbances such as wildfire, wind, insect outbreaks, and timber harvesting at large spatial

(>100,000 ha) and long temporal (centuries) scales. In the model, living and dead biomass (rather than stem density) are tracked within cohorts of species on each cell, and several parameters are included that represent aboveground productivity and mortality. LANDIS-II is a primarily process-based model that encapsulates distinct ecological or physical processes as independent extensions that act on the biomass of cohorts within cells on the landscape. The independent operation of each extension on the extant biomass of each species cohort on each landscape cell produces forest dynamics that are an emergent property of the interacting extensions. The drought extension as implemented by Gustafson and Sturtevant (2013) modeled drought using empirical relationships, while the other extensions (e.g., succession, timber harvest) used a process-based approach.

To estimate empirical drought models for the upper Midwest U.S., Gustafson and Sturtevant (2013) constructed a data set containing records of percent biomass lost to mortality (*pm*) by species on each FIA plot in each inventory and a measure of drought stress (PDSI) during each inventory period obtained from the National Climate Data Center (URL: http://www1.ncdc.noaa.gov/pub/data/cirs/). The FIA inventory records covered the period 1965 to 2010 (varied by state), with inventories at approximately 13 year intervals. Mixed linear models were estimated for four categories of species drought sensitivity and tested against a 30 % random sample of observations that were not used in developing the estimates. They found that, in the U.S. Midwest, drought length was a better predictor of mortality than drought severity.

A LANDIS-II drought extension was constructed to use the empirical models to simulate drought-induced biomass loss to mortality. At each time step, a measure of drought is drawn from a user-specified distribution and the regression coefficients are used to calculate the 95 % confidence interval (CI) of *pm*. For each cell on the landscape, and for each species in the cell, a value of *pm* is selected from the CI such that older cohorts will have a *pm* value found in the upper part of the CI and younger cohorts in the lower portions, consistent with other empirical observations (Allen et al. 2010; Ganey and Vojta 2011). Biomass is removed from species cohorts (beginning with oldest cohort) until the selected *pm* value has been reached. To simulate loss of seedlings to drought stress, the probability of establishment (P_{est}) for the species is modified (for the current time step only) to 0.0 if its seedlings are relatively sensitive to drought, and by half if seedlings are moderately sensitive to drought (Hanson and Weltzin 2000). For species relatively insensitive to drought P_{est} is unchanged. After simulating drought, normal establishment processes of sprouting and seed dispersal/germination are simulated using the succession extension. Additional details of the empirical models and the extension can be found in Gustafson and Sturtevant (2013).

3.3.2.1 Case Study 1—Oconto County, Wisconsin

To provide a heuristic example of studying the effect of drought on forest composition, we used the LANDIS-II drought extension of Gustafson and Sturtevant

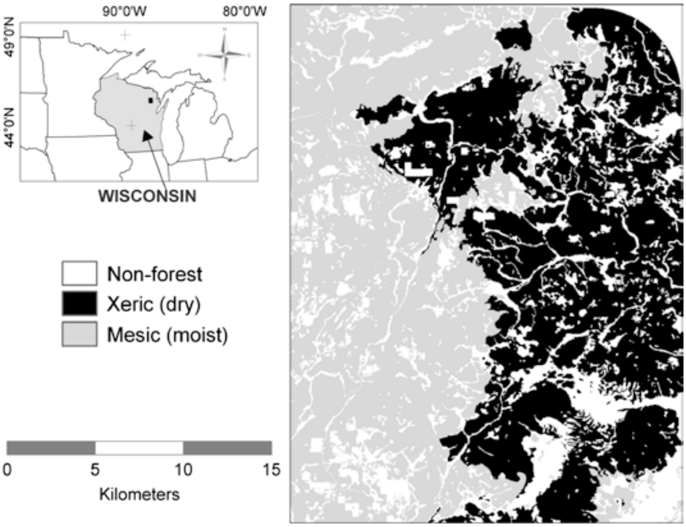

Fig. 3.1 Map of simulation study area in Oconto County, Wisconsin (USA)

(2013) to explore the effect of increasing drought length. We simulated three scenarios of mean drought length (years): no droughts, the current drought regime as simulated by Gustafson and Sturtevant (2013) (lognormal distribution of drought length with $\mu = 0.3$, $\sigma = 0.7$), and a drought regime with markedly longer droughts ($\mu = 1.2$, $\sigma = 0.7$). We conducted simulations on a 65,733 ha landscape on the Chequamegon-Nicolet National Forest in northeastern Wisconsin, USA (Fig. 3.1). We used the initial conditions map and LANDIS-II parameters described by Gustafson and Sturtevant (2013) that reflect current forest conditions and tree species vital attributes on each of the landforms. Because shade-intolerant species disappear without disturbance we also simulated each drought scenario with stand-replacing harvests on 5 % of the landscape per decade, with aspen (*Populus* spp.) and birch (*Betula* spp.) cut on an 80 year rotation and all other species on a 320 year rotation. We used version 6.0 (Scheller et al. 2007) of LANDIS-II with the Biomass Succession v3 (Scheller and Mladenoff 2004) and Biomass Harvest (Gustafson et al. 2000) extensions. Simulations were run for 300 years with three replicates and all extensions used a 10-year timestep. We evaluated the effect of increased drought on the amount of biomass killed by drought and on living biomass, by drought-susceptibility class (Table 3.1).

We found that, regardless of drought scenario, without harvesting the drought-susceptible pioneer species disappeared from the landscape by year 150 (Fig. 3.2a). As droughts lengthened, the total living biomass on the landscape declined modestly, and the relative abundance of somewhat drought-intolerant species decreased while that of the drought-tolerant class increased modestly

Table 3.1 Species assignments to the four drought sensitivity classes (reproduced from Gustafson and Sturtevant 2013)

Drought sensitivity class	Common name	Scientific name
Intolerant	Quaking aspen, big-toothed aspen, paper birch, black ash	*Populus tremuloides*, *P. grandidentata*, *Betula papyrifera*, *Fraxinus nigra*
Somewhat intolerant	Eastern hemlock, White spruce, Northern white cedar, yellow birch, balsam fir	*Tsuga canadensis*, *Picea glauca*, *Thuja occidentalis*, *Betula alleghaniensis*, *Abies balsamea*
Somewhat tolerant	Red maple, sugar maple, black cherry, white ash, basswood, American larch, black spruce	*Acer rubrum*, *A. saccharum*, *Prunus serotinus*, *Fraxinus americana*, *Tilia americana*, *Larix laricina*, *Picea mariana*
Tolerant	Red pine, white pine, jack pine, red oak, white oak	*Pinus rubra, P. strobus, P. banksiana, Quercus rubra, Q. alba*

(Fig. 3.2a). The amount of biomass lost to drought remained at equilibrium under the current drought regime, although the proportion lost by more drought-tolerant classes increased as the drought-intolerant class disappeared (Fig. 3.2b). Under the longer drought regime the total biomass lost to drought was higher than that under the current regime but also decreased over time as the drought-susceptible class disappeared.

When harvests were included, the drought-intolerant class actually increased through time (Fig. 3.3a) because that class is composed primarily of shade-intolerant species that require disturbance to persist (Table 3.1). As the length of droughts increased, the total living biomass decreased, with the somewhat drought-intolerant class losing relatively more biomass through time. The drought-intolerant class seemed to flourish under long droughts because with the addition of harvesting disturbance tolerant, single species stands were retained, resulting in vigorous regeneration and high rates of growth even after drought disturbance. This contrasts with observations in Alberta, Canada, where mature aspen dieback was related to drought severity and interactions with logging were not considered (Hogg et al. 2008). The amount of biomass lost to drought was higher when harvests occurred, with extremely high losses under the long drought scenario (note y-axis scaling in Fig. 3.3b). These losses were almost entirely from the drought-intolerant class, which became very abundant on the landscape because of harvesting and was especially susceptible to long droughts. It is interesting to note that this class maintained its presence on the landscape under both drought scenarios, and continued to increase in relative abundance through year 300. This example is quite simple, but it nonetheless provides insight into interactions between drought and harvest in the context of empirical studies (e.g., D'Amato et al. 2013).

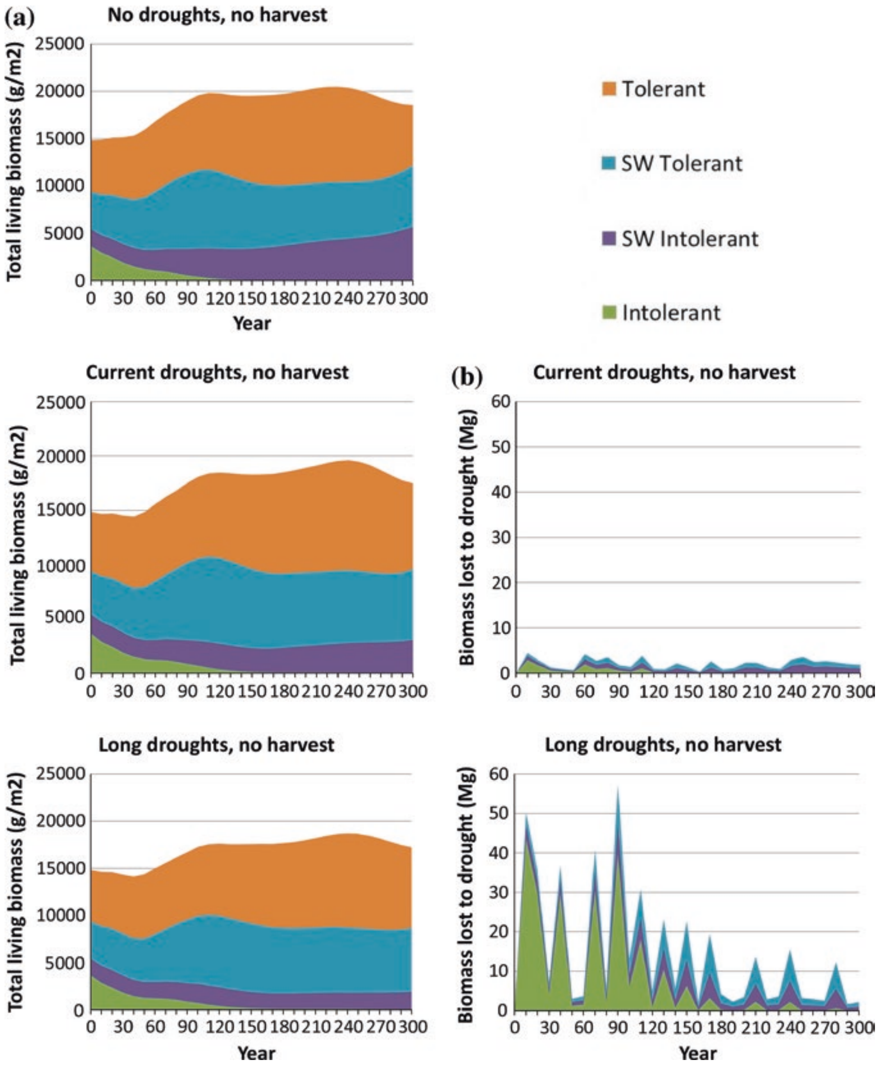

Fig. 3.2 Living (**a**) and killed (**b**) biomass by drought susceptibility class (Table 3.1) in simulated drought scenarios without timber harvesting for Oconto County, Wisconsin (USA)

3.3.2.2 Critique of the Empirical Approach

The empirical approach has two major advantages. First, empirical relationships are conceptually simple and are therefore relatively easy to build and test given an adequate data set. Second, relative to a mechanistic approach few parameters are needed to simulate drought mortality, reducing both the effort needed to estimate parameters and the cumulative error associated with additional parameters. Furthermore, the algorithms are simple, resulting in faster computation.

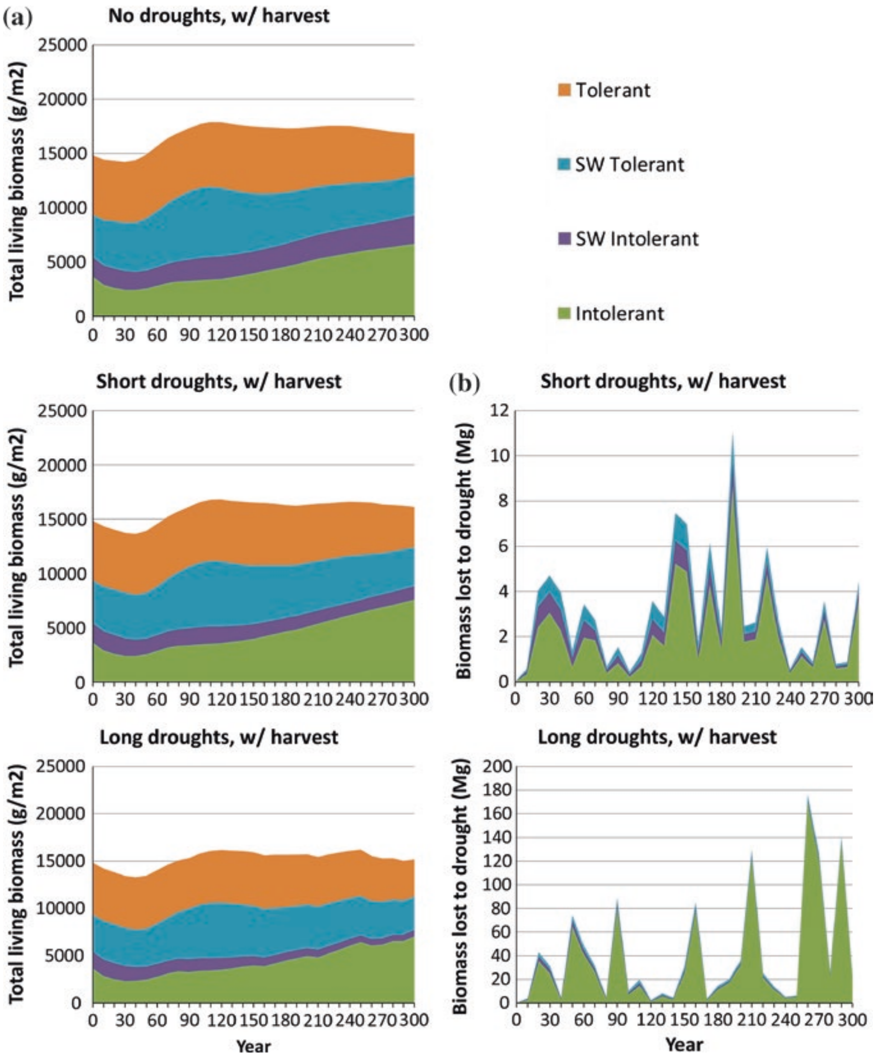

Fig. 3.3 Living (**a**) and killed (**b**) biomass by drought susceptibility class (Table 3.1) in simulated drought scenarios with timber harvesting for Oconto County, Wisconsin (USA). Note y-axis scaling differences in the right-hand plots

On the other hand, the empirical approach has several shortcomings. The most important is the increasing evidence that the known (past) relationships between drought and mortality are very unlikely to be valid into the future. If only the distribution of measures of drought varied under climate change, then the empirical approach might remain valid. But the increased evapotranspirative demand caused by concomitant higher temperatures indicates that moisture stress will increase in a way that is not linearly related to precipitation (Dale et al. 2001). And even when a drought index is used that better accounts for both temperature and precipitation (e.g., the moisture index of Thornthwaite (1948) that calculates moisture stress as a function of potential evapotranspiration and precipitation), the potential shuffling of community assemblies will likely change competitive dynamics. We expect that species will not shift their ranges in unison and therefore communities will re-assemble (Iverson et al. 2008). This change in competitive interactions coupled with increasing drought stress may alter species susceptibility to mortality.

There are also other disadvantages: (1) Because the estimation of empirical models usually requires records that span long time periods, few suitable data sets are available for estimating the statistical models. Even the long-term FIA database may not always be adequate for building empirical models (e.g., Gustafson 2014). (2) Relationships between measures of drought and tree mortality may be only weakly significant, likely because of statistical noise (Gustafson and Sturtevant 2013). This results in uncertainty that may be unacceptably high, especially when coupled with the uncertainty inherent in other components of the LDSM (Xu et al. 2009). (3) The general applicability of empirical models has yet to be established. Gustafson (2014) attempted to use empirical models constructed in the U.S. Midwest in the U.S. northeast. However, it was difficult to verify that their validity, because droughts were rare in that region during the period for which records were available. Moreover, empirical models for northeast species not found in the Midwest did not exist. (4) Moisture stress reduces growth rates and can ultimately lead to mortality by several associated causes (Bréda et al. 2006), but growth rates and mortality are not coupled in the empirical approach. Thus, the LDSM will simulate normal growth during a drought, even though some portion of cohort biomass is lost to mortality. In reality, the effects of drought on growth varies among species (Bréda et al. 2006), which may affect competition and ultimately successional outcomes, apart from the mortality effects of drought.

3.3.3 Deterministic Approach

Ideally, projections of future drought frequency, severity, and extent should incorporate the influence of enhanced evaporative demand under climate change using GCM-derived projections and temperature-sensitive drought indices (Dai 2010; Wehner et al. 2011). However, such climate variables are not typically incorporated directly into process-based LDSMs, and thus drought projections may need to be deterministically integrated, such that simulations of future drought effects on forest ecosystems can include temporally and spatially synchronized interactions with climate change effects on species establishment and productivity, as well as other disturbance events (e.g., wildfire).

3.3.3.1 Case Study 2—Voyageurs National Park

To illustrate, we projected future drought occurrences using GCM outputs for the period 2000–2099 and simulated potential drought effects on a 157,000 ha southern boreal forest landscape (52 % forested, 48 % lakes/wetlands) in Voyageurs National Park (VNP) and vicinity in northern Minnesota, USA (Fig. 3.4). We used an established model to generate a self-calibrating drought index (SC-PDSI) compatible with climatological regions (Wells et al. 2004), that requires inputs for monthly average temperature, monthly total precipitation, normal mean temperature and precipitation, latitude, and available soil water holding capacity (AWHC). We derived future monthly climate values from the Canadian Centre for Climate Modelling and Analysis (CCCma) Coupled Global Climate Model (www.cccsn.ec.gc.ca) under the SRES-A2 emissions scenario (IPCC 2007), used 1961–1990 climate means as normals, and derived AWHC values from the State Soil Geographic (STATSGO2) database (http://websoilsurvey.nrcs.usda.gov/). Compared to the normal period, the A2 climate scenario predicts a nearly 6°C increase in mean annual temperature and a ≈90 mm increase in annual precipitation (and with greater variability) by the end of the twenty-first century.

Species establishment, growth, and mortality were simulated using LANDIS-II with the biomass succession, base fire, and wind disturbance extensions (Scheller et al. 2007; and as described in the case study in Sect. 3.3.2.1). Species life history traits and disturbance parameterization largely followed Shinneman et al. (2010). Species probability of establishment (P_{est}) and maximum aboveground net primary productivity (ANPP) inputs for the biomass succession extension (Scheller and Mladenoff 2004) were calculated under contemporary and future climate scenarios using PnET for LANDIS (Xu et al. 2009). The PnET extension for LANDIS uses equations from the PnET-II (Aber et al. 1995) ecosystem process model to generate estimates of maximum ANPP, and equations from the LINKAGES (Pastor and Post 1986) forest gap model to estimate species establishment probabilities, under different climate conditions. Input values for species ecophysiological parameters were obtained from relevant sources (e.g., Reich et al. 1999; Peters et al. 2013), and key site and climate parameters (and sources) are nearly identical to those for the drought model described above. Thus, P_{est} and maximum ANPP values for each tree species in the VNP landscape were estimated annually using climate parameters that temporally and spatially correspond to those used for annual drought projections. Inputs were calculated for three primary ecoregion types (two upland types, one wet forest type), delineated using soil (STATSGO2) and recent forest classification maps (http://www1.usgs.gov/vip/voya/voya.zip).

Drought effects were simulated in LANDIS-II using a recently developed empirical stress-mortality extension that simulates the effects of stress events on tree mortality and biomass at predetermined time steps (Shinneman et al. in prep). Specifically, future drought events were simulated via the extension for each year in which projected growing-season (March–August) cumulative PDSI values sum to -12 or lower (capturing moderate to extreme droughts). Each occurrence of a

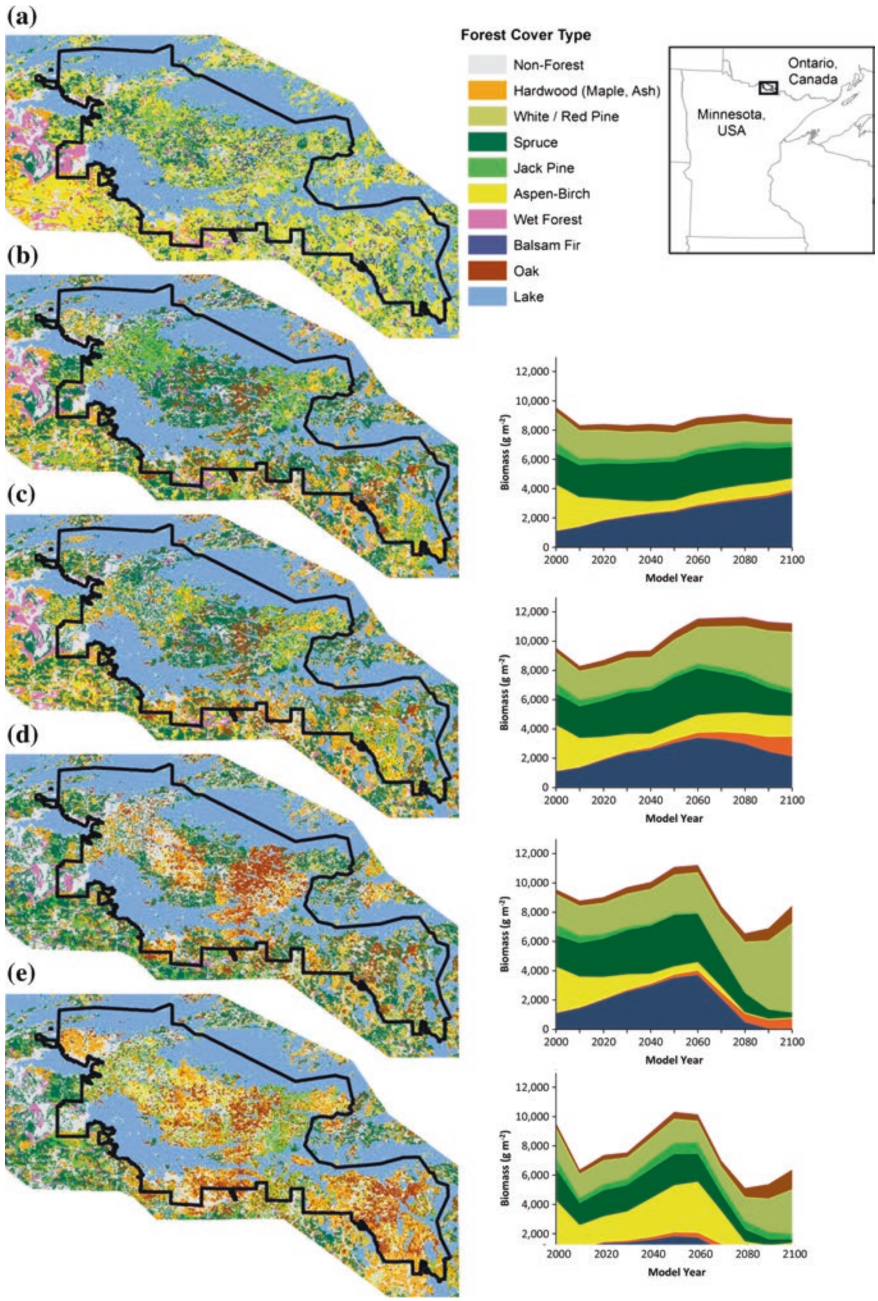

Fig. 3.4 Forest composition and aboveground biomass over time for Voyageurs National Park and vicinity, relative to the contemporary (i.e., recently mapped and classified, not modeled) landscape (**a**) and four modeled future scenarios: contemporary climate, contemporary fire regime, and no drought (**b**); future climate, contemporary fire regime, and no drought (**c**); future climate, contemporary fire regime, and climate change-induced drought (**d**); and future climate, future fire regime, and climate change-induced drought (**e**)

drought event triggered predetermined amounts of biomass reduction from mortality for selected species-age cohorts, ranging from 5 to 33 % for older cohorts across the drought-intolerant to tolerant species groups (refer to Table 3.1), respectively, and with generally lower mortality rates for younger cohorts (Gustafson and Sturtevant 2013). Although drought mortality rates associated with each species were not available for the study area, a simulated maximum rate of 33 % for oldest cohorts of drought-sensitive species is comparable to extensive drought-induced mortality documented for similar forests nearby (e.g., Jones et al. 1993; Michaelian et al. 2011). Finally, if consecutive drought years resulted in >90 % biomass reduction for any species-age cohort, complete cohort mortality was triggered.

Here we present model output for the VNP landscape, as a prototype for a regional model currently in development (Shinneman et al. in prep.) that demonstrates potential interactions among drought mortality, wildfire, and climate change effects on species establishment, growth, and productivity. Spatial resolution for forest conditions was 1 ha, and temporal resolution varied depending on the process simulated, but drought inputs were at annual resolution, while most output was reported for 10-year time steps. We present results at the end of a 100-year period (2000–2100) under four successively altered scenarios: (1) contemporary climate, contemporary fire regime, and no drought, (2) future climate, contemporary fire regime, and no drought; (3) future climate, contemporary fire regime, and climate change-induced drought; and (4) future climate, future fire regime, and climate change-induced drought. Thus, in all scenarios, forest composition and biomass were affected by both fire and climate-driven species establishment probabilities, and two scenarios additionally simulated mortality from drought. All scenarios also included modest amounts of wind disturbance (Shinneman et al. 2010). Contemporary fire regimes for VNP were simulated to achieve an approximately 400 year mean fire rotation, based on recent fire records for the region, while future fire rotation was reduced to about 200 years, based on fire rotations projected under climate change (Flannigan et al. 2005). Biomass output results are limited here to the dominant upland forest ecoregion type in VNP, which is characterized by generally shallow, nutrient-poor, coarse-textured soils with low water holding capacity. Projected SC-PDSI values derived from the CGCM-A2 climate scenario indicate that moderate to severe drought will be common across the three land types in the latter half of the twenty-first century, occurring in 35 to 65 % of the growing seasons between 2060 and 2099, with the upland forest ecoregion type most vulnerable.

Results show that under the current climate scenario, with a contemporary fire regime and no drought mortality (Scenario 1), regional forest composition transitioned from primarily aspen-dominated (due to past timber harvest and wildfire) in the contemporary landscape (Fig. 3.4a) to large expanses of late-successional boreal conifers, especially shade-tolerant, fire-sensitive balsam fir (*Abies balsamea*) (Fig. 3.4b). Similar projections have been made for the region using other models (Shinneman et al. 2010). Accordingly, biomass of shade-tolerant and fire-intolerant species increased over time, while biomass decreased for most early successional and fire-dependent species, especially white pine (*Pinus strobus*)/red pine (*Pinus resinosa*), and aspen (Fig. 3.4b). With warmer temperatures and no drought (Scenario 2), the shift in composition toward boreal conifers was less pronounced, as spruce (*Picea* spp.)-fir biomass declined substantially after 2060 under less favorable climate, while white pine and hardwood species biomass increased (Fig. 3.4c), similar to other LDSM projections for the region (Ravenscroft et al. 2010). However, when drought effects were simulated under climate change (Scenario 3), oak (*Quercus* spp.) and white pine biomass and cover increased more substantially, while boreal species biomass declined more precipitously after 2060 (Fig. 3.4d). Under drought, climate change and more frequent wildfire (Scenario 4), forest composition was similar to Scenario 3, but with more even proportions of forest cover types at the landscape scale, and a substantial decline in mean forest biomass (75 % of the mean forest biomass of Scenario 3 at year 2100; 57 % of that in Scenario 2).

Thus, scenarios in which the effects of warmer temperatures and associated drought were simulated shifted the landscape away from dominance by boreal forest species—spruce, jack pine (*Pinus banksiana*), and aspen—which declined from about 78 % of the forest landscape area at model year 2000 to less than 50 % at model year 2100, and from 75 % of mean upland forest biomass at year 2000 to only about 5 % in 2100. In contrast, temperate forest species increased under these scenarios, with more oak, white pine, maple (*Acer* spp.), and ash (*Fraxinus* spp.). When fire frequency increased under warmer, drought-filled climate conditions, the forest landscape shifted further toward temperate species and overall upland forest biomass declined substantially, suggesting a shift toward open forest structures dominated by early successional, drought-tolerant, and fire-tolerant (or resprouting) species, and representing the effects of recently burned forest (about 10 % of the initial forest area). Boreal spruce-fir cover types mostly remained dominant in ecoregions with higher soil water content (e.g., wetland-forest and clay soil ecoregions, Fig. 3.4a-e maps; biomass output not shown). Warmer temperatures without drought (Scenario 2) did not have these dramatic effects, as more of the upland forest area and biomass was represented by boreal species, although the area covered by these species still diminished steadily after 2060.

3.3.3.2 Critique of the Deterministic Approach

The primary advantage of incorporating a relatively deterministic approach within an otherwise stochastic LDSM is that climate effects on species establishment/growth and drought-induced mortality are more directly linked in time and space. Although the fire events simulated in the above example were not directly linked to climate-induced drought events, advanced fire and fuel extensions have been developed that do allow climate to directly influence fuel conditions and fire occurrence (Sturtevant et al. 2009). However, a more seamless approach would be to develop the ability to directly integrate user-provided climate inputs among all relevant processes and their extensions in LANDIS-II (and similar LDSMs), further unifying the influence of climate on ecological processes and disturbance interactions across time and space. Indeed, if such climate-input functionality used a random weather generator approach (e.g., LARS-WG), stochasticity inherent in many LDSMs (providing estimates of variation in future forest conditions) would be preserved. A climate library extension for LANDIS-II that will provide much of this capability is nearing completion (Robert Scheller, pers. comm.)

A potential disadvantage to modeling drought using a deterministic approach is that predetermined drought events of a minimum intensity trigger a uniform rate of mortality for each species-age cohort. Moreover, the data and empirically derived relationships needed to parameterize drought-induced mortality for species-age cohorts in many forest ecosystems are likely to be insufficient, primarily due to a lack of long-term, tree mortality data that can be directly attributable to the effects of drought (Gustafson and Sturtevant 2013), but also due to uncertainty about changing ecosystem responses under future climate conditions. Thus, further development of the stress-mortality extension used in the above example might include the ability to represent a continuum of drought intensity, with mortality rates determined by integration with mechanistic, process-based models (discussed below).

Finally, when projecting future drought under climate change, careful consideration should be given to selecting appropriate drought indices, GCMs, and downscaling methods. Precipitation projections in particular can vary substantially among GCMs and may be more difficult to effectively downscale from global to landscape scales (IPCC 2007). Although use of a multi-model ensemble approach could reduce the uncertainty among models, ensemble climate models may also unrealistically reduce the variability of drought intensity predicted by the more reliable individual GCMs (Wehner et al. 2011).

3.3.4 Process-Based (Mechanistic) Approach

In many cases using a direct, mechanistic approach to model drought effects on forests may be advantageous as it allows explicit simulation of the physiological processes that induce drought stress and lead to altered rates of cohort establishment, growth, and mortality in response to changes in water and light availability. Although LDSMs can be externally coupled with ecosystem process models (e.g., to define species growth and establishment input parameters, as in our case studies), such an approach limits the direct response of key processes to drought stress. Incorporating changing water and light availability directly into an LDSM not only permits ready simulations of drought-enhanced rates of biomass loss and mortality among species as a stochastic and spatially explicit process, but the effects of specific drought events can be incorporated into the model, affecting future competitive interactions and disturbance events, including the effect of future drought.

Such a mechanistic approach may become feasible with the development of a new LANDIS-II succession extension that includes moisture and light as limited resources to simulate competition among tree cohorts. The new extension (PnET-Succession) incorporates elements of the PnET-II biogeochemical model (Aber et al. 1995; Ollinger et al. 1998) into an extension based on the Biomass Succession extension (Scheller and Mladenoff 2004) to calculate growth as a function of limited light and soil water resources. This new capability allows growth rates to vary at each time step in response to competition for light, and more importantly for this discussion, for water.

A full description of the PnET-Succession extension is well beyond the scope of this chapter, but can be found in De Bruijn et al. (2014). However, a few key elements will illuminate how the extension can facilitate the simulation of drought mortality as a process. First, species cohort growth rates are calculated as a function of photosynthesis, which depends fundamentally on soil water availability, defined as the ratio of transpiration and potential transpiration. Soil water is tracked at the grid-cell level using a bulk hydrology model based on precipitation, air temperature, and consumption by species cohorts. Cohorts compete for water and light in each cell, and cohort biomass determines the priority of access to radiation and soil moisture, with the largest cohorts having first access to both resources. When water is adequate, the rate of photosynthesis (leaf area index) for a given species cohort increases with light that is available to the cohort (dependent on canopy position and leaf area), atmospheric carbon dioxide (CO_2) concentration and foliar nitrogen (N), and decreases with age and departure from optimal temperature. As soil water availability decreases, photosynthesis also decreases. The PnET-Succession extension accounts for reductions in photosynthesis by respiration such that foliar respiration rate depends on temperature and moisture, while maintenance respiration depends only on temperature.

Thus, in the PnET-Succession extension, photosynthetic rates (and therefore growth rates) vary by species and cohorts monthly as a function of precipitation and temperature (among other factors), which directly affects competition and ultimately successional outcomes. Capitalizing on this approach of simulating growth via the process of photosynthesis, drought-induced mortality would result when carbon reserves are depleted by respiration. Such mortality may further depend on the length of time that water limitations occur, based on the drought-tolerance of species. For studies of the effects of climate change on forest successional dynamics, a “weather stream” of temperature, precipitation, and radiation from downscaled global circulation models would allow growth and establishment rates to vary at each time step in response to temperature and precipitation, and drought-induced mortality would be simulated when moisture stress depresses growth rates below respiration levels for a prolonged period. An initial test of the ability of PnET-Succession to simulate drought effects compared empirical physiological measurements from a precipitation manipulation experiment in a piñon-juniper ecosystem (Pangle et al. 2012) with values predicted by PnET-Succession. For the purposes of landscape modeling of forest growth and succession over long time periods, net photosynthesis is the key output of the model, and it responded similar to the empirical measures under both precipitation diversion and irrigation treatments (Gustafson et al. 2015). Modeled carbon reserves also varied consistently with empirical measures under drought and wet conditions, and modeled carbon reserves for experimental plots were well correlated with observed mortality rates. These results suggest that this simple physiological approach holds promise to mechanistically simulate drought effects under climate change at broad temporal and spatial scales. Additional testing is ongoing.

3.3.4.1 Critique of the Mechanistic Approach

The primary advantage of the mechanistic approach is that it is built on first principles. The physiology of tree water use in response to availability is well studied and relationships between water availability and growth rates are well established. Mortality becomes deterministic as a consequence of physiological moisture stress and carbon balance, rather than the outcome of a probability density function. The sophistication of the modeling of those processes can be small or great, depending on the research or management question. De Bruijn et al. (2014) added elements of the PnET-II model into LANDIS-II, but other physiology models could be used instead. Additionally, mechanistic approaches to simulate direct drought-induced mortality are almost certainly more robust under climate change scenarios than empirical approaches (Keane et al. 2001), but indirect mortality (e.g., by insects) may also need to be explicitly simulated. Robustness under novel conditions is one of the key criteria for assessing the utility of models to forecast forest dynamics as a consequence of global changes (Gustafson 2013). Another advantage is that the mechanistic approach is general and can be applied in any system for which the physiological relationships of water stress and photosynthesis are known. Finally, a mechanistic, process-based approach overcomes the decoupling of moisture stress and growth rates that is inherent in the empirical approach.

One important disadvantage is that process-based models are more complex, requiring more parameters that increase uncertainty and potentially requiring more time for computation. Validation of performance under future conditions that do not yet exist (e.g., increased atmospheric CO_2 concentrations) also remains a challenge. Model users must rely on validation of the process model under the range of historical conditions or from experimental studies, and assume that the physiological processes of growth and death will not fundamentally change in the future.

3.4 Future Prospects

Modeling drought effects in LDSMs is still in its infancy, and no current approach is clearly robust. In part, this is related to the newness of the modeling attempts, but is also the result of lingering ambiguity about the physiology of tree mortality from moisture stress (Sala et al. 2010), as well as challenges inherent in projecting future drought events under climate change (Dai 2010). It is very likely that new and innovative techniques will be developed, perhaps involving a combination of empirical and process-based approaches. In the face of climate change, the key to achieving robust capabilities is to model the links between the important factors that determine moisture stress (e.g., precipitation, temperature, and other biotic and abiotic factors) and tree mortality. Somewhat robust tree- and site-scale models already exist, but innovations are needed to successfully implement such approaches at broader temporal and spatial scales.

Although many aspects of the physiology of photosynthesis, growth, water use, and carbon allocation within trees are well known, the fundamental mechanisms determining tree survival or mortality during drought remain poorly understood despite decades of research (Bréda et al. 2006; Allen et al. 2010; Sala et al. 2010). Manion's (1991) decline spiral model posits that drought triggers mortality of trees that are already under stress by factors such as old age, poor site conditions, and air pollution, allowing them to be killed by tissue damage or biotic agents such as wood-boring insects and fungal pathogens. McDowell et al. (2008) suggest three mutually non-exclusive mechanisms by which drought could lead to forest mortality: (1) extreme drought kills trees through cavitation of water columns within the xylem, (2) long-term water stress produces plant carbon deficits that lead to death or reduced ability to defend against biotic agents such as insects or pathogens, and (3) extended warmth during droughts can result in increased populations of biotic agents, allowing them to overwhelm their already stressed tree hosts. Although these hypotheses have growing support, the physiology of tree death by moisture stress is not unambiguous (Bréda et al. 2006; Sala et al. 2010), and the process is to some extent still simulated by proxy. Moreover, drought effects may be offset or vary unpredictably among species due to increasing atmospheric CO_2 concentrations and N deposition, which affect plant water use and photosynthetic efficiency (Wang et al. 2012).

We have alluded to several knowledge gaps that hinder our ability to model drought effects on forested landscapes, not the least of which includes critical uncertainties related to the physiology of drought-induced mortality for most tree species. Although long-term empirical and experimental climate change studies are few, their findings should be incorporated into LDSMs, as should remote sensing data that provide additional information about the relationships between drought and tree response (e.g., Breshears et al. 2005). There may also be value in combining existing models that use different approaches and operate at different scales, as demonstrated by the joining of the LANDIS-II and PnET-II models (as described in Sect. 3.3). Ultimately, advances are needed to allow modelers to link changes in fundamental environmental drivers to their differential effects on tree species as well as their interactions with growth, competition, mortality, and various natural and anthropogenic disturbances.

3.5 Conclusions

Based on our review of the literature and experience, as well as results from the relatively heuristic case studies provided here, we can draw some general conclusions: (1) Because of changing climate, drought stress will increasingly affect the dynamics of forested landscapes, resulting in altered ecosystem composition, structure, and function. (2) Because climate change will produce new environmental conditions and stressors (including drought) that will interact in complex ways with forest growth, succession, and disturbance, to reliably project future forest dynamics LDSMs must better link the variability in climate with that inherent in the fundamental drivers of ecosystems. (3) Inclusion of drought as a process that alters forests in LDSMs is in its infancy but, because of the increasing importance of drought, these capabilities must be rapidly advanced.

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Chapter 4
Modeling Wildfire Regimes in Forest Landscapes: Abstracting a Complex Reality

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4.1 Introduction

Fire is a natural disturbance that is nearly ubiquitous in terrestrial ecosystems. The capacity to burn exists virtually wherever vegetation grows. In some forested landscapes, fire is a principal driver of rapid ecosystem change, resetting succession (McKenzie et al. 1996a) and changing wildlife habitat (Cushman et al. 2011), hydrology (Feikema et al. 2013), element cycles (Smithwick 2011), and even landforms (Pierce et al. 2004). In boreal forests, for example, recurring wildfires are the main cause of compositional and spatial patterns (Wein and MacLean 1983), where a fire-induced "shifting spatial mosaic" governs the heterogeneity in ecosystem patterns and processes on the landscape (Goldammer and Furyaev 1996). In forest ecosystems where dominant species are long-lived, mature trees may provide a buffer against extreme weather such as drought or heat waves, but fires and other disturbances such as insect outbreaks eliminate the buffering of the canopy, leaving a hotter and drier microclimate conducive to the establishment of new species. In a warming climate, fire is expected to amplify and accelerate changes in forest composition, spatial pattern, and structure (Littell et al. 2010; Loehman and Keane 2012; Raymond and McKenzie 2012; Cansler and McKenzie 2014). Anticipating these changes will be a key to successful forest management and conservation.

The value that land managers place on wildfires varies widely, as do strategies for their management (Bowman et al. 2011). In some parts of the world (e.g., Mediterranean), wildfires are seen as a natural hazard to human settlements, and attempts are made to reduce or eliminate their occurrence (Rego and Silva 2014). In other regions (e.g., Fennoscandia) wildfires have been virtually eliminated by centuries of aggressive fire suppression, and now are being re-introduced to restore biodiversity patterns and ecosystem processes (Wallenius 2011). Analogously, in North America, emulating natural disturbances such as fire is a growing forest-management paradigm, mostly where spatial and temporal patterns of wildfires are used as templates for silvicultural prescriptions (Perera et al. 2004). All these approaches to management demand spatially reliable and spatio-temporally explicit knowledge of wildfires in forest landscapes.

Fire is a dynamic stochastic process. Observed fires and time series of fire events can be seen as single realizations of that process (Lertzman et al. 1998; McKenzie et al. 2011). Rarely will two fire events be the same, because each event includes unique instances of fire ignition, spread, and extinguishment. The array of geo-environmental factors that control these three steps (in the case of wildfires), and social factors that modify their effects (in the case of man-made and managed fires), make each fire event different. Climate and weather, vegetation (fuel) composition and spatial arrangement, and topography interact to produce *fire regimes* with aggregate properties that reflect these drivers. We define fire regimes broadly, sensu Krebs et al. (2010), as characteristic combinations of antecedent conditions (i.e., climate, fuels, topography), fire attributes, and fire effects. For example, topographic complexity engenders characteristic fire shapes and sizes over time,

Table 4.1 Properties of wildfire regimes versus individual wildfires

	Individual fire	Fire regime
Temporal properties	Fire date(s)	Fire frequency (fire return interval or fire cycle), fire season
Cause	Specific ignition source (e.g., lightning, arson, fireworks, smoldering)	Characteristic ignition (lightning or human)
Process	Fire behavior: fireline intensity, flame length, spread rate, torching, crowning Fire effects: consumption, emissions, plant mortality	Productivity, fuel build-up, succession, leaf phenology, disturbance interactions (e.g., insects, pathogens, windthrow)
Material	Fuel loading, fuel connectivity (horizontal and vertical)	Species composition, biomass
Climate and weather	Wind, humidity, temperature, fuel moisture	Water balance deficit, summer temperature, winter precipitation, drought frequency, El Niño Southern Oscillation
Extent	Fire size, fire perimeter	Annual area burned (mean and variance), fire-size distribution
Spatial pattern	Simple versus complex, fire progression, fire severity classes or spatial variability	Spatial pattern of landscape fuel types (fuel mosaic), patch size distributions (fire area and fire severity)
Management	Initial attack, suppression, backfires, evacuations	Fuel treatments, let burn versus suppression, demographic planning, education

Lists are meant to be representative but not exhaustive

even though individual fire perimeters and areas are generally not well predicted (Kennedy and McKenzie 2010; McKenzie and Kennedy 2012). Similarly, fire and climate interact with vegetation across multiple spatial and temporal scales, producing characteristic fire patterns at broad scales (Higuera et al. 2009; Gedalof 2011). Understanding fire regimes comprehensively, especially broader characteristics such as fire-return intervals, fire-size distributions, spatial probabilities of occurrence, and spatial patterns of severity, is the primary value to the aforementioned management interests (Krebs et al. 2010; Table 4.1).

To understand wildfire regimes in forest landscapes, we seek a level of generality that is different from what is required for the behavior of individual fires and cannot be achieved by simply "summing over" fire events and their effects. For example, fire-scarred trees provide a temporally accurate record of historical fires, but a spatially imperfect one because the extent and perimeters of fire events are known only imprecisely, even when sophisticated interpolations are applied (Falk et al. 2011; Swetnam et al. 2011). Interpolation errors accumulate such that aggregate statistics and general characteristics of the fire history are biased or unacceptably inaccurate.

Unlike historical fire regimes for which we have incomplete records, contemporary wildfires take place within a rich data matrix: fire weather and fuels may be known with greater accuracy. With sufficient input data, at appropriate temporal and spatial resolutions, individual fires can be simulated reasonably well, particularly with "full-physics" models (Linn et al. 2002; Mell et al. 2007), but sensitivity to initial conditions, especially with extreme events that involve convective fire plumes and long-distance spotting, still leads to considerable uncertainty in outcomes (Werth et al. 2011). Furthermore, full-physics models are currently impractical at the scale of forest landscapes, in that their grid spacing is on the order of centimeters. This may always be the case, because not only is their execution at the scales required computationally infeasible, but also they will encounter the so-called "middle-number" problem (McKenzie et al. 2011): a combinatorial explosion of spatial variation in parameters across their domain that cannot be compensated by judicious choices of averages or other summary statistics.

In this chapter, we confront a conceptual issue in modeling whose clarification should enhance the appropriate use of simulation models that focus on wildfire regimes (hereafter "WRSMs," as distinct from finer-scale models that focus on individual fires) in forest landscapes. Many good overviews of landscape fire models are available (e.g., Keane et al. 2004; Cary et al. 2006, 2009; Scheller and Mladenoff 2007) and we eschew more coverage of the same territory. Instead, we examine what (and how) we abstract by WRSMs and how the *level of abstraction* characteristic of a WRSM depends on the resources available to initialize, compute, inform, and evaluate the model (Kennedy and McKenzie 2012). We provide an analogous overview of model complexity, drawing on Keane et al. (2004), and show how models fall along an orthogonal (to abstraction) gradient of complexity. We focus on aspects of WRSMs that deal explicitly with fire, acknowledging that the fire regime is only one component of landscape forest dynamics.

We draw on a decades-long history of addressing issues of complexity and abstraction in ecological models (Levins 1966; Scheffer and Beets 1993; Logan 1994; Cale 1995; Jackson et al. 2000), which provides much useful discussion but understates the independence of the two concepts or does not explicitly contrast them. For example, Levins (1966) emphasizes tradeoffs among *generality*, *realism*, and *precision*, each of which overlaps both complexity and abstraction. Jackson et al. (2000) equate abstraction and complexity, setting the stage for us to propose that these concepts are as likely to be orthogonal as to be parallel. We build on this earlier work with a conceptual model that maps the WRSM "landscape" onto a two-dimensional space of abstraction and complexity. We provide three contrasting examples of working models and their levels of complexity and abstraction, and suggest that relevant information available to the modeler will guide the model's "position" in that space. We conclude with recommendations for making explicit choices about what to include in WRSMs in forests, guided not only by the ideas of complexity, abstraction, and available information, but also by more general considerations.

4.2 Abstracting Reality and Defining Complexity

Science builds models of reality. In contrast to other disciplines such as history or fiction-writing, however, scientific models must be continually confronted with data (Hilborn and Mangel 1997). All models of reality entail a degree of *abstraction*; otherwise they would be mere replicates. In this chapter we adopt the idea that abstractions of reality may be "formed by reducing the information content of a concept or an observable phenomenon, typically to retain only information that is relevant for a particular purpose." (https://en.wikipedia.org/wiki/Abstraction). Consequently, the level of abstraction of a WRSM reflects how much its information content is reduced and generalized to inform the model's objectives (Kennedy and McKenzie 2012). Depending on these objectives, processes modeled at different scales will be subject to more or less abstraction.

Some models have lower bounds on their level of abstraction than do WRSMs. For example, the aim of weather-forecast models would appear to be to mimic reality as closely as possible, because they have no other purpose. In contrast, the purpose of most WRSMs is to ask scientific questions whose answers will be models of reality (accepting that reality can never be known perfectly) rather than explicit predictions of future conditions.

In landscape ecology, the *complexity* of models is more common parlance than their abstraction. For example, a detailed comparison of the complexity of WRSMs, with respect to several metrics, is in Keane et al. (2004). While acknowledging the value of this work, we take a more generic view of complexity as associated with the amount of information required to describe the regularities or patterns in a system (Gell-Mann 1994). As such, complexity is defined quantitatively (Gell-Mann and Lloyd 1996), while being distinguishable from both purely information-theoretic definitions and subjectively chosen metrics. Abstraction and complexity are both properties of models, but the opposite of "abstract" is "concrete," not "simple," whereas both "complex" and "complicated" are opposites of simple. We further propose that complexity and abstraction can be viewed orthogonally, such that models, both existing and possible, live in a two-dimensional space bounded by limits on four edges (Fig. 4.1).

In modeling wildfire regimes, we seek to match the levels of abstraction and complexity with (1) the resources available to initialize, compute, inform, and evaluate the model, and (2) the specific objectives of the model. For example, if we have no fuels data to validate model inputs, does it even make sense to specify fuel loadings, even though fuels are a critical driver of the size and severity of fires. These data are typically lacking for both historical and future fires. Two alternatives are (1) [increase complexity—yes, by introducing more state variables] to estimate fuels allometrically from other variables, sensu Loehman and Keane (2012) and many other studies, or (2) [increase abstraction while reducing complexity] to replicate fuel-dependent dynamics via a more abstract representation of fire (Kennedy and McKenzie 2010).

A useful corollary to level of abstraction in a WRSM is the level of *aggregation*, both in model dynamics and model outcomes. At the most concrete level,

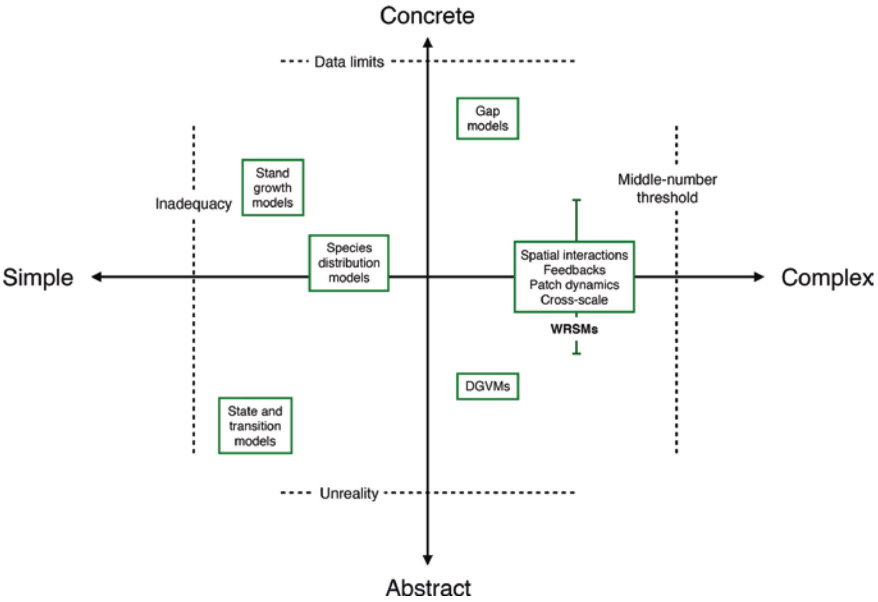


Fig. 4.1 Qualitative positions of different ecological models in the two-dimensional space of complexity and level of abstraction. Wildfire regime simulation models (WRSMs) are generally complex, but a heuristic "error bar" is placed around the associated processes on the abstraction axis, because they often vary more in this dimension than in complexity. In practice, the domain is bounded by the dotted lines, beyond which models would be either infeasible (beyond data limits or the middle-number threshold) or not useful (inadequate or unrealistic). DGVM = Dynamic Global Vegetation Model. See text for further explanation

individual fires are simulated (Keane and Finney 2003). Such models are appropriate when fire perimeters and fire progression need explicit representation. In contrast, if aggregate properties of the fire regime, such as annual area burned or spatial patterns of fire severity, are the key outcomes, explicit simulation of fire behavior and fire spread may introduce unneeded precision, and with it the potential for cumulative errors (McKenzie et al. 1996b, 2014).

Besides informing model objectives, model abstraction, or aggregation, should match available information. Within the realistic complexity bounds defined heuristically in Fig. 4.1, available information corresponds to the optimal position a model can occupy along gradients from abstract to concrete and from simple to complex (Fig. 4.2). Models simulating time-specific outcomes, such as past fire regimes or the future, will be compromised in different ways. For example, a model of Holocene fire may use sediment charcoal data that are spatially resolved to 1 km or finer, but have no better temporal resolution of fire, climate, or vegetation than centuries. A model of future fire regimes may have finely resolved downscaled climate, but essentially no data for evaluation. Note that Fig. 4.2 represents available information for the present as informing a model at a level of detail that exceeds the middle-number threshold. This figure reiterates how either complexity or available information can be a limiting factor for model concreteness.

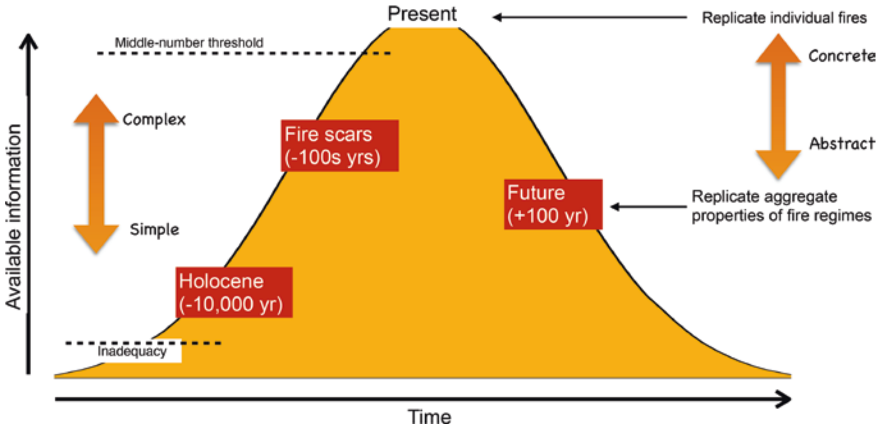


Fig. 4.2 The level of detail in a model is constrained by available information, e.g., input data, calibration data, and robustness of algorithms. Points on the information axis in this figure refer to data, specifically: vegetation, fuels, weather or climate, land use, etc. Available information provides a constraint on both concreteness and complexity, and ideally helps to identify an optimum (see text) on both axes. Landscape fire models are also constrained by the middle-number threshold of complexity (Fig. 4.1), such that whereas they can, for example, simulate individual fires in the present, inferences must be restricted to more aggregate properties, even if information is rich. This is because of the cumulative error associated with representing too many processes explicitly (see text)

An obvious goal for modeling is to find optima along the continua of abstraction and complexity. At least two distinct efforts are required to achieve this. First, model content and structure must be ecologically informed in a way specific to the model objectives (Keane et al. 2015). Whereas it is a truism to claim that ecological models should be ecologically informed, here we mean that processes should be simulated at scales that match the questions being asked. For example, returning to the aggregate properties of fire regimes, suppose we want to estimate patch-size distributions of high-severity fire in a warmer climate, and contrast those with current observations. A model that simulates individual fires, capturing their perimeters and spatial patterns of severity, will accumulate errors (and false precision) by misplaced concreteness (i.e., we seek patch structure, not the shape of any individual fire), no matter how ecologically sophisticated (Kennedy and McKenzie 2010; Swetnam et al. 2011). In contrast, a more abstract and less complex model, still ecologically informed, has fewer calculations and parameters, and one could argue that if each parameter has uncertainty associated with it the reduced cumulative error of this type offsets errors of omission associated with aggregating key processes, particularly if the characteristic scales of these processes are not violated.

Second, all models must be "confronted with data" (Hilborn and Mangel 1997). This confrontation should be "unguarded," so that any discrepancies that are revealed will be informative (see Sect. 4.4.4 below). At an early stage in model development, attention to discrepancies can inform not only model structure and

Table 4.2 Contrasting elements of the three example models, drawing from properties in Table 4.1

	FireBGCv2	WMFire	BFOLDS
Fire time step	Sequential not linked to vegetation	Sequential not linked to vegetation	Hourly linked to weather
Cause	Random ignition based on fire-return interval	Random ignition	Random ignition associated with weather
Process	Mainly mechanistic, partly stochastic	Stochastic	Mainly mechanistic, partly stochastic
Material	Fuel loading, fuel connectivity (horizontal and vertical)	Fuel loading (from RHESSys vegetation)	Forest cover, fuel
Climate and weather	Wind, humidity, temperature, fuel moisture, foliar moisture	Wind, fuel moisture as surrogate	Wind, humidity, temperature, fuel moisture, moisture
Extent	Fire size, fire perimeter, max extent prescribed	Fire size, fire perimeter, max extent emergent	Fire size, fire perimeter
Spatial pattern	Generated by rule-based percolation	Generated by probabilistic fire spread	Generated by mechanistic fire behavior
Management	Implemented in scenarios	Not implemented	Not implemented

algorithms, but also levels of abstraction and complexity that are manageable; only later will the data confrontation be used to tune model parameters (Kennedy and Ford 2011). In our example of patch-size distributions, confronting a model with explicit polygons and dates would fail globally, because to achieve this level of concreteness would exceed the middle-number threshold (Fig. 4.1). Confronting it with aggregate properties of patches is manageable, and therefore informative.

We emphasize that optimal abstraction and complexity are not necessarily to be found at the high ends of what is possible. Indeed they are closely tied to available information, though not strictly parallel or correlated (Fig. 4.2), and coupled to model objectives, as many have observed (Keane et al. 2015). Below we provide three examples of different solutions to the questions “how abstract” and “how complex.” Differences among the models are outlined in Table 4.2.

4.3 Example Modeling Approaches

4.3.1 FireBGCv2: Complex, Concrete

A detailed description of FireBGCv2 is given in Chap. 8. Here we highlight briefly the aspects of the model that are germane to our discussion. The FireBGC models have evolved over 15+ years under the guidance of Robert Keane (Keane et al. 1996, 2011), and simulate fire and succession on Rocky Mountain landscapes.

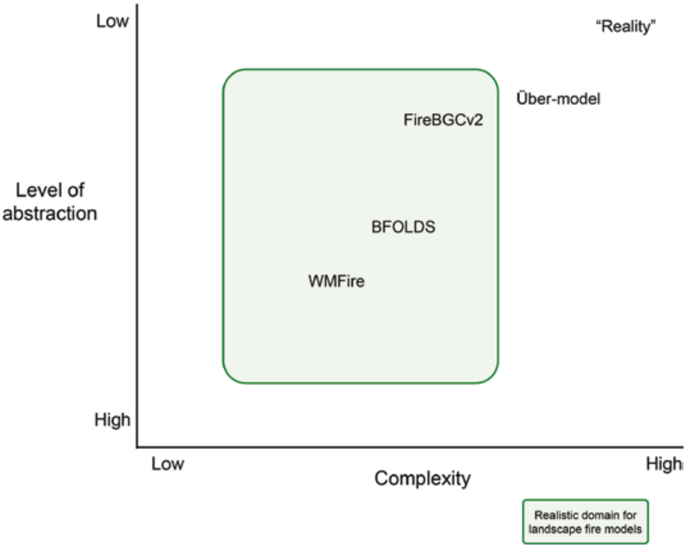


Fig. 4.3 Domain of landscape fire models on two axis (see Fig. 4.1), with positions of models discussed in the text. Reality is more concrete, and more complex, than any existing model or the "über-model" envisioned by Keane et al. (2015). The concreteness of FireBGCv2 approaches the limit of feasibility and desirability, whereas its complexity is still less than what might be desired. See text for further explanation

The model is standalone and includes detailed biogeochemistry (the BGC part) coupled with a gap-like model to represent individual-tree-based succession. The current version operates at five distinct spatial scales, from individual tree to "landscape." Finer scales are used for physiological processes such as photosynthesis, respiration, and decomposition, whereas fire is implemented stochastically at the landscape scale at which its explicit spatial nature can be represented. Finer-scale processes are made as mechanistic as possible, combining theoretical models from the literature with parameters calibrated to specific ecosystem types.

FireBGCv2 operates at the high end of complexity and concreteness for existing landscape fire models (Keane et al. 2004). Indeed it may be at the high end of what is feasible (Keane et al. 2015; Fig. 4.3). As such, it could be said that no key ecological process is left unrepresented, to be a source of unexplained variability. A key strength of the model is that not only are all these processes included, but they are also modeled as mechanistically as possible instead of arising from purely empirical approaches, particularly those that are so much in vogue in the era of "big data." Because of their emphasis on pattern-matching, empirical approaches can be very suspect when extrapolated outside their original domain (Cushman et al. 2007).

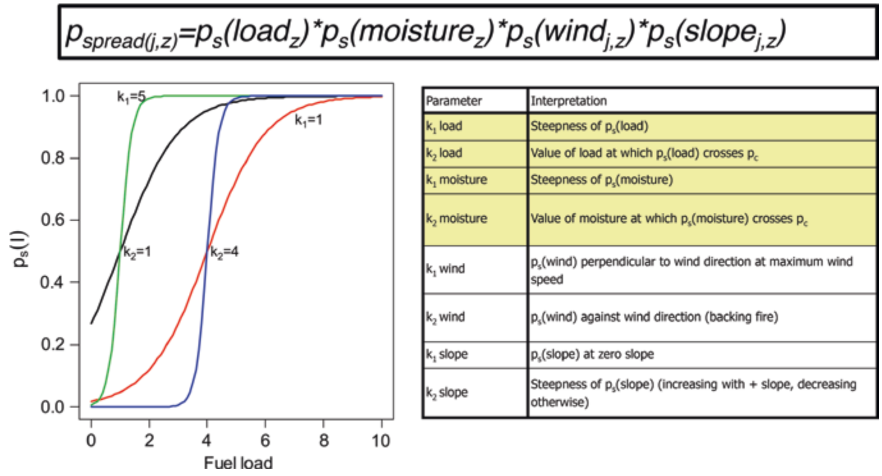
A model this complex is subject to several limitations, as acknowledged by Keane et al. (2011). With literally hundreds of parameters, model behavior can be unstable and highly nonlinear. Fire-return interval, which may interact with individual species dynamics to produce unrealistic outcomes (Keane et al. 2011), is a key source of model sensitivity. The developers recommend frequent and thorough comparisons of model output with observations (good advice when building any model). A difficulty with this for a complex model is that comparisons can lack transparency because of the high-dimensional space (many simultaneous comparisons), or lack validity simply because of the dearth of historical data for comparison. A further limitation is the cumulative uncertainty from multiple approximations in complex processes. For example, the developers found that coarse-graining of spatial processes from 30 to 100 m, when simulating large landscapes, preserved most of the important details in the outcome. This likely illustrates a "balance" of errors between loss of resolution and the multiplicative errors associated with detailed process-based modeling replicated at many sites over many years.

4.3.2 WMFire: Less Complex, Abstract

WMFire arose from a need to incorporate fire into a process-based ecohydrological model, RHESSys (Regional HydroEcological Simulation System; Tague and Band 2004), which simulates the effects of climate change on forested watersheds of the western United States. WMFire's design and structure were motivated by the successful reconstruction of the spatial properties of historical fire regimes by inverse modeling that combined probabilistic fire spread and Monte Carlo methods to fit fire-spread parameters to historical fire-scar records (Kennedy and McKenzie 2010; McKenzie and Kennedy 2012). WMFire receives an input watershed-scale database from RHESSys and a weather stream, spreads fire stochastically following a product of probabilities, each associated with a weather, fuel, or topographic variable (Fig. 4.4), and passes the record of burned cells back to RHESSys. Fire severity and fire effects are then computed within RHESSys by coupling an index of fire weather with a western United States-wide database of fire effects (Ghimire et al. 2012).

Simulation of both fire itself and vegetation dynamics and succession are substantially less complex, and more abstract (especially fire) in the WMFire-RHESSys combination than in FireBGCv2, except that RHESSys has hydrological routing, absent in FireBGCv2. In comparison, the WMFire approach has advantages and disadvantages. Its key advantage (over most landscape fire models, including many that are less complex than FireBGCv2) is that its relative simplicity permits a formal optimization procedure to fit parameters in such a way that output can be compared to observations robustly. Multi-criteria optimization (Kennedy and Ford 2011) quantifies (and therefore can minimize) the multivariate distance between model output and a comparison data set. This optimization is possible only if a model is simple enough that evaluation does not become a middle-number problem (see text above and Fig. 4.1), and is not feasible for a complex mechanistic model.

