REVIEW

Is successional research nearing its climax? New approaches for understanding dynamic communities

Scott J. Meiners*,†[1], Marc W. Cadotte[2], Jason D. Fridley[3], Steward T. A. Pickett[4] and Lawrence R. Walker[5]

[1]*Department of Biological Sciences, Eastern Illinois University, 600 Lincoln Avenue, Charleston, Illinois 61920, USA;* [2]*Biological Sciences, University of Toronto-Scarborough, Scarborough, Ontario M1C 1A4, Canada;* [3]*Department of Biology, Syracuse University, 107 College Place, Syracuse, New York 13244, USA;* [4]*Cary Institute of Ecosystem Studies, 2801 Sharon Turnpike, PO Box AB, Millbrook, New York 12545-0129, USA; and* [5]*School of Life Sciences, University of Nevada Las Vegas, Las Vegas, Nevada 89154, USA*

Summary

1. Succession has been a focus of extensive ecological study for well over a century. Despite this sustained interest, succession remains a central theme in ecological research and is positioned to continue that prominence in this era of expanding human impacts. Community ecology is currently experiencing a profound conceptual expansion, providing many new insights into succession.

2. Here we present an existing conceptual framework of successional drivers that includes variation in site conditions, species availability and species performance, and expand it to include both evolutionary and geographic sources of variation. This framework is useful because it specifies relationships among individual drivers and is causally complete. While we generally think about succession as a within-site process, the inclusion of phylogenetic and geographic processes allows integration across broader scales.

3. We use the conceptual framework to highlight several opportunities for successional research that have developed within community ecology, but have not been fully integrated into succession work. These ideas represent not only individual drivers of succession, but also potential synergistic processes operating through interaction with other drivers. The complexity of drivers in succession strongly argues for the need to move away from single factor studies towards combinatorial studies that incorporate multiple drivers.

4. Utilizing a trait-based approach should allow researchers to address successional drivers at multiple ecological scales and lead to new insights that integrate ecological systems. Our ability to do this will depend on the availability of equivalent data across multiple systems, suggesting the need for more standardization in successional studies.

5. Addressing the research opportunities highlighted here will not only produce insights into successional systems, but also expand our understanding of fundamental questions in community ecology as a whole. Of particular importance is the ability to address broader scale questions that go beyond the idiosyncrasies of individual sites and systems. Understanding the dynamics of successional systems will remain critical to understanding, managing and predicting anthropogenic impacts on natural systems.

Key-words: community phylogenetics, environmental gradients, geographic variation, plant succession, plant traits, propagule pressure, site history, soil biofeedbacks

'Every one [sic] has heard that when an American forest is cut down, a very different vegetation springs up; but it has been observed that ancient Indian ruins in the Southern United States, which must formerly have been cleared of

---

*Correspondence author. E-mail: sjmeiners@eiu.edu
†Order of authors alphabetical after the first author.

trees, now display the same beautiful diversity and proportions of kinds as in the surrounding virgin forests. What a struggle must have gone on during the long centuries between the several kinds of trees, each annually scattering its seeds by the thousand; what war between insect and insect – between insects, snails and other animals with birds and beasts of prey – all striving to increase, all feeding on each other, or on the trees, their seeds and seedlings, or on the other plants which first clothed the ground and thus checked the growth of the trees.'

C. R. Darwin. 1859. The Origin of Species by Means of Natural Selection

The origins of nearly everything that ecologists study today can be found in Darwin's writings. Succession is no different. In Darwin's words, we actually see a fairly detailed description of what he thought would generate successional transitions. Darwin's text portrays a diversity of driving mechanisms – dispersal, herbivory and competition are clearly listed, with transitions in life-form and trophic interactions implied. This causal complexity is in sharp contrast to the single driver approach of many studies that form our base knowledge of succession.

As one of the earliest foundational concepts of ecology (McIntosh 1985), succession has a long history and many researchers who have contributed conceptually. The list reads as a who's who of plant ecology over the last century – Cowles, Clements, Gleason, Tansley, Oosting, Watt, Keever, Egler, Odum and Bazzaz, with many more contemporary researchers. With all of this attention, is there any real benefit to continuing to focus on succession as a process? We certainly think so. Current rates of landscape change, scale and type of human impacts, and globalization of species pools were not apparent during the developmental period of successional thought. We now have much stronger analytical methods available to us and have expanded the pool of mechanisms that may be controlling community composition and dynamics. We suggest that these new conditions and improved methods argue for the continued importance of succession to ecological thought and that more effort should be made to understand its mechanisms.

In this article, we show how placing succession in a broader temporal and spatial context can clarify relationships among its various drivers and provide a conceptual framework that suggests further research approaches.

A scale-specific successional framework

Decades of research on succession have yielded a plethora of successional drivers, some strongly supported, and some less so. This complexity has resulted from a reductionist approach, one that encourages researchers to study individual drivers in individual systems. This approach makes it difficult to determine interactions among drivers within a particular example of succession, to evaluate the relative importance of these drivers or to compare the influence of drivers across multiple successional pathways. To address this challenge, a hierarchical conceptual framework has been developed over the last several decades that functions to organize the disparate drivers of succession (Pickett, Collins & Armesto 1987a; Pickett & McDonnell 1989; Pickett & Cadenasso 2005; Pickett, Meiners & Cadenasso 2011). The framework divides successional drivers into three classes using three broad sources of variation or differentials: (i) site conditions and history, (ii) species availability and (iii) species performance (Table 1). Each of these broad classes then contains the individual drivers of succession. Variation in any of these drivers may then lead to changes in the composition or structure of a plant community resulting in succession. By separating drivers hierarchically, the framework highlights different modes of action, which can then help to identify critical interactions among drivers.

Site conditions and history reflect characteristics of a site's present and past disturbance regimes and resource availability. While little research has focused on this class of successional drivers, site conditions and history have become a primary focus of restoration ecology (e.g. Luken 1990; Bakker & Berendse 1999; Kardol & Wardle 2010). Primary and secondary successional sequences differ widely in this as the starting conditions are dramatically different. *Species availability* encompasses the processes that determine the ability of species to disperse into a recently disturbed site or survive a disturbance as propagules (Noble & Slatyer 1980). This class includes not only species characteristics, but also landscape context as a source of propagules and the characteristics of the dispersal vectors that move seeds. The importance of this broad category to constraining succession is highlighted by the concept of initial floristics where succession is determined by initial colonists (Egler 1954) and is critical to neutral theory, which focuses on stochastic dispersal

Table 1. Successional drivers organized into differentials within three broad classes

Site conditions and history	Species availability	Species performance
Disturbance type and history	Vagility	Life history
Resource availability	Seed bank persistence	Competitive ability
Local climatic conditions	Dispersal mode	Phenology
Nutrient deposition	Vector movement patterns	Plant–microbe interactions
	Landscape position/ connectivity	Herbivory/Pathogens
	Location of seed sources	Resource use/ Allelopathy

Within each broad class or drivers, specific drivers of succession are hierarchically nested. While only a few specific drivers are listed under each class as examples, these classes are sufficiently broad to capture all potential drivers of succession within a site.

and colonization events (Hubbell 2001). Finally, *species performance* contains all of the mechanisms by which species interact and sort themselves within a community. This class has received the most attention and therefore contains the greatest diversity of potential successional drivers. It covers Tilman's competition-based resource ratio hypothesis (Tilman 1985), the interaction-based views of Connell & Slatyer (1977) and even Clements (1916), as well as the majority of trait-based sorting suggested by Grime (2001). Together, the three broad classes that comprise the core of the hierarchical view should be able to contain all of the known and potential drivers of succession (Pickett, Meiners & Cadenasso 2011).

