CHAPTER 4

Community assembly dynamics in space

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4.1 Introduction

Species live in a complex web of interactions in the ecological community. What effects do species exert on one another, and how strongly? If species interactions are mostly strong, how do species cope with one another and coexist in the same community? In other words, what level of species diversity and what patterns of species composition should we expect to see if species interactions strongly affect community structure? These are some of the fundamental questions that community ecologists seek to answer (Morin 1999).

Much remains unknown to fully answer these questions, and one major challenge is that species interactions can bring about two contrasting types of community dynamics (Fig. 4.1). In theory, strong interactions can make communities either deterministic or historically contingent (Samuels and Drake 1997; Belyea and Lancaster 1999; Chase 2003; Fukami *et al.* 2005). When deterministic, the effect of species interactions on community structure is determined by environmental conditions. On the other hand, when historically contingent, community structure diverges among localities as

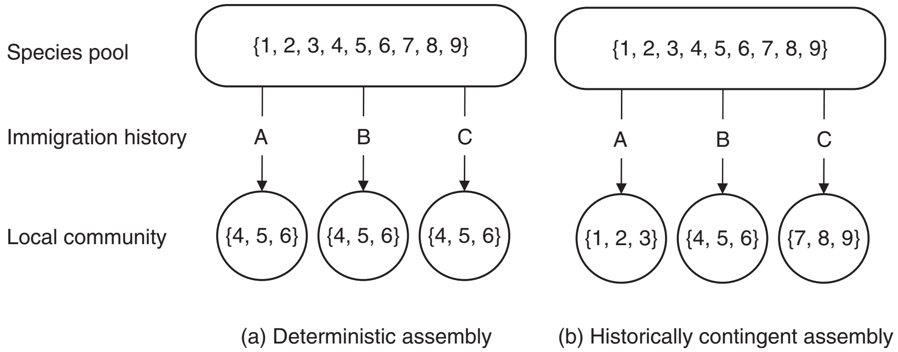

Figure 4.1 (a) Deterministic and (b) historically contingent community assembly. Numbers represent hypothetical species, sets of numbers in brackets represent the species composition of local communities, arrows from the species pool to local communities represent species immigration, and alphabets represent different immigration histories. Deterministic community assembly refers to situations in which different patches converge to the same species composition regardless of immigration history as long as the communities initially share the same environmental conditions. Historically contingent community assembly refers to situations in which different patches diverge to contain different sets of species if immigration history differs between them, even if the communities initially share the same environmental conditions. Specific species compositions in the figure are arbitrary. Modified from Fukami (2008). See also Chase (2003).

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a result of stochastic variation in the history of species arrivals, even under identical environmental conditions and an identical regional species pool.

It is difficult to determine which of these two scenarios happens in natural communities. One main reason is simply that the immigration history of most communities is unknown. This problem is apparent in observational studies of community assembly. First popularized by Connor and Simberloff (1979) in response to Diamond (1975), these studies use statistical methods called null models to compare observed community structures with what would be expected if species interactions did not exert significant effects on structure (Gotelli 2001). The null models are a useful tool for detecting effects of species interactions, but only when used with caution. An incorrect assumption sometimes made when using null models is that strong interactions should always lead to community structures that are significantly different from null expectations. Strong interactions, when combined with variable immigration history, can result in historically contingent community development, which can produce apparently random community structure. As pointed out by Wilbur and Alford (1985) and Drake (1991), species interactions, even when strong, do not necessarily create community structures that are distinguishable from null expectations that are based on deterministic effects of species interactions. This limitation arises largely because most null-model studies use data taken at only one point in time. Temporal changes in community structure, let alone the history of species immigration, are usually not considered, simply because such data are rarely available.

Is it possible at all, then, to deepen our understanding of species interactions and community structure without historical information on species immigration? Studies have recently begun to evaluate possible conditions that make community assembly deterministic or historically contingent. For example, it has been suggested that the rate of nutrient supply determines the extent of historical contingency (Chase 2003; Steiner and Leibold 2004). If this is true, then we should be able to calculate at least how predictable community structure will be, based on nutrient supply rate. These studies indicate a potentially promising way in which we can deepen our understanding of community structure without knowing immigration history. Building on this framework, this chapter will consider the spatial scale of community assembly dynamics as a potentially important yet relatively overlooked factor that may critically determine the likelihood of deterministic versus historically contingent community assembly. My aim here is not to provide a comprehensive review of community assembly research. I will instead use the results of several recent studies to highlight ideas that I believe are worthy of further exploration.