Two key limitations are associated with a model as simple as WMFire (this propagates to the WMFire-RHESSys combination). First, some potentially



$$p_{spread(j,z)}=p_s(load_z)*p_s(moisture_z)*p_s(wind_{j,z})*p_s(slope_{j,z})$$

Parameter	Interpretation
k_1 load	Steepness of p_s(load)
k_2 load	Value of load at which p_s(load) crosses p_c
k_1 moisture	Steepness of p_s(moisture)
k_2 moisture	Value of moisture at which p_s(moisture) crosses p_c
k_1 wind	p_s(wind) perpendicular to wind direction at maximum wind speed
k_2 wind	p_s(wind) against wind direction (backing fire)
k_1 slope	p_s(slope) at zero slope
k_2 slope	Steepness of p_s(slope) (increasing with + slope, decreasing otherwise)

Fig. 4.4 Pixel-to-pixel fire spread (here from cell *j* to cell *z*) forms the core of WMFire. Fire spread depends nonlinearly on fuel abundance (*load*), fire weather (moisture and wind), and topography (*slope*). The shape of the response of the fire-spread probability (p_{spread}) depends on two parameters (*k*) associated with each variable. Monte Carlo analysis on multiple fires in modeled watersheds is used to fit the parameters such that fire regimes emerge from combinations of the biophysical variables. See text for further explanation

important questions cannot be answered because the relevant processes are not simulated. For example, exact times and places of individual fire events, with simulated fire behavior that replicates these events as accurately as possible, will not be represented by simulating fire spread stochastically, because this method focuses on aggregate properties of fire regimes. Similarly, individual species responses to climate change cannot be projected, because tree species composition is ignored in RHESSys.

A second more subtle limitation is associated with the problem of attribution. With a simple model that produces aggregate properties of systems, a many-to-one relationship exists between drivers and outcomes. We suggest below (Sect. 4.4.4) that transparency of outcomes is an important property of a simulation model. A model that is too simple or too abstract may have *reduced* transparency in that the sensitivity to initial conditions (i.e., previous time steps or inputs) is muted by a model algorithm to the point that many starting points may produce the same outcome. Differences in dynamics represented in a complex model, important for future projections, may collapse when abstracted or aggregated.

4.3.3 BFOLDS: Intermediate Complexity and Abstraction

BFOLDS (Perera et al. 2008) was designed to explore Ontario's boreal forest fire regime. By mechanistic and spatial simulation of fire, this model overcomes the limitations of reliance on fire-history information (Li et al. 1997), temporal-only projections (Boychuk and Perera 1997), and includes spatio-temporal changes in vegetation cover explicitly (Yemshanov and Perera 2002). It is a hybrid model that simulates individual fires mechanistically and forest cover transitions empirically. Each fire event is modeled as a result of spatially explicit placement of ignitions on a forest landscape, with its realization determined by spatially explicit fire-weather patterns and fuel conditions at that point. If ignited, the fire spreads on a raster grid based on the rates of fire spread computed from input of fire weather, fuel patterns, and topography. Extinguishment is also mechanistic—based on fuel patterns and fire weather. Parameter choices use the principles of the Canadian Fire Behavior Prediction system (Forestry Canada Fire Danger Group 1992). The forest cover changes are temporally discrete, governed by a time-dependent Markov chain model populated with probabilities of state transitions (Yemshanov and Perera 2002) with spatially explicit interactions with geo-environment (Weaver and Perera 2004). Vegetation cover generates the fuel-pattern grids for fire-event simulations.

In the model multiple fire events are simulated daily during a fire season guided by fire weather, fuel, and topography information for a given area. As such, no presumptions are made of the number of fires, sizes of fires, or their locations during the simulations; the ensuing fire regime is an emergent property of the model function (logic, assumptions, and data). By replicated simulations, BFOLDS constructs probability distributions of aggregate properties of fire regimes: fire-size distribution, fire-return interval, fire severity, as well as spatial biases in these properties. Therefore, BFOLDS is typically applied to explore, discover, and understand regional-scale fire regimes (>10 million ha, >100 years) and inform forest policy development and analysis (Rempel et al. 2007; Perera and Cui 2010).

Although fires are simulated far less intensively than in a physical model, and the types of input data required are fewer, BFOLDS is still data- and information-hungry. This is mostly true for weather data (wind, precipitation, temperature). The resolution and extent of data demand (1 ha) and periods (hourly over a fire season) exceed what is typically collected. Therefore, the model relies on interpolation and extrapolation to produce continuous surfaces and temporal series. This is an abstraction of input data that may not be evident to model users, and may lead to false expectations of model precision. Another source of false precision is in fixing model parameters. Simulation steps of some physical processes, for example, fire extinguishment and smoldering, require an understanding of fine-scale dynamics that exceeds the present state of knowledge. This leads to model assumptions, though explicit, that contribute to false precision. Most such limitations should be overcome in time as data resolutions, extents, and scientific knowledge improve. In the short term, clear communication of model limitations and the degree of abstraction is essential to avoid misinterpretation of accuracy and precision.

4.4 Some Criteria for Developing and Applying WRSMs

We have framed fire-regime models in terms of gradients of abstraction and complexity, and given three examples that occupy distinct positions along those gradients. We now turn to more general criteria for building models that we believe should apply at most levels of abstraction and complexity. We draw heavily on the discussion in McKenzie et al. (2014), while noting that those authors were addressing regional-scale models of climate change, whereas we focus on forest landscapes, with their own characteristic key processes, such as contagious disturbance. For each criterion, we suggest how consideration of the polarities simple–complex and concrete–abstract is germane. Our hope is that the modeling criteria that follow are robust across spatial and temporal domains, and across a wide range of objectives in ecological modeling.

4.4.1 Be Clear with Scale and Goal

As computing power and empirical knowledge of fire science improves, wildfire regime modelers will find it difficult to resist the temptation to simulate every detail of fire process possible. This is a futile pursuit since the accuracy of input data at regional scales, where fire regimes are modeled, will never match those accuracies expected by modelers. Instead, they must pursue improving robustness of models at the correct scale. It also behooves the modelers to stress the goals of simulations: is it the past (backcasting), future (forecasting), or what could be (what-if potential) that they seek? Model applications commonly overlook that the first two are subsets of the last (Fig. 4.5; Perera and Cui 2010). A model must be **complex** enough to capture fire process (but no more complex), but **abstract** enough to be robust, i.e., not tied to particulars that will not be stationary in new regimes.

4.4.2 Wildfire Regimes Should Be Emergent Rather than Prescribed

A potential critique of all simulation models is that by their very nature they reproduce the expectations of modelers. Clearly this is an inferior situation to reproducing reality, at whatever level of abstraction is optimal in the context. With fire regimes, aggregate properties are often specified in simulation models, with individual fire events remaining stochastic (see Sect. 4.3). For example, a mean fire-return interval (FRI) may be associated with each of the different vegetation types but individual fires depend on suitable weather and fuel condition and abundance (Lenihan et al. 2008). If conditions repeatedly do not favor a fire, fire extent when it does occur can be adjusted to match the prespecified FRI, particularly

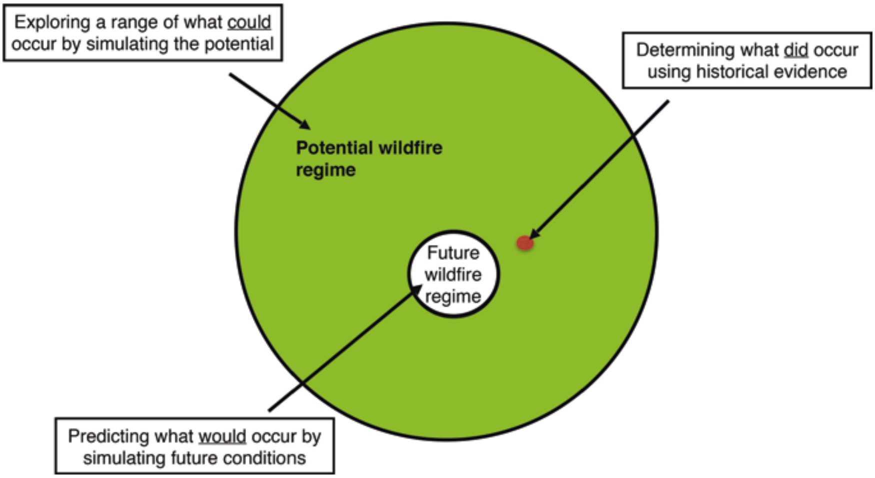


Fig. 4.5 A Venn diagram of the conceptual domains of wildfire modeling goals. Forecasting and backcasting are nested subsets of the potential wildfire regimes—what could happen. The broad goal of wildfire regime modeling, given that future conditions are uncertain, must be simulating what-if scenarios, i.e., to expand the smaller domain by improving robustness of models, but narrowing the larger domain (*green circle*) to what is plausible given all uncertainties associated with the future drivers of fire (adapted from Perera and Cui 2010)

in the case where fire frequency is area-based, e.g., via a natural fire rotation or fire cycle. A limitation of this approach, even (or especially) if it calibrates well to observations, is that in a non-stationary climate, FRIs can change more rapidly than vegetation types, making this model with a prescribed FRI less robust for future projections. Such a model is too **simple** and too **concrete**.

Alternatively, one can build a model that also generates fire events from first principles, such as thresholds of fire weather and fuel moisture, but lets the aggregate fire-regime properties emerge from the cumulative effects of individual events (Perera and Cui 2010). In this paradigm, future or potential fire regimes are less constrained to predetermined values, and projections should be more robust to a changing climate, but evaluating the model with current observations will be more challenging because of the lack of simple metrics such as FRIs for comparison (see also Sect. 4.4.4). We note that this particular criterion does not apply universally to all modeling objectives. For example, if we seek to understand vegetation response to wildfire scenarios we have identified explicitly, they are best specified in advance.

4.4.3 Distributions Are Better than Points

The Climate Model Intercomparison Project (CMIP5; Taylor et al. 2012) evinces the value of ensemble simulations rather than individual model runs. Stochastic variation within the same model can produce very different and sometimes contradictory outcomes (Deser et al. 2012). Whereas running multiple models in the same project may be infeasible to forest landscape modelers, sensitivity to a reasonable amount of stochastic variation in the model of choice can reveal weaknesses or uncertainties in both model structure and inferences about results. Because fire itself is a realization of a stochastic process, multiple instances are needed to capture fire-regime properties, from annual area burned to fire-size distributions or proportions of area in different severity classes. As Perera and Cui (2010) showed, each of these properties has characteristic variability, in current and potential conditions. Here the **complexity** associated with ensembles is irreducible, but necessary. In such ensembles, complexity may be traded for **abstraction**, e.g., the **concreteness** of a model such as FireBGCv2 may make an ensemble approach prohibitive.

A caveat to the call for looking at ensemble projections is associated with understanding extreme events (McKenzie et al. 2014). The "regression to the mean" that occurs when focusing on distributions and ranges of variation should be balanced by a vigilance toward outliers that may inform the answers to research questions. For example, what is the future likelihood of what is now a 95th-percentile event (Stavros et al. 2014)?

4.4.4 Methods Must Be Transparent

Different replications from one model may give qualitatively different results. It is important to understand why the results differed. Did you get the right answer for the wrong reasons (Dennis et al. 2010)? Sensitivity analysis provides quantitative transparency, along with an understanding of model variation, but just as important are semantic and logical transparency. Can you explain, for example, why the one realization that is an outlier gave you the outcome it did? For landscape fire models, a particularly useful time for model transparency is when extreme events (see Sect. 4.4.2) occur in some realizations but not others. Did these fires emerge realistically from their precursors, or are they artifacts of some coincidence in parameter space that is opaque to evaluation? This need for transparency, for developers and for users, limits how **complex** and how **abstract** a model can be.

4.4.5 Aim for Progressive Improvements

This criterion is general and is difficult to associate directly with complexity and abstraction, except that it is clearly linked to model transparency (Sect. 4.4.4). Observations, and "validation," are important for simulation modeling, but bringing them in too soon and tuning the model to fit them will be counter-productive: it may camouflage basic errors in model content or not account for feedbacks that are present in observations (Ford 2000). Being “wildly wrong” at some stage may be the most informative thing that could happen. Maximizing the concurrence of a model with observations by uncritically adding predictor variables and statistical interactions (in an empirical model), or finding the most parsimonious calibration to match “reality” (in a simulation model) makes a model less robust to predictions outside its domain (Cushman et al. 2007).

On the other hand, it is possible to start out with faulty assumptions that ensure the inevitability, rather than the chance, of being wrong. For example, as discussed in Sect. 4.4.2, a potential pitfall is assuming that the natural fire regimes for particular vegetation types are stationary. Such a model is very likely wrong from the outset, and correspondence with the real future will be coincidental.

4.4.6 Implications for Model Development and Use

As all models are abstractions of reality, how much detail can be subsumed into thoughtful parameter choices, aggregated in some other way to produce emergent properties of the system faithfully, or even simply ignored? The expression “as simple as possible, but no simpler” is attributed to Einstein, and can be a useful heuristic along both our axes: complexity and abstraction (Fig. 4.1). Ecological science, and with it ecological modeling, is of course filled with contingencies and “unsimple truths” (Mitchell 2009). This limits our ability to generalize about optimal levels of abstraction or complexity, as does the universal need for models to be designed and run with research objectives in mind.

Given this contingent optimality, and the other criteria we have proposed above (Sect. 4.4), we suggest three further considerations for abstraction and complexity. First, there will always be tradeoffs between model complexity and the feasible amount of replication. There may be cases in which a refined algorithm should be sacrificed for a parallel but cruder one that admits to an ensemble approach wherein multiple realizations “solve” the original algorithm without introducing false precision. A higher level of abstraction (in which a totally different algorithm is used) may also give a more realistic outcome, even if less precise.

Second, what are the limits on information available for evaluating increased complexity? For example, our best measurements of landscape fire are for the contemporary period. For the historical period (roughly pre-1900) we have no fuels data, no fire-start dates, and usually only a rough idea of fire perimeters. Historical fire spread must be reconstructed indirectly, and with necessarily simpler models (Kennedy and McKenzie 2010). For the future, no measurements are available other than the range of possibilities starting at the present, which we can only simulate. The many complexities in those simulations, though manageable for the present for which we have observations, constitute false precision when applied to the future, especially for fire (Kennedy and McKenzie 2012).

Third, decide which uncertainties you can live with for your objectives. At what level of abstraction do you need outcomes? For example, if you need fire sizes and shapes to predict landscape connectivity and distance to seed source in the interior of high-severity patches, you will need different precision (and will need to accept different levels of uncertainty, proportionally) than if you are projecting the likelihood of extreme fires in future decades.

4.5 Conclusion

We have offered a conceptual framework for WRSMs in the hope of providing modelers with a different view, and different filters, for developing and using these tools for simulating forest landscapes. In doing so, we step back from the many valid day-to-day concerns of modelers to a level of abstraction that may be useful particularly when modelers encounter obstacles that are ill-defined or embedded in layers of processes that are hard to separate. We believe that re-assessing the levels of abstraction and complexity in a model, and how they depend on available information, can be a useful reflective pause at any stage in the modeling process.

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Chapter 5
Modeling Insect Disturbance Across Forested Landscapes: Insights from the Spruce Budworm

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Contents

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5.1 Introduction

Insects are important disturbance agents affecting temperate and boreal biomes (Wermelinger 2004; Johnson et al. 2005; Cooke et al. 2007; Raffa et al. 2008). Defoliating insects in particular have historically affected a staggering area of North American forests, particularly across the boreal biome (Fig. 5.1). Principal among these boreal forest defoliators is the spruce budworm (*Choristoneura fumiferana* Clemens) that in the 1970s affected over 50 million hectares of fir (*Abies* spp.) and spruce (*Picea* spp.) forests at its peak in Eastern Canada and the Northeastern United States, making it among the most economically and ecologically important forest insects on the continent. Its significance is reflected in an extensive history of research to support modeling and management activities (e.g., Morris 1963a; Greenbank et al. 1980; Royama 1984; Sanders et al. 1985). The most recent review of spruce budworm modeling was by Régnière and Lysyk (1995, but see also Cooke et al. 2007). Since 1995 (when spruce budworm became primarily endemic), 1103 papers were published with the keyword *C. fumiferana* (Web of Science, accessed December 2014), indicating a strong need for new synthesis.

Modeling insect outbreak dynamics requires understanding of the insect's population dynamics, phenology, host preferences (i.e., species, size), feeding dynamics, and factors affecting outbreak severity in time and space. Spruce budworm defoliates balsam fir (*A. balsamea*) and spruce species, emerging from winter hibernacula as tiny second instars that bore into emerging buds and then feed on

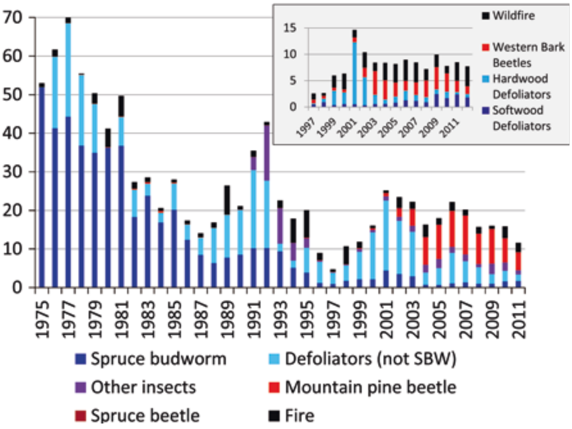

Fig. 5.1 Comparative disturbance statistics for major insect species in the contiguous 48 states of the United States (*inset*) versus the Canadian provinces (Canadian Council of Forest Ministers 2013; http://nfdp.ccfm.org National forestry database program. Canadian Forest Service, Ottawa, Ontario, Canada)

the new foliage as shoots expand. Its population cycles are longer than most other defoliating species, both in terms of time between outbreaks and their duration (Cooke et al. 2007; Myers and Cory 2013). Mortality generally begins after 5 to 6 consecutive years of heavy defoliation (MacLean 1980) in balsam fir, followed by white spruce (*P. glauca*) and then red spruce (*P. rubens*) and black spruce (*P. mariana*) (Erdle and MacLean 1999). Adult budworm moths are strong fliers that actively use wind currents to facilitate long-distance dispersal (Greenbank et al. 1980; Anderson and Sturtevant 2011; Sturtevant et al. 2013).

The most commonly reported outbreak interval is on the order of 30–40 years (e.g. Jardon et al. 2003), and the species is best known for regionally synchronized outbreaks (Royama 1984; Peltonen et al. 2002) that cause widespread forest decline over broad areas (MacLean 1984). However, a wide range of outbreak frequencies and spatial scales of synchronization have been observed in different parts of the insect's extensive range (e.g., Williams and Liebhold 2000; Robert et al. 2012). Despite its apparent "destructive" nature and economic impacts (Chang et al. 2012a, b), the spruce budworm is an integral part of boreal forest ecology, with extensive outbreaks observed over several centuries within the dendroecological record (Boulanger and Arseneault 2004; Boulanger et al. 2012) and over several millennia within the paleoecological record (Simard et al. 2006).

Current understanding of budworm disturbance ecology comes from two divergent areas of research, both with extensive histories and both involving modeling of budworm disturbance. The first group of researchers sought empirical solutions to assess risk and effects of defoliation, primarily by building defoliation-growth reduction and defoliation-mortality relationships into stand growth models, as a means of prioritizing individual stands for either aerial spraying or preemptive salvage logging or for estimating effects of budworm outbreaks on timber supply (e.g., Baskerville and Kleinschmidt 1981; Erdle and MacLean 1999; MacLean et al. 2001). The second group researched the details of the budworm's population biology and dynamics to develop simulation models for evaluating feedback between forest conditions and budworm populations, and to inform population management (e.g., Morris 1963b; Jones 1977; Ludwig et al. 1978; Royama 1984). The two approaches have not been well integrated, in part because they derive from different disciplines, objectives, and traditions with respect to modeling uncertainty. However, an early and effective example of integration is reflected in the Holling–Baskerville efforts to use the Jones (1977) defoliation effects model in the Report of the Task Force for Budworm Control Alternatives (Baskerville 1976). This work also inspired defoliation impact field work (e.g., Erdle and MacLean 1999) by exposing key information gaps related to tree growth-defoliation and tree survival-defoliation relationships.

More recently, we have observed parallel developments in modeling of budworm disturbance at landscape scales. The first development involves applying budworm defoliation effects on forest stands at landscape-scale within a timber supply and scheduling framework (MacLean et al. 2001; Hennigar et al. 2007). This strategy is generally used as decision support for tactical planning of forest resources during a given outbreak. The second development is the integration of budworm defoliation disturbance within landscape disturbance and succession models (e.g., Sturtevant et al. 2004; James et al. 2011; Sturtevant et al. 2012). This strategy is applied for ecological insights, strategic planning, and development of broad-scale policy over longer time periods (e.g., centuries). As of the writing of this chapter, these divergent areas of research and parallel landscape modeling strategies have not been integrated. Recent advancements in the understanding of budworm population biology and ecology (Régnière and Nealis 2007; Eveleigh et al. 2007; Régnière et al. 2012, 2013), in combination with the recent increase in budworm outbreak activity in Eastern Canada (Canadian Council of Forest Ministers 2013) warrant a fresh synthesis of budworm science and modeling approaches to inform the next generation of budworm disturbance models.

In this chapter, we examine the history of spruce budworm disturbance modeling to provide insights into landscape insect disturbance modeling more generally. We do so by first outlining the evolution of competing approaches to budworm population modeling, illustrating the interplay of models and data, and highlighting key insights (including failures and advances) into the roles of reciprocal feedbacks among trophic levels (i.e., budworm, its forest host, and its natural enemies), and broader-scale processes (i.e., dispersal, synchronization, climatic variation and change). Second, we overview studies relating budworm defoliation to its effects on forests, culminating in spruce budworm decision support tools designed for forest operations planning. Third, we summarize more recent contributions using landscape disturbance and succession models focused on long-term responses of forested landscapes to a given budworm disturbance regime, and examine the opportunities for synthesis provided by this modeling framework. We conclude with our recommendations for a modern synthesis based on lessons learned from over five decades of research and modeling in the budworm-forest system, and its implications for the modeling of analogous defoliator-forest systems in North America and elsewhere.

5.2 Population Dynamics

Authoritative reviews have been written on the biology and dynamics of *Choristoneura* species (Volney 1985), including the comparative dynamics of the spruce budworm relative to other closely related defoliator species (Cooke et al. 2007). The spruce budworm is an early season herbivore whose dynamics are influenced by a large array of agents, operating at a range of spatial scales, including many species of vertebrate and invertebrate natural enemies, various host plant effects, a range of weather effects, and dispersal. With so many agents contributing to the system’s dynamics it is perhaps not surprising that no fewer than 15 budworm models have been published over the last five decades (Table 5.1).

Table 5.1 A contrast of classes (eruptive, cyclic, and gradient) of whole-system models of spruce budworm disturbance dynamics illustrating major model advances and limitations

Class	Description	Emphasis	Limitations	Source
Eruptive	Eruptive	Predation on large larvae	Space	Watt (1963)
	Population collapse	Epidemic behavior; host foliage limitation	Endemic phase processes and dynamics	Morris 1963b
	Budworm site model	Host foliage energetics and productivity	Space; delayed density-dependent predation	Jones (1977)
	Spatialization of Jones 1977	Dispersal	Delayed density-dependent predation	Clark et al. (1979)
	Analytical abstraction of Jones 1977	Outbreak as slow–fast cusp catastrophe	Delayed density-dependent predation	Ludwig et al. (1978)
	Re-parameterization of Jones 1977	Reduced role of bird predation interaction with host size; opportunity for aggressive suppression given local extinction	Delayed density–dependent predation	Stedinger (1984)
	Re-abstraction of Jones 1977	Overriding influence of generic host effects	Delayed density–dependent predation	Hassell et al. (1999)
Cyclic	Time series	2nd order density-dependence effect on cycling	Space; degradation of host forest	Royama (1984)
	Time series parameterization and scaling	2nd order density-dependence; spatial variation and scaling	Dispersal through space	Fleming et al. (1999; 2002)
	Cycle synchronization	Role of dispersal in homogenizing spatial differences in cycle frequency	Degradation of host forest	Régnière and Lysyk (1995)
	Dispersal mortality	Role of host degradation in promoting risky dispersal of herbivores	Landscape scale; space	Régnière and Nealis (2007)
	Tri-trophic interaction	Multifrequential cycling behavior and synchronization	Positive density dependence of mate finding	Cooke et al. (2007)

(continued)

Table 5.1 (continued)

Class	Description	Emphasis	Limitations	Source
Gradient	Phenological synchrony across trophic levels	Extreme weather; transients under climate change; genetic capacity for adaptation to climate change	Spatial disequilibrium caused by dispersal lags	Fleming and Volney (1995), Volney and Fleming (2000)
	Phenology	Climate warming on development times and survival rates	Dispersal through space	Fleming (1996)
	Climate change	Belt-shaped outbreak distribution and climate-driven range shift	Fast temporal dynamics	Régnière et al. (2012)

5.2.1 *Data Sources and Modeling Challenges*

To understand the evolution in the thought behind model development it helps to first understand (1) how the data sources developed over time, and (2) how improvements in computational tools and technologies facilitated the development of ever more powerful methods of hypothesis testing. Over the course of the last century, three major phases in data acquisition, analysis, and modeling may be discerned (Fig. 5.2). The earliest studies of spruce budworm ecology and population dynamics indicated that researchers were well aware of the recurring nature of budworm outbreaks (Blackman 1919), and of the roles of multiple factors in influencing the rising and declining phases of population change (Swaine and Craighead 1924). Analytical tools at this time were limited to graphical and conceptual models. During a second phase of discovery through the 1950s to the early 1980s, studies became more comprehensive and methods became more quantitative. Intensive data collection from the Green River Watershed in New Brunswick, Canada (Morris 1963a; Fig. 5.2) led to the simple (yet formal and mathematical) multiple equilibrium model of Watt (1963), followed by the more complex budworm site model of Jones (1977) and its elegant mathematical simplification, which resulted in the cross-scale manifold model of Ludwig et al. (1978) (Table 5.1). A third phase of synthesis centers intellectually around the publication by Royama (1984), in which he offered an alternative interpretation of the Morris (1963a) database via time series analyses, and that by Royama (1992), in which he attempted to place the spruce budworm system in a broader ecological content by comparing it with other animal systems with cyclical population dynamics. Consequently, more intensive studies necessary to accurately distinguish among factors regulating budworm populations over time were established in the 1980s,

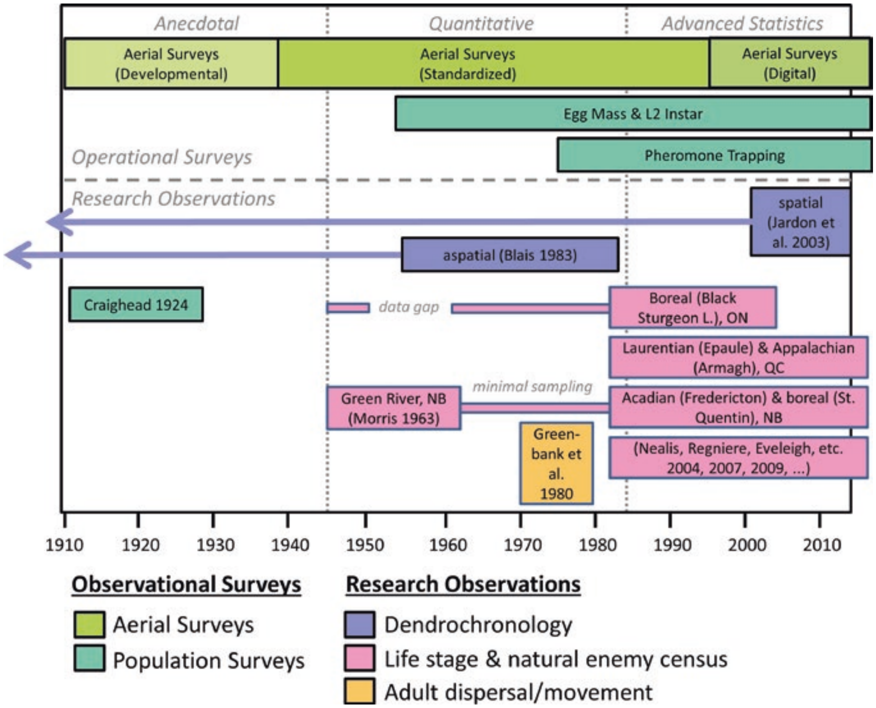

Fig. 5.2 The evolution of data sources describing spruce budworm system behavior. Scientific advances have followed concurrent methodological improvements in data collection, data analysis, and simulation modeling

while the availability of geographic information system (GIS) technology and spatial data sets in the 1990s provided opportunity to quantify factors affecting outbreak synchronization and dynamics in space (Fig. 5.2). Advanced statistical methods in both time series and spatial analysis methods are leading to increasingly nuanced characterizations of system behavior that require a revised understanding of the budworm–forest system.

Clearly, the time scale of observation influences one's ability to infer cyclic behavior. The earliest quantitative models (listed in Table 5.1) were developed on the empirical basis of just one cycle from the 1950s. For example, Turchin (1990) concluded that budworm populations were nonstationary (i.e., insufficient data to declare the trend-like pattern cyclic) based on plot-level population data from across New Brunswick available from 1945 to 1972 (Fig. 5.3). Similarly, Williams and Liebhold (2000) concluded that budworm populations were not regulated by density-dependent feedback based on 1945–1988 aerial survey data from across Eastern North America. The later models benefitted from two cycles of observations and insights garnered through the 1970s and 1980s. As the length of the time series increases the evidence in favor of cyclic dynamics increases (Fig. 5.3). Data limitations help to explain in part some of the evolution in modeling behavior, i.e.,

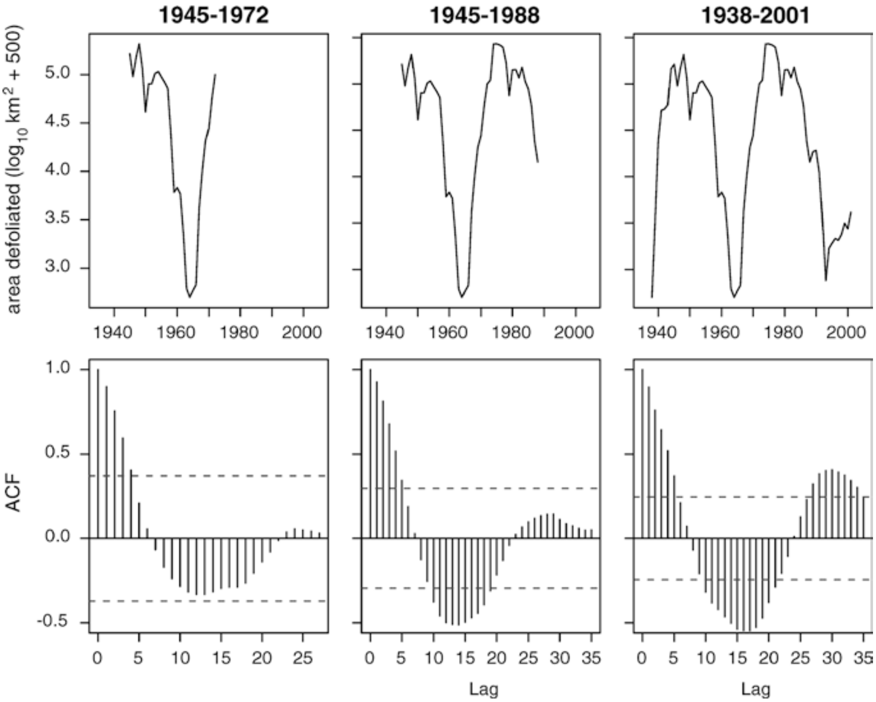

Fig. 5.3 The history of spruce budworm area defoliated in Quebec, Canada 1938–2001. The province-wide time series in the far right column has been divided to create two additional, shorter series, and all three subjected to autocorrelation analysis (bottom row; ACF = autocorrelation function). The shorter time frames were chosen to match those used in time series studies by Turchin (1990) and Williams and Liebhold (2000) (see text)

the emphasis on eruptive behavior in the early phase of modeling and on cyclical behavior in the more recent phase.

Authors of the earliest models were nonetheless aware of the recurrent nature of budworm outbreaks, due to numerous tree-ring studies by Blais (1954, 1961, 1965, 1968). As groundbreaking as these early studies were, Blais did not explicitly recognize the role of scale in interpreting the tree-ring data. The relevance of scale is exemplified by, for example, Boulanger et al. (2012) in a locally intensive study that illustrated the remarkable stability of the budworm outbreak cycle through multiple centuries, while Jardon et al. (2003), using dendroecological studies placed on a systematic spatial grid across much of Quebec, Canada, emphasized the complexity in patterns of recurrence and a lack of repetition in the spatial pattern of outbreak progression. Apparently, just as the temporal scale of observation may influence the perception of cyclicity, so may the spatial scale of observation influence the perception of outbreak cycle homogeneity and synchrony, as budworm populations do not behave identically everywhere.

5.2.2 Competing Hypotheses and Modeling Paradigms

Two major paradigms underlie budworm outbreak models (Table 5.1). The first paradigm, peaking in the 1970s, focused on the role of the forest in precipitating and terminating devastating budworm outbreaks (i.e., multiple equilibrium "eruptive" models). The second paradigm emphasized the role of natural enemies in generating periodic outbreaks that do not necessarily result in host forest collapse (i.e., cyclic predator–prey models). These paradigms differ in two primary areas. The first is the relative strength of top-down versus bottom-up effects (Box 5.1). The second is the relative significance of dispersal in generating complex dynamic behavior and spatial patterning. Both paradigms persist in the literature to the present day.

BOX 5.1

Two elegant mathematical models represent alternative paradigms of the fundamental processes underlying budworm population dynamics. In the Ludwig-Jones-Holling model (LJH; Ludwig et al. 1978) budworm dynamics were assumed to be fundamentally eruptive, owing to positive and nonlinear feedbacks between budworms and forest and the effect of predators on budworms, which was thought to vary as a function of tree size. Royama (1992), in contrast, emphasized the role of delayed feedback from natural enemies in a generic predator-prey model (which Royama (1984) and Fleming et al. (2002) implemented in a univariate autoregressive form, as in our Fig. 5.4) that induced a periodic harmonic oscillation. In each case, a factor viewed as critical in one model was downplayed in the other. Specifically, Ludwig et al. (1978) represented the effect of predation as being conditional on budworm populations and tree size, where predator density was not modeled explicitly, and used two nonlinear feedback equations to describe vegetation dynamics. In contrast, Royama (1992) largely ignored vegetation dynamics by treating food resource competition as a fixed effect, and represented predation as a delayed reciprocal feedback process.

Although Ludwig et al. (1978) contended that their model was an accurate abstraction of the dynamics of the original Jones budworm site model (Jones 1977), Hassell et al. (1999) showed that Ludwig et al. (1978) actually mischaracterized the Jones model by including the predation saturation effect (i.e., the second term in the budworm (B) equation; Fig. B5.1), which in addition to the nonlinear foliage equation (E) (Fig. B5.1) contributed to the relaxed oscillation dynamic that produces the same effect. In contrast, in the Jones model the oscillation dynamics are driven by nonlinear foliage dynamics alone. This finding only serves to strengthen the degree of contrast between eruptive and forest-dominated versus non-eruptive/cyclic and predator-dominated modeling paradigms.

Notably, Royama never actually suggested that the budworm could be adequately represented by any univariate, or even predator-prey, model.

Indeed, his use of the second-order autoregressive model in his 1984 monograph was for ancillary demonstrative purposes only. Moreover, in the synthesis to his Chap. 9 on spruce budworm, Royama (1992) specifically referred to budworm oscillating about a single, conditional equilibrium state, which would vary as a function of forest conditions and natural enemy community composition. Rather than ignoring vegetation dynamics per se, it is more accurate to state that Royama (1992) chose not to attempt to summarize the effect of forest conditions in quantitative terms

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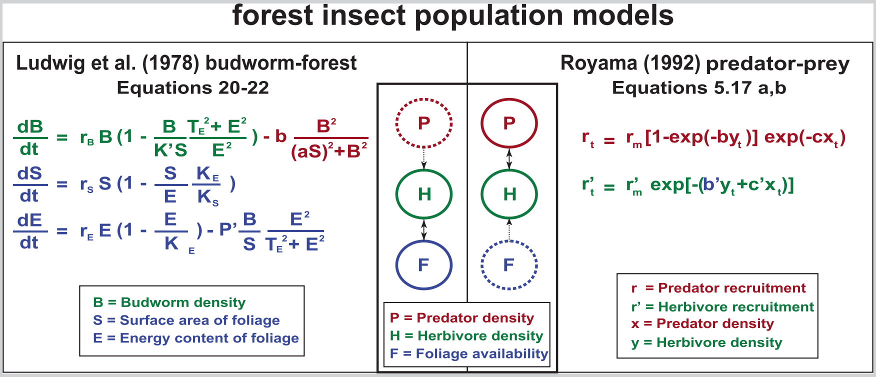


Fig. B5.1 Tri-trophic interactions in the spruce budworm system as depicted by two simple models from the metastable eruptive (*left*) versus harmonic oscillation (*right*) paradigms, in two common modeling frameworks. The center panel highlights congruencies and differences in the two system models, color-coded to link variable or mathematical expressions to each of the three dominant trophic levels (predators, herbivores, foliage). Solid circles indicate trophic levels represented by dynamic state variables and double arrows indicate inter-trophic relationships that are characterized by reciprocal feedback. In the Ludwig-Jones-Holling model predation is a variable effect; there is no equation for predator population rate of change. In the Royama model the intensity of feeding competition for foliage is a fixed effect; there is no equation for forest foliage dynamics

Clearly, although the two models (and modeling paradigms) differ starkly in terms of which trophic level is emphasized, such a difference could be reconciled through the development of a hybrid model that allows for either fixed or dynamical effects of both trophic layers below and above the budworm (i.e., predators, forest). To examine the effect of ancillary factors, such as weather or dispersal, on budworm tritrophic interactions, a hybrid model (see Fig. 5.8 in text) might be considered that would allow for altering critical assumptions about the nature of the feedbacks occurring among trophic levels.

5.2.2.1 Multi-equilibrium Model

The suite of models produced under the eruptive outbreak paradigm, summarized previously (Cuff and Baskerville 1983; Fisher 1983), emphasized a critical role for tree size, and hence forest age, in shaping the budworm's ability to acquire food and shelter and to evade natural enemies. Large amounts of host foliar biomass were assumed to be a necessary condition for budworm outbreaks, and sharp declines in available host foliar biomass were assumed to be a necessary condition for population collapse. Consequently, these models shared a "relaxed oscillation" dynamic characterized by alternating host depletion and regrowth. This dependence on bottom-up constraints was thought to explain why the duration between outbreaks was so long in relation to other periodic defoliators, which tend to erupt at roughly decadal intervals (Myers and Cory 2013). The primary differences between alternative models developed under the eruptive outbreak paradigm are reflected in different hypotheses about the relative importance of factors triggering population eruption (Fisher 1983): temperature (e.g., Watt 1964), sufficiently large quantities of host to overcome low-density predator regulation or a so-called predator pit (e.g., Jones 1977; Ludwig et al. 1978), and external invasion by adult moths (e.g., Stedinger 1984). All shared the assumption that forest collapse was responsible for outbreak decline.

The evolution of budworm models under the eruptive paradigm led to seminal insights into insect disturbance modeling. The first computer simulation model (Watt 1963) was characterized by "bistability," referring to the simultaneous existence of two distinct alternative stable equilibrium states (i.e., endemic and epidemic), both of which are accessible at any moment in time, and neither of whose existence is "conditional" on varying environmental conditions. The Jones (1977) model and the Ludwig et al. (1978) abstraction were characterized by "metastability," which refers to the temporary existence, and conditional stability, of multiple equilibrium states that arise through dynamic interplay among multiple regulatory processes operating at distinct timescales. The interaction between fast and slow consumptive and regenerative processes gives rise to a "manifold" characterized by a cusp, or critical bifurcation point, which separates two flexible domains of attraction, and a "hysteresis" effect of irreversibility, where return to a basal equilibrium state is inevitable, but requires the slow passage of time to precipitate a critical change in environmental circumstances. Berryman et al. (1984) used the term "metastable" to refer to the forest–insect limit cycle (i.e., also termed a "relaxation oscillation") that results from the inevitability of a "slow" forest regeneration cycle after a fast process of insect population eruption and forest collapse.

Authors of early budworm models were also pioneers in the simulation of spatial dynamics of outbreaks (e.g., Clark et al. 1979). Spatial processes were recognized as important because budworm densities "were not solely determined by local factors, but remain at least partially synchronized with neighboring areas" (Fisher 1983, p. 107). Under the eruptive model paradigm, adult dispersal was a key factor underlying the radial expansion of outbreaks from so-called "epicenters" (Hardy et al. 1983), analogous to how we currently understand the spread of bark beetle epidemics (Powell et al. 1998). The primacy of wind-mediated dispersal of budworm moths underlying the spatial spread of outbreaks under the eruptive paradigm—and the implications for budworm suppression programs—was underscored by an unprecedented research program to investigate the aerobiology of spruce budworm dispersal (Greenbank et al. 1980) (Fig. 5.2).

5.2.2.2 Harmonic Oscillation Model

Despite the obviously destructive nature of budworm outbreaks, several widespread observations were inconsistent with the multi-equilibrium models (Royama 1992). First, budworm outbreaks frequently end before host foliar biomass is fully depleted. Second, these outbreaks occur at fairly regular intervals ranging between 20 and 40 years between peaks (Burleigh et al. 2002; Jardon et al. 2003; Boulanger et al. 2012) that are less than even the "pathological rotation age" of balsam fir (70 years; Burns and Honkala 1990). While the eruptive models of this era (Table 5.1) were not scale-specific, they were typically applied at the resolution of a "forest block" (e.g., Clark et al. 1979; 170 km^2). If budworm outbreaks resulted in forest collapse at this scale every three to four decades then very rarely would forests have the opportunity to develop into the mature and overmature age classes that are frequently observed in the boreal forest. Likewise, immature and mixed species stands generally show only partial stand mortality (MacLean 1980; Su et al. 1996). Finally, cyclic budworm outbreaks are often synchronized at regional scales, despite high spatial variability in forest conditions, suggesting broad-scale population fluctuations are governed by more than just local forest conditions.

An alternative paradigm, elaborated most forcefully by Royama (1984), is that something other than forest age and abundance—such as natural enemies—restricts generation recruitment of budworm. By acting in a delayed density-dependent manner, these agents induce a harmonic (i.e., sinusoidal) oscillation, much like a predator–prey cycle (Box 5.1), resulting in a system that is statistically "stationary" in its cycling (i.e., autoregressive) properties, including time series mean and variance. According to Royama's model no upper (or lower) stable state is ever realized; the unique equilibrium state is never achieved because of an unending regime of stochastic perturbations that continually force the system away from its globally stable single-point attractor. Royama (1984) noted that, according to this theory, some population cycles may not rise to a level where defoliation becomes observable. This, he suggested, might explain the occasional missing cycle in long time series records—defoliation events that could not easily be detected by aerial surveys and tree-ring analysis.

The paradigm is parsimoniously expressed in a model phase space diagram (Fig. 5.4a). Using a second-order density-dependent approach that is essentially a phenomenological predator–prey model, one can produce long cycle lengths by careful selection of an appropriate parameter space. Zone IV of the parameter

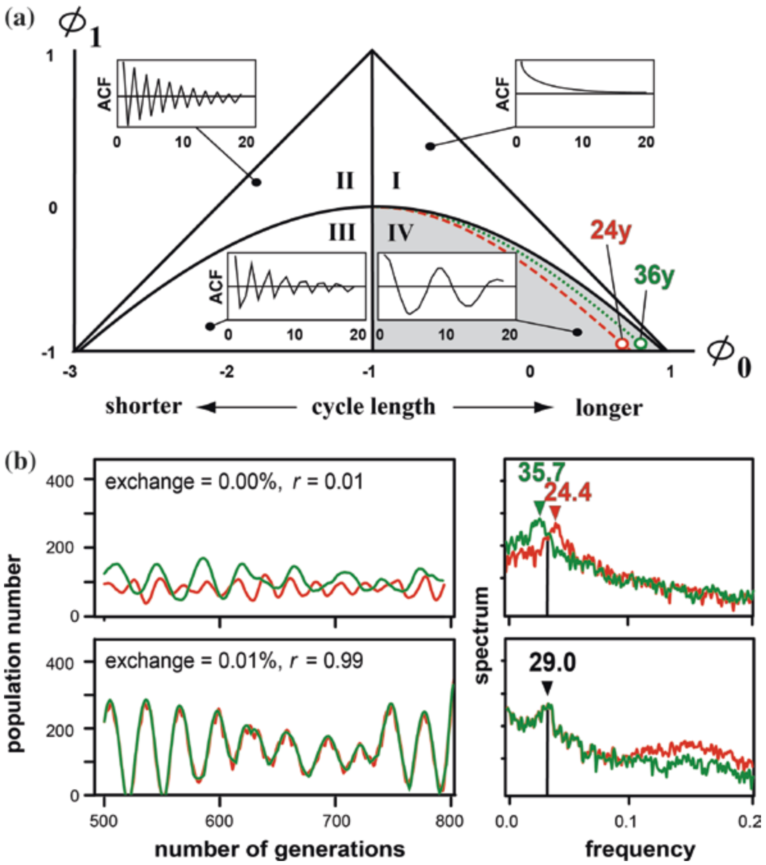


Fig. 5.4 **a** The parameter space of a delayed feedback time series model (Rt = Φ0Nt + Φ1Nt-1 + et) overlaid on a phase plane diagram representing different zones of model behavior (Royama 1992; see *inset*), where Zone IV parameter space generates low-frequency dampening oscillations. Tiny variations in the delayed feedback parameter (Φ_0) are sufficient to generate large difference in cycle frequency, as indicated by the parameter sets (Φ_0, Φ_1) required to generate sustained oscillations of 36- and 24-year periodicity. **b** The effect of coupling via reciprocal dispersal on two populations cycling at differing frequencies. Even when the strength of dispersal coupling is low (exchange rate = 0.01 % amongst populations), the 36- and 24-year cycling populations (*top left*) converge on a phase-synchronized 29-year cycle (*bottom left*), as demonstrated by corresponding spectral peaks in the respective time series (*right*), with correlations (r) rising from ~ 0 to ~1

space (Fig. 5.4a) produces slow-damping cyclical behavior consistent with the idea of "phase-forgetting quasi-cycles" (Nisbet and Gurney 1982). Royama (1984) illustrated parameter combinations in Zone IV that generate low-frequency, high-amplitude cycling, and Fleming et al. (2002) discussed these parameterizations in the context of the spruce budworm. Figure 5.4a illustrates two contrasting parameterizations that lead to robust 36- and 24-year cycling behavior (stochastic realizations illustrated in Fig. 5.4b). A 36-year outbreak cycle (i.e., time between peaks) is indicative of budworm outbreak dynamics in the northeastern boreal forest (e.g., Jardon et al. 2003), while a 24-year cycle is more common to the Appalachian region (Cooke et al. in prep.), to Western Canada (Burleigh et al. 2002), and also to western spruce budworm, *C. occidentalis* Freeman (Alfaro et al. 2014). Clearly, a 24-year outbreak cycle is not sufficiently long for forest regrowth, particularly in Northwestern Canada where balsam fir is absent, and the dominant conifer is the relatively long-lived white spruce. Notably, very small differences in parameter values may result in significantly different cycle lengths (Fig. 5.4).

Trophic interactions affecting budworm populations were recently documented to show a complex food web involving at least 56 different species, including alternative parasitoid hosts, predators, and hyperparasitoids (Eveleigh et al. 2007). One might ask how a 56-dimensional trophic interaction could possibly be represented in a simple two-dimensional autoregressive model. The answer lies in Royama (1971, 2001). The competitive interaction between parasitoid species that occurs with multiparasitism may serve a compensatory mechanism whereby a reduction in one parasitoid species is readily offset by compensatory gains in another parasitoid species with a similar attack phenology. Trophic redundancy thus may result in a relatively stable predator–prey multispecies complex that behaves more or less as a pure two-species predator–prey system.

In theory, a more rapid response of predators translates into lower amplitude, higher frequency predator–prey cycles. With a very large food web, relatively small changes to just a few key budworm parasitoid species might produce such differences. In this way, interaction between forest composition and the spruce budworm natural enemy complex may help to explain the lower amplitude and higher frequency cycle more typical of the floristically diverse Laurentian forests relative to the higher amplitude, lower frequency cycle more typical of the less diverse boreal forest (Cooke, unpublished manuscript). Indeed, it is interesting to speculate on the potential role of the closely related hardwood defoliators in the *Choristoneura* genus (e.g., *C. conflictana* and *C. rosaceana*), whose presence or absence would serve to perturb the natural enemy communities that surround the spruce budworm (see Sect. 5.3 for discussion on reduced budworm defoliation in hardwood-rich stands and forests of New Brunswick).

Analyses of recent data that included high-frequency sampling of parasitoids (Nealis and Régnière 2004a, b; Régnière and Nealis 2007) support Royama's assertion that "the primary oscillation is governed by lagged, negative feedbacks between budworm density and generational survival as influenced by the impact of natural enemies on late-feeding stages of the insect" (Régnière and Nealis 2007, p. 14). Yet host mortality was also clearly documented as contributing to the decline—just not consistently across study sites. Among the strongest sources of bottom-up feedbacks are dispersal mortality within young instars when seeking food resources in heavily defoliated stands (Nealis and Régnière 2004a). In short, substantial losses in host foliar biomass can certainly contribute to—but is not a requirement for—outbreak decline.

5.2.2.3 Upscaling Local Dynamics to Landscapes and Regions

As indicated previously, the champions of each model paradigm further differed in the relative significance of dispersal in generating complex dynamic behavior and spatial patterning of budworm outbreaks. While Royama (1980, 1984, 1992) acknowledged that dispersal by both larvae and adults was an integral part of budworm life history, he invoked Moran's (1953) theorem to argue that synchronized patterns of outbreaks are primarily caused by weather-driven (i.e., density-independent) fluctuations in recruitment between the adult and egg stage, where egg-laden female moths are prone to dispersal within and between forest stands. Under Moran's theorem, modest environmental perturbations that are regionally autocorrelated in space can synchronize independently oscillating populations, even when the environmental factor is independent of the cause of the population oscillation. This "Moran Effect" has since been identified as an important factor contributing to the regional outbreak synchrony for a wide range of Lepidopteran species (Ranta et al. 1997; Myers 1998; Bjørnstad et al. 1999; Myers and Cory 2013), including two species of lymantrids with females that cannot fly (Mason 1996; Bjørnstad et al. 2008).

The interaction between dispersal and spatiotemporal dynamics of outbreaks depends in part on how immigration affects local population dynamics, i.e., the underlying population model, or harmonic oscillation versus metastable eruption. For the latter, dispersal acts as successive triggering of eruptions through a spatial chain reaction, similar to a "domino-effect" (Clark et al. 1979) also known as a traveling wave (Bjørnstad et al. 2002). This so-called "epicenter hypothesis" fell out of favor with the advent of the harmonic oscillation paradigm that emphasized the Moran effect (Royama 1984). Régnière and Lysyk (1995) later proposed a high-resolution spatial model that illustrated how dispersal may act as a significantly more robust synchronization process that forces independently oscillating systems to converge to a common cycling frequency even if their intrinsic cycling frequencies differ (as illustrated in Fig. 5.4b). Régnière and Lysyk (1995) fundamentally changed the nature of the discussion of cycle synchronization to place equal emphasis on weather and dispersal as potential synchronizing forces (e.g., Peltonen et al. 2002). More recently, Régnière et al. (2013) empirically documented an "Allee effect" (Allee 1931) within low-density budworm populations—not in the form of a predator pit as proposed by Holling and colleagues (Ludwig et al. 1978), but due to low mate-finding success at very low densities. This Allee effect, i.e., the positive dependence of population growth rates on population densities when densities are low, suggests that a low endemic state can be overcome via immigration. If dispersal can produce both kinds of effects, i.e., synchronization and traveling waves, then hybrid models that include both effects may be necessary to fully capture the relevant dynamics.

The recent data and syntheses suggest that neither of the supposedly competing paradigms (i.e., host abundance vs. natural enemies, and Moran Effect vs dispersal) is sufficient to characterize the full range of budworm outbreak behavior in time and space. Insights from landscape ecology, including recognition of the critical role of neighborhood effects, spatial heterogeneity, and the appropriate scaling of ecological processes (Addicott et al. 1987) suggests that the discrepancy between paradigms might be related to the spatial and temporal scale of observation and empirical data. This perspective is supported by the multiscale modeling efforts of Fleming et al. (1999, 2002) who showed that finely resolved gridded data differ qualitatively in behavior from models parameterized using coarsely gridded data. More specifically, whereas local dynamics appear to conform to an eruptive hypothesis, the landscape scale dynamics appear to conform to a cyclic hypothesis. Although the models used were purely phenomenological and univariate, the results are consistent with Holling's idea of "cross-scale drivers" (Holling 1973, 1986), with eruptive behavior emerging locally as the result of a fast process (in this case positively density-dependent mating success or predator escape), and cyclic behavior emerging at the landscape scale as the result of some slow process (in this case delayed density-dependent parasitism and dispersal-driven cycle synchronization, as illustrated in Fig. 5.4b). The spruce budworm thus appears to behave as hybrid cyclic-eruptive, with the characteristic oscillatory and eruptive relaxation behaviors emerging at distinct, well-separated spatial scales of landscapes versus stands.

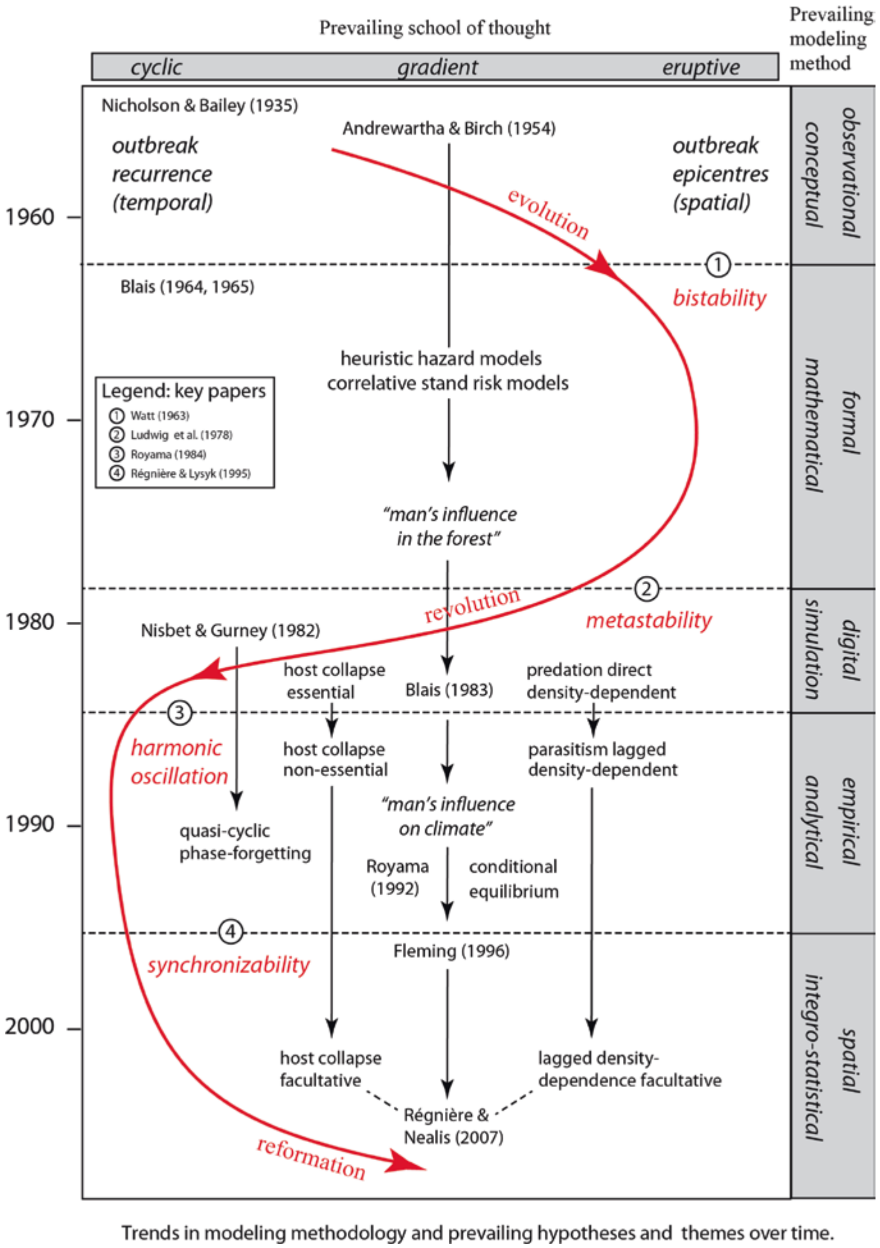
5.2.3 Gradient Models and Climate Drivers

In his synthesis of the spruce budworm system, Royama (1992) emphasized the conditional nature of its equilibrium state, with cycle frequency, amplitude, and time series mean and variance all potentially varying depending on environmental factors, effectively serving as "gradients" in space and time. He suggested these environmental factors might include forest composition, food web composition, and climate. Recognition of gradients affecting insect population dynamics (Table 5.1) derives from the notion that population densities are controlled by environmental carrying capacities (Andrewartha and Birch 1954). Indeed, as early as the 1950s, spruce budworm "outbreaks" were occasionally referred to as "gradations" (Morris et al. 1958). Very early "hazard-rating" models were built on this same premise of the outbreak as a spatial gradient, substituting the forest resource for the environment (e.g., Webb et al. 1956). Hazard modeling has become increasingly sophisticated with time and is elaborated in Sect. 5.3. However, the concept of environmental gradients—and more specifically climate—as a key factor contributing to nonstationary budworm outbreak dynamics in time and space both transcends the two modeling paradigms summarized above and has emerged most recently as fundamental to the understanding of outbreak behavior (Fleming and Candau 1998).

There are two fundamental approaches to understanding the climate–budworm outbreak interaction. The first approach relates to processes underlying budworm outbreak response to climate: investigations of the underlying process and empirical pattern analysis of past outbreaks using climate variables as covariates. Results from models used to investigate the process suggest climate and weather interact with budworm on multiple levels, i.e., growth, survival, and movements of both the budworms and their natural enemy complex (Fleming 1996). Gray (2008) argued that it is challenging to understand the cumulative effects of these multiple interacting processes. Pattern analyses of broad-scale aerial surveys clearly indicate an overall climatic signal affecting the budworm outbreak dynamic, but to date these types of analyses have been limited to a single outbreak cycle (e.g., Candau and Fleming 2005; Gray 2008, 2013). Régnière et al. (2012) simplified the processes to two dominant temperature-dependent limitations on population dynamics: development rate (Régnière and You 1991) and consumption of energy reserves over winter during diapause (Han and Bauce 1997, 2000). Consequently, budworm outbreaks become limited by the budworm's ability to complete its phenological life cycle at the northern (or altitudinal) extent of its range, and by the exhaustion of energy reserves due to higher metabolism at the southern extent of its range. The key insight from this combined body of modeling (i.e., process- and pattern-based) is that climate is an influential environmental factor. Climate change is anticipated to significantly affect future outbreak dynamics, with a northward shift in periodic outbreak behavior (much as predicted by Fleming and Volney 1995), a reduction in outbreak cycle amplitude in regions that have historically seen the most regular oscillations, and the elimination of detectable defoliation at the southern range limit (Régnière et al. 2012). Indeed evidence is mounting that northward range shift of spruce budworm may be attributable to climate warming, and that climate and forest composition both influence outbreak dynamics (Gray 2013).

5.2.4 *Insights Following Five Decades of Research and Modeling*

The evolution of thought and the interplay of data and modeling over time can be described by five phases of model development (observational, formal, digital, empirical, spatial), punctuated by the publication of four revolutionary papers (Fig. 5.5) (Watt 1963; Ludwig et al. 1978; Royama 1984; Régnière and Lysyk 1995). As the data accumulate over time, and as the methods evolve, we see that the prevailing paradigm oscillates from cyclic to eruptive to cyclic and is currently settling on a hybrid between these extremes. A unifying theme that emerged in the background of these opposing paradigms was the idea of population regulation by environmental factors such as forest and climate. One is led to conclude that this system may exhibit all three features of cyclic, gradient, and eruptive behavior (Table 5.1). Ideas that were once dismissed as unimportant or improbable (e.g., epicenter theory; anthropogenic forcing) come back into vogue as new data emerge, as the role of heterogeneity and scale become increasingly explicit, and as the demands of operational management force modelers to consider the full array of actual dynamic behavior across multiple spatial scales.



Trends in modeling methodology and prevailing hypotheses and themes over time.

Fig. 5.5 Evolution in thinking on the nature of spruce budworm outbreaks, marked by distinct phases where key papers had a lasting influence

5.3 Budworm Risk, Impacts, and Decision Support

5.3.1 Empirical Understanding

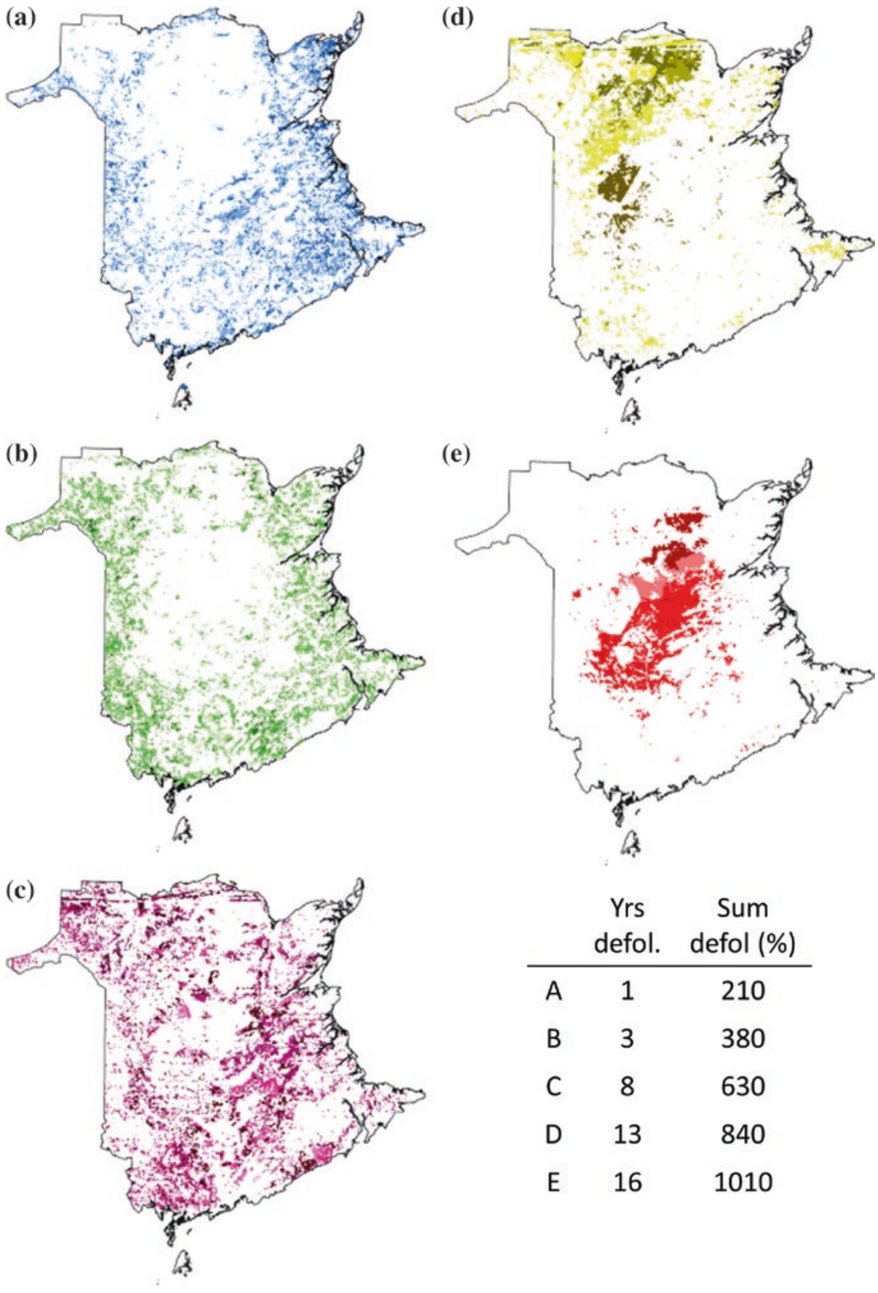
The historical spruce budworm modeling of Holling and colleagues (Jones 1977; Clark et al. 1979), in collaboration with Baskerville, directly contributed to forest policy discussions (Baskerville 1976) and considerations of timber supply and effects of defoliation on provincial economy and employment (e.g., Baskerville 1982). It also contributed to broader development of timber supply modeling and forest management decision-making frameworks in New Brunswick (e.g., Baskerville and Kleinschmidt 1981; Hall 1981), and was the precursor of stand- and forest-level modeling inherent in the modern spruce budworm decision support system (SBWDSS). Here we (1) review empirical relationships between defoliation levels and reductions in stand growth and survival, and the factors that influence them; (2) relate the population processes from Sect. 5.2 to the impacts measured at tree-, stand-, and neighborhood scales; and (3) describe the foundation and functioning of the SBWDSS.

