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

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Contents

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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.

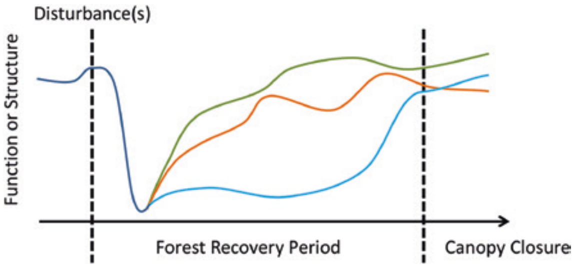

Fig. 10.1 A forest stand may follow one of many possible trajectories depending on initial conditions, disturbance (type, intensity, size, and heterogeneity), biological legacies, recolonization, and management. Sensitivity to initial conditions and long-term uncertainty defines a *complex* process.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

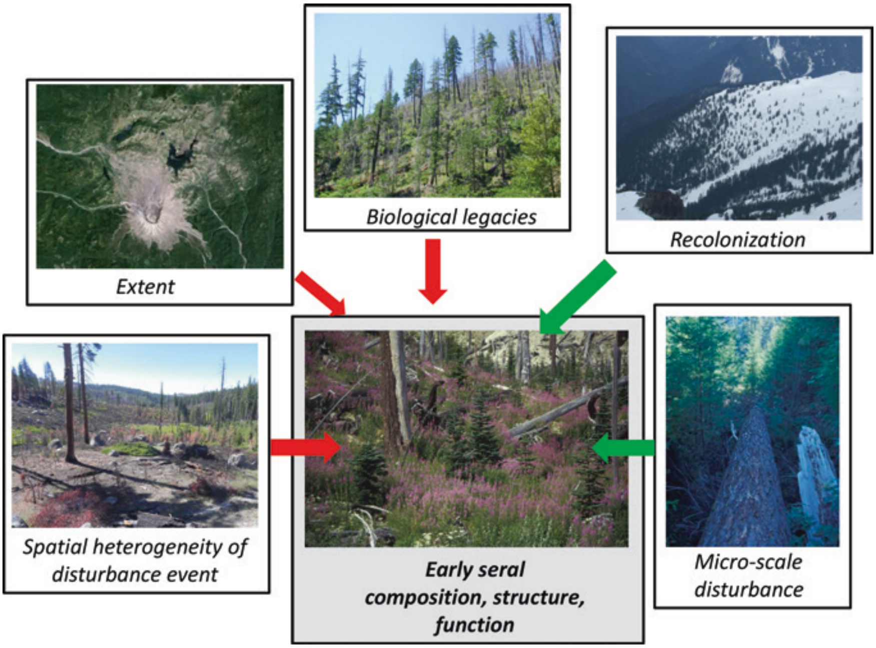

Fig. 10.2 The composition, structure, and function of early seral pre-forest ecosystems depend on the combination of processes associated with behavior of the generating disturbance (*red arrows*) and processes that occur subsequent to the disturbance (*green arrows*)

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.

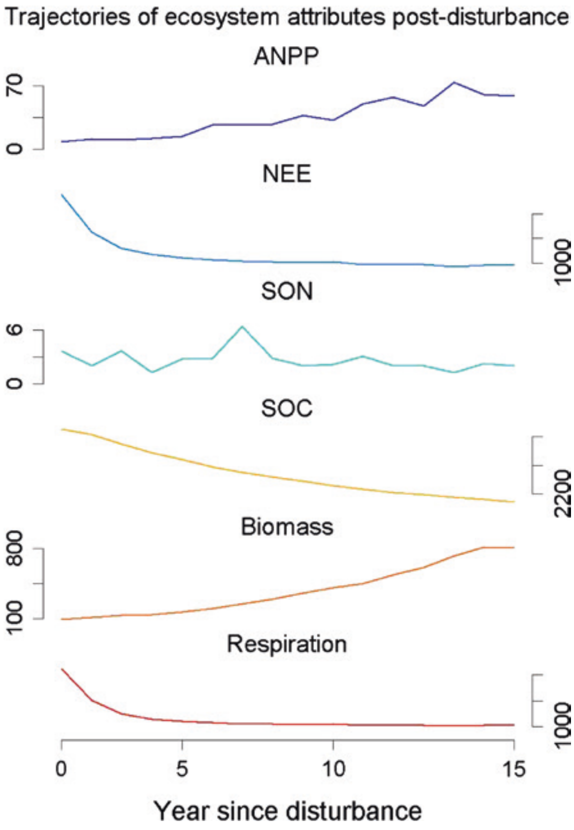

Fig. 10.3 Temporal dynamics of xix biogeochemical metrics immediately following simulated wildfire in the Lake Tahoe Basin, California and Nevada, United States. ANPP is aboveground net primary productivity (g biomass m^{-2} $year^{-1}$); NEE is net ecosystem exchange (g C m^{-2} $year^{-1}$); SON is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