4.2 Determinism and historical contingency in community assembly

Before considering spatial issues relating to community assembly, I would first like to clarify what is meant by determinism and historical contingency. In this chapter, I define community assembly as the construction and maintenance of local communities through sequential arrival of potential colonists from an external species pool (Drake 1991; Warren *et al.* 2003). As Warren *et al*. (2003) pointed out, ‘viewed in this way, community assembly emphasizes changes in the community state rather than embracing all evidence for pattern in community structure, the broader context in which the term assembly is sometimes used’.

While community assembly can be historically contingent or deterministic in the absence of species interactions, the focus of this chapter will be comparison of the two scenarios in their presence. Community assembly starts with a disturbance, such as a fire, flood or hurricane. Because space, nutrients and other resources are often abundant in the recently disturbed area, competition and other interspecific interactions are unlikely to exert strong effects on community structure at this stage. Also, of the potential colonists that can immigrate into the disturbed area, only some will have reached the new patch thus far, and which species have arrived can be a matter of chance (e.g. Walker *et al.* 2006). In this sense, communities are historically contingent, but not as a joint consequence of immigration history and species interactions. Once more time has passed since disturbance, most potential colonizers may have arrived, even though species interactions have not yet started to affect community structure (e.g. Mouquet *et al.* 2003). In other words, most species expected to be found there are present. In this sense, community structure is deterministic, but because this determinism does not involve species interactions, it is not what I would like to focus on here, either.

Given more time after disturbance, species interactions will start to influence community composition more strongly as each species increases in abundance in the patch. These species interactions can make community structure become either deterministic or historically contingent. It is these two contrasting outcomes that are the focus of this chapter. According to the deterministic view, the environmental conditions under which community assembly happens determine which of the species from the regional pool will remain in the community as a consequence of species interactions. In this case, immigration history does not influence the final species composition of the community. Such communities are said to follow deterministic 'assembly rules' (Weiher and Keddy 1995; Belyea and Lancaster 1999). This idea is rooted in Clements's (1916) climax concept of succession. More recently, deterministic assembly rules have been indicated to drive community assembly not just through immigration, but also through evolutionary diversification (Losos *et al.* 1998; Gillespie 2004).

In contrast, if communities are historically contingent, environmental conditions do not determine a single climax community. Instead, even if two communities are originally under the same environmental conditions, they may contain different sets of species if they have different immigration histories. Lewontin (1969) is often cited as the first author to articulate this idea. Here there is more than one final stable state (called alternative stable states, multiple stable points, multiple stable equilibria, etc.; see Schröder *et al*. 2005) that communities may approach through assembly; once a community assumes a stable state, it cannot move to another stable state unless heavily disturbed. This phenomenon is caused by 'priority effects', in which early-arriving species affect, either negatively or positively, the performance of species that arrive late in terms of population growth (see Almany 2003 and references therein). A simple example of priority effects involves pre-emptive competition, in which species that arrive early make resources unavailable, by virtue of being there first, to other later-arriving species that need those resources to survive and grow (e.g. MacArthur 1972; Sale 1977; Tilman 1988). However, priority effects need not involve only competition, and can happen via predation (e.g. Barkai and McQuaid 1988; Holt and Polis 1997), environmental modification (e.g. Peterson 1984; Knowlton 2004) and other types of species interactions. Recently, experiments have shown that not only community assembly over ecological time, but evolutionary assembly through diversification can also be historically contingent (Fukami *et al*. 2007).

Ever since Lewontin's early writings (1969), much emphasis has been placed on alternative stable states in studying historically contingent assembly. Historical contingency should be considered from a broader perspective, however. There are two ways that communities can be historically contingent even when there is only one final stable state to which communities tend over time.