The purpose of the original conceptual framework was to organize successional thought in a useful and logical manner (Pickett, Collins & Armesto 1987b). While there is no specific temporal or spatial scale associated with the original hierarchical view, it can easily be rearranged into a filter model to describe successional dynamics within a single site. In this usage, each level constrains lower levels, but there is also the potential for feedback among levels (Fig. 1). Simply, site conditions filter out species able to survive under local conditions from those that reach the site and those are then sorted out via competition or other determinants of performance. This general structure can be amended to the specifics of a system. It also provides an opportunity to place succession within a site, the usual object of study, and into a broader ecological context, a much less explored opportunity. In addition, the dynamics
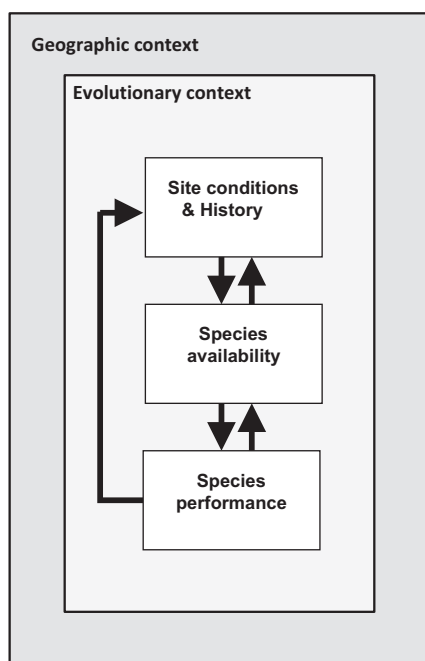
of an individual site can be placed in the larger context of the evolutionary processes that formed the community and the characteristics of the species. As species pools, environmental conditions and evolutionary processes are likely to vary geographically, this is then nested in a broader geographic context. Placing succession into the broader context of geography and evolutionary processes is a necessary next step in moving successional thought forward and should yield new perspectives.

There is room for continued research in all classes of successional drivers. The following sections will outline research opportunities within our framework. For this manuscript, we explore each class of drivers in the framework, although we recognize that there are many other potential avenues of research. Above all, there is a need for an integrative view of succession that encompasses both the diversity of drivers and perspectives applied to successional systems.

Site conditions, past and present

Following a disturbance, there are a set of abiotic and biotic site conditions that determine successional responses. These conditions can vary along a fertility gradient from the nearly sterile surfaces of fresh lava flows to the potentially nutrient-rich forest soils found under a tree damaged by strong winds. Other environmental gradients (e.g. degree of vulnerability to further disturbances such as erosion, flooding or fire; degree of shade; or proximity to or survival of colonizers) represent additional variability in site conditions created by the scale, severity and frequency of the disturbance. Anthropogenic disturbances further complicate local and regional disturbance regimes (the sum of all disturbances in an area), often increasing disturbance scale, severity and unpredictability, and sometimes introducing novel conditions (e.g. toxic mine wastes; Walker 2011) or novel communities (e.g. from invading, non-native species). This variability creates a distinct challenge to the development of generalizations about succession, but two recent approaches offer promise.

First, there is a growing recognition that reciprocal adjustments are made between abiotic and biotic variables. These adjustments occur at all ecological time-scales, from the interaction of geomorphology and evolution (Corenblit *et al.* 2008) to plant–soil feedbacks that occur nearly instantaneously (van der Putten *et al.* 2013) and can drive or constrain successional responses (Walker & Wardle 2014). Secondly, recent advances in environmental measurements are permitting more comparisons among sites and improving our understanding of the spatial dynamics of disturbances and subsequent community assembly. Historical disturbance regimes can now be reconstructed from dendrochronology and sediment data (McLauchlan *et al.* 2014). Current environments are also being more easily and widely analysed. For example, improvements are being made in sensor technology (e.g. remote sensing of microclimates), and data from many field observations and

Fig. 1. A filter model of succession placed into an evolutionary and geographic context. While most studies focus on only one box within this conceptual model, studies need to account for multiple causes and contexts to develop a broader and more synthetic view of community dynamics to move succession conceptually forward.

experiments are being compiled into meta-analyses (Prach & Walker 2011). Such measurements allow increasing comparisons of successional responses to disturbances across multiple environmental gradients.

These two approaches to understanding the range of post-disturbance site conditions, along with many others, indicate that ecological processes are clearly linked across multiple temporal and spatial scales. Historical environmental conditions are now interpreted in light of their influence on current patterns (e.g. of biodiversity, Fritz *et al.* 2013) or processes (e.g., community assembly, Cavender-Bares *et al.* 2009). Spatial patterns of resources are seen as driving processes from molecules to ecosystems (Chave 2013). Successional dynamics (past or present) can be interpreted as a temporal composite of all of these influences, from interacting abiotic and biotic variables to local and regional spatial conditions. Generalizations about succession will be most useful for addressing current challenges of ecosystem disruption when they incorporate these multiple influences on site conditions.

Propagule pressure as a successional driver

A foundational idea in plant population ecology is the idea of seed limitation – whether populations are limited by the availability of seeds rather than by safe sites for germination and establishment (Turnbull, Crawley & Rees 2000). The concept of propagule pressure, or the number of individuals colonizing a site, is a community-level extension of seed limitation studies that has developed within invasion biology. Propagule pressure essentially quantifies species availability to a location rather than presence/absence in the local species pool. Suitably high propagule pressure (numbers of seeds or dispersal events) can conceivably regulate the establishment of a new species in a system, potentially overriding community resistance to invasion (Rouget & Richardson 2003; Lockwood, Cassey & Blackburn 2005). Operationally, this idea is not completely equivalent to seed limitation as it does not separate seed and safe site limitation. Propagule pressure may influence colonization when a colonizing species occupies niche space that is incompletely utilized and thereby increase total establishment opportunities in the community, overcoming seed limitation at the community scale. If a colonizing species utilizes niche space in similar ways to resident species, then we would still expect colonization to increase as the invading species comes to dominate the propagule pool but without changes in the total number of establishment opportunities – propagule swamping.

The separation of community propagule pressure into separate processes yields mechanistic insights. If safe site limitation is in operation, then the probability of colonization should increase with the probability of dispersal into those locations. As appropriate microsites become filled, then colonization should asymptotically decrease until the system is saturated (Fig. 2). In contrast, if propagule swamping is functioning, then colonization should increase
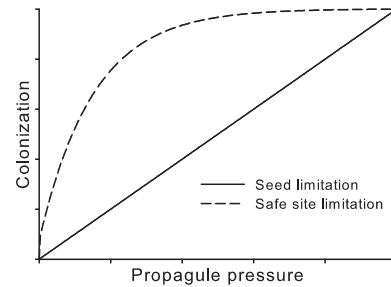

Fig. 2. Functional responses of plant colonization to increasing propagule pressure under two ecological scenarios. When safe sites are limiting, colonization will increase until appropriate microsites are saturated. Under seed limitation, colonization will increase with the proportional abundance of the colonizing species in the seed pool – propagule swamping. Under both scenarios, increasing propagule pressure will lead to increasing likelihood of successful colonization but are driven by different processes.

proportionally with the relative abundance of the colonizing species in the seed pool – effectively lottery recruitment (Lavorel & Lebreton 1992; Turnbull, Crawley & Rees 2000). We might expect safe site limitation very early in succession or in species poor systems, where there may be underexploited microsites that can be better utilized by species not present or at low abundance in the community. In contrast, propagule swamping is much more likely to occur whenever regeneration opportunities occur in more species rich communities. As long as the colonizing species is ecologically similar to resident species currently expanding in the site, for example mid-successional shade-intolerant perennials, then abundance in the plant community should increase following the proportional abundance of the colonizing species in the seed pool.

