Chapter 8
Insects and Forest Succession

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8.1 Introduction—Foundations of "Succession" in Plant Ecology

There is a long-standing, even ancient, belief in Western thought that forests, particularly unmanaged forests relatively free from obvious human impacts, are never-changing; this is the connotation of the German word "urwald" or "original forest" that influenced early thinking on forests from the origins of the emerging scientific disciplines of forestry and ecology in the 1800s. However, all forests, including extant ancient forests, are in fact in a state of flux. In addition to changes due to seasonality and forest responses to vicissitudes of the environment, forests nearly always show directional changes in species composition, structure, and ecosystem processes that are termed **succession** (Box 8.1). In general, forest succession is initiated by **disturbance** (Box 8.1), defined as a (more or less) discrete event in which some or all vegetation is destroyed or removed from the system. The most common agents of forest disturbance are fire, windstorms, floods, and (very commonly) tree removal by human activities; however, animals, including insects, and microbes such as fungal pathogens, can also be important disturbance agents in many forest ecosystems. Succession may in general be viewed as the process of biotic recovery of the system following such a disturbance event.

Citation: Thomas, S.C. (2021) Insects and forest succession. In: Forest Entomology, J. Allison, editor, Springer-Verlag, New York. In press.

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J. D. Allison et al. (eds.), *Forest Entomology and Pathology*,
https://doi.org/10.1007/978-3-031-11553-0_8

Box 8.1 Definitions of succession and disturbance

"Disturbance" and "succession" are both terms that have a long use in the ecological literature, and a correspondingly long history of debate over precise definitions. To most ecologists, "disturbance" connotes a large and sudden reduction in biomass that is associated with a discrete event, such as a fire, windstorm, or forest harvest. A definition of disturbance based on loss of biomass of primary producers has been promoted by Grime (1979, 2006), and is the most commonly cited definition. Grime argues that broader definitions include too many types of environmental perturbations to be useful: forest community responses to atmospheric pollutants or climate variation, for example, generally have little in common with changes following clearcut harvesting. Likewise, some proposed definitions of "succession" encompass any change in the structure, function, or composition of community (or ecosystem). However, such all-encompassing definitions have been widely critiqued as overly broad, including patterns and processes that range from community drift (stochastic variation in populations of individual species under stable conditions), to responses to atmospheric pollutants.

While recognizing that alternative definitions exist, the present chapter (and most of the ecological and forestry literature) adheres to the following definitions that essentially paraphrase Grime (1979; 2006):

Disturbance: an event that removes biomass.

Succession: a directional change in community structure over time.

Understanding successional changes in structure, species composition, and diversity of dominant vegetation following disturbance has been a central focus of ecology since the discipline's inception. Many early ideas and generalizations concerning succession—such as the idea of an unchanging "urwald"—have remained surprisingly influential, even when convincingly falsified. An historical approach is therefore taken here as a framework.

The earliest[1] formal studies of ecological succession focused on dune vegetation (Cowles 1899, 1901), but ecologists soon began to examine this process in forest ecosystems (Gleason 1917; Lee 1924). Due to the long lifespan of trees, changes in forest community composition driven by succession can take place over centuries to millennia. This timescale has presented a long-standing challenge to

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[1] As an historical note of particular interest to entomologists, an earlier but strikingly similar development of theory on ecological succession was the work of Pierre Mégnin in the 1880s (Michaud et al. 2015). Mégnin, trained as a veterinarian and entomologist, was the first to systematically investigate the timing of insect colonization of human corpses, with a view toward supporting the work of forensic scientists in court cases. He described eight "squads" of colonizing insects that formed a predictable sequential series on corpses and used the term "succession" to describe this pattern (Mégnin 1894). The predictability of this pattern was then challenged in the literature by American physician Murray Motter (Motter 1898), paralleling aspects of the Clements-Gleason debate, but predating it by more than two decades (Michaud et al. 2015).

understanding mechanisms that determine patterns of forest succession, since manipulative experiments or even sequential observations at the correct temporal scale are rarely possible. Models, ranging from simple conceptual representations to complex simulation models, have thus played a central role in the study of forest succession. Some of the earliest ecological computer simulation models, such as the forest “gap models” JABOWA and FORET (Botkin et al. 1972; Shugart 1984), were specifically aimed at elucidating mechanisms of forest succession. This focus on forest succession has continued as a central preoccupation in ecological modeling to the present (e.g. Pacala et al. 1993; Liu and Ashton 1995; Grimm et al. 2005; Taylor et al. 2009; Ma et al. 2022). However, early inquiry on succession relied on simpler conceptual models that remain influential.

Historically, the works of Frederic E. Clements (1916, 1936) had great influence on the conceptualization of the process of succession and the ecological mechanisms involved. Clements formulated two central theories. The first was the idea that succession generally operated by means of facilitation, with colonizing species creating conditions that lead to the success of other species. For example, early colonizing tree species would enhance soil organic matter and nutritional status in a manner that would enable later-successional species to successfully establish and grow (Clements 1916). The second theory was that of the climax community, toward which succession under a given set of soil (edaphic) and climatic conditions would gradually converge (Clements 1936). Climax communities were hypothesized to be stable over long time periods, showing no directional change in species composition.

Both the climax community concept and predominance of facilitation processes in succession were hotly debated in ensuing years. Most prominently, Henry Gleason promoted an individualistic view of succession, which proposed that ecological communities form and develop in a non-deterministic way (Gleason 1926). Another influential ecologist, Alexander Watt, described systems in which succession appeared to by cyclic, with no set end point (Watt 1947). Frank Egler presented evidence that species coming to dominate late in succession were generally present early in succession, and that there could be “precedence effects” in which early presence of plant species could strongly influence subsequent successional patterns (Egler, 1954). Egler argued strongly against what he termed the “relay floristics” model of Clements, and even offered a $10,000 reward to any ecologist who could demonstrate a clear example of Clementsian succession through at least 5 stages (Anderson 2018). The award was never collected.

The concept of a climax community likewise has been extensively critiqued, and in modern ecology is viewed as an abstraction not actually observed in nature. Thus, a given forest may be thought of as “late seral” (i.e. dominated by species not typical of early stages of succession, and not undergoing rapid successional change in species composition), but essentially no forest is a true ecological climax that does not show directional change. The main reasons for the non-existence of true ecological climax communities are: (1) a mis-match of current communities with climatic conditions; (2) persistence of disturbance, including disturbances that are “endogenous” to communities (such as treefall gaps formed following the death of individual trees); and (3) a sufficiently short return interval for large-scale disturbance such that the community cannot reach equilibrium (Pickett and McDonnell 1989).

A host of commonly used terms and concepts attach to ecological succession (Box 8.2). It has been argued that there is substantial redundancy in terminology related to ecological succession (Pulsford et al. 2016); however, in any discussion of succession it is difficult to avoid the terminological morass. Succession has classically been described as falling into categories of primary succession and secondary succession (on "new" and "previously occupied" substrates, respectively); in secondary succession individuals and structures that derive from the pre-disturbance community are termed "biological legacies". Additional descriptors have often been applied to describe the pattern of succession, including "progressive", "retrogressive", "cyclic", and "arrested" succession. Species that initially colonize sites following disturbance are most often referred to as "pioneer" species. Although the term and concept of a "climax community" in a Clementsian sense have been discarded in modern ecology, forest communities late in succession are often termed "late-seral", and such forests are typically characterized by intrinsically generated small-scale disturbance events as individual trees senesce and die, forming gaps. The formation of such gaps, together with the process of forest regrowth at gap sites, is termed "gap-phase dynamics", and is characteristic of most late-seral forests.