First, communities can exist in what is called a permanent endcycle. Morton and Law (1997) suggested that there are theoretically two types of final states that communities reach. One is called a permanent endpoint, and the other a permanent endcycle. Permanent endpoints consist of subsets of species from the species pool that are resistant to invasion by any species that are not members of the endpoint. When ecologists refer to alternative stable states, they are in many cases referring to alternative permanent endpoints. In contrast, a permanent endcycle is 'the union of the sets of species that occur in a cyclic or more complex sequence of communities' (Morton and Law 1997). Each set of species in a permanent endcycle can be invaded by at least one of the other species in the endcycle, but cannot be invaded by any species not in the endcycle (Fig. 4.2). Communities in a permanent endcycle are contingent on immigration history, because species composition at a given point in time depends on the sequence of species invasion as the communities go through the endcycle (Lockwood *et al*. 1997; Fukami 2004b; Steiner and Leibold 2004; Van Nes *et al*. 2007). This is true even with just

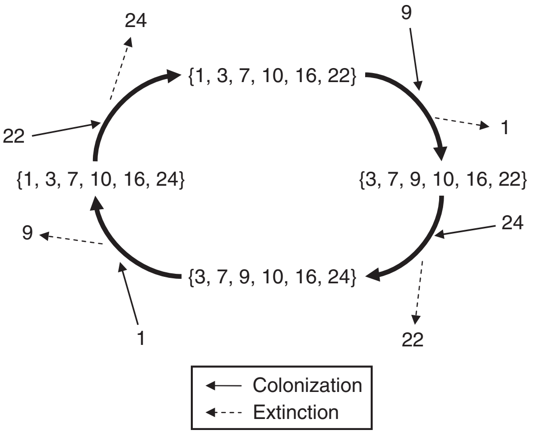

Figure 4.2 An example of a permanent endcycle. Numbers represent hypothetical species in a computer simulation. In this simulation, species 1–12 are autotrophs and species 13–24 are heterotrophs. Sets of numbers in brackets represent species composition of a local community, thick arrows represent temporal changes in species composition, thin arrows represent species colonization, and dotted arrows represent local species extinction. In the example shown here, the species pool consists of 24 species, but only those that participate in the endcycle are shown. Modified from Morton and Law (1997) and Fukami (2008).

one final permanent endcycle, in the absence of alternative final states.

Second, communities can also exhibit alternative long-term transient dynamics. It can take a long time, relative to the generation times of the species involved, for a community to reach a stable state. In such cases, communities will be historically contingent for a long time on their way to a stable state if they follow alternative successional trajectories (Fukami 2004a). For example, suppose that species A competitively excludes species B regardless of immigration history. Even so, species B can remain dominant for a long time if it arrives before species A, and before competitive exclusion eventually occurs. This phenomenon is particularly likely when dispersal ability and competitive ability are similar among species (Sale 1977; Knowlton 2004; Fukami *et al.* 2007; Van Geest *et al.* 2007). For the rest of this chapter, I will consider permanent endcycles and long-term transients as well as alternative stable states in discussing community assembly.

4.3 Community assembly and spatial scale

Having clarified what is meant by determinism and historical contingency, I would now like to develop the main thesis of this chapter, namely that explicit consideration of spatial scale should help us to better understand the conditions in which community assembly is deterministic and those in which it is historically contingent. Drawing on recent theoretical and empirical studies, I will focus on three factors relating to spatial scale: (1) patch size, (2) patch isolation and (3) environmental heterogeneity. In discussing these, it will become clear that it is the relative spatial scale of all of these factors simultaneously considered that brings us the closest to a full understanding of community assembly dynamics.

4.3.1 Patch size

The local patch is the scale at which community assembly occurs (Fig. 4.1). Recent research has suggested that the size of local patches can affect the degree of historical contingency in community assembly. In their pioneering work, Petraitis and Latham (1999) proposed that historical contingency leading to alternative stable states occurs only when patch size exceeds a threshold value. When a newly created patch is too small, the species dominant in and around the patch before disturbance quickly colonize it from adjacent areas and continue to dominate. In this sense, the fate of community assembly in the patch is deterministic. In contrast, when the patch is large, species that are not dominant in adjacent areas may immigrate from a certain distance away and subsequently become abundant before adjacent dominant species take over the patch. In this situation, the history of species immigration can influence community membership. Thus, this is a historically contingent assembly.

Petratis and Latham's (1999) idea is mainly derived from their work on rocky intertidal communities in the New England region of North America, where each patch appears to be in either of two states, algal-dominated or mussel-dominated. It was suggested that, for a disturbance such as ice scour to cause a patch to move from algal-dominated to mussel-dominated or vice versa, patch size needed to be sufficiently large to prevent nearby dominants from always driving community assembly. It should be noted here, though, that there is some debate about whether these really represent two alternative stable states (Bertness *et al.* 2004).