The ability of propagule pressure to override local controls on abundance (differential performance) is a potentially important, yet unexplored area for succession. The composition of the propagule pool is typically thought of as constraining everything that follows in succession, not as a potential determinant of those species interactions. Propagule pressure likely has large, but brief impacts in setting the composition of early successional communities where the first colonists have the potential to expand dramatically (Turnbull, Crawley & Rees 2000). Propagule pressure seems unlikely to be able to move succession towards an earlier phase as the characteristics of early successional species should strongly limit their success in older communities. Propagule pressure is likely important in establishing composition during transitional periods in succession. For example, when conditions first allow the colonization and expansion of woody species, dominance of the propagule pool by a species will likely result in at least temporary dominance by that species. An additional level of complexity may result when the timing of seed arrival influences community composition and develops long-lasting priority effects (e.g. Ejrnæs, Bruun & Graae 2006; Körner *et al.* 2008; Helsen, Hermy & Honnay 2012). Ultimately, species persistence in the community should be determined by the

suitability of their traits for local environmental conditions and biotic interactions. Whether propagule pressure consistently has the potential to generate long-term changes in community dynamics is unclear (Řehounková & Prach 2008), as is its ability to override species interactions. Of course, propagule pressure also operates in the context of varying site conditions, species pools and geography.

Biofeedbacks as a determinant of differential performance

Interactions between plants and soil microbial communities have emerged as major drivers of community structure, diversity and dynamics (Kardol *et al.* 2007; Bever *et al.* 2010; van der Putten *et al.* 2013) and therefore represent potential drivers of successional processes as regulators of differential performance. Individual members of the soil community vary dramatically in their impacts on plant species, with interactions ranging from strongly antagonistic to strongly mutualistic. Furthermore, the direction and strength of interaction between individual plant species and their microbes can vary based on the identity of the microbe, even within mutualists (Klironomos 2003). Variation in species composition and specificity of interactions within the soil microbial system results in a complex interaction landscape that produces net effects on plant performance and may further alter the soil microbial community.

Feedbacks generated by soil communities are context-dependent and can lead to population replacement or stasis based on the direction of the net interaction (Klironomos 2002; Callaway *et al.* 2003; Reynolds *et al.* 2003; Padilla *et al.* 2012). Disturbances impact plant and soil microbial communities, altering composition. While successional dynamics have perhaps been best characterized for mycorrhizae, microbial interactions are still a relatively unexplored aspect of successional biology (Fierer *et al.* 2010). Mycorrhizal densities are often low immediately following a disturbance, but rapidly recover as succession proceeds (Allen & Allen 1984; Johnson *et al.* 1991; Titus, Whitcomb & Pitoniak 2007). Plant communities may respond to these changes as early successional species are often less dependent on mycorrhizae than are later successional species. Longer lived plants also tend to be more dependent on mycorrhizae than are shorter lived plants (Janos 1980; Wilson & Hartnett 1998; Reinhart, Wilson & Rinella 2012). However, it is not only fungal densities which change during succession, but likely also their composition and function. Chagnon *et al.* (2013) proposed a functional transition for mycorrhizae based on Grime's (2001) plant strategies. They propose that successional transitions in mycorrhizal function follow the availability of nutrients as well as the dependence of the plants themselves on the fungi. Though the dynamics of other microbial groups have not been explored in detail, we may also expect changes in their abundance and function during succession as has been documented in mycorrhizae. Most

importantly, it is the net community impact that determines feedbacks and microbial influences on succession, not the behaviour of any one functional group (Kardol, Bezemer & van der Putten 2006).

Fewer taxa of microbes should be present following disturbance, both from the physical impacts of the disturbance and the lack of sufficient plant hosts to support populations (Thrall *et al.* 2007). Mutualists such as mycorrhizae are expected to rapidly increase based on the development of positive feedbacks and their generalist nature. Antagonistic microbes are likely to be slower to colonize than mutualistic microbes because of their host specificity under low diversity conditions such as early successional communities (Thrall *et al.* 2007), and because they likely inhibit their own spread through reducing host performance. These changes may result in an initial period of minimal net microbial effects followed by a rapid increase in net mutualism as beneficial organisms increase in the soil (Fig. 3). As succession continues, antagonistic microbes will accumulate in the system, shifting microbial function towards greater negative effects on plant performance (Reynolds *et al.* 2003). Similar shifts in microbial communities may occur as new plant species come to dominate communities. For example, a newly colonizing shrub species may initially encounter a largely benign or beneficial soil microbial community, but would likely build up antagonistic microbes as it came to dominate (Clay *et al.* 2008). The rate of these shifts will influence the ultimate abundance of the species in the site and the successional persistence of the population.

While soil microbial communities clearly have the potential to alter plant community composition and turnover, it is important to establish their importance relative to other successional drivers. Similarly, changes in the magnitude and direction of soil microbial interactions during succession are conceptually feasible, but have rarely been tested (*e.g.* Kardol, Bezemer & van der Putten 2006). Assess-
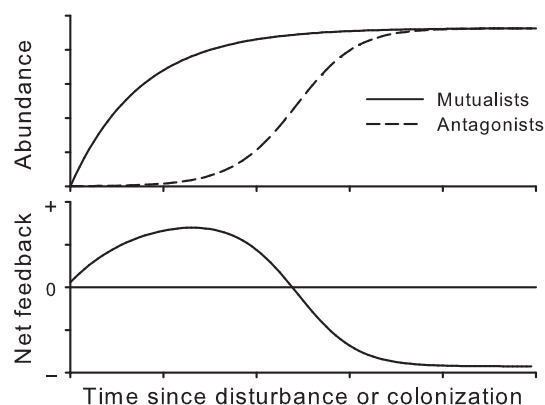

Fig. 3. Hypothetical changes in soil microbial communities during succession. The upper panel illustrates the time lag between density increases of mutualistic and antagonistic soil microbes. The net feedback (lower panel) changes as a function of the relative densities of these two groups, leading to shifts in the role of the soil microbial community over succession or as a species colonizes.

ments following a suite of species across a successional gradient will be necessary to separate species-specific responses from community-wide trajectories. Both approaches will be important to improve our understanding of the influences of microbial communities on plant succession. Overall, the relative impacts of plant–microbial interactions on succession likely change geographically with productivity and may be contingent on disturbance history, the identity and phylogenetic relatedness of the species pool and other factors.