Box 8.2 Forest succession concepts and terminology

Community: a set of interacting organisms in a given space and time, generally quantified as the relative abundances of these organisms.

Primary succession: succession occurring in areas lacking a prior community, such as plants colonizing newly formed geological deposits.

Secondary succession: succession occurring in areas that have a pre-existing community.

Progressive succession: succession accompanied by an increase in total biomass.

Retrogressive succession: succession accompanied by a decrease in total biomass.

Cyclic succession: succession in which species reciprocally replace each other over time.

Arrested succession: succession in which the typical progression of successional stages does not occur, often associated with anthropogenic or invasive species effects.

Pioneer species: species that are early colonizers following disturbance; synonyms include "ephemeral species", "fugitive species", and "opportunist species".

Gap phase dynamics: the process of tree death and subsequent forest regrowth characteristic of late-seral forest systems.

Initial floristics: theory that all species, including those dominating later successional stages, are present early in succession but change in abundance.

Relay floristics: theory that groups of species colonize and disappear from a given site through the course of succession, and characteristically act to make the site less suitable for themselves and more suitable for subsequent sets of species.

Biological legacy: structures or organisms that carry over from pre-disturbance communities.

Sere: successional stage.

Late-seral community: a community dominated by late-successional (non-pioneer) species.

Primary forest: forest that has not been logged.

Old-growth forest: variously defined—a common ecological definition is a late-seral forest showing gap-phase dynamics.

The term "old-growth" is somewhat problematic. It has connotations of a Clementsian climax community, and for this reason is avoided by some ecologists and foresters. In many regions there are working definitions of "old-growth forest" based on management objectives or specified in a legal framework. For example, in the province of Ontario, Canada, regulations define "old-growth" as forests with dominant trees older than 70–150 years, depending on biogeographic region and dominant tree species (Uhlig et al. 2001). From a modern ecological perspective, "old-growth" is commonly used as a synonym for a late-seral forest showing gap-phase dynamics; as noted below this is the common usage in relation to stages of stand structural development. However, recent analyses of usage emphasize that the precise meaning of "old-growth" varies widely in both the ecological and forestry literature (Wirth et al. 2009).

8.2 Successional Changes in Forest Communities—Models and Mechanisms

There are several reasons to use studies of plant ecology as a basis for understanding successional patterns in other organisms, including insects. As noted above, the historical development of thinking on succession in ecology was based almost entirely on plant communities. It is also widely accepted that plants are generally of primary importance in determining diversity of other organisms, in particular insects (Siemann et al. 1998; Castagneyrol and Jactel 2012). One would therefore generally expect that the same ecological processes that drive plant species turnover and changes in diversity through succession would be reflected in the insect community. Changes in plant species composition may or may not be the main mechanism by which vegetation affects insect communities. Recent studies have emphasized the importance of changes in forest stand structure and dynamics (as distinct from changes in plant community composition) in understanding successional patterns in forest insects. In addition, age-related changes in the morphology and physiology of individual trees themselves may have important consequences for insect communities in guilds that interact closely with live trees such as herbivores and pollinators.

Broad generalizations or “laws” of succession—of the sort sought by early plant ecologists—have remained elusive. Pluralistic reconciliations of alternative views of patterns and mechanisms were offered in the 1970s by Drury and Nisbet (1973) and Connell and Slatyer (1977), who focused on mechanisms rather than resulting patterns. The general mechanisms may be classified as involving processes of facilitation, tolerance, or inhibition. In “facilitation”, species alter the environment in a way that makes it more suitable for colonization of other species. A tolerance process in succession involves progressive lowering of resource levels, and a sorting of species by their ability to tolerate low resources; models of succession based on tolerance have been developed in detail by David Tilman (1982, 1985). “Inhibition” processes involve resistance of all species to displacement, such that early colonizers persist until they have completed their life cycle. It should be noted that the meanings of the terms “mechanism” and “model” themselves have a long history of debate in relation to ecological succession (Pickett et al. 1989). Very generally, a “mechanism” is a process operating at a lower hierarchical level of organization that explains a pattern observed at a higher level. Some recent efforts to conceptually unify community ecology advocate a focus on processes and mechanisms analogous to those operating on gene frequencies in population genetics (i.e. selection, drift, immigration, and speciation: Vellend 2016); however, this focus seems to discard the study of succession entirely.

A central question that received research attention from the 1960s onwards is the development of ecological diversity (most commonly species diversity as measured by local species richness or a diversity index) through succession. An early generalization was that increases in species diversity through the course of succession were universal (Margalef 1968; Odum 1969). However, empirical data from plant communities did not generally support this claim (Drury and Nisbet 1973), though evidence that species diversity is maximized in late-seral stands was found in tropical forests (Brünig 1973). In contrast, communities with high natural disturbance rates commonly were found to show a peak in plant species diversity early in succession, as in the case of Australian schlerophyll woodland communities (Purdie and Slatyer 1976), and a number of western conifer forests (Habeck 1968; Peet 1978). Other studies have presented strong evidence for peaks in forest plant diversity at intermediate successional stages (a hump-shaped pattern through succession) in a variety of systems (e.g. Schoonmaker and McKee 1988; Sheil 2001).

An observed peak in species richness at an intermediate successional stage in tropical forest (Eggeling 1947) was used as a principle illustration in Joseph Connell's exposition of the influential intermediate-disturbance hypothesis (Connell 1978). This hypothesis states that species diversity is expected to be maximized at an intermediate intensity or frequency of disturbance: only a few species (generally pioneer species) will be able to persist under a high disturbance regime, and under very low disturbance a small number of species are expected to out-compete other species. Although commonly attributed to Connell, the main elements of the intermediate-disturbance hypothesis go back earlier (Wilkinson 1999), particularly to works by Grime (1973) and Horn (1975).

While intuitive, the intermediate-disturbance hypothesis has repeatedly been questioned on theoretical grounds (Huston 1979; Fox 2013), and is not particularly well supported empirically (Mackey and Currie, 2001; Bongers et al. 2009). In particular, the point was made early on that the response of local (alpha) diversity to disturbance is expected to vary with site productivity (Huston 1979, 2014: Fig. 8.1). Huston's demographic equilibrium theory predicts that in very low productivity systems with low growth rates any disturbance can drive species locally to extinction; in this case peak diversity is expected at low disturbance rates. In very high productivity systems with high growth rates, competitive exclusion can take place rapidly, and peak diversity is expected at high disturbance. This analysis suggests that the intermediate-disturbance hypothesis only applies at intermediate levels of productivity. Although the intermediate disturbance hypothesis was developed in part as a potential explanation for a hump-shaped successional pattern in diversity, its application to such patterns also remains somewhat ambiguous. Neither the intermediate disturbance hypothesis nor the dynamic equilibrium model makes explicit predictions regarding how much diversity is expected immediately following a disturbance event, since this largely depends on colonization and "legacy" effects that are not part of either model.