Defoliation links insect budworm population factors to stand responses (MacLean 1980; Erdle and MacLean 1999). Current defoliation is directly correlated with late larval stage population density, so current and cumulative defoliation link budworm population dynamics to stand responses. From the standpoint of predicting or inferring effects of budworm outbreaks on growth and yield or timber supply, defoliation is easier to assess at the branch-, tree-, stand-, or landscape scale than are budworm population levels. Current defoliation sampling methods include manually assessing percentage defoliation by foliage age class, on shoots, branches, or trees (e.g., Fettes 1950; Sanders 1980; MacLean and Lidstone 1982) and also well-developed aerial survey techniques (e.g., Dorais and Kettela 1982; MacLean and MacKinnon 1996) that rely on the reddish coloration of foliage resulting from budworm larvae severing and webbing together needles as they feed. Repeated annual measurement of current and cumulative defoliation on individual trees in permanent sample plots, and relating cumulative defoliation to growth and survival of those trees over time, is the basis for much of our empirical understanding of budworm impacts.

So what do we know about budworm defoliation, impact relationships, and effects on trees and stands? First, budworm population density is the main driver of annual current defoliation (e.g., Figure 5.3), and several factors influence budworm population trends. But host tree species also influence current defoliation, with an extensive permanent sample plot data set (>27000 tree and 1117 stand measurements from 1984 to 1992) revealing a clear and consistent hierarchy of host species defoliation. Regardless of budworm population density (defoliation severity) and various stand variables tested, white, red, and black spruce had approximately 72, 41, and 28 % as much current defoliation as balsam fir, respectively. Phenology of host bud burst and budworm larval development may be the leading cause of reduced defoliation on red and black spruce compared with balsam fir and white spruce. Red and black spruce bud burst occurs on average 2 weeks later than on balsam fir (Greenbank 1963), causing lower early instar larvae survival on red-black spruce and lower percent defoliation relative to other host species (Lawrence et al. 1997; MacLean and MacKinnon 1997).

Second, host tree defoliation and tree growth reduction and mortality are consistently reduced when host trees are mixed with deciduous trees not just within stands, but also in relation to surrounding stands (Bergeron et al. 1995; Su et al. 1996; Campbell et al. 2008). Reduced budworm impacts within mixed forests may be attributed at least in part to the effect of hardwood species on the abundance and composition of budworm natural enemy communities. Tachinid parasitism of larvae and ichneumonid parasitism of pupae were elevated in stands mixed with or surrounded by deciduous species (Cappuccino et al. 1998), and a similar response was observed for egg parasitism by a hymenopteran species (Quayle et al. 2003). Importantly, stands with a hardwood tree species component contain many alternative host Lepidoptera species for multivoltine parasitoids that parasitize budworm. This can be critical as multivoltine parasitoids need to subsist on an alternate host in the late summer and autumn to continue their life cycle (Maltais et al. 1989). High levels of non-host deciduous species could also contribute to significant losses of first- and second-instar larvae during dispersal to other hosts (Kemp and Simmons 1978). The effects outlined here refer to factors affecting levels of defoliation at the plot to neighborhood scale (e.g., 1 km radius; Campbell et al. 2008). We speculate that the feedback between forest composition and budworm population dynamics may scale up to influence regional differences in outbreak frequency (Fig. 5.4) and intensity (Cooke, unpublished manuscript).

Third, growth reduction and mortality impacts at the tree- and stand scale are strongly related to cumulative defoliation over successive years (e.g., Erdle and MacLean 1999; Ostaff and MacLean 1995). Tree mortality rates are also a function of species and age class, whereas growth reduction has been observed to be similar, for a given level of 5-year cumulative defoliation among balsam fir, white spruce, and red–black spruce (Erdle and MacLean 1999). The relationships between growth, survival, and cumulative annual defoliation, by species, appear to be robust among differing outbreaks and studies, and can largely be considered deterministic. Outbreak severity and duration largely determines the amount of cumulative defoliation. However, real-world defoliation patterns are generated by the multiscaled interaction among forest conditions, nonlinear budworm population dynamics, complex trophic interactions, and the climatic and weather drivers affecting the predator–prey interaction (Sect. 5.2). For example, recent cluster analysis of aerial survey data for the last major outbreak in New Brunswick shows spatially aggregated regions with current defoliation ranging between 1 and 16 years (Zhao et al. 2014; Fig. 5.6). Other authors have identified analogous spatial heterogeneity in defoliation within an outbreak cycle across much of the boreal forest (Candau and Fleming 2005; Gray 2008). Such variability in current and cumulative defoliation underscores the importance of drawing together budworm population modeling and impact/decision support system modeling approaches.



	Yrs defol.	Sum defol (%)
A	1	210
B	3	380
C	8	630
D	13	840
E	16	1010

Fig. 5.6 Cluster analysis of spruce budworm defoliation in New Brunswick, Canada, from 1966 to 1993 resulted in 28 representative defoliation patterns, which were grouped into five categories (**a**–**e**) with divergent defoliation duration (ranging from 1 to 16 years; Yrs. defol.) and amounts (equivalent to removal of 2 to 10 age classes of foliage; Sum defol. %) (Zhao et al. 2014). Duration and severity of spruce budworm defoliation determines the resulting magnitude of impacts

Fourth, stand and site characteristics, and tree vigor, have been observed to influence current defoliation, growth reduction, and survival in some studies (e.g., Lynch and Witter 1985; Hix et al. 1987; Osawa 1989; Archambault et al. 1990; Dupont et al. 1991; MacKinnon and MacLean 2003) but not in others (Bergeron et al. 1995; MacLean and MacKinnon 1997). These appear to be weaker relationships, which break down during severe defoliation episodes.

5.3.2 Spruce Budworm Decision Support System (SBWDSS)

Advances in computer and information gathering technology have made the evaluation of alternative management practices through model simulation a feasible and valuable tool for forest managers (MacLean 1996). The SBWDSS, originally developed conceptually by Erdle (1989) and refined into a software application by Canadian Forest Service researchers (MacLean et al. 2001), was developed to project effects of budworm outbreaks on tree growth, mortality, and timber supply, and to incorporate potential management actions into a decision-making framework. It is built on the empirical impact relationships described in the previous subsection. Annual defoliation data obtained from aerial surveys and various user-defined defoliation scenarios are converted into cumulative 5-year defoliation. The model is deterministic and thus multiple defoliation scenarios are used but could eventually be coupled to population dynamic models as these improve. Estimates for the different scenarios are used to model tree growth reduction and stand mortality in a GIS forest inventory database (MacLean et al. 2001). Hennigar et al. (2007) improved the SBWDSS modeling framework by integrating stand-level budworm volume impacts into a forest estate model (Remsoft Spatial Planning System 2010), allowing pest management decisions such as foliage protection, harvest rescheduling, and salvage to be considered when maximizing timber flows during a budworm outbreak (MacLean et al. 2000, 2002).

The latest iteration of the SBWDSS allows integration between forest management planning and optimization models and underlying tree impact information derived from pest management decision support tools (McLeod et al. 2012). This tool can assist land managers in quantifying marginal benefits of protecting forest stands against insect defoliation (e.g., in terms of timber volume in m^3 ha^{-1} or value as \$ ha^{-1}). Protection cost: benefit analyses can be conducted using existing forest inventory and insect monitoring data in combination with forest management planning models to project the effects of foliage protection strategies on forest development and forest values.

This decision support system (DSS) comprises several specialized tools that allow users to simulate insect impacts on trees, stands, and forests (McLeod et al. 2012). These tools leverage stand growth modeling capabilities (FORUS Research, Fredericton, NB) and allow forest impact analyses to be conducted with existing strategic forest management optimization models (Remsoft Spatial Planning System 2010). These capabilities permit efficient exploration of cost-effective foliage protection or wood salvage scenarios. The tools can be divided into those used in estimating stand effects for strategic forest impact analysis (nonspatial tools) and those used for optimal spatial design of operational spray blocks (spatial tools). Nonspatial tools can be used to calibrate and implement the SBWDSS.

Strengths of the SBWDSS approach include robust stand-scale relationships, integration with existing forestry modeling tools, and use in tactical decision-making. Limitations of empirical DSS are that outbreak severity (number of years of >30 % annual defoliation) varies considerably and is scale- and context-dependent; studies are underway to better understand spatial and temporal variability of historic defoliation patterns in New Brunswick and Maine, United States, and to relate variability to budworm sample numbers. Since the SBWDSS stand impact matrix includes effects of all possible combination of cumulative defoliation on volume production, analyses can be scaled to differing outbreak severities. Nonetheless, until population modeling can actually project outbreak severity in time and space several years into the future, the stand growth/DSS approach will likely continue to use "what if," user-specified defoliation scenarios that are typically based on previous outbreak patterns, as well as monitoring and annual updating of stand-scale defoliation conditions during outbreaks using aerial survey or potentially remote sensing.

5.3.3 Transcending Traditional Disciplines

A commonality between the budworm population modeling and hazard modeling implied by Fig. 5.5 is the predominant absence of spatial context, particularly with respect to supporting data collected at plot (e.g., Royama 1984) and stand (e.g., MacLean 1980) scales. Analogous to insights described in the previous section (Fleming et al. 1999, 2002), landscape ecology left its mark on traditional impact studies starting with the recognition by Bergeron et al. (1995) that neighborhood and spatial context had implications for budworm damage, including the community composition and abundance of natural enemies (Cappuccino et al. 1998). The fact that both budworm and its natural enemy complex are mobile and therefore sensitive to spatial context could no longer be ignored.

An important consideration is that the vegetation equations underlying the eruptive class of models (Table 5.1) were not developed from data and have never been validated. The vegetation equations, which Hassell et al. (1999) showed to exhibit intrinsically explosive dynamics, were derived from Jones (1974, 1977), which in turn were supposedly inherited from an unpublished 1973 M.Sc thesis by a J.M. Stander at the University of British Columbia, Canada. Given the critical dependency of the eruptive models on vegetation dynamics, and the absence of vegetation dynamics in Royama's framework (Box 5.1), any modern hybrid modeling approach should revisit the question of how foliar biomass changes as trees and forests grow and prune themselves, and how this variable responds to budworm defoliation. Forest empiricists may be well-positioned to address this question, and in so doing, greatly inform the scaling of budworm populations to stands and landscapes. Likewise, budworm disturbance scenarios projected by the SBWDSS generally operate on the premise that budworm population dynamics are not affected by slower dynamics such as changes in forest conditions and climate—in other words, past dynamics are reasonable indicators of future outbreak behavior. We suggest that SBWDSS projections could be improved by incorporating feedback between forest and budworm defoliation scenarios in a way that is consistent with a modern synthesis of past modeling paradigms.

To fully understand critical feedbacks between forests and budworm dynamics relevant to both populations and their effects, we need to understand both tree losses (growth reduction and tree mortality) and tree response, i.e., regeneration and infilling of small or large gaps by surrounding trees (e.g., Spence and MacLean 2012). The former represents short-term hazard analysis, that is, within the realm of the current DSS. The latter represents long-term risk to timber supply and implications for future forest conditions, and requires a process-based modeling approach such as is embedded in landscape disturbance and succession models.

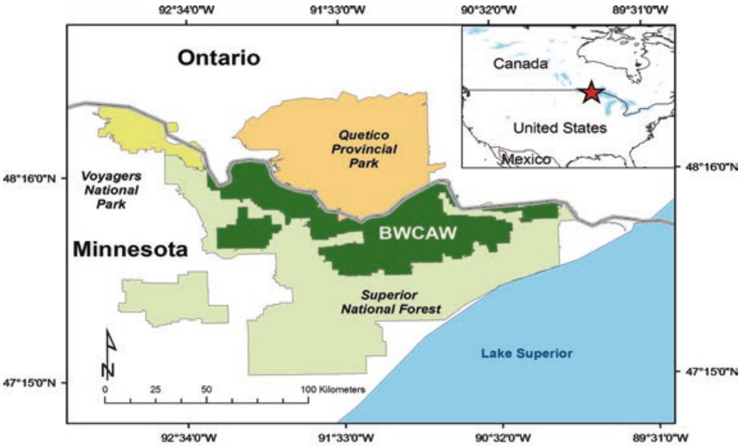
5.4 Landscape Disturbance and Succession Models

Landscape disturbance and succession (LDSM) models form a subset of forest landscape simulation models, identified by their explicit simulation of dynamic interactions between vegetation and disturbances in both space and time, and thus address the need to evaluate long-term risk by modeling long-term forest dynamics (Scheller and Mladenoff 2007). These LDSMs share a set of common traits, albeit with differing levels of sophistication, process, and complexity. Each simulates vegetation change in response to one or more disturbances and over time in the absence of disturbance. Each includes some environmental representation of the biophysical template (*sensu* Urban 2005) that affects the growing environment. While these processes generally operate and manifest locally at the level of a grid cell or polygon, they may be affected by neighborhood processes (e.g., seed source), environmental change (e.g., climate change), or vegetation–environment interactions (e.g., nutrient cycling). Simulated disturbance processes also vary in their respective degree of sophistication and coupling with other model processes. Unlike the deterministic optimization approach characteristic of the coupled SBWDSS and timber scheduling software described in the previous section, LDSMs explicitly incorporate the stochastic nature of disturbance and vegetative processes that reflects their intended purpose—to project future landscape conditions over comparatively longer timescales (e.g., centuries to millennia compared with DSS projections of years to decades). Spatial interactions among processes are fundamental to the approach because they “produce emergent behavior that contributes to the evolution of landscape pattern and changes in spatial heterogeneity at multiple scales” (Scheller and Mladenoff 2007, p. 493–494).

Implementation of defoliator disturbance regimes within the LDSM framework requires methods to (1) define outbreak dynamics in time and space, (2) define the spatial distribution of resulting impacts, and (3) implement the vegetation response to those impacts (Sturtevant et al. 2004). As should be apparent from the previous sections, predicting outbreak severity and duration across a complex landscape cannot be done with any certainty (e.g., Figure 5.6). Uncertainty is factored into LDSMs by applying disturbance processes according to stochastic functions. To date these functions have been defined simply, where outbreak periodicity and extent may be derived empirically from either dendrochronological studies (e.g., Jardon et al. 2003; Bouchard et al. 2006) or aerial survey data (e.g., Peltonen et al. 2002; Gray and MacKinnon 2006, 2007).

Simulating the characteristic spatial patterns of budworm-related mortality within a given outbreak (i.e., aggregation, severity, etc.) requires scaling the plot- and stand-scale impact relationships defined in the previous section to heterogeneous landscapes. Section 5.3 describes how forest composition, age, and growing environments can contribute to heterogeneity in defoliation impacts. The consequence of these combined relationships is that, in pure fir stands, mortality can be stand replacing, i.e., coarse scale, large opening (e.g., Baskerville 1975; MacLean 1980) but in mixed species stands overstory mortality is partial, forming small canopy gaps (e.g., Kneeshaw and Bergeron 1998; D'Aoust et al. 2004; Kneeshaw et al. 2008). Sturtevant et al. (2012) therefore scaled plot-level relationships between host abundance and disturbance impacts to landscapes as disturbance probabilities, resulting in a gradient of patchy "gaps" (i.e., isolated disturbed cells) where hosts were rare to more continuous mortality where hosts were dominant (Fig. 5.7). Neighborhood effects, such as reduced impacts within forests dominated by hardwoods (Su et al. 1996; Cappuccino et al. 1998), may be similarly approximated by adjusting disturbance probabilities based on neighborhood context (James et al. 2011). Nonetheless, considerable variability remains in defoliation impacts that both overlay and interact with the landscape structure and composition (e.g., Belle-Isle and Kneeshaw 2007). Such methods can be further refined by quantifying spatial patterns of defoliation mapped using remote sensing (e.g., Foster 2011).

Forecasting forest dynamics following spruce budworm outbreaks requires that tree species recruitment is understood as a function of overstory mortality. One of the simplest conceptual models of budworm-related forest succession is the cyclical model of balsam fir replacing itself in fir-dominated stands (Baskerville 1975; MacLean 1980). This model is based on the high shade tolerance of balsam fir (Kneeshaw et al. 2006) and its ability to form dense seedling banks that are released following overstory mortality (Morin et al. 2009). As suggested by Baskerville (1975), this model becomes more complex as forest structure and composition increase in complexity. For example, Kneeshaw and Bergeron (1998) show that budworm-caused mortality can lead to both the maintenance of shade intolerant hardwoods and the increase of non-host shade tolerant species such as eastern white cedar (*Thuja occidentalis*) in mixed species stands. Others have shown that outbreak periods are associated with recruitment peaks of many companion species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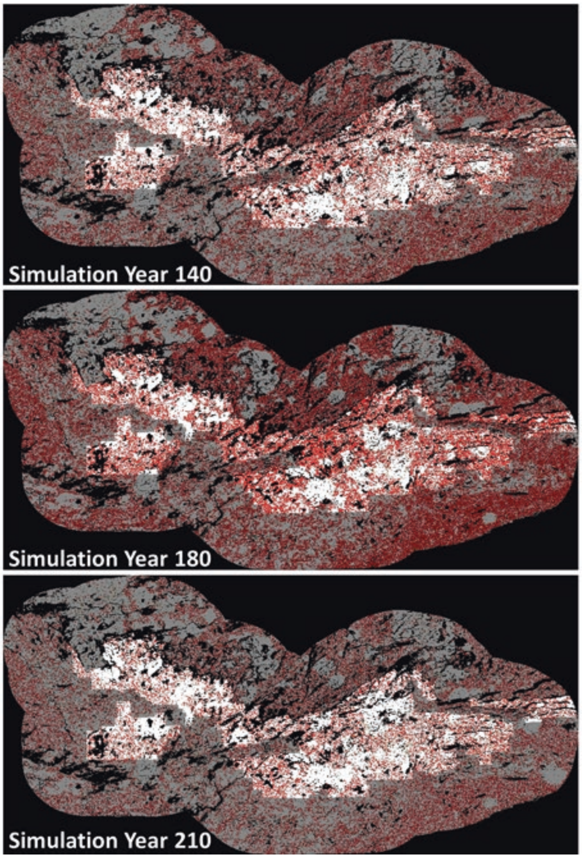
Simulation Year 140
Simulation Year 180
Simulation Year 210

◀ **Fig. 5.7** Simulated budworm disturbance within a landscape disturbance and succession model (Sturtevant et al. 2012), illustrating realistic simulation of budworm defoliation disturbance in both time (e.g., alternating moderate and severe outbreaks) and space (i.e., diffuse mortality moderated by spatial heterogeneity in host tree species). Large patches where budworm damage is absent reflects absence of host due to recent fires. Importantly, outbreaks were predefined to occur every 33.5 ± 10.6 years (mean ± SD) constrained to a 10-year time step. Alternating moderate and severe outbreaks emerged from the lagged response of regenerating host species

in addition to balsam fir (Bouchard et al. 2006). An increase in the presence of competing shrub species has also been linked to budworm outbreaks (Batzer and Popp 1985; Kneeshaw and Bergeron 1999; Kneeshaw and Prevost 2007).

Modeling of post-outbreak forest dynamics will be improved by a better understanding of understory seedling dynamics and their interactions with overstory composition and spruce budworm populations. For example, in some cases the forest may be too young or dominated by mixed species such that advance balsam fir regeneration banks are sparse. In other cases, as budworm populations increase and exhaust food resources in the overstory, the larvae may disperse downward (“down-spinning”) and defoliate the understory regeneration layer (Ruel and Huot 1993). This can then lead to a patchy forest structure and permit the recruitment of species other than balsam fir. However, knowledge of the effects of larvae down-spinning and defoliation of the understory seedling bank is lacking limiting our ability to establish the budworm population densities at which this process occurs.

The above elements are sufficient to examine budworm–forest interactions, with useful insights. For example, emergent behavior, such as alternating low severity and high severity outbreaks (Blais 1981; Bouchard et al. 2006), may be observed due to the inertia of host recovery following severe outbreaks (Fig. 5.7). Interactions between budworm, forest composition, and other disturbance regimes including fire and harvesting have also been investigated using LDSMs (James et al. 2011; Sturtevant et al. 2012). Nonetheless the current “state of the art” in insect modeling within LDSMs lags somewhat behind that of some other disturbances, such as fire. For example, nonstationary fire “regimes” may be derived from the emergent behavior of the underlying processes affecting fire ignition, spread and extinguishment, and the interactions of these processes with forest conditions, weather, and climate (McKenzie and Perera, in this volume). Coupled forest–budworm feedbacks have not yet been attempted within the LDSM framework, despite empirical evidence for such feedbacks at the landscape scale (as described above) (Candau and Fleming 2005; Bellier et al. 2007; Robert et al. 2012). Including such feedbacks could generate additional complexity in outbreak patterning, such as alternating patterns in per capita impact on host trees (i.e., high intensity in one outbreak, low intensity in the next), as reported by Bouchard et al. (2006). This alternating pattern in outbreak *intensity* would constitute a multiplicative effect over and above the far more intuitive pattern of outbreaks that vary in *extent* in proportion to host cover. Such scenarios can then serve as the basis for sensitivity analysis and scenario testing within the SBWDSS framework.

Landscape applications of the eruptive era models (i.e., Clark et al. 1979; Stedinger 1984; Fleming and Shoemaker 1992) used very coarse resolution forest compartments, with dispersal between them. Environmental factors have considerable influence on local dynamics (Gray 2013), such that spatial heterogeneity in landscapes is an important consideration. LDSMs can supply the more realistic forest responses that include spatial heterogeneity, although this opportunity for scaling has yet to be taken advantage of. Yet other processes—in particular the multiple scales and magnitudes of movements by both budworm and their natural enemies—remain unresolved. Computational demands of such multiscaled movements may also restrict their practical application within LDSMs, despite exponentially increasing computing technologies. Consequently, the same fundamental problem limiting SBWDSS also limits LDSMs, albeit at a different temporal scale (i.e., decade vs. century).

The development of such coupled modeling will also be critical for evaluating the effect of climate change on budworm–tree dynamics. LDSMs are already commonly applied to investigate the effects of climatic change on vegetation dynamics, typically by using climate–envelope relationships to define vegetation response to changing environments (e.g., Scheller and Mladenoff 2005; Keane et al. 2008; Ravenscroft et al. 2010). Among the many insights from these investigations is that spatial heterogeneity can influence vegetation response to environmental change (Scheller and Mladenoff 2008) and that indirect consequences of climate change, particularly consequent changes to disturbance regimes, can have larger consequences than the direct effects of environmental change on vegetation (Gustafson et al. 2010).

While LDSMs provide opportunity to investigate climate–budworm–landscape interactions, the science of climate–insect interactions has not yet been integrated into this framework. The regional empirical analyses of Gray (2008) and Candau and Fleming (2011) provide some guidance for how to parameterize future outbreak patterns under a warming climate. Alternatively, the processes underlying climatic constraints on population dynamics may include the ability of budworm to complete its life cycle based on cold temperature constraints on growth at high latitudes, and energetic constraints on survival of overwintering larvae at low latitudes (Régnière et al. 2012). Fleming (1996) suggested temperature-dependent predation or parasitism rates may also be involved, and as yet no evidence suggests these processes are not operating simultaneously. Other authors suggest that differences in weather variability across the same latitudinal gradient may also affect budworm population dynamics (Cooke et al. 2007; Dukes et al. 2009; Cooke, unpublished manuscript). To date, conceptual insights and advances have not been integrated into a single modeling framework.

The strength of the LDSM approach lies in its integration of processes occurring at different spatial and temporal scales, with both direct and indirect feedback between vegetation, multiple disturbances, and environment in time and space. The degree of complexity in the way these processes are represented can range from purely empirical functions based on past observations to theoretical relationships grounded in first principles. Stochasticity is fundamental to the approach to account for what we can and cannot project reliably. With respect to insect disturbance in general, and budworm disturbance in particular, applications have been weighted more toward empirically derived functions with associated probabilistic uncertainty.

The extensive research and modeling of budworm population and disturbance processes summarized in the previous two sections provides a rigorous basis for incorporating additional insect disturbance processes into the LDSM approach. In essence, the LDSM provides dynamics of critical vegetation and environmental gradients in time and space that could determine the "conditional equilibrium state" affecting harmonic oscillations of budworm populations (sensu Royama 1992). To simulate the disturbance process more precisely, empirical relationships underlying the SBWDSS could be adapted into impact functions. Insect movement could be simulated to interact with spatial heterogeneity of vegetation and environment to account for neighborhood and synchronization processes, while the flexible architecture of the LSDM may allow evaluation of competing hypotheses in a way that remains sensitive to scale. Integration of these processes with climate drivers affecting population dynamics provides opportunity for a "whole-system" approach to the question of climate change effects that may be compared directly for consistency with empirical study (e.g., Gray 2013).

Equally important is clear recognition of the appropriate domain of applicability for the LDSM approach. It is intended to capture spatial patterns at the landscape scale and temporal patterns on the order of a century or longer. This approach is therefore more amenable to strategic questions such as evaluation and consequences of alternative future scenarios at the above spatial and temporal time scales. It is not well-suited to address tactical decisions such as the specific placement of forest treatments in time and space, nor short-term projections of impacts and system response.

5.5 Opportunities for Synthesis

5.5.1 Model Integration

It is not surprising that multiple modeling paradigms have persisted over time: the data, as good as they are, have been insufficient to fully parameterize or refute any one model. Data uncertainties and model uncertainties were such that conjectures went unrefuted for long periods. Hypotheses that fell out of favor were revisited as new data, new methods, and new operational needs emerged (Figs. 5.2 and 5.5).

Consequences of the modeling paradigm for using insecticides for population control were particularly acute. For example, logical consequences of the cyclic model by Royama (1984) suggested local-scale foliage protection could be pursued without any threat of prolonging the region-wide cycle due to the role of natural enemies in promoting cyclic behavior (Royama et al. 2005), while the eruptive model by Ludwig et al. (1978) that minimized the role of natural enemies indicated foliage protection would necessarily prolong the outbreak. Similarly, Stedinger (1984) suggested that spruce budworm populations could be driven to local extinction if intense insecticide spraying occurred early enough in the growth phase of the outbreak cycle, while Royama (1984) contended that very little could be done to manage area-wide outbreaks, and that epicenter suppression would always end in futility when landscape-wide cycles proceeded to rapid synchronization via the Moran effect (Moran 1953; Royama 1984, 1997, 2005; Régnière and Lysyk 1995; Cooke et al. 2007). The most recent documentation of Allee effects (Régnière et al. 2013) and the renewed interest in dispersal as a synchronizing agent affecting the spatial scale of outbreaks (Régnière and Lysyk 1995; Sturtevant et al. 2013) has revitalized the debate about the efficacy of early intervention programs to manage outbreaks versus simply protecting foliage. Such divergent policy implications underscore the importance of clarifying model assumptions and of the role of science in reducing the most critical uncertainties. Meanwhile, recent warming of the North American boreal forest is changing the rules under which outbreaks have historically developed (Gray 2013).

As illustrated repeatedly by the spruce budworm modeling history, there is a natural tension between the inclusion of detail (model specificity) versus keeping models simple (model generality). This tension cuts across the contrasting paradigms outlined here, in that Ludwig et al. (1978) and Royama (1984) both advocated parsimonious models of minimal complexity (see Box 5.1), whereas Jones's original (1974) site model is aptly described as a "big, ugly model" (sensu Logan 1994) with a high degree of complexity. We suggest that a middle ground is necessary to attain a qualitatively well-specified model of the feedback couplings that give rise to the major features of budworm disturbance regimes. The opportunity for a modern synthesis can be represented by a hybrid model involving two levels of reciprocal feedback, one for the herbivore and its host tree, and one for the herbivore and its parasites, each contained within the larger context of dynamic climate gradients (Fig. 5.8). While simple in concept, model behavior will be complicated by the movement of budworm and their natural enemies, by coupled nonlinear relationships among trophic levels, and by cross-scale interactions among processes occurring at different temporal rates and spatial scales. Such complexities were well-recognized by budworm modelers as far back as the 1970s (e.g., Ludwig et al. 1978). What was underappreciated by followers of either paradigm was the *combination* of major features of outbreak behavior necessary to minimally characterize its dynamics in time and space, i.e.:

- Synchronizable (phase-forgetting), low-frequency oscillations that are more frequent (every 20–40 years) than the average rate of stand replacement
- High-frequency sawtooth oscillations (every 4–7 years), associated with fluctuations in fecundity and dispersal propensity
- Eruptive epicenters that serve as early sources for area-wide outbreaks
- Outbreak cycles that tend to alternate between non-stand replacing and stand replacing (i.e., not all outbreaks rising to the same level of devastating impact)
- Climatic gradients that track northward with climate warming

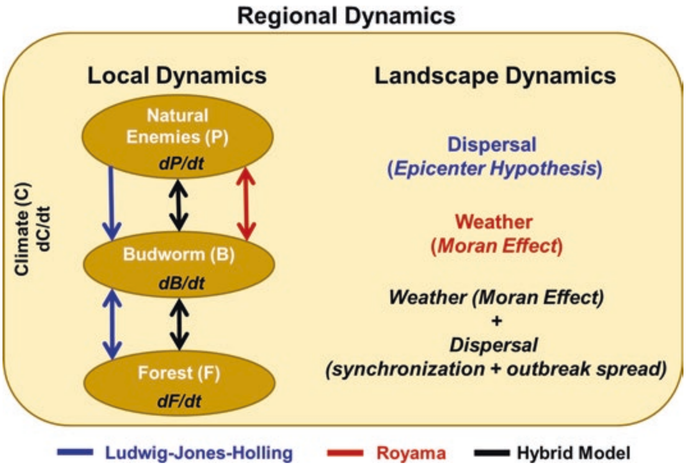

Fig. 5.8 Multiple equilibrium models championed by Holling and colleagues (Ludwig et al. 1978; *blue*) included predation; however, strong reciprocal feedback centers on the budworm–forest interaction. In contrast, the harmonic oscillation model championed by Royama (1992; *red*) emphasized strong reciprocal feedback in the higher trophic levels, with budworm–forest interactions as a secondary consideration. A modern synthesis (*black*) would consider both levels jointly, including the potential for eruptive and cyclic behavior, as well as the broader-scale context of climate

Likewise, decades of empirical study of budworm impacts on forests (Sect. 5.3) suggest the following common response, in decreasing order of strength and consistency of relationships:

- Host species composition and age determine mortality
- Outbreak severity and duration determine the magnitude of impacts
- Host species influences defoliation
- Deciduous content within stands and neighborhoods reduces host defoliation
- Stand and site characteristics and tree vigor show influence under some circumstances but are the weakest effect

Of these five drivers of budworm impacts, outbreak severity and duration are notoriously variable (Fig. 5.6) with major implications for projecting effects on forest. Accurate modeling of spruce budworm population trajectories may never be useful for precise predictions at an operational scale. Yet we expect consistent, high-resolution monitoring of forest conditions will improve the utility of the SBWDSS approach for decision-making. In addition, insights from complementary modeling (e.g., climate drivers, LSDMs) may improve the current approach (i.e., using past behavior to predict the future) by developing more plausible and informative alternative outbreak scenarios. For example, one might expect a light or moderate outbreak to follow a severe one, but what is the relative plausibility of such a scenario? Likewise, how might current climate affect the severity of the next outbreak cycle?

Integration of coupled landscape–climate–insect feedbacks—using insights and relationships from population and impact modeling approaches, respectively—within an LDSM framework can address many pressing issues facing land managers today. These include the cumulative effects of land management activities on insect disturbance frequency and intensity (Miller and Rusnock 1993), the direct influence of climate change on outbreak dynamics (Régnière et al. 2012; Gray 2013), and the interactions between these factors as they affect forest resilience to novel anthropogenic change. Among the key uncertainties are:

- Multiscaled insect movement as mediated by heterogeneity in resources and weather patterns
- Adaptive response of budworm to novel climates
- Defoliation effects on advance fir regeneration and subsequent successional pathways
- Responses of parasitoids to new habitats, landscape configuration, and climate

5.5.2 *Transferability of Insights Among Defoliator Systems*

Spruce budworm is arguably one of the most studied insects on the planet. Spruce budworm share many elements of system behavior with other important forest-defoliator systems (Cooke et al. 2007), and many of the lessons learned under the extensive budworm research programs may be transferable to modeling these systems. Features common among many forest defoliator systems include the near universal role of the Moran effect as a regional synchronization factor (Bjørnstad et al. 2008), prevalence of simultaneous top-down and bottom-up drivers affecting population cycling behavior (Myers and Cory 2013), and the importance of climate drivers affecting system behavior—including outbreak dynamics and range expansion (Jepsen et al. 2008; Bentz et al. 2010; Zografou et al. 2014) and the robust empirical relationships between defoliation and growth reduction and mortality (e.g., Osawa 1989; Erdle and MacLean 1999). Indeed, the generalized framework of the SBWDSS has also been applied to insects other than spruce budworm. It has been used to calibrate and predict timber supply impacts of balsam fir sawfly (*Neodiprion abietis*) and eastern hemlock looper (*Lambdina fiscellaria*) defoliation scenarios in Newfoundland, Canada (Iqbal et al. 2012). It also includes defoliation impact modeling data for jack pine budworm (*C. pinus*). Likewise, a generic insect disturbance approach for LDSMs used budworm as a demonstration (Sturtevant et al. 2004) and has since been applied to defoliation disturbance in China (Chen et al. 2011) and Siberia (Gustafson et al. 2010), and enhanced to simulate effects of defoliation on carbon cycling within eastern deciduous forests of North America (Foster 2011; Kretchun et al. 2014).

Berryman (1986) proposed that individual forest insect pest systems could be classified into discrete categories "eruptive," "cyclical," "gradient," "pulse," and "sustained" according to the dominant pattern of fluctuation in space and time.

After five decades of research on a cross-scale system such as spruce budworm it is apparent that the system exhibits a broad array of complex dynamics, any facet of which may be observed, depending on the spatial and temporal scale of observation. There is little reason to suspect that other cross-scale systems, being regulated both from above and below and by weather and climate, should behave any more simply. For example, the forest tent caterpillar (*Malacosoma disstria*) system has also been approached from two divergent perspectives: the eruptive paradigm (Rose and Harmsen 1981) versus that of the harmonic oscillation (Cooke et al. 2012). Although evidence is mounting that the effect of specialist and generalist parasitism is strong enough to induce a predator–prey oscillation in this system (Roland and Taylor 1997; Roland 2005), there is also evidence of traveling waves of eruption (Cooke et al. 2009), which may be a result of the positive density dependence of mating success on population density at low population densities (Sjostrom and Roland, unpublished data), as reported for spruce budworm (Régnière et al. 2013). Indeed, it is increasingly clear that the forest tent caterpillar also responds strongly to spatial and temporal gradients in both climate conditions (Daniel and Myers 1995) and landscape structure (Roland et al. 1998; Cooke and Roland 2000, Wood et al. 2010), suggesting a remarkable parallel with spruce budworm. We suggest that the most fruitful modern avenue of research in forest–insect–climate interactions is in testing inclusive hypotheses that allow for multiple processes acting simultaneously using integrative, multiscale landscape models that embrace the possible existence of a range of dynamical behaviors.

Research and modeling of other defoliator systems can likewise inform modeling of spruce budworm. One of the major limiting factors restricting understanding of budworm cycling dynamics is its unusually long cycle length that exceeds most scientific careers. Other systems that cycle more frequently are more amenable to both statistical modeling and model validation, providing valuable insights into the processes underlying outbreak dynamics in time and space (e.g., larch bud moth (*Zeiraphera diniana*): Johnson et al. 2006, forest tent caterpillar: Cobbold et al. 2005; Hughes 2012; Robert 2014; European gypsy moth (*Lymantria dispar*): Haynes et al. 2009). Similarly, the detailed study of the invasion by the gypsy moth in North America offers unique insights into processes such as Allee effects in time and space, while multiscaled and multi-trophic level study of the forest tent caterpillar offers unique insights into scale-specific factors affecting host–parasitoid dynamics (Roland and Taylor 1997; Roth et al. 2006). Insights from these other systems suggest fruitful areas of research within the spruce budworm system.

5.6 Concluding Remarks

The spruce budworm case study is a dramatic illustration of the interplay between data and modeling, the broader challenge of simulating insect–forest interactions in time and space, and the conflicting management guidance that can emerge from such activities. Indeed, foundational concepts such as cross-scale theory (Holling 1992), adaptive cycles and ecological resilience (Gunderson and Holling 2002), spatial population dynamics (Bjørnstad et al. 1999), and aerobiology (Gage et al. 1999) can all trace pivotal roots to the collective spruce budworm research program. Such broad influence speaks to the power of modeling on the scientific enterprise and its interaction with land management and policy. While not emphasized here, there is an undeniable human dimension to the artistic and nonscientific aspects of model development that are apparent in the divergent perspectives applied to the problem (Table 5.1; Box 5.1; Fig. 5.5). The budworm case study illustrates how insights from each perspective can be complimentary, and how conflict and debate among these perspectives provided deeper insights that ultimately led to more complete understanding of the system. It also illustrates how aspatial perspectives can lead to conflict in data interpretation, and how appreciation of scale, spatial heterogeneity, and movement can help reconcile seemingly disparate schools of thought. Such lessons and insights have clear implications not only for budworm as the latest widespread outbreak to hit North America develops (i.e., 3.2 million ha of moderate-to-severe defoliation in Quebec in 2013; QMRNF 2013), but also insect disturbance modeling more generally.

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Chapter 6

Individual-Based Modeling: Mountain Pine Beetle Seasonal Biology in Response to Climate

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6.1 Introduction

Over the past decades, as significant advances were made in the availability and accessibility of computing power, individual-based models (IBM) have become increasingly appealing to ecologists (Grimm 1999). The individual-based modeling approach provides a convenient framework to incorporate detailed knowledge of individuals and of their interactions within populations (Lomnicki 1999). Variability among individuals is essential to the success of populations that are exposed to changing environments, and because natural selection acts on this variability, it is an essential component of population performance.

Initially viewed simply as an alternative modeling technique to classical differential- or difference-based deterministic models of theoretical ecology, IBMs are in fact fundamentally different (De Angelis and Mooij 2005). These models have four essential characteristics: (1) an organism’s life cycle can be depicted in full detail (e.g., thermal responses, behavior, fecundity); (2) variability among individuals of the same life stage, be it caused by genetic or environmental differences, is accounted for; (3) resources exploited by the modeled organisms are explicitly accounted for; and (4) population sizes are represented by integer numbers because they are composed of individuals (Uchmanski and Grimm 1996). An IBM focuses on the fates of individuals with explicitly different traits, and on the biotic and abiotic circumstances to which each responds. The full complexity of an organism’s life cycle can therefore be described and modeled. Such models provide a helpful framework within which to conceptualize and interconnect natural processes, design research, analyze results, and synergistically combine empirical studies and modeling (Van Winkle et al. 1993).

Dealing with individuals simplifies the mathematical formulation of rules and relationships that dictate their responses to environmental conditions or to each other. Individuals can thus differ in many ways, either genetically or because of their environmental context, and it is these differences and their consequences that determine the behavior and the effects of populations on their environment. The object-oriented programming techniques upon which IBMs rest are particularly well suited to discuss adaptation of organisms to varying environmental conditions, because of the property of inheritance from parents and to progeny (Warren and Topping 2001). As is true of all objects in this programming paradigm, specific traits of parents can be passed on, intact or modified, to progeny (children). In a biological context, this occurs when individuals are “copied” at reproduction.

Adaptive characteristics that allowed the survival of parents are thus inherited by their progeny, modifying the relative frequencies of various individual traits according to their survival and fecundity (fitness) under current environmental conditions. Thus, the frequency distributions of various traits can change in simulated populations much as they do in nature.

IBMs are well suited to describing the temperature-dependent processes of organisms sensitive to varying environmental conditions, and can help to model the responses of populations to a changing climate. Many insect species, including those deemed pests due to their significant ecological and economic impact, have been influenced by a changing climate (Bale et al. 2002). Prime examples are bark beetles in the genus *Dendroctonus* for which a clear connection between weather and population irruptions and subsequent landscape-scale tree mortality has been shown (Hansen et al. 2001; Berg et al. 2006; Aukema et al. 2008; Chapman et al. 2012; Preisler et al. 2012; Hart et al. 2014). Changing climatic conditions are also responsible for a range shift in at least one species, *Dendroctonus ponderosae*, the mountain pine beetle (MPB). This irruptive species attacks and kills most *Pinus* species in western North America (Wood 1982). Genetic data suggest that MPB migrated north following the postglacial Holocene recolonization of British Columbia by several *Pinus* species (Richardson et al. 2002; Mock et al. 2007; Godbout et al. 2008; Samarasekera et al. 2012). Recent warming has increased the speed of this MPB migration into new regions in Alberta, British Columbia, the Yukon, and Northwest Territories, Canada (Bentz et al. 2010; Safranyik et al. 2010; Cudmore et al. 2010; de la Giroday et al. 2012), with exposure to at least one new host tree species, jack pine (*Pinus banksiana*) (Cullingham et al. 2011, 2012). Jack pine extends across the boreal forest of Canada and into the northern part of the mid-western United States, and there is concern about the potential for MPB to invade eastward across Canada and into central and eastern states (Nealis and Cooke 2014). Long-lived high-elevation pines (e.g., *P. albicaulis*) with life history strategies not suited for large-scale disturbance events may also be at risk (Logan et al. 2010; Tomback and Achuff 2010). Sustained MPB outbreaks are now occurring in high elevation forests where persistent activity was previously constrained by cold temperatures (Amman 1973; Logan and Powell 2001; Bentz et al. 2011a). The capacity of MPB to continue expanding into new thermal habitats, however, remains unclear.

Issues surrounding the effects of climate on the distribution and performance of species have been investigated by a range of methods, including correlative approaches such as climate matching or species distribution modeling (Elith and Leathwick 2009) that correlate presence/absence observations with climatic and geographic variables and extrapolate the results to novel regimes. Mechanistic approaches include more detailed (if less comprehensive) process modeling (Sutherst and Bourne 2009; Régnière et al. 2012a). In this chapter, we present a prototype mechanistic IBM that describes in detail the fitness (population growth rate) responses of MPB to temperature, based on understanding of the insect's developmental and survival responses to temperature, and on the resulting consequences through its interactions with host trees. We realize that many aspects of

MPB life history and the role of hosts at tree and stand scales are not accounted for within this prototype. However, this “working” model allows us to investigate climate change effects on the invasiveness of MPB and provides a useful demonstration for the general application of an IBM approach to insect disturbance modeling.

6.2 The Insect

The behavior and ecology of MPB have been extensively studied (see Safranyik and Carroll 2006). Most populations across the insect’s range are univoltine (one generation per year) although 2–3 years can be required in colder environments or years (Amman 1973; Bentz et al. 2014). Bivoltinism (i.e., two generations in 1 year) appears to currently be limited in MPB due to evolved developmental thresholds that serve to reduce cold-induced pupal mortality (Bentz and Powell 2014). MPBs develop through four larval instars before pupating and becoming adults. Except for a brief adult flight period, the entire lifecycle is spent in the phloem, and the host tree is typically killed as part of successful offspring production. Adults emerge from trees in the summer months to attack new hosts using a coordinated attack mediated by beetle-produced pheromones. A well-synchronized adult emergence facilitates mass attack, and is important in the development of MPB outbreaks because the insects must overcome host defenses to successfully colonize healthy trees (Raffa et al. 2008). Temperature directly influences MPB development rate (Bentz et al. 1991; Régnière et al. 2012b), and stage-specific development thresholds help synchronize adult emergence (Powell and Logan 2005). Mortality due to extreme cold also conditions MPB population success (Safranyik and Linton 1998). Cues of declining temperature initiate glycerol synthesis and lower supercooling points (SCP), increasing MPB larval cold tolerance (Bentz and Mullins 1999). Before this acclimation occurs or when it is disrupted by warm periods, significant mortality can occur during cold snaps. Reproductively active MPB adults also supercool to some extent (Lester and Irwin 2012). In areas where MPB population growth has historically been limited by cold mortality, warm temperatures associated with climate change have increased population success and may allow continued population expansion (Stahl et al. 2006; Sambaraju et al. 2012).

6.3 The Model

The influence of climate on MPB population success has been the subject of considerable modeling attention. Empirically driven, statistical approaches have been proposed (Safranyik et al. 1975; Aukema et al. 2008; Preisler et al. 2012; Reyes et al. 2012), and mechanistic models have also been developed (Bentz et al.

1991; Gilbert et al. 2004; Régnière and Bentz 2007; Powell and Bentz 2009), to analyze the role of temperature in MPB population outbreaks using historic and future climate data (Logan and Bentz 1999; Logan and Powell 2001; Hicke et al. 2006; Bentz et al. 2010; Safranyik et al. 2010). While empirical models have good descriptive power for the range of conditions for which they were derived, they need to be used with caution under unobserved multivariate contexts such as encountered when crossing ecoregional boundaries. In contrast, mechanistic models are more suitable for predicting MPB population success in novel climate regimes. Previous mechanistic model development, however, has used frameworks that do not allow inclusion of processes other than the influence of temperature on insect development time. For example, Powell and Bentz (2009) were successful in linking phenology, temperature, and population growth rates; although their approach is based on cohorts, it is unsuited to linking with other aspects of MPB life history such as cold tolerance (Régnière and Bentz 2007). MPB has no obligate diapause stage. The age distribution of overwintering populations, and therefore winter survival, are thus largely determined by summer phenology. Modeling cold tolerance requires an individual beetle's history of cold exposure. An IBM can potentially succeed where other modeling approaches have failed because it allows life history traits relevant to beetle success to be projected onto individuals (i.e., age-specific development time, exposure to cold, fecundity), and collaboration among individuals to overwhelm host responses can be incorporated. We develop an IBM that integrates the influence of temperature on insect development time and cold mortality, and their consequences on the interaction between MPB and its host trees.

Our model allows two operating modes: *incipient* or *outbreak*. In the outbreak mode, attacking brood adults lay eggs in successfully attacked trees, and their progeny are allowed to produce successive generations. Only in the first year is an input initial attack pattern provided; subsequent timing and intensity of attacks are determined by the timing of brood adult emergence. This can lead to overlapping generations (e.g., when the semivoltine descendents of year $n-1$ and univoltine descendents of year n overlap to attack trees in year $n+1$). As in a real-world outbreak, very rapidly so many beetle objects are available that brood trees are overwhelmed almost with impunity as only a small proportion of attacks are warded off by tree defenses. In incipient mode, new attacks in a single focus tree are initiated each year, and the number of successful attacks generated by the progeny of this initial attack in the subsequent year or two (depending on voltinism) is recorded. Thus, each initial attack is allowed only a single generation. The incipient mode thus describes the process whereby an incipient population subsists on limited, ephemeral resources, and is unable to develop to the outbreak phase by mass attacking new hosts. This mode predicts the circumstances under which incipient populations can become outbreak populations, while the outbreak mode describes the effect of temperature on the natural course of an outbreak. In both cases, population growth rate (R) is expressed as the ratio of successful attacks in successive years or generations.

6.3.1 Objects

This IBM is nonspatial, in the sense that trees and insects do not have specific locations in space, and movement is assumed to occur throughout (and only within) the modeled forest. The model contains four kinds of objects: a forest, two kinds of host trees, and beetles.

The forest is a "container object" that tracks the number and states of tree and beetle individuals. The forest has a total size, F_s (km^2), with tree density F_d (trees km^{-2}) used solely to determine the number of available host trees. There are two types of trees: focus and brood, all the same size, differing only in their defensive capability. An area, F_0 (km^2), of forest containing defenseless focus trees receives initial beetle attacks. Brood trees are attacked by adults emerging from these focus trees, and from previously attacked brood trees. Brood trees can ward off attacks at a constant daily rate of a_0 (beetles m^{-2} of bark per day), and support a maximum number of attacks $a_{\max}$ (beetles m^{-2} of bark), reflecting maximum colonization density of individual trees. Brood trees whose defense capacity (a_0) is exceeded are killed, and their numbers F_k accumulate F_k over time t (years). Insect objects are contained either in focus or brood trees. In this model, only females are modeled. In MPB, sex ratio varies systematically over the course of an outbreak (Amman and Cole 1983). While this would be an interesting parameter to explore because of possible sex-differential mortality and maternal choice of sex ratios, we chose to use a constant 60 % female sex ratio to create female eggs.

Each insect object is distinct in three characteristics, expressed relative to the population mean: eight uncorrelated stage-specific development rates, potential fecundity, and larval cold tolerance. Individuals develop, reproduce, and survive independent of one another, except when the newly emerged adults attack new hosts. At that time, the number of adults attacking on a given day determines the probability of survival given host tree defenses. Because the number of individual beetles becomes very large, especially when the model runs in outbreak mode, a "super-individual" approach (Scheffer et al. 1995) is used in which beetle objects represent several individuals with the same characteristics (development rates, age, potential, and realized fecundity).

6.3.2 Development, Reproduction, Variability

Descriptions of MPB thermal responses in development and oviposition were taken from Régnière et al. (2012b). Development and oviposition are simulated by a unimodal rate equation with a distinct set of parameters for each life stage and for egg laying. At creation, each individual is assigned relative development rates in each of the seven life stages and relative fecundity, represented by eight random numbers that are drawn from lognormal distributions with means of 1. Development in successive life stages and oviposition are summed at each time step (4 h). Individuals change stages when their physiological age (starting at 0 for eggs) reaches a new unit (1: instar 1, 2: instar 2, 3: instar 3, 4: instar 4; 5: pupae, 6: teneral (unemerged) adult, 7: ovipositing adult) with two exceptions. Teneral adult emergence can be delayed without further aging if temperature remains below an emergence threshold, $T_e = 18$ ℃ (Safranyik and Carroll 2006). Adults emerging on any given day collectively attack new trees and become ovipositing adults. Ovipositing adults die once they have laid 95 % of their potential fecundity (average 82 eggs/female), which simulates old age mortality.

6.3.3 *Survival*

A constant "attrition" rate *s*, representing all mortality not specifically described, is applied at the creation of new eggs. The main cause of dynamic mortality in the model is exposure to cold. All eggs, pupae, and teneral adults are assumed to be killed as soon as temperature drops below −18 ℃. Larval cold tolerance is modeled following Régnière and Bentz (2007). The probability distribution of cold tolerance is a population trait that varies over time in response to temperature. The proportion of the larval population in one of three states, each with its SCP distribution, is calculated from the daily series of minimum/maximum temperatures. A composite distribution of SCP is compiled each day. Probability of cold mortality is based on this distribution and daily minimum temperature. The maximum mortality rate experienced by larvae is applied to each super-individual at the end of larval development.

In ovipositing adults, cold tolerance varies seasonally and is modeled in relation to time of year, independent of temperature. For this purpose we fitted a cosine function of calendar date to the observations of Lester and Irwin (2012, their Fig. 5a; $\mathrm{SCP}_a = -20.2 - 6.09 \cos\left[2\pi\left(t/365\right)^{1.365}\right]$; $R^2 = 0.946$). Adults exposed to a temperature $\leq \mathrm{SCP}_a$ die immediately.

6.3.4 *Attack*

The beetle population is initialized using a Gaussian distribution of attacks over time on the forest's defenseless focus trees. Mean date (t_0) and standard deviation (σ_0) of the initial attacks are specified as inputs. The number of females per m^2 of bark in this initial attack is $n_0 + a_{\max}(F_0 \times F_d - 1)$, so that when a single focus tree ($F_0 = 1/F_d$) is used, the model simulates an incipient outbreak with an initial density of n_0 females m^{-2} of bark. Females in the initial attack lay eggs, generating the brood adults that will attack new host trees at emergence.

When an adult emerges from a tree, it joins the day's collection of emerging adults (n_e) that generate that day's new attack on surviving host trees in the stand. All successfully attacked trees are killed. To limit population growth, a proportion

S_l of emerging beetles succeeds at finding live hosts to attack while the remainder is lost. This loss is a function of the proportion of the trees in the forest that have already been attacked and killed:

$$S_l = 1 - \left(\frac{F_k}{F_s \times F_d}\right)^{\alpha} \tag{6.1}$$

where F_k is the number of trees in the forest that have already been attacked, and $F_s \times F_d$ is the total number of trees in the forest. The exponent $\alpha \geq 1$ specifies how rapidly resource depletion inhibits host encounter. We use $S_l = 40$, large enough so that the effect of resource exhaustion occurs abruptly as tree mortality approaches 100 %. Thus, in the simulations produced here, α is used only to produce a sudden limit to growth.

Total emerging adults attacking new hosts is $n_a = S_l n_e$. Our model assumes that beetles are perfect host finders, consistently aggregating on available hosts and reaching maximum attack density on those trees before switching. The number of trees attacked is determined by:

$$F_a = \max\left(1, \frac{n_a}{a_{\max}}\right) \tag{6.2}$$

The daily number of attacking beetles killed by tree defenses is

$$A = a_0 F_a \tag{6.3}$$

In an incipient outbreak, where beetles emerge from a single focus tree, the proportion of attacking beetles killed by host defenses can be fairly high, as A can easily exceed n_a on any given day. But once F_a becomes large enough in a developing outbreak, survival from host defenses S_h is determined solely by the ratio $a_0/a_{\max}$.

6.4 Calibration/Validation

6.4.1 Seasonality of Adult Emergence

We compared output of our model with field observations to verify that the seasonality it predicted was close to reality. Beetle development time and associated phloem temperatures were monitored in the field at a range of latitudes and elevations (Fig. 6.1; Bentz et al. 2014). Beetle attacks and the subsequent emergence of brood adults were monitored on individual host trees every 1–4 days during the entire attack period. Hourly phloem temperature records were obtained from the north and south aspects of tree boles, just under the outer bark, 1.8 m above ground. Hourly mean air temperature was recorded at each site. These measurements were made continuously from initiation of attacks to adult emergence 1 or 2 years later.

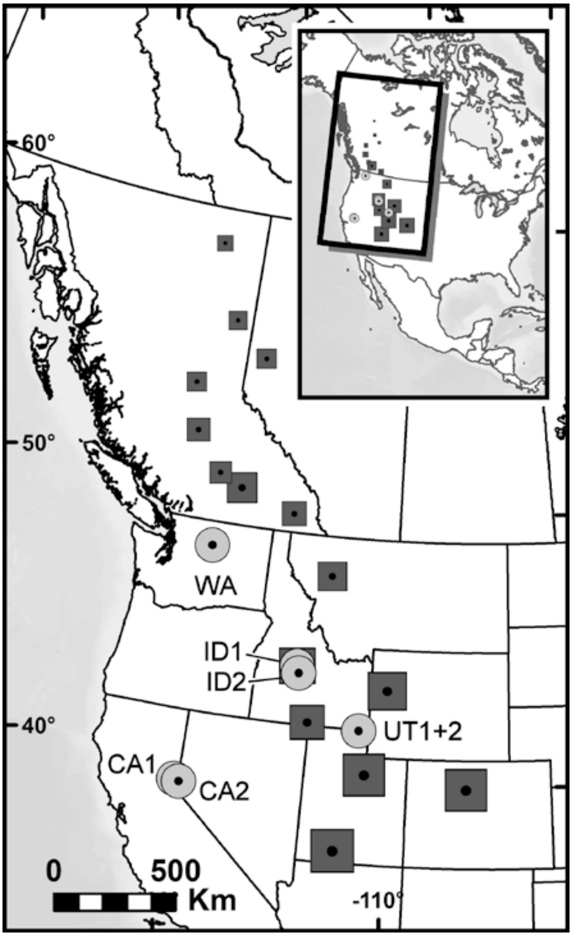

Fig. 6.1 Map of western North America illustrating sampling locations for validation of adult emergence phenology (*circles*, Table 2; Bentz et al. 2014) and simulation of population growth rates between 1950 and 2012 (*squares*, sizes proportional to elevation)

Our model requires as input daily minimum and maximum temperatures, and these were extracted from the observed hourly temperature records. We calculated bark temperatures by averaging north- and south-aspect daily minimum and maximum observations and developed a phloem microclimate filter to transform daily minimum and maximum air temperature (T_n, T_x) into phloem temperature (T'_n, T'_x). Because phloem temperatures are not usually available, and air temperatures modified with the microclimate filter will be used in model application, we present model test results obtained with this input, except when otherwise mentioned. For each set of MPB attack and emergence observations (i.e., location and year), the attack data were summarized by calculating the mean and standard deviation of attack dates, used as model inputs. The model interpolates between successive minima and maxima and runs on a 4-hr time step (Allen 1976).

The dates when 10, 50, and 90 % emergence were observed in the field were compared to model-predicted dates. Because an IBM is inherently stochastic, each simulation was replicated 30 times and results averaged. The dates predicted by the model, using the published parameters for development rates, variability, and fecundity (Régnière et al. 2012b), were well-correlated with observations ($r = 0.87$), but the model predicted events an average of 12.0 days later than observed, and the observed–predicted regression line had a slope of 0.76 (significantly less than 1; Fig. 6.2a). Based on these results, we made two modifications to the model. To restrict the duration of the oviposition period, the total number of eggs laid was limited to 50 % of individuals' potential fecundity, set to $\bar{E}_0 = 82$ eggs per female (Régnière et al. 2012b). This reduction was obtained by trial and error, and may reflect adult mortality not otherwise explicitly considered in the model. To better represent the observed variability of the adult emergence period, we also reduced the variability of development rates of all immature stages by half, again by trial and error. It is quite possible that the methods used to determine insect development rates under laboratory conditions (see Régnière et al. 2012b) exaggerated their normal variability. These changes increased the observed–predicted correlation ($r = 0.94$), made the bias nonsignificant (average 1.2 days), and increased the observed–predicted regression slope to 0.8 (still significantly less than 1). Given the input initial attack patterns (left column of Fig. 6.3) and observed air temperatures modified for bark microclimate, modeled

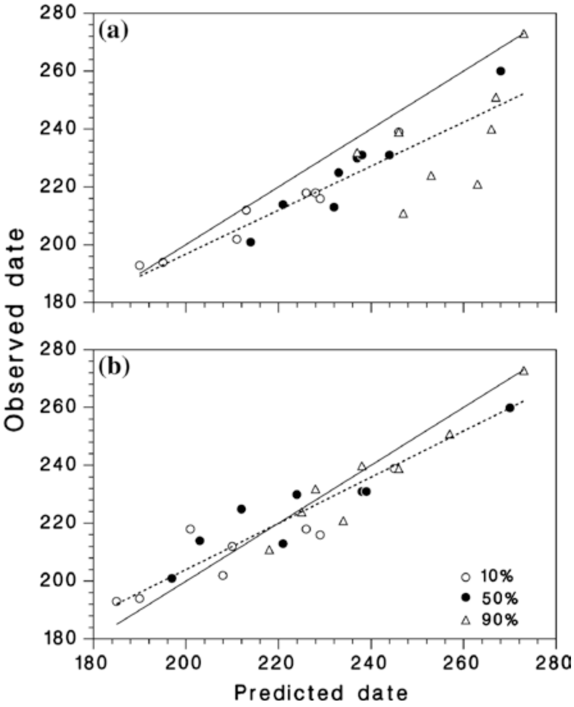

Fig. 6.2 Relationship between observed and simulated dates of 10, 50, and 90 % cumulative emergence of univoltine adults in 8 site-years in the western United States between 2002 and 2012. **a** Unmodified model; **b** modified model; parameters that describe fecundity and development time variance were altered. *Solid lines* equality; *dotted lines* regression

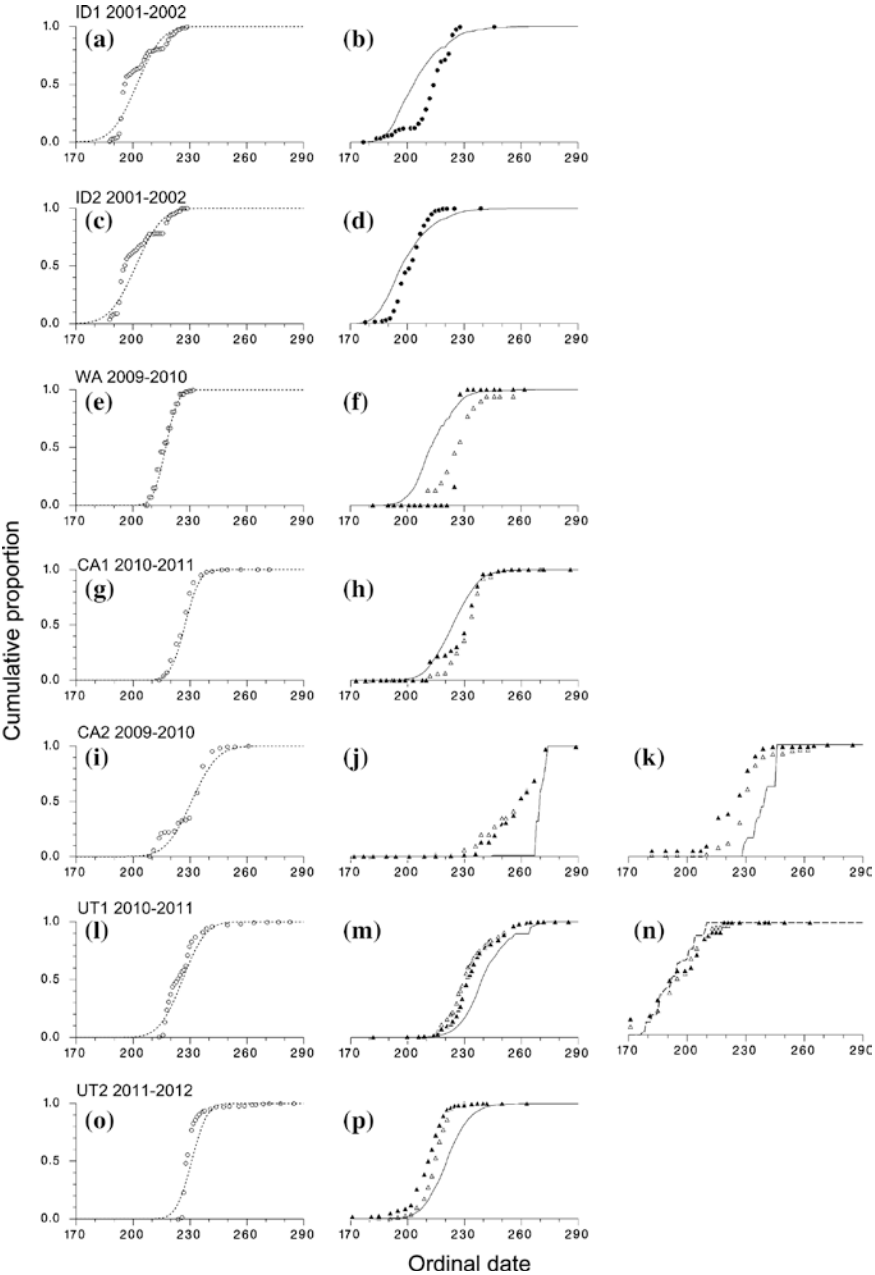

Fig. 6.3 Comparison of observed and simulated mountain pine beetle emergence in seven locations and years. The figure is divided in three columns. On the left are the observed (*white circle*) and Gaussian (*dotted line*) attack patterns (model input) for each plot-year. In the center are the observed (*black circle* all orientations; *black triangle* south bole; *white triangle* north bole) and simulated (*dash line*) univoltine adult emergence patterns in the following summer. On the right, in the case of sites CA2 and UT1, are semivoltine adult emergence patterns 2 years after the initial attack. The dashed line in the right panel for UT1 was generated using north bole temperatures as model input

univoltine adult emergence patterns generally agree well with observations (center and right columns in Fig. 6.3), although emergence timing of semivoltine adults was less accurate (Fig. 6.3k). The need to reduce developmental variability and oviposition period to obtain a better fit with field observations suggests that important development and mortality processes may be missing in our model. Nevertheless, observed and simulated development times ranged from 400 to 800 days; a precision of <15 days over such a long simulation period is sufficient to predict climate impacts on MPB seasonality and performance.

6.4.2 *Fitting to Observed Annual Growth Rates*

Estimates of observed MPB outbreak growth rates obtained from aerial detection surveys conducted by United States Forest Service for the Sawtooth National Recreation Area (SNRA), Idaho, were described in Powell and Bentz (2009). We collected MPB-infested tree phloem and air temperature data at multiple sites between 18 July 1992 and 15 October 2004, using the methods described in Sect. 6.4.1, from four sites in the SNRA, forming a continuous thermal record of daily minimum and maximum temperatures. Assuming that the density of trees is relatively constant, the area growth rate (calculated as the ratio of area affected in year $n + 1$/area affected in year n) approximates the growth rate in number of MPB-infested trees.

Additional daily minimum and maximum air temperature data for the period lacking phloem temperature observations between 1986 and 2010 were obtained from the nearest weather stations in the National Climatic Data Center daily observations databases, using the distance-weighted averaging and thermal gradient approach of BioSIM (Régnière et al. 2014). These records were then transformed with a multiple regression relating daily air temperature minima and maxima to observed 1992 phloem temperatures:

$$\begin{aligned} T_n' &= 2.55 + 1.00T_n + 0.298(T_x - T_n) \\ T_x' &= 1.88 + 1.04T_x + 0.080(T_x - T_n) \end{aligned} \tag{6.4}$$

This provided a means to complete our time series of daily minimum and maximum phloem temperature to cover the period 1986–2010.