Phylogenetic processes and succession

Evolutionary history is key to understanding the mechanisms driving successional change. Evolution generates the pool of species available to colonize patches and often results in adaptations that determine when and where species exhibit optimal performance. The signature of evolutionary history is observed as phylogenetically non-random species assemblages (Webb *et al.* 2002). The species pool almost always contains a large number of species representing a diverse array of evolutionary lineages (Srivastava 1999; Lessard *et al.* 2012), and ecological processes select non-random subsets of this pool during community assembly and succession (Webb *et al.* 2002; Cavender-Bares & Wilczek 2003; Fig. 4a). Space-for-time substitution studies (e.g. Letcher 2010; Purschke *et al.* 2013) suggest that late successional communities are typi-

cally phylogenetically over-dispersed, while early successional communities tend to be phylogenetically clustered or random (Fig. 4b). The intuitive interpretation of these patterns is that early successional environments exert strong filtering that selects for groups of closely related species that share traits adapted to colonization and success in early environments. In late successional communities, competition is often presumed to be the dominant structuring mechanism, which selects for species that are ecologically dissimilar (Fig. 4a). However, these intuitive inferences make important assumptions about the mechanisms that generate community structure and the evolution of species differences. Here we will examine the potential hypotheses that explain the shift from phylogenetically clustered to overdispersed communities during succession.

Phylogenetic clustering in early successional communities necessarily means that something is selecting for traits shared by close relatives. This selection can happen by two different mechanisms. The classic explanation is that environmental conditions in early succession, such as high light, water stress and other manifestations of disturbance, are stressful for many plant species. The second mechanism, largely absent from phylogenetic analyses, is that closely related species may also possess life-history traits that give them a temporal fitness advantage independent of any stress effect. Early succession species are typically those that reproduce quickly and often, and disperse well (e.g. Bazzaz 1979; Connell, Noble & Slatyer 1987; Huston
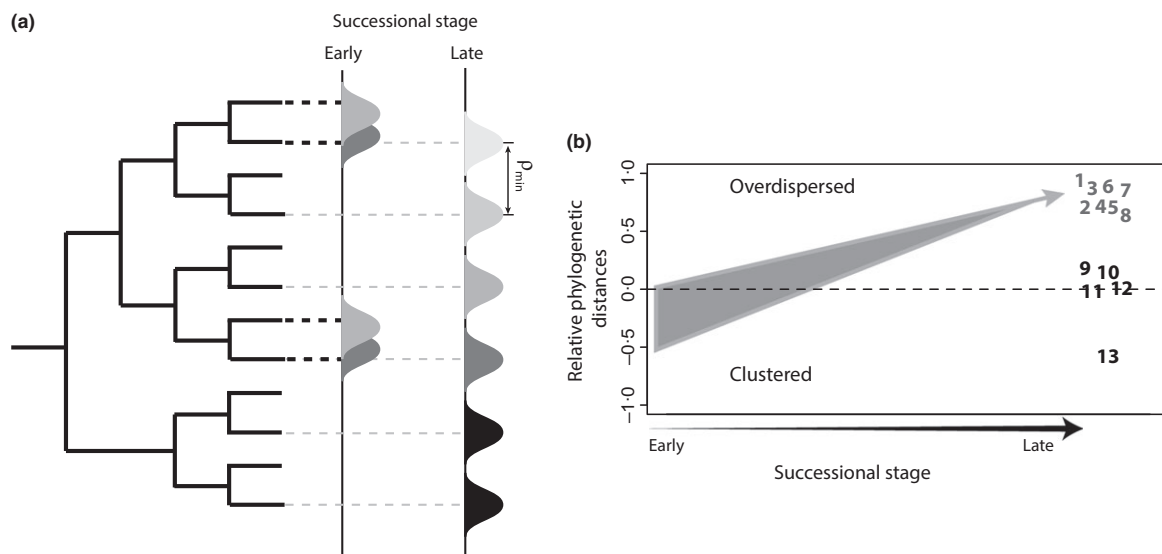

Fig. 4. The assembly of early and later successional communities from a regional species pool of variously related species. Early succession communities are dominated by species from relative few clades that possess traits allowing them to thrive in the environmental conditions associated with early succession. Late succession communities contain more distantly or evenly related species. In these late assemblages, competition is more important, and species with minimum niche or resource requirement differences (ρ_{min}) coexist and are likely more distantly related than a random assemblage (a). The majority of studies support the observation that late communities tend to be phylogenetically overdispersed, while early communities or clustered or random (b). Numbers correspond to individual studies showing: significant overdispersion with succession (top, greater phylogenetic distance); studies with inconsistent or non-significant results are near the axis; below the axis indicates a study that observed clustering. Studies are as follows: 1- (Swenson *et al.* 2007); 2- (Gonzalez *et al.* 2010); 3- (Letcher 2010); 4- (Ding *et al.* 2012); 5- (Letcher *et al.* 2012); 6- (Whitfeld *et al.* 2012); 7- (Purschke *et al.* 2013); 8- (Yang *et al.* 2014); 9- (Webb, Gilbert & Donoghue 2006); 10- (Verdú *et al.* 2009); 11- (Norden *et al.* 2012); 12- (Mo *et al.* 2013); 13- (Kunstler *et al.* 2012).

& Smith 1987; Turnbull, Crawley & Rees 2000), or are less reliant on mycorrhizal symbionts, as discussed above. The colonization of early successional patches is likely a combination of traits associated with high population growth rates that overcome the perils of small population sizes, for example Allee effects (Cadotte 2007). These types of traits are often associated with colonizing species that are poor resource competitors, but instead compete for access to newly open patches through lottery competition, where the first to colonize a patch is the local competitive winner (Levins & Culver 1971). Therefore, the mechanism generating phylogenetic clustering may be better informed by competition theory than by environmental filtering (Mayfield & Levine 2010). Thus, early successional strategies represent a suite of traits that are likely evolutionarily stable and shared among close relatives.

Regardless of whether stress tolerance or life-history traits regulate the colonization of early successional plants, the net result would be phylogenetically clustered assemblages if key traits show a phylogenetic signal. However, phylogenetic clustering can be complicated by the convergence of distantly related evolutionary lineages on similar strategies. For example, in eastern North America, annuals or short-lived perennials from several distantly related families (e.g. Asteraceae, Poaceae and Brassicaceae) frequently dominate early successional habitats. This ecological convergence is a real evolutionary signal and requires approaches that combine traits and phylogeny (Cadotte, Albert & Walker 2013). Measures based on nearest taxon distances should still detect phylogenetic clustering in this context as long as there are multiple species from each converged lineage within the habitat (e.g. multiple grasses and asters). However, measures based on a full tree or mean distances among taxa may not pick up non-random relatedness patterns.

Phylogenetic overdispersion in older habitats has been the most frequent result in the literature (Fig. 4). This pattern happens when local ecological processes select for dissimilar traits possessed by distantly related species through two potential mechanisms. First is the traditional explanation – which competition selects for species that are sufficiently different from one another (Cavender-Bares & Wilczek 2003) through classic niche competition where similar species compete most intensely (Gause 1934; Chesson 2000). In this scenario, overdispersion in the local community means that there are a sufficient number of different niches or resources available to minimize competitive exclusion. The second potential mechanism is if local habitats contain high resource or niche heterogeneity, which may select for distantly related species via species sorting (Questad & Foster 2008). This selection can happen by the process of differential success itself, where increasing biotic complexity creates new niches and resource space –in essence diversity begetting diversity. For example, later successional communities may have greater vertical light stratification than early communities, allowing the coexistence of a greater number of functional traits linked to light availability.