Fukami (2004a) proposed a hypothesis that seems contradictory to the Petraitis and Latham (1999) hypothesis. Experiments showed that community assembly was historically contingent to a greater extent in smaller rather than larger patches. Microbial communities were assembled in the laboratory by introducing 16 species of freshwater protists and rotifers in four different orders in each of four different microcosm sizes. The results showed that species diversity was affected more by immigration history in smaller microcosms. This was explained as follows. Given the same initial population size, early arriving species can achieve high population density more quickly in smaller patches. Consequently, resource availability and other conditions in patches are more greatly altered by early immigrants in smaller patches, which then has a greater effect on late-arriving species in smaller patches (see also Orrock and Fletcher 2005).

The apparent contradiction between Petraitis and Latham (1999) and Fukami (2004a) stems partly from different assumptions made about the source of immigrants. Petraitis and Latham assume that immigration rates, particularly of species that are dominant near the patches, are higher for smaller patches. Immigration history itself is, then, more deterministic there, resulting in more deterministic assembly. On the other hand, Fukami assumes that immigration rate and history do not vary with patch size. In this situation, the inverse relationship between patch size and the rate of increase in population density causes larger patches to be more deterministic.

Which assumption is more realistic? The answer depends partly on the environment around the patch. Petraitis and Latham's assumption would be more realistic if patches are surrounded by areas that provide immigrants. Besides rocky intertidal patches, forest gaps (e.g. Hubbell 2001) are possible examples. On the other hand, Fukami's assumption may be more realistic if the source of immigrants is distant from the patches. Examples may include entire islands acting as patches that undergo community assembly after an island-wide volcanic eruption (e.g. Thornton 1996) and entire ponds acting as patches that undergo assembly after drought and subsequent refilling of water (e.g. Chase 2007).

But even in patches distant from the species pool, immigration rates may vary with patch size. Just as darts are more likely to hit a larger dartboard, species may be more likely to arrive at a larger patch. Under this target size effect (Lomolino 1990), larger patches receive more individuals, consequently reducing the between-patch difference in the population density of early-arriving species. The effect of patch size on historical contingency suggested by Fukami (2004a) may not be as strong then. It is also possible, however, that slower immigration rates in smaller patches make more time available for early immigrants to alter the environment before other species arrive. This can strengthen priority effects in smaller patches relative to larger ones, making the difference in the extent of historical contingency between small and large patches more pronounced. The relative importance of these two opposing ways in which patch size affects historical contingency requires further investigation.

Clearly, the effects of patch size on community assembly are complex. In particular, it has become clear that considering the effect of patch size necessitates consideration of the areas surrounding the patches as well. The following sections will explore surrounding areas a little further. I will first consider the degree of patch isolation and then the spatial scale at which environmental heterogeneity is observed relative to the scale of patches.

4.3.2 Patch isolation

Several studies suggest that community assembly is more sensitive to immigration history when the patch is located farther from the species pool. Robinson and Edgemon (1988) assembled microbial communities by introducing phytoplankton species into aquatic microcosms in three different orders at three different rates. Results showed that the effect of introduction order on species composition was greater when communities were assembled with lower immigration rates. Because immigration rate is generally expected to be lower when the distance from the species pool is greater (MacArthur and Wilson 1967), Robinson and Edgemon's results suggest that community assembly is historically contingent to a greater extent when the patch is more isolated.

In a related study, Lockwood *et al.* (1997) conducted computer simulation of community assembly using Lotka–Volterra equations modelling competition and predation within patches. Using two immigration rates, they found that immigration history influenced species composition under both immigration rates, but that the type of effect differed between the two rates. When immigration rate is low, different immigration histories lead communities to alternative stable states, whereas when immigration rate is high, permanent endcycles occur. The likely reason for this difference has to do with whether the assembling communities approach an equilibrium between immigration events. Low immigration rate allows for this, eventually resulting in a stable state of species composition. In contrast, high immigration rate prevents the community reaching any possible equilibrium between immigration events. Thus, high immigration rate maintains species composition in a transient state of change, resulting in permanent endcycles.

Fukami (2004b) used a similar Lotka–Volterra model to find that community assembly resulted in permanent endcycles regardless of immigration rate, but that the number of species involved in permanent endcycles was greater when immigration rate is low. As a result, immigration history has a greater effect on species composition when immigration rate is lower (see also Schreiber and Rittenhouse 2004).