An additional hypothesis that may provide an alternative explanation for variable patterns of species diversity through succession is that diversity is maximized in the successional stages that are most frequent at the landscape scale under the prevailing disturbance regime (Denslow 1980). The gist of this argument is that the regional species pool is a function of habitat area, following from island biogeographic theory (MacArthur and Wilson 1967). Thus, regions with infrequent disturbance are expected to show maximal diversity in late-seral stands since there has been greater opportunity for immigration and speciation to add to the regional pool of species adapted to late-seral conditions. Conversely, regions with frequent disturbance, and regions with slow recovery from disturbance, are expected to accumulate a larger species pool adapted to early-successional habitats. This theoretical framework leads to a prediction that successional patterns of species diversity may show pronounced biogeographic differences as a function of the regional disturbance regime.

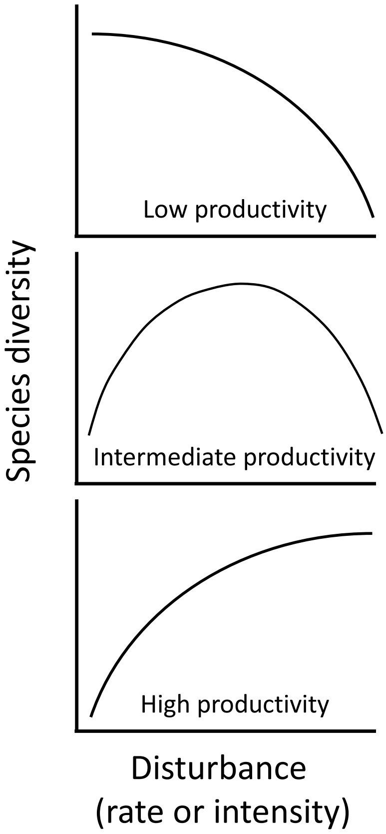

Fig. 8.1 Hypothesized relationships between species diversity and disturbance regime based on the demographic equilibrium model (Huston 1979, 2014); at intermediate levels of productivity the "intermediate disturbance hypothesis" pattern is expected

8.2.1 Forest Stand Structure and Dynamics

Successional patterns per se have predominantly been analyzed in terms of the species composition of communities (i.e. patterns of species abundance and diversity), rather than structural characteristics. However, as detailed below, there is also a long-standing applied forestry literature that has focused on stand structure rather than species composition in describing patterns of forest regrowth following a disturbance event. Stand structure is in fact often considered of primary importance in determining forest biodiversity patterns (e.g. Spies 1998; McElhinny et al. 2005). Forest structure here is generally defined in terms of patterns of macroscopic habitat elements, such as tree density and basal area, leaf area index, gap size distributions, and the amounts and decay classes of coarse woody debris, and also encompasses edaphic characteristics such as litter layer thickness, humus form, and the development of pit-and-mound topography associated with gap-phase regeneration (Spies 1998; Franklin et al. 2002).

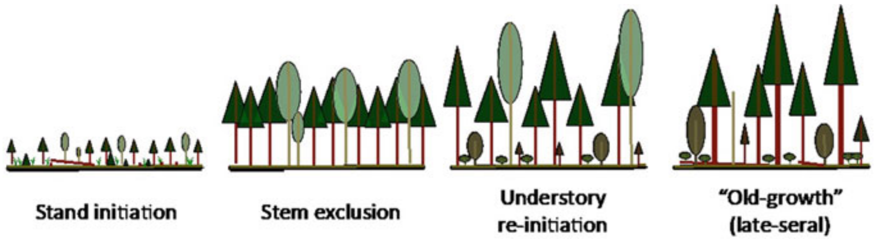

Fig. 8.2 Stages of stand development following a stand-replacing disturbance. Note presence of dense herbaceous vegetation and legacy structures during the stand initiation stage, even, closed canopy and lack of understory vegetation in the stem exclusion stage, presence of small inter-crown gaps and recruitment of shade-tolerant vegetation in the understory re-initiation stage, and uneven structure, canopy gaps, coarse wood, and patches of shade-tolerant understory vegetation in the "old-growth" stage

A four-stage scheme for forest stand development described by Oliver (1980) has been widely utilized (note that similar descriptions were commonly given in older forestry texts (e.g. Toumey and Korstian 1937), and derive from the German forestry literature of the 1800s). The four-stage scheme (Fig. 8.2) divides stand development into: (1) stand initiation, in which a new cohort of trees establishes; (2) stem exclusion, in which trees compete strongly for resources and there is high density-dependent mortality; (3) understory re-initiation, in which sufficient gaps form in the canopy to allow development of ground-layer vegetation and recruitment of shade-tolerant trees; and (4) old-growth, characterized by senescence of individual trees and gap-phase dynamics.

Recent critiques and extensions of this scheme have made a number of important refinements (Franklin et al. 2002). First "legacy" inputs from pre-disturbance stands, including dead and live trees, can critically affect stand development, particularly at the stand initiation stage. Second, the old-growth stage is an aggregate of multiple distinct stand development stages. Many forests have species that qualify as "long-lived pioneers", trees that colonize open area but that can survive for 100s to 1,000 + years (such as Douglas-fir (*Pseudotsuga menziesii*) in western North America). Late-seral forests that retain these long-lived pioneer trees are generally distinct in structure and species composition from later stages. In part due to this effect, there is commonly a peak in biomass accumulation in late-seral stands that should often be considered distinct from "old-growth" stands: the term "transition old-growth" has sometimes been used to describe such stands (Wirth et al. 2009). In some systems there is a pronounced long-term pattern of "ecosystem retrogression" with declining productivity, often accompanied by soil acidification; this is particularly well documented in boreal forests (Wardle et al. 2003) but appears to be common to many forest systems (Wardle et al. 2004). Third, there are important events and processes that may or may not correspond to the described transitions between stand development stages. For example, canopy closure commonly is used to distinguish stand initiation from stem exclusion stages; however, density-dependent mortality is not observed immediately following canopy closure. The development of gaps between individual tree crowns is a signature characteristic of the understory re-initiation stage; these canopy openings often arise through “crown shyness” effects (e.g. Fish et al. 2006) that vary greatly among tree species and in response to environmental conditions, such as the prevailing wind regime. As noted above, the term “old-growth” is also problematic in its connotation of Clementsian “climax” community, so the later stages of stand development might better be termed “late-seral” or “gap phase dynamic” stages.

In addition to the point that forest structure rather than composition may be a better predictor of community patterns of forest organisms—in particular arthropods—a focus on stand structure and dynamic stages is important for developing broad generalizations on forest succession. First, it is clear that there is high stochasticity in community composition, particularly early in succession, such that clearly defined “successional communities” do not generally exist. In contrast, there is evidence that stand structural characteristics often follow similar and predictable patterns in a wide variety of forest systems (Oliver and Larsen 1996). Stand structural patterns, in addition to being closely linked to a number of mechanisms of importance from the perspective of insect habitats (e.g. legacy structures such as coarse woody debris, canopy tree senescence, and tree gap formation), may thus also enhance comparability across studies.

A general concept of stand structure as a predictor of arthropod diversity was proposed by John Lawton in the 1980s (Lawton 1983); however, the conceptualization of forest structure differed from that presented above. Lawton focused on canopy structural complexity and did not consider coarse woody debris or edaphic factors. Lawton also predicted a continuous increase in structural complexity with stand age, whereas a stand development perspective notes that legacy structures and patchy regeneration commonly results in higher environmental heterogeneity soon after disturbance events, and low environmental heterogeneity during the stem exclusion phase. One may thus consider the hypothesis of stand structural development as a predictor of successional patterns in insect communities as an extension of, but distinct from, Lawton’s plant architecture hypothesis.