Tests for overdispersion assume that competition selects for species that are more different than a random expectation; however, it is possible that competition produces relatedness patterns that do not appear different than random expectations. If evolutionary pressures (i.e. divergent selection) have produced species that accumulated differences over relatively short evolutionary time-scales, then coexisting species need not be very distantly related. Further, if the evolution of differences has produced sufficient differences for coexistence (i.e. the interval of species pairwise distances that are not very different than random expectations), then again randomization tests may not detect significantly non-random patterns. Thus, significant overdispersion represents potential evidence of competition, but random phylogenetic patterns do not mean that competition is not important. Furthermore, phylogenetic signals are likely contingent on historical disturbance regimes, interactions with the microbial communities of related species and species introduction patterns, complicating phylogenetic successional trajectories.

Geographic variation in successional dynamics

As case studies of primary and secondary succession accumulated over the first half of the 20th century, it became apparent that regional differences in the nature and rate of succession were large, even under relatively similar ecological circumstances (Tansley 1939; Oosting 1942; Bazzaz 1968; Keever 1983). Despite this recognition, attempts at geographic synthesis have been attempted only recently in secondary (Anderson *et al.* 2006; Wright & Fridley 2010) and primary succession (del Moral & Magnússon 2014). Studies of the interplay between local and regional drivers of successional dynamics remain poorly developed in relation to other core ecological themes, such as community diversity (Ricklefs 1987). Just as a regional perspective has made seminal contributions to our understanding of species richness patterns, the promise of putting successional dynamics in a geographic context lies in solidifying our conceptual framework (Fig. 1). Viewing succession from a geographic context will encompass large variation in site conditions, composition and phylogenetic structure of the species pool, and performance of species under varying circumstances. This will allow us to assess the relative importance of these mechanisms and their interactions at a coarser scale. To the extent that geographic patterns are correlated with global change factors (e.g. temperature, soil moisture, nutrient loading), they are also useful in predicting the impact of atmospheric and land use change on local successional dynamics (Prach *et al.* 2014). Here we describe two recent succession frameworks that have distinct geographic components. While both frameworks come from secondary successional systems, similar geographic variation in successional processes can be found in primary succession (Walker & del Moral 2003).

Wright & Fridley (2010) introduced a geographic model of secondary succession based on factors controlling the intensity of competition between woody and herbaceous species. This model emphasizes the interaction of site conditions and species performance, and suggests early successional dynamics are a function of the ability of woody seedlings to recruit in different herbaceous assemblages (see also Smit & Olff 1998). Secondary succession on fertile substrate typically promotes early dominance by high resource demanding herbs that are able to usurp light and soil resources and that strongly inhibit woody colonization (Grime 2001). Poor substrate, such as nutrient-deficient clays of highly weathered soils or relatively sterile glacial outwash sands, often promote early but patchy colonization instead by stress tolerant herbs, particularly C_4 bunchgrasses (Bazzaz 1968), leaving bare mineral soil to be rapidly colonized by (often) gymnosperm trees (e.g. *Pinus*, *Juniperus*) that pave the way for later successional tree species, thereby speeding up the rate of succession by decades (Wright & Fridley 2010). Here the ultimate driver of successional dynamics is soil fertility, which exhibits strong geographic variation, in addition to the regional composition of early successional species and the traits they exhibit in relation to competitive ability (Fig. 5). Similarly, historical disturbances, particularly agricultural practices, may lead to enhanced or depleted soil fertility that alter successional rates.

If soil fertility is of paramount importance to successional dynamics, a simple prediction that can be applied globally to mesic ecosystems is that herbaceous communities are able to persist longer without disturbance on substrates of high nutrient availability, even under high dispersal rates of woody species. To our knowledge, this prediction has yet to be tested outside of a few cases in eastern North America and Europe. For example, Smit & Olff (1998), Bornkamm (2007) and Rebele (2013) found forest regeneration to be delayed in northern Europe on high fertility sites, with herbaceous competition implicated as the mechanism in all studies. Similarly, Fridley & Wright (2012) found site fertility to be more important than climate regime in a latitudinal study of woody seed-

ling recruitment across the Eastern United States. Further, there are suggestions that some types of mesic meadows and grasslands may persist for decades or more due to the same mechanism (Peet 2000; Wright, Jones & Flecker 2002). Soil fertility may also regulate the rate of transitions within herbaceous species (Carson & Barrett 1988), potentially altering succession in herbaceous dominated communities as well.

Geographic patterns of successional dynamics may also have an important climatic component, suggesting rates of succession are likely to change with local climate conditions even under a constant regional species pool. For example, Anderson *et al.* (2006) extended the metabolic theory of ecology to include predictions of the rate of woody biomass accumulation after forest disturbance. Assuming that the rate limiting step of carbon assimilation is the carboxylation potential of Rubisco, the authors showed that the rate of ecosystem biomass increase should increase with average growing season temperature, independent of differences in growing season length. This was confirmed in a global analysis of woody biomass accumulation across 64 forests (Anderson *et al.* 2006). This effect may be compounded by the climate-induced migration of early successional species poleward, for example, Fridley & Wright (2012) found southern US pioneer species such as *Pinus taeda* established in old fields faster than most northern pioneer species, even at sites north of their current range, only to be subsequently killed by winter temperatures.

Geographically based theories of succession share a need for systematic data on rates of successional dynamics across a full range of environmental gradients and ecological contexts. Unfortunately the availability of such data is extremely limited, particularly for early, herb-dominated successional stages. Because successional dynamics are measured in multiple ways (species turnover, compositional change, ecosystem state changes, biomass accrual), there is as yet no common currency for placing a comprehensive model of successional dynamics (Del Moral & Chang In press; Fig. 1) into a biogeographic context. This seems to be a fertile area for conceptual advances in suc-
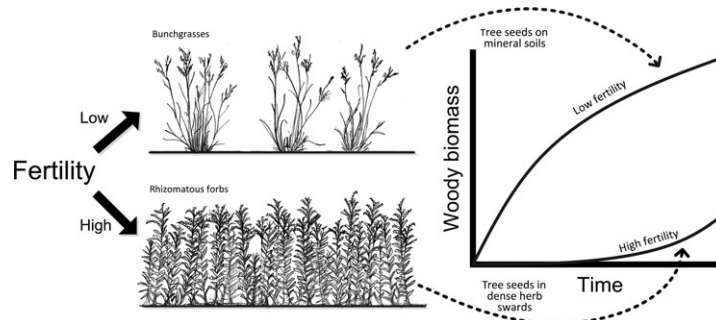

Fig. 5. A model of tree regeneration in secondary succession based on soil fertility as an example of geographic variation in successional processes. This model emphasizes the interaction of geographic variation in soil resource supply and the traits of early herbaceous dominants, which in turn influences the rate at which tree seedlings establish. See text for details. Similar geographic variation in primary succession may occur where fertility alters the abundance of nitrogen fixing plants and their interactions.

cession research, particularly for placing successional studies firmly in a global change context. Furthermore, documenting geographic variation in any of the successional drivers discussed here will provide a much needed perspective on how successional dynamics are regulated.