These studies all assume that the species pool that provides immigrants exists externally, such that patch community dynamics do not affect the species pool (Fig. 4.3b). The model of community assembly based on this assumption is typically referred to as the mainland-island model. An alternative model has been termed the metacommunity model, which describes a collection of multiple local patches each undergoing community assembly through occasional dispersal of species between the patches (Wilson 1992; Leibold *et al.* 2004; see Chapter 5). In metacommunities, the species pool is internal instead of external, and local patches serve as the source of immigrants (Fig. 4.3a). In terms of patch isolation, when patches are more isolated from one another, the rate of *internal* dispersal is lower (Fig. 4.3a), whereas when patches are more isolated from the species pool, the rate of *external* dispersal is lower (Fig. 4.3b).

Computer simulations show that higher internal dispersal (or how isolated patches are to one another) could make community assembly more deterministic (Fukami 2005). This theoretical result is consistent with findings from empirical studies (e.g. Chase 2003; Cadotte 2006). However, Fukami (2005) also showed that whether this effect of

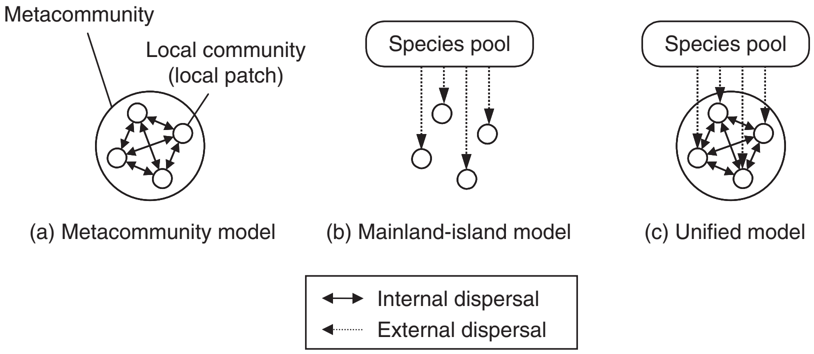

Figure 4.3 (a) Metacommunity model, (b) mainland-island model and (c) unified model of community assembly. Arrows represent dispersal between patches within the metacommunity (referred to as internal dispersal). Dashed arrows represent dispersal from the external species pool (referred to as external dispersal). Modified from Fukami (2005).

internal dispersal occurs depended on the rate of external dispersal. Specifically, frequent internal dispersal reduces the extent of historical contingency if external dispersal is not frequent, but internal dispersal does not affect historical contingency if external dispersal is frequent. Therefore, the two dispersal types can reciprocally provide the context in which each affects species diversity. These results indicate that in order to understand historical contingency in community assembly, it is important, though rarely done, to distinguish internal and external dispersal and to know the relative frequency of the two types of dispersal (Fig. 4.3c).

4.3.3 Scale of environmental heterogeneity

Many studies, including those discussed above, assume that local patches share identical environmental conditions. They also assume that the region within which local patches are embedded is homogeneous across space. Clearly these assumptions are not met in many ecological landscapes. An interesting question then is how the scale at which environmental heterogeneity is observed may influence the degree of historical contingency in community assembly.

A study by Shurin *et al.* (2004) is relevant here. They used a mathematical model to study conditions for coexistence of two competing species at a regional scale. The region modelled consists of multiple patches that vary in resource supply ratio. In the absence of variation among patches in resource supply ratio, one of the two species competitively excludes the other. When patches vary in the ratio, historical contingency occurs in terms of which species occupies a given patch. Specifically, in patches where resource supply ratio is intermediate, the species that arrives first prevents the other from colonizing that patch. In other patches where the ratio takes more extreme values, one or the other species dominates. These patches serve as a species pool that provides immigrants to patches of intermediate environmental conditions for historically contingent community assembly to be realized there (though it involves only two species in the model). Historically contingent assembly occurs only when there is an external species pool that is not influenced by the patches in which historical contingency is observed.

In terms of the spatial scale of environmental heterogeneity, the results of Shurin *et al.* (2004) can be interpreted as follows. Historically contingent assembly occurs when environmental conditions are sufficiently heterogeneous across patches (Fig. 4.4d) rather than within patches (Fig. 4.4c). Thus, it is the scale of environmental heterogeneity relative to the patches in question, rather than its absolute scale independent of patch size, that affects the degree of historical contingency in community assembly.