8.2.2 Tree Ontogeny

Another recent perspective on potential mechanisms for forest successional patterns of particular relevance to arthropod communities is age-related changes in tree physiological and functional biology. The lifespan of individual canopy trees commonly continues through the duration of observed successional patterns; in managed forests and forests with short disturbance-return intervals, this is essentially always the case. Trees generally show large and predictable changes though ontogeny not only in structural features, but also in physiology, including large changes in leaf and woody tissue chemistry (Meinzer et al. 2011). Some tissue-level ontogenetic changes important from an arthropod perspective include: (1) increased leaf thickness and leaf mass per area (Thomas and Winner 2002); (2) reduced leaf nitrogen concentrations and a concomitant reduction in leaf photosynthetic capacity (Bond 2000); and (3) increased leaf toughness (Mason et al. 2013). The mechanisms for such changes include limitations on tree water transport that increase as trees grow (Bond 2000; Koch et al. 2004), as well as changes in allocation patterns including the effects of increasing allocation to reproductive structures as trees age (Thomas 2011). Some important traits show strongly non-linear trends, possibly as a result of reproductive allocation effects: for example, in temperate hardwoods leaf nitrogen and photosynthetic capacity show a hump-shaped pattern with a peak in younger trees (Thomas 2010). It is hypothesized that ontogenetic trends may reflect in part selective pressure for leaf herbivore defense (Boege et al. 2011; Mason and Donovan 2015). However, there appears to be no general pattern in production of herbivore defensive compounds in relation to tree age (Barton and Koricheva 2010), and indirect defenses and herbivory tolerance likewise show variable patterns (Boege et al. 2011).

Ontogenic changes in macroscopic aspects of tree structure are also common, and some of these have long been recognized to be important to arthropod habitat use. Trees add progressive layers of bark (periderm) cells produced by the cork cambium; thus, bark thickness increases with tree age, and declines from the base to the peripheral branches. Sucking insects such as scale species (Hemiptera suborder Sternorrhyncha) that feed on woody tissues must penetrate bark tissues but can benefit from reduced moisture stress in bark crevices. This tradeoff is thought to result in a peak in scale abundance on trees of intermediate size that has been seen in some systems (Wardhaugh et al. 2006). Production of large branches can result in the trapping of soil within three canopies, producing unique “canopy soil” environments that are the habitat of specialized arthropod communities in some systems (Lindo and Winchester 2006). As noted by Lawton (1983), increasing complexity of branching structure through tree ontogeny may contribute importantly to arthropod habitats. Another macroscopic pattern is age-related crown thinning, as documented in both temperate (Nock et al. 2008) and tropical (Quinn and Thomas 2015) trees. Intra-crown leaf area index of older trees declines to as little as 1/2 or 1/3 of that observed in younger trees just entering the canopy. The canopies of older trees showing crown thinning likely present a dramatically different thermal environment for canopy insects. In addition, many tree species have long-delayed reproduction, and trees generally show increased reproductive allocation through ontogeny (Thomas 2011); these patterns are certain to affect arthropods reliant on flowers or fruits as resources or habitat elements.

8.3 Key Questions on Forest Insect Succession

Forest management generally results in a replacement of late-seral forests with younger forests of simplified structure and altered tree species composition. Insects and non-insect arthropods comprise the majority of macroscopic taxa in most forest ecosystems, so an understanding of insect community changes in relation to forest stand development is essential. The mechanisms and processes involved in these responses are likewise of central importance in developing conservation and management approaches to mitigate detrimental effects of wide-scale forest management. In addition to forest-level successional patterns in insect communities, one expects to find successional processes associated with aging of individual live trees, and in structures associated with trees, such as dead wood. These patterns are both of fundamental interest and contribute to whole-forest successional patterns important from a management perspective. Moreover, some insects are themselves a cause of stand-replacing disturbance events and may influence forest succession processes via herbivory and other interactions.

The remainder of this chapter addresses the following questions: (1) How do forest arthropod communities change in relation to stand development in terms of species richness, overall abundance, and community composition, and what mechanisms account for these patterns? (2) Is there evidence for more than two distinct successional stages in forest arthropod communities? (3) Does arthropod diversity essentially track plant diversity through succession? (4) What insect groups are typically dependent on late-seral forests, and what mechanisms and processes account for this dependence? (5) Do forest arthropod communities closely associated with trees vary with tree size and age? (6) Given the importance of coarse woody debris in driving many patterns in forest insect arthropods, what is the evidence for insect succession on woody debris itself? I conclude with a brief overview of insect effects on successional processes in forests, including insects that cause stand-replacing disturbance events, and the effects of insects on forest succession generally.

8.3.1 Observed Successional Patterns in Forest Arthropod Assemblages

The form of the relationship between diversity and forest age is a central descriptor of successional patterns (Fig. 8.1). However, many published studies on forest insect succession have been based on a small number of (often only 2) stand age, successional stage, or stand development categories. Frequently studies have also lacked true replication, making it impossible to distinguish successional patterns from stand-to-stand variation. Table 8.1 summarizes empirical studies that have true replication (or examined continuous variation with 12 or more sampled stands) and included more than 2 categories and spanned at least 15 years of post-disturbance recovery in terrestrial forest arthropods.

As has been found in syntheses aimed at testing the intermediate disturbance hypothesis generally (MacKey and Currie 2001; Shea et al. 2004), hump-shaped relationships as predicted by the hypothesis are not consistently observed in individual studies, though may emerge in synthesizing large data sets (Bongers et al. 2009; Yeboah and Chen 2016). Qualitative successional patterns of species richness of forest arthropod communities seem to vary considerably among studies and specific systems (Table 8.1). Overall a somewhat greater proportion of studies found negative rather than positive trends in species richness with stand age (33% vs. 27%); only 15% of studies exhibit a hump-shaped relationship, with a peak at intermediate stand age, while 9% of studies show a "U-shaped" pattern (Table 8.1). However, a dichotomy in patterns is apparent with respect to biome: in boreal and temperate forests most studies (68%) find a decreasing or U-shaped pattern of species richness with stand age, while in tropical forest most studies (80%) show either increasing species or hump-shaped patterns (Table 8.1).

One of the only published works to assess patterns across a full range of stand ages and development stages is that of Paquin (2008). This study provides compelling evidence for a "U-shaped" relationship between species richness and stand age in Carabid beetles in boreal forest (Fig. 8.3). Many other boreal and temperate forest studies have not had a sufficient range of stand ages or sufficient replication to possibly observe an increase in species richness among very old stands. Thus, observed negative relationships may correspond to "truncated" U-shaped patterns. The other boreal study that covers a very large age is that of Gibb et al. (2013), who note an increase in species richness mainly in the oldest stands in a long chronosequence (and who did not sample stands younger than 5 years post-harvest). Two other well-supported U-shaped patterns have also been published: a study on carabid beetles in pine plantations in Spain (Taboada et al. 2008), and a study of chrysomelid beetles in thorn forests in northern Mexico (Sánchez-Reyes et al. 2019).