Using this daily minimum and maximum phloem temperature time series as input, the model was run in outbreak mode, using a simulated annealing algorithm to estimate the value of the attrition survival parameter ($s = 0.43$) and initial infestation size in 1986 ($F_0 = 0.03$ km^2) on the basis of minimum sum of squared deviations between observed and simulated total forest area killed over time. Other parameter values were fixed ($F_s = 2800$ km^2; $F_d = 75{,}000$ trees km^{-2}; $a_0 = 5$ attacks day^{-1} m^{-2}; $a_{\max} = 120$ attacks m^{-2}; $T_e = 18$ °C; $N_0 = 60$ attacks; $t_0 = 200$, $\sigma_0 = 5$ days, and $\alpha = 40$).

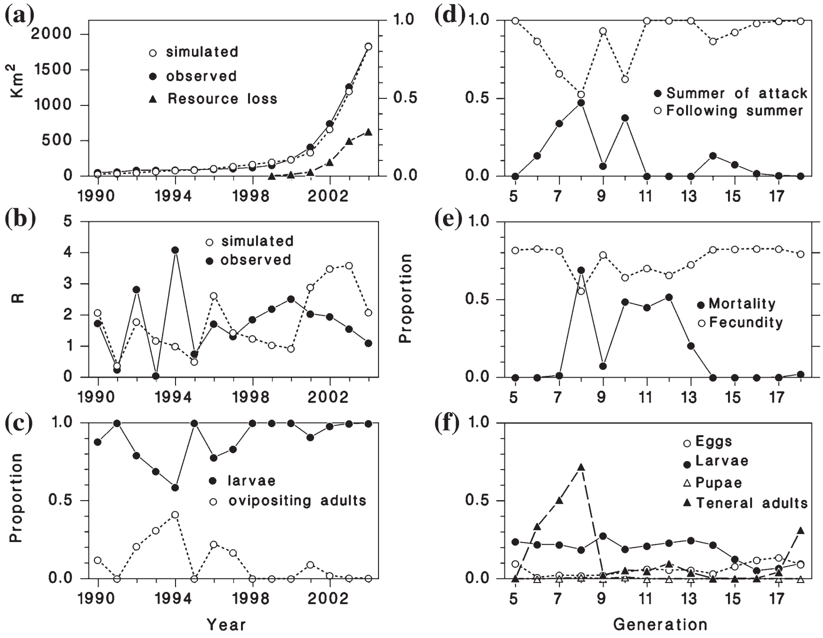

Fig. 6.4 Observed (*white circle*) and simulated (*black circle*). **a** Infestation size (also, value of survival from resource-loss S_l *black triangle*); **b** annual infestation growth rates; **c** proportion of overwintering individuals in larval stages (*black circle*) or as ovipositing adults (*white circle*); **d** proportion of adults emerging in the year of attack (*black circle*) or in the following year (*white circle*); **e** winter mortality rate of ovipositing adults (*black circle*) and average realized fecundity (*white circle*); **f** winter mortality of immature stages (eggs: *white circle*; larvae: *black circle*; pupae: *white triangle*; teneral adults: *black triangle*). Year is the year of attack. Generation 5 was produced in 1990, with univoltine adults emerging in 1991

The resulting predicted and observed cumulative forest mortality (km^2) were highly correlated ($r = 0.997$; Fig. 6.4a). The annual outbreak area growth rates (Fig. 6.4b), however, were not significantly correlated with the simulated annual growth rates of successful attacks ($r = 0.12$, $P = 0.67$; Fig. 6.4b), although average observed (1.733 ± 1.014) and simulated (1.757 ± 1.006) growth rates were nearly identical ($P = 0.95$). The model is set up to assume an exact correspondence between the number of successful MPB attacks and tree mortality because the density of successful attacks per tree is constant, all trees are equally likely to be attacked and killed, and there is no spatial variation in tree density. In nature, none of these are constant, and deviations between beetle population performance and tree mortality rates may vary accordingly. Growth rates were significantly reduced by resource-loss in the last 2 years of the simulated outbreak through Eq. (6.1), as the total area killed (F_k) approached total forest size, estimated here at $F_s = 2800$ km^2 (black triangle line in Fig. 6.4a). Model results indicate that most individuals in the SNRA during the study period spent winter as larvae (Fig. 6.4c).

Years with a large proportion of individuals spending winter as ovipositing adults corresponded to those with a higher proportion of individuals emerging as adults in the same summer as they were oviposited (Fig. 6.4d; $r = .86$). Winter mortality among overwintering adults was the main source of variation in realized fecundity (Fig. 6.4e; $r = -0.96$). Winter mortality of eggs and pupae was very low (Fig. 6.4f) because very few individuals were predicted to spend winter in those stages. Larval winter mortality averaged only 20 %, but mortality in the teneral adult stage was highly variable, with high mortality rates associated with years when a high proportion of individuals reached the ovipositing adult stage in the summer of attack ($r = 0.66$), as many individuals were unable to emerge prior to winter. Because in these simulations the initial population was already in outbreak mode (0.03 $\text{km}^2 \times 75{,}000$ trees $\text{km}^{-2} = 2250$ trees), the number of MPB attacking was well beyond a tree's defensive capacity, and the proportion of attacks warded off by trees is near constant at 4 % ($a_0/a_{max} = 5/120$).

6.5 Model Behavior

6.5.1 Seasonality and Elevation

We ran the model at three elevations near Jasper, Alberta, where MPB is well established: one point at Jasper (1062 m), two at the same latitude and longitude but at fictional elevations: low (400 m) and high (1500 m). Actual weather observations for the period 2007–2010 were used as input. The nearest Environment Canada weather station was chosen for each simulation point using BioSIM (Régnière et al. 2014), compensating for differences in coordinates with regional latitude, longitude, and elevation thermal gradients.

We ran the model in incipient mode using (1) 60 females/m^2 in the initial attack, with $t_0 = 200$ (17 July) and $\sigma_0 = 5$, (2) attrition survival $s = 1$, and (3) adult emergence threshold $T_e = 18$ ℃. Two different simulations were run: (a) no winter mortality and (b) winter mortality in all life stages. The distribution of life stages and adult emergence over time resulting from these simulations are illustrated in Fig. 6.5.

At the fictional low elevation site, ignoring winter mortality, a very small proportion of adults emerged in October of the initial attack year. The majority of brood adults emerged the following summer (i.e., univoltine). Some individuals developed to the teneral adult stage prior to winter, and the predicted emergence of these individuals was as early as April when temperatures exceeded 18 ℃. However, most individuals spent the winter in the larval and pupal stages and emerged in July. When cold mortality was applied, overwintering eggs, pupae, and teneral adults were killed, along with a portion of overwintering larvae. As a result of this mortality, the relative importance of the first summer's late (October) flight was inflated. As none of the eggs laid by those late-summer attackers would have survived winter, their contribution to the population would be null. Mortality of

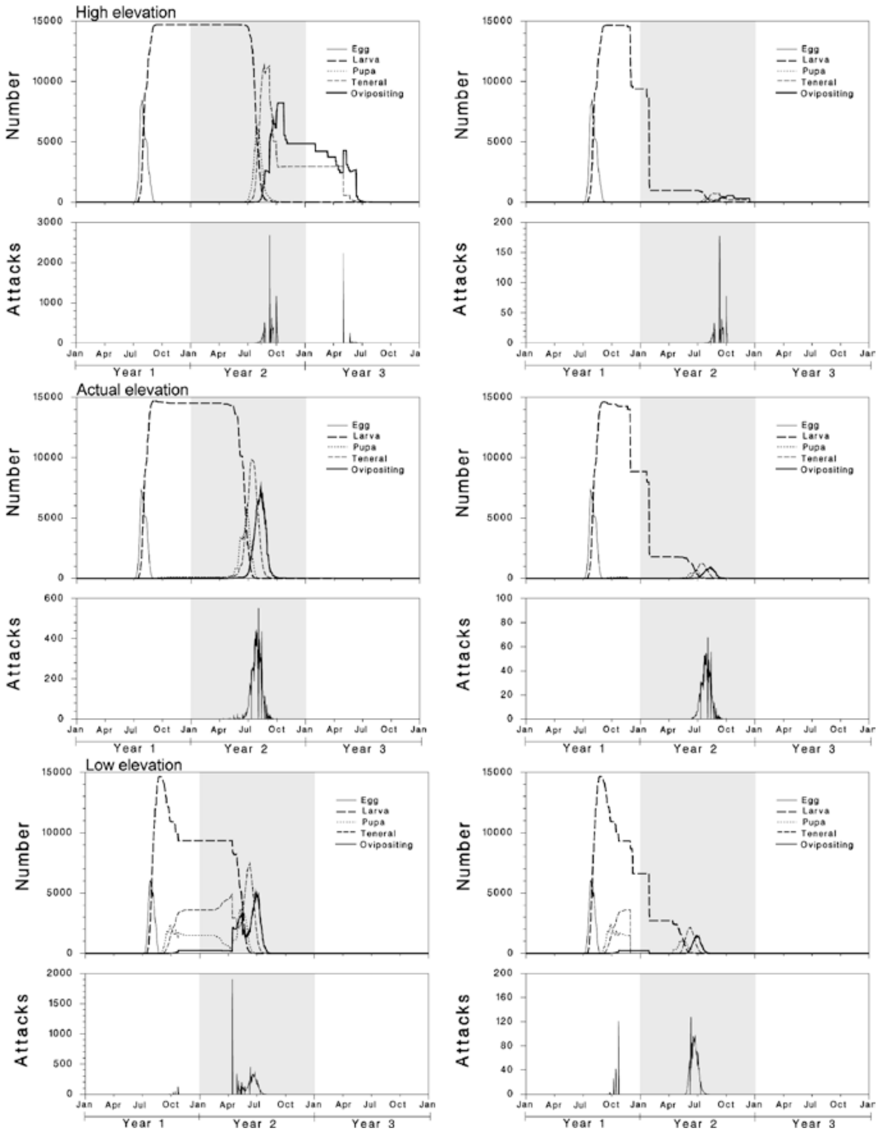

Fig. 6.5 Predicted life stage frequencies and attack timing following a Gaussian initial attack centered on July 17 (day 200 ± 5 days). Temperature was estimated for three elevations at the latitude and longitude of Jasper, Alberta, Canada (52.88°N, −118.07°E): 1500 m (*top row* of 4 panels), 1062 m (actual elevation, *center row*) and 400 m (*bottom row*). *Left column*: simulations with no winter mortality. *Right column*: winter mortality in all life stages

pupae and teneral adults also eliminated the brood adults that would have emerged in early spring, leaving only the individuals that spent winter in the larval stages to contribute to the next summer's brood adult flight in June and July.

At the middle elevation (actual elevation of Jasper), all individuals spent winter as larvae, mostly in the 4th instar. Brood adult emergence occurred in July of the following summer (univoltine). Mortality due to cold did not change the timing of adult emergence, although the total number of emerging brood adults was reduced. At the highest elevation, the population also overwintered as larvae, and a high proportion of individuals emerged in August to October of the following year (univoltine). The remaining individuals spent the second winter as teneral adults and emerged 2 years after the initial attack (semivoltine). Many of the univoltine adults would have overwintered as ovipositing adults. When cold-induced mortality is added, teneral adults are predicted to die during the second winter, resulting in emergence of univoltine beetles only.

These simulations illustrate important consequences of climate on MPB dynamics. First, at low elevation locations where summer development is accelerated, but with sufficient cold to kill the most sensitive life stages, brood adults emerging in late summer of the year of initial attack may not reproduce successfully due to mortality of eggs during winter. Ovipositing adults are also likely to be killed overwinter. Thus, warmer climates can lead to lower overall population fitness as a result of poor synchrony between winter cold and the most cold-hardy life stages (larvae). However, in still warmer conditions where winters are not cold, this effect would disappear. In colder climates with slower summer development and a mix of univoltine and semivoltine beetles, winter mortality in the teneral and ovipositing adult stages can also result in high mortality during the second winter. These results confirm previous research suggesting that climates leading to well-synchronized, strictly univoltine phenology are the most adaptive for the insect (Amman 1973; Safranyik 1978). As winter temperatures warm, however, complete univoltinism does not appear to be mandatory for population growth as long as adult emergence remains synchronous (Bentz et al. 2014).

6.5.2 Latitudinal Gradient

We ran the model over the period 1951–2010 at 15 locations along a latitudinal gradient within the geographical range of lodgepole pine (*P. contorta*), between Strawberry Point, Utah, USA (37.45°N, −112.34°E, 2695 m) and Fort Nelson, British Columbia (58.78°N, −122.73¨E, 395 m). There was a strong negative correlation between elevation and latitude among the sites ($r = -0.90$; squares, Fig. 6.1). The model was run in incipient as well as outbreak mode. Weather inputs were provided by BioSIM, from the two daily NCDC weather stations nearest to each simulation point, compensating for differences in latitude, longitude, and elevation with local thermal gradients derived from several nearest normals-generating weather stations. We provided the same Gaussian initial attack pattern (mean: 17 July, standard deviation: 5 days) as input. Each simulation was replicated 30 times and results were averaged to reduce stochastic effects. General

Linear Models were used to relate several key output variables (single-generation population growth rates R, winter survival S_w, voltinism, fecundity, and attacking adult survival from host defenses S_h) to year, latitude L, and elevation E. For this analysis, latitude and elevation were combined into a single variable that we called "effective latitude" ($L_E = L + k$E) where k transforms elevation into degrees latitude. The value of k was chosen to maximize the correlation between average growth rate and L_E (1°N per 165 m elevation). This value is similar to that estimated by Bentz et al. (2014) using degree hours >15 ℃ required for completion of a generation.

Simulated growth rates increased significantly between the 1950–1959 and 2010–2012 time periods. In both incipient and outbreak modes, effective latitude negatively affected growth rates, and the increase of population growth rates through time was most pronounced at the highest effective latitudes (time × latitude interactions highly significant in both modes; Fig. 6.6a, f). Winter survival also increased significantly over time and decreased significantly with effective latitude (Fig. 6.6b, g). However, no significant interaction was apparent between effective latitude and time period in either incipient or outbreak mode in the effect on winter survival. These effects were identical in incipient and outbreak modes. Year, effective latitude, and their interaction also significantly affected voltinism in the two simulation modes (Fig. 6.6c, h). These results suggest that MPB populations across the 15 sites in this latitudinal/elevational gradient have been mostly univoltine, and increasingly so over the period 1950–2012. This strong tendency to univoltinism reflects the choice of our simulation locations, all situated within the main distribution of lodgepole pine. The exceptions to univoltinism occurred mostly between 1950 and 1980, with 30 % of adults emerging in less than a year in Cassia, Idaho, USA (42.1°N, −114.1°E, 1965 m), and 20 % as semivoltine in Vernon, British Columbia (50.35°N, −119.11°E, 1452 m). Realized fecundity did not change significantly over the simulation period, but dropped significantly with effective latitude (Fig. 6.6d, i).

Fecundity was more variable in incipient mode, probably as a result of the smaller number of adults surviving host defenses (Fig. 6.6e, j). In incipient mode, this factor increased significantly over time and declined with effective latitude, with a significant interaction. However, as expected, outbreak-mode survival from host defenses was very high and essentially constant. To summarize these results, a regression model using log S_w (winter survival), and log S_h (attacking adult survival from host defenses) as predictors explained 98.6 % of the variation in log R between years, locations, and simulation modes.

The modeled changes in MPB survival and recruitment rates over time and space described here were caused by corresponding changes in observed thermal regimes, in particular extreme minimum and mean annual temperatures (Fig. 6.6k, l), and to a lesser extent mean maximum temperatures (Fig. 6.6m). There was also a slight increase in precipitation over the years (Fig. 6.6n), but because of a gradual increase in mean annual temperature this did not translate to a change of aridity, calculated as the annual sum of monthly differences between potential evapotranspiration and precipitation (Fig. 6.6o).

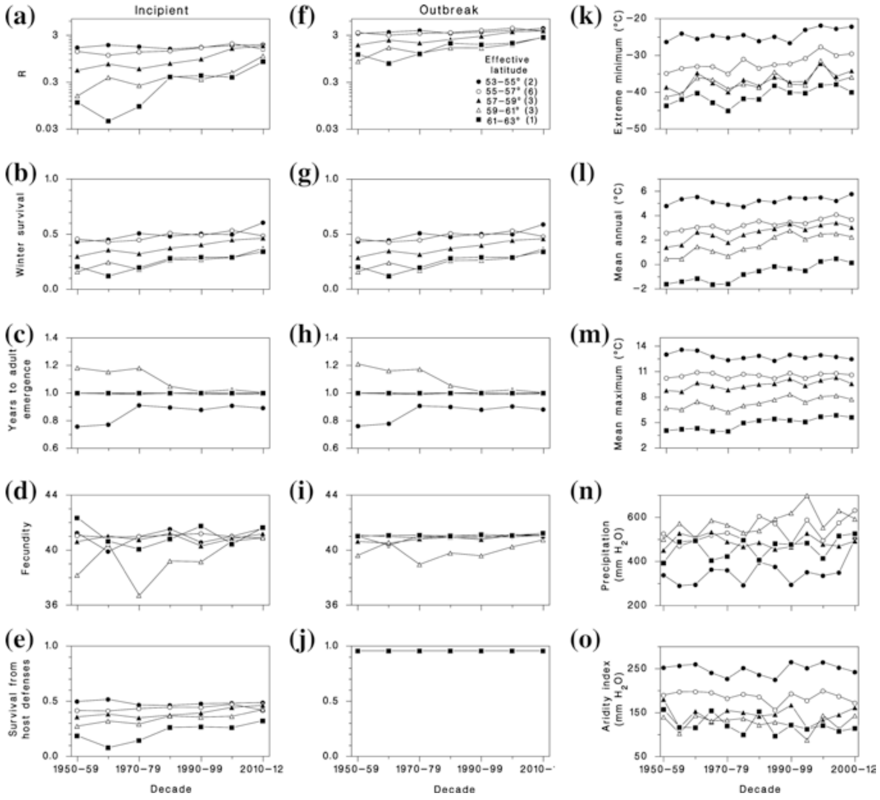

Fig. 6.6 Decadal average model inputs and outputs in incipient and outbreak modes for an array of 15 locations in western North America over the period 1951–2012. Sites grouped into five effective latitude classes of 2° (number of sites per class in parentheses). *Left column* incipient mode. *Center column* outbreak mode. *Right column* weather statistics. **a**, **f** Generation growth rate; **b**, **g** winter survival (all stages); **c**, **h** mean number of years to complete a generation (development in 1 year is univoltine); **d**, **i** realized fecundity; **e**, **j** survival from host defenses; **k** extreme annual minimum, **l** mean annual and **m** mean maximum air temperature; **n** annual precipitation; and **o** aridity index

6.6 Climate Change

Simulated past and future (1961–2100) daily minimum and maximum temperatures on a 201 × 193 grid over North America were obtained from the Canadian Regional Climate Model (CRCM) version 4.2.0 runs ADJ and ADL (Music and Caya 2007). These runs are based on the Intergovernmental Panel on Climate Change (IPCC) A2 emissions scenario (IPCC 2007), which has been realistic thus far given actual emissions estimates (Raupach et al. 2007). The IPCC A2 is intermediate between Representative Concentration Pathway RCP6 and RPC8.5 scenarios (IPCC 2013).

From these data, 30-year normals were computed for several decades in the interval 1961–2050, and the “delta” method (differences between modeled decadal normals and the reference 1981–2000) was used to generate unbiased decadal sets of 30-year normals into the future. We used as model input 10 years of observed daily minimum and maximum temperatures for the decades 1961–1970, 1981–1990, 2001–2010, and 10 years of daily values generated stochastically from climate-changed normals (Régnière and St-Amant 2007) for decades 2021–2030 (normals 2011–2040) and 2041–2050 (normals 2031–2060).

Two sets of model output maps were prepared, one for western North America, and one for the whole continent, north of Mexico. The model was run in incipient and outbreak modes for 10,000 simulation points located randomly across western North America, and 30,000 points across the whole of North America north of Mexico, with increased point density in mountainous areas. Elevations were obtained from digital elevation models (DEM) at 30 arc-second resolution obtained from Shuttle Radar Topography Mission SRTM 30 (http://dds.cr.usgs.gov/srtm/version2_1/SRTM30/; Accessed 6 January 2015). Because of the stochastic nature of the model and of weather inputs when generated from normals, each model run was replicated 10 times, and model output was averaged over replicates and years. From these averaged outputs, maps were generated by universal kriging with elevation provided by the input DEM as external drift variable. Log population growth rates were used for interpolation. Model output was masked using polygons that estimate the twentieth century distributions of pine habitat in the United States and Canada (all *Pinus* species mapped by Little 1971; refer to United States Geological Survey 1999).

Predicted MPB population growth rates over the distribution of western pine species increased considerably in every decade between 1961–1970 and 2001–2010, and are predicted to continue increasing under climate change (Fig. 6.7). Over the historical period (1961–1970 to 2001–2010), these changes coincided with changes in the thermal regime (Fig. 6.6). The maps suggest that numerous forested areas, particularly in south-central British Columbia, coastal regions and low latitudes and elevations in the United States, have historically had high probability of MPB outbreak development. Periodic MPB outbreaks have been observed in these areas (Preisler et al. 2012). However, factors other than temperature that are not accounted for in our model affect MPB population dynamics. These include stand density, host tree age and size (Fettig et al. 2007), and moisture conditions that can influence fungal symbionts (Rice et al. 2007), tree defense capacity, and phloem drying. The latter factor is a major cause of mortality among MPB immature stages (Cole 1981; Safranyik and Carroll 2006). Along our latitudinal gradient, annual precipitation (Fig. 6.6n) and mean temperature combined to generate a strong aridity gradient, undoubtedly a factor involved in limiting MPB population growth rates in the southern proportion of the insect’s range. Also, MPB developmental responses to temperature in the southwest United States differ from those in the northern part of the insect’s range (Bentz et al. 2011b) from which our model parameters were obtained. Therefore, model predictions are less reliable in these areas. Western pine forests at higher elevations in the United States and

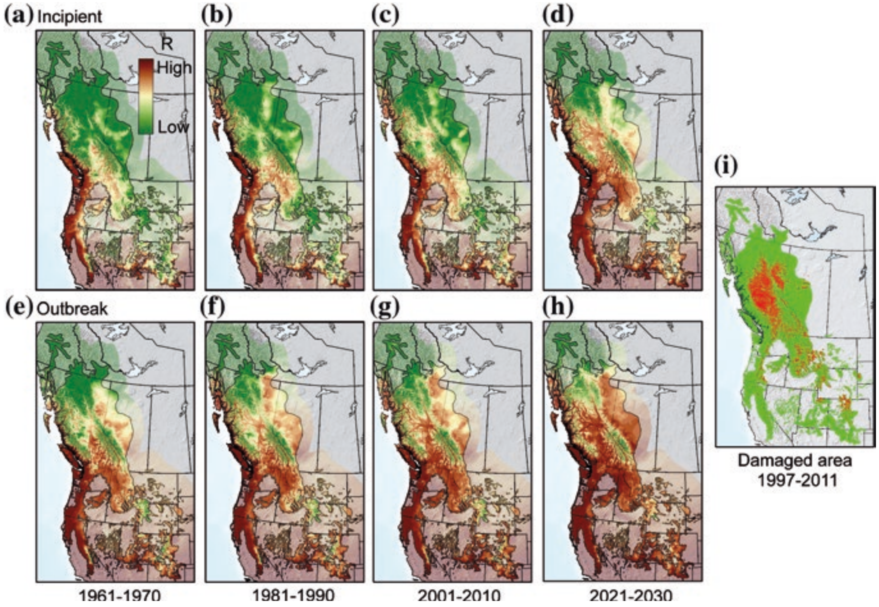

Fig. 6.7 Incipient (**a**–**d**) and outbreak (**e**–**h**) population growth rates during 1961–1970 (**a**, **e**), 1981–1990 (**b**, **f**), 2001–2010 (**c**, **g**), and expected in 2021–2030 (**d**, **h**). **i** Map overlaying areas affected by mountain pine beetle in western North America, 1997–2011 (*red*) on the twentieth century distribution of western pines not including jack pine (data compiled by G. Thandi, Natural Resources Canada, and provided by: BC Ministry of Forests, Alberta Environment and Sustainable Resource Development, USDA Forest Service, Natural Resources Canada). Western pine species distribution compiled from U.S. Geological Survey 1999

Canada, and at higher latitudes in British Columbia and Alberta historically had a low probability of MPB outbreaks. These areas are predicted to become increasingly suitable to MPB with climate change. Many of these areas are currently experiencing widespread MPB outbreaks (Safranyik et al. 2010; Meddens et al. 2012; Fig. 6.7i), and the climate change scenario maps (Fig. 6.7d, h) show that this trend can be expected to continue, with increasing risk in the Yukon, Northwest Territories, and Alberta.

In 2006, MPB populations were observed infesting jack pine in central Alberta (Cullingham et al. 2011). This population expansion was aided by long-distance dispersal of beetles from epidemic populations west of the Rocky Mountains (de la Giroday et al. 2012), and possibly by high reproductive success in naïve hosts (Cudmore et al. 2010). The current distribution of MPB-caused tree mortality in Alberta (Fig. 6.7i) corresponds well with predicted population growth rates in outbreak mode, for the period 2001–2010 (Fig. 6.7g). By the middle of this century, predicted population growth rates will be moderate to high in most of Alberta, although moderate to low in the northern and eastern Canadian Provinces where it is actually predicted to decline slightly in the future. These results highlight

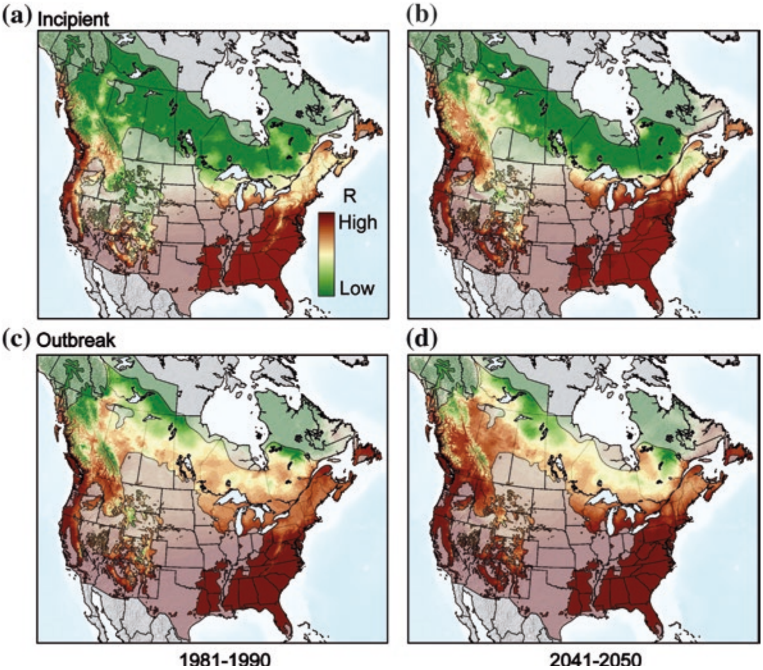

Fig. 6.8 Incipient (**a**, **b**) and outbreak (**c**, **d**) MPB population growth rates during 1981–1990 and expected in 2041–2050 in North America north of Mexico. Model output is masked with the twentieth century distribution of all pine species (U.S. Geological Survey 1999)

the differential effect of temperature on MPB cold tolerance and population synchrony. Increasing minimum temperatures may result in higher overwinter survival, but univoltinism will be disrupted when temperatures are too warm (Bentz et al. 2010; Sambaraju et al. 2012; Bentz and Powell 2014). MPB outbreak potential and population growth is also influenced by stand conditions, measured using indices of stand structure, volume, density and composition. Safranyik et al. (2010) found that stands east of Alberta generally have low suitability, and when combined with our model results suggest that future population growth across the boreal forest will be less than that recently observed in British Columbia.

Incipient model results indicate areas where thermal conditions are highly conducive to the transition between incipient and outbreak populations, although population growth is artificially halted in the model. By the middle of this century, model predictions suggest that thermal conditions in much of Alberta and northwestern British Columbia will become more suitable for transition from the incipient phase, without the need for large surrounding populations. The Canadian boreal forest and some high elevations areas in the western United States, however, will not necessarily be suitable for this transition (Fig. 6.8b), although if population growth is unconstrained due to other factors, populations will be moderately successful (Fig. 6.8d). Pine forests in the eastern United States are also predicted to have high population growth potential by the middle of this century. Suitability of eastern pines for MPB reproduction is unknown, however, and our process models of development and cold tolerance are not parameterized for these regions.

6.7 Modeling Conclusions

Our integrated model of phenology and cold tolerance provides a tool to evaluate climate influences on the invasiveness of MPB, a native insect limited in distribution by climate. Simulations illustrate important consequences of climate on MPB dynamics. When run across a latitudinal gradient, winter survival and the ability of adults to overcome host defenses, a consequence of developmental timing, explained 98.6 % of the variation in population growth between years, locations, and simulation modes. Winter survival and population growth rates increased significantly between 1950 and 2012, particularly at the highest effective latitudes. When run across an elevation gradient, thermal regimes that resulted in univoltinism and larval overwintering were optimal. Warm summers at the lowest elevation accelerated development, resulting in adult emergence the year of attack. Oviposition was late enough in the fall, however, that a high proportion of the life stages most sensitive to cold were killed during winter, emphasizing the low overall population fitness resulting from poor phenological synchrony between winter cold and the most cold-hardy life stages at warmer temperature. Using climate projections, simulations suggest that much of the central Canadian boreal forest fits this scenario. Future environmental suitability for population growth and expansion, as measured by the influence of temperature on MPB physiological processes, will lie between the relatively low suitability values predicted by the incipient mode simulations (where host tree defenses play a large role) and the higher values predicted in outbreak mode (where host defenses are negligible).

This prototype mechanistic model illustrates the importance of accounting for both cold mortality and life-stage-specific phenological details, in full interaction. This is a benefit of this IBM that an aggregated modeling approach could not have provided. We acknowledge gaps in our understanding of these processes, including cold tolerance of life stages other than larvae, and constraints on fecundity. Moreover, host tree abundance and connectivity that affect the beetle's host-finding and mass attack abilities, and important indirect effects of climate on host trees and MPB community associates, are not currently incorporated in the model.

The MPB has been migrating for the past 8000 years, following a northerly expansion of its host tree species. As temperature increased, expansion has been extraordinarily rapid in the past few decades, so rapid that no loss of genetic variability was detected in expanding populations (Samarasekera et al. 2012). Our model explains the role of weather in this expansion, and predicts that the pace of population growth in Alberta and northern British Columbia will continue to increase. Thermal conditions across the boreal forest into eastern Canada will not be as favorable for population growth. Adaptation in thermally dependent MPB life history traits to rapid warming could alter this prediction, and should be a high priority topic for future research. Moreover, IBMs provide an excellent framework for including adaptive potential. In addition to expansion north and east in Canada, MPB could extend its range south into pine forests of Mexico. The MPB is currently active in high elevation pine forests of southern Arizona. Genetic differences in developmental parameters between northern and southern populations (Bentz et al. 2011b; Bracewell et al. 2010), however, limit using the current model to predict MPB invasiveness in the south. Additional processes such as phloem drying in response to aridity (Cole 1981), and developmental parameters specific to southern MPB populations, will allow for a comprehensive tool to predict MPB invasiveness across the range of pines.

6.8 IBM as Generalized Modeling Approach for Insect Disturbance Modeling

An ongoing argument in ecological literature relates to the generality and utility of simple versus complex models. Evans et al. (2013) wrote "*Modellers of biological, ecological, and environmental systems cannot take for granted the maxim 'simple means general means good'. We argue here that viewing simple models as the main way to achieve generality may be an obstacle to the progress of ecological research. We show how complex models can be both desirable and general, and how simple and complex models can be linked together to produce broad-scale and predictive understanding of biological systems*". The data requirements of complex models also are a topic of controversy in the literature (e.g., Lonergan et al. 2014; Evans et al. 2014). We do not intend to answer these issues in detail here.

We believe that the choice of approach to model insect disturbance is dictated by several criteria: the objectives, the prediction precision and extent of specificity sought, the level of detail and specificity available in our understanding of a species' behavior, and the availability of data. While IBMs such as the one developed here may seem complex, they are in fact relatively simple because they make reference to few abstract concepts or theoretical constructs that can be very difficult to parameterize. They rely on adequate understanding of just what data are needed to capture the essential behavior we need to mimic of nature. As such they are data hungry, but only to the extent that the demands placed on their specificity and precision are high. In our individual-based modeling of the responses of the spruce budworm (*Choristoneura fumiferana* Clem.; Cooke and Régnière 1996; Régnière et al. 2012a), and its congener the western spruce budworm (*C. occidentalis*), to climate (Nealis and Régnière 2014), we used an amount of data very similar to that required for the present MPB IBM. As has been the case here, we achieved fairly high precision in predictions, as well as a good level of understanding of the fundamental interactions between positive and negative influences of climate in their ecology. But perhaps the greatest achievement of these models is that they allow us to identify areas where we do not know enough or where the most pressing data needs exist. They are also easy to expand to include new processes and behaviors, because of their object-oriented nature.

For most pests that have significant economic or ecological impact, basic data are available for the elaboration of IBMs. The great advantage of insect IBM is that their structure is generalizable. Descriptions of thermal responses (development of the various life stages, reproduction), of movement, of interactions between individuals in competition for resources, and other key processes are common to most species. The details (life history strategies, number of life stages, developmental parameters, the most influential factors) vary between species. The object-oriented programming paradigm underlying IBMs allows for re-use and straightforward modification of model structures.

But the IBM approach to disturbance ecology is far more broadly generalizable. Our model deals with individual insects and trees. In the same manner, a disturbance model can focus on forests as collections of individual stands, each with its specific traits (size, composition, age, damage level, treatment history, spatial location). In the end, no matter the modeling approach used, the requirements for detail and data are directly proportional to the specificity of the questions being asked, and the degree of precision required of the answers.

6.9 IBM as a Scaling Strategy for Insect Disturbance Modeling

The IBM approach used here provided a simple framework for integration across temporal and mechanistic scales. It allowed us to predict MPB population growth rates, which depend on extreme cold temperatures (at the hourly/daily scale), nonlinear developmental responses to temperature (at the weekly/monthly scale), effects of developmental variability (at the seasonal scale) and accumulation of population momentum to become a full outbreak (at the multi-yearly scale). Description of processes at the scale of individual beetles allowed us to model emergent properties at broader scales resulting from superposition of individuals, without pre-ordained or coerced aggregative effects.

Our IBM is nonspatial. It operates at the scale of a forest. Individual trees within the forest are represented however, and the model could therefore include tree-level effects such as individual host demography, stress history, and moisture availability. It may be possible to combine the developmental, survival, and reproductive processes included in our model with those describing the kairomonal interactions underlying the swarming behavior of adult MPB in another IBM developed by Perez and Dragicevik (2011). However, as pointed out by Powell and Bentz (2014), spatially explicit prediction at the tree scale is unrealistic. Data demands that would allow for accurate predictions from mechanistic models increase exponentially as the scale of prediction decreases. These data demands include a complete demography and stress status for all trees across a landscape, and microclimate variables that dictate the shape and directions of odor plumes from individual host trees. Assuming that pattern prediction at the tree scale is not required, the IBM approach provides an efficient way to assess the impact of host demography and stress on MPB outbreaks at stand scale.

At a broader scale, the IBM presented here could easily be adapted to include dispersal of MPB in a matrix of stands comprising a forest or landscape. The current limitation on numbers of successful attacks, Eq. (6.3), would need replacing, because it is the spatially implicit resolution of a spatially explicit process (searching for new hosts). The situation is analogous to the relationship between an earlier stand-level outbreak model (Powell and Bentz 2009) and a more recent spatially explicit outbreak model (Powell and Bentz 2014). Rather than predict a successful search probability within the stand using Eq. (6.3), MPB in a spatial model must be allowed to disperse from their source stands, whereupon their success in exceeding attack thresholds can be assessed.

The question of how to disperse beetles accurately is not straight forward. In a simple cellular automaton setting, a constant fraction of beetles can be allowed to move between adjacent cells. In fact, some large-scale regression approaches (e.g., Aukema et al. 2008) include the impact of nearby cells and could be used to parameterize a cellular dispersal model. A more complicated approach would be to disperse individual beetles in the IBM according to a dispersal kernel, as was parameterized by Heavilin and Powell (2008). Individual dispersal distances are generated as samples from the dispersal kernel, which allows for accurate resolution of dispersal independent of model structure. This differs from a cellular automaton, which inflicts its gridded structure on model results. A more nuanced dispersal approach is based on ecological diffusion (Powell and Bentz 2014) and includes the effects of available hosts, which serves to slow down beetle movement in some patches, and presence of non-host areas through which beetles disperse much more rapidly. Regardless of dispersal specifics, spatial waves of killed trees will progress from patch to patch as local susceptible hosts are exhausted and locally produced brood are exported to nearby cells. Exact rates of dispersal will depend on the precise details of the dispersal mechanism and density of susceptible host trees, similar to other epidemiology models (Heavilin et al. 2007).

At still larger scales, IBMs offer an opportunity for resolving unlikely dispersal events with potentially large consequences, as in the dispersal episode that led to MPB crossing the Rockies from British Columbia to Alberta (de la Giroday et al. 2012). In deterministic spatial modeling approaches it is very difficult to resolve a low-probability event such as long-distance dispersal via storm cells. In a deterministic model of outbreak progression, low-probability events would become small magnitude certainties driving unrealistically rapid outbreak propagation. However, in an IBM, low-probability events are resolved as infrequent samples of individuals. Low-probability events appear as tails in a distribution in deterministic models, but in an IBM low-probability events are samples of mostly zero. When an event that could trigger an outbreak occurs however, individual beetles could be dispersed realistically to distant locations, allowing an IBM to simulate continental-scale events.

The drawback of IBMs in space is the sheer computational scale of keeping track of individuals. IBMs lend themselves to parallel approaches, particularly for a system such as MPB where the critical effects of temperature on the population are all projected onto individuals independently, and relevant calculations can occur in parallel. However, continental landscapes involve millions of hosts that produce tens of thousands of beetles. Even with a "super-individual" approach, an overwhelming number of objects must be tracked. The continental-scale maps that we prepared here do not constitute a true scaling-up of the MPB outbreak process, as model runs were completely independent of one another from location to location. At least for the near future, explicit spatial modeling of MPB outbreaks with IBMs is likely to be restricted to forest scales.

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Chapter 7
Southern Pine Beetle Herbivory in the Southern United States: Moving from External Disturbance to Internal Process

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7.1 Introduction

The southern pine beetle (*Dendroctonus frontalis* Zimmermann; herein referred to as SPB) is the most destructive pest of pine forests in the southern United States (U.S.). To reproduce, adult SPBs must find, attack, and kill a suitable host tree (i.e., pine species; *Pinus* spp.). Across most of the beetle's range (Fig. 7.1), it kills trees grown for commercial timber, recreation, or other ecosystem services, placing SPB in direct conflict with those who manage the forests. The damage it causes occurs in large, unpredictable pulses in space and time. Most years, populations occur at low densities and are almost undetectable within a forest. Periodically, populations undergo rapid growth, leading to regional outbreaks. During outbreaks, spatially discrete aggregations of dead and infested trees occur across a broader forest landscape of healthy trees (Fig. 7.2). Regional outbreaks may last for several years before population densities return to endemic levels.

In the U.S., SPB damage is estimated to cost timber producers approximately $43 million per year (Pye et al. 2011). But SPB's unpredictability creates an added dimension to its pestilence. First, the periodic nature of outbreaks and the speed with which they develop, make it difficult to plan and mobilize resources for management. Second, the southeastern U.S. forest is managed by a mix of private

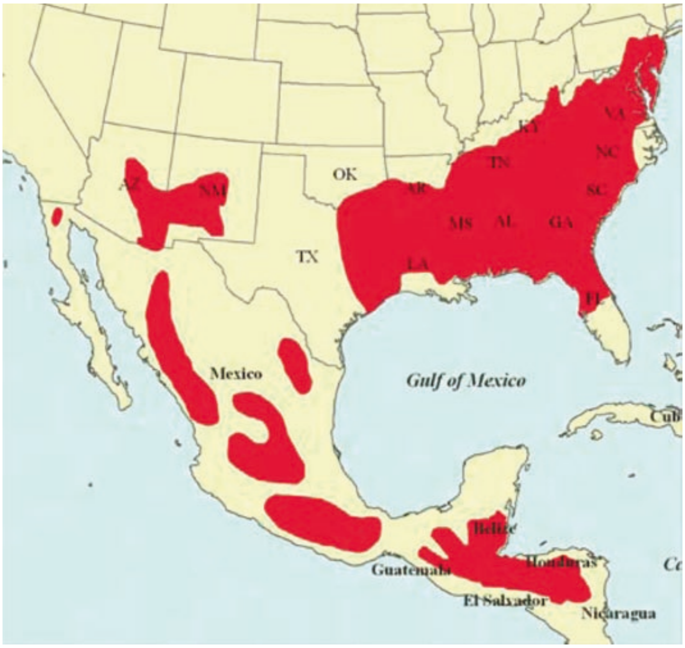

Fig. 7.1 The distribution of southern pine beetle in North and Central America. The large contiguous region in the southeastern United States marks the approximate boundary of what we refer to in this chapter as the southern forest (from Clarke and Nowak 2009)

Fig. 7.2 Examples of tree mortality caused by southern pine beetle. *Top* A large active infestation. *Middle* A typical expanding infestation showing trees with *red* (dead) and *yellowing* crowns (infested). *Bottom* Spatially discrete dormant infestations. Photographs reproduced with permission from Ron Billings, Texas Forest Service

landowners, commercial foresters, and state and federal entities. The occurrence of damage into spatially discrete and largely unpredictable infestations leads to equally unpredictable impacts that are unevenly distributed amongst forest stakeholders.

This chapter deals with SPB populations, and their impact on forests and forest managers. The central thesis is that modeling is essential to understand SPB, and consequently, to effectively manage its impacts. First, we outline the ecology of SPB and the forest system it inhabits. Our intent is to illustrate the scale of the problem, and the importance of thinking about SPB as a complex system that involves three interacting components: SPB populations, host pines, and humans that manage the forest. We build on this viewpoint by introducing our concept of an ecological disturbance, and suggest how this provides a useful way of looking at the SPB problem. Finally, we discuss why modeling is important for SPB, and how it can be used to organize and communicate ideas and data to help solve the SPB problem. We take the view that modeling should be a creative, iterative process where a variety of approaches are used to add value to current SPB data and knowledge.

7.2 Biology of the Southern Pine Beetle and Southern Forests

7.2.1 Southern Pine Beetle Population Ecology

The SPB is a small insect, approximately 3 mm in length that infests pine trees. To reproduce and complete a generation, adult beetles kill their host tree. The cycle of infestation begins with one or more pioneer adult beetles landing on the bole of a suitable host. Beetles usually select trees older than 10 years, with diameters greater than 15 cm, although the suitability of hosts (host selection) varies considerably depending on the abundance of SPB. Adult beetles attack potential hosts by chewing through the outer bark of the tree. The primary defense mechanism of host pines is to exude resin that engulfs or entraps (pitches out) beetles, restricting further attacks and often killing them. To increase the probability of a successful attack, beetles release pheromones that attract conspecifics to the potential host. If the tree becomes sufficiently weakened by attacks, adults bore into the phloem, and construct galleries (ca 10–20 cm long) into which eggs are deposited. Depending on the number of attacking beetles, gallery construction may extend from a height of 1 m above the ground to the live crown. Many of SPB's key life history rates such as egg production and development are driven by temperature and other site specific factors (e.g., population density, host susceptibility). Under favorable environmental conditions, females typically excavate galleries for 7–14 days and deposit approximately 1–3 eggs per day (Wagner et al. 1981), before reemerging to initiate attacks on new hosts. Eggs develop within the galleries through 4 larval instars that feed on phloem, and a pupal stage. After approximately 30–90 days, second generation adults emerge from the natal tree to repeat the cycle.

The main factor that makes SPB populations important to humans is that tree mortality damage is concentrated within outbreaks. Outbreaks are time periods and spatial areas delimited by a phase of rapid population growth and subsequent population decline. In turn, outbreaks comprise one or many infestations—spatially discrete areas of the forest that comprise trees that are currently infested, or have been infested by SPB (examples of which are shown in Fig. 7.2). The change in population size that is associated with outbreaks occurs over large forested areas or regions, typically between two and 100 counties (across most of its range a county area is approximately 2500 km^2). These elevated (epidemic or outbreak) populations may persist for 1–5 years before returning to endemic population levels. Figure 7.3 illustrates contrasting spatial patterns of SPB outbreaks across the United States for two different years (Birt 2011b). Figure 7.4 illustrates the frequency of outbreaks across the southern U.S. Since records began (ca 1960), at least one outbreak has occurred every year in the U.S. An outbreak is defined by the USDA Forest Service as greater than 1 infestation per 1000 ha of host per year; and an infestation by a group of greater than 10 dead or infested trees. A key characteristic of both outbreaks and infestations is that they occur unpredictably in space and time.

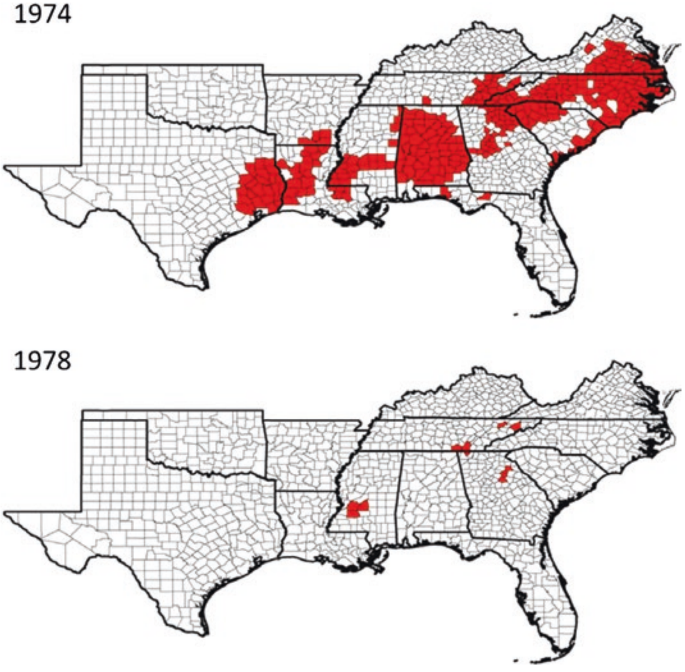

Fig. 7.3 An example of two contrasting annual patterns of southern pine beetle outbreaks across the southeastern United States. Counties considered to be in outbreak (>1 infestation per 1000 ha of host tree species) are shown in *red*

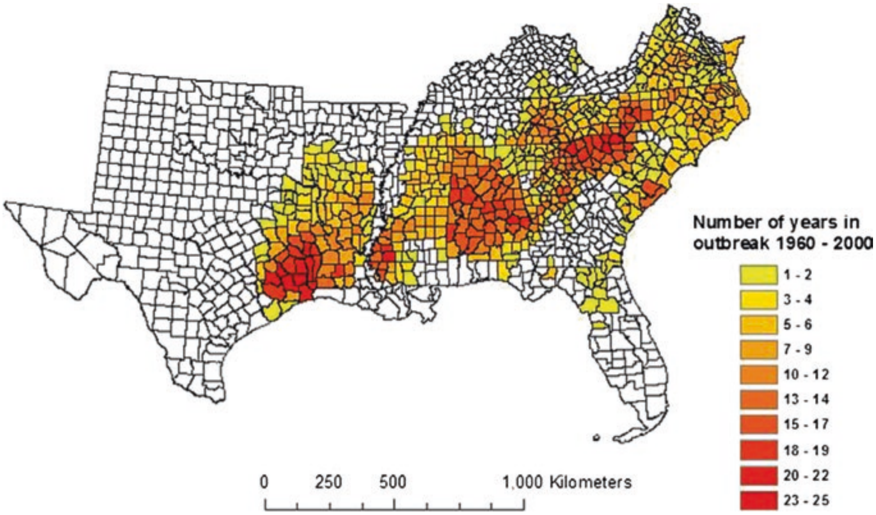

Fig. 7.4 Map of southern pine beetle (*SPB*) outbreaks, by county, between 1960 and 2000. The map effectively illustrates the frequency of outbreaks but does not provide information for other important aspects of SPB disturbance, most notably the number of infestations per outbreak and characterizations of the size of each outbreak

Within active infestations (Fig. 7.2), trees can be categorized as being: dead (no longer colonized), colonized (or infested), in the process of colonization, or under attack. Large infestations can contain many hundreds of dead trees, and often comprise one or more discrete aggregations of colonized trees—called an active head. At the periphery of a head, emerging and reemerging beetles initiate pheromone coordinated attacks on healthy hosts. These "mass attacks" increase the probability of successful colonization. In younger infestations, the availability of "attacking" adults may occur in pulses because the emergence of each generation of adults is synchronized by the timing of colonization and the development rates of the insect. As an infestation matures reemergence behavior and overlapping generations (caused by differences in the development times of egg cohorts), leads to a steady stream of attacking adults, and therefore increased tree mortality. Under these conditions, tree mortality, SPB population growth, and the growth rates of infestations can become very high.

Outbreaks and infestations present highly visible evidence of SPB populations. However, most of the time, SPB is almost undetectable in a forest landscape. As Fig. 7.4 illustrates, although some counties have experienced outbreaks 25 times in 40 years, this frequency is somewhat misleading because outbreaks tend to persist in a region for multiple years. In reality, outbreaks are interspersed with relatively long periods during which SPB populations are either present at low densities (herein endemic population phase), or not at all. For example, east Texas, historically an area of high concentration of SPB activity, has not experienced an outbreak for 16 years. During endemic population phases, mass attacking of trees is probably prevented by low densities of adult beetles. Instead, SPB probably search for and colonize highly susceptible trees that have been weakened by other biotic or biotic processes such as lightning strikes, or other bark beetles (Coulson et al. 1986).

A central challenge for SPB research is to understand how the ecological processes that drive colonization of an individual tree can also lead to the complex patterns of outbreak and endemic populations in space and time. To understand the entire SPB population cycle parsimoniously, the *same* biological and ecological processes that explain outbreak population dynamics must also be capable of explaining low density endemic population dynamics. Additionally, these processes, driven by key environmental variables, must also explain the differences in SPB dynamics across the wide range of environmental conditions it inhabits. In other words, variations in population dynamics during outbreak and endemic phases, and across its broad geographic range, must be explainable by a fixed and parsimonious set of life history constraints and ecological processes. Despite a large body of research into the fine-scale ecology of SPB (see Hain et al. 2011; Stephen 2011; Sullivan 2011; Ayres et al. 2011; Birt 2011a, b for reviews), the ecological or environmental processes that drive shifts in populations from endemic to epidemic and the spatio-temporal pattern of infestations are not fully understood.

7.2.2 Impacts of Southern Pine Beetle Damage

7.2.2.1 Socioeconomic Impacts

Although SPB is an interesting ecological problem in its own right, research is largely driven by the impact of its damage on humans. These impacts are most often described in terms of economic loss to forest managers, often reported as reduction in timber value, and costs associated with remediating (clearing and replanting) damaged areas. When outbreaks occur they cause large-scale tree mortality within a region. Landowners scramble to harvest dead and infested trees, or even to harvest noninfested trees in an attempt to offset the risk of future damage. Regionally, these activities cause an excess of harvested trees that local sawmills are unable to process, and which are prohibitively expensive to transport to other areas. Although SPB outbreaks do cause a considerable net loss to regional economies, the real economic impacts of an SPB outbreak are actually more complex, and involve the redistribution of monetary value from individual landowners (losers) to timber processing operations (winners) (Pye et al. 2011).

The regional cost of SPB damage is just one way of measuring its impacts. At a finer scale, SPB affects organizations and individuals. In the southern U.S., forest lands are managed by a variety of stakeholders including independent private foresters, large-scale commercial timber companies, and federal or state agencies (e.g., USDA Forest Service). For individuals and organizations, the unpredictability of outbreaks is possibly the biggest impediment for efficient management. This unpredictability leads to difficulty allocating and maintaining resources between outbreaks. One of the key resources for dealing with outbreaks is the experience, knowledge, and skills of forestry workers involved in SPB decision-making activities (identifying, documenting, and remediating), including trained forestry technicians and the landowners themselves. Although certain characteristics of forest stands predispose them to infestation, the ability to predict whether a particular stand will become infested is relatively low (Birt 2011c). Proactive management of trees, such as prescribed thinning, is currently seen as the best way to prevent SPB infestations, but involves cost to the landowner. And SPB's unpredictability means that, potentially, an individual forest manager could still incur an infestation even if they follow all "best practice" guidelines for stand management.

When infestations do occur on a landowner's property, questions arise as to how to manage them to prevent further damage. Clearly, the growth of an infestation is driven by the dynamics of the beetle population and currently we do not understand enough about SPB population dynamics to be able to accurately predict how much damage an infestation will ultimately cause. Even if we did, uncertainties in the future weather patterns that drive much of SPB's ecology would naturally affect the confidence placed in any prediction. Affected landowners often face an agonizing wait to find out how much damage will occur, and how much this damage will ultimately cost them. In most cases, pesticides are not a viable treatment option because of environmental risk, expense, and poor efficacy. Instead, recommended treatments most often involve cutting trees at and around the active head of an infestation (buffer strips). Cut trees may then be left in situ, removed, or burned. In all cases, management is expensive, offers no guarantee of efficacy, and is usually required during times when forest management resources are under severe strain.

7.2.2.2 Positive Impacts

Several authors have investigated the role of SPB in structuring forest landscapes and maintaining ecosystem function such as forest productivity, biodiversity, and hydrological function. Tchakerian and Coulson (2011) provide a comprehensive review of this research. Damage caused by SPB can facilitate primary production by releasing resources (sunlight and nutrients) from "mature stands" dominated by older, less productive trees. Under natural (non-managed) conditions, these releases are relatively slow and begin a few months after infestation with leaf fall; followed by destruction of woody debris from the crown; breakdown and modification of standing dead wood; and culminating in fallen, rotting trunks on the forest floor. Following SPB damage, gaps in the forest canopy also lead to a change in plant species composition towards herb and shrub species, and favor the growth of juvenile pine and hardwood species. Leuschner and Maine (1980) estimated an increase in herbage production beneath loblolly pine (*Pinus taeda* L.) stands following tree mortality caused by SPB. One consequence of this restructuring is that damaged areas may provide increased resources for wildlife. Maine et al. (1980) estimated increased food availability following SPB damage and suggested a positive effect for several other species (e.g., quail, woodpeckers, turkey, deer, and small mammals).

Historically, the southern pine region comprised three fairly distinct forest systems: the Coastal Plain; the southern Appalachian Mountains; and the Piedmont. On the flat, poorly drained Coastal Plain, loblolly pines and hardwoods were the dominant species. In mountainous regions, changes in elevation drive a heterogeneous and species rich pattern of vegetation cover, with relatively small patches of white pines (*Pinus strobus* L.) interspersed among mixed hardwood and hardwood stands. But within the Piedmont region, longleaf pine (*Pinus palustris* Mill.) was the dominant forest type (Schowalter 2012). Longleaf pine is more resistant to SPB damage (Schowalter et al. 1981a) and once occupied an estimated 38 of 142 million hectares of the total forest area of the southeastern U.S. (Croker 1968; Frost 2006; Hanson 2010). It is thought that fire and SPB were responsible for the successional dynamics of these longleaf pine forests, leading to open, monospecific forests with an understory of grasses and herbaceous vegetation that supported considerable game (Franklin 1997). In the late nineteenth century, longleaf pine forests were heavily exploited for timber and naval stores (tar, turpentine, rosin). As stocks of red pine (*Pinus resinosa* Ait.) and white pine in the northeastern U.S. declined, the south also became the U.S.'s principal supplier of timber (especially the products from the longleaf pine forest), with production reaching a peak in 1909. Although the precise impact of SPB on the successional dynamics of pre-settlement forests are unknown, SPB may once have been an integral component of productive, pre-settlement forest systems.

7.2.3 The Current Southern Forest

Although the SPB is native to the southeastern U.S., the southern forest has changed considerably over the past 100 years. The exploitation of pine forests in the early twentieth century has led to considerable changes in the SPB's environment. Following the first wave of human exploitation, the area of the southern forest has declined to 60 % of its original area, and has also become fragmented. This fragmentation has been driven by conversion of forest to agriculture and urban land uses. Additionally, much of the forest has been managed to maximize timber production, often by planting genetically selected loblolly pine and slash pine (*Pinus elliottii* Engelm.) in large, even aged stands.

Another way of looking at the current state of the forest is by who owns it, and how they manage it. Ownership of the southern forest is split into three broad groups: private individuals (56 % by area), commercial timber companies (30 %), and public forest (14 %) (Zhang et al. 2012). The objectives of forest management in each ownership category (and the effects of this management on forest structure) may be very different. While the industrial forestry sector and many private commercial landowners are necessarily driven by economic factors, the USDA Forest Service's current management objective emphasizes the diverse values of forest landscapes to communities and individuals.

Generally, public land holdings occur in fairly large contiguous areas that can be managed according to well-defined and fairly consistent objectives. However, forest tracts owned by the industrial forestry sector and private individuals are currently undergoing considerable change. Historically, most commercial landholdings were owned and managed by large industrial timber companies. These were companies that owned and managed both the land (forest), and the processing mills. The rationale was that, by owning both, the company had control over both the supply and condition of its raw materials (i.e., the forest). More recently, this type of commercial ownership has been replaced by entities called Real Estate Investment Trusts (REITS) and Timberland Investment Management Organizations (TIMOS). Between 1980 and 2007, REITS and TIMOS have taken over two thirds of the forest area once owned by industrial timber companies (Coulson and Meeker 2011). Although TIMOs and REITs employ professional foresters, uncertainty surrounds how different management objectives of these organizations (driven by changes in their financial objectives) may affect the composition and structure of the forest over the long term.

By area, private individuals (i.e., families) own and manage most of the southern forest. This group contains the most diverse range of management plans spanning economic timber production, hunting, aesthetics, or even no management. In the current southern forest, the average size of a holding is approximately 12 ha. However, 59 % of family owners have small areas of forest, ranging in size from <1 to 4 ha. This results in a fragmented forest landscape that has and continues to be driven by estate disposal and urbanization (Butler and Wear 2012). For small private owners, management plans are likely to be driven by a broad range of factors that include resource constraints; whether a tract of land remains large enough for commercial harvest; and education or forestry knowledge, including whether an individual is suitably informed of "best" management practices.

7.2.3.1 Reciprocal Interactions Between Southern Pine Beetles and Humans

Most researchers agree that SPB damage is to some extent driven by the composition and structure of the forest. The scientific basis for these beliefs come largely from stand risk modeling (or other correlative models), which has repeatedly shown that certain factors (e.g., high basal area, drought, damage) predispose stands to infestations. Many foresters proactively manage stands in an attempt to prevent SPB damage, for example, through selective thinning, uneven aged silviculture, or planting more resistant species (e.g., longleaf pine). The importance of collective forest stewardship is widely recognized by state and local forestry agencies, which often provide subsidies to offset some of the expense of this management. Even at a federal level, the Healthy Forests Restoration Act (2003) provides legislation that attempts to reduce large-scale disturbance events (including SPB) through proactive forest management.

The SPB has the potential to change the structure and composition of the forest both directly through tree mortality; and indirectly when landowners are forced to modify management plans following SPB damage on their own land or within the surrounding forest landscape. If the science behind forest management incentives is correct, management before and after SPB damage *should* reduce the impacts of SPB, and consequently improve the net productivity of forests. However, a multitude of factors drive changes in the way forests are managed. These include other disturbances (e.g., fire, drought, hurricanes), the demand for timber products, and changes in the "values" landowners attach to their forest.

The relationship between SPB damage, forest management, and forest dynamics suggest that the forest landscape might be best conceptualized as a coupled socio-economic and ecological system. Intuitively, patterns of SPB damage are driven by the current structure and composition of the forest, which in turn is a consequence of the collective decision-making of forest managers. It is also probable that SPB damage has a reciprocal effect on how individuals and organizations manage the forest in the future. For example, one could imagine that changes in management plans could be influenced by factors such as an individual's past exposure to damage, whether the forest is a primary income source, how long they have been involved in forestry (experience), the values they attach to the forest (why they own forest), and their willingness to adopt experiential knowledge versus scientific knowledge to solve problems.

Modeling the southern forest as a coupled socioeconomic–ecological system has the potential to address a broad range of questions about its sustainability and future productivity. For example, it is possible that both the short- and long-term impacts of SPB disturbance "naturally" drive forest management towards reductions in future damage (i.e., ecosystem resilience), thereby maintaining socioeconomic productivity. Alternatively, short- and long-term impacts of SPB may drive changes in forest dynamics that reduce the productivity and stability of this system.

7.3 What Is an Ecological Disturbance?

Despite its widespread use in ecology, no single and unambiguous definition exists for ecological disturbance (Coulson and Tchakerian 2010) and terms such as perturbation and stress have often been used synonymously, inconsistently, and ambiguously to describe ecological damage (Rykiel 1985). Furthermore, ecologists have classified different kinds of disturbances, for example, the terms "press" and "pulse" are often used to describe changes in the ecological environment that are either long term and low magnitude (presses), or short-term and high magnitude (pulses) (e.g., Glasby and Underwood 1996).

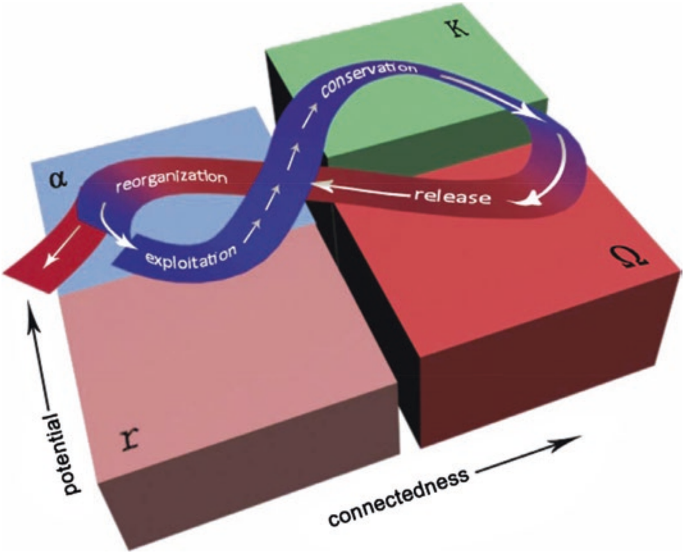

Fig. 7.5 The adaptive cycle of ecosystem succession. The cycle comprises four phases of succession: growth or exploitation (*r*); conservation (*K*); collapse or release (*Ω*); and reorganization (*α*). The *arrows* indicate the speed of flow in the cycle: *short and closely spaced arrows* indicate slow and gradual changes and *long arrows* represent a rapidly changing situation. In our definition of disturbance we suggest that, intuitively, disturbances involve forces that affect the release phase (pulses) and *r* phase (presses) of the cycle and reduce the connectedness or order (*x*-axis) of the system

Any general definition of disturbance should help ecologists understand ecological systems. Intuitively, these systems are dynamic and undergo constant change in both their abiotic and biotic components. Changes in any measured entity within the ecosystem can be characterized in several ways, for example, by magnitude, frequency, or predictability. Given that change is a fundamental component of all ecosystems, the central problem of defining disturbance lies in why certain measurable changes in an ecosystem should be classified as a disturbance, and why others should not.

The concept of ecological disturbance is intricately tied to the way ecologists view the dynamics of natural and modified ecosystems (Wu and Loucks 1995). The adaptive cycle (Fig. 7.5; Gunderson and Holling 2001) illustrates a contemporary view of ecological stability and succession in a spatially defined ecosystem. In the adaptive cycle, an exploitation phase is characterized by changing (successional) communities of r-strategy organisms exhibiting high growth and reproduction rates; the conservation phase (K) represents a relatively stable, organized ecological state dominated by K-strategy organisms. The K and r phases of the adaptive cycle are linked by release (Ω) and reorganization phases (α). These are characterized by episodic events of sufficient energy to "release" the matter stored (conserved) in the K phase (e.g., wind, floods, drought, fire, herbivory), followed by a more gradual release and reorganization of these materials. In some cases, release and reorganization may lead to considerable changes in the trajectory of ecological succession, and to a different K-state. This conceptual model of ecosystem dynamics illustrates two types of ecological change: increases in system order (connectivity in Fig. 7.5) that occur during the exploitation and conservation phases and decreases in order that occur during the release and reorganization phases. We propose that, scientifically and intuitively, disturbance usually involves processes that decrease the order of a system.