The experiment conducted by Drake (1991) provides additional insight into environmental heterogeneity and community assembly. Similar in design to Robinson and Edgemon (1988) and Fukami (2004a), Drake (1991) assembled aquatic microbial microcosms through sequential introductions of species in various orders using two different sizes of microcosms. The results showed that, in small patches, the same species dominated the assembled community regardless of introduction order, whereas, in large patches, species introduced early dominated over those introduced late. These results

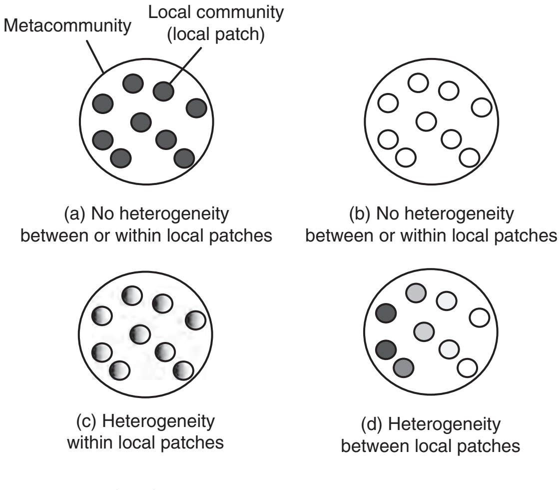

Figure 4.4 (a–d) Spatial scale at which environmental heterogeneity is observed. Shading indicates variation in environmental conditions (e.g. rate of nutrient supply). Heterogeneity is drawn arbitrarily as a gradient. Modified from Fukami (2008).

appear to contradict those of Fukami (2004a) discussed above, while being congruent with those of Petraitis and Latham (1999). But neither seems to be the case. Drake (1991) invoked differences in environmental heterogeneity between small and large patches to explain his results, whereas neither Fukami (2004a) nor Petraitis and Latham (1999) explicitly considered environmental heterogeneity. Drake postulated that environmental heterogeneity increased with patch size (light availability was more variable in larger microcosms owing to increased depth; depth was standardized across patch size in Fukami (2004a)), and that variation among species in their competitive ability was small when environmental heterogeneity was great. Communities are thought to be more sensitive to historical contingency when species are competitively more similar (e.g. MacArthur 1972; Hubbell 2001). If this applies to Drake's microcosms, then it explains smaller historical contingency in smaller patches. Drake's (1991) explanation would need to be tested to be rigorously validated, but the suggested potential relationship between patch size, environmental heterogeneity, competitive relationship and historical contingency remains novel to this day.

4.3.4 Synthesis

In summary, I have considered patch size, patch isolation and the spatial scale of environmental heterogeneity as three spatial factors influencing the degree of determinism and historical contingency in community assembly. These factors do not affect community assembly independently of one another. Instead, their scale and consequently their role in community assembly are determined relative to those of the others. Through consideration of these three factors, several conditions for historical contingency have emerged. Specifically, community assembly is hypothesized to be historically contingent to a greater extent when (1) immigration rate is lower, (2) immigration history is more variable and (3) the species pool that provides immigrants to local patches undergoing assembly exists more independently of the community dynamics within the patches.

4.4 Community assembly and species traits

Ultimately, consequences of patch size, patch isolation and environmental heterogeneity for community assembly depend on the spatial scale of species movement (Cadotte and Fukami 2005). For this reason, it is important to know the dispersal ability of the species involved in community assembly in question, in order to address the determinism versus historical contingency question. Furthermore, the degree of variation in dispersal ability among species can also influence historical contingency in community assembly. This is because the more similar species are in dispersal ability, the more stochastic immigration history is expected to be, which can then lead to less deterministic assembly. Smaller variation in competitive ability should also result in less deterministic assembly, as priority effects act stronger between competitively more similar species.

Furthermore, dispersal ability and competitive ability are thought to sometimes show a trade-off, such that species that are good dispersers are poor competitors, and vice versa (e.g. Petraitis *et al.* 1989; Cadotte 2007). In terms of succession, this means that early-successional species are competitively inferior to late-successional species (Petraitis *et al.* 1989). This trade-off, too, may influence historical effects in community assembly. For example, assembly may be more deterministic when the species show a clearer trade-off between these two traits. This is because, under a clear trade-off, community assembly is expected to progress predictably to eventually end with a predictable set of late-successional competitive species dominating the community.