In general, the patterns reported in Table 8.1 do not appear to support predictions of either the intermediate disturbance hypothesis or of the demographic equilibrium model (Huston 1979, 2014) that builds upon it. North temperate and in particular boreal forests have much lower productivity than most tropical forests, and so would be predicted to show a less pronounced decline in diversity with stand age (due to competitive exclusion effects) than tropical forests. However, precisely the opposite trend is found. Some of the best-replicated studies show U-shaped patterns of species richness through succession, which is essentially the opposite of the predicted pattern. The patterns observed are generally more consistent with mechanisms based on stand structural development. Important habitat elements such as coarse woody debris are often abundant as structural legacies in young stands, particularly after natural disturbance events such as fire and wind-throw. Coarse woody debris decays slowly in northern ecosystems, and so these legacy effects would be expected to persist for decades. The recruitment of new coarse woody debris, particularly in the form of large standing dead trees and large-dimension logs, requires that trees complete their life cycle, which may require 100 years or more. U-shaped patterns of arthropod diversity would thus be predicted as a consequence of coarse woody debris inputs and dynamics. In the tropics coarse woody debris is more ephemeral as a result of high temperatures, consistent high moisture, and the abundance of termites and other organisms that rapidly consume dead wood. Thus, legacy structures may be less likely to influence arthropod successional patterns in the tropics. Also, tropical forests likely present more structural habitat elements that consistently increase through stand development, such as those related to lianas and epiphytes. The prevailing positive trend in arthropod diversity through succession in the tropics thus also appears consistent with a stand structure mechanism.

Table 8.1 Studies examining successional patterns in forest arthropods; studies listed included assessments in 3 or more stand age categories spanning at least 15 years with true replication (or spanning a continuous age sequence with at least 12 total samples). Qualitative patterns of successional patterns in total abundance (abund.) and species richness (rich.) are described as follows: “ – ” and “ + ” indicate decline or increases with stand age or successional stage, respectively, “hump” and “U” indicates a maximum or minimum at intermediate age/stage, and “null” indicates no detectable response

Taxon	Biome	Location	Stages	Ages (y)	abund	rich	Reference
Spiders	boreal	Finland	4	0–60	–	–	Niemelä et al. 1996
Carabid beetles	boreal	Finland	4	0–60	–	–	Niemelä et al. 1996
Ants	boreal	Finland	4	0–60	–	–	Niemelä et al. 1996
Spiders	boreal	Canada	3	1–29	null	+	Buddle et al. 2000
Carabid beetles	boreal	Finland	5	5–60	null	–	Koivula et al. 2002
Carabid beetles	boreal	Canada	cont	0–341	?	U	Paquin 2008
All beetles	boreal	Sweden	cont	5–290	+	+	Gibb et al. 2013
Spiders	temp	USA	4		–	–	McIver et al. 1992
Spiders	temp	Canada	4		?	–	Brumwell et al. 1998
Carabid beetles	temp	Canada	4		?	–	Brumwell et al. 1998
Spiders	temp	USA	cont	0–15	null	null	Niwa and Peck, 2002
Carabid beetles	temp	USA	cont	0–15	null	null	Niwa and Peck 2002
Ground-dwelling beetles	temp	USA	4	5–	U	–	Heyborne et al. 2003
Butterflies	temp	Japan	4	1–	–	–	Inoue 2003
Carabid beetles	temp	Spain	5	2–80	U	U	Taboada et al. 2008
Carabid beetles	temp	New Zealand	6	1–29	–	null	Pawson et al. 2009
Orthoptera	temp	Germany	3		hump	hump	Helbing et al. 2014
Spiders	temp	Japan	cont	1–107	–	–	Haraguchi and Tayasu 2016

(continued)

Table 8.1 (continued)

Taxon	Biome	Location	Stages	Ages (y)	abund	rich	Reference
Chrysomelid beetles	sub-trop	Mexico	4	4–	+	U	Sánchez-Reyes et al. 2019
Butterflies	trop	Cameroon	4		?	+	Lawton et al. 1998
Canopy beetles	trop	Cameroon	4		?	null	Lawton et al. 1998
Canopy ants	trop	Cameroon	4		?	null	Lawton et al. 1998
Leaf litter ants	trop	Cameroon	4		?	hump	Lawton et al. 1998
Termites	trop	Cameroon	4		?	+	Lawton et al. 1998
Bees	trop	Malaysia	3	20–	+	–	Liow et al. 2001
Geometrid moths	trop	Malaysia	6		null	+	Beck et al. 2002
Butterflies	trop	Indonesia	3		?	+	Schulze et al. 2004
Dung beetles	trop	Indonesia	3		?	+	Schulze et al. 2004
Pyraloid moths	trop	Malaysia	6		?	+	Fiedler and Schulze 2004
Arctiid moths	trop	Ecuador	3		hump	hump	Hilt and Fiedler 2005
Butterflies	trop	Indonesia	4		hump	+	Vedderler et al. 2005
Geometrid moths	trop	Ecuador	3		?	hump	Nöske et al. 2008
Arctiid moths	trop	Ecuador	3		?	hump	Nöske et al. 2008
Galling insects	trop	Brazil	cont	0–21	?	hump	Fernandes et al. 2010

The attention in most studies of successional patterns in forest arthropods has been on species richness patterns and changes in species composition. Most studies have not directly reported patterns in overall arthropod abundance; however, where this is done it appears that overall arthropod abundance commonly shows similar patterns to that of species richness (Table 8.1). For example, Niemelä et al. (1996) report declines in both abundance and species richness through succession in Carabid beetles, spiders, and ants in boreal forests. Abundance patterns themselves are of interest in terms of trophic interactions, nutrient cycling, and other processes. Abundance patterns should also be taken into account in assessing species richness (Gotelli and Colwell 2001). Most recent studies have done this through use of rarefaction

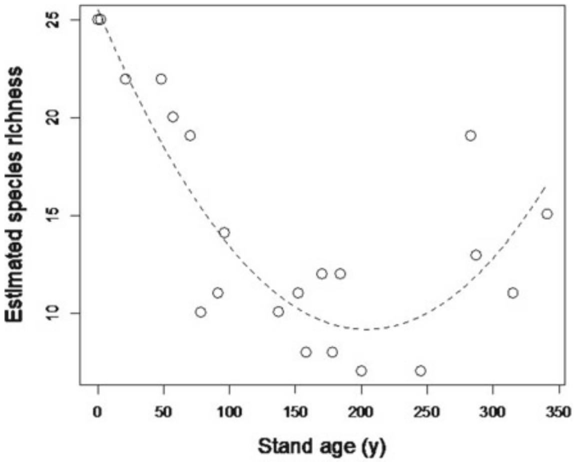

Fig. 8.3 Relationship between estimated species richness of Carabid beetles (abundance-based coverage estimator, derived from analysis of species accumulation curves: Chao and Yang 1993) and stand age in naturally regenerated post-fire stands of black spruce (*Picea mariana*) sampled in western Quebec, Canada. Redrawn from Paquin (2008)

curves and related statistics (e.g. Paquin 2008). Of course, biodiversity more broadly may be assessed through numerous metrics including conventional species diversity measures that weight evenness and richness (such as Fisher's alpha, Shannon–Wiener index, Simpson index, and others: Magurran 2013), functional diversity measures (Mouchet et al. 2010), and phylogenetic diversity measures (Cadotte et al. 2010).