The adaptive cycle provides a conceptual model of ecosystem change, important for addressing fundamental societal issues such as the sustainability, resilience, and productivity of artificial and natural ecosystems. However, as Figs. 7.6 and 7.7 illustrate, the interpretation of disturbance within the adaptive cycle depends a great deal on how a focal ecosystem is defined spatially, temporally, and by the ecological entities of interest. For convenience, we will call this a bounded system. Defining a system in this way simplifies the problem of understanding its dynamics because it allows processes that occur within the system (endogenous) to be studied, described, and understood in detail. The trade-off is that processes and interactions external to the focal system (exogenous) must be represented implicitly, and with less detail. Examples of processes that are endogenous to a bounded system include the vital rates and competitive interactions of focal organisms. Conversely, weather is often viewed as an exogenous process in many bounded systems because, although it can be affected by the state of a system, these processes are complex, and usually occur at broader scales than can be represented in useful conceptual and mathematical models.

A number of authors have attempted to define disturbance. For example, Rykiel (1985) defines disturbance as a physical force, agent, or process, either abiotic or

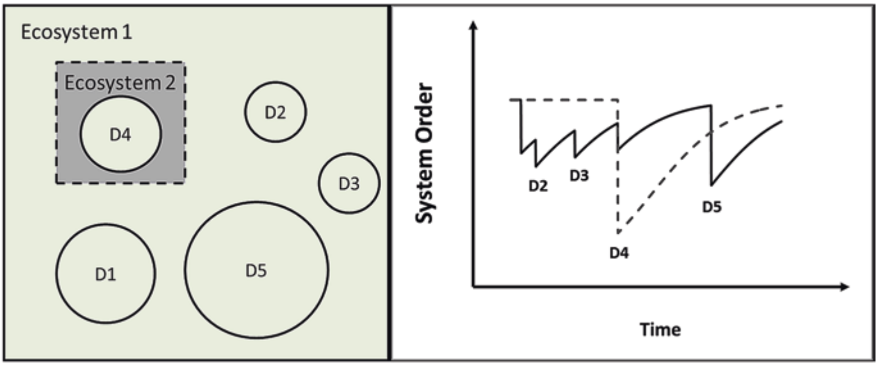

Fig. 7.6 Illustration of the relationship between spatial scale and disturbance magnitude. The *left panel* shows two ecosystems subject to several disturbance events (*circles* labeled *D1–D5*). The *right panel* shows the temporal pattern and magnitude of these disturbances relative to Ecosystem 1 (*solid line*) and Ecosystem 2 (*dashed line*). Event D4 represents a much larger proportional disturbance to Ecosystem 2 relative to Ecosystem 1, highlighting the difficulty of characterizing a disturbance by the magnitude of its effect alone

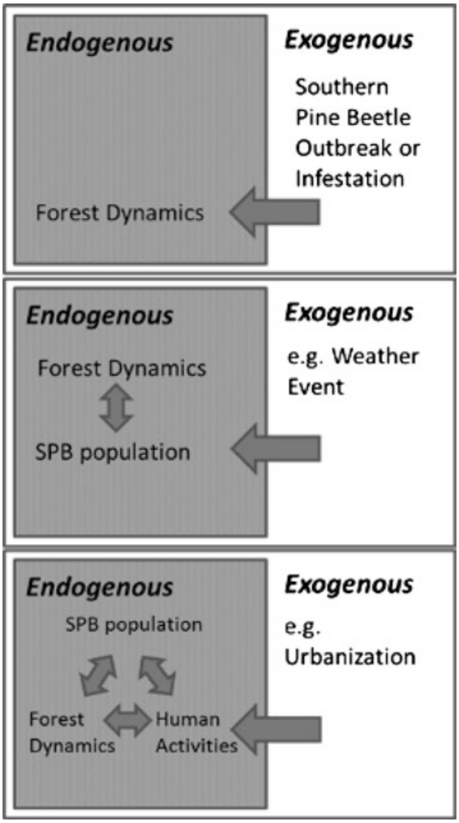

Fig. 7.7 Illustration of how a disturbance may be redefined depending on the spatial and temporal scale and the entities and processes of interest in a bounded system. The *top panel* illustrates a case where the bounded system is defined so that southern pine beetle (*SPB*) is an exogenous disturbance (the initiation of the disturbance event is not driven by processes within the bounded system). In the *middle panel*, understanding the relationships between forest dynamics and SPB populations may shift the initiating cause of a disturbance to a different exogenous event, for example, weather. The *bottom panel* illustrates reciprocal relationships between forest dynamics, humans, and SPB populations that could further redefine the nature of disturbance in relation to human activities such as urbanization or landscape domestication

biotic, causing a perturbation (an effect or change in system state) in an ecological component or system, relative to a specific reference state and system, and defined by specific characteristics. A simpler, more practical definition is provided by Coulson and Tchakerian (2010), who define disturbance as an initiating cause (physical force, process, or event) that produces an effect (consequence) that is greater than average, normal, or expected. In this chapter, we view a disturbance as an event that originates outside of a bounded system that is delimited by time, space, and explicit ecological processes and which causes a change in the dynamics of the focal system. This concept of disturbance (as an external process) is clearly dependent on an a priori definition of the bounded system of interest. As such, our intent is not to definitively classify whether a particular driver of ecosystem change *always* or *never* constitutes a disturbance, or to replace the colloquial use of the word. Instead, it is to facilitate how the term can be used to more explicitly model (whether conceptually or mathematically), and therefore understand, the dynamics of ecological systems. In many cases, the use of the term ecological disturbance represents a paradox: at some scales the effect of a disturbance is to reduce system order; but when viewed at broader scales, or using a different set of system entities, the same "disturbance" may actually have the effect of maintaining a dynamic equilibrium. Examples of disturbance events *might* include hurricanes or other extreme weather; fire, environmental pollutants; invasive or irruptive species; and human activities because they can be conceptualized as a force with the potential to reduce system order and change the dynamics of a bounded system. However, in our view, the key to them being a disturbance depends on a specific context—the definition of the bounded system in question. Specifically, whether the event can be wholly explained or modeled using explicit endogenous processes of the system, or whether it cannot and therefore must be represented by exogenous processes described by fixed, immutable patterns (e.g., frequency, regularity, location, intensity) of the event in space and time.

7.3.1 Why Is This Concept of Disturbance Important to the Southern Pine Beetle Problem?

In our working definition, the magnitude of a disturbance event, and descriptions and explanations of its causes and effects, are intrinsically linked to the spatial and temporal scale and the entities represented in a bounded system (i.e., Fig. 7.6). The impacts of SPB damage are most often defined from the viewpoint of humans that manage the forest. For example, individual forest stands are disturbed by discrete infestations and larger forest landscapes are disturbed by regional outbreaks. Therefore, to individuals that manage the forest, SPB damage is most naturally viewed as an exogenous disturbance. Currently, we are unable to predict when and where damage will occur through an understanding of SPB's broad scale population dynamics. Instead, predictions about damage rely on characterizations of the frequency, severity, and location of historical outbreaks and infestations. This entirely exogenous view of SPB damage has important implications for effectively managing the southern forest because, as Sect. 7.2.3 illustrates, the composition and configuration of the southern forest has and continues to undergo considerable change. Consequently the historic patterns of SPB disturbance may not be relevant to the current or future states of the forest.

Southern pine beetle damage is therefore most naturally thought of as an exogenous disturbance because of the limited spatial and temporal scales at which we conventionally view the problem. These scales are (understandably) driven by its impacts on those who manage the forest. However, SPB has always been a component of the southern forest landscape and, therefore, has likely always caused periodic and spatially aggregated tree mortality. If the SPB has always been an integral, endogenous component of the southern pine forest, should it be viewed as a disturbance? Our view is that it could be, but that a more productive way of looking at the problem is to view SPB as an endogenous component of the forest system whose dynamics are driven by other, exogenous factors. These may include short-term weather events, climate change, or human–forest interactions. The major questions that arise from this viewpoint are: what are the real disturbances that change the frequency and magnitude of SPB damage? How do they affect the long-term dynamics of southern pine forests? And how do changes in these dynamics of the forest affect their utility to the humans who manage them?

Obtaining parsimonious explanations of an ecological system such as SPB requires models that describe the system using as many endogenous, and as few exogenous, processes as possible. The SPB has a complex ecology (including many interactions with hosts, other biota, and probably even humans), and occupies a broad range of environmental conditions. Developing a better understanding of SPB dynamics will require an iterative, exploratory process of defining many conceptual bounded systems (defined by different spatial and temporal limits, abiotic and biotic entities, and processes) and comparing their dynamics with those of observed ecosystems (pattern). Figure 7.7 illustrates that throughout this exploratory process, it may be possible to replace events that were previously considered exogenous with explicitly described endogenous processes. As Rykiel (1985) suggests: “a disturbance at any level can be absorbed by moving up the hierarchy (of linked ecosystems), in effect, placing the disturbance within a new and larger system… This larger system has properties different from the former system and the disturbance now appears to be part of the internal workings of the system rather than a disturbance to the system”.

7.4 Modeling Southern Pine Beetle Damage

7.4.1 Why Model Southern Pine Beetle Populations?

Models are used in conjunction with observation, experience, and experimentation to understand which components are most important for developing a greater understanding of a system. Models can take the form of diagrammatic representations of concepts, graphical summaries, statistical summaries, mathematical equations, or computer simulation models. As such, models have always been used in ecology. Even heavily designed (manipulated) experiments require models to summarize results and test hypotheses (e.g., statistical models such as t-test, ANOVA, linear regressions). Generally speaking, as a system becomes less amenable to experimentation or direct observation, increasingly complex, nonstandard models are needed to make sense of observations and data. This is the case with the SPB system. Many of the questions important for understanding the causes and impacts of SPB damage cannot be investigated by experimentation or observations alone. Instead, the dynamics of the southern forest system are only amenable to investigation by integrating patterns and processes that can be measured directly.

7.4.2 Data Constraints for Modeling Southern Pine Beetle Populations

Models (whether conceptual or mathematical) that describe SPB populations must be formulated using ideas and parameters that are based on observations or data from the "real world". In the following section, we describe the challenges associated with observing and collecting SPB data, and how this constrains our understanding of (1) the spatio-temporal pattern of SPB damage and (2) the population ecology and dynamics that drive SPB damage.

7.4.2.1 Characterizing Historical Patterns of Southern Pine Beetle Damage

The factors that trigger SPB populations to transition from low density to high density phases are unknown and highly debated within the scientific community. As such, historic data provides an essential starting point for understanding higher level impacts of SPB damage on forest systems, for detecting cause and effect relationships between SPB damage and environmental factors, and for developing and validating a mechanistic understanding of broad scale SPB population dynamics. Figure 7.4 shows the outbreak frequency of SPB across the southern forest between 1960 and 2000. However, one of the key problems of characterizing SPB damage lies in the complexity of its pattern. Although these maps present a useful view of a single dimension of disturbance (the frequency of outbreaks at an approximate spatial scale of a U.S. county), in reality SPB damage is characterized by more detailed temporal and spatial dimensions. For example, the initiation of outbreaks usually occurs in spring or summer when a number of discrete infestations first appear across a regional landscape (e.g., a 1000–5000 km^2 area), which then become epicenters of SPB population growth and tree mortality. Throughout the course of an outbreak, each of these infestations will grow to different sizes (and shapes) and may also lead to the initiation of new infestations on the landscape. This spatio-temporal pattern is essential for developing and validating SPB models, but it is difficult data to collect, store, and communicate.

The principal source of data detailing the broad scale patterns of SPB damage comes from monitoring surveys conducted by agencies responsible for managing forests. Aerial surveys are used to detect the initiation of outbreaks and monitor their progression. Surveyors look for groups of trees with red crowns (dead and vacated trees), surrounded by other trees with yellow or fading foliage (trees likely to contain active populations). Flights occur on flight lines approximately

1.5–8.0 km apart, and may cover many hundreds of km^2 of forest in a day, including private and public lands. Modern techniques use digital sketch maps to record the location and size of infestations. Following aerial detection, ground crews are used to find the exact location of an infestation, identify and notify the landowner, verify SPB as the causal agent of the damage, survey the status of the population (number of dead trees and infested trees), and estimate rate of infestation growth (Billings 2011). Although aerial surveys and associated ground surveys are important for monitoring and managing outbreaks, they are designed primarily for operational control of SPB and not scientific enquiry. As Sect. 7.2 illustrates, when outbreaks occur in a region, forestry professionals often become overwhelmed to the extent that ground sampling of infestations needs to be prioritized. In most cases, this limits repeated sampling at the same site, which in turn limits the availability of infestation growth and decline data. In some cases, data may be difficult to collect because of the local terrain (e.g., mountainous areas), or access (e.g., infestation on private property). Additionally, the range of SPB also includes regions in Central America, where damage is rarely documented or reported.

The difficulty and cost of measuring SPB damage therefore affects the availability and quality of data for modeling. These data constraints are exacerbated by the rarity and unpredictability of SPB. As Fig. 7.4 shows, outbreaks are actually relatively infrequent in most regions and highly unpredictable in space and time. Because of this unpredictability, large amounts of data, collected over long time periods, and over broad spatial scales are required to provide accurate statistical summaries of actual patterns—an enterprise that involves considerable collective effort and organization by SPB stakeholders. Even more data is required to develop statistical models to detect the initiating cause of outbreaks. To detect causal relationships, data that describes *potential* causes (e.g., conditional state of the forest) must be recorded alongside damage information (effects). Most obviously, it is important to know the characteristics of forested areas that are affected by SPB, but less intuitively, to analyze the spatial and temporal pattern of damage relative to the underlying structure and composition of the forest, it is essential to know the characteristics of areas that did *not* incur damage. This requires ongoing maintenance of accurate forest inventories (at scales appropriate to SPB), a task that requires a long-term collective effort, and specialist skills (e.g., remote sensing).

7.4.2.2 Constraints for Understanding Southern Pine Beetle Population Dynamics and Life History

Certain characteristics of SPB ecology make the development of population models difficult. For example, broad scale population dynamics of SPB are difficult to measure directly and completely. While broad scale patterns of tree mortality (discussed above) are the best indicators of population dynamics, these two measures are not directly equivalent for several reasons. Factors such as the number of beetles that occupied each dead tree, the success rate of attacking beetles, and the time delay between observed tree mortality (indicated by a fading, or reddening crown) and actual tree mortality all conspire to influence the relationship between measurements of tree mortality and population levels. In fact, direct observations of population dynamics and ecology are restricted to relatively small spatial and temporal scales (e.g., within individual trees or infestations). This highlights the importance of models for integrating "observable" pieces of information into more complete descriptions of population dynamics. At the same time, issues surrounding the availability of data, and the difficulties associated with collecting them, are essential for understanding the amount of interpretation that is necessary to integrate SPB ecology into population models, and therefore, for interpreting their results.

One natural bias in SPB data is caused by the difficulty of observing low density populations in the field (i.e., those occurring between less frequent regional outbreaks). During the endemic population phase, SPB completes generations in isolated trees weakened by other environmental forces (e.g., lightning). Ordinarily, healthy host trees are able to repel attacking SPB individuals by exuding sticky resin that prevents adults from constructing galleries and laying eggs. The theory is that dispersing SPB locate weakened trees relatively efficiently within the forest (aided by host volatiles), but do not grow to high enough population densities to allow the successful attack of neighboring, healthy hosts. Several explanations for the regulation of endemic populations are offered, including the importance of predators and parasites, the mortality costs associated with dispersal in search of weakened trees, and the local and regional strength of host defenses. The difficulty of measuring endemic populations is driven by the extensive forest landscape, and the rarity of SPB infested trees. Because it is difficult for humans to perceive exactly what a weakened tree looks like (except for those with lightning damage), searching for these trees in forested areas, and investigating colonization rates is difficult. To overcome these measurement difficulties, Coulson et al. (1986) used an alternative approach to measuring colonization rates by experimentally manipulating (i.e., weakening) hosts by simulating lightning struck trees using explosives. Manipulations occurred in an area with no visible beetle activity within 5 km. Despite the low apparent beetle density, colonization occurred within only a few days following summer treatments, and approximately 133 days following winter treatments, illustrating that beetles readily find and colonize weakened trees. However, the precise mechanisms by which they do this, where the beetles come from, and how many of all the dispersing adults in the forest actually located the weakened trees are unknown.

Because of the difficulties involved in locating SPB populations during endemic phases, much of our ecological knowledge of SPB comes from studies of active infestations. During outbreaks, many active infestations appear across a regional landscape making the beetle much easier to study. Within active infestations, high densities of beetles lead to the mass attack of potential hosts. Mass attack behavior occurs as beetles emerge from their natal tree and attack in high enough numbers to overcome the natural defenses of the host (oleoresin production). Although many adult beetles may die during a mass attack, once a host's defense has been overcome by attacking beetles, it is readily colonized by other beetles in the local population or by beetles immigrating from adjacent populations. The tree may remain as a viable resource for a period of time that depends on the colonization rate of the tree (the phloem of each tree has limited space) or on the natural deterioration of the phloem driven by environmental factors. When population densities are high, and colonization of trees rapid, female beetles may attack one host, lay a complement of eggs, then re-emerge to attack another host. This complex mass attack behavior is driven by pheromones and host volatiles (Sullivan 2011). These compounds facilitate communication between individual beetles, structuring the population to maximize population growth by focusing attacks on particular hosts, affecting reemergence rates, and possibly driving dispersal from an infestation to new locations within the forest. Although these pheromones have been extensively studied in the laboratory, they are much more difficult to measure in the field.

Despite the visibility of SPB damage in infestations, many of the detailed ecological processes that affect population growth are hidden to observers. For example, most SPB activity occurs under the surface of the bark, and at heights between 1 and 20 m from the ground. Under these conditions, estimates of population size in a single tree require climbing equipment, skilled technicians, and statistical methods to accurately sample the population in a single tree (e.g., Pulley et al. 1977; Rain et al. 1978). Sampling methods may include destructive sampling (removing samples of bark) or nondestructive sampling (estimating populations using entry holes and emergence holes). Some of the most valuable information for understanding SPB ecology has been evaluated from meticulous laboratory studies. For example, development, survival, and reemergence rates have been measured under different constant temperature regimes (e.g., Gagne 1980) using noninvasive X-ray photography, providing much of the necessary life history ecology required to develop models driven by environmental temperature.

Infested trees may also be colonized by predators, parasites, or symbionts, all of which are potentially important for understanding SPB population dynamics (Klepzig and Hofstetter 2011). Recording this information for a single tree, over the generational time of the insect presents a considerable challenge. As infestations grow, the number of affected trees, and therefore the size and complexity of data for the "within tree" population quickly becomes overwhelming. Although it is possible to construct spatiotemporal maps of infested trees (e.g., Schowalter et al. 1981b), measuring and recording all of the information that may be relevant to understanding life history such that the data can be easily understood and reused by other researchers is logistically difficult.

Given the difficulty of observing SPB directly, several authors have experimentally manipulated populations within infestations to focus on particular ecological processes. For example, manipulations of attack density have shown that intraspecific competition may be an important regulator of population growth rates within a single tree (Reeve et al. 1998); predator exclusion experiments have been used to measure the effect of predators on survival and therefore population growth rate (e.g., Turchin et al. 1999); and mark–recapture experiments, linked to diffusion models, have been used to estimate SPB dispersal distances from active infestations (Turchin and Thoeny 1993). Less directly, Schrey et al. (2008) attempted to evaluate dispersal among populations using genetic techniques. They found only very small genetic distances among beetles sampled within five National Forests in Mississippi during a 2004–2005 outbreak. These locations span the entire area of the state (approximately 480 km × 240 km), and suggest that either the outbreak consists of a single interbreeding (and therefore highly mobile) population or that it comprises several non-mixing meta-populations originated from a single relatively undifferentiated source population.

7.4.3 Types of Models

Southern pine beetle ecology is complex, and involves many processes that are difficult to observe directly. In the absence of a complete understanding of SPB ecology, our view is that effective SPB modeling requires a broad range of models that help ecologists organize, integrate, communicate, and understand the large body of research that has been undertaken on ecological process and patterns of damage.

All models are designed to represent a complex real-world phenomenon in a simpler form (abstraction). Abstraction occurs whenever a complex system is represented by a simpler conceptual, pictorial, or mathematical representation. For example, population growth rate could be used to represent complex interactions among multiple finer scale processes (rates of development, survival, and reproduction), making the model easier to express mathematically and easier to interpret. On the other hand, if the real world is simplified too much, then models are often criticized as being unrepresentative. For example, although population growth rate may be an effective abstract parameter for a model of population dynamics; a life history theorist might argue that population growth rate is actually a product of the way in which an organism allocates "energy" between growth, reproduction, and dispersal and is driven by evolutionary processes that maximize an organism's fitness. At an even finer scale, physiologists might argue that development (i.e., cell division and organism growth) is driven by biochemical processes driven by chemical energy.

By definition, abstraction ensures that no model can or should represent all processes that occur within a system. Instead, it is the role of the modeler to decide which are most important based on the ecological questions that are to be addressed. For statistical approaches, a large body of research exists that helps to objectively guide the complexity of models relative to their predictive power. However, we argue that not all models in ecology need to be statistical or predictive. In fact, ecological research and researchers would benefit from broadening the remit of modeling away from trying to develop, or expecting, purely statistical, or predictive models. As Sect. 7.4.2 illustrates, data associated with SPB are difficult to measure, often incomplete, and highly interpretable. Therefore, models are also essential for summarizing and communicating complex and valuable data and expressing ideas for how different ecological processes, often measured independently, integrate to influence higher level behavior of a system. Given the philosophical implications of abstraction, we also suggest that searching for a single model of a system is futile. Instead, especially in a system as complex as SPB, multiple working models are required to develop the depth of understanding necessary to confidently use model "results" to understand the frequency, magnitude, and effects of populations and damage: "The multiplicity of models is imposed by the contradictory demands of a complex, heterogeneous nature and a mind that can only cope with a few variables at a time; by the contradictory desiderata of generality, realism and precision; by the need to understand and also to control" (Levins 1966).

A common way of expressing the level of abstraction in an ecological model is on a gradient of mechanistic to nonmechanistic. In the former, model processes are represented in ways that explicitly conform to underlying theories or processes for how a system works (i.e., less abstract). In contrast, nonmechanistic models often use parameters and functions that represent underlying processes less explicitly, if at all. For ecological applications, mechanistic models are often considered especially useful. For example, Bolker (2008) suggests: "All other things being equal, mechanistic models are more powerful since they tell you about the underlying processes driving patterns. They are more likely to work correctly when extrapolating beyond the observed conditions." The rationale for this viewpoint is intuitive and persuasive. First, ecology is subject to general, scientific theories that, logically, should be the starting point for developing models. Second, for most ecological problems (especially complex ones), a great deal of data and information (i.e., prior knowledge) already exist that partially explain how a particular system works. Much of this theory and prior information is wasted unless it can be usefully integrated to provide a higher level view of a system.

Although we agree with the potential advantages of mechanistic models, we also argue that mechanistic versus nonmechanistic characterizations can be misleading. Models are constructed to represent a designed and simplified view of a system so *interpreting* the results of the model in relation to the "real world" is essential but often overlooked. Interpretation of model outputs or of fitted parameters is a human-centric activity that ensures that modeling is a useful way of communicating knowledge about a system. With careful interpretation, mechanistic models can be statistical, and statistical models can also be mechanistic. In the former case, statistical methods exist to evaluate how well a mechanistic model represents observed data and these can even be extended to objectively include the influence of prior knowledge. However, if the stated goal of the modeler is to develop a highly integrative mechanistic model, the consumer of the model should also be prepared to see the value of the model beyond a strict, statistical analysis of the model outputs (prediction). Equally, standard statistical models (e.g., linear regression) or heavily abstracted models (e.g., those that use population growth rate) can be useful in understanding finer scale processes that lead to an observed phenomenon. This is especially true if some time is taken to interpret the abstractions and reimagine them as more complex mechanistic processes that have been simplified for mathematical convenience.

We suggest that there are considerable and necessary advantages of broadening and defining the utility of different types of ecological models, especially for a problem as large and complex as SPB. Instead of focusing on what models can predict, our view is that ecological models would be more usefully classified into the categories based on how they add value to data to help understand specific problems:

(1) Descriptive: Models that summarize complex data, and present them in a way that enhances communication of data, information, or knowledge (Fig. 7.8).
(2) Integrative, exploratory, or a priori: Models that integrate known ecological processes and are used to generate outputs that provide insights into a more complete system (Fig. 7.9).
(3) Inferential or statistical: Models that are used to statistically estimate (infer) unknown processes using measurements from a higher level view of a system (Fig. 7.10).

In the next sections we describe each approach in more detail and provide examples from the SPB literature.

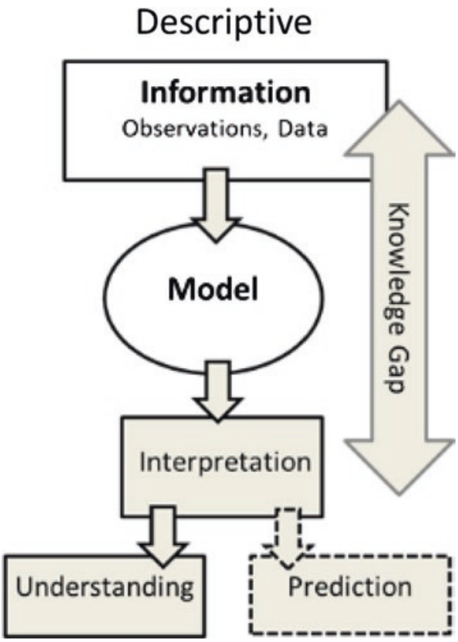

Fig. 7.8 Diagram illustrating the components of descriptive ecological models. These models serve to simplify raw observations and data to enhance understanding and communicate ideas. Descriptive models may consist of data summaries (e.g., statistical summaries or annotated diagrams) or graphical representations of conceptual ideas

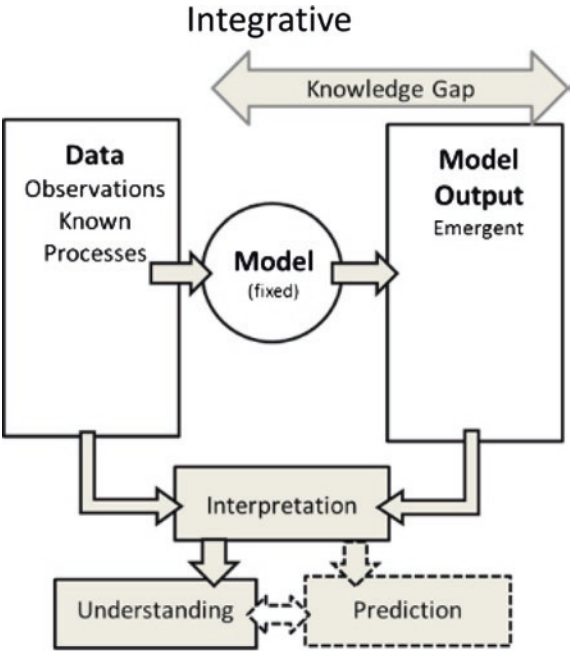

Fig. 7.9 Diagram illustrating the components of integrative models. These models integrate known processes and can be used to generate output that represents a higher order process. Model output depends on the assumptions used to drive the interaction among components. Interpretation of model outputs is based on the data used in its construction. The model can be used to develop understanding by manipulating these assumptions and observing their effects on model output (e.g., sensitivity analysis, scenario testing)

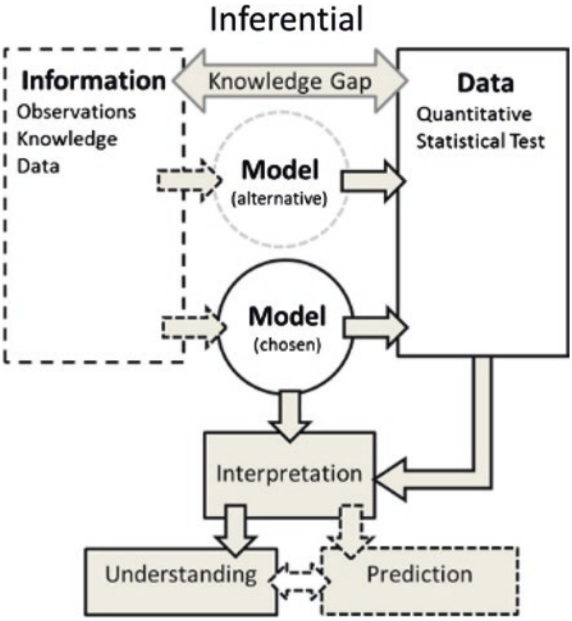

Fig. 7.10 Diagram illustrating the components of inferential models. Models are constructed and statistically tested against data, often representing a higher level process. The goal is to infer statistical support for a model based on well-defined data sets. *Dashed lines* show optional processes: for example, information, knowledge, and data may guide some development of the model; multiple models may be constructed and selected to best fit the data; and prediction may occur following interpretation of model results

7.4.3.1 Descriptive Models

Figure 7.8 provides a diagrammatic view of the role of descriptive models. Analogous to descriptive statistics, their main objective is to simplify complex data and observations into a form that improves the understanding of these processes and aids communication. Examples from the SPB literature include the fine-scale behavior of adult beetle host finding (Fig. 7.11; Bunt et al. 1980) and models of the essential stages of tree utilization (Fig. 7.12; Payne 1980). Another important example is the Southern Pine Beetle Information System (SPBIS): a USDA Forest Service program designed to collect and disseminate historical and current infestation data. It comprises a spatial database of SPB damage assessed using aerial detection and ground surveys (Peacher 2011). The database is used primarily to aid decision-making during regional outbreaks, and contains information on infestation growth and suppression treatments. It is included here because potentially this data is important for researchers who wish to first understand the spatial and

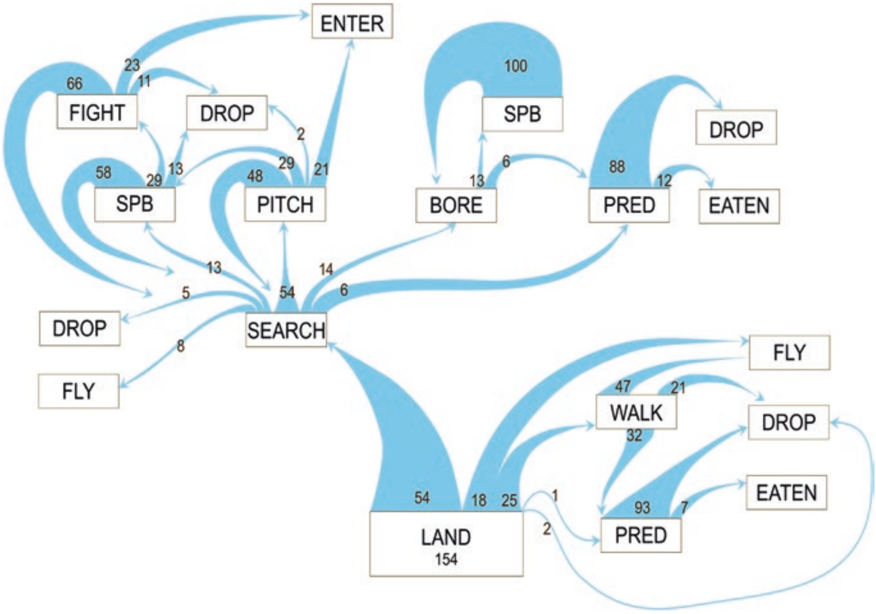

Fig. 7.11 Example of a descriptive model illustrating the processes involved in host selection by southern pine beetle (*SPB*). Activities of beetles landing on a host tree were divided into 12 categories. *Arrows* show the percentage of beetles within a behavior category that proceed to another category. The diagram begins with 154 beetles observed from after an initial landing event on the tree (*LAND box*). The categories of on-bark behavior are landing (*LAND*), walking (*WALK*), searching (*SEARCH*), investigating an entrance hole (*PITCH*), encountering another SPB (*SPB*), encountering a predator (*PRED*), and fighting with another SPB (*FIGHT*). Termination behavior is divided into flew from the tree (*FLY*), dropped from the tree (*DROP*), captured by a predator (*EATEN*), bored a gallery (*BORE*), and entered entrance hole (*ENTER*). Data from Bunt et al. (1980), redrawn in Sullivan (2011)

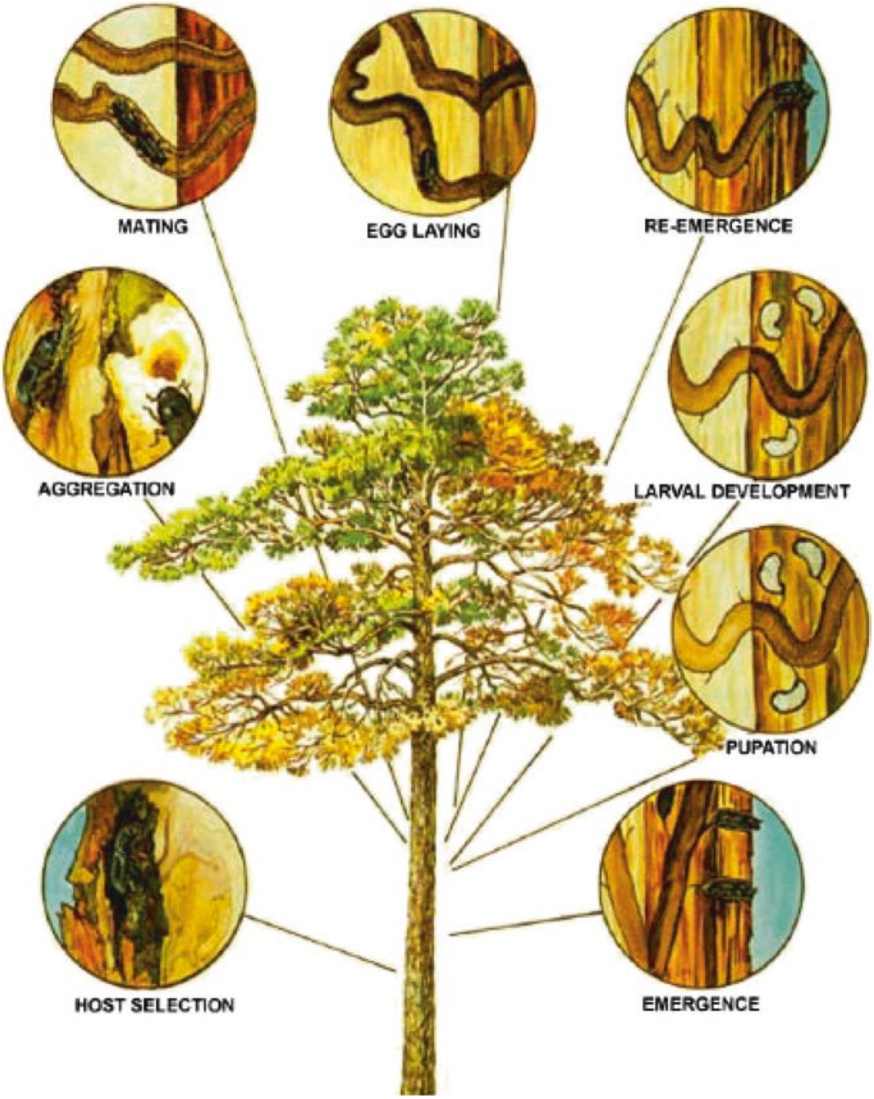

Fig. 7.12 Example of a descriptive model illustrating the various stages of southern pine beetle host utilization. Even simple drawings of life cycles can be efficient and powerful tools for communicating information and knowledge. Reproduced from Payne (1980) and Hain et al. (2011)

temporal pattern of SPB infestations during an outbreak. In this case, we would argue that the database itself is not the ecologically relevant model. Instead, SPBIS provides a useful, ecological model to the extent that it is able to deliver this complex information to an individual in a simple, descriptive way.

Descriptive models attempt to fill a large knowledge gap, and are the first step before developing more complex models. Their practical use requires much interpretation, which may take the form of conducting further research or utilizing their data in other types of models. This interpretation is most likely to enhance understanding rather than allowing prediction.

7.4.3.2 Integrative, Exploratory, or a Priori Models

The main objective of this type of modeling approach is to integrate disparate life history processes to deduce a higher level view of a system (Fig. 7.9). Often, this higher level view is not obvious by observing each component of the system independently. In this approach, the modeler uses knowledge of observable phenomenon, and orders and interprets them deciding (a priori or up front) those which are/are not important to the system. The result is a mathematical or simulation model that produces output that represents a higher level view of the system, based on the assumptions that have been made about how these processes interact (model parameters and functional relationships).

Examples from the SPB literature include the use of LANDIS (a landscape simulation model) to understand the impacts of SPB herbivory (disturbance) on forest succession (e.g., Cairns et al. 2008). LANDIS is a modeling framework that can be parameterized using simple assumptions about the environmental characteristics of a landscape (i.e., spatial pattern of ecological zones), life history characteristics of relevant tree species (e.g., seed dispersal, tree establishment rates, mortality, and shade tolerance), and disturbance (e.g., exogenous patterns of SPB damage). Using these parameters it then simulates the change in the composition of tree species (forest communities) over long timeframes (100–1000 years), providing a higher level view of forest succession (emergent property of the system) that is not possible to measure directly. Another example is provided by Fig. 7.13. Here we have used the development rates of SPB (Wagner et al. 1984) and spatially interpolated temperature data (Thornton et al. 1997) to calculate the potential number of generations that could be achieved by SPB across its range (again, an emergent property that is not directly obvious from the input parameters and data). Further examples include TAMBEETLE (Coulson et al. 1989; Feldman et al. 1981) and HOGModel (Salom et al. 2001; Satterlee 2002), both simulation models that represent the growth of an infestation under different stand conditions (basal area, DBH, and temperature) using temperature-driven life history parameters (e.g., survival, development, reproduction) collected under laboratory conditions.

In this category of models, the outputs do not necessarily require explicit statistical validation (although this could and should be done if appropriate measurements exist). Rather, the models serve to explore "what if?" scenarios. As such, experimentation is important for achieving a better understanding of the system. This involves manipulating parameters to explore how they affect the behavior of the system. For example, in the LANDIS model, simulations are created to explore different scenarios (manipulations of parameters) that investigate the state of the system under different levels of disturbance by SPB and fire. Equally, parameters and processes could be excluded or included in a model to explore how these affect model output.

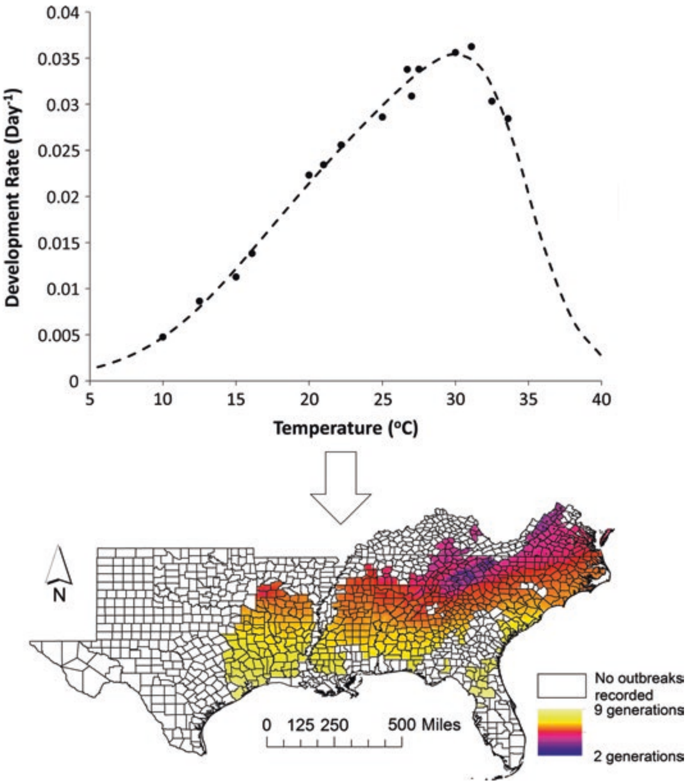

Fig. 7.13 Example of an integrative model estimating the number of generations of southern pine beetle across the southern United States. The number of generations is estimated using temperature-driven development rates model (illustrated in the *graph*) derived from laboratory experiments, and spatially interpolated temperature data

7.4.3.3 Inferential Models

Inferential models use explicit statistical methods to guide and challenge model development (Fig. 7.10). In this category, data must be available in a highly organized form that is amenable to statistical analysis. Here, the goal is to infer one or more unknown parameters from a set of known data. This can be done by creating one model (a priori), and then comparing its output to some real-world data. Or by developing "competing" models (each representing different processes), then statistically determining which provides the most parsimonious explanation of an observed phenomenon. Hilborn and Mangel (1997) provide an excellent text that deals with inferential modeling in ecology. Logistic regression is an example of a statistical model that has been used to understand the risk of stands becoming infested by SPB (e.g., Daniels et al. 1979; Zarnoch et al. 1984). Here, the dependent variable (whether a given stand has been infested or not) is compared to several independent variables (measurable properties of the stand such as the size and density of trees) to understand the relative importance of each of these factors in driving infestation probability.

Another example is provided by Turchin et al. (1991). Here, a data set illustrating the number of infestations in east Texas between 1958 and 1990 was used to infer the ecological processes most likely to have driven these patterns. Two competing models were proposed: SPB damage driven by weather and SPB driven by

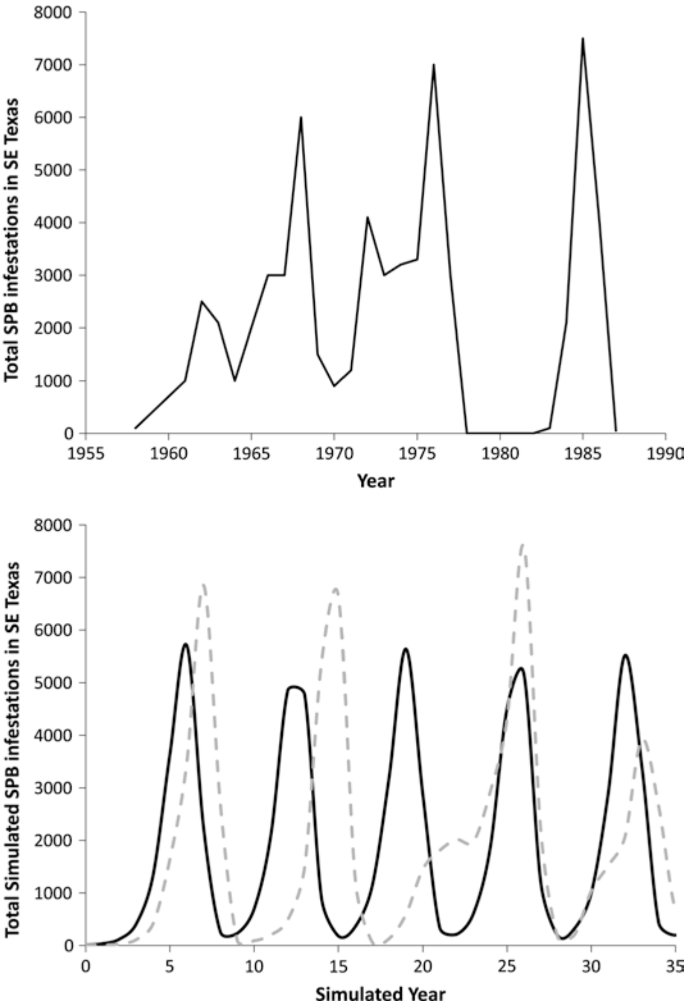

Fig. 7.14 The *top graph* shows the number of southern pine beetle (*SPB*) infestations per year between 1958 and 1988 as measured by the Texas Forest Service. The *bottom graph* shows the simulated number of infestations over the same time period based only on a model of delayed density dependence. In the *bottom graph*, *solid lines* show deterministic outputs of the model, *dashed lines* show a model with some error added to the process. The model is derived from a statistical analysis (inferential) of real-world data

changes in predation. Statistical methods were then used to infer which model was best supported by the data, leading to the conclusion that the cycles of SPB activity are most likely driven by delayed density effect occurring between SPB and its predators. Figure 7.14 shows the outputs from the model inferred from this study, compared to observations. This example is important for the SPB literature for several reasons. First, it provides the only existing mathematically plausible explanation for endogenous cycles of SPB damage (outbreaks). Second, their results have led to considerable and productive research (and a more detailed understanding) of the role of predators on SPB based on experimentation and observation at the scale of a single tree (e.g., Reeve 1997; Turchin et al. 1999), and on the behavior of potential predators. Finally, when retested with new data, the original conclusions of delayed density dependence did not hold (Friedenberg et al. 2008). This illustrates that the insights that can be gained from models come from carefully interpreting their results, even if they have been statistically validated.

Inferential modeling provides the highest level of scientific objectivity when determining causal relationships. Out of necessity, the examples above use relatively simple models to describe a higher level process. However, in theory, complex models can be fit to ecological data either by increasing the availability of data, or by constructing models where some of the processes are assumed to be known, and the unknowns (knowledge gaps) are estimated using statistical techniques. In practice, the limitations of inferential models are that data may not be available either in a format, or quantities, that allow vigorous statistical analysis.

7.5 Conclusions

The SPB has been studied intensively for nearly 100 years (St. George and Beal 1929). Despite this effort, we still do not fully understand the population dynamics of the insect, and therefore are unable to accurately predict when and where the damage resulting from infestations will occur. Put another way; although we know a lot about the fine-scale ecology of SPB, we do not yet understand how these processes interact to drive SPB population change. Although this statement could be true for almost any species, several factors make it especially relevant to the SPB. First, SPB populations fluctuate greatly in space and time. These fluctuations are difficult to explain mathematically based on our current knowledge of SPB ecology. Second, SPB population dynamics are almost impossible to observe directly, or to manipulate experimentally. Finally, because SPB significantly affects individuals and communities, our inability to understand when and where damage will occur has a significant cost to society. These characteristics define the specific nature of the SPB problem. Table 7.1 provides an interpretative overview of the SPB system, and how our concept of ecological disturbance, and classification of ecological models, could be used to address specific characteristics of the problem.

The most pressing research need for SPB is to develop models that are capable of explaining the initiation and decline of outbreaks, and within them, realistic

Table 7.1 Summary of the characteristics of the southern pine beetle (SPB) problem, consequences of specific issues, and potential solutions based on the concept of disturbance ecology and the value of different types of models

Issue	Consequence	Potential solution
SPB damage is unpredictable in space and time	SPB has similarly unpredictable effects on those who manage the forest	Rather than viewing SPB as a disturbance, conceptualize and model infestations and outbreaks as an endogenous property of the forest system to understand how system dynamics are affected by different spatial and temporal scales and ecological processes. Investigate the effects of exogenous disturbances on system dynamics
SPB damage has significant economic impacts	The temptation is to develop models that are predictive and *immediately* useful for decision making	Refocus efforts on developing models that improve understanding of the system
The forest system is undergoing considerable change from human activities	Historical patterns of SPB damage may not be applicable to the current state of the system	Identify the true disturbances to the system (e.g., climate change, human activities) and understand how they are affecting the frequency and intensity of outbreaks
Forest management has, and continues to have, the largest impact on the structure and composition of the southern forest	Changes in the structure of the forest, driven by human activities, influence SPB. Equally, SPB damage has a large impact on the way humans manage the forest	Consider representing the system as a coupled socio-ecological system. Represent management activities as endogenous processes of the system, where decision making and management (hence the structure of the forest) are influenced by beetle activity, and vice versa
SPB has been studied for over 100 years, across a range of environmental conditions, and from the perspective of many areas of interests and expertise	Much information and data is available with which to develop a holistic understanding of SPB population ecology. However, the breadth and amount of this information and data requires considerable organization and interpretation	Embrace different model types for different purposes:
		(1) Descriptive models to effectively communicate complex data and/or ideas
		(2) Integrative models to explore the dynamics of different representations of the system
		(3) Inferential models for statistically rigorous assessments of outputs and parameters
SPB occurs over a broad geographic range, and is a native, endogenous component of a complex ecological system	The logical constraint is that SPB population models should be representative of endemic and outbreak dynamics and is applicable for populations across its range	Although the goal should be to understand SPB as an endogenous component of the system, use simpler models to iteratively explore and understand subcomponents of the SPB problem

patterns of the initiation and decline of infestations. Given our concept of disturbance, these models should represent SPB damage as an innate (endogenous) property of a system that is driven by relatively few exogenous driving variables (see Fig. 7.7). So far, delayed density dependence is the only plausible ecological mechanism that has been shown to be mathematically capable of driving the characteristic oscillations of SPB populations (Turchin et al. 1991; Friedenberg et al. 2008). Even so, this model describes only temporal changes in population size and questions remain whether, or under what conditions, these same processes could drive the characteristic spatial pattern of infestations during outbreaks. In the context of disturbance, it is also interesting to note that the delayed density dependence model is capable of describing the occurrence of irruptive outbreaks without any external forces (disturbances) to the system. However, under these conditions it describes outbreaks that are regular and periodic, and therefore not representative of real SPB outbreak dynamics. However, when a stochastic term is introduced to the model (one interpretation of which is a representation of an external disturbance such as weather variation), it produces irregular dynamics much more similar to actual SPB outbreak patterns.

Our conceptual view of ecological disturbance provides a useful way of thinking about models of SPB. Currently, SPB damage is often viewed as a "disturbance" because the spatial and temporal scales that humans use to interpret and manage forest landscapes are relatively small compared to the ecological complexity and the broad temporal and spatial scales that drive SPB populations. However, SPB has always been an integral component of southern pine forests. Conceptualizing SPB as an endogenous property of a broader forest system may lead to new ideas about the factors that actually drive SPB damage, which may in turn lead to more effective forms of management. In other words, we can use the dual concepts of a bounded system and disturbance to think critically about what actually constitutes a disturbance to SPB populations and the forest landscape, defined by different spatial and temporal scales and entities. It is axiomatic that SPB causes periodic damage to the forest. But what external factors (disturbances) if any are actually driving this damage, and how do they affect the dynamics of the system and our ability to manage it? For example, do irregularities in weather patterns cause outbreaks, and if so, how large must these disturbances be to initiate an effect? Are changes in forestry practices or land use affecting the frequency and severity of outbreaks, and therefore the long-term persistence and resilience of the system? Exploring these questions will require considerable experimentation into how different "bounded systems" (e.g., spatial and temporal scale and processes of interest) and endogenous and exogenous processes affect system dynamics (Fig. 7.7).

Given past and future changes in the structure and composition of the southern forest, we suggest that a useful way of looking at the southern forest would be as a coupled socio-economic and ecological system. In other words, human management should increasingly be considered as a potential driver of SPB damage; and certainly one of the biggest factors likely to influence the long-term dynamics of the southern forest system. According to our working definition of disturbance, reciprocal links between human management, forest structure, and SPB damage would usefully redefine the nature of SPB disturbance. Instead of being viewed as an exogenous disturbance (i.e., the result of an unexplained SPB outbreak or infestation), SPB damage could be better described as the visible ecological effect of an exogenous human disturbance. Reframing models of the system in this way may lead to pragmatic but effective ways of managing SPB centered on human activities that are, by definition, within some control of forest managers.

Successfully modeling SPB damage as an endogenous property of the system will require a change in the way models are used and interpreted among SPB practitioners (see Sect. 7.4.3). Many of the ecological processes that are important to understanding broad scale population dynamics are difficult to observe directly or measure unequivocally. The life history of SPB is complex and intricately linked to other biotic (e.g., hosts, predators, parasites) and abiotic entities (e.g., pheromones and wind, temperature). Most often these processes are described qualitatively (for example in this chapter and in other referenced texts). However, quantitative approaches are also required to integrate this information into progressively more complete, unambiguous, and accurate descriptions of SPB populations. All types of models are important to this process. Descriptive models help summarize complex data (patterns of damage and ecological processes) to improve its clarity and accessibility to other scientists. Integrative models can be used to test ideas about how different ecological processes (defined by different bounded systems) interact to generate higher order properties of a system. And inferential models provide the means to rigorously test or compare hypotheses. Adopting this viewpoint, an enlightened view of the value of modeling is that it should allow different views of how a system works to be more formally documented, communicated, and tested. For SPB, this has special importance given the multidisciplinary nature of research, the ecological and sociological complexity of the problem, and because the periodic and transient nature of SPB damage requires information to be well organized, rapidly available, and easy to understand. As such, we should not expect any model to be *correct*. Instead, model building should be a creative, iterative, and exploratory process where competing or complementary models contribute collectively to an improved understanding of the SPB and how to manage its pestilence.

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Chapter 8
Exploring Interactions Among Multiple Disturbance Agents in Forest Landscapes: Simulating Effects of Fire, Beetles, and Disease Under Climate Change

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8.1 Introduction

Global climate varies naturally at millennial time scales, but humans, primarily through combustion of fossil fuels, have now added sufficient greenhouse gases to the atmosphere to cause rapid climate warming at a rate unprecedented in the last 10,000 years (IPCC 2007). In light of its potential adverse effects on natural, political, social, and economic systems, ecologists have been called upon to investigate the consequences of anthropogenic climate change on the world's ecosystems (Bachelet et al. 2001; Schneider et al. 2007). However, questions pertaining to the numerous, complex, and multi-scale interactions among ecological processes, disturbance agents, and climate drivers present intractable challenges with respect to scientific exploration, as traditional field methods used to explore ecosystem responses to environmental change are inadequate to capture complex interactions that occur across large areas and long time periods (Fig. 8.1). Multi-scale ecological interactions often result in nonlinear feedbacks that produce novel and unanticipated landscape responses to changing climates (Lauenroth et al. 1993; Temperli et al. 2013). These can be explored using simulation modeling, in which computer programs are developed to quantitatively simulate complex ecological processes and their interactions over decades or centuries (McKenzie et al. 2014).

In our opinion, most ecological responses to climate change are best evaluated and simulated at landscape scales using landscape models (LMs). Because of their limited spatial extent, finer-scale stand models cannot fully incorporate spatial aspects of disturbance regimes (Bugmann 2001), and coarser-scale Dynamic Global Vegetation Models (DGVMs) are not designed to simulate important species- and plant-level disturbance effects such as successional trajectories and disturbance survival (Flannigan et al. 2009). Spatially explicit simulations using LMs

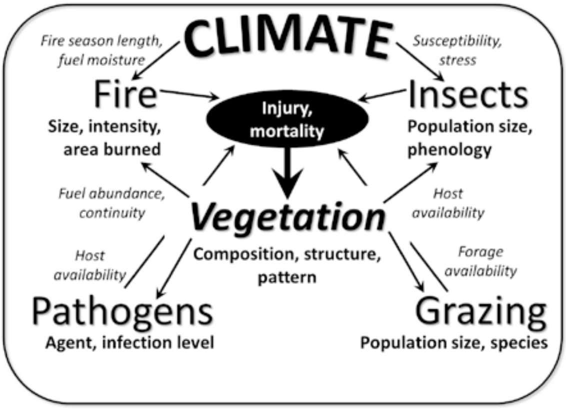

Fig. 8.1 The direct and indirect interactions among disturbances and vegetation that dictate landscape dynamics. Shown are four of the most common disturbances currently affecting landscapes around the world: wildland fire, insects, pathogens (disease), and grazing by native and exotic ungulates

have greatly improved our ability to explore and understand complex interactions (Scheller and Mladenoff 2007; Perry and Millington 2008). Several sources provide details on landscape change modeling (Mladenoff and Baker 1999), ecosystem dynamics (Canham et al. 2004), and spatial fire spread and effects (Gardner et al. 1999). In various reviews, LMs are classified based on their design, structure, detail, resolution, and geographical area (see Keane et al. 2004; He 2008; Baker 1989; Moran and Corcoran 2012; Scheller and Mladenoff 2007, respectively). To realistically predict climate change effects, LMs must be structured to simulate disturbance processes, vegetation growth and mortality, and species composition and distribution as well as their interactions across multiple scales (Bachelet et al. 2000; Purves and Pacala 2008). However, the level of mechanistic detail needed to realistically simulate important interactions among these processes and variables remains a central challenge in landscape modeling (Gustafson 2013).

In this chapter, we explore a unique subset of the many ecological interactions that occur at landscape scales—the interactions among disturbances (Fig. 8.1). Disturbances influence vegetation distribution, structure, and composition, and may indirectly and directly interact with one another and with changing climate to create novel landscapes (Kitzberger et al. 2012). Warming climates have already altered interactions among disturbance regimes resulting in highly visible and rapidly occurring changes in landscape composition and structure, and the importance of these interactions have been shown in studies across the world (Green and Saladin 2005; Parker et al. 2006). In the United States, Bachelet et al. (2000) documented the interactive effects of fire and grazing on vegetation conditions in South Dakota pine forests, while Buma and Wessman (2011) showed that fire, windthrow, and salvage logging interactions dictated vegetation response. Allen (2007) attributed the cause of forest dieback in New Mexico to the interactions of fire, grazing, erosion, and severe drought, and Beh et al. (2014) found that unique interactions between sudden oak death (*Phytophthora ramorum*) and wildfire contributed to the intensity of ambrosia beetle species attacks in California tanoak (*Notholithocarpus densiflorus*) forests. In South America, Matson and Bart (2013) showed that the interaction of fire and grazing dictate shrub encroachment in the Andes mountains. Lewis and Lindgren (2002) found that interactions between tomentosus root disease (*Inonotus tomentosus*) and spruce beetle (*Dendroctonus rufipennis*) controlled tree mortality and wood volume lost in boreal forests of British Columbia, Canada, while the importance of drought, grazing, and fire interactions to the structure and composition of grasslands was documented by Koerner and Collins (2014) in South Africa and Hobbs et al. (2003) in Australia.

To demonstrate the importance of effects of single and interacting disturbances on landscapes, we focused this chapter on a subset of disturbances that are common across many US Rocky Mountain landscapes: wildland fire (any fire that occurs in a non-developed or sparsely developed area), mountain pine beetle (*Dendroctonus ponderosae*), and white pine blister rust (*Cronartium ribicola*). Based on a review of the literature, we discuss the mechanisms of each disturbance type, including possible interactions from each combination of the three disturbances. We then use a landscape simulation model to evaluate how single and interacting disturbances respond to changes in climate and influence landscapes. Because the magnitude, trend, and type of disturbance interactions differ across ecosystems, our simulation results cannot be wholly extrapolated to other landscapes; however, our goal in this chapter is to demonstrate the general importance of disturbance interactions in influencing future landscape composition and structure.

8.2 The Simulation Model and Application

FireBGCv2 (Fire BioGeoChemical model Version 2) is a bottom-up, mechanistic, individual tree, forest succession model containing stochastic properties implemented in a spatial domain (see Keane et al. 2011 for complete model documentation). It can be categorized as a landscape fire succession model (Keane et al. 2004), a forest landscape model (He 2008), or a landscape dynamics model (Mladenoff and Baker 1999). Versions of the model have been used to address a wide variety of research questions including climate change effects on stream temperatures, wildlife, and vegetation composition (Loehman et al. 2011a); management effectiveness; grazing interactions with fire; landscape structure; fuel-snag dynamics; and carbon emissions (Keane et al. 1997). FireBGCv2 contains five hierarchical levels of spatial organization from coarse, fixed-boundary sites defined by similar topography, weather, soils, and potential vegetation to dynamically created stands that differ by existing vegetation composition and structure; simulation plots on which ecosystem processes are modeled for computational efficiency; species with well-defined physiological parameters; and individual trees, each of which is explicitly represented with attributes, such as age, height, diameter at breast height (DBH), and height to live crown. FireBGCv2 simulates basic processes such as tree growth, organic matter decomposition, and litterfall using detailed physical and biogeochemical relationships (Keane et al. 2011). Long-term daily weather streams drive primary canopy processes (e.g., transpiration, photosynthesis, and respiration), vegetation phenology (e.g., curing, leaf fall), and fire dynamics (e.g., ignition, fuel moisture, spread, intensity) within the simulation landscape.

Weather, tree species and structural traits, and landscape composition determine fire, mountain pine beetle, and white pine blister rust activity within a simulation (Fig. 8.2). In the simulations presented here, fire ignition was based on historical distribution of the Keetch Byram Drought Index, fuel loading, and fuel moisture, while fire spread was modeled on slope and wind vectors, fuel characteristics, and fuel moisture. Blister rust infections for five-needle pines were simulated when site daily relative humidity was above 90 % and daily mean temperature was above 10 °C (Loehman et al. 2011a); and mountain pine beetle epidemics were initiated in the model when lethal temperature thresholds (below −40 °C for a single day, or below −20 °C for 2 weeks) were not met for 40 years, and host pine species comprised more than 30 % of the simulation landscape (Keane et al. 2011).

We simulated all combinations of wildland fire, mountain pine beetle, and white pine blister rust for two forested landscapes that comprise a range of

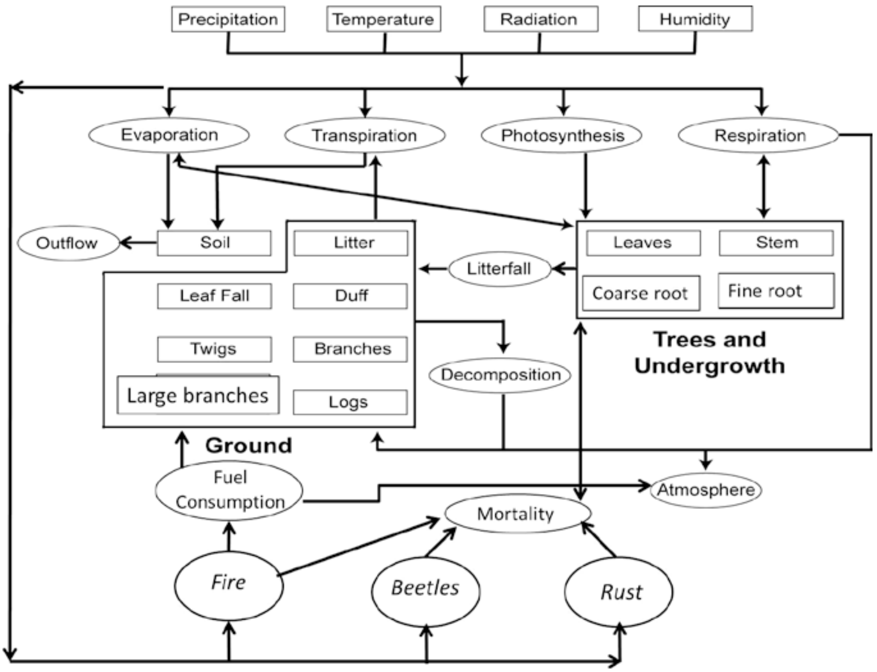

Fig. 8.2 An illustration of the complex linkages among disturbances (bottom) and the ecological processes and components with which they interact to drive landscape behavior. This diagram depicts the interacting ecological processes simulated by the FireBGCv2 landscape model (Keane et al. 2011)

climate, vegetation, and fire regime types common to the US Rocky Mountain region (Fig. 8.3):

- **East Fork of the Bitterroot River (EFBR)**: A 128,000 ha dry mixed-conifer ecosystem in western Montana, USA, with an historical low- to high-frequency, mixed-severity fire regime. Lower-elevation stands comprise primarily ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii)*, and higher elevation stands are dominated by lodgepole pine (*Pinus contorta* var. *latifolia)*, whitebark pine (*Pinus albicaulis*), subalpine fir *(Abies lasiocarpa),* and Engelmann spruce (*Picea engelmannii*).
- **Yellowstone Central Plateau (YCP)**: An 80,000 ha, high-elevation lodgepole pine ecosystem in Yellowstone National Park, USA, with an historical low-frequency, high-severity fire regime. Stands contain minor amounts of Douglas-fir, whitebark pine, subalpine fir, and Engelmann spruce.

We simulated disturbance interactions under two climate scenarios:

- **Current climate**: The recorded daily weather for the last 50+ years collected within or near each of the simulation landscapes, compiled by the National Climatic Data Center. Weather years were used in sequence, repeated for multiple cycles over a 250-year simulation period.

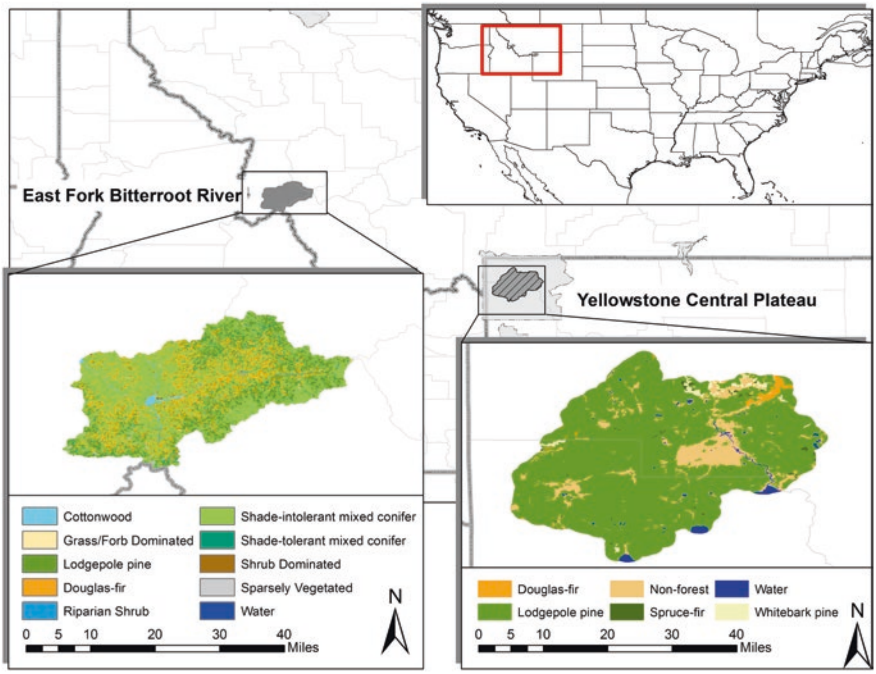

Fig. 8.3 FireBGCv2 simulation landscapes: the East Fork Bitterroot River (EFBR) and Yellowstone Central Plateau (YCP), both within the northern Rocky Mountains, USA

- **Warmer climate**: A climate change scenario in which temperatures increase by an average of 2.8 °C relative to historical weather. Climate offsets for each landscape represent an ensemble average of climate model projections for the A2 emissions scenario (IPCC 2007) downscaled to 12 km for the period 2070 to 2099 (Girvetz et al. 2009).