Traits as a way to integrate successional drivers

The focus on species functional traits has been hailed as a unifying perspective in ecology (e.g. Weiher *et al.* 1999; Diaz *et al.* 2004; Wright *et al.* 2004; McGill *et al.* 2006; Westoby & Wright 2006; Shipley 2010). The perspective has been applied successfully to successional dynamics as well (e.g. Prach, Pyšek & Smilauer 1997; Garnier *et al.* 2004; Navas *et al.* 2010; Raevel, Violle & Munoz 2012). While a systematic review of trait-based ecology and its intersection with succession is beyond the scope of this paper, the benefits of a functional approach to succession are worth mentioning. At first glance, trait-based ecology may appear to fit nicely under differential species performance in our conceptual framework. However, the approach manifests itself at all levels of the framework. Traits will also determine a species' response to local environmental conditions and disturbance history and will influence the dispersal ability of a species in a landscape. As many traits determine differential success within communities, we would also expect them to be under selection pressure and that these selection pressures may change regionally. While the operation of traits within all levels of the conceptual framework may appear problematic, this integration allows functional traits to be useful regardless of spatial or temporal scale of investigation. We suggest that functional approaches will allow studies that encompass multiple classes of successional drivers in our conceptual model, providing the ability to cross ecological scales.

By focusing on functional traits, successional studies more directly address mechanistic processes than traditional taxonomic-based studies. More importantly, a functional approach has the potential to generalize across systems with dramatically different species composition (Cadotte, Carscadden & Mirotchnick 2011). Much of the functional ecology work done to date has examined the trait structure or assembly of communities in response to environmental factors and inferred process from the analyses – a complex version of a space-for-time substitution design. This approach may be problematic as it assumes that current environmental conditions represent those that shaped the community, something that is not likely to occur when succession generates large changes in substrate or physical structure (Walker *et al.* 2010). Furthermore, a functional approach would allow a regional perspective on succession and cross-system comparisons. One of the major limitations to such an integrative approach is our ability to focus on a few important traits in the way that ecosystem ecologists focus on productivity, decomposition and mineralization rates across systems. Having a standard set of plant traits, similar to those applied to leaf characteristics (e.g. Wright *et al.* 2004) would allow broad scale questions about succession to be addressed and would represent a major new perspective in successional biology.

Conclusions

The sections above outline several opportunities for how successional science can continue to develop and grow. However, the mechanistically complex nature of succession necessitates movement from single factor approaches towards multifactorial experiments and studies. Single factor studies are useful in identifying the potential role of an individual driver in a particular system and may help to identify the key drivers of that system. However, multifactorial study designs are necessary to evaluate the relative strength of drivers and to place them in an appropriate ecological context (Prach & Walker 2011). A particularly useful strategy would be studies replicated across geographic gradients (Fridley & Wright 2012) or historical contexts. This would allow ecologists to move away from simplistic questions such as 'is competition important in succession?' towards the inherently more valuable question of 'when is competition important?'

In outlining research opportunities, we have specifically avoided any prioritization or ranking of the sections within the conceptual framework. All successional sites occur in the full context of the framework – they have historical and current conditions and are colonized by an interacting suite of species drawn from the regional pool. The species present have varying evolutionary relationships formed by historical interactions with biotic and abiotic conditions that shape contemporary interactions under current site conditions. Finally, all of this occurs within a specific geographic context, forming the broad conditions, species pools and evolutionary history that constrain species interactions. Placing research in a conceptual framework such as we have presented allows researchers to set their work in a broader context and understand the contingencies that may be operating. History is always present, as is the phylogenetic and geographic context of a particular system. Viewing communities and their dynamics as the integrated outcome of all these processes should allow plant succession to continue to be both foundational and at the forefront of ecological thought.

References

Allen, E.B. & Allen, M.F. (1984) Competition between plants of different successional stages: mycorrhizae as regulators. *Canadian Journal of Botany*, **62**, 2625–2629.

Anderson, K.J., Allen, A.P., Gillooly, J.F. & Brown, J.H. (2006) Temperature-dependence of biomass accumulation rates during secondary succession. *Ecology Letters*, **9**, 673–682.

Bakker, J.P. & Berendse, F. (1999) Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology & Evolution*, **14**, 63–68.

Bazzaz, F.A. (1968) Succession on abandoned fields in the Shawnee Hills, southern Illinois. *Ecology*, **49**, 924–936.

Bazzaz, F. (1979) The physiological ecology of plant succession. *Annual Review of Ecology and Systematics*, **10**, 351.

Bever, J.D., Dickie, I.A., Facelli, E., Facelli, J.M., Klironomos, J., Moora, M. *et al.* (2010) Rooting theories of plant community ecology in microbial interactions. *Trends in Ecology & Evolution*, **25**, 468–478.

Bornkamm, R. (2007) Spontaneous development of urban woody vegetation on differing soils. *Flora - Morphology, Distribution, Functional Ecology of Plants*, **202**, 695–704.

Cadotte, M.W. (2007) Competition-colonization trade-offs and disturbance effects at multiple scales. *Ecology*, **88**, 823–829.

Cadotte, M.W., Albert, C.H. & Walker, S.C. (2013) The ecology of differences: integrating evolutionary and functional distances. *Ecology Letters*, **16**, 1234–1244.

Cadotte, M.W., Carscadden, K. & Mirotchnick, N. (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, **48**, 1079–1087.

Callaway, R.M., Mahall, B.E., Wicks, C., Pankey, J. & Zabinski, C. (2003) Soil fungi and the effects of an invasive forb on grasses: neighbor identity matters. *Ecology*, **84**, 129–135.

Carson, W.P. & Barrett, G.W. (1988) Succession in old-field plant communities: effects of contrasting types of nutrient enrichment. *Ecology*, **69**, 984–994.

Cavender-Bares, J. & Wilczek, A. (2003) Integrating micro- and macroevolutionary processes in community ecology. *Ecology*, **84**, 592–597.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A. & Kembel, S.W. (2009) The merging of community ecology and phylogenetic biology. *Ecology Letters*, **12**, 693–715.

Chagnon, P.-L., Bradley, R.L., Maherali, H. & Klironomos, J.N. (2013) A trait-based framework to understand life history of mycorrhizal fungi. *Trends in Plant Science*, **18**, 484–491.

Chave, J. (2013) The problem of pattern and scale in ecology: what have we learned in 20 years? *Ecology Letters*, **16**, 4–16.

Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, **31**, 343–366.

Clay, K., Reinhart, K., Rudgers, J., Tintjer, T., Koslow, J. & Flory, S.L. (2008) Red queen communities. *Infectious Disease Ecology: The Effects of Ecosystems on Disease and of Disease on Ecosystems* (eds R.S. Ostfeld, F. Keesing & V.T. Eviner), pp. 145–178. Princeton University Press, Princeton, NJ.

Clements, F.E. (1916) *Plant Succession, An Analysis of the Development of Vegetation*. Carnegie Institution, Washington, D.C.

Connell, J.H., Noble, I.R. & Slatyer, R.O. (1987) On the mechanisms producing successional change. *Oikos*, **50**, 136–137.

Connell, J.H. & Slatyer, R.O. (1977) Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist*, **111**, 1119–1144.

Corenblit, D., Gurnell, A.M., Steiger, J. & Tabacchi, E. (2008) Reciprocal adjustments between landforms and living organisms: extended geomorphic evolutionary insights. *Catena*, **73**, 261–273.

Del Moral, R. & Chang, C.C. (In press) Multiple assessments of succession rates on Mount St. Helens. *Plant Ecology*. doi:10.1007/s11258-014-0425-9

Diaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A. *et al.* (2004) The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science*, **15**, 295–304.

Ding, Y., Zang, R.G., Letcher, S.G., Liu, S.R. & He, F.L. (2012) Disturbance regime changes the trait distribution, phylogenetic structure and community assembly of tropical rain forests. *Oikos*, **121**, 1263–1270.