Additional methodological limitations pertinent to succession studies on forest arthropods bear mention. Essentially all studies involve chronosequences that substitute space for time. Some of the biases and limitations of a chronosequence approach are overcome with true replication of stands; however, chronosequence studies implicitly assume constant environmental conditions (Pickett 1988; Johnson and Miyanishi 2008). Given the long time periods involved in forest succession, there is not really an alternative; however, future studies could profitably apply emerging approaches that combine chronosequence data with direct temporal data (Damgaard 2019). The available data are also highly skewed to a few taxonomic groups. For example, most studies in temperate and boreal systems have focused on carabid beetles or spiders, both of which are readily sampled using pitfall traps. Major forest arthropod groups that have received almost no attention in terms of successional patterns include many non-insect arthropods (e.g. isopods, centipedes, millipedes, opiliones - but see Schreiner et al. 2012), and major insect groups, including Diptera, Hemiptera, and non-ant Hymenoptera.

8.3.2 Two or More Distinct Successional Stages in Forest Arthropod Communities?

In essentially all studies of forest arthropod succession, differences in community composition have been detected between post-disturbance sites and late-seral stands

(Table 8.1). In general, one finds a set of species associated with more open habitats, a set of forest species, and a gradual transition between these two groups. However, a few studies have presented evidence for a distinct mid-successional community of forest arthropods. Niemalä et al. (1996) present evidence from boreal forest in southern Finland that carabid and ant communities immediately post disturbance are more similar to late-seral communities than are communities in younger, closed-canopy stands. In a study of *Pinus sylvestris* plantations in northern Spain, Taboada et al. (2008) found that the youngest stands showed carabid beetle communities similar to surrounding open habitats, while after canopy closure (i.e. in the stem exclusion stage: Fig. 8.2), communities differed strongly in composition and were highly depauperate; older stands showed more similar species composition to natural pine forests in the region. Analyses presented by Paquin (2008) provide evidence for four distinct successional communities of carabid beetles in black spruce succession following fire: a “burned” seral community found only in the first 2 years post-fire with a set of 6 indicator species, and “regenerating”, “mature”, and “old growth” communities each with 2–4 distinctive characteristic species. The “regenerating” community corresponds to the progressive decline in overall carabid beetle diversity from year ~ 3–170 (Fig. 8.3).

The only temperate or boreal study included in Table 8.1 to find a hump-shaped response pattern, examining succession patterns of Orthoptera in pine woodlands in the northern Alps, also presents evidence for 3 distinct insect communities (Helbing et al. 2014). In this case, the earliest seral stage had a high proportion of bare ground, and was inferred to be poor in food resources, while the second seral stage had some tree recruitment but was essentially still open; closed-canopy forest was not found until the third stage, and this corresponded to a large decline in species richness. This study, although superficially seeming to support intermediate disturbance, thus also strongly implicates changes in forest structure as a main driver of successional patterns.

In sum, studies that have looked in detail at arthropod community patterns through succession, at least in boreal and temperate forest systems, have commonly found evidence for a distinct intermediate stage. In terms of stand development, this appears to generally correspond to the stem exclusion stage, and likely includes species that can persist under low light conditions with little understory vegetation and little coarse woody debris.

8.3.3 *Relationships Between Arthropod and Vegetation Diversity Through Forest Succession*

As noted earlier, it is widely accepted that there is a pervasive relationship between arthropod diversity and plant diversity. Many herbivores and seed predators have narrow host ranges; widespread specialization in forest insect communities was famously the basis for early extrapolations of global insect diversity based on host tree canopy insecticidal fogging (Erwin 1982). Siemann et al. (1998) present evidence for a general relationship between arthropod and vegetation diversity based on large-scale experimental manipulations of herbaceous plant communities. As they note, the overall relationships were significant, but with low intercepts and R^2 values (0.14 for observed total species richness), and stronger relationships between species richness of insect herbivores and higher trophic levels (predators and parasitoids). Subsequent studies have noted similar patterns (e.g. Haddad et al. 2009), and comparable effects have been seen in relation to plant genetic diversity (Johnson et al. 2006). Observational studies have indicated strong relationships between insect diversity and plant diversity, specifically in forest ecosystems (Basset et al. 2012), and in heterogeneous landscapes (Zhang et al. 2016). However, a recent experimental study that manipulated local woody plant diversity did not find effects on insect diversity (Yeeles et al. 2017).

Do changes in arthropod diversity through succession track patterns for plants? Few of the studies listed in Table 8.1 examined these relationships, however Beck et al. (2002) found a strong correlation between vegetation diversity and insect diversity in a study of geometrid moths in Malaysia, and Nöske et al. (2008) found similar results in montane forests in Ecuador. In the broader literature, a notable counterexample is a study reporting no significant relationship between geometrid moth diversity and vegetation diversity along a successional gradient on Mt. Kilimanjaro (Axmacher et al. 2004). However, in this case the oldest vegetation class was a monodominant high-elevation forest that was spatially disjunct and at higher elevation than other sites. Additional tropical studies showing relatively strong correlations between vegetation diversity and insect diversity through succession include a study of butterflies and dung beetles in Sulawesi, Indonesia (Schulze et al. 2004), and of gall-forming insects in a tropical dry forest in Mexico (Cuevas-Reyes et al. 2004). A meta-analysis on broader patterns suggests that positive correlations are generally observed between insect and plant diversity (with a pooled correlation coefficient of ~ 0.45), but that this relationship is stronger between habitats and stronger for primary consumers than secondary consumers (Castagneyrol and Jactel 2012).

8.3.4 What Insect Groups Depend on Late-Seral Forests?

Observations on general associations of arthropod groups with open vs. forested habitats are certainly as old as entomology as a science: Orthoptera, Hemiptera, and most bees and Lepidoptera are likely to be found in open areas, whereas most Isoptera, Blattoidea, and millipedes favour forest habitats. Of course, casual observations can be misleading (and biased toward the most apparent species); specific associations with late-seral forests are often less obvious, though critically important from a conservation perspective.

Studies represented in Table 8.1 may give some indication of patterns. The most important point is that essentially all studies find variable patterns within taxa, with some species associated with late-seral stands. Among broad taxonomic groups,

Fig. 8.4 *Rhysodes sulcatus*: an example of a woody-debris-dependent insect of conservation concern. This endangered saproxylic beetle is native to Eurasia, and currently extinct in much of its European range (Photo: Credit Nikolas_Rahme-Flickr14929651712_09f4855d2b_k)

those that appear to most consistently show positive relationships with stand age include most Lepidoptera and Isoptera, at least in the tropics. Consideration of this question illustrates how sparse these data are: hundreds of similar studies covering all arthropod groups would be required for an adequate assessment.

In the absence of such data, lists of threatened and endangered arthropod species provide some useful information. The most comprehensive assessments to date have been in the European Union: among non-aquatic insect groups assessed, 15% of saproxylic beetles are considered threated, compared to 9% of bees, and 9% of butterflies (Nieto et al. 2014). Eckelt et al. (2018) provide a list of 168 beetles that are strongly associated with late-seral stands in Germany. Beetle species that require large coarse woody debris in closed forest habitats appear to be among those most systematically threatened (Fig. 8.4).