FireBGCv2 simulations are usually performed with multiple replicates to account for stochastic model elements (e.g., Loehman et al. 2011a), but we did only one run per scenario for the purposes of illustration. For each 250-year simulation, disturbances were implemented beginning in the initial simulation year. We report two response variables sensitive to disturbance interaction effects: species composition (dominant species of each modeled stand) and tree basal area (m^2 ha^{-1}).

8.3 Disturbances

In an ecological context it is not particularly informative to talk about disturbance in terms of a single event because it is the *pattern* of disturbances through time that shapes ecosystems. A disturbance regime defines the spatial arrangement, frequency, intensity, and ecological consequences of disturbance events repeated

Table 8.1 Glossary of terms often used to describe disturbance regimes

Disturbance characteristic	Description	Example
Agent	Factor causing the disturbance	Mountain pine beetle is an agent that kills trees
Source, cause	Origin of the agent	Lightning is a source for wildland fire
Frequency	How often the disturbance occurs or its return time	Years since last fire or beetle outbreak (scale dependent)
Intensity	A description of the magnitude of the disturbance agent	Mountain pine beetle population levels; wildland fire heat output
Severity	The level of impact of the disturbance on the environment	Percent tree mortality resulting from mountain pine beetle infestation; fuel consumption in wildland fires
Size	Spatial extent of the disturbance	Mountain pine beetles can kill trees in small patches or across entire landscapes
Pattern	Patch size distribution of disturbance effects; spatial heterogeneity of disturbance effects	Fire can burn large areas but weather and fuels can influence fire intensity and therefore the patchwork of tree mortality
Seasonality	Time of year when disturbance occurs	Species phenology can influence wildland fire effects; spring burns when plants are growing can be more damaging than fall burns when plants are dormant
Duration	Length of time that disturbances occur	Mountain pine beetle outbreaks usually last 3–8 years; fires can burn for a day or for an entire summer
Interactions	Disturbances interact with one another, as well as climate, vegetation and other landscape characteristics	Mountain pine beetles can create fuel complexes that facilitate or exclude wildland fire
Variability	The spatial and temporal variability of the disturbance characteristics listed above	Highly variable weather and mountain pine beetle mortality can cause highly variable burn conditions resulting in patchy burns of various sizes

over space and time. Assessments of a disturbance regime must encompass an area of land that is large enough that the full range of disturbance sizes are manifest, and long enough so that the full range of disturbance characteristics are captured. Disturbance regimes are generally described by 11 characteristics (Table 8.1; Simard 1991; Agee 1993; Skinner and Chang 1996; Keane 2013). These characteristics illustrate the great complexity that confounds any simplistic representation of interacting disturbance regimes in land management. The following is a description of three important disturbances, and their interactions within the US northern Rocky Mountains.

8.3.1 Wildland Fire

Wildland fire is ubiquitous throughout forest ecosystems of the northern Rockies and is arguably the most dominant landscape disturbance in the region. Wildland fire is very responsive to variability in environmental conditions on the landscape, including vegetation type and distribution, climate, weather, and topography. Where rates of vegetation production outpace decomposition, sufficient biomass is available to support fires. Wildland fuels lose moisture and become flammable in the region's typically warm and dry summers, during which there are ample sources of ignition from lightning strikes and humans. Therefore, the active fire season (period conducive to active burning) is in the summer, typically from late June through October, with shorter seasons at higher elevation sites where snowpack can persist well into July. Regionally, widespread fire years are correlated with drought (Heyerdahl et al. 2008; Morgan et al. 2008). At landscape scales, topography can influence the spatial pattern of fire spread. In dissected mountainous areas, topographic features (e.g., barren slopes) can form barriers to fire spread (Grissino-Mayer et al. 2004), but where drainages are aligned with prevailing winds, topography can facilitate the spread of large fires (Sharples 2009).

The composition and structure of forests in the northern Rockies is strongly determined by climate, elevation, topographic position, and fire history. In general, fire regimes vary along environmental gradients, with fire frequency decreasing and fire severity increasing with elevation. For example, at the lowest and driest elevations where forests are dominated by ponderosa pine, frequent surface fires historically consumed litter and dead wood, and killed seedlings and smaller trees. Adaptive traits such as thick bark allowed mature ponderosa pines to survive many repeated fires over time and tree densities were kept low.

Fire exclusion since the 1920s has increased surface fuel loads, tree densities, and ladder fuels, especially in low-elevation, dry conifer forests (Schoennagel et al. 2004). As a result, fires in these forests may be larger and more intense, and may cause higher rates of tree mortality than historical fires. In higher elevation forests, however, where fires were historically infrequent, fire exclusion has not affected the fire regimes (Romme and Despain 1989; Schoennagel et al. 2004). For example, lodgepole pine forests in Yellowstone National Park historically were subject to large, stand-replacing fires (Romme 1982), and lodgepole pine has the unique ability to regenerate prolifically after these severe fires from seeds released from the tree's serotinous cones (Turner et al. 2003).

Future climate projections for the northern Rocky Mountains have dramatic implications for fire regimes. The fire season is expected to grow longer, allowing more fires to occur and those fires to burn for longer periods and across larger areas (Westerling et al. 2006). Earlier onset of snow melt will reduce fuel moisture during the fire season, making a larger portion of the landscape flammable for longer periods of time (Miller et al. 2011).

8.3.2 Mountain Pine Beetle (MPB)

The principal agent of insect-caused mortality in northern Rocky Mountain pine forests is mountain pine beetle (MPB). The MPB is a native, cambial-feeding bark beetle of several western pines, including ponderosa pine, western white pine (*Pinus monticola*), whitebark pine, limber pine (*Pinus flexilus*), and lodgepole pine (Safranyik and Carroll 2006; Gibson et al. 2009). The entire life cycle is spent beneath the bark of host trees, except when adults emerge from brood trees and fly in search of new host trees. Tree defense against MPB is complex, including both physical (e.g., resin flow) and chemical (e.g., terpenoid compounds) defenses, but these match-head-size beetles can overwhelm host defenses through sheer numbers with a mass attack strategy. The MPB is an integral component of forest ecosystem processes because of its role in stand thinning and redistribution of resources and nutrients important for tree regeneration. It is also recognized as an aggressive and economically important forest insect responsible for tree mortality across large areas (Gibson et al. 2009). Beetle-induced tree mortality influences biogeochemical processes with effects that are nonlinear in time and space and depend on the stage of beetle infestation and rate of ecosystem recovery (Griffin et al. 2011; Edburg et al. 2012). For example, Edburg et al. (2012) found that the timing and amount of snow melt, as well as the quality of water, may be substantially modified following bark beetle outbreaks, and Kurz et al. (2008) report that widespread tree mortality during MPB outbreaks greatly reduced forest carbon uptake and increased carbon emissions from decay of killed trees.

Mountain pine beetle populations are typically innocuous, infesting a few damaged or suppressed trees scattered throughout the forest. However, populations periodically erupt into large-scale outbreaks (Safranyik and Carroll 2006). Such outbreaks can cause dramatic tree mortality over extensive areas in only a few years, often killing the largest host trees in high-density stands. Although some stands may sustain nearly complete mortality (Amman 1977), average mortality in mature lodgepole pine stands across the landscape is usually 30–45 % (Safranyik and Carroll 2006). Mortality of reproductive whitebark pine can exceed 95 % (Schwandt 2006; Logan et al. 2010).

Periodic MPB outbreaks have occurred for millennia (Brunelle et al. 2008) with, for example, pre-twentieth century dates of MPB-caused mortality inferred from whitebark pine tree-ring records (Perkins and Swetnam 1996). From 1990 to 2014, 6.6 million ha of forest in the western United States have been infested by MPB (Jenkins et al. 2012), and the MPB outbreak that has been ongoing in British Columbia over the past decade is the largest recorded in the twentieth century (Sambaraju et al. 2012). Moreover, evidence suggests that the suitable climatic window for MPB is expanding to encompass additional territory, and outbreaks are occurring further north, further south, and at higher elevations than occurred previously (Safranyik et al. 2010; Cullingham et al. 2011; Lynch and O'Connor 2013). For example, MPBs are now found in hybrid lodgepole pine/jack pine (*Pinus banksiana*) stands and are able to infest natural jack pine stands at the leading edge of the Canadian front, which could facilitate a host-range expansion into areas of the boreal forest (Cullingham et al. 2011).

An important focus of current research is the degree to which changes in climate are likely to affect tree host populations and beetle dynamics. Climate is known to govern beetle survival and growth because beetle development and dispersal are sensitive to temperature (Bentz et al. 2010). Recent evidence confirms that MPB activity has been influenced by changes in climate. For example, MPB flight season in the Colorado Front Range now occurs at least one month earlier and for twice as long as recorded historically (Mitton and Ferrenberg 2012). Statistical models based on historical climate and beetle distributions demonstrate that minimum winter temperatures and drought conditions in current and preceding years influence outbreak size (Preisler et al. 2012). Coops et al. (2012) modeled areas of vulnerable host trees and areas of potential beetle expansion under future climate and suggested that timing and location of future outbreaks will depend on complex interactions among climate-driven effects on tree distributions and tree stress, as well as independent effects on MPB phenology and outbreak dynamics.

8.3.3 White Pine Blister Rust (WPBR)

White pine blister rust (WPBR) is an exotic fungus, inadvertently introduced into the United States from Europe around 1910 (Bingham 1983; Tomback and Achuff 2011). Its complex life cycle requires two hosts, with two spore-producing stages on white pine and three separate spore-producing stages on the alternate hosts, *Ribes* spp. The WPBR is a fungus that infects only five-needle pine species, and all nine North American five-needle pine species are susceptible. Infection begins when basidiospores, produced on *Ribes* leaves in late summer, are wind dispersed to pines in the vicinity. The basidiospores germinate on the pine needles and hyphae grow through the stomata into the cell tissues, needles, and stem (Patton and Johnson 1970). Cankers form when the fungus reaches large branches and the main stem, and canker formation and colonization of the phloem by the hyphae, which initially cause branch dieback and top kill, eventually kill the tree. Cankers form blisters that erupt through the bark, releasing aeciospores, the spore stage that infects *Ribes* (see Schwandt et al. (2013) for a detailed description of the WPBR life cycle). Basidiospores are short-lived and disperse relatively short distances, but aeciospores are hardy and can disperse long distances (>100 km; Frank et al. 2008). Basidiospores have a narrow window for production and successful infection of pine needles, requiring warm temperatures (>20 °C) and high humidities (>98 %) (McDonald et al. 1981). The time required for WPBR to kill its host varies by species (5–10 years for western white pine and over 20 years for whitebark pine) (Hoff and Hagle 1990). Native pine populations show some heritable resistance to WPBR but frequency of resistance is low; often less than 1 % of trees show resistant traits (Hoff et al. 1980). Tree mortality affects stand structure and species composition, but the most serious impact of WPBR is long-term effects to white pine regeneration capacity, with direct mortality of the more susceptible seedlings and saplings and the loss of cone and seed production following branch dieback and top kill.

8.4 Disturbance Interactions

8.4.1 Wildland Fire and Mountain Pine Beetle

Wildland fires and insect outbreaks are the two primary natural disturbance processes in conifer forests of western North America (Hicke et al. 2012; Jenkins et al. 2012). How wildland fire and bark beetles interact has been an important research topic since the early twentieth century (Miller and Patterson 1927; Evenden and Gibson 1940; Weaver 1943) with research primarily focused on the potential for increased fire hazard following outbreaks. Results of multiple studies have indicated changes in fire behavior, extent, and severity result from bark beetle-caused mortality in pine forests, with variability in fire patterns heavily influenced by climate, weather, topography, forest type, and disturbance history (see Hicke et al. 2012 for a summary). Fewer studies have addressed the influence of wildland fires on bark beetle disturbance regimes, and fewer still have examined the reciprocal interactions of beetles and fire through several disturbance cycles (but see Parker et al. 2006). Climate factors, in particular drought and increased temperatures, are recognized as key drivers of both wildland fires and bark beetle outbreaks (Hicke et al. 2012). Anthropogenic climate change has been recognized as a causal factor in recent increases in annual area burned by wildfires (Littell et al. 2009) and area affected by bark beetle outbreaks (Bentz et al. 2010). Predictions of warmer temperatures and increased drought stress suggest that the total area susceptible to or affected by beetle outbreaks and large or severe fires may increase in the coming decades (Williams et al. 2013). Acting independently or synchronously in space and time, wildland fires, and MPB outbreaks can substantially influence forest structure, composition, and function; abruptly reorganize landscapes; and alter biogeochemical processes such as carbon cycling, water supply, and nutrient cycles (Fettig et al. 2007; Kurz et al. 2008; Edburg et al. 2012; Falk 2013; Hansen 2014).

Though MPB can be found in fire-damaged trees (McHugh et al. 2003; Schwilk et al. 2006; Six and Skov 2009), it is only weakly attracted to fire-scorched trees (Geiszler et al. 1984; Davis et al. 2012). MPBs rarely contribute significantly to post-fire tree mortality (Geiszler et al. 1984; Powell et al. 2012; Jenkins et al. 2014), and beetle-caused mortality is usually limited to the immediate vicinity of the fire (Ryan and Amman 1996). However, it has been shown that fire injury can increase tree susceptibility to MPB attack, and MPB can kill fire-damaged trees (McHugh et al. 2003; Davis et al. 2012; Jenkins et al. 2014). Although fires can contribute to maintaining local MPB populations (Elkin and Reid 2004; Davis et al. 2012; Powell et al. 2012), fires are not known to initiate MPB outbreaks (Mitchell and Sartwell 1974; Powell et al. 2012).

Fire effects on MPB populations are time-dependent. For example, fire-weakened trees are colonized only when fire occurs near the time when beetles are searching for new host trees, so that beetles encounter the trees before phloem resources become unsuitable (Parker et al. 2006). Although MPB reproduce in fire-damaged trees, this resource benefit lasts only a few months or years after a fire (Davis et al. 2012; Powell et al. 2012). Wildland fires can affect beetle activity indirectly over longer time periods by altering species composition and structure of forests (e.g., removing fire-intolerant species) and providing increased water, light, and nutrients for surviving trees (i.e., growth release), thus influencing the availability and vigor of suitable host trees (Hessburg et al. 2005; Fettig et al. 2007; Keeling and Sala 2012). In addition, stand-replacing fires can reduce the likelihood of MBP attack until regenerating forests have attained a threshold diameter sufficient to attract beetles, especially when beetle populations are relatively low (Kulakowski et al. 2012).

Mountain pine beetle activity influences wildland fire by altering the quantity, type, vertical and horizontal arrangement, and chemical and moisture properties of dead and live vegetative biomass (fuel) available to burn (Hicke et al. 2012). Thus, a MPB outbreak has the potential to change the probability of fire occurrence, potential for crown fire, rate of fire spread, and burn severity patterns and variability (Table 8.1). Beetle-caused tree mortality can also influence the balance of light, water, and nutrients available for growth of overstory and understory plants, thereby altering species composition and stand structure (i.e., fuel characteristics) for years after an outbreak (Hansen 2014).

Mountain pine beetle impacts in forests occur in three phases important for fire behavior: the endemic phase, in which beetles are restricted to stressed or damaged trees; the epidemic phase, in which large beetle populations attack and kill as many as 80–95 % of susceptible host trees within stands; and the post-epidemic phase, which lasts for approximately five years after an epidemic (Jenkins et al. 2008; Safranyik et al. 2010; Hansen 2014). During the endemic phase, beetle influence on fuels and subsequent fire behavior is fairly limited, as few trees are affected (Page and Jenkins 2007). In the epidemic and post-epidemic phases, fuel and fire characteristics depend on time since attack (Hicke et al. 2012). One to three years after initial attack, when needles are yellowing or red but still attached to branches, attacked trees have lower foliar moisture content, and therefore higher flammability and torching potential, than green trees. Because aerial fuel continuity is maintained, active crown fire potential is high (Page et al. 2012; Jenkins et al. 2014). Four to ten years after attack, standing dead trees have lost their needles and small branches, making active crown fire potential lower than in non-attacked stands, but increased fine surface fuel loads result in higher surface fire rates of spread, flame lengths, and torching potential (Hicke et al. 2012; Schoennagel et al. 2012). The highest fire hazard is assumed to occur in the post-epidemic phase, decades after attack, as a result of accumulation of heavy, large-diameter fuels (snags and large branches), regeneration, and increased wind speeds and drying of fuels resulting from the loss of sheltering vegetation (Jenkins et al. 2008). Fire behaviors and fire effects associated with post-epidemic stands include increased duration of flaming and smoldering, increased fireline intensity, increased potential for crown fire initiation, and increased fire severity (Jenkins et al. 2008; Hicke et al. 2012; Schoennagel et al. 2012).

Consistent with the interactions described above, our modeling results indicate that interactions of wildland fire and MPB activity influence the abundance

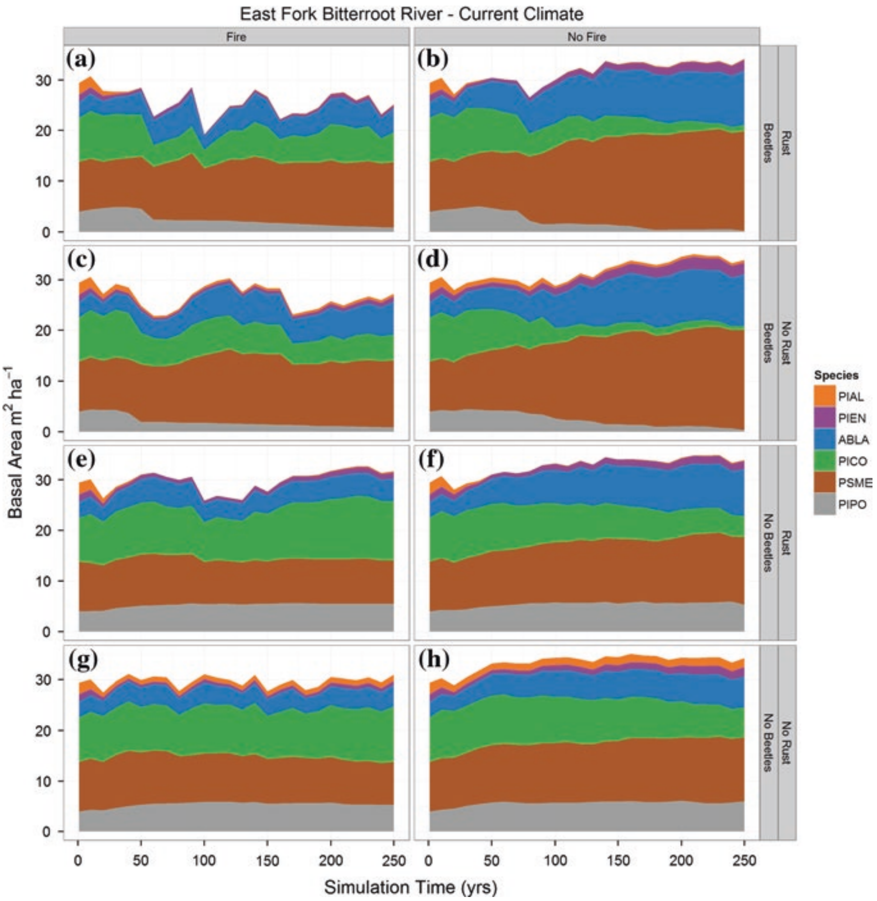

Fig. 8.4 Landscape composition of species cover types mapped using the plurality of basal area for current climate (CC) for the East Fork of the Bitterroot River (EFBR) landscape with all combinations of fire, white pine blister rust (WPBR), and mountain pine beetle (MPB): **a** fire, WPBR, and MPB, **b** no fire, WPBR, MPB, **c** fire and MPB, **d** MPB only, **e** fire and WPBR, **f** WPBR only, **g** fire only, and **h** no disturbances. *Species* PIAL-whitebark pine, PIEN-Engelmann spruce, PICO-lodgepole pine, PSME-Douglas-fir, and PIPO-ponderosa pine

of individual species on the landscape (Figs. 8.4 and 8.6). Species responses are directly linked to the physiological and life history characteristics that control response to fire and suitability as host species for MPB. As a result of differences in species composition and landscape configuration in each of our simulation landscapes, climate (current vs. projected future) influences fire and beetle interactions in different ways. For example, the EFBR landscape is dominated by low-elevation conifers that are adapted to relatively frequent fire and are MPB hosts, with smaller components of high-elevation, fire-intolerant, and non-host species (Fig. 8.4a). Under current climate and without additional MPB or WPBR disturbance, simulated fires limit the basal area of fire-intolerant whitebark pine, Engelmann spruce, and subalpine fir and, where their distributions overlap, favor lodgepole pine over Douglas-fir (Fig. 8.4g). Simulated MPB activity in the absence of fire substantially decreases the basal area of host species (lodgepole pine, ponderosa pine, and whitebark pine), allowing for an increase in non-host species such as Douglas-fir, Engelmann spruce, and subalpine fir (Fig. 8.4d). The interaction of MPB and fire produces some of the lowest landscape basal areas. Significantly, we found that fire-mediated MPB effects at the individual species level restrict the abundance of subalpine fir and Engelmann spruce at higher elevations and maintain small but viable populations of lodgepole pine and ponderosa pine at lower elevations. Compared to current climate, the simulated warmer climate has little effect on total basal area in the absence of disturbance, but increases the basal area of Douglas-fir at the expense of lodgepole pine (Fig. 8.5h). Similar to current climate scenarios, in a warmer climate fire reduces the basal area of fire-intolerant trees (Fig. 8.5a, c, e, g), and the interaction of fire and MBP decreases basal area of MPB host tree species and high-elevation conifers, with or without the influence of WPBR (Fig. 8.5a, c). However, the warmer climate decreases fire rotation, increases annual average area burned, and increases the percent of high severity fires for all disturbance scenarios, but these results are more variable across time (Table 8.2).

The vast majority of the YCP landscape is dominated by lodgepole pine, a fire-sensitive and MPB host species, with lesser amounts of high-elevation, non-host species (Engelmann spruce, subalpine fir), and minor populations of Douglas-fir and whitebark pine (Fig. 8.6). Under current climate, simulated wildland fires exert minor and short-term control over species basal area (Fig. 8.6c). Simulated MPB activity, one of the dominant disturbance processes on the YCP landscape, causes periodic and substantial declines in lodgepole pine, allowing for a persistent increase in subalpine fir and Engelmann spruce over initial levels (Fig. 8.6a, b, c, d). The interaction of MPB and fire nearly doubles the percent of high-severity fire as the result of increased surface fuels from MPB-killed trees (Table 8.2) and limits subalpine fir and Engelmann spruce growth, but does not mediate beetle effects on lodgepole pine (Fig. 8.6c, g). Simulated climate change is not a strong enough stressor to alter species or landscape basal area in the absence of disturbance; however, under a warmer climate fires increase in severity and reduce species basal area (Fig. 8.7; Table 8.2). Fires also facilitate increased Douglas-fir representation by freeing resource space previously occupied by lodgepole pine, allowing for the expansion of this more fire-tolerant species, but Douglas-fir representation is also driven by seed source limitations (Fig. 8.7a, c, g).

8.4.2 Wildland Fire and White Pine Blister Rust

Effects of wildland fire on WPBR are minor and primarily indirect, with the exception of the possibility that smoke may kill rust spores produced at the time of the fire (Parmeter and Uhrenholdt 1975). Fire indirectly affects WPBR by

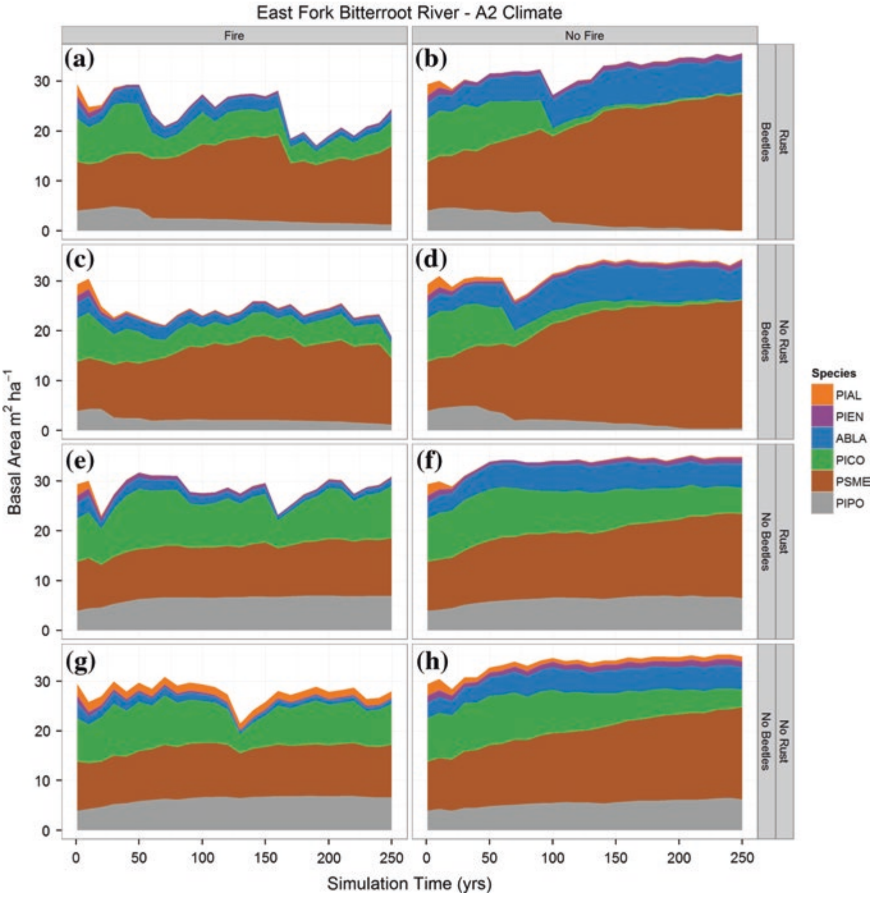

Fig. 8.5 Landscape composition of species cover types mapped using the plurality of basal area for a warmer climate (A2) for the East Fork of the Bitterroot River (EFBR) landscape with all combinations of fire, white pine blister rust (WPBR), and mountain pine beetle (MPB): **a** fire, WPBR, and MPB, **b** no fire, WPBR, MPB, **c** fire and MPB, **d** MPB only, **e** fire and WPBR, **f** WPBR only, **g** fire only, and **h** no disturbances. Species: PIAL-whitebark pine, PIEN-Engelmann spruce, PICO-lodgepole pine, PSME-Douglas-fir, and PIPO-ponderosa pine

changing the size, distribution, and abundance of its two hosts—five-needle pines and *Ribes* spp. Most five-needle pines of the western United States are somewhat (whitebark pine, limber pine) to highly (western white pine) fire-adapted, with thick bark, high canopies, and deep roots (Ryan and Reinhardt 1988). Mixed and high severity fires are common in forests where WPBR is present (Arno et al. 2000; Murray 2007). These fires can create favorable conditions for pine regeneration because most five-needle pine seeds are rodent- and bird-dispersed and thus better adapted to spread into post-fire landscapes than seeds of their tree competitors (Lanner 1989; Morgan et al. 1994). Severe fires that kill rust-resistant pine

Table 8.2 Summaries of wildland fire characteristics from the FireBGCv2 model for two simulation landscapes: The East Fork Bitterroot River and Yellowstone Central Plateau for current climate and warmer climate scenarios

Scenario	Fire return interval (years)	Fire rotation (years)	Annual average area burned (%)	High severity fires (%)	Average tree mortality (%)
East Fork Bitterroot River (EFBR)—current climate (CC)					
Fire only	107 (41.64)	119	1.51	4.6	26.8 (0.10)
Fire, WPBR	96 (45.30)	110	1.72	3.9	27.0 (0.08)
Fire, MPB	109 (36.45)	112	1.37	8.6	31.3 (0.13)
Fire, MPB,WPBR	89 (62.06)	98	1.64	3.9	27.7 (0.12)
East Fork Bitterroot River (EFBR)—warmer climate (A2)					
Fire only	31 (30.77)	47	3.22	6.2	24.6 (0.08)
Fire, WPBR	43 (40.88)	56	3.09	6.4	22.3 (0.08)
Fire, MPB	48 (43.73)	36	2.90	5.3	27.1 (0.10)
Fire, MPB,WPBR	89 (61.56)	62	2.81	9.1	27.4 (0.10)
Yellowstone Central Plateau (YCP)—current climate (CC)					
Fire only	145 (43.46)	284	0.47	40.1	46.1 (0.32)
Fire, WPBR	259 (33.95)	310	0.24	52.4	38.6 (0.36)
Fire, MPB	254 (27.34)	518	0.23	77.3	75.1 (0.30)
Fire, MPB,WPBR	238 (32.07)	387	0.33	81.9	58.3 (0.39)
Yellowstone Central Plateau (YCP)—warmer climate (A2)					
Fire only	132 (59.14)	98	0.93	57.9	62.5 (0.22)
Fire, WPBR	215 (13.03)	204	0.48	52.0	58.8 (0.25)
Fire, MPB	214 (12.75)	239	0.46	75.9	64.6 (0.38)
Fire, MPB,WPBR	116 (73.50)	131	0.92	65.9	63.9 (0.33)

Disturbance types implemented are white pine blister rust (WPBR), mountain pine beetle (MPB), and wildland fire (Fire). Results are annual values averaged over the 250-year simulation period, with standard deviations in parentheses

trees ensure continued high rust infection rates and mortality (Keane et al. 2012), however, where rust-resistant five-needle pines survive fire they can provide the seeds for populating future landscapes resilient to both rust infection and fire mortality (Keane et al. 2012). Finally, studies have indicated that fire exclusion has increased competition stress, weakening pine trees and perhaps facilitating rust infection (Parker et al. 2006; Heward et al. 2013).

Stands that are both burned and rust-infected have a higher overall potential for tree mortality. Trees infected with WPBR are weakened, and may be more susceptible to fire-caused damage and mortality (Stephens and Finney 2002). As WPBR kills pine trees slowly, dead foliage and wood added to the fuelbed may increase fire intensity. As occurs after MPB outbreaks, WPBR infection results in

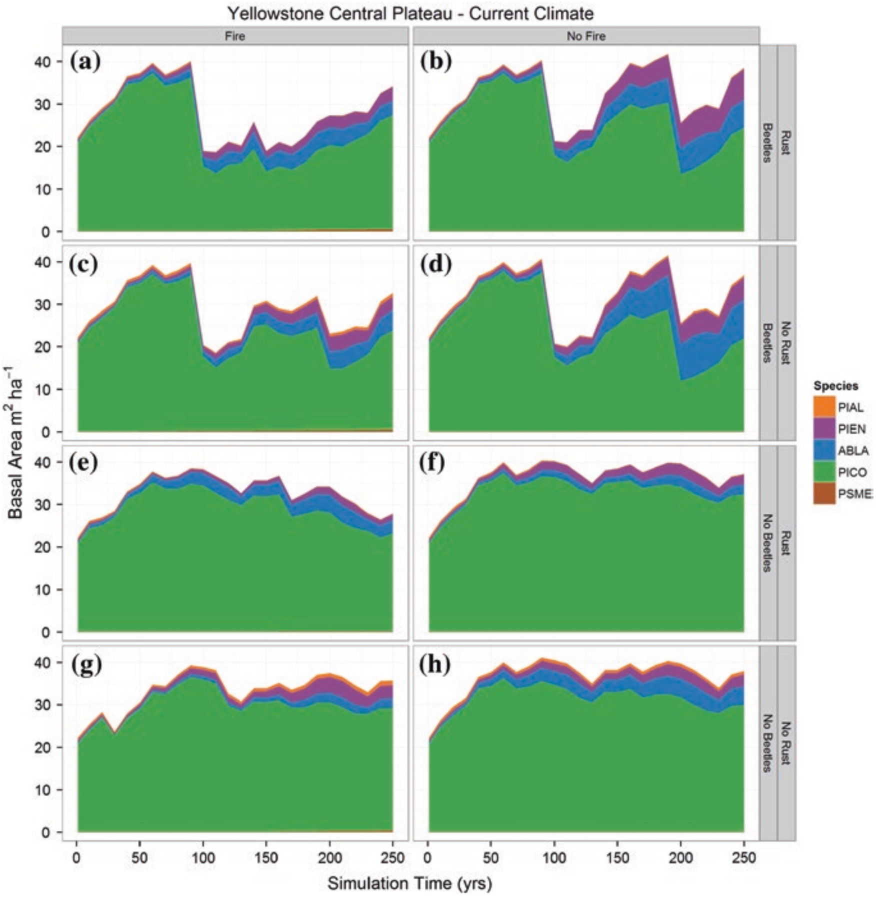

Fig. 8.6 Landscape composition of species cover types mapped using the plurality of basal area for current climate (CC) for the Yellowstone Central Plateau (YCP) landscape with all combinations of fire, white pine blister rust (WPBR), and mountain pine beetle (MPB): **a** fire, WPBR, and MPB, **b** no fire, WPBR, MPB, **c** fire and MPB, **d** MPB only, **e** fire and WPBR, **f** WPBR only, **g** fire only, and **h** no disturbances. Species: PIAL-whitebark pine, PIEN-Engelmann spruce, PICO-lodgepole pine, PSME-Douglas-fir, and PIPO-ponderosa pine

elimination of the shade-intolerant pine overstory, allowing shade-tolerant competitors to occupy the openings. This creates substantially different canopy fuel conditions, such as lower canopy base heights, higher canopy bulk densities, and greater canopy cover, which facilitate crown fires (Keane et al. 2002; Reinhardt et al. 2010). Shade-tolerant competitors are also more susceptible to fire damage, resulting in high post-fire tree mortality in rust-infected landscapes.

Three five-needle pine species are present on our simulation landscapes: western white pine, whitebark pine, and limber pine. The FireBGCv2 simulations indicate that interactions between fire and rust have a minor influence on landscape

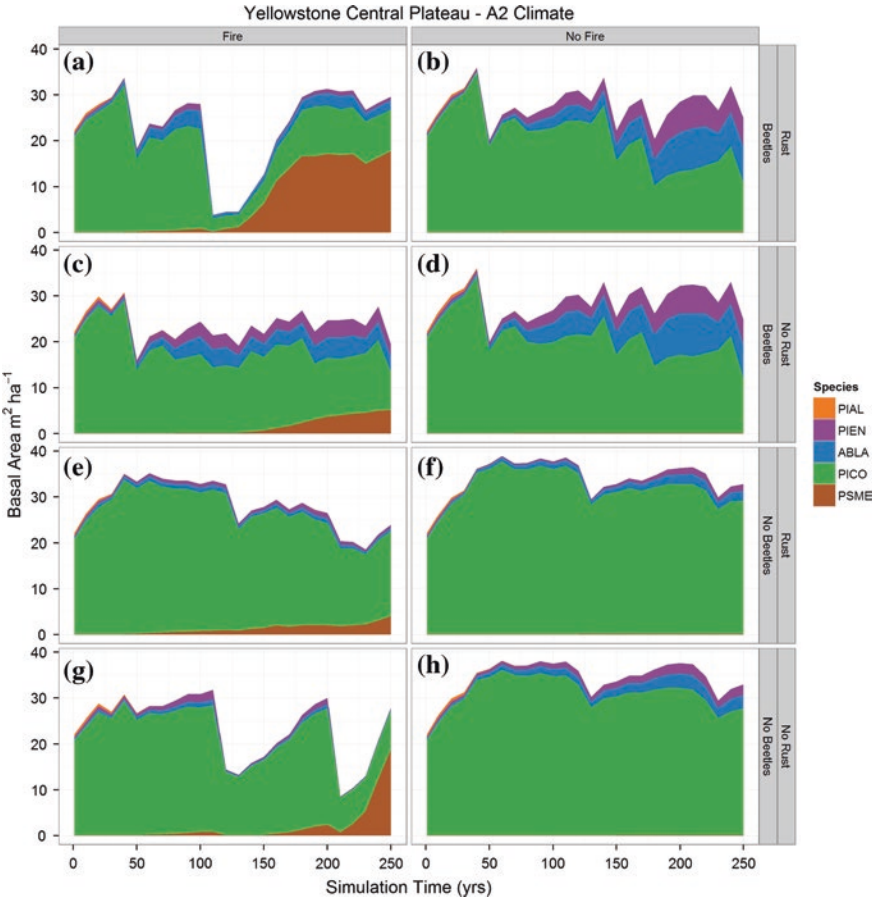

Fig. 8.7 Landscape composition of species cover types mapped using the plurality of basal area for a warmer climate (A2) for the Yellowstone Central Plateau (YCP) landscape with all combinations of fire, white pine blister rust (WPBR), and mountain pine beetle (MPB): **a** fire, WPBR, and MPB, **b** no fire, WPBR, MPB, **c** fire and MPB, **d** MPB only, **e** fire and WPBR, **f** WPBR only, **g** fire only, and **h** no disturbances. *Species* PIAL-whitebark pine, PIEN-Engelmann spruce, PICO-lodgepole pine, PSME-Douglas-fir, and PIPO-ponderosa pine

composition of host species because our landscapes contain relatively few of these trees. For example, whitebark pine represents only 3.7 % of the EFBR landscape basal area in the absence of simulated WPBR infection, and limber pine is so rare that it is not shown in our modeling results. In WPBR-only simulations, whitebark pine is replaced over time by subalpine fir (Fig. 8.4f), but when fire disturbance is included, whitebark pine remains on the landscape at low levels (1.23 % of landscape basal area; Fig. 8.4e; Table 8.3). In contrast, fire does not buffer WPBR infection effects on whitebark pine at YCP, where it comprises about 2 % of the landscape basal area in simulations with fire and without rust (Fig. 8.6g), but decreases to less than 1 % of basal area when rust is simulated with or without fire (Fig. 8.6e, f).

Table 8.3 Summaries of vegetation and biomass characteristics from the FireBGCv2 model for two simulation landscapes

Scenario	Basal area ($m^2\ ha^{-1}$)	Basal area of PIAL ($m^2\ ha^{-1}$)	Basal area of pines ($m^2\ ha^{-1}$)	Above ground C burned (%)	Basal area killed by WPBR (%)	White pine basal area killed by WPBR (%)	Basal area killed by MPB (%)	Pine basal area killed by MPB (%)
East Fork Bitterroot River (EFBR)—current climate (CC)								
No disturbance	33.37 (1.66)	0.05 (0.01)	0.46 (0.04)	–	–	–	–	–
Only WPBR	32.67 (1.9)	0.01 (0.02)	0.4 (0.06)	–	0.3 (0.6)	24.1 (34.8)	–	–
Only MPB	31.68 (2.18)	0.02 (0.02)	0.23 (0.16)	–	–	–	2.8 (2.9)	11 (9.6)
WPBR, MPB	31.54 (2.19)	0.01 (0.02)	0.23 (0.16)	–	0.4 (0.6)	25.6 (37.2)	2.4 (2.7)	9.5 (8.7)
Fire only	29.81 (1.12)	0.04 (0.01)	0.54 (0.02)	0.1 (0.6)	–	–	–	–
Fire, WPBR	29.97 (2.22)	0.01 (0.02)	0.53 (0.03)	0.1 (0.2)	0.3 (0.5)	21 (33.9)	–	–
Fire, MPB	27.06 (2.38)	0.02 (0.02)	0.33 (0.09)	0.3 (0.5)	–	–	3.3 (3)	9.4 (6.7)
Fire, MPB,WPBR	25.92 (2.75)	0.01 (0.02)	0.35 (0.08)	0 (0.1)	0.3 (0.4)	17.4 (36.1)	3.7 (4.5)	9.9 (10.5)
East Fork Bitterroot River (EFBR)—warm, dry climate (A2)								
No disturbance	33.54 (1.87)	0.03 (0.01)	0.41 (0.06)	–	–	–	–	–
Only WPBR	33.72 (1.72)	0.01 (0.02)	0.43 (0.04)	–	0.6 (1.1)	40 (37.6)	–	–
Only MPB	32.13 (2.32)	0.02 (0.02)	0.19 (0.16)	–	–	–	3.3 (3.9)	14.8 (11.6)
WPBR, MPB	32.26 (2.39)	0.01 (0.02)	0.18 (0.18)	–	0.3 (0.6)	32.4 (35.2)	2.5 (3.3)	12.5 (14.2)
Fire only	27.83 (2.01)	0.06 (0.01)	0.58 (0.03)	0.3 (1.1)	–	–	–	–
Fire, WPBR	28.7 (2.27)	0.01 (0.02)	0.56 (0.04)	0.2 (0.4)	0.2 (0.3)	21.2 (31.7)	–	–
Fire, MPB	24.64 (2.4)	0.02 (0.02)	0.31 (0.07)	0.6 (1.9)	–	–	4.1 (4)	12 (8.5)
Fire, MPB,WPBR	24.24 (3.82)	0.01 (0.02)	0.35 (0.09)	0.7 (2)	0.8 (1.2)	47.1 (36.3)	4 (3.9)	10.7 (8.1)
Yellowstone Central Plateau (YCP)—current climate (CC)								
No disturbance	36.63 (4.54)	0.02 (0)	0.88 (0.05)	–	–	–	–	–

(continued)

Table 8.3 (continued)

Scenario	Basal area ($m^2\ ha^{-1}$)	Basal area of PIAL ($m^2\ ha^{-1}$)	Basal area of pines ($m^2\ ha^{-1}$)	Above ground C burned (%)	Basal area killed by WPBR (%)	White pine basal area killed by WPBR (%)	Basal area killed by MPB (%)	Pine basal area killed by MPB (%)
Only WPBR	36.37 (4.47)	0.01 (0.01)	0.91 (0.03)	–	0.2 (0.2)	22.4 (21.1)	–	–
Only MPB	31.84 (6.86)	0.02 (0)	0.8 (0.17)	–	–	–	7.9 (15.5)	9.7 (19.2)
WPBR, MPB	32.5 (6.76)	0.01 (0.01)	0.81 (0.14)	–	0.2 (0.2)	19.4 (15.7)	7.5 (15)	9.1 (18.4)
Fire only	33.3 (4.54)	0.02 (0.01)	0.91 (0.06)	0 (0.1)	–	–	–	–
Fire, WPBR	32.71 (4.4)	0.01 (0.01)	0.89 (0.05)	0.5 (1.8)	0.2 (0.2)	21.8 (17.2)	–	–
Fire, MPB	29.09 (6.17)	0.02 (0)	0.86 (0.11)	0.1 (0.2)	–	–	7.1 (14.4)	8.2 (16.4)
Fire, MPB,WPBR	28.08 (7.07)	0.01 (0.01)	0.85 (0.1)	0.1 (0.3)	0.3 (0.3)	23.4 (17.1)	5.4 (13.2)	6.3 (14.9)
Yellowstone Central Plateau (YCP)—warm, dry climate (A2)								
No disturbance	34.16 (3.97)	0 (0.01)	0.91 (0.04)	–	–	–	–	–
Only WPBR	34.02 (4.04)	0 (0.01)	0.94 (0.03)	–	0.1 (0.2)	34.8 (36.9)	–	–
Only MPB	28.61 (3.82)	0 (0.01)	0.73 (0.15)	–	–	–	11.9 (12.9)	15.6 (16.1)
WPBR, MPB	27.67 (3.86)	0 (0.01)	0.75 (0.19)	–	0.1 (0.3)	34.1 (35)	13.3 (14.5)	16.9 (18.5)
Fire only	23.46 (7.12)	0 (0.01)	0.86 (0.17)	0.2 (0.6)	–	–	–	–
Fire, WPBR	28.33 (5.02)	0 (0.01)	0.9 (0.05)	1.8 (5.7)	0.1 (0.2)	30.9 (33.1)	–	–
Fire, MPB	23.69 (3.32)	0 (0.01)	0.73 (0.16)	0.6 (1.5)	–	–	10.5 (13)	13.8 (16)
Fire, MPB,WPBR	23.24 (9.01)	0 (0.01)	0.61 (0.26)	0.2 (0.6)	0.1 (0.2)	29 (27.8)	6.3 (10.9)	9.9 (11.8)

The East Fork Bitterroot River and Yellowstone Central Plateau for current climate and warmer climate scenarios. Disturbance types implemented are white pine blister rust (WPBR), mountain pine beetle (MPB), and wildland fire (Fire). Results are annual values averaged over the 250-year simulation period, with standard deviations in parentheses

Although the combination of fire and WPBR implemented for EFBR and YCP affect percent of fires that are high-severity and landscape fire rotation differently than fire-only scenarios, these differences are relatively minor because whitebark pine is a small component of the landscape (Table 8.2). However, as mentioned previously, for both simulation landscapes the warmer climate scenario substantially alters fire rotations, average annual area burned, and percent of fires that are high severity (Table 8.2).

8.4.3 Mountain Pine Beetle and Blister Rust

Few researchers have investigated the interactions between the native MPB and exotic white pine blister rust. In their endemic phase, MPB populations may weaken five-needle pines and facilitate infection by WPBR, but these interactions are strongly governed by climate and biophysical environment (Tomback and Achuff 2011). However, the ubiquitous presence of WPBR spores and low resistance to the disease ensures that most five-needle pines will eventually become infected and die from WPBR, regardless of MPB endemic levels (Hoff et al. 2001). More importantly, MPB influences WPBR through regulation of the tree species that are host to both disturbance agents (Campbell and Antos 2000). For example, although whitebark pine stands in the Greater Yellowstone Ecosystem show little WPBR-related mortality, levels of MPB-related mortality are high (Kendall and Keane 2001). Many stands of healthy five-needle pines in Yellowstone have been subjected to a major MPB outbreak over the last decade as a result of high densities of large-diameter trees coupled with prolonged warm, dry conditions. These outbreaks resulted in substantial mortality of rust-resistant whitebark pine trees (Logan et al. 2009).

Effects of WPBR on MPB infestations are also highly variable and subtle. Archibald et al. (2013) found less MPB activity in trees that had high WPBR damage, whereas Bockino and Tinker (2012) found that whitebark pine selected as hosts for MPB had significantly higher WPBR infection, but this varied by tree size (diameter), stand type, and disturbance pattern (Larson 2011). Kulhavy et al. (1984) found that over 90 % of western white pine trees infected by bark beetles had either WPBR or some type of root disease, whereas Six and Adams (2007) found little evidence of interaction effects between MPB and WPBR.

The FireBGCv2 simulations validate the importance of species composition in relation to disturbance interactions, even though effects of MPB and WPBR interactions are minimal because of the scarcity of WPBR host species in our study areas. The EFBR simulations of MPB disturbance under current climate result in a decline in both lodgepole and whitebark pine, with a corresponding increase in subalpine fir and Douglas-fir (Fig. 8.4d; Table 8.3), with little change from the addition of WPBR (Fig. 8.4b). The WPBR-only EFBR simulation (Fig. 8.4f) shows little difference in species composition compared to the no-disturbance scenario (Fig. 8.4h). Similar results are seen for the YCP landscape, except that the decline in lodgepole pine is not countered by increases in subalpine fir because of dry site conditions (Fig. 8.6b, d, f, h). These trends are enhanced under a warmer climate, where lodgepole pine declines are greater and stands are mainly replaced by Douglas-fir (Fig. 8.7a, g), but WPBR interaction has minor effects on species composition (Fig. 8.7b, d).

8.4.4 Fires, Beetles, and Rust

Real-world studies of the complex interactions among fire, beetles, and rust are rare, but in our simulations the presence of MPB and WPBR reduces the basal area of pine species. Fire, while reducing pines in the short term, appears to ensure their long-term persistence by eliminating competitors, as noted by Keane and Morgan (1994). In previous modeling efforts, decades or centuries were required to re-establish populations of rust–resistant pines after die-off (such as would occur with MPB). Simulated wildland fires killed some trees, but prevented encroachment by shade-tolerant non-pine species and maintained five-needle pines on the landscape (Loehman et al. 2011b). Observationally, the greatest decline in whitebark pine has been found in those areas affected by both WPBR and MPB but not fire (Campbell and Antos 2000).

Interactions among fire, MPB, and WPBR can only occur in areas that have the potential to support five-needle pines, which are rare in our simulation landscapes. However, we found that fire rotations in EFBR and YCP under current climate are about 10 % lower when all three disturbances are allowed to interact, and average landscape tree mortality is also lower (Table 8.2). Under a warmer climate, fire rotation decreases (from 98 to 62 years for EFBR, and from 387 to 131 years for YCP), and the percent of high severity fires increases for both landscapes. Landscape basal areas are lower when all three disturbances are included, and the basal area of pines is significantly lower for multiple disturbance scenarios than other disturbance combinations, for both current and warmer climates (Table 8.3). Douglas-fir and subalpine fir dominate the EFBR landscape when all three disturbances are active under current climate without fire (Fig. 8.4a); however, when fires are included, pines are maintained on the simulation landscape (Fig. 8.4b). With a warmer climate Douglas-fir dominates both the EFBR (Fig. 8.5a) and YCP (Fig. 8.7a) landscapes, but both whitebark and lodgepole pines are still present because of continued fire. Thus, interactions among disturbances create different landscapes than when each disturbance acts separately, or in the absence of disturbance.

8.5 Discussion

Interactions among disturbance agents can dramatically influence ecosystems. Our literature review and simulation modeling experiments demonstrate that interactions among various disturbance types may cause easily detectable, direct, and immediate effects such as differential tree mortality, but at landscape scales, effects of long-term and coupled disturbance regimes can lead to complex feedbacks and nonlinear behaviors causing landscape trajectories to differ significantly (Figs. 8.4, 8.5, 8.6 and 8.7; Tables 8.2 and 8.3). Another finding from this effort is that most of the interaction effects are mediated through vegetation response rather than direct interactions between disturbances, such as a fire killing beetles and fungi. More importantly, we found that the effects of climate change on landscape conditions result mainly from the effects of disturbances and their interactions on vegetation; direct vegetation response to climate change rarely causes significant landscape change.

Many factors determine the magnitude, trend, and direction of interacting disturbance effects. The physical environment is perhaps the most important factor: as shown by our simulations, climate has enormous influence (Figs. 8.4, 8.5, 8.6 and 8.7; Tables 8.2 and 8.3), with a warmer climate allowing for greater MPB activity and more wildland fire, altered landscape composition and structure, and changes in WPBR infection and mortality rates. Topography is also an important influence affecting rate of fire spread, water and radiation balance, and microclimatic conditions that in turn may influence potential for rust infection and host vulnerability. Species composition also influences disturbance interactions. For example, the abundance of host species for both MPB and WPBR may dictate the intensity and magnitude of interactions between these two disturbances, and resulting tree mortality patterns dictate wildland fuel dynamics that then influence fire regimes. The current climate-mediated MPB outbreak in North America might have been less intense and more localized if wildland fires had not been suppressed over the last century, since fire exclusion has increased the abundance of host species of sufficient size and distribution for insect and disease epidemics (Catchpole et al. 2001; Carroll et al. 2003).

Comprehensive simulations of multiple disturbance interactions demand a mechanistic, process-based approach to ensure most effects are appropriately represented (Gustafson 2013). Direct links from climate to both disturbance and vegetation processes are needed to simulate those important ecophysiological interactions that dictate ecosystem response (Keane et al. 2015). In our simulations, for example, wildland fire often killed trees, which increased water availability because of decreased leaf area and evapotranspiration, resulting in increased fitness of surviving trees thereby reducing insect and disease mortality. This result is possible because the model simulated daily the effects of rainfall, snow dynamics, and temperature on soil water, plant phenology, evapotranspiration, photosynthesis, and respiration across an entire landscape (Keane et al. 2011). Phenomenological approaches, such as statistical analysis and modeling, do not incorporate the full suite of ecophysiological responses to climate change into model structure (Gustafson 2013; Keane et al. 2015).

Incorporating the complexity of mechanistic biophysical and biotic drivers for multiple disturbances at landscape scales across decades of simulation is a challenge for even the most comprehensive LMs (Keane et al. 2015). Ecological surprises may emerge due to inadequate model predictive power, particularly for understanding spatially heterogeneous, scaled, and nonlinear interactions of coupled disturbance processes. Moreover, as disturbance regimes increasingly move beyond historical observations (Westerling et al. 2011), interactions with other disturbance agents become less predictable because modeled relationships cannot be based on observed data. Feedbacks of disturbance-caused ecosystem changes to subsequent disturbance susceptibility are also likely to confound predictive models; for example, MPB epidemics can decrease or increase modeled crown fire susceptibility depending on assumptions about ecosystem productivity and the rate of canopy recovery, which may depend on biophysical setting as well as the severity of the outbreak. Considering that changes in climate can alter disturbance regimes and host vulnerability as well as determine trajectories of ecosystem recovery, potential ecological surprises seem to inhabit an infinite state space.

We must recognize the great need for models that represent coupled systems (e.g., disease and host) to realistically represent complex forest ecosystem dynamics across multiple scales of space and time. In a recent review of climate change effects on plant diseases, Pautasso et al. (2012) identified several key research gaps including the need to (1) focus on mountain and boreal ecosystems, (2) integrate climate drivers other than temperature (e.g., precipitation), and (3) couple long-term observational data sets with climate change scenarios to predict impacts on plant pathogens and their hosts. As in studies of human health, an understanding of coupled systems is needed to fully recognize system vulnerability, resistance, and resilience (Hausermann et al. 2012). Development of such models requires theoretical, field, and modeling work to identify key processes, interactions, and ecological thresholds that cause cascading and nonlinear ecosystem responses. Although there is still a long way to go to represent disturbance interactions in LMs (Keane et al. 2015), newer efforts to couple niche models with more complex ecosystem, population, and disturbance models are promising (see Iverson et al. 2011; Fordham et al. 2013; Tanentzap et al. 2013).

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Chapter 9

Simulating Forest Landscape Disturbances as Coupled Human and Natural Systems

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9.1 Introduction

The global human population is projected to increase from 7.2 billion in 2013 to 9.6 billion in 2050 (United Nations Department of Economic and Social Affairs 2013). Increasing numbers of people and households are placing escalating pressure on global forests through demand for wood and other forest resources. In addition, the geographic expansion of human populations results in deforestation and subsequent conversion of forested areas to agricultural and developed land uses. These human impacts interact with changing climate and natural forest disturbances such as wildfires and insect outbreaks to create a complex system of interacting processes that drive forest dynamics and affect ecosystem services such as timber production, wildlife habitat, water quality, and carbon sequestration. Spatial simulation modeling of forest landscape change is an important technique for exploring the potential outcomes of these interactions over large areas and long time periods. Landscape simulation models are widely used for reconstructing historical landscape patterns driven by natural disturbance regimes, projecting future landscape trajectories under alternative forest management scenarios, and conducting simulation experiments to examine how multiple processes and their interactions affect landscape patterns and trajectories of change (Wimberly et al. 2012).

Human activities affect forest landscapes over a range of spatial and temporal scales, with diverse influences on forest vegetation patterns and dynamics. Conversion of forests to agricultural and developed land uses has the most significant ecological impact because the affected areas are removed from the forested land base. The replacement of forests with developed land uses is effectively a permanent change over the time scale of common planning horizons. Agricultural conversion is also frequently viewed as a persistent long-term change. However, there are many historical examples of broad-scale agricultural abandonment and forest recovery (Foster 1992), and afforestation is occurring in many areas around the globe (Stanturf et al. 1998). Although land use conversions occur at the individual parcel level as a result of landowner decisions, broader patterns of change are driven by regional and global economic and demographic forces. These trends include urban sprawl resulting from the growth of large metropolitan areas as well as cropland expansion driven by increasing global demand for agricultural commodities. Land use changes often exhibit distinctive patterns that influence fragmentation of the remaining natural vegetation (Fig. 9.1). For example, forms of urban growth range from the gradual expansion of urban centers to “leapfrog” patterns of more dispersed development (Herold et al. 2003), and patterns of agricultural conversion can be influenced by transportation networks and infrastructure (Geist and Lambin 2002).

In forests where timber production is a primary land use, silvicultural activities modify stand structure through the removal of trees, and the resulting changes in density, species composition, and tree size distribution influence the development of the residual stand. In wildfire-prone forest landscapes, a variety of fuel management activities such as thinning, prescribed burning, mastication, and mechanical removal can be applied to reduce wildfire severity and improve the

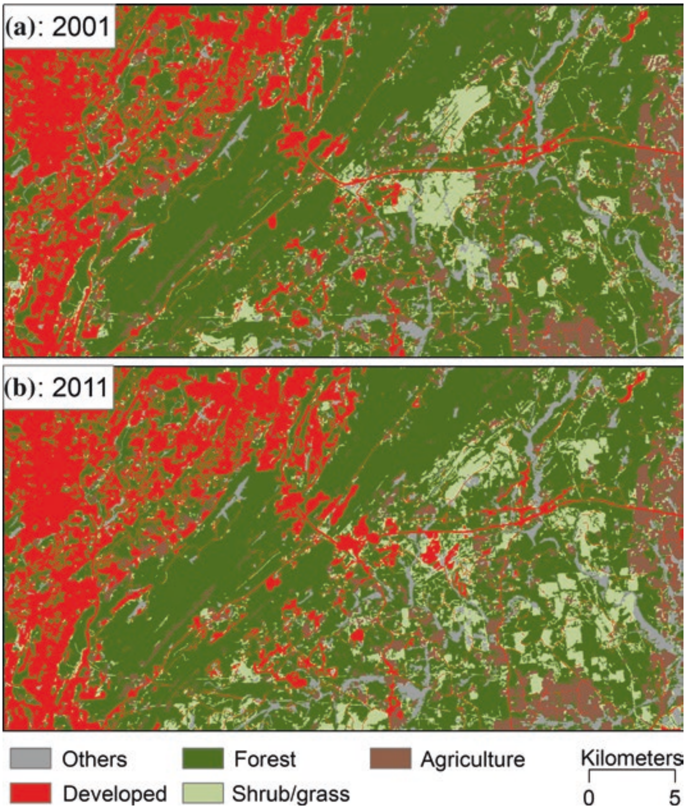

Fig. 9.1 Expansion of developed land in the vicinity of Birmingham, Alabama from 2001 to 2011 illustrating expansion of existing developed patches as well as "leapfrog" growth along transportation corridors. Land cover data are from the National Land Cover Database

effectiveness of fire suppression activities (Agee and Skinner 2005). The sizes and shapes of the harvest units, along with their spatial arrangement, determine forest patterns and influence habitat fragmentation in managed forest landscapes (Fig. 9.2). The persistence of these changes depends on the specific management practices being applied. An old-growth stand will take centuries to recover its late-successional habitat characteristics following clearcutting (Franklin et al. 2002), whereas surface fuel loads may recover to pre-treatment levels within a few years after prescribed burning (Fernandes and Botelho 2003). The cumulative effects of the frequency of harvesting, the degree to which the stand structure is modified, and the rate of vegetation recovery create a continually shifting forest mosaic and determine critical ecosystem functions such as the amount of carbon storage in dynamic landscapes (Smithwick et al. 2007).

Roads are another pervasive human influence on forest landscapes; they facilitate forest conversion to other land uses and provide access for forest management

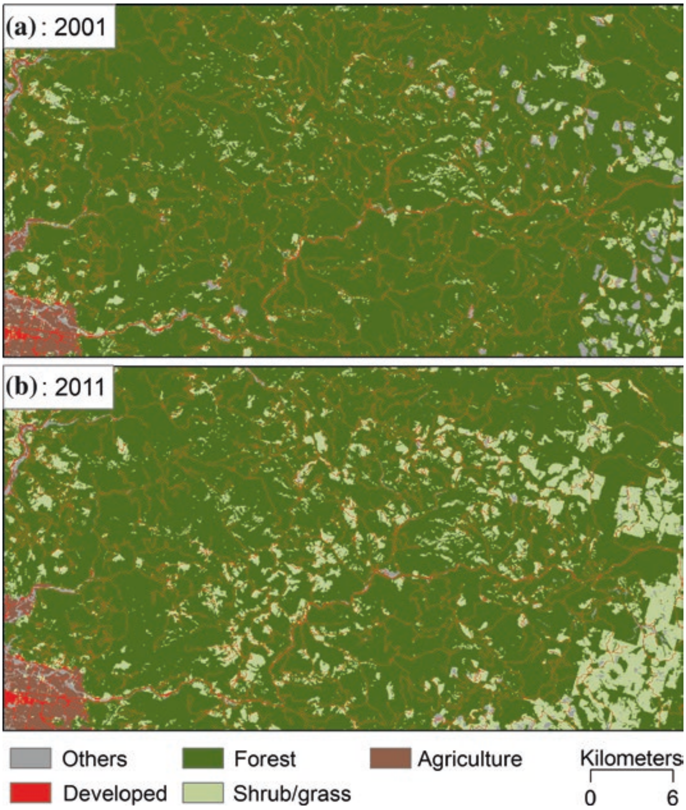

Fig. 9.2 Landscape patterns of human disturbance resulting from timber harvesting in the Tillamook State Forest, Oregon. Land cover data are from the National Land Cover Database

activities such as timber harvesting and fuel treatments. In addition, forest roads affect disturbance regimes and habitat characteristics. For example, in a dry forest landscape in the western United States, the frequency of human-ignited fires increased with road density (Narayanaraj and Wimberly 2012). Fire boundaries were also spatially associated with roads, reflecting their functions as fuel breaks and transportation corridors that facilitate fire suppression (Narayanaraj and Wimberly 2011). In addition, roads affect the structure and composition of roadside forests (Watkins et al. 2003), facilitate the spread of invasive species (Parendes and Jones 2000), and increase the risk of disturbances such as floods and landslides (Jones et al. 2000). Direct effects of roads on adjacent forest environments are generally limited to a relatively narrow zone of influence (often <50 m from roadside). However, the pervasiveness of forest road networks across large areas greatly magnifies their effects across broader landscapes (McGarigal et al. 2001).

These human disturbances do not occur independently of one another. In particular, broader patterns of land use can affect forest dynamics through their interactions with forest management practices and natural disturbance. These types of interactions frequently occur in the transition zone between natural forest and developed areas, referred to as the wildland–urban interface (WUI), which has resulted from the expansion of human populations into forests and other wildland areas (Mell et al. 2010). The permanent presence of low-density settlements in fire-prone ecosystems increases the probability of human-ignited wildfires (Syphard et al. 2007b), but also reduces the frequency of forest management activities and increases the costs associated with treating hazardous fuels (Wear et al. 1999; Berry and Hesseln 2004; Kline et al. 2004). Human land use also influences fire regimes in tropical forests in developing countries through the expansion of agricultural land, resulting in deforestation and fragmentation of the remaining forests, and increased use of fire for land clearing and agriculture (Nepstad et al. 2008). In particular, the spread of fire from human-dominated areas into the edges of remaining forests can lead to further deforestation through a positive feedback loop of fire, tree mortality, and increased susceptibility to fire because of increased fuel loads and modified understory microclimate (Cochrane et al. 1999). Thus, agricultural expansion can ultimately lead to deforestation even in protected areas where direct land use conversion is prohibited.

The human disturbance processes and interactions discussed thus far fall within the scope of coupled human and natural systems (CHANS). Such systems have emerged as an important basis for understanding the reciprocal interactions and feedbacks that connect human activities and ecosystem responses through couplings that occur at multiple spatial and temporal scales (Liu et al. 2007a, b, 2013). By exploring such linkages over a broad range of scales from local interactions to global telecoupling, research on CHANS aims to disentangle these complex relationships and has the potential to generate new insights that are highly relevant to environmental policy. As a result, the CHANS approach has been widely applied as a framework for studying a variety of human–environment interactions including wildlife habitat relationships and conservation in human-dominated landscapes (Carter et al. 2012); the interactions of fire management, air quality, and human health in fire-prone ecosystems (Johnston and Bowman 2014); complex interactions of multiple drivers of land cover and land use change (López-Carr et al. 2012); and the emergence of infectious disease outbreaks as a result of human influences on the ecologies of pathogens, vectors, hosts, and the landscapes they inhabit (Meentemeyer et al. 2012).