Egler, F.E. (1954) Vegetation science concepts. I. Initial floristic composition, a factor in old-field vegetation development. *Vegetatio*, **4**, 412–417.

Ejrnæs, R., Bruun, H.H. & Graae, B.J. (2006) Community assembly in experimental grasslands: suitable environment or timely arrival? *Ecology*, **87**, 1225–1233.

Fierer, N., Nemergut, D., Knight, R. & Craine, J.M. (2010) Changes through time: integrating microorganisms into the study of succession. *Research in Microbiology*, **161**, 635–642.

Fridley, J. & Wright, J. (2012) Drivers of secondary succession rates across temperate latitudes of the Eastern USA: climate, soils, and species pools. *Oecologia*, **168**, 1069–1077.

Fritz, S.A., Schnitzler, J., Eronen, J.T., Hof, C., Böhning-Gaese, K. & Graham, C.H. (2013) Diversity in time and space: wanted dead and alive. *Trends in Ecology & Evolution*, **28**, 509–516.

Garnier, E., Cortez, J., Billès, G., Navas, M.L., Roumet, C., Debussche, M. *et al.* (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, **85**, 2630–2637.

Gause, G.F. (1934) *The Struggle for Existence*. Hafner Publishing Company, New York, NY.

Gonzalez, M.A., Roger, A., Courtois, E.A., Jabot, F., Norden, N., Paine, C.E.T. *et al.* (2010) Shifts in species and phylogenetic diversity between sapling and tree communities indicate negative density dependence in a lowland rain forest. *Journal of Ecology*, **98**, 137–146.

Grime, J.P. (2001) *Plant Strategies, Vegetation Processes, and Ecosystem Properties*. John Wiley & Sons, Chichester.

Helsen, K., Hermy, M. & Honnay, O. (2012) Trait but not species convergence during plant community assembly in restored semi-natural grasslands. *Oikos*, **121**, 2121–2130.

Hubbell, S.P. (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NY.

Huston, M. & Smith, T. (1987) Plant succession: life history and competition. *The American Naturalist*, **130**, 168–198.

Janos, D.P. (1980) Mycorrhizae influence tropical succession. *Biotropica*, **12**, 56–64.

Johnson, N.C., Zak, D.R., Tilman, D. & Pfleger, F.L. (1991) Dynamics of vesicular-arbuscular mycorrhizae during old field succession. *Oecologia*, **86**, 349–358.

Kardol, P., Bezemer, T.M. & van der Putten, W.H. (2006) Temporal variation in plant–soil feedback controls succession. *Ecology Letters*, **9**, 1080–1088.

Kardol, P. & Wardle, D.A. (2010) How understanding aboveground-belowground linkages can assist restoration ecology. *Trends in Ecology & Evolution*, **25**, 670–679.

Kardol, P., Cornips, N.J., Kempen, M.M.L.v., Bakx-Schotman, J.M.T. & Putten, W.H.v.d. (2007) Microbe-mediated plant-soil feedback causes historical contingency effects in plant community assembly. *Ecological Monographs*, **77**, 147–162.

Keever, C. (1983) A retrospective view of old-field succession after 35 years. *American Midland Naturalist*, **110**, 397–404.

Klironomos, J.N. (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature*, **417**, 67–70.

Klironomos, J.N. (2003) Variation in plant response to native and exotic arbuscular mycorrhizal fungi. *Ecology*, **84**, 2292–2301.

Körner, C., Stöcklin, J., Reuther-Thiébaud, L. & Pelaez-Riedl, S. (2008) Small differences in arrival time influence composition and productivity of plant communities. *New Phytologist*, **177**, 698–705.

Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmermann, N.E. *et al.* (2012) Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. *Ecology Letters*, **15**, 831–840.

Lavorel, S. & Lebreton, J.D. (1992) Evidence for lottery recruitment in Mediterranean old fields. *Journal of Vegetation Science*, **3**, 91–100.

Lessard, J.P., Borregaard, M.K., Fordyce, J.A., Rahbek, C., Weiser, M.D., Dunn, R.R. *et al.* (2012) Strong influence of regional species pools on continent-wide structuring of local communities. *Proceedings of the Royal Society B-Biological Sciences*, **279**, 266–274.

Letcher, S.G. (2010) Phylogenetic structure of Angiosperm communities during tropical forest succession. *Proceedings of the Royal Society B-Biological Sciences*, **277**, 97–104.

Letcher, S.G., Chazdon, R.L., Andrade, A.C.S., Bongers, F., van Breugel, M., Finegan, B. *et al.* (2012) Phylogenetic community structure during succession: evidence from three Neotropical forest sites. *Perspectives in Plant Ecology, Evolution and Systematics*, **14**, 79–87.

Levins, R. & Culver, D. (1971) Regional coexistence of species and competition between rare species (mathematical model/habitable patches). *Proceedings of the National Academy of Sciences of the United States of America*, **68**, 1246–1248.

Lockwood, J.L., Cassey, P. & Blackburn, T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution*, **20**, 223–228.

Luken, J.O. (1990) *Directing Ecological Succession*. Chapman and Hall, London.

Mayfield, M.M. & Levine, J.M. (2010) Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters*, **13**, 1085–1093.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, **21**, 178–185.

McIntosh, R.P. (1985) *The Background of Ecology*. Cambridge University Press, Cambridge.

McLauchlan, K.K., Higuera, P.E., Gavin, D.G., Perakis, S.S., Mack, M.C., Alexander, H. *et al.* (2014) Reconstructing disturbances and their

biogeochemical consequences over multiple timescales. *BioScience*, **64**, 105–116.

Mo, X.-X., Shi, L.-L., Zhang, Y.-J., Zhu, H. & Slik, J.W.F. (2013) Change in phylogenetic community structure during succession of traditionally managed tropical rainforest in Southwest China. *PLoS One*, **8**, e71464.

del Moral, R. & Magnússon, B. (2014) Surtsey and Mount St. Helens: a comparison of early succession rates. *Biogeosciences*, **11**, 2099–2111.

Navas, M.L., Roumet, C., Bellmann, A., Laurent, G. & Garnier, E. (2010) Suites of plant traits in species from different stages of a Mediterranean secondary succession. *Plant Biology*, **12**, 183–196.

Noble, I.R. & Slatyer, R.O. (1980) The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio*, **43**, 5–21.

Norden, N., Letcher, S., Boukili, V., Swenson, N. & Chazdon, R. (2012) Demographic drivers of successional changes in phylogenetic structure across life-history stages in plant communities. *Ecology*, **93**, S70–S82.

Oosting, H.J. (1942) An ecological analysis of the plant communities of Piedmont, North Carolina. *American Midland Naturalist*, **28**, 1–126.

Padilla, F.M., Mattingly, W.B., Swedo, B.L., Clay, K. & Reynolds, H.L. (2012) Negative plant–soil feedbacks dominate seedling competitive interactions of North American successional grassland species. *Journal of Vegetation Science*, **23**, 667–676.

Peet, R.K. (2000) Forests and meadows of the Rocky Mountains. *North American Terrestrial Vegetation* (eds M.G. Barbour & W.D. Billings), pp. 75–122. Cambridge University Press, Cambridge.

Pickett, S.T.A. & Cadenasso, M.L. (2005) Vegetation dynamics. *Vegetation Ecology* (ed. van der Maarel E.), pp. 172–198. Blackwell Publishing, Malden, MA.