Of course, dispersal ability and competitive ability are just a few of many traits that characterize species. There has recently been a renewed interest in explaining community dynamics from species traits (e.g. Fukami *et al.* 2005; McGill *et al.* 2006; Ackerly and Cornwell 2007). Other traits that can influence community assembly include disturbance tolerance, intrinsic rate of growth and predator avoidance. Including these traits in a framework for community assembly should enhance our predictive power. For example, even when there is a clear trade-off between dispersal ability and competitive ability, community assembly can be historically contingent in the presence of predators. Recent experimental work suggests that the timing of predator arrival at the local patch can influence the final structure of prey communities under a competition–colonization trade-off (Olito and Fukami 2009).

Dispersal ability and other traits may ultimately be determined by the spatial scale of patches that the species have experienced over evolutionary time (Denslow 1980). Patch sizes that species have experienced in the past and those of the present are not necessarily the same. This is particularly true in the presence of anthropogenic disturbance, habitat fragmentation and exotic species introduction. Anthropogenic disturbance can be evolutionarily novel; habitat fragmentation can create new kinds of patch size and isolation; and exotic species can differ from native species in the spatial scale of patches that they have adapted to, consequently differing in the way native and exotic species perceive spatial scale. How do these anthropogenic changes in the scale of community assembly affect historical contingency in assembly? We currently know little to answer this question. A better understanding of the role of scale in community assembly may contribute to advancing not only community ecology as a basic science, but also solving applied issues regarding the community-level impacts of species invasions.

4.5 Conclusions and prospects

I have discussed how the spatial scale at which community assembly occurs may influence the degree to which community assembly dynamics are deterministic versus historically contingent. As spatial factors, I have focused on patch size, patch isolation and the scale at which environmental conditions vary. In combination, these factors are proposed to jointly affect three elements of community assembly dynamics: the rate of immigration to local communities, the degree to which the species pool is external to local community dynamics and the extent of variation in immigration history between local communities. I have argued that these three elements will in turn determine the extent of historical contingency and determinism in community assembly. Additionally, I have briefly pointed out that the spatial scale of community assembly is defined relative to dispersal ability of species involved. But dispersal ability is often not independent of other traits such as competitive ability, disturbance tolerance and predator avoidance. Explicit consideration of these traits should lead to a better understanding of the conditions for contingent versus deterministic assembly.

As discussed in the introduction, much of community assembly research has traditionally relied on null-model approaches using observational data. This is because experimental assembly of natural communities is difficult in most situations owing to the large spatial and temporal scales involved in this type of work. However, direct experimental manipulation of immigration history is necessary in order to rigorously evaluate historical effects in community assembly (Schröder *et al.* 2005). For this reason, I expect that experiments will become increasingly important in community assembly research. Experiments have so far been limited mainly to those with microorganisms in the laboratory owing to their logistical advantages, but we will also need to do more field experiments to ensure that the concepts we develop are firmly placed in natural context. Though difficult, field experiments are feasible by, for example, incorporating experimental research into ecological restoration projects (e.g. Fukami *et al.* 2005; Weiher 2007).

In addition, research on community assembly has mainly considered systems in which environmental conditions do not vary considerably except when pulse disturbance events initiate a new round of community assembly. However, environmental conditions can of course fluctuate greatly in many systems. How do temporal fluctuations affect the role of spatial scale in determining the degree of historical contingency in community structure? Does the temporal scale of environmental fluctuations relative to that of community assembly affect the extent of historical contingency? These questions remain unanswered. My focus here has been spatial scale, but temporal scale should also be explored further in future research in relation to community assembly, over both ecological and evolutionary time.

This chapter has largely consisted of exploration of ideas rather than evaluation of data. We do not yet have sufficient data to draw general conclusions as to how often or to what extent natural communities are governed by historical contingency. If it turns out in the future that many communities are indeed highly sensitive to historical effects, then one may question whether community ecology can be called a science in the first place. The answer could be no if science was defined as discovering general patterns in nature and explaining these patterns within a predictive framework. In fact, we do know that clear general patterns are rarely observed in community structure. Historical contingency may well be a main reason behind the absence of such patterns. Nonetheless, like other authors (e.g. Long and Karel 2002; Chase 2003), I believe a good understanding of the conditions for determinism versus historical contingency will contribute to building a predictive theory of community ecology. Here I have sought to provide a first step in this endeavour, with a special focus on the spatial scale of community assembly dynamics. Many of the ideas presented here are only exploratory, and some may prove wrong. Even so, it is my hope that they serve to stimulate further research on the dynamics of community assembly.

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