The CHANS framework is also highly applicable to the study of human interactions with disturbance-driven forest ecosystems. In particular, the interrelationships between anthropogenic disturbance and natural processes in forest landscapes can generate a variety of emergent behaviors, including self-reinforcing feedback loops (Cochrane et al. 1999; Lindenmayer et al. 2011), threshold effects (Bodin et al. 2006; de Filho and Metzger 2006), and alternative stable states (Hirota et al. 2011). These effects cannot be fully understood or predicted without considering the interactions of multiple processes across large areas and long time periods. Therefore, spatial simulation models are important tools for understanding the effects of coupled human and natural processes in forest landscapes and for developing appropriate management strategies to sustain forests and the ecosystem services that they provide.

In this chapter, we review the current capabilities for simulating interactions between human activities and forest landscape dynamics by grouping models into two main categories: forest landscape models (FLMs), which focus on landscapes where forests are the dominant land cover, and land change models (LCMs), which encompass mosaics of different land cover and land use classes that include forests in addition to other land uses such as developed areas and agricultural lands. Dynamic Global Vegetation Models (DVGMs) and similar coarse-grained ecological models that do not directly incorporate two-dimensional spatial representations of landscape patch structure and associated ecological processes (Fisher et al. 2010) are outside the scope of this review. Our synthesis highlights the strengths and limitations of existing models for simulating human disturbances and offers suggestions for future development of integrated models that can more effectively simulate forests as CHANS.

9.2 Forest Landscape Models

9.2.1 Background

During the late 1980s, the emergence of landscape ecology offered new perspectives for understanding ecological dynamics and addressing forest management issues at broad spatiotemporal scales encompassing thousands of hectares and extending from decades to centuries. At these scales, natural and anthropogenic disturbances such as wildfire, windthrow, insect outbreaks, and timber harvesting emerge as important drivers of landscape pattern and dynamics. Forest landscape models were developed to study the effects of these disturbance processes on forest landscapes. Most early FLMs were designed to simulate a single disturbance type, such as fire (Li et al. 1997) or timber harvesting (Gustafson and Crow 1996). More recently, FLMs have benefited from a variety of technological advances, including increased computing capacity, widespread adoption of geographic information systems (GIS), increased utilization of satellite remote sensing for mapping large forest landscapes, and advanced software engineering techniques. The models are usually designed to simulate multiple processes and their interactions in a spatially explicit manner, although individual models vary considerably in their representation of forest landscapes, level of spatial interaction, and overall complexity (Scheller and Mladenoff 2007; He 2008; Xi et al. 2009).

A distinctive characteristic of FLMs is that they track spatially explicit details about tree species, ages, sizes, and/or biomass as state variables (Fig. 9.3a). As a result, the simulation of site-level succession is a core process that is modeled using a variety of approaches, ranging from simple methods that use stand age as a proxy for even-aged stand development (Boychuk and Perera 1997; Li et al. 1997) to more sophisticated techniques that model transitions among discrete successional stages as a function of time and multiple types and severities of disturbance (Keane et al. 2002; Chew et al. 2004; Wimberly and Kennedy 2008). Alternatively succession can be simulated as a competitive process driven by

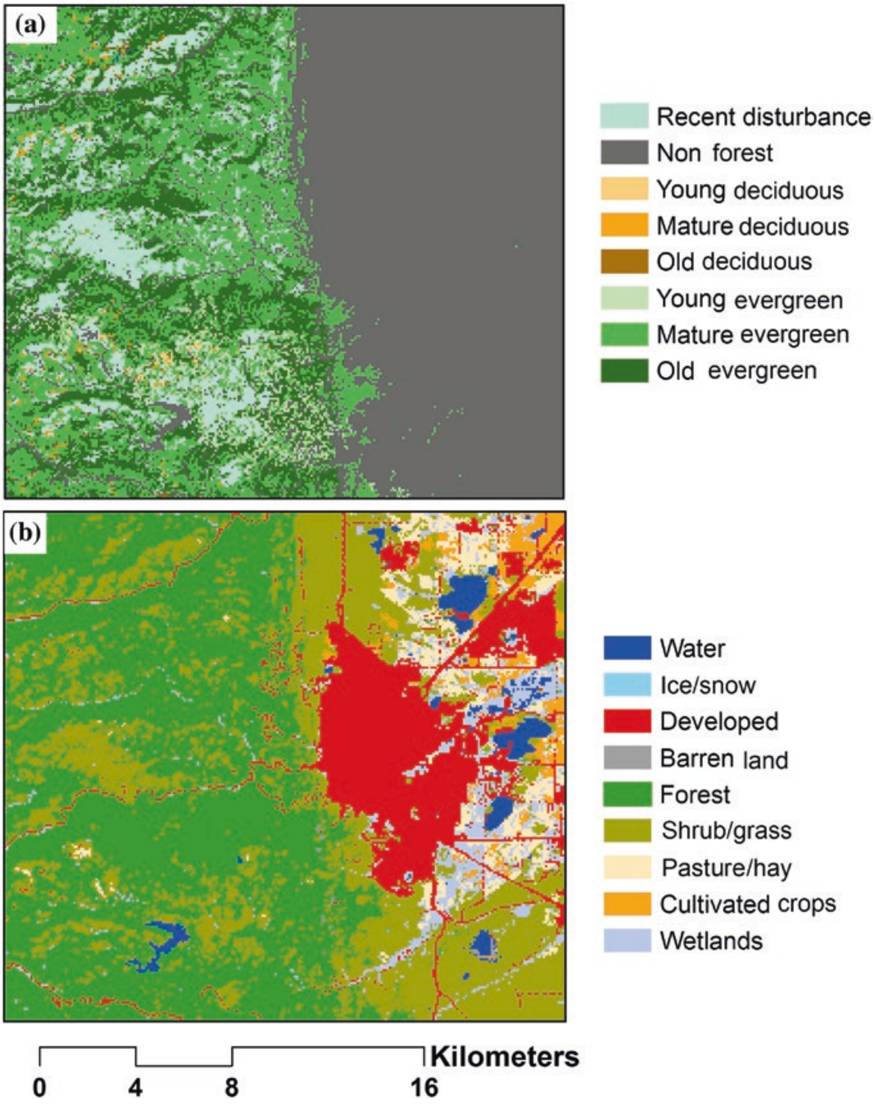

Fig. 9.3 Examples of land cover representations for the same landscape in forest landscape models (FLMs) versus land change models (LCMs): **a** FLMs are used to simulate forest succession and species characteristics, but not to evaluate non-forest land cover, **b** in LCMs all forests are often aggregated into a single cover class, but multiple categories of land cover and land use are simulated in non-forested areas

species characteristics such as longevity, fire and shade tolerance, maturity, regeneration niche, and growth rate (He and Mladenoff 1999) or using a meta-modeling approach that derives successional trajectories from more detailed, individual-tree based models of stand development (Bettinger et al. 2005; Lischke et al. 2006;

Seidl et al. 2012). Natural disturbances such as wildfire, windthrow, and insect outbreaks are simulated using algorithms that model disturbance initiation and spread based on top-down drivers such as climatic variation, and local susceptibility as a function of vegetation, topography, and other environmental characteristics (Keane et al. 2006; Wimberly and Kennedy 2008). More recent development of FLMs such as LANDIS-II has allowed the simulation of ecosystem processes such as nutrient cycling and their interactions with forest succession, environmental conditions, and fire and biomass harvesting regimes (Scheller et al. 2011; Karam et al. 2013). Other important FLM developments include adding functionality to project climate change impacts (Gustafson et al. 2010; Gustafson and Sturtevant 2013), and utilizing large forest inventory databases to simulate and validate forest landscape change over very large spatial extents (Wang et al. 2013b, 2014).

9.2.2 Simulating Forest Management Activities

Many FLMs can be used to simulate the effects of silvicultural practices on forest landscape patterns and ecosystem dynamics over large spatial and temporal scales. In the early stages of development, the use of FLMs was often focused on understanding the effects of alternative timber harvesting strategies (e.g., aggregation versus dispersion of harvest units) on landscape patterns and forest fragmentation (Li et al. 1993; Gustafson and Crow 1996; Baskent 1997). Results from these studies highlighted the fact that harvesting pattern is a key driver of the spatial pattern of managed landscapes, with aggregated harvest areas creating less fragmentation and producing more interior forest area than dispersed harvest areas (Baskent 1997). Within the past two decades, FLMs have been further developed to simulate a wide range of forest management practices, such as thinning, single tree removal, group selection, clearcutting, and reforestation (Gustafson et al. 2000; Fraser et al. 2013). These developments have paralleled the implementation of more detailed and realistic approaches for characterizing and simulating successional changes in forest composition and structure. For example, only clearcutting can be simulated with a model that uses a single stand age variable as a proxy for stand development, whereas other activities such as thinning and single tree removal can be incorporated into more complex successional models that track multiple cohorts of trees, simulate biomass dynamics, or model transitions between various forest structure classes.

Forest harvesting disturbances are modeled based on a set of rules and parameters that define the spatial pattern, temporal frequency, and stand-level effects of harvests (Gustafson et al. 2000; Bettinger et al. 2005; Fraser et al. 2013). The users typically provide spatial data layers that determine the boundaries of individual harvest areas and broader management areas for which harvesting regimes are specified. The management areas can be defined to exclude riparian buffers, conservation areas, and other locations where timber is not harvested. The rate of harvesting is typically specified either as a desired rotation length or as an area to be harvested or treated within each time step of the simulation. Specific stands are selected for treatment based on a priority ranking algorithm that can be based on stand age, stand composition and structure, economic value, or other factors that determine the stand's suitability for treatment. Spatial constraints can also be applied to either disperse treated harvest units across the landscape or aggregate them into larger harvest blocks. At the stand level, a set of rules are applied to determine how stand characteristics are modified by harvesting. Depending on the methods used to model vegetation succession, harvests may remove cohorts of trees, reduce live stand biomass, or trigger a transition to a different stand structure class.

Wildfire is a key natural disturbance process that has been incorporated in most FLMs, and many of these models also include the capability to simulate the effects of fire management activities. Fire suppression can be simulated mechanistically at the level of the individual fire (Loepfe et al. 2011), or statistically at the fire regime level by manipulating parameters such as frequency and size distribution (Shang et al. 2007). Fuel management aimed at preventing the occurrence of uncharacteristically large, high-severity wildfires is currently an important management practice in the United States and in other temperate forest ecosystems around the world (Agee and Skinner 2005). As a result, modules for simulating fuels and responses to fuel treatment activities such as thinning, mastication, and prescribed burning have been incorporated into some FLMs (He et al. 2004; Ryu et al. 2006; Sturtevant et al. 2009a). Fuel loads can be modeled as a simple function of time, reflecting gradual accumulation since the last fire (He et al. 2004), or using more sophisticated ecosystem models that track the accumulation, mortality, and decomposition of various categories of live and dead fuels (Ryu et al. 2006). Within the FLM simulation framework, fuel treatments can alter the effects of subsequent wildfire by modifying the amounts of available fuels, and by altering stand structure and species composition in ways that affect the probability of wildfire-induced mortality. Forest landscape models can then be applied to assess how different strategies for implementing multiple fuel treatments over large areas and long time periods influence the fire regime and the resulting patterns of forest vegetation (He et al. 2004; Sturtevant et al. 2009b). However, to date relatively few studies have examined the effects of different fuel treatment strategies on processes such as carbon sequestration, nutrient cycling, and emissions.

FLMs have been used to assess the effects of alternative forest management practices on ecological responses such as reduction of fire risk, climate change adaptation, shifts in species abundance and distribution, changes in wildlife habitat, carbon sequestration, and nutrient cycling. For example, Shang et al. (2004) concluded that mechanical treatment (thinning and coarse woody debris removal) coupled with prescribed fire effectively controlled fuel loads and reduced potential fire risk in Central Hardwood Forests of the United States. In the same forests, Wang et al. (2013a) reported that group selection and clearcutting were the most effective management alternatives for mitigating oak (*Quercus* spp.) decline over short and medium time frames. Bu et al. (2008) found that certain harvesting and planting strategies can delay the northern migration of warming-adaptable species in a temperate forest of northeastern China. Scheller et al. (2011) found that forest harvesting reduced carbon storage in U.S. Lake States Mesic Forests, with whole-tree removal resulting in a greater loss of carbon storage than standard harvesting practices such as delimbing on site. A modeling study by Karam et al. (2013) assessed the relative influences of fire exclusion and multiple harvesting strategies on nutrient pools in the Lake Tahoe Basin, United States. This variety of studies highlights the breadth of forest ecosystems in which FLMs can be applied as well as the some of the wide range of interactions between management activities and natural processes that can be explored.

9.3 Land Change Models

9.3.1 Background

In contrast to FLMs, LCMs encompass land cover types beyond forests, but the land surface is typically classified into relatively few discrete land cover types that may include one or more forest classes in addition to other natural and anthropogenic classes such as developed, agricultural, non-vegetated, grassland and shrubland (Fig. 9.3b). In this review, we generically refer to LCMs as "land *use* change models" because their underlying processes typically reflect changes in land use such as urban growth, agricultural expansion, agricultural land abandonment, and afforestation. However, most spatially explicit LCMs do not actually model changes among different land use categories, but instead simulate transitions between land cover types such as forest, developed, cropland, and grassland. LCMs typically use these broad land cover classes as state variables because they can be readily mapped using satellite remote sensing, whereas land use cannot always be directly inferred from land cover. A variety of different approaches can be used to model transitions among these states (Table 9.1); some of the most common LCM methodologies and examples of where and how they have been applied are summarized below.

9.3.2 Markov Chain and Cellular Automata Models

Land cover change through time can be measured over large areas using multi-date satellite imagery, and the resulting data used to derive empirical transition probabilities among land cover classes. These probabilities can then be applied to project change using Markov chain models, which are stochastic models in which the current state of a grid cell determines conditional probabilities for future state changes. Markov chain frameworks have been used to model land use change (Bell 1974) as well as other processes such as gap dynamics and succession in forested lands (Shugart et al. 1973; Horn 1975) since at least the 1970s, and these techniques remain in use worldwide. For example, Brown et al. (2000) used multi-date Landsat imagery to parameterize a Markov chain model for projecting forest cover

Table 9.1 Distinguishing characteristics of four major types of land change models (LCMs)

Model characteristics	Markov chain	Cellular automata	Demand allocation	Agent-based
State variables	Multiple land cover and land use classes	Usually one or a few land cover and land use classes	Multiple land cover and land use classes	States of autonomous agents representing individuals or groups
Dynamic functions	Transitions driven by current state at a given location	Transitions driven by current state at neighboring locations	Transitions sensitive to spatial driving variables	Land use decisions in response to other agents and spatial driving variables
Strengths	Simple, can be parameterized using historical land cover and land use maps	Spatially explicit, can model complex behaviors based on simple adjacency rules	Intermediate complexity, separation of demand and allocation makes parameterization straightforward	Realistic, provides insights into the underlying processes that drive land cover and land use change
Limitations	No spatial interactions, historical transition probabilities may not be relevant in the future	Simple rules may not capture all relevant interactions, can be difficult to parameterize	Sensitive to future demand assumptions, requires suitable data for modeling allocation probabilities	Can be difficult to parameterize, simulation of many agents over large regions is computationally demanding

change in the Upper Midwest of the United States. Guan et al. (2008) used four dates of Landsat imagery to determine transition probabilities between six land use classes (including "forestland"), using a Markov chain model to project change from 2010 to 2050 in Kitakyushu, Japan. Petit et al. (2001) used multi-date SPOT imagery to parameterize a Markov chain model for southeastern Zambia, projecting rapid forest decline due to conversion to cultivated land. In all these examples Markov chain models were used to project changes in forested area, but did not explicitly address the effects of disturbance or management within these forests.

Cellular automata (CA) models build on the concept of Markov chain models by utilizing transition rules that are not only dependent on a cell's current state, but also on the state of adjacent or neighboring grid cells. These models can be used to represent complex, nonlinear relationships among processes affecting land use change, with landscape patterns resulting from interactions among processes such as self-organization, emergence, and path dependence (Walsh et al. 2006; Liu et al. 2008; Stanilov and Batty 2011). CA models have been widely applied to model landscape change, and especially to simulate patterns of urban growth. The Slope, Land Cover, Exclusion, Urbanization, Transportation, and Hillshade (SLEUTH) model (Clarke et al. 1997) has been used since the 1990s for a multitude of urban modeling projects (Claggett et al. 2004; Jantz et al. 2010; Liu et al. 2012). The Spatially Explicit Regional Growth Model (SERGoM) (Theobald 2005; Bierwagen et al. 2010) and Metronamica model (Stanilov and Batty 2011) have similarly been used to model urban growth. In such models, change in forest land cover or land use is usually not explicitly modeled but arises as a consequence of the expansion of urban development into forested areas.

Less frequently, CA models have been used to simulate transitions among multiple vegetation and land cover classes, including forested lands. Ozah et al. (2012) used a deterministic CA model to simulate changes between seven land use and land cover classes, including forest, in the Lake Chad basin in Africa. Walsh et al. (2006) modeled cassava, forest, and rice for northeastern Thailand using a CA modeling framework, including deforestation that occurred as a result of cropland expansion. Yang et al. (2012) linked CA and Markov chain models to project land use near Beijing, China, and forest was one of the five explicitly modeled classes. The LandShift model was designed to simulate anthropogenic land use change at national to global scales, and an application of the model in India simulated forested land as part of a study of demand for human settlement, biofuel production, and food production (Schaldach et al. 2011). In all of these examples, forest was treated as a land cover or land use class, and forest disturbance, other than direct conversion of forest to other land use classes, was not explicitly modeled.

9.3.3 Demand-Allocation Models

One of the significant challenges in modeling land cover and land use change is that underlying processes operate over an array of spatial scales, ranging from broad macroeconomic and demographic drivers to local constraints that affect land use within individual parcels. To account for processes at multiple scales and to incorporate both spatial and non-spatial data, many LCMs use separate modules to model the "demand" and "allocation" of land change. Demand provides aggregate land use proportions at the regional level (quantity of land use change), and is generally driven by "top-down" drivers that affect demand for land-based commodities, such as population growth, commodity prices, or global trade. The allocation component ingests the amount of change from the demand component and produces spatially explicit maps of the locations of land cover or land use change. Allocation is dependent on site-level, spatially explicit data such as elevation, slope, soil attributes, climate, and access to transportation networks, all factors that affect the ability of a land parcel to support a given type of land use. The concepts of "demand" and "allocation" modules were established during the development of the Conversion of Land Use and its Effects (CLUE) model (Veldkamp and Fresco 1996; Verburg et al. 2002), but have since been widely adapted for use in other modeling frameworks.

Demand-allocation models have been used to explore land use at a variety of spatial and thematic scales. Unlike many CA models that are focused on urban change, demand-allocation models have typically been used to project changes among multiple land use categories, including forest. Wassenaar et al. (2007) used the CLUE framework to model cropland and pasture expansion into forested areas of the tropics in Central and South America, while more recently Barreto et al. (2013) used CLUE to model soybean expansion into forested areas of Brazil. In these applications, forest was treated as one of several land use classes, with no explicit representation of forest disturbance or management. Pontius et al. (2001) used GEOMOD to model land use change in Costa Rica, emphasizing forest disturbance. However, they simply modeled the locations of recently disturbed (cut) forest lands, assuming no regrowth, and did not consider other land use changes such as afforestation due to agricultural land abandonment. Of the commonly used demand-allocation modeling frameworks, the Forecasting Scenarios (FORE-SCE) of land use change model has treated forested lands and forest disturbance with the most detail. FORE-SCE has been used to model up to 18 land cover classes, including three classes of forested land (deciduous, mixed, and evergreen) and can also be used to simulate land cover transitions resulting from forest clearcutting (Sohl and Sayler 2008; Sohl et al. 2012). However, FORE-SCE does not represent other forms of disturbance (e.g., fire, insects) or other forest management activities (e.g., thinning, fuel treatments). The modeling of natural vegetation succession has not been incorporated into any of these demand-allocation frameworks.

9.3.4 Agent-Based Models

Agent-based models (ABMs) are process-oriented frameworks that simulate the decision-making processes of "agents", individuals, groups, or entities responsible for land management decisions. Other modeling frameworks that aggregate the collective behavior of agents may miss important aspects of decision-making (Manson and Evans 2007). The decision-making process is often represented by a series of decision rules, with an individual agent's land use decision based on expected response to a set of prescribed input conditions. Landscape patterns emerge from the aggregate interaction among individual agents with heterogeneous behaviors; the agents can interact both with each other and their environment. ABMs have a shorter history of application in land use modeling than the approaches outlined in the previous sections. The most common use of ABMs to date has been by the research community to explore interactions among drivers of land use change, rather than for practical application or policy-making (Matthews et al. 2007). Agent behavior is often modeled at the individual or household level, with model parameter data gathered through household surveys or interviews; as a result, many applications of ABMs have been at a local scale.

As with other types of LCMs, ABMs often focus on modeling changes in agricultural or developed land uses, with changes to forests occurring as an indirect result of agricultural and urban expansion. Castella et al. (2005) used a role-playing game to inform an ABM for simulating land use decisions of farmers in northern Vietnam, with changes in forest area resulting from decisions to plant upland crops or rice. Robinson and Brown (2009) examined potential impacts of land use development policies on forest cover for a township in southeastern Michigan, United States. These studies all occurred on relatively small geographic areas, a common trait for ABM applications because of the computational cost of modeling the interactions of multiple agents across broad geographic regions. Valbuena et al. (2010) described a conceptual framework for applying ABMs to regional settings that uses an agent typology and a probabilistic decision-making approach to represent the variability of agent behavior in a population. ABMs have also been used to represent forest management decisions by agents. For example, Leahy and Gorczyca (2013) developed an agent-based model to represent forest harvest decisions by small-scale forest landowners in Maine, United States. Perez and Dragicevic (2010) modeled insect infestations in British Columbia, Canada, in which the agents were the mountain pine beetle (*Dendroctonus ponderosae*) and lodgepole pine (*Pinus contorta*) trees, along with a forest management agent.

9.4 Coupled Models of Land Change and Forest Dynamics

Traditionally, FLMs have been applied to forest-dominated landscapes with other land cover and land use classes treated as a generic "background" for which change is not explicitly modeled. In contrast, LCMs have been applied to transitions between forests and other broad classes such as croplands and urbanized areas, but have not been used to explicitly simulate changes in forest structure and composition within the forested areas. However, several examples of modeling efforts bridge the gap between these two approaches. In the Coastal Landscape Modeling and Assessment (CLAMS) project, an FLM that simulated forest management activities and the resulting changes in stand structure and landscape patterns was coupled with an LCM that predicted changes in building densities as a result of human population expansion into forested areas (Johnson et al. 2007; Spies et al. 2007). The FLM was the Landscape Management Policy Simulator (LAMPS), which was designed to simulate forest dynamics over extremely large areas (millions of ha) while providing detailed information about the distribution of tree species and sizes within each stand (Bettinger et al. 2005). This FLM was used to simulate the spatial pattern of forest management activities by modeling the interaction of forest landowner behavior with the constraints imposed by various forest policies (Bettinger and Johnson 2003). The LCM was used to simulate increases in building densities using an empirical model driven by historical building densities, topography, land use zoning, and a gravity index that quantified developed pressure as a function of distance from cities (Kline et al. 2003).

The FLM and LCM were combined to project future trends in forest composition and structure across the Coast Range of western Oregon, United States. The two models were coupled via a *spatial overlay* approach, in which a set of rules was used to modify forest management and forest cover at a given location based on building density at the same location (Fig. 9.4a). Timber harvesting was halted and forest cover was maintained at locations that reached a minimum rural residential building density, and locations were eliminated from the forested land base once they reached a minimum urban building density. Overall, expanding development resulted in a 6 % reduction in private industrial forests and a 36 % reduction in private nonindustrial forests available for timber production over the 100-year simulation period (Johnson et al. 2007). This application was an example of *loose coupling*, in which the LCM was run first and the time series of land use change was then used to constrain the projections of management activities and forest structure change made by the FLM. No reciprocal effects of forest vegetation characteristics on land use change were modeled.

In the preceding example, changes in land use interacted with forest landscape dynamics via the influence of housing density and timber harvesting, and ultimately through the conversion of forests to urban areas. Another important process linking human land use and forest dynamics is fire, and several integrated modeling projects have focused on this linkage. Syphard et al. (2007a) projected future patterns of WUI expansion, wildfire, and vegetation dynamics in southern California, United States, by coupling an FLM (LANDIS) with an LCM that predicted urban expansion using a CA framework. Vegetated areas were eliminated by urban growth, and the influences of urbanization on forests were captured via a *spatial interaction* approach where fire frequency was increased within a 90 m WUI buffer surrounding roads and urbanized areas (Fig. 9.4b). Two types of model coupling were implemented: a loose coupling in which the urban growth model first projected WUI change through 2050 and then incorporated the future land use pattern into LANDIS simulations, and a tight coupling in which both the

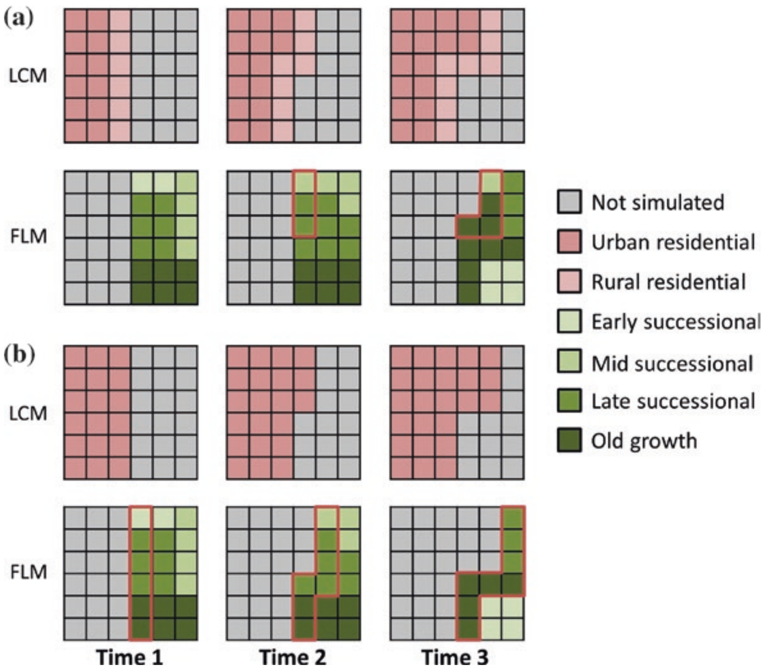

Fig. 9.4 Examples of two general approaches to coupling land change models (LCMs) and forest landscape models (FLMs): **a** In the spatial overlay approach, forests are eliminated by urban residential development, but are retained and influenced by human activity in areas of rural residential development (pixels outlined in *red*). **b** In the spatial interaction approach, forests are eliminated by urban residential development, and the remaining forests are influenced by human activity within a buffer surrounding developed areas (pixels outlined in *red*)

land use pattern and the vegetation map were updated after each 1-year time step. Incorporating the effects of urban growth did not have a large effect on total area burned, but did influence the spatial and temporal patterns of vegetation and fire because of shifts in ignition locations over time as a result of changes in the location of the WUI.

Thompson et al. (2011) coupled a FLM (LANDIS-II) with a land use change model in a way that combined the *spatial overlay* and *spatial interaction* approaches. The LCM simulated forest conversion to developed areas over a range of patch sizes and development intensities. As in the previous CLAMS example, forest composition and structure was still modeled in these converted areas. Development was effectively treated as a disturbance, where species composition and age structure were modified and future regeneration was suppressed. Both forest conversion and the spatial pattern of timber harvesting were sensitive to spatial interactions with socio-economic characteristics in the surrounding landscape, including population density, home values, and road density. The coupled model was used to simulate future scenarios of regional forest change in Massachusetts, United States. Based on these simulations, it was shown that potential increases in aboveground biomass resulting from climate change were more than offset by decreases in aboveground biomass caused by forest conversion and timber harvesting.

Other research efforts have focused on the effects of deforestation and fires resulting from anthropogenic ignitions in tropical forest landscapes. Silvestrini et al. (2011) conducted a simulation experiment across the Amazon basin in which the projected land use changes from the SimAmazonia model (Soares-Filho et al. 2006) were used as inputs to a spatial simulation model of fire that incorporated the effects of deforestation and distance to roads on anthropogenic ignitions. They projected that burned area outside of protected areas would increase in the future, with land use change having a stronger influence on fire patterns than climate change. However, land use change and climate change also had synergistic influences on fires; their combined effects increased the projections of area burned by an amount that was greater than the sum of their individual effects. Soares-Filho et al. (2012) expanded on this approach by developing the Fire Ignition, Spread, and Carbon (FISC) model, which integrated simulation models of land use change and fire with the Carbon and Land Use Change (CARLUC) model, a stand-level simulator of tree growth, mortality, and carbon dynamics. They used the FISC model to conduct simulation experiments under various land use change, climate change, and forest restoration scenarios for the Xingu region of the Amazon. Their results showed that the major driver of fire was forest fragmentation resulting from land use change, and that forest restoration had the potential to limit the amount of understory fires in the region by reducing forest fragmentation. They also found that land use change had a stronger influence on projected carbon balance than climate change, shifting the Xingu region from a net carbon sink to a carbon source in the absence of forest restoration activities.

Another coupled FLM and LCM simulation application has been developed by integrating the demand-allocation land cover and land use change algorithms from the FORE-SCE model (Sohl and Sayler 2008; Sohl et al. 2012) into the Landscape Dynamics Simulator (LADS) model of natural disturbance and forest succession (Wimberly 2002; Wimberly and Kennedy 2008). The new model, entitled the Coupled Human and Natural Geospatial Environments (CHANGE) simulator, uses the FORE-SCE algorithms to control transitions among a set of land cover and land use classes, and then applies the LADS algorithms to simulate natural vegetation dynamics within the land cover classes that are dominated by natural vegetation (Lamsal et al. 2014). The integrated model can also be used to simulate the growth of the WUI, which includes areas of low-density human development that are dominated by natural vegetation. The WUI is modeled using a *spatial overlay* approach in which the land use change models growth and tracks the location of WUI areas, but forest succession and natural disturbances such as fire are still simulated in these areas. The CHANGE model has been applied in central Colorado to explore the interaction of WUI growth and changing fire regimes under alternative future climate scenarios (Liu et al. 2014).

9.5 Synthesis and Perspectives

To date, the development of FLMs and LCMs has mostly occurred along parallel tracks, with relatively few examples of simulation models that have bridged the gap between these two modeling frameworks. However, both FLMs and LCMs have been coupled with other types of models to address broader questions about the interaction of landscape dynamics with biophysical processes. Forest landscape models have been linked with metapopulation models to explore the influences of disturbance regimes on species abundance and population viability in dynamic landscapes (Akcakaya et al. 2004; Wimberly 2006). Land change models have been coupled with spatial models of hydrology (Tang et al. 2005; Wijesekara et al. 2012), erosion and sedimentation (Verburg 2006), and even with other LCMs operating at different spatial scales and levels of complexity (Moreira et al. 2009). In some cases, these linkages highlighted important feedback loops that constrain the process of land use change. For example, agricultural land use influences erosion and sedimentation, and the resulting redistribution of soils across the landscape affects local suitability for agriculture and the spatial distribution of future land use transitions (Claessens et al. 2009). Integrated modeling efforts that link simulations of anthropogenically driven land use change with timber harvesting, natural disturbances, and forest succession have the potential to highlight similar feedback loops and other complex CHANS behaviors. Developing new conceptual frameworks and technological tools to more effectively link FLMs and LCMs will be a critical step toward understanding the dynamics of CHANS in forested landscapes.

The differences between existing FLMs and LCMs partially reflect the different domains of scale at which these types of models operate (Table 9.2). FLMs have historically been applied to smaller landscapes (10^3–10^6 ha) at finer spatial resolutions (0.1–10 ha), whereas LCMs have often been applied across larger regions (10^5–10^8 ha) at coarser spatial resolutions (1–100 ha). However, this distinction is not absolute and there is considerable overlap in both the grain and extent of these two classes of models. Both FLMs and LCMs are generally applied at similar

Table 9.2 Main characteristics of forest landscape models (FLMs) compared to those of land change models (LCMs)

Model characteristics	Forest landscape models	Land change models
Spatial grain	0.1–10 ha	1–100 ha
Spatial extent	10^3–10^6 ha	10^5–10^8 ha
Time step	1–10 years	1–10 years
Simulation length	10–10^4 years	10–100 years
Attribute detail	Tree species, cohort ages, successional stages, biomass	Forests represented by one or a few discrete cover classes
Anthropogenic activities	Clearcutting, partial harvesting, thinning, fuel treatments, planting	Development, agricultural expansion, agricultural land abandonment, afforestation

temporal resolutions (1–10 years) and projected over similar time frames (decades to centuries). In some applications, FLMs have been run for much longer time periods (thousands of years or longer) to simulate historical disturbance regimes and estimate the historical amounts and spatial patterns of forest seral stages (e.g., Wimberly et al. 2000; Karau and Keane 2007).

Perhaps a more important difference is that these types of models have historically been developed by scientists from different disciplines and applied to address problems in different types of landscapes. As a result, FLMs and LCMs have evolved distinctive approaches to landscape characterization and process representation. In the United States, for example, FLMs have been primarily developed by ecologists and foresters and have often been used to evaluate the effects of alternative forest management strategies in National Forests and in other areas dominated by publically owned forest land. In contrast, LCMs have been developed by geographers and planners and have been applied across more heterogeneous regions with multiple land uses to project and analyze the outcomes of processes such as urban sprawl, agricultural land abandonment, and agricultural expansion. As a result, new interdisciplinary initiatives will be an important step toward effectively integrating these two classes of models within a CHANS framework (Roy et al. 2013).

Despite these differences in spatial scale and disciplinary scope, many commonalities in model design emphasize underlying similarities between FLMs and LCMs. At the most basic level, almost all of these models run on gridded landscapes in which multiple categorical (e.g., land use classes, species) or quantitative (e.g., stand age, biomass, tree size) state variables are tracked within each grid cell. The underlying spatial algorithms used to model change are often generic enough to be extended to different processes. For example, the FORE-SCE model adapted the demand-allocation algorithms originally developed for land use change modeling to simulate timber harvesting (Sohl and Sayler 2008; Sohl et al. 2012). This modification was accomplished by including separate land use classes to represent clear-cut forest, specifying the amount of clearcutting that occurs via the demand module, modeling the location of clear-cuts via the allocation module, and tracking forest stand age to ensure representation of realistic cutting cycles and regrowth of clear-cut areas. More generally, the approach used by many FLMs to simulate timber harvesting, as described in Sect. 9.2.2, can be conceptualized as a type of demand-allocation algorithm in which a desired volume or area of harvests is allocated spatially depending on management unit locations, forest vegetation characteristics, accessibility limitations, and adjacency constraints.

Several other spatial modeling approaches have been implemented in both FLMs and LCMs. CA algorithms, similar to those used to simulate urban sprawl, have also been used to model various aspects of forest disturbance. The ABMs used to simulate social systems and land use change are closely connected with the individual-based models that have been used to simulate many ecological systems, including forest dynamics. Perez and Dragicevic (2012) used an ABM in combination with CA to model tree mortality patterns resulting from insect infestation. Cellular automata models have also been widely applied to model fire spread in forested environments (Karafyllidis and Thanailakis 1997; Hernández Encinas et al. 2007; Vahidnia et al. 2013). These and other similarities in model structure and algorithms between FLMs and LCMs suggest strong potential for developing integrated modeling platforms that can utilize the same model structure and basic algorithms to simulate land use change, forest management activities, natural disturbances, and forest vegetation dynamics within a tightly coupled modeling framework.

This type of integrated modeling approach will be needed to address many of the complex forest management issues that arise from increasing interactions between humans and natural systems. In the western United States, for example, the continued expansion of the WUI creates in a variety of subtle yet significant feedbacks between low-density residential land use, forest management and fuel treatment activities, and the risk of insect outbreaks, wildfires, and other large disturbances. Modeling studies have been carried out to explore various aspects of the WUI in the United States, including projections of future changes in housing density in the vicinity of protected areas across the United States (Radeloff et al. 2010), modeling experiments to explore the effects of fuel treatments on fire regimes and landscape structure (Ager et al. 2010), and assessment of the potential effects of wildfire on housing loss under different future development scenarios (Syphard et al. 2013). However, no model currently exists that combines all of these processes and their potential interactions into a unified framework. Such a model would be useful to project how expanding human populations will interact with changing climate and wildfire in future landscapes (Wimberly and Liu 2014). Strategic implementation of fuel treatments could help to reduce housing loss, but increasing population densities may also create a feedback loop that limits the potential for implementing fuel treatments in areas with high rural population densities and small ownership parcels (Fig. 9.5). The integration of FLMs and LCMs is thus a critical research need for projecting future change scenarios in the WUI.

From a broader global perspective, continued population growth is resulting in increased pressure on protected areas and other zones of high conservation value worldwide (Cincotta et al. 2000; Wittemyer et al. 2008). In many parts of the developing world, human land use affects disturbance and succession in adjacent forests through fire spread (Cochrane and Barber 2009), illegal logging (Curran et al. 2004), and edge effects resulting from forest fragmentation (Laurance et al. 1998). Protection of forests and other natural resources may also affect population growth and socio-economic characteristics in surrounding communities through associated infrastructure development, employment opportunities, and provision of ecosystem services (McDonald et al. 2007; Andam et al. 2010; Naughton-Treves et al. 2011). These types of interactions are highly sensitive to the spatial patterns and dynamics of human populations and land use (Cincotta et al. 2000). Thus, integrated modeling of land use change, anthropogenic and natural forest disturbances, and resulting effects on forest ecosystems has the potential to aid in the development of conservation strategies that protect biodiversity while sustaining local communities (Fig. 9.6). Further development of integrated landscape modeling approaches is needed to increase the capacity to simulate a variety of human–natural synergies across a broad range of geographic settings.

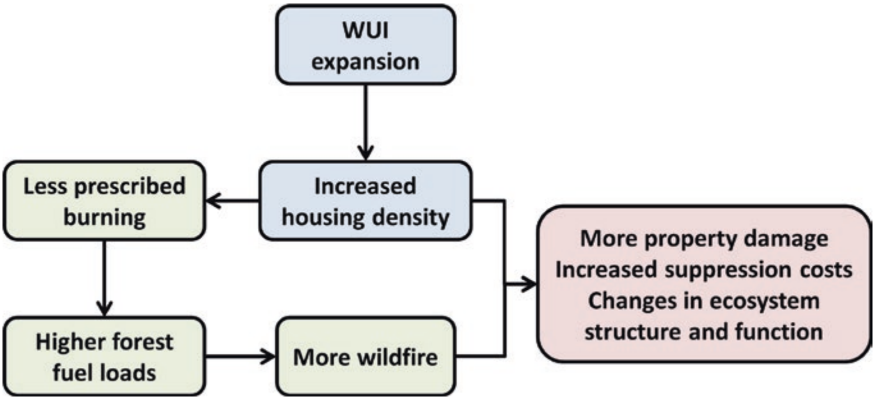

Fig. 9.5 Flowchart illustrating hypothetical interactions of expanded development in the wildland–urban interface (WUI) with forest management activities, ecosystem processes, and natural disturbances. *Blue boxes* indicate processes represented in land change models; *green boxes* are those represented in forest landscape models; the *red box* highlights potential outcomes

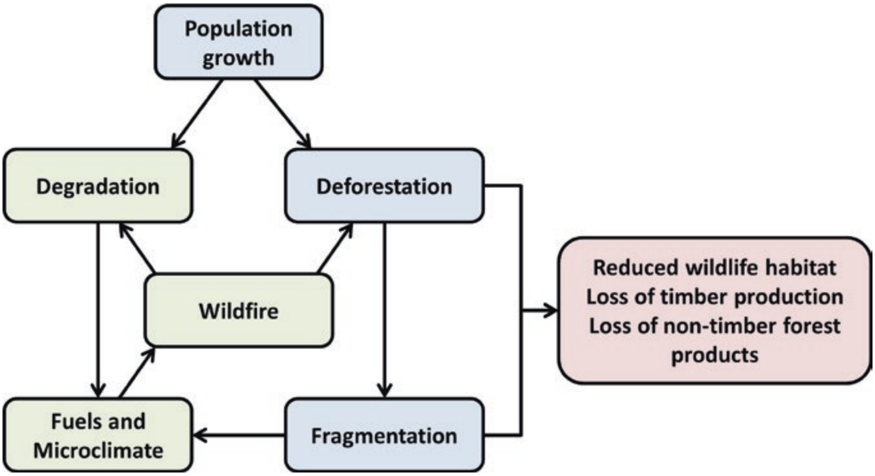

Fig. 9.6 Flowchart illustrating hypothetical interactions of population growth in tropical landscapes with deforestation, degradation, and fire. *Blue boxes* indicate processes represented in land change models; *green boxes* are those represented in forest landscape models; the *red box* highlights potential outcomes

9.6 Conclusions

Existing landscape models simulate a wide range of human disturbances. Forest landscape models typically focus on timber harvesting and fuel treatments as the primary human impacts on forests without considering the broader landscape context, whereas LCMs usually simulate transitions between forests and other land cover types without explicitly modeling succession and disturbance within forested areas. Although roads are often used as a driving variable in simulations of land cover land use change or fire ignitions, most current FLMs and LCMs do not explicitly model the expansion of road networks or consider other influences of roads on adjacent forests. Further development of integrated models that consider the interactions of land use and land cover change with forest management and natural disturbance regimes are needed to more effectively conduct large-scale assessments of future change scenarios in regions where an expanding human footprint is both causing deforestation and altering ecosystem processes in the remaining forests. In future, additional work is needed to more clearly elucidate the processes that connect forest disturbances and succession with broader patterns of land use change, and to develop new modeling tools for assessing future scenarios of forest disturbance and succession in an increasingly human-dominated world.

The similarities of landscape representation and spatial algorithms in FLMs and LCMs provide a framework upon which to build coupled models. As a result, the technical barriers to this type of integration are now relatively low. For example, both agent-based and cellular automata modeling techniques have been used to implement FLMs as well as LCMs, and thus either of these approaches could provide a strong foundation for implementing a coupled model. There is also a strong potential to add functionality for land cover and land use change modeling to existing FLMs (e.g., Thompson et al. 2011), and to incorporate processes such as forest succession, natural disturbances, and forest management activities into existing LCMs (e.g., Sohl and Sayler 2008). However, these types of coupled models will add an additional layer of complexity to the underlying FLM or LCM. As a result, there will be greater demands for data for model initiation and parameterization, and greater challenges in specifying and parameterizing a wider array of function to drive the simulation of forest dynamics, land change processes, and their interactions. To address these challenges, ecologists and foresters will need to work more closely with other disciplines such as geography, planning, and economics. The ultimate goal will be to implement forest landscape disturbance modeling in a CHANS framework that recognizes the contextual effects of regional land use and other human activities on the forest ecosystem while capturing the reciprocal influences of forests and their disturbances on the broader land use mosaic.

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Chapter 10
Simulating Forest Recovery Following Disturbances: Vegetation Dynamics and Biogeochemistry

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10.1 Introduction

Although much effort has been devoted to simulating disturbance processes (see Chaps. 2–7) and their interactions (Chaps. 8 and 9), less attention has been paid to the simulation of forest recovery immediately following disturbance(s). Forest recovery is the process of re-establishment of tree cover (aka stand re-initiation) and associated ecological functions on disturbed sites and is therefore a direct connection between disturbance and resultant stand development. "Forest recovery" can be a value-laden term as "recovery" implies greater benefit accrued from a return to a tree-dominated forest condition. However, recent work on early seral forest ecosystems (commonly defined as the period between a substantial disturbance causing >50 % canopy mortality and canopy closure) has called attention to the special values associated with this stage (King et al. 2011; Swanson et al. 2011). Although often regarded as fleeting or transient—often to the point of exclusion within forest simulations—forest recovery can be protracted (Poage et al. 2009; Freund et al. 2014) due to a variety of factors often ignored within the context of modeling forested systems. Regardless of implicit values or duration, understanding the process of forest recovery is critical to forecasting forested landscapes and disturbance dynamics because long-term successional trajectories depend on this period of regeneration and altered biogeochemical fluxes.

The duration of forest recovery may determine population dynamics of species that require mature stands. Large areas in early succession may fragment landscapes, especially when few biological legacies remain, a high contrast with adjacent mature forest is created, and/or high interspersion with the mature forest matrix is created (Franklin and Forman 1987; Bailey 2007). In landscapes or regions where late seral habitats are considered limiting, it has been proposed that early seral systems be aggressively reforested to facilitate a return to closed-canopy conditions (Sessions et al. 2004).

Early seral habitat is itself critical for many species and is subject to fragmentation as a result of land use changes and alterations to disturbance regimes (Litvaitis 1993; Miller and Hammond 2007). A complete review is beyond the scope of this chapter, but some examples of the characteristics and importance of early seral habitat include:

- Dominance of broadleaf vegetation, including forb, shrub, and tree forms (especially important in conifer-dominated zones; Hagar 2007).
- Forage for several ungulate species (Miller 1970; Irwin and Peek 1983; Nyberg and Janz 1990; Alldredge et al. 2001; Kie et al. 2003).
- Habitat for moths and butterflies (Pyle 2002; James and Nunnallee 2011), including many species of conservation concern (Miller and Hammond 2007).
- Structural and trophic resources for many bird species (Meslow 1978; Fontaine et al. 2009; Betts et al. 2010), including in forest industry landscapes (Bosakowski 1997; Keller et al. 2003) or landscapes with clearcuts (Vitz and Rodewald 2006). Woodpeckers and their allies (family Picidae) frequently

benefit during the early stage, as their insect prey increases dramatically with the abundance of snags and down woody debris (Hutto 1995).

- Abundance of fruiting and flowering vegetation, creating improved forage for many vertebrates and invertebrates, for example bears and their seasonal use of fruiting shrubs (such as *Vaccinium* and *Shepherdia*) in disturbed areas (Zager et al. 1983; Hamer 1996; Samson and Huot 1998; McLellan and Hovey 2001).

Early seral forests often exhibit a high degree of complexity whereby there is sensitivity to initial conditions that magnifies long-term uncertainty (Fig. 10.1). Such complexity is generated by several factors, including the spatial heterogeneity associated with the original disturbance (Foster et al. 1998), size of the disturbance event (Turner et al. 1997; Sturtevant et al. 2014), the behaviors of colonizing organisms (Halpern 1989), the characteristics and spatial pattern of biological legacies of the pre-disturbance forest ecosystem (Franklin et al. 2000), and smaller-scale disturbance processes during the forest recovery period itself (Lutz and Halpern 2006) (Fig. 10.2). Critically, post-disturbance management typically reduces ecological complexity with consequences for the pace of forest recovery. As a result of these factors and their interactions—each operating at unique scales—uncertainty is high with the potential for divergent future stand trajectories (Frelich 2002).

The net outcome is that forest recovery presents numerous challenges to accurately simulating the relevant processes and their consequences at appropriate scales. Many important drivers (e.g., high live canopy fuel density, animal density and herbivory) are widely ignored when modeling forest development. In this chapter, we first review the critical drivers of early succession and attendant processes. Next we review the modeling approaches to forest recovery applied to date. Then we provide two examples of forest disturbance and recovery simulations, each emphasizing a unique but critical perspective on the topic. Finally, we assess the challenges for improving simulation efforts and provide our thoughts on necessary steps forward.

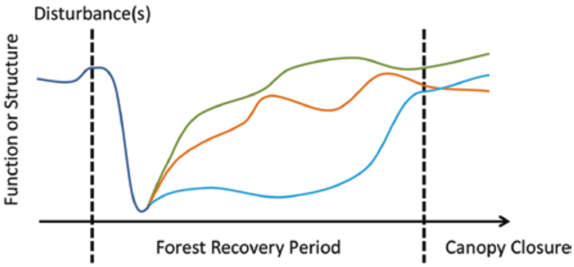

Fig. 10.1 A forest stand may follow one of many possible trajectories depending on initial conditions, disturbance (type, intensity, size, and heterogeneity), biological legacies, recolonization, and management. Sensitivity to initial conditions and long-term uncertainty defines a *complex* process. The y-axis may represent many defining characteristics of closed-canopy forests. The *blue line* represents delayed recovery which may favor early successional wildlife

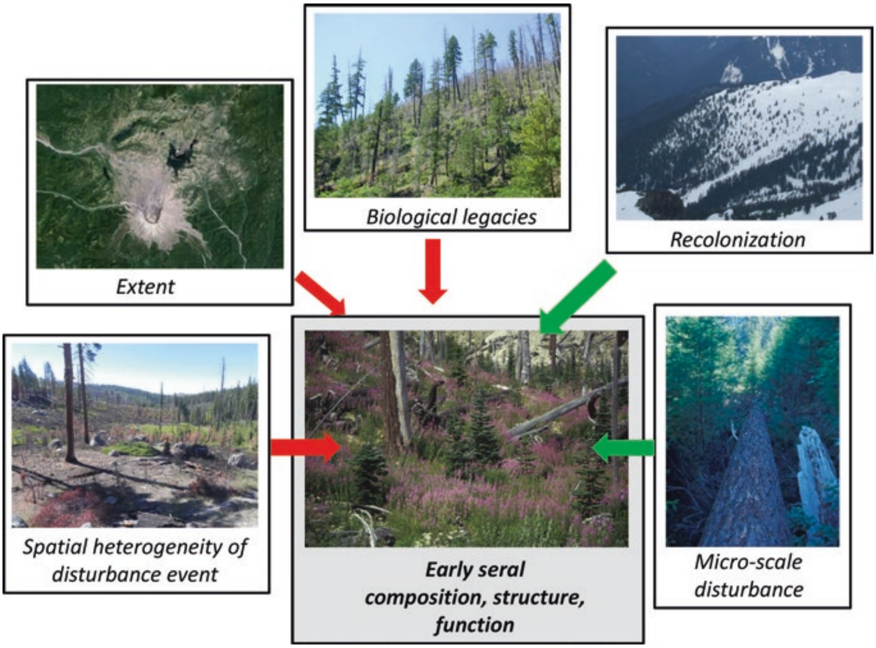

Fig. 10.2 The composition, structure, and function of early seral pre-forest ecosystems depend on the combination of processes associated with behavior of the generating disturbance (*red arrows*) and processes that occur subsequent to the disturbance (*green arrows*)

10.2 Drivers of Forest Recovery

Any attempt to simulate forest disturbance and subsequent recovery must begin with an assessment of the primary processes that determine the eventual outcome—the status of the forest following recovery. We provide examples of four drivers that have a large net effect on forest recovery: biological legacies (presence, amount, and types), altered forest nutrient and water fluxes, regeneration, and management activities. These four drivers—and the examples given below—reflect our own research in central and western United States but are broadly applicable.

10.2.1 Biological Legacies

Biological legacies are living and dead elements of the pre-disturbance ecosystem that persist into early succession (Franklin et al. 2000; Perera and Buse 2014). The amount, type, and spatial arrangement of biological legacies vary widely depending on the disturbance, the susceptibility of trees and shrubs to the disturbance, and any subsequent management actions. The large variety of possible outcomes highlights the ecological complexity inherent to forest recovery. The notable exception to this variation is salvage logging (see below) that reduces biological legacies.

Biological legacies have ramifications that extend throughout succession (Franklin et al. 2000). As an example, the localized rate of stand development following broad-scale stand-replacing wildfire in the Cascades Range of Oregon and Washington depends on proximity to areas that served as partial or complete fire refugia for late-succession tree species (Keeton and Franklin 2005). In the boreal forest, proximity to live residuals following fire has a similar effect on tree regeneration (Greene and Johnson 2000). Large diameter snags may crush young trees as they fall in the early seral period, creating spatial heterogeneity in regenerating tree cohorts (Lutz and Halpern 2006). Snags and downed woody material also reduce erosion and provide partial shelter, increasing soil moisture (see below), which is critical for the regeneration of many tree and shrub species. Biological legacies may also enhance connectivity (Greene and Johnson 2000; Lindenmayer and Franklin 2002; Lindenmayer and Fischer 2006). Individual legacy trees scattered throughout a young forest matrix offer many values, including enhanced wildlife use (Irwin et al. 2000; Mazurek and Zielinski 2004; Lindenmayer and Possingham 1995), and maintenance of mycorrhizal communities (Cline et al. 2005).

10.2.2 Altered Forest Fluxes: Carbon, Nitrogen, Water

Early succession is a time of substantially modified fluxes of energy and material in the forested landscape. Many fluxes are magnified, as the moderating and stabilizing influence of mature forest is removed, and the rate of many ecosystem processes accelerates (Klinger et al. 1994). Nutrient availability may be enhanced due to higher mineralization rates (McClain et al. 1998; Neary et al. 1999) and successional influences on species composition (Brais et al. 1995). At the same time, many fluxes are diminished. Due to the loss of canopy, photosynthesis and evapotranspiration, litter fall and internal nutrient cycling, latent heat, and gross carbon (C) assimilation are all retarded (Leuschner and Rode 1999).

The classic watershed studies at Hubbard Brook (Bormann et al. 1968) demonstrated the flux of nitrogen following clearcut harvesting and herbicide application, revealing the importance of early seral vegetation in capturing nutrients mobilized by decomposition. More recent research has highlighted how post-disturbance conditions (higher temperatures, increased solar radiation) can accelerate heterotrophic respiration, causing a relatively rapid loss of C from the system, above and beyond C lost immediately during the original disturbance(s) (Janisch and Harmon 2002; Campbell et al. 2007). This net flux can vary as a function of disturbance type and variable dead wood legacies and other factors (Mkhabela et al. 2009). Magnified forest fluxes also include more rapid water loss (and the risk of floods as seen in Colorado, USA, in 2013) and more rapid leaching and flow of nitrogen (N) and other nutrients (Vitousek et al. 1979; Boerner 1982; Neary et al. 1999), often affecting neighboring surface waters, e.g., Lake Tahoe (Karam et al. 2013). The net effect of such rapid fluxes may include erosion and loss of top soil (DeBano et al. 2005), reduced regeneration due to low available nitrogen (Beatty 1984), and reduced water retention that disadvantages many small-seeded trees, such as hemlock (e.g., *Tsuga* spp.).

10.2.3 Regeneration

The density, composition, and multi-scale pattern of tree regeneration is determined by many factors (Turner et al. 1998), such as disturbance type (Foster et al. 1998), topographic position and site quality within the disturbed area (Host et al. 1987; Larson and Franklin 2005), distance to seed sources (McClanahan 1986), reproductive strategies of dominant tree species (e.g., serotiny; Turner et al. 1997), micro-topographic features of the disturbed area (Birchfield 2011), and ungulate browsing (Rooney and Waller 2003; Weisberg and Bugmann 2003; Cavieres and Fajardo 2005). The interaction among these factors may be of great significance for regeneration. As an example, if a good seed mast year coincides with a disturbance, regeneration may be significantly enhanced (Vernon et al. 2005). The seasonality of the disturbance may also determine the rate of tree establishment. Examples include fires that occur late in the growing season permitting abundant regeneration from mature canopy seed banks, as observed in Douglas-fir (*Pseudotsuga menziesii*) forests (Larson and Franklin 2005) or survival, as in the snow bank refugia for true fir (*Abies* spp.) associated with the spring eruption of Mt. St. Helens (Washington State, USA) in 1980 (Crisafulli et al. 2005).

Regeneration largely determines the duration of the forest recovery period and the subsequent successional trajectory. Frelich (2002) outlined alternate stable states for boreal forests dependent on seed sources and the time between wildfires. If the time since the last wildfire was relatively brief, jack pine (*Pinus banksiana*) seed sources may not be mature ("immaturity risk"; Zedler 1995) and quaking aspen (*Populus tremuloides*) will be favored with a long delay until the emergence of late-successional species (Frelich 2002). If ungulate populations are high, as is common in the eastern United States, ungulate browsing of regeneration can radically alter the successional trajectory following disturbance (Hobbs 1996; Putman 1996; Rooney and Waller 2003). Artificial regeneration efforts may set a disturbed area on a very different developmental trajectory than that associated with natural regeneration. Again, Mt. St. Helens provides an example, with salvage-logged areas dominated by replanted Douglas-fir and noble fir (*Abies procera*) in the western part of the blast zone contrasting sharply with naturally regenerating areas on federal lands (Titus and Householder 2007).

10.2.4 Management Actions

Management actions are often the largest determinant of forest recovery outcomes, depending on the effort and expense invested. Management actions vary widely and may include post-disturbance replanting, removal of "hazard snags," or some combination thereof. Forest recovery can be accelerated by, for example, planting trees and controlling competing shrubs (Swanson et al. 2011) or retarded through such activities as aggressive salvage logging (Donato et al. 2006). In landscapes where timber revenue is a primary objective (e.g., industrial forest lands) and the generating disturbance is of a natural mechanism (wildfire, wind, avalanche), salvage logging may be performed, followed by reforestation. More recently, some have advocated for using disturbances (including logging) as opportunities to promote ecosystem resilience to climatic change via facilitated migration (Millar et al. 2007; Duveneck and Scheller 2015). Facilitated migration following disturbance is an active intervention in biogeographic shift, whereby managers attempt to pre-emptively assist species in their dispersal along expected migration trajectories, either across elevation or across geographic distances.

Timber managers typically seek a relatively quick recovery of closed-canopy conditions (Oliver and Larson 1996; Smith et al. 1997) and this is frequently accomplished via aggressive application of herbicide and relatively dense planting of seedling stock (Nyland 2002). Salvage logging curtails the early seral stage and reduces its structural complexity (Lindenmayer and Noss 2006; Lindenmayer et al. 2008; Swanson et al. 2011). Titus and Householder (2007) used the case of forest industry lands and National Forest lands within the Mt. St. Helens blast zone as examples of differing successional trajectories resulting from management actions: the establishment of a productive (but low diversity) conifer plantation following salvage and replanting, and the development of diverse early seral habitats where these activities were not conducted.

10.3 Review of Approaches

The range of modeling approaches used to simulate forest recovery and the model choice for a particular application is largely driven by the emphasis given to the drivers reviewed above and the choice of scale. If forest recovery is strongly dictated by management actions that prescribe a narrow range of possible successional trajectories, a relatively simple model of forest recovery will suffice. On the contrary, if the application requires consideration of the full suite of drivers and potential tree diversity (particularly functional diversity) is high, a more nuanced modeling approach will be necessary.

When considering broader scales (>1000 ha), estimates of the rate and trajectory of forest recovery should take into account spatial processes and landscape context and therefore the choice of scale is critical. Spatial processes include the dispersal of vegetative propagules (in addition to those present within the seed bank) and disturbances that depend to some degree on the biotic substrate (e.g., fires and fuel; insect and preferred hosts). Spatial context determines the probability of any given spatial process intersecting with any given location; no forests operate as islands distinct from the broader landscape matrix although the degree of connectivity varies widely. Similarly, models represent spatial context and processes using a wide diversity of approaches. However, simulations of relatively small extents (<10 ha) necessarily exclude multiple interacting disturbances by design.

Here we review modeling approaches that are specifically focused on two primary outcomes of forest recovery: vegetation and biogeochemistry (specifically the magnitudes and rates of change of C and N). Most models have focused on either vegetation or biogeochemistry although hybrid approaches are now emerging.

10.3.1 Vegetation

Forests models may be highly *deterministic* in regard to vegetation where stand type (inclusive of the characteristic tree species) is immutable. Many early forest models were deterministic "growth and yield" models and did not simulate vegetative change; it was assumed that management controlled the general stand type. Immediately following any major disturbance or management activity the stand would essentially be reset to a younger version of itself after which the size classes (e.g., Landscape Age-Class Dynamics Simulator; Wimberly 2002) increment over time or the size of individual trees (e.g., Forest Vegetation Simulator; Robinson and Monserud 2003) increase over time or the amount of biomass (e.g., BIOME-BGC; Running and Hunt 1993) increases over time. Succession in BIOME-BGC is determined by the dominant vegetation or potential vegetation type (PVT) (e.g., Neilson 1995) which reflects broad climatic and edaphic gradients. In landscapes with steep topography (and strong abiotic sorting), these models continue to be applied. Simulated PVTs—and particularly associated fuel types—typically interact with simulated wildfire although the period of forest recovery is often treated as inflammable and therefore forest recovery serves primarily to reduce fuel continuity across the landscape (e.g., Kennedy and Wimberly 2009).

In contrast, many models add a level of stochastic behavior to forest recovery: the infinite vagaries of vegetative establishment and competition are simplified to a tractable set of outcomes via probability distribution functions. In the simplest case, the stand type or initial community is randomly chosen from a fixed suite of potential types or communities; the probability of a given type is usually inferred from historic patterns. After this stochastic assignment, the stand follows a successional pathway as described above. And again, in such models the period of forest recovery typically has little interaction with the broader landscape aside from its effect on wildfire spread. An example of a model with stochastic types is the Vegetation Dynamics Development Tool (VDDT) (Klenner et al. 2000) wherein multiple initial states or types may each be associated with a probability following specific disturbance types.

A more *mechanistic* (an abstraction of the ecological process or mechanism) approach is to simulate establishment during forest recovery as a function of dispersal from neighboring areas and germination from the seed bank or other on-site propagules (e.g., resprouting from root collars). Dispersal is highly stochastic, depending on spatial context and the life history characteristics of individual tree species. For example, aspens and other ruderal species typically have small, wind-blown seeds with long dispersal distances (aka "leptokurtotic"; Clark et al. 1998). In contrast, acorns typically have short dispersal distances except when or where dispersal is facilitated by vertebrates. Seed source strength is also important (Iverson et al. 2004). If the area undergoing forest recovery is relatively large, establishment at the center, farthest from potential seed sources, may be delayed by years or decades. Implementing seed dispersal within a model requires a dispersal algorithm (either away from seed sources or into potential sites) and estimates of the dispersal distributions (Clark et al. 1998). Although the necessary algorithms deploy relatively simple trigonometry, the large area of potential sources (dependent upon maximum seed dispersal distance) requires recursive computational searches for sources across larger landscapes. And data to parameterize dispersal distributions are typically lacking. The net effect is large uncertainty when simulating the establishment of vegetation during forest recovery, including the potential for delayed recovery. In contrast to such mechanistic regeneration approaches, the PVT approach (both deterministic and stochastic) described above encompasses all community components, including grasses, forbs, mosses, lichens, etc. Despite the computational cost, mechanistic dispersal simulation forges a much stronger link between forest recovery and landscape processes.

10.3.2 Biogeochemistry

Similar to vegetation dynamics, the biogeochemistry of forest recovery can be modeled as deterministic or stochastic processes. In general, simulated biochemical modeling has few feedbacks to the larger landscape; they are typically treated as vertical processes, mediating only the interactions among atmosphere, soil, and biotic components. The exception is watershed models that project water quality and quantity, e.g., the Soil and Water Assessment Tool (SWAT; Srinivasan and Arnold 1994). These models typically include information about the amount and location of early seral forests (if not the vegetation type) as they have large effects on water flow and timing. To our knowledge, these effects on water cycling have not been directly incorporated (although a loose coupling is common) into models designed primarily to project forest change.

In the deterministic approach, live and dead C (and less frequently N) pools change through time as a function of growth (net primary productivity), mortality, and decay (heterotrophic respiration, Rh) (Janisch and Harmon 2002; Scheller and Mladenoff 2004). Disturbance may occur at any time along these C trajectories therefore generating novel live, dead, and soil C pools at the onset of forest recovery. However, the *rates* of growth, mortality, and Rh are *fixed* for a given vegetation type or climate-vegetation combination. Examples of such models include the Carbon Budget Model-Canadian Forest Sector (CBM-CFS; Li et al. 2002) and LandCarb (Mitchell et al. 2012).

Stochastic biogeochemical models of forest recovery incorporate the effects of dynamic climate (e.g., PnET; Pan et al. 2009), dynamic soils (e.g., CENTURY; Smithwick et al. 2009), and/or dynamic vegetation (e.g., LANDIS-II with the Century extension; Scheller et al. 2011) on C and N cycles. Most of these models are dynamic in multiple dimensions although no model is *fully* dynamic: every model has some fixed parameters dependent upon the goals and temporal scales considered. For example, soil clay, sand, and loam percentages are typically fixed.

10.3.3 Disturbance Feedbacks

How simulated forest recovery feeds back to disturbance regimes typically mirrors the effect of spatial context on forest recovery. However, within models the strength of this feedback is often underrepresented—early seral stands are often assigned relatively static properties whereby they do not contribute vegetative propagules and have reduced (or no) probability of fire spread (as noted), reduced insect host preference, and reduced vulnerability to wind mortality. The opposite may be true. Birds that favor edges, e.g., jays, may facilitate seed dispersal, or snags may concentrate seed fall from animal dispersers (McClanahan and Wolfe 1987). Clearcuts can create wind "fetches" that increase wind speed at forest edges. Young conifer forests are often highly flammable (high live canopy fuel density) and experience higher wind speeds—and therefore higher fire severity—than mature forests. This is reflected in the occurrence of "reburn" events that occur during the early seral period (Gray and Franklin 1997; Thompson et al. 2008; Fontaine et al. 2009). Finally, early seral shrubs can harbor diseases that affect surrounding mature forests. White pine blister rust is the best known example; shade intolerant gooseberry (*Ribes* spp.) is the host for this fungal pathogen and was widely distributed following the "great cutover" in the U.S. Midwest (Hunt and Pandalai 2003). Although some models provide the flexibility to accommodate early seral fuel types (e.g., Sturtevant et al. 2009), to our knowledge few models capture these other important effects on landscape disturbances.