8.3.5 *Insect Succession Related to Tree Age and Size*

Lawton (1983) noted that natural history observations suggest associations of specific insects with trees of specific age but was unable to locate any data on this phenomenon. Recent observations that there are large systematic differences in tree physiology through tree ontogeny have motivated studies on the effects of tree size/age on insect communities closely associated with trees, in particular insect herbivores. There are thus now a number of studies that allow tests for patterns of abundance of specific insects through the whole of tree ontogeny. Ontogenetic succession in myrmecophytic trees has been the subject of a number of studies. These tree species require some time to attract ants as a consequence of developmental constraints and ant dispersal limitation (e.g. Del Val and Dirzo 2003); ant inhabitants subsequently have strong effects on herbivore communities, and initial ant colonizers are commonly displaced by other species (e.g. Feldhaar et al. 2003; Fonseca and Benson 2003; Dejean et al. 2008). These studies thus provide clear examples of distinct insect successional communities that track tree age and ontogenetic stage.

Aside from studies of myrmecophytes, assessments of tree ontogeny effects on arthropod communities have focused primarily on herbivore communities. LeCorff and Marquis (1999) compared herbivore communities on understory saplings and mature trees of two oak species, finding differences in community composition and higher herbivore abundance and diversity in the understory. Other "sapling vs. mature tree" studies have yielded different results. Basset (2001) found increased herbivore abundance and diversity in mature trees of the neotropical pioneer species *Pourouma bicolor*. Jeffries et al. (2006) sampled herbivore communities from *Quercus alba* leaves across a broad chronosequence, finding an increase in the number of species per unit leaf area (from ~ 0.8 to 1.2 species/m^2 leaf sampled). Thomas et al. (2010) present data on the frequency of herbivore damage types, most of which may be traced to one or two main species, on canopy leaves of *Acer saccharum* sampled in an uneven-aged forest. These data show a positive correlation of the diversity of damage types with tree size and age (Fig. 8.5). Available data, albeit scarce, thus suggest a general trend of increasing diversity of herbivore communities with tree age (as distinct from stand age).

Sessile arthropods may have particularly strong ontogenetic associations with their hosts. As noted above, scale insect abundance commonly reaches a maximum at trees of intermediate size (Wardhaugh et al. 2006). In a tropical dry forest, Cuevas-Reyes et al. (2004) found a general tendency for increased levels of gall formation (mainly by Cecidomyid midges) on saplings than on mature trees and inferred that this may be caused by greater availability of undifferentiated meristems favorable to gall development. In contrast, maple spindle gall mite increases dramatically in

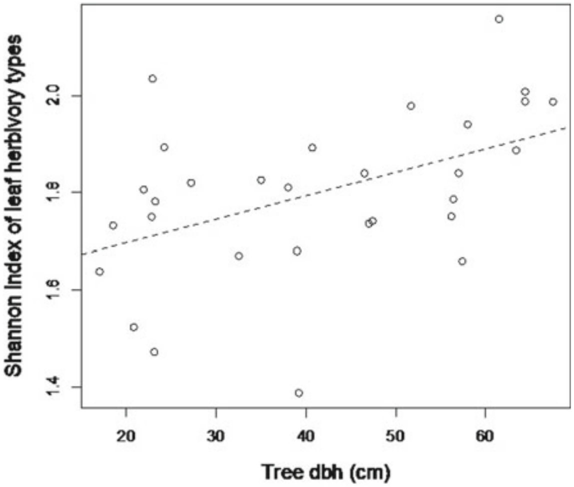

Fig. 8.5 Increase in diversity of arthropod herbivory types on canopy leaves of sugar maple (*Acer saccharum*). Linear regression line is shown ($R = 0.473$; $P = 0.008$). Data are from Thomas et al. (2010)

abundance with tree age, and galling is associated with substantial declines in leaf physiological performance (Patankar et al. 2011); a predaceous mite that invades and lays eggs within galls also tracks this pattern (Patankar et al. 2012).

8.3.6 Insect Succession on Coarse Woody Debris and Other Discrete Habitat Elements

As detailed above, the early literature on succession as an ecological process focused largely on plant communities. Nevertheless, there was at least one influential early entomological study, that of Savely (1939), who described successional patterns of arthropods on pine and oak logs in the southeast US. Logs were initially colonized by phloem-feeding taxa during the first year, in particular beetles in the families Cerambycidae, Buprestidae, and subfamily Scolytinae. These species enhanced wood decomposition by fungi, which were in turn linked with a variety of fungivorous and predaceous species that later colonized the logs (Savely 1939). Although the patterns described clearly had an affinity with prevailing ideas of Clementsian succession, Savely sought an understanding of insect succession on the basis of physical processes, with a focus on log microclimate and chemistry.

Insect succession patterns on coarse woody debris have received renewed research interest in recent years, with a focus on saproxylic beetles. In general, species with a narrow host range initially colonize, and more generalist species are found in later decay classes (Grove 2002). Varying patterns have been found with respect to diversity. Ulyshen and Hanula (2010) found the highest diversity of beetles in loblolly pine in the earliest decay class. In contrast, Hammond et al. (2004) found increasing beetle diversity through decay in poplar logs. Boulanger and Sirois (2014) describe a distinct community of beetles that colonizes standing dead trees following fire, and another than colonizes burnt trees once fallen. Ferro et al. (2012) report peak beetle diversity in mid decay class logs, with distinct communities found in early, mid, and late decay classes (Fig. 8.6).

There are a variety of other discrete (and often ephemeral) habitat elements analogous to coarse woody debris on which succession in forest arthropod communities is common. Examples include ant communities in domatia (e.g. Fonseca and Benson 2003), insects associated with decomposition of animal carcasses (e.g. Matuszewski et al. 2010), small natural ephemeral pools (phytotelmata) such as those formed by tree holes and bromeliads (Greeney 2001; Rangel et al. 2017), and larger vernal pools (Bischof et al. 2013) and animal wallows (Vanschoenwinkel et al. 2011). One might expect the successional patterns in these habitats to be affected by the local forest environment, which itself is strongly affected by stand successional status and structure. Successional patterns within these habitat elements would also be expected to contribute to overall successional patterns with stand age. These interactions have received little attention.

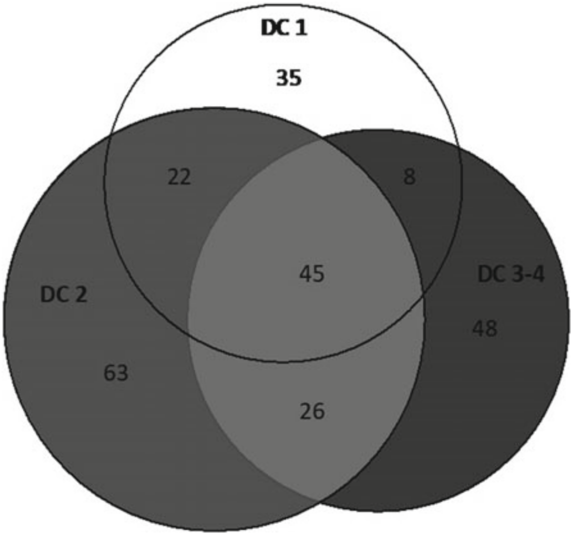

Fig. 8.6 Venn diagram showing species overlap of dead-wood-inhabiting beetles sampled from coarse woody debris by decay class. The area of circles is proportional to the total number of observed species. The largest distinct community occurs on mid-decay logs. Redrawn from Ferro et al. (2012)

The importance of coarse woody debris as a habitat element stems from its provision of resources and effects on micro-environmental conditions over an extended period. Another forest disturbance legacy that is beginning to receive attention is charcoal generated from fire events, which has marked effects on soil properties and commonly strongly stimulates tree growth (Wardle et al. 1998; Thomas and Gale 2015). Uniquely, charcoals are exceptionally long-lived in the natural environment, potentially persisting for 1,000s or 10,000s of years, and thus are expected to remain through multiple stand-replacing disturbance events. Recent studies have addressed both recent "biochar" additions to soil (i.e. charcoals designed for use as a soil amendment), and effects of long-persistent natural chars. Although data on forest arthropods are very limited, research to date suggests the potential for large changes in soil arthropod communities associated with deposition of charcoals (Domene 2016). Recent studies also suggest unique arthropod communities associated with Amazonian "terra preta" soils defined by incorporation of chars by pre-contact Amerindians (Demetrio et al. 2019).