Pickett, S.T.A., Collins, S.L. & Armesto, J.J. (1987a) A hierarchical consideration of causes and mechanisms of succession. *Plant Ecology*, **69**, 109–114.

Pickett, S.T.A., Collins, S.L. & Armesto, J.J. (1987b) Models, mechanisms, and pathways of succession. *The Botanical Review*, **53**, 335–371.

Pickett, S.T.A. & McDonnell, M.J. (1989) Changing perspectives in community dynamics: a theory of successional forces. *Trends in Ecology and Evolution*, **4**, 241–245.

Pickett, S.T.A., Meiners, S.J. & Cadenasso, M.L. (2011) Domain and propositions of succession theory. *The Theory of Ecology* (eds S.M. Scheiner & M.R. Willig), pp. 185–216. University of Chicago Press, Chicago.

Prach, K., Pyšek, P. & Smilauer, P. (1997) Changes in species traits during succession: a search for pattern. *Oikos*, **79**, 201–205.

Prach, K. & Walker, L.R. (2011) Four opportunities for studies of ecological succession. *Trends in Ecology and Evolution*, **26**, 119–123.

Prach, K., Řehounková, K., Lencová, K., Jírová, A., Konvalinková, P., Mudrák, O. *et al.* (2014) Vegetation succession in restoration of disturbed sites in Central Europe: the direction of succession and species richness across 19 seres. *Applied Vegetation Science*, **17**, 193–200.

Purschke, O., Schmid, B.C., Sykes, M.T., Poschlod, P., Michalski, S.G., Durka, W. *et al.* (2013) Contrasting changes in taxonomic, phylogenetic and functional diversity during a long-term succession: insights into assembly processes. *Journal of Ecology*, **101**, 857–866.

van der Putten, W.H., Bardgett, R.D., Bever, J.D., Bezemer, T.M., Casper, B.B., Fukami, T. *et al.* (2013) Plant–soil feedbacks: the past, the present and future challenges. *Journal of Ecology*, **101**, 265–276.

Questad, E.J. & Foster, B.L. (2008) Coexistence through spatio-temporal heterogeneity and species sorting in grassland plant communities. *Ecology Letters*, **11**, 717–726.

Raevel, V., Violle, C. & Munoz, F. (2012) Mechanisms of ecological succession: insights from plant functional strategies. *Oikos*, **121**, 1761–1770.

Rebele, F. (2013) Differential succession towards woodland along a nutrient gradient. *Applied Vegetation Science*, **16**, 365–378.

Řehounková, K. & Prach, K. (2008) Spontaneous vegetation succession in gravel–sand pits: a potential for restoration. *Restoration Ecology*, **16**, 305–312.

Reinhart, K.O., Wilson, G.W.T. & Rinella, M.J. (2012) Predicting plant responses to mycorrhizae: integrating evolutionary history and plant traits. *Ecology Letters*, **15**, 689–695.

Reynolds, H.L., Packer, A., Bever, J.D. & Clay, K. (2003) Grassroots ecology: plant-microbe-soil interactions as drivers of plant community structure and dynamics. *Ecology*, **84**, 2281–2291.

Ricklefs, R.E. (1987) Community diversity: relative roles of local and regional processes. *Science*, **235**, 167–171.

Rouget, M. & Richardson, D.M. (2003) Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. *American Naturalist*, **162**, 713–724.

Shipley, B. (2010) *From Plant Traits to Vegetation Structure*. Cambridge University Press, Cambridge, UK.

Smit, R. & Olff, H. (1998) Woody species colonisation in relation to habitat productivity. *Plant Ecology*, **139**, 203–209.

Srivastava, D.S. (1999) Using local-regional richness plots to test for species saturation: pitfalls and potentials. *Journal of Animal Ecology*, **68**, 1–16.

Swenson, N.G., Enquist, B.J., Thompson, J. & Zimmerman, J.K. (2007) The influence of spatial and size scales on phylogenetic relatedness in tropical forest communities. *Ecology*, **88**, 1770–1780.

Tansley, A.G. (1939) *The British Islands and Their Vegetation*. Cambridge University Press, Cambridge.

Thrall, P.H., Hochberg, M.E., Burdon, J.J. & Bever, J.D. (2007) Coevolution of symbiotic mutualists and parasites in a community context. *Trends in Ecology & Evolution*, **22**, 120–126.

Tilman, D. (1985) The resource-ratio hypothesis of plant succession. *American Naturalist*, **125**, 827–852.

Titus, J.H., Whitcomb, S. & Pitoniak, H.J. (2007) Distribution of arbuscular mycorrhizae in relation to microsites on primary successional substrates on Mount St. Helens. *Botany-Botanique*, **85**, 941–948.

Turnbull, L.A., Crawley, M.J. & Rees, M. (2000) Are plant populations seed-limited? A review of seed sowing experiments. *Oikos*, **88**, 225–238.

Verdú, M., Rey, P.J., Alcántara, J.M., Siles, G. & Valiente-Banuet, A. (2009) Phylogenetic signatures of facilitation and competition in successional communities. *Journal of Ecology*, **97**, 1171–1180.

Walker, L.R. (2011) Integration of the study of natural and anthropogenic disturbances using severity gradients. *Austral Ecology*, **36**, 916–922.

Walker, L.R. & del Moral, R. (2003) *Primary Succession and Ecosystem Rehabilitation*. Cambridge University Press, Cambridge.

Walker, L.R. & Wardle, D.A. (2014) Plant succession as an integrator of contrasting ecological time scales. *Trends in Ecology & Evolution.*, **29**, 504–510.

Walker, L.R., Wardle, D.A., Bardgett, R.D. & Clarkson, B.D. (2010) The use of chronosequences in studies of ecological succession and soil development. *Journal of Ecology*, **98**, 725–736.

Webb, C.O., Gilbert, G.S. & Donoghue, M.J. (2006) Phylodiversity-dependent seedling mortality, size structure, and disease in a Bornean rain forest. *Ecology*, **87**, S123–S131.

Webb, C.O., Ackerly, D.D., McPeek, M.A. & Donoghue, M.J. (2002) Phylogenies and community ecology. *Annual Review of Ecology and Systematics*, **33**, 475–505.

Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E. & Eriksson, O. (1999) Challenging theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science*, **10**, 609–620.

Westoby, M. & Wright, I.J. (2006) Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution*, **21**, 261–268.

Whitfeld, T.J.S., Kress, W.J., Erickson, D.L. & Weiblen, G.D. (2012) Change in community phylogenetic structure during tropical forest succession: evidence from New Guinea. *Ecography*, **35**, 821–830.

Wilson, G.W.T. & Hartnett, D.C. (1998) Interspecific variation in plant responses to mycorrhizal colonization in tallgrass prairie. *American Journal of Botany*, **85**, 1732–1738.

Wright, J.P. & Fridley, J.D. (2010) Biogeographic synthesis of secondary succession rates in eastern North America. *Journal of Biogeography*, **37**, 1584–1596.

Wright, J., Jones, C. & Flecker, A. (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia*, **132**, 96–101.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. *et al.* (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.

Yang, J., Zhang, G., Ci, X., Swenson, N.G., Cao, M., Sha, L. *et al.* (2014) Functional and phylogenetic assembly in a Chinese tropical tree community across size classes, spatial scales and habitats. *Functional Ecology*, **28**, 520–529.