10.4 Case Studies: Forest Recovery in Two Forests

To illustrate how the drivers of forest recovery have been modeled and applied, we chose two examples with similar approaches but divergent purposes. For both examples the LANDIS-II modeling framework was used (Scheller et al. 2007). This model emphasizes spatial interactions, such as seed dispersal and fire spread, and tracks the location of age-defined cohorts of individual tree or shrub species through time. It also offers a large degree of flexibility, allowing different processes to be emphasized depending on the question and application. For each example, we also highlight unique challenges and opportunities for future research.

10.4.1 Harvest Regeneration and Carbon in Chile

Our first example is of modeling *Nothofagus* forests in Tierra del Fuego, Chile (Swanson 2009). In this region, the effects of harvesting on forest regeneration are of particular concern and a simulation modeling approach was chosen to examine the consequences and trade-offs of harvesting at broad scales. Regeneration is particularly sensitive to harvesting because many of the tree/shrub species have low or mid shade tolerance and many management regimes incorporate planting, limiting the range of successional trajectories. The simulations conducted suggest that regeneration affects long-term C storage and planting, if successful, can substantially increase C storage as compared to natural regeneration alone (Swanson 2009).

The focus on regeneration during forest recovery as a driver of long-term C storage highlighted numerous opportunities for further research. First, how important is disturbance size? There may be critical size thresholds at which regeneration becomes much more limiting, dependent in part on the seed dispersal capacities of trees found in neighboring forests. And what determines the success of artificial planting? Many models, including LANDIS-II, assume that any planting is successful. However, planting success is always less than 100 % and is highly dependent upon microclimatic conditions and seasonal patterns of precipitation.

The motivating questions included: Can the artificial regeneration failure rate be incorporated into broad-scale models and what information is necessary? The parameterization of LANDIS-II in this case included a higher rate of regeneration under a residual live forest canopy, such as may be created in the natural partial-wave wind disturbance regime (whereby wind events over decadal time scales blow down portions of a stand progressively in the prevalent down-wind direction, resulting in a spatially diverse uneven-aged stand condition) in the actual landscape (Rebertus and Veblen 1993; Rebertus et al. 1997) or in shelterwood harvesting (Schmidt and Urzúa 1982; Rosenfeld et al. 2006).

This application revealed areas where model refinement was needed to represent early seral dynamics. Improved accuracy requires better accounting of the spatial variability of regeneration (i.e., assessment of founder effects, where long-term dispersal may influence available genotypes) obtained under a residual canopy, especially as a function of soil moisture availability. In the drier eastern portions of Tierra del Fuego, heterogeneity of moisture availability, especially as a function of location in gaps and substrate type (e.g., woody debris acting as a moisture reservoir) has significant implications for density and pattern of tree establishment. On the other extreme, wet soils can inhibit regeneration or favor more hydrophytic vegetation. Shrub competition (especially from *Berberis* spp.) was also not modeled, and this can be a significant factor in delaying return to a closed-canopy forest structure, especially along the immediate coast in Tierra del Fuego.

In summary, even sophisticated models that incorporate disturbance intensity and size and specific variation in seed rain density may not capture local substrate variability and competition that is critical to estimating regeneration dynamics. To obtain the information needed to populate more detailed models, resampling post-disturbance plots at a high frequency will be required, similar to approaches used to generate the data necessary to fit statistically rigorous trend models (e.g., Huisman et al. 1993).

10.4.2 Biogeochemical Cycling in the Lake Tahoe Basin

Our second example is from the Lake Tahoe Basin in California and Nevada, United States (Loudermilk et al. 2013, 2014). In this landscape, forest harvesting for timber is generally excluded and wildfire and thinning to prevent or ameliorate wildfire effects are important drivers of forest change. Loudermilk et al. (2013) focused on the effects of disturbance on net biogeochemical cycling, specifically the response of C pools to the long-term effects of wildfire and thinning. Although the emphasis was on long-term forest change, the Century extension used within the LANDIS-II framework allows for a finer-scale temporal analysis of C and N responses immediately post-disturbance.

We averaged the response of multiple ecosystem biochemical attributes to simulated wildfires separated in space and time, focusing on the 15 years immediately following a wildfire (Fig. 10.3). Of the six attributes highlighted, one simulated attribute was relatively stable (soil organic nitrogen), three changed linearly (aboveground net primary productivity, soil organic carbon, aboveground biomass), and two were nonlinear [net ecosystem exchange (NEE), heterotrophic respiration (Rh)] over this relatively short period. The initial decline of NEE and Rh was caused by the rapid decay of large amounts of organic material immediately after fire (e.g., Janisch and Harmon 2002). For all six metrics, the rate of change exceeded the average rate of change over 100 years by at least an order of magnitude.

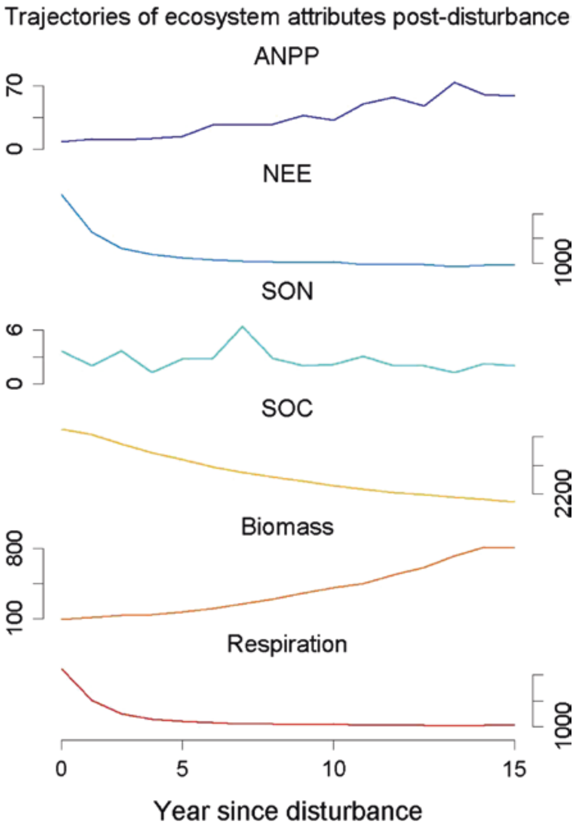

Fig. 10.3 Temporal dynamics of xix biogeochemical metrics immediately following simulated wildfire in the Lake Tahoe Basin, California and Nevada, United States. ANPP is aboveground net primary productivity (g biomass m^{-2} $year^{-1}$); NEE is net ecosystem exchange (g C m^{-2} $year^{-1}$); SON is soil organic nitrogen (g m^{-2}); SOC is soil organic carbon (g m^{-2}); biomass is aboveground live biomass (g m^{-2} $year^{-1}$); respiration is heterotrophic respiration (g C m^{-2} $year^{-1}$)

The substantial decay immediately post-fire highlights the need to consider relatively short-term and transient dynamics when simulating C trajectories. Longer time steps could potentially "average out" this period of heightened heterotrophic respiration and thereby could overestimate both coarse woody debris remaining on site and landscape-scale C in woody detritus.

This example highlights a substantial challenge: frequent (weekly or monthly) measurements are rarely collected immediately following disturbance and model calibration and validation generally depend on landscape-scale and longer-term empirical data. The result may be a broadly accurate forecast of landscape-scale dynamics with poorly measured or understood local accuracy. A common compromise becomes apparent: principles and algorithms derived from landscape-scale data may have poor predictive capacity at local scales where management policies are implemented. The alternative is a highly parameterized local-scale model that cannot incorporate disturbance regimes and interactions among disturbances. Therefore a broader understanding (derived from empirical and modeling studies) of the circumstances under which the various drivers of forest recovery need to be included is required.

10.5 Future Challenges and Opportunities

10.5.1 Process Uncertainty

There are many domains within which models and data about processes critical to understanding forest recovery are inadequate. This is not to say that complete knowledge or information about other processes or stages exists, but rather that some processes have proven more difficult to translate into suitable modeling approaches. This reflects the increasing recognition of the ecological complexity of forest recovery. The net result is the need to become more mechanistic (Gustafson 2013). However, the mechanistic simulation of all processes acting during early succession is generally not feasible. We focus on two related domains that particularly merit further investment in data collection and modeling: the role of biological legacies and the role of partial disturbances.

Biological legacies in particular remain poorly understood or modeled for most systems. To what degree do they influence successional trajectories? To what degree do they ameliorate the effects of disturbance? Keeton and Franklin (2005) describe a negative exponential distribution of regeneration density with distance from old-growth shade-tolerant trees that survived stand-replacing wildfire in the south Washington Cascades, creating gradients of composition strongly related to topographic features. Topographically driven patterns of fire survival combined with seed dispersal patterns created heterogeneous successional states as a function of distance from refugial watercourses and/or fuel-limitations. However, changing disturbance regimes can alter the influence of living or dead biological legacies, such as when higher fire severity reduces seed source and changes the post-disturbance substrate (Johnstone et al. 2010). Although progress has been made in quantifying dispersal over large distances (McLachlan et al. 2005), much uncertainty remains in how far seeds travel over annual or decadal scales and under what conditions. Seed dispersal has large implications for simulating the effects of disturbances and successful colonization often depends on sufficient disturbance severity and the removal of competitive barriers (Iverson et al. 2004).

Many landscape models now simulate variable severity disturbances, which affects the distribution and density of live residuals, thus incorporating some of the complexity associated with partial disturbance. Often, however, less data is available from which to estimate the survival of individual shrub and tree species. This is due in part to a focus on catastrophic disturbances. The most severe disturbances attract the most media attention and this translates into management pressure and research agendas. However, low and moderate/mixed severity disturbances are generally more common and have a more nuanced effect on forest landscapes (Perry et al. 2011). The effects of variable fire regimes and timber harvest have been simulated in a spatially explicit manner at stand scales (e.g., Miller and Urban 2000). However, modeling mixed-severity fire regimes, and their spatially explicit outcomes, at the landscape scale is a greater challenge, especially due to the interaction of terrain, fuel beds, and climate drivers at multiple temporal scales. The resulting complexity leads to the realization of nonequilibrium dynamics at landscape scales, such as in the mixed-conifer forests of eastern Washington State (Hessburg et al. 2007). Adding a further layer of uncertainty to the template established by a disturbance regime is the variable response of tree regeneration as determined by climate (Brown and Wu 2005) or the interaction of disturbance and climate (North et al. 2005). This makes the modeling of forest dynamics more challenging and "data-hungry" in these areas than in forest regions where few topographic and interannual climatic constraints on tree regeneration exist.

10.5.2 Linking Community Dynamics with Biogeochemistry

Improved model representation of forest recovery will require tighter integration of community dynamics and biogeochemistry. For example, it is not clear what effect detrital inputs following disturbance have on long-term heterotrophic respiration (Schmidt et al. 2011). In part, this is because few biogeochemical data are collected during or immediately following (within weeks) disturbance events (Lindenmayer et al. 2010). Biogeochemical data is typically expensive and is collected at fine scales and the imputation of these data to the landscape-scale of forest models is difficult. For example, flux tower measurements are rarely paired with localized disturbances (although see Clark et al. 2012).

10.5.3 Model Formulation

Most models are *sequential*: events happen in a given (either specified or random) order. Many of the processes outlined above, however, happen simultaneously, e.g., seed dispersal and ungulate browsing are continuous and overlapping processes. One solution is to increase the spatiotemporal resolution and use increasingly finer increments of time and distance in simulation models. The representation of forest recovery at a high spatial and temporal resolution is at odds with the need to be computationally efficient when simulating large landscapes over long durations. In particular, the expectation of a changing climate necessitates the incorporation of temperature and precipitation variables into the simulation of forest recovery (Dale et al. 2001), especially when the model time horizons are many decades (He et al. 2002). These changes are actively being developed and the next substantial hurdle will be integration of forest recovery processes into dynamic global vegetation models and global circulation models. Currently such models generally only consider mature forests. However, if increased extreme weather events (Collins 2014) and forest disturbances (Hicke et al. 2013) push a substantial portion of forested landscapes into early seral stages, the integration of forest recovery processes will be necessary to accurately capture global carbon budgets.

10.6 Conclusions

Models that incorporate forest recovery and the duration and character of early seral forest conditions, although imperfect, can aid in the assessment of potential landscape trajectories and associated values over time. If landscape management objectives are dominated by timber production or the maintenance of mature forest habitat, then such models can help assess the rate of recovery of closed forest conditions. Another value of these models is for representing early seral habitat and requires understanding the spatial characteristics, compositional traits, and duration of early seral pre-forest conditions. As the understanding develops of the value of early seral habitat for the maintenance of rare or threatened species (Swanson et al. 2014), models of forest recovery may become crucial tools for predicting the stability and connectivity of such habitats (e.g., Severns et al. 2013).

However, successful representation of forest recovery and early seral forests requires that forest ecologists (and their modeling efforts) embrace the ecological complexity inherent to the forest recovery process (Green and Sadedin 2005; Puettmann et al. 2013). The rates of key fluxes change quickly immediately following a disturbance and sensitivity to initial conditions and circumstance (e.g., disturbance severity) become more prominent. Emergent behaviors are produced that increase the uncertainty of the forest recovery process and have the potential to produce divergent long-term outcomes (Fig. 10.1). Unfortunately, the ecological complexity of early seral stages is often grossly simplified within models.

Success will also require improved data sources. Understanding the emergent outcomes of disturbance regimes over relatively long temporal scales will require landscape models in both reconstructive and predictive applications. An important opportunity to test models of forest recovery would be reconstruction of the long-term effects of large disturbances on the biota at regional scales (e.g., Crisafulli et al. 2005; Swanson et al. 2013). The benefits of large disturbances are their variable intensity across large scales, diversity of biological legacies, temporal synchrony, and their "charismatic" nature that often promotes long-term funding for monitoring. Simultaneously, remote sensing can serve as the long-term (multi-decadal) and large-scale window for validating models of forest recovery following mixed-severity disturbances (Sturtevant et al. 2014). Finally, "citizen scientists" could be trained to collect data about establishment following disturbances. The technology now available to the average person with a mobile phone represents a unique opportunity to engage recreational forest users in monitoring forests to inform ecological forecasts (e.g., LeafSnap: Kumar et al. 2012). These data could augment existing inventory data that are typically sparse, infrequent, and not designed to capture the period immediately after disturbance. Such data could also capture finer-scale regeneration and substrate variability than is typically captured by inventory data. We can imagine future cell phone applications that would inform a recreational hiker when they are approaching a recent disturbance and prompt them to collect regeneration or snag data via a simple interface.

Finally, disruptive or sudden climate change and associated increases in disturbances may necessitate a much more active role for management during forest recovery, e.g., immediately planting tree species not currently extant within the broader landscape (Duveneck and Scheller 2015). Therefore, disturbances can serve as important windows of innovation and experimentation that enable us to test and explore novel manipulations of the recovery process. Such radical (or "transformative"; Puettmann et al. 2013) management actions likely will only be acceptable if models can quickly and convincingly demonstrate the net benefits of such actions to forest recovery and the forest beyond.

In summary:

- Forest recovery may be the most complex stage of succession, with high variability in terms of outcomes, due to the multitude of drivers and scales that influence regeneration and biogeochemical cycling.
- To date, simulations of forest dynamics have largely focused on the dynamics of the resulting overstory and subsequent disturbances. More attention must be paid to the forest recovery stage that determines long-term successional trajectories.
- Further empirical research is necessary to improve model formulation and performance for the period of recovery following forest disturbance.
- Opportunities for data collection and scientific inquiry exist following "charismatic" or well-publicized disturbance events that are synchronized in time and with large area of variable disturbance intensity. Remote sensing is also rapidly emerging as a coarse-scale data source for model calibration and validation.
- Continued research is urgently necessary to help develop novel strategies for manipulating forest recovery to rapidly adapt to climate change disruptions. Improved modeling approaches are a key component of addressing this need.

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Chapter 11
Simulation Modeling of Forest Landscape Disturbances: Where Do We Go from Here?

Ajith H. Perera, Brian R. Sturtevant and Lisa J. Buse

Contents

It was nearly a quarter-century ago when Turner and Gardner (1991) drew attention to methods of quantifying landscape patterns and processes, including simulation modeling. The many authors who contributed to that seminal text collectively signaled the emergence of a new field—spatially explicit simulation modeling of broad-scale ecosystem dynamics. Of particular note are the

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works of Turner and Dale (1991), who produced a first comprehensive overview of the prospect of modeling landscape disturbances, and of Sklar and Costanza (1991), who summarized the limited state of landscape modeling across various systems ranging from natural to anthropogenic and from terrestrial to aquatic, all in a single chapter. Concurrent with the growth in landscape ecology, the field of modeling at broader scales has expanded and diversified quite rapidly since these early summaries. This growth is evident in that less than a decade later, Mladenoff and Baker (1999) were able to assemble an entire text on landscape modeling with a focus on the dynamics of forest landscape disturbances. The subsequent proliferation of landscape disturbance simulation modeling has been captured in several reviews (e.g., Keane et al. 2004; Scheller and Mladenoff 2007; He 2008) and compilations (Sturtevant et al. 2004). For brevity, we refer to these models as *forest landscape disturbance models* (FLDMs), an inclusive term that embraces not just forest landscape disturbance and succession models, but also models of risk and hazard assessment, decision-support tools, land-use and cover change models, and models of individual-based processes. This term and its abbreviated form (i.e., FLDMs) were created for convenience only: our intent is not to add to the plethora of terms and acronyms in landscape modeling parlance.

The evolution of FLDMs has been marked by many changes, but we emphasize three aspects in particular. First, there has been an increase in the number of disturbance types and agents being simulated, and a change in how they are perceived by modelers. Early efforts focused on wildfire and some insect pests, but now the suite of disturbances included in FLDMs, at least in North America, is numerous and continues to expand. During the early stages, disturbance processes were generally simulated as individual external disturbance agents that periodically influenced forest landscapes, independent of vegetation dynamics. Now, there is an explicit recognition of the synergistic effects of interactions among individual disturbances and the dependence of those dynamics on changes in the forest landscape's composition and spatial patterns.

The second aspect relates to a gradual shift in modeling approaches. Early on, there was a heavy emphasis on empirical approaches that primarily relied on observations of past disturbance events based on the assumptions that the patterns exhibited by disturbance agents were stationary and that the responses of the forest landscape were static. Now, modelers are beginning to dispel the belief that knowledge of past disturbances is sufficient to understand what could happen in the future; instead, they are promoting an understanding of the mechanisms that drive disturbances as well as the dynamics of landscape composition. The nonstationary characteristic of forest landscape disturbances, driven by changes in contextual factors such as climate and anthropogenic influences, is an often-discussed topic among FLDM developers.

The third aspect relates to the advances in computing technology and data capture. The early limitations of computing capacity—hardware, programming languages, networking, and affordability—and the limited availability of high-resolution data are far less relevant now than they were even a decade ago.

Technological advances in computation have surpassed the underlying science that supports the processes being simulated by FLDMs, except perhaps in few extreme circumstances. Progress in technology has enabled modelers to develop common (shared) modeling platforms, adopt modular designs that foster interactions among modelers, and remotely exchange vast amounts of information. An unfortunate consequence of advanced computing and data technology is the misplaced goal of pursuing technologically advanced models, which may occur at the expense of models that are imbued with rich and relevant science.

Our goal in this chapter is twofold. First, we present a synopsis of the contents of this book. Beyond being a summary of the salient points that were made in various chapters, we hope that the emergent messages described here will present an adequate view of the current state of our topic—simulation modeling of forest landscape disturbances. Thus, despite the small sample size of only 10 chapters, we hope to capture what is "here and now" based on the examples provided by the contributions of other chapter authors. Second, we present thoughts on future directions or "where do we go from here?" addressed to the community of forest landscape disturbance modelers. Rather than specific prescriptions and remedies, these are general considerations about modeling (not disturbance ecology) that modelers should ponder as their modeling efforts grow, advance, and diversify.

11.1 Where Are We Now?

As mentioned above, we have assumed that the types of disturbances addressed in the preceding chapters, and the modeling approaches and methods described therein, provide a reasonable overview of the present state of FLDMs. This includes many facets of quantifying and simulating forest landscape disturbances: the behavior of disturbance agents, including their interactions with forest landscapes and the effects of contextual factors (i.e., broader-scale and external drivers such as climate and socioeconomic factors); the response of forest landscapes to disturbance agents; the recovery of forest landscapes; and assessment of the risk of disturbances. Even though this book includes only 11 chapters, its 28 authors represent a variety of topics, geographies, perspectives, and views that collectively embody more than 250 years of experience in FLDM development and application. Admittedly, a more complete and global picture of the present state of FLDMs could be constructed through a thorough and exhaustive literature review and synthesis, but that's a task we leave to colleagues who will be motivated by the discourse presented in this chapter.

In the following sections, we summarize the main points made by authors in each chapter, guided by Table 11.1, which provides an overview of their respective focus and key messages. We have grouped the chapters using the broad categories of abiotic, biotic, and integrated disturbances, followed by landscape recovery based on Fig. 1.1 in Chap. 1.

Table 11.1 Summary of the present state of modeling, major knowledge gaps, and future needs for each disturbance type presented in the individual chapters in this book

Chapter number/ authors	Chapter type	Modeling focus *Disturbance type*	Chapter focus	Main messages	
				Present state	Major knowledge gaps and future needs
2. Mitchell and Ruel	Review	Windthrow *Pulse*	A review of empirical and hybrid empirical–mechanistic modeling approaches to simulate windthrow susceptibility, with scaling from tree to stand and landscape scales	• There are many empirical models based on tree- and stand-scale outcomes • Many hybrid mechanistic models link tree vulnerability to environmental and management factors	• Representation of airflow through complex stands and partial harvests • Understanding of tree collisions and damage propagation within stands • Model validation across a broader range of forest conditions
3. Gustafson and Shinneman	Case study and review	Drought *Press*	An illustration of empirical approaches and a review of the potential for mechanistic approaches to simulating effects of drought-induced mortality on stand composition	• The primary focus is empirical, but mechanistic models in development are also discussed	• Understanding of the mechanisms of tree mortality related to moisture stress • Empirical studies to link tree mortality to multiple stressors • Approaches to scale from trees and sites to broader scales (e.g., landscapes)
4. McKenzie and Perera	Synthesis	Wildfire regimes *Pulse*	An exploration of the modeling approaches used in wildfire-regime simulation models, based on the orthogonal concepts of abstraction and complexity.	• Approaches range from empirical to hybrid and mechanistic • This is a relatively mature field of simulation modeling.	• Understanding of nonstationarity and dynamical properties of fire regimes • Modeling of interactions with other disturbances • Approaches that minimize `cumulative error and increase the transparency of outcomes

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Table 11.1 (continued)

Chapter number/ authors	Chapter type	Modeling focus *Disturbance type*	Chapter focus	Main messages	
				Present state	Major knowledge gaps and future needs
5. Sturtevant et al.	Review and synthesis	Spruce budworm (SBW) *Pulse*	A synthetic review of the evolution of modeling approaches to describe SBW dynamics	• Modeling approaches are well developed, but poorly integrated with other ecological processes and with ecosystem recovery.	• Ability to simulate outbreak severity and duration • Appropriate scaling techniques (time and space) • Improved integration of insect population dynamics with host tree effects • Integration of elements from different scientific paradigms that are consistent with current science
6. Regnière et al.	Case study	Mountain pine beetle (MPB) *Pulse*	An illustration of the individual-based model (IBM) approach to evaluate the response of MPB to climate change	• IBMs represent a new and expanding topic • The MPB IBM is limited to nonspatial processes	• Knowledge of insect biology; effects of tree distribution on host finding by the MPB and its attack ability; indirect effects of climate on host trees • For spatial modeling, how to accurately simulate MPB dispersal • For scaling up, how to manage a large number of objects (here, individuals)
7. Birt and Coulson	Review	Southern pine beetle (SPB) *Pulse*	A synthetic exploration of modeling SPB dynamics while considering the disturbance agent as an endogenous property of the forest landscape system	• SPB models exist, but are not well integrated into a holistic and integrated modeling approach	• Knowledge of the processes underlying the transition from endemic to an outbreak state • Scaling techniques (time and space) • Integrated modeling as a coupled human–forest–insect system • Need to move from predictive modeling to exploratory modeling using mechanistic approaches

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Table 11.1 (continued)

Chapter number/ authors	Chapter type	Modeling focus *Disturbance type*	Chapter focus	Main messages	
				Present state	Major knowledge gaps and future needs
8. Keane et al.	Case study	Disturbance interactions *Pulse and press*	A demonstration of highly integrated mechanistic modeling of abiotic and biotic disturbances to examine their emergent interactions	• Integrated mechanistic modeling is in the early stages of development • Most ecological responses to disturbances will result from complex interactions • Computing technology enables the development of integrated and complex disturbance simulation models	• Understanding of the relationships among disturbances and their effects • Inclusion of additional abiotic and biotic disturbance mechanisms • Mechanistic response functions for ecological processes
9. Wimberly et al.	Review	Coupled human–natural systems *Press*	A review of modeling approaches to simulate the reciprocal effects of anthropogenic and natural disturbances by coupling forest landscape models (FLMs) with land change models (LCMs)	• FLMs and LCMs are fairly well developed, but independently of each other • Integration is possible with existing models, but is still at its very early stages	• Data to initiate and parameterize more complex integrated models • Understanding of processes to connect disturbance effects with land-use change • Common inputs, algorithms, and model structures • New conceptual framework that captures feedbacks and reciprocal influences

(continued)

Table 11.1 (continued)

Chapter number/ authors	Chapter type	Modeling focus *Disturbance type*	Chapter focus	Main messages	
				Present state	Major knowledge gaps and future needs
10. Scheller and Swanson	Case study and review	Forest recovery	An examination of the modeling of key ecological processes involved in the recovery of forest landscapes from disturbances	• The post-disturbance recovery stage is often overlooked or oversimplified in models • Models are moving from empirical toward mechanistic approaches	• Understanding of the drivers and processes to clarify which must be included in models • Scale-appropriate data to populate more detailed models • Approaches to model mixed severity and simultaneous overlapping disturbances • Integration of the forest recovery stage in other models

11.1.1 Abiotic Disturbances

As Mitchell and Ruel (Chap. 2) explain, empirical windthrow models can represent site and management conditions at the tree and stand-scale and provide insights into landscape-scale patterns of wind disturbance. However, empirical models offer limited insights into the underlying mechanisms and are of limited use in as-yet unobserved situations. Hybrid–mechanistic modeling approaches are used to predict the behavior of individual trees under wind loads—individual trees fail if the critical wind load exceeds the stem strength or anchorage strength—and can be aggregated to simulate stand- and landscape-scale outcomes. Some spatial effects, such as sheltering by upwind trees, are accounted for, while others, such as tree-to-tree collisions, are not. By including regional wind patterns and incorporating the models into decision-support systems, climate change scenarios can be explored. Many knowledge gaps remain, some of which can be addressed through expert knowledge. Predictive models can be improved via interdisciplinary collaboration.

Using case studies, Gustafson and Shinneman (Chap. 3) present two stages of modeling in the relatively new field of simulating the effects of drought on forest landscapes: empirical correlations between stress and species responses and mechanistic simulations of the mortality induced by moisture stress. Although moisture stress has been modeled for decades, modeling drought as a disturbance (i.e., as episodes of drought-caused tree mortality) is recent and is still in the early stages of development. Deterministic approaches, although common and simple, have many disadvantages: they are not realistic, they simulate uniformity and homogeneity in disturbance patterns, and they do not account for changes in the climatic context. Furthermore, drought-based tree mortality is a confounded outcome: cumulative stress resulting from drought can predispose trees to biotic disturbance agents, such as insects and diseases, whose prevalence may be independently affected by climatic change. Additional drivers such as changes in atmospheric chemistry can likewise affect plant water use and moisture stress. Mechanistic modeling approaches based on tree physiology are poised to better address the cumulative effects of stress agents, and their effects on forest mortality.

In their synthesis, McKenzie and Perera (Chap. 4) observe that modeling of wildfire regimes is a relatively mature field of study, so that current paradigms in this field can inform simulations of other forest landscape disturbances. For example, it is clear that the stochasticity of wildfire events and the effects of a changing climate are not replicated in observations of the past. Therefore, predefining properties of individual disturbances or fire regimes in general will fail to capture the dynamism, emergence, and stochasticity that characterize forest landscapes and will not be robust to changes in disturbance regime characteristics. Mechanistic modeling has advantages in this regard, but it is also possible to "over-model" by including extraneous mechanisms, which can produce false precision at fine scales, and to misrepresent wildfire disturbance at broad scales. The degree of abstraction and complexity embedded in simulation models must be question- and situation-specific, and most importantly, must be scale-specific.

11.1.2 Biotic Disturbances

In reviewing the evolution of spruce budworm (*Choristoneura fumiferana*) modeling over a period of five decades, Sturtevant et al. (Chap. 5) illustrate the long-term process of model building to inform our understanding of complex disturbance dynamics. Advances in spruce budworm modeling have been neither linear nor continuous, but rather they have emerged from competing and often incomplete paradigms that explain limited observations collected at inherently restricted spatial and temporal scales. Insect disturbance modeling is often complicated by nonlinear and cross-scale interactions among components that operate at various scales. Despite extensive investments in research, comprehensive modeling approaches have not readily emerged because of the inherent unpredictability and specificity of these ecological systems, as is the case for biotic disturbances in general. Sturtevant et al. present a vision of a hybrid approach that blends scientific paradigms, modeling approaches, and empirical and mechanistic relationships, using the framework of landscape disturbance and succession models.

In describing an individual-based model (IBM) that simulates mountain pine beetle (*Dendroctonus ponderosae*) responses to temperature changes, Regnière et al. (Chap. 6) present an excellent example of a highly mechanistic simulation model of the behavior of a disturbance agent. Their chapter is unique in that it focuses on a single model, and their in-depth case study illustrates a specific modeling paradigm (i.e., IBM). The IBM approach can help to identify knowledge and data gaps and can be used to simulate low-probability events. In this approach, the built-in responsiveness to changes in the climate context is governed by relatively simple rules that affect individual responses to the environment. IBM is a generalizable strategy that is particularly well-suited to insect disturbance, since outbreaks are emergent properties that result from the summation of individual responses. However, there are difficulties involved in up-scaling coupled disturbance mechanisms from tree (individual) to landscape scales and in applying the IBM approach to simulate outbreak behavior in time and space, which may be beyond the current computing capacity.

Birt and Coulson (Chap. 7) discuss many considerations for advancing models of the forest disturbance caused by the southern pine beetle (*Dendroctonus frontalis*). The vision of potential positive effects of disturbances is often overlooked because of the common socioeconomic perspective that disturbances are destructive. However, if considered as an integral part of a broader ecological system, beyond the scale of the “destroyed” forest stand, disturbances can be perceived as agents of ecosystem renewal. This point, which the authors present for southern pine beetle, is applicable to other disturbances. For some disturbances, adopting a holistic outlook that includes socioeconomic processes will help modelers to better quantify the disturbance regimes and their consequences, and will also help them to communicate about disturbances and educate forest managers. Birt and Coulson argue in favor of simulation models based on mechanisms, although a variety of complementary modeling approaches will ultimately yield the most insight for complex systems. As well, they reiterate the view that past disturbances may not inform the future because of the dynamic nature of forest landscape drivers and the patterns they produce.

11.1.3 Integrated Disturbances

Using a case study of simulating the interactions among three disturbance types (i.e., fire, insects, and disease), Keane et al. (Chap. 8) demonstrate that the indirect effects of climate change on disturbance regimes and their interactions can have far greater influence on ecosystem dynamics than the direct effects. Since these disturbances can act synergistically, their combined effects can be elucidated only with mechanistic models that include the underlying drivers, and cannot be discerned based solely on past observations. Recent advances in landscape models are enabling investigations of such interactions among disturbances; however, empirical knowledge of the underlying drivers that affect disturbance interactions remains a limiting factor. Emergent properties of integrated disturbances, through their reciprocal interactions, can be counterintuitive. Although the specifics of such interactions may be unique to each study area and set of circumstances, the approaches to understanding such interactions are transferable to other landscapes and situations.

Wimberly et al. (Chap. 9) review the coupling between natural and anthropogenic disturbances and the potential for combining land change models (LCMs), which address socioeconomic phenomena, with forest landscape models (FLMs), which focus on ecological phenomena. Although the spatial scales and approaches may differ between LCMs and FLMs, the common conceptual design in both approaches makes their integration possible. Real and complex interactions are inherent in these coupled systems, indicating that the effects can be direct and immediate (as is the case with forest harvesting) or they can be indirect or delayed (as is the case with road networks). Recent efforts in the landscape-scale modeling of coupled human–natural systems have relied primarily on loose coupling of FLMs and LCMs, in which the input from one model is used to drive the other model. Given the reciprocal nature of human and ecological processes, further progress will require interdisciplinary efforts to more tightly couple these modeling approaches.

11.1.4 Recovery

Scheller and Swanson (Chap. 10) focus on modeling a system's recovery after a disturbance. Reciprocal feedbacks between the disturbance and both vegetation and biogeochemical processes are integral to understanding the effects of disturbance on forest landscapes. The complexity and short time horizon of the recovery processes, as well as the many interacting factors and influences complicate modeling efforts of short-term forest landscape recovery, and lead to uncertainty in the outcomes. Four major drivers influence recovery dynamics: biological legacies, nutrient and water fluxes, regeneration mechanisms, and management activities. The two contrasting case studies presented in this chapter demonstrate both the importance of modeling the recovery stage of forest dynamics and the challenges associated with this modeling. Mechanistic approaches are essential to reflect the complexity of the processes involved in forest recovery. Critical requirements to support these approaches are data to parameterize such models, the reconstruction of disturbance effects at regional scales, remote sensing of post-disturbance recovery, and the enlistment of "citizen scientists" to fill data gaps.

11.1.5 Emergent Messages

The chapters in this volume not only spanned a broad range of disturbance types, they also present disturbance modeling from different perspectives. For example, three sequential steps relevant to modeling forest landscape disturbances are addressed in the chapters at different levels of focus and detail (Fig. 11.1). Chapters 5 and 7 focused on methods of simulating the disturbance agent's behavior and the response of the forest landscape separately, whereas other chapters (3, 4, 8 and 9)

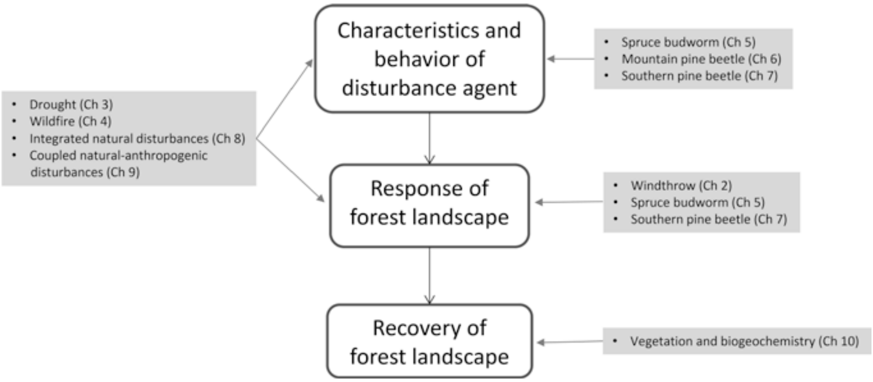


Fig. 11.1 The three major steps involved in simulating forest landscape disturbances, and the modeling domains addressed in the chapters of this book

addressed these steps together. Chapter 6 detailed only the first step, and Chap. 2 focused on the second. Chapter 6 described simulation of the behavior of a disturbance agent (mountain pine beetle), given certain forest characteristics and climate drivers, whereas Chap. 2 addressed the response of a forest's structure to a physical disturbance agent (windthrow, given the presence of wind storms). Even though most chapters alluded to post-disturbance vegetation changes, only Chap. 10 focused explicitly on the recovery of forest landscapes after disturbances.

To illustrate the emergent messages that result from synthesis of the discussion in the preceding 10 chapters, we created a word cloud based on the relative frequency of occurrence of the key terms (Fig. 11.2). This shows that concepts such as interactions, complexity, mechanistic modeling, abstraction, and anthropogenic effects were more commonly addressed by chapter authors than stochasticity, validation, hypotheses, communication, and model parsimony. It appears that these "common" terms in the word cloud are interrelated. Below, we examine the concepts associated with these terms first and address the "less common" terms later in the text.

Spatially explicit interactions are inherent in forest landscape disturbances: a common theme in this book is the relative strength of the reciprocal interactions between vegetation and the various disturbance agents in time and space. Abiotic disturbance agents—particularly those that are most directly linked to weather and climate patterns (i.e., in this book, wind, drought)—have comparatively limited feedback with vegetation in terms of modifying disturbance regimes. Although vegetation does have a localized influence on disturbance effects, for example via size- or species-specific susceptibility to the disturbance (e.g., the likelihood of being blown over, as in Chap. 2; the relative tolerance of drought, as in Chap. 3), its relative influence on the behavior of disturbance agents is limited compared with larger-scale factors, such as hurricane frequency and regional drought episodes. In contrast, biotic disturbance agents have comparatively strong reciprocal feedbacks with vegetation dynamics (e.g., Chaps. 5–7). Furthermore, the absence of a host species can make its associated biotic disturbance agent become irrelevant. Wildfire disturbance lies between these two extremes because it is an abiotic disturbance that is strongly influenced by both weather and climate and by the specific fuels

Fig. 11.2 The relative importance (frequency of mention) of 10 key terms in the independent contributions in this volume (Chaps. 1–10). The font size is proportional to the frequency of occurrence of the words in the text; however, the terms are randomly positioned within the figure

produced by the vegetation (Chaps. 4 and 8). Thus, it is more general than most insect pests (fire occurs in most of the world's forest ecosystems), but less general than wind (all trees become susceptible to windthrow at extreme wind speeds).

Moreover, interactions among disturbances are complex, a fact that all chapter authors point out. Press disturbances influence pulse disturbances. (See Chap. 1 and Table 1.1 for their definitions.) For example, drought stress may change the characteristics of the forest landscape, and this, in turn, will influence the behavior of wildfire. As well, some pulse disturbances influence other pulse disturbances. For example, a windthrow event may modify forest fuel availability, thereby altering the behavior of wildfire. Anthropogenic disturbances may alter natural disturbances both directly and indirectly; for example, indirect press disturbances such as road networks can change water tables (thus, can affect wildfire spread) and direct pulse disturbances such as harvesting can change stand properties (thus, can affect windthrow), thereby affecting subsequent disturbance dynamics. The relative strength of reciprocal interactions between disturbance agents and vegetation dynamics has important consequences for overall system complexity. Changes in contextual factors such as climate may be subtle until thresholds are reached, after which the response can be pronounced; examples include changes in temperatures and precipitation (drought) and in lightning patterns (wildfires).

As our knowledge of individual disturbance domains matures, there is a concurrent move by modelers of all disturbances toward mechanistic modeling. All authors in this book argued in favor of such a move, and noted that the limitations of simple empirical models and extrapolations appear to be increasingly recognized by researchers. The once-popular and primary method of understanding forest landscape disturbance regimes solely based on past occurrences is either being replaced or complemented by scenario-based simulations that depend on an understanding and quantification of the underlying ecological processes. This is evident in simulations of the susceptibility to a disturbance and the vulnerability if one occurs (Chap. 8). This area of research stems from a long tradition in risk and hazard analysis, but has become quite sophisticated in terms of the science underlying the description of risk factors and their interactions with disturbance processes in time and space (e.g., Chaps. 2 and 5). It is also evident in approaches for addressing the concept of emergent disturbance regimes, where disturbance events initiate, spread, and terminate based on first principles of biology, physics, and chemistry to generate dynamic disturbance regimes that are influenced by both external drivers (e.g., climate variables) and internal properties (i.e., reciprocal interactions among vegetation composition, arrangement, and structure). It is possible to model disturbance behavior that emerges from an even lower level of organization, such as the cumulative behavior of individual disturbance agents rather than disturbance events. This method is suitable for simulating biotic disturbances such as insects or human disturbances, as affected by the behavior of individuals (e.g., Chaps. 6 and 9). Simulating disturbances as emergent system properties sets the stage for investigations of the interactions among disturbances—the consequences of which are often greater than the sum of their parts (Chap. 8).

All authors in this book recognize the complexities that are involved in mechanistic modeling, and the difficulties in scaling and selecting the ecological processes that need to be modeled. Limitations emphasized by several authors include those related to data, and specifically the quality, resolution, and extent of the data resources needed to parameterize, initialize, or validate models. More importantly, significant scientific limitations remain as a result of incomplete understanding and knowledge of various processes; for example, we do not fully understand the drivers underlying the "death spiral" associated with tree stress (Chap. 3), cross-scale interactions (Chaps. 5 and 7), and thresholds that influence many disturbance types, including insect outbreaks, diseases, and wildfire (Chap. 8), nor the key drivers and processes crucial for forest recovery (Chap. 10). Nonetheless, landscape disturbance modeling, like virtually all other disciplines in ecological modeling, will always be subject to the middle-number paradox in ecosystems (sensu Allen and Hoekstra 1992), and expectations must be tempered accordingly (Chap. 4).

The shift toward mechanistic modeling is also perhaps motivated by the recognition of the nonstationarity of contextual factors. This includes a wide acceptance of the prospect of changing climatic conditions as well as inclusion of anthropogenic influences on a forest landscape's structure and function. The latter are perhaps more complex and unpredictable because many social, political, and economic factors influence the behavior of human populations. Still, many have argued that simulating forest landscape disturbances in isolation from anthropogenic effects is only an academic exercise, because "real-world systems" include human effects through modification of landscape patterns (e.g., by forest harvesting, road construction, and the control of disturbance agents that considerably modify the behavior of landscape-scale disturbances). Therefore, the integration of socioeconomic phenomena as constraining and controlling factors may be essential.

Some common knowledge gaps also emerged from the individual discourses by chapter authors. Foremost was the uncertainty involved with understanding which ecological processes are crucial for inclusion in mechanistic FLDMs, and extending those key fine-scale mechanisms to broader scales; this was echoed by all chapter authors. Paucity in knowledge is also evident in relation to factoring in anthropogenic influences, as emphasized by Chaps. 7 and 9. As the processes are scaled from fine to broad, and multiple mechanisms are added, the relative lack of knowledge on error propagation (Chap. 4) and validation (Chap. 2) also could become an impediment to developing mechanistic FLDMs. Some of these difficulties can be, at least in the short term, alleviated by resorting to expert knowledge (Chap. 10).

In summary, the following messages resonate throughout the chapters in this book:

- *Disturbance regimes are complex*, but they nonetheless need to be examined and understood in a way that accounts for as much of the complexity as possible. Abstraction of the ecological system and of the disturbance and recovery processes can be simple or complex, depending on the question and the modeling goal.

- *Disturbances in forest landscapes are dynamic and therefore nonstationary*. They are dynamic because there are many interactions and feedback mechanisms with other ecological processes. They are nonstationary because the forest landscape patterns (and processes) change over time, and the contextual factors (that are beyond the scale of the disturbance mechanisms) can change outcomes.
- *Past disturbance processes are informative, but they may not indicate what is possible or probable in the future*. Simple extrapolation of past information into the future, however convincing and accurate, may be inappropriate in dynamic systems that are moving into novel conditions.
- *Understanding the mechanisms that govern the behavior of disturbance agents, the responses of the forest landscape, and its recovery processes is very important* and, however daunting, will be the solution to exploring disturbances under possible future scenarios, as well as testing models as hypotheses to advance science. This is true notwithstanding the need to be parsimonious with the mechanisms that are quantified and modeled.
- *Excluding anthropogenic influences, focusing on one disturbance at a time, and ignoring forest landscape recovery mechanisms are no longer the most effective strategies*. Simulating scenarios with long time trajectories may not be valid unless the human effects, climate change, and interactions with other disturbances, as well as how forests landscapes evolve, are considered and included in modeling efforts.
- *Computing and data-gathering techniques may have advanced well beyond our capacity, as ecologists, to conceive and quantify ecosystem processes*. These former bottlenecks are rarely an impediment to developing sophisticated FLDMs, with few exceptions such as extending IBMs to large forest landscapes. At the same time, FLDMs must not be guided and motivated by technological advancements. What is needed is not a consideration of what is technologically *feasible*, but rather what is ecologically *sensible*.

11.2 Where Do We Go from Here?

With increasing and broadening awareness of ecological disturbances and their consequences in forest landscapes, we expect the role of FLDMs to continue to expand. They have been and will continue to be fundamental tools to inform research on disturbance ecology through the iterative process of model development, confrontation of models with data, and refinement or development of new models to incorporate the resulting insights. The scientific role of model development has a special meaning in the field of forest landscape ecology, since landscape-scale experimental manipulation is complicated, if not impossible. Consequently, scientific advances in FLDM development will likely be supported by the growing demand for modeling tools by forest landscape managers,

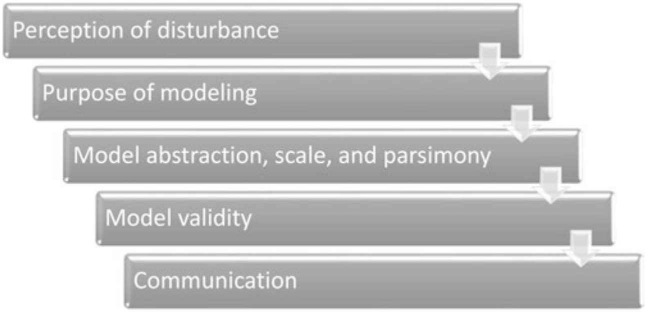


Fig. 11.3 Considerations for developers of forest landscape disturbance models. The directionality implied by the arrows is not necessarily linear; there are many feedback loops involved in successful model development based on continuous learning and adaptation

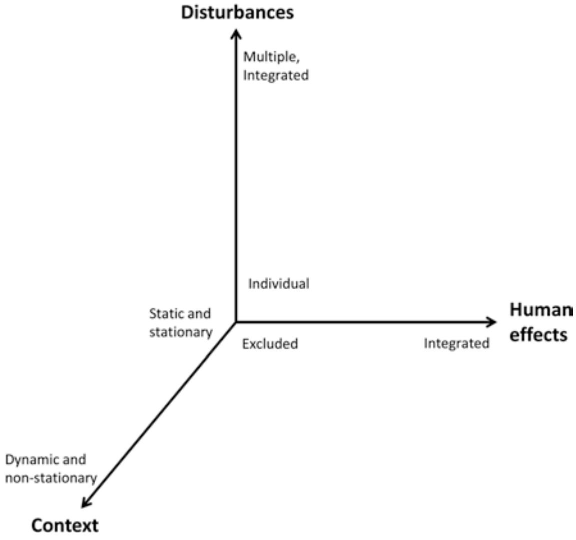
who increasingly view FLDMs as an integral part of their strategic and tactical decision-making. Also, FLDM developers will have access to rapidly advancing scientific knowledge, improved empirical data on forest landscape patterns and processes, as well as superior computing technology and programming languages.

In the rest of this chapter, we present a collection of considerations for those who develop FLDMs with the goals of advancing science and applied decision-support (Fig. 11.3). We address these considerations from five perspectives: the perception of disturbances; the purposes of modeling; abstraction, scaling, and parsimony of models; model validation; and communication.

1. **Perception of forest landscape disturbances**

Disturbances can be perceived as continua in multiple dimensions (Fig. 11.4). For example, they can be considered simultaneously based on:

Fig. 11.4 The characteristics of the forest landscape disturbances that are included in a simulation model can be perceived along many dimensions. This illustration shows only three such axes, and does not necessarily suggest orthogonality among the dimensions, nor linearity in scale



(a) The number of disturbances considered, starting with a simplified scenario of a single “type” of disturbance (i.e., a single causal factor), and progressing toward a complex suite of many interacting (integrated) disturbances
(b) The influence of human activities, ranging from no anthropogenic influence to indirect influences on disturbances through anthropogenically altered landscape patterns and direct influences by controlling the disturbance agents. For example, socioeconomic factors such as vagaries in the markets for forest products, shifts in cultural perceptions, demographic changes, and changes in human settlements can all influence forest landscape disturbances.
(c) Ecological context changes, starting with the assumption of stationary contexts and extending to dynamic (nonstationary) contexts that dynamically influence disturbance processes. Evolution of novel ecosystems as a consequence of changes in context, such as climate change, atmospheric pollution, and species invasions, is a distinct probability.

“Real world” applications demand a high degree of complexity from FLDMs, and a more inclusive view of disturbances by model developers. Although model developers may envision and pursue an idealistic and complex FLDM that would capture all disturbances, including all human activities, under a range of scenarios related to context changes, in reality the success of such a pursuit will not initially be high. Such a pursuit may go beyond current theoretical knowledge, technological and information capacity, and even computing capabilities. We therefore caution modelers that FLDM development should move in the direction of developing comprehensive models only with due rigor, as knowledge and capacity make this expansion both rational and feasible. In the meantime, they should eschew models that try to address as many issues as possible and that therefore address none well, since such models may be less useful than simpler models that address a few select disturbances well. During this process of advancement, while FLDMs continue to evolve and become more complex, an explicit articulation of the domain in which we perceive a disturbance to occur (which we consider essential state assumptions for modeling) will help define the FLDM’s scope for its developers, and will clarify its intent and utility to those who apply the FLDM.

2. **Purposes of modeling**

As we pointed out in Chap. 1, the differences among the purposes of FLDMs (i.e., prediction, forecasting, projection, and scenario exploration) are not mere academic distinctions; they matter greatly because they affect how models are developed, perceived, and applied by users. Nearly 40 years ago, Overton (1977) noted that the modeling literature did not contain clear statements of models’ goals and objectives. This is still true, as Evans et al. (2013a) echo in their meta-review of ecological model typologies that range from tactical uses to strategic purposes. Here, we reiterate that for successful development and use of FLDMs, both the model developers and the users must clearly understand the purpose of the model. This is especially the case for constraining how the FLDM output must be viewed (Fig. 11.5).

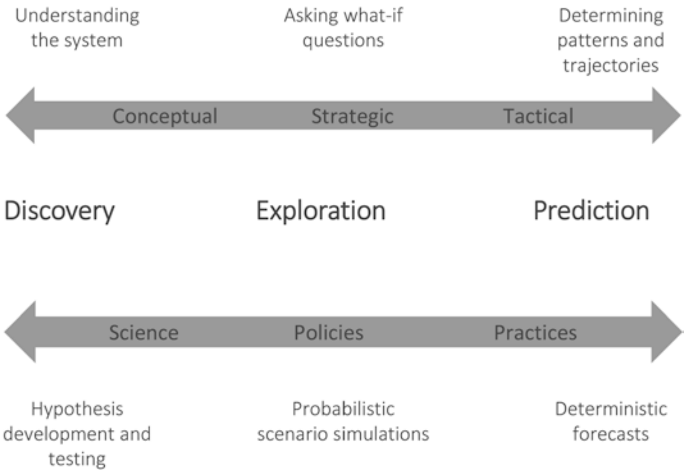


Fig. 11.5 The range of purposes and expected outcomes of forest landscape disturbance models. Adapted from Hall and Day (1977) and Bugmann (2003)

It is common for practical users of FLDMs, such as forest managers, to demand precise and deterministic predictions of where and how forest landscape disturbances will occur. Though other fields of ecology may argue for predictive models (e.g., Evans et al. 2013b), we contend that the degree of certainty required to make such predictive and forecasting applications suitable for tactical purposes is an impossible expectation with current FLDMs. The most appealing and robust use of some FLDMs is to support long-term explorations of how forest landscapes are disturbed, and how they recover. For example, all chapter authors in this book note the need for discovery, and we emphasize that a robust understanding of the emergent properties of forest landscapes must be the goal of FLDMs. These would include the properties that are evident when individual-based disturbance events are scaled up to populations, which will elucidate the synoptic characteristics of the disturbance. Such discoveries could be made either by mechanistic modeling or by sophisticated statistical modeling of past disturbance events, provided that the latter cover a large enough sample space to capture the spatial, temporal, and stochastic variability of the system that is being simulated. Another possible discovery is a depiction of the properties that may emerge from interactions among disturbance agents, which is only feasible with mechanistic modeling efforts. Such explorations of synoptic properties of forest landscape disturbances and scenario-based simulations of future possibilities of ecosystem patterns and processes must be the primary goal of FLDMs. In this context, it is the responsibility of the model's developers to clearly articulate the purpose of their model (including its limitations) to those who will want to apply the model.

3. **Abstraction, Scaling, and Parsimony of Models**

Numerous interrelated ecological factors—structures and functions—are linked to a given landscape disturbance process. Scoping the domain of the modeled processes, identifying which processes are relevant, and selecting only the most significant ones can be a difficult task. However, as philosophers have reiterated, it is abstraction that leads to universality, parsimony, and rigor, as well as to clarity in science. Therefore, abstracting the essence of complex and interrelated ecological phenomena in forest landscape disturbances is not just desirable, but is an essential task in developing FLDMs.

Strong arguments have been made for increased complexity in ecological models (e.g., Evans et al. 2013a), but this does not mean that the inclusion of more mechanisms will necessarily make models better or that these more complex models will advance the science more effectively. In fact, Duarte et al. (2003) note the pseudo-complexity of ecological models and the tendency for “mechanism creep” (i.e., the incorporation of insufficiently well understood or of low-importance mechanisms) during model development. We think that the temptation to over-model a system can be prevented by carefully considering the scale-relevancy of ecological processes. Even though advances in computing and data-acquisition technologies have immensely helped forest landscape modelers, this progress could become an impediment to making FLDMs appropriately parsimonious. That is, models should only include mechanisms that we understand sufficiently well to be confident the model will produce more realistic results, and must exclude mechanisms that do not have important effects on the model’s outcomes. With increased computing capacity and efficiency in programming languages, and the ready availability of high-resolution data, modelers may feel compelled to develop more complex models, just because they can. Although it may appear ridiculous to suggest this, it is not inconceivable to expect FLDMs to include molecular-level processes! But even if such complex models are elegantly built, they would have very high uncertainties and an increased risk of error propagation.

Appropriate scaling of ecological processes is a crucial step in model conception. Since most ecological processes are scale-specific, adoption of an appropriate scale is the key to correctly representing a forest landscape system and its processes, as well as to the discovery of emergent properties. Because ecologists are typically burdened by the intuitive familiarity of the phenomena they study and by their anthropocentric views, objectively choosing the correct scale can be difficult (Wiens 1989; Allen and Hoekstra 1992). Fortunately, many excellent explanations of ecological scale exist to assist FLDM developers (e.g., Wiens 1989; King 1991; Levin 1992; and many chapters in Peterson and Parker 1998). Also of value for forest landscape disturbance modelers is hierarchy theory (sensu Allen and Starr 1982; O’Neill et al. 1986), which helps to further unravel issues of scale and abstract ecological processes. Understanding the hierarchy of ecological process relationships will help simplify the view of complex interrelationships that might otherwise appear relevant and important (Fig. 11.6). As a starting point, we argue that FLDM developers should aim for no more than three hierarchical levels of

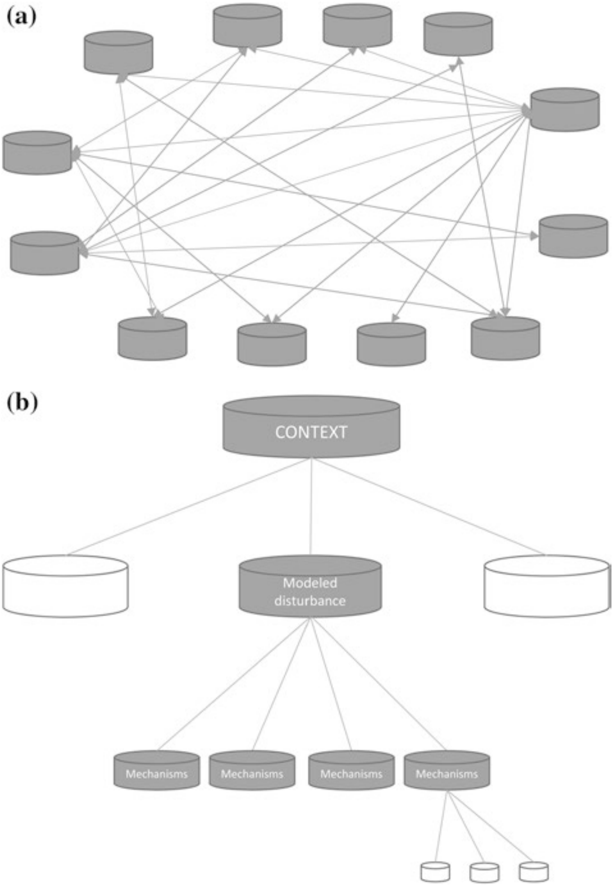


Fig. 11.6 An abstract depiction of how scaling can help simplify model conception. **a** Many interrelated ecological processes related to disturbance processes appear essential, complex, and detailed if they are not scaled hierarchically. **b** After scaling as a nested hierarchy, three levels emerge: the context, the focal disturbance process, and the key mechanisms that drive the disturbance process. This helps modelers to comprehend and address only the essential processes (*gray*), and ignore superfluous processes (*white*)

ecological processes: the context, the focal disturbance process, and the key mechanisms that drive the disturbance process.

4. **Model validation**

It is clear that for ecological models to be credible, they must be considered *valid*. However, it is not necessarily clear what "validity" means. Borrowing from the allometric and other statistical models used in ecology, many modelers consider model validation to be the simple act of comparing model outputs to empirical observations. The ecological modeling literature is replete with such examples. However, this ignores the possibility that an incorrect model can still produce results that match observed data, and the possibility that a correct model can produce results that do not match the observed data. This is especially true for FLDMs, which aspire to simulate ecological patterns and processes at scales that exceed our capacity to observe, and that produce probabilistic scenarios. Simple confrontation of past observations (single data points) with a set of simulated patterns (a probability distribution), even if statistically viable, may not prove that FLDMs are valid and credible. Many, in particular Oreskes and her colleagues (e.g., Oreskes et al. 1994; Oreskes 1998, 2003; Oreskes and Blitz 2001), have stressed that establishing model credibility involves verification, evaluation, and assessment of the *whole* modeling procedure (Fig. 11.7). This includes "validation" of the assumptions, input data, and model logic (conception, scale, and subprocesses), and finally, and only then, assessment of the output. Accordingly, the major focus and the responsibility of model developers should be on establishing the credibility of the model's structure: its logic, components, and assumptions.

5. **Communication**

There are two important facets to communicating in the context of FLDMs, especially with the user community. First, model developers must articulate about their FLDMs. This aspect of knowledge transfer—the necessity to unambiguously and explicitly communicate the premise, value, and limitations of a model to a user community—was raised by landscape ecology modelers nearly a decade ago (King and Perera 2006), but this topic has still not gained sufficient recognition. Modelers must not assume that users are aware and informed of the purpose,

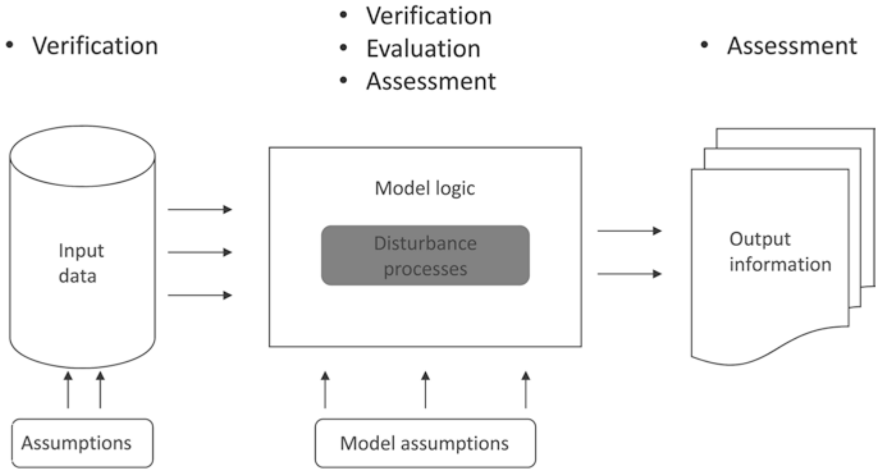


Fig. 11.7 Validation of an FLDM involves critical examination, evaluation, and verification of all steps in the simulation of a disturbance process, not just comparing the model outcome to observed data

assumptions, structure, limitations, and results of a FLDM. This is a risky assumption, since miscomprehension by users will lead to misuse and abuse of models, and that may lower the credibility of both models and modelers, perhaps even more so than poorly constructed models. Although enthusiastic efforts to clarify the value of FLDMs are admirable, model developers must be careful not to engage in aggressive marketing and promotion of their products, as this leads to poor communication and possibly unmet expectations. Also, ambiguity in expressions, including the use of incorrect terminology, can lead to incorrect use and expectations of FLDMs. An example is the frequently incorrect use of the phrase "prediction" in modeling parlance that leads to applications of models for inappropriate purposes, and misinterpretations of model outcomes.

Second, model developers can use models to communicate about forest landscape disturbances. Simulating scenarios as what-if explorations provides powerful tools to gain insights about forest landscape disturbances that are otherwise beyond the bounds of empirical observations. For example, the spatial and temporal probabilities and heterogeneity of disturbances are hard to comprehend based on few historical observations. As well, the notion that history will repeat, and therefore that past disturbances are predictive of future disturbances, can be challenged using FLDMs. This is especially true for disturbance regimes that are nonstationary in response to changing contexts. Another aspect worth communicating is that, from an ecological perspective, not all disturbances are destructive. When some disturbance agents are viewed at a broader scale, above the scale of the forest communities that have been disturbed, the agents may appear as endogenous and the disruptions they create as integral to the broader ecological system.

11.3 Conclusions

During the two decades since their naissance in North America, simulation models have become a mainstay in landscape ecology research. They are also vitally important tools that aid policy development, strategic plans, and decision-making in land management. This trend is nowhere more evident than in modeling broad-scale disturbances in forest landscapes. Aided by advances in technology—more powerful computing and better data acquisition—the field of forest landscape disturbance modeling has flourished. The many and different discourses in this volume provide evidence for that growth, including the variety of disturbance types that are modeled and how they are modeled. The relative degree of maturity in modeling and understanding of disturbance agents is a continuum, ranging from wildfire and insect pests, which have been studied and modeled at broad scales for decades, to phenomena such as drought and disease modeling, which are relatively new topics.

Nonetheless, several common messages have emerged:

- a shift toward mechanistic models that are based on understanding and quantifying ecological processes,
- integration of nonstationarity in disturbance behavior due to feedback from many stochastic dynamics in forest landscapes and changes in climatic and other contextual factors,
- including interactions with many other simultaneous disturbance processes, and
- integrating anthropogenic influences in simulations of forest landscape patterns and processes.

Such advances in process-based modeling, including the integration of multi-scale feedbacks among processes and the interactions among multiple disturbance types, were not available even a decade ago. In addition, modeling of the recovery of forest landscapes has also begun to mature. The responses that are being studied and tracked now include biochemical and geochemical processes and biomass, which are important complements to projections of a forest's species composition.

We believe the future of FLDMs to be promising. The topic of forest landscape disturbances is drawing increased attention from scientists and forest managers alike. The variety of disturbances being modeled, the rigor of the modeling procedures, and the number of FLDMs are all increasing. However, despite the progress that has been made in this field, potential traps exist. One is the pursuit of increased complexity. The detailed inclusion of all possible ecological processes is not synonymous with enhanced rigor; on the contrary, it may be the opposite. In many cases, more parsimonious models are more appropriate. Another trap is viewing amplified computing power as a goal rather than as a tool for achieving a goal. Although technology is a great aid to modelers, it is not, by itself, a reason for developing simulation models.

Modelers can maintain their momentum and avoid such pitfalls by adhering to a suite of best practices. Specifically, modelers should:

(a) pursue, whenever possible, parsimonious rather than complicated models;
(b) conceive and scale the modeled processes based on ecological concepts rather than based on the available computing technology and data;
(c) develop models collaboratively to facilitate ensemble modeling and cross-comparisons;
(d) evaluate a model's structure, logic, and assumptions rather than validating models based solely on the match between their outcome and observed data;
(e) treat models as hypotheses, and vigorously strive to test those hypotheses, and continuously improve the model's logic; and
(f) communicate about models to users continuously and actively rather than passively.

With this, we echo many other colleagues who have voiced the same sentiment: imbue simulation models with rich science, consider the models as hypotheses, and strive to simplify models to focus on the fundamental drivers over extraneous detail.

Finally, FLDMs are a powerful and indispensable tool for policy developers and managers of forest landscapes. They can be applied to help propose strategic objectives, examine plausible scenarios, and evaluate alternative management goals—all without having to rely exclusively on past experiences and evidence. When broad-scale experimentation is impossible, and when state assumptions based on a description of the past will not remain valid under a changing context (e.g., climate change, anthropogenic change), only the virtual explorations facilitated by FLDMs can inform us of potential emergent ecological patterns and processes in forest landscapes.

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