8.4 Effects of Insects on Forest Succession

The most dramatic and obvious effects of arthropods on forest succession processes are the relatively few species of insects that themselves can be the direct cause of stand-replacing disturbance events by killing the majority of canopy trees over a short time period. These cases are mainly restricted to boreal and north-temperate forests, and specifically include several species of Scolytine beetles—namely mountain pine beetle (*Dendroctonus ponderosae*), European spruce bark beetle (*Ips typographus*), and southern pine beetle (*Dendroctonus frontalis*), as well as three species of Lepidoptera: spongy moth (*Lymantria dispar*), spruce budworm (*Choristoneura* spp.), and eastern tent caterpillar (*Malacosoma americanum*). In addition, there are cases of invasive species that do not cause stand-replacing disturbances in their native range but can do so in their introduced range. Notable examples of include Asian long-horned beetle (*Anoplophora glabripennis*), and emerald ash borer (*Agrilus planipennis*).

The tree host ranges of these species, at least those within their native range, are relatively small. For example, mountain pine beetle essentially impacts *Pinus contorta*, but also can feed to some extent on sugar pine (*P. lambertiana*), western white pine (*P. monticola*) and ponderosa pine (*P. ponderosa*) and has recently reproduced on jack pine (*P. banksiana*) (Cullingham et al. 2011). The species acts as stand-replacing disturbance agent only because *P. contorta* forms essentially monodominant forests in large areas of British Colombia, Alberta, and the Western US. This raises the issue of future forest succession: is it possible that beetle-kill areas will show a complete change in species composition or possibly enter a state of arrested succession and lose forest cover entirely? This is a critically important question in view of the recent unprecedented mountain pine beetle impacts in western Canada. Although mountain pine beetle is the most extreme case, similar questions arise in essentially any case of insects as agents of stand-replacing disturbance.

Recent work on vegetation responses following complete tree mortality of lodgepole pine stands due to beetle kill suggests a large initial positive response of understory herbaceous vegetation in terms of both productivity and diversity (Pec et al. 2015). Lodgepole pine has serotinous cones and is adapted to regenerate following stand-replacing fires. In central British Colombia lodgepole pine is essentially absent from tree recruitment following beetle kill and the existing seedling bank of subalpine fir (*Abies lasiocarpa*) is the only source of tree regeneration (Astrup et al. 2008). However, higher lodgepole pine regeneration has been seen in areas of the US (Collins et al. 2011; Kayes and Tinker 2012), and in boreal forest regions where the mountain pine beetle represents a novel impact (Campbell and Antos 2015). Thus, it appears that in only some areas is there likely to be a complete change in species composition following stand-replacing mountain pine beetle outbreaks.

Given the relatively narrow host ranges of insects, it is not surprising that insects as true stand-replacing disturbance agents are essentially restricted to boreal forests and low-diversity temperate forests. However, large-scale insect outbreaks, though perhaps not true stand-replacement events, are also found in the tropics. Anderson (1961) observed stand-level defoliation, likely by a species-specific lepidopteran, in areas dominated by the dipterocarp species *Shorea albida*. This tree species forms nearly monospecific stands in peat swamp areas in Borneo. A similar example has been documented in another monodominant tropical forest in the neotropics, dominated by *Peltogyne gracilipes* (Nascimento and Proctor 1994). Dyer et al. (2012) compiled other known examples in natural tropical forests. In general, stand-level defoliation events have been reported only from low-diversity tropical forests, in particular areas where a single species dominates.

Other than extreme cases of insects causing stand-replacing disturbance events, are there more general effects of insects on the succession process in forests? It has been hypothesized that insect herbivory can act to decelerate succession (Brown 1985) by reducing overall growth and competition among plant species. Alternatively, insect herbivory might accelerate succession by herbivores having a larger effect on poorly defended early-successional species (Davidson 1993). Manipulative studies (mainly on amenable non-forest systems) have yielded variable effects depending on the system (Brown et al. 1988). It has also been hypothesized that granivory or seed predation has effects on successional processes distinct from herbivory (Davidson 1993). Seed predators generally impact large-seeded late-successional trees more so than pioneer species, and thus might be expected to favor the latter. Important insect seed predator taxa include Curculionid, Scolytid, and Bruchid beetles, Lygaeid hemipterans, Gryllid orthopterans, and members of the orders Diptera, Hymenoptera, Lepidoptera, and Thysanoptera. I am not aware of any formal test of herbivory or seed predation effects on successional patterns in forest systems. The potential importance of seed predation on tropical forest dynamics is suggested by the phenomenon of mast fruiting in the Dipterocarpaceae of Southeast Asia, thought to be an evolutionary response to seed predation pressure (Janzen 1974; Lyal and Curran 2000). Analyses of successional patterns in insect taxa important as seed predators are also lacking. One might expect large increases in diversity in these groups through forest succession, particularly an increase in species associated with large-seeded host taxa.

8.5 Conclusions

Succession has been a notoriously contentious topic from the time of Clements and Gleason to the present. In any reading of the empirical literature on insects and forest succession, it is obvious that many entomologists simply avoid broader ecological theory, being satisfied with narrow descriptions of patterns specific to a given system. Two problems arise from such narrow description. First, it is inherently important that scientific contributions form a basis for broader generalizations and test existing theory. Second, if theory is not articulated, it is often still present in the mind of the investigator in the form of unstated assumptions and bias. The uncritical assumption that old-growth forests are climax communities in the Clementsian sense is a particularly common popular misconception, as is the bias toward assuming that older forest stands must have higher species richness. The intermediate disturbance hypothesis has been the most important theoretical touchstone of studies on forest insect succession, but forest entomologists should be aware that support for this theory is generally weak, and that the foundations of the theory itself are questionable. Successional processes are almost certainly system-specific and idiosyncratic in many respects; however, the main conclusion that emerges from the present review is that forest structural development (and possibly direct effects related to tree ontogeny) is generally more useful as a framework for understanding patterns of forest insect succession than more abstract theoretical representations.

Acknowledgements I thank Sandy Smith for discussions on the topic, and the editors of this volume for constructive criticisms that helped improve the paper. I acknowledge the members of my academic "pedigree" (F.A. Bazzaz, L.C. Bliss, W.D. Billings, H.J. Oosting, W.S. Cooper, and H.C. Cowles), who largely dedicated their careers to the study of plant succession. I also thank J. Weiner, with whom I first studied much of the basics covered here, and J. Allison for entrusting a chapter in an entomology text to an unrepentant botanist.

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