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Assembly rules within a contingent ecology

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Ecologists have searched for general principles, or assembly rules, which determine how species combine to form communities. Two major strands of research highlight the interaction of assembly rules operating at different levels of community organisation, and within uncertain local and historical contingencies. Here, we review the literature on community assembly within the context of three principal determinants: dispersal constraints, environmental constraints and internal dynamics. This classification separates external factors (dispersal and environmental constraints) from internal processes (internal dynamics). We assert that assembly rules are general, deterministic and mechanistic, and operate on internal dynamics within the constraints imposed by the local environment and the history of species invasions. Several assembly rules have been proposed to operate within and across trophic levels, as well as on whole systems. The rules act through resource dynamics and spatial dynamics to select species or subsets of species that can coexist, and may lead to patterns of increasing biomass and non-random spatial distributions. Environmental constraints restrict species establishment and mediate interactions among successful colonists; a change in environmental constraints, either exogenous or endogenous, may drive community change. Even in systems at equilibrium, environmental constraints influence the outcome of assembly rules. Dispersal constraints determine the pool of potential colonists available at a particular time and place, and are a complex amalgam of species-specific traits, storage effects, landscape ecology, and history. The order and timing of species invasions (dispersal constraints) interact with assembly rules to produce priority effects. The directionality of community assembly may be lost if either the rate of species invasions or the rate of non-selective species extinctions exceeds the rate at which species are selected by assembly rules. The falling apart, or disassembly, of a community through breakdown of species interactions may follow different rules or a different assembly trajectory.

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"Let's construct our theoretical community from scratch"
– (Plato: 59)

How do species arriving at a site combine to form a community? This question captures the central idea of community assembly, and intersects with several subdisciplines in ecology (Fig. 1). The notion of community assembly dates back to the 4th century BC with Plato's discussion of the sociological assembly of human communities. Ecological studies in community assembly encompass a range of different approaches and perspectives, but generally address one of two themes. Firstly, does the sequence in which species colonise a site influence development of the community? Secondly, do general principles or "assembly rules" hold across communities with different histories? These two themes highlight the interaction between a contingent ecology, where community assembly is dependent on uncertain local and historical effects, and a deterministic ecology, where community assembly conforms to general principles.

Community assembly entwines many aspects of ecology and has the potential to stimulate new and exciting avenues of research. Its wide-ranging remit, however, also poses challenges for coherent investigation. This review was motivated by our frustration with inconsistencies in the way different authors view the subject, often related to differences in subdiscipline and methodology, and the dearth of explicitly stated assembly rules, despite the idea being more than 20 years old. Our main objectives are, firstly, to synthesise previous studies of community assembly that have used diverse approaches, and, secondly, to summarise existing "assembly rules" so that underlying mechanisms and resultant patterns are stated explicitly. Throughout, we emphasise the interaction between deterministic and contingent ecologies. The

Fig. 1. Venn diagram illustrating one way in which the three determinants of community assembly might bridge various subdisciplines of ecology.

literature review is not exhaustive, but we hope that it covers the major approaches to community assembly in an integrative rather than divisive way.

Determinants and rules

One of the first challenges in reviewing the community assembly literature is to define the term "assembly rule". The range of phenomena proposed as rules is so diverse that the word is in danger of losing its meaning. Compare, for example, Haefner (1981), Lawton (1987), Weiher and Keddy (1995a), Morris and Knight (1996), and Samuels and Drake (1997). Few studies (e.g., Fox 1987) contain explicit statements of hypothesised rules for how communities change over time; even fewer state rules explicitly and propose underlying mechanisms (e.g., Holt et al. 1994, Morris and Knight 1996). The current ambiguity and confusion surrounding the term "assembly rule" highlight the need for a clear definition. Based on the English language definition of a rule, we identify two essential elements. Firstly, a rule is a fundamental "principle" that applies across many different situations. Secondly, a rule constrains the behaviour of an "action or procedure", i.e., a *process*. Within the context of community assembly, rules should therefore arise from processes occurring within the community, rather than describe patterns arising in particular circumstances for particular taxa. The same rule may apply to communities that differ historically, leading to similar or divergent trajectories. Non-random community structure may reflect the outcome of assembly rules, but pattern detection is a far cry from defining the rules which generated that pattern (Keddy 1992, Weiher and Keddy 1995b, Weiher et al. 1998). Hence, *assembly rules are general and mechanistic, and operate within the case-specific constraints imposed by colonisation sequence and environment.*

We use the term "rules" to describe general principles arising from mechanisms operating within the community and to which the assembly of a community conforms. For example, the *mechanism* of consumer-resource dynamics (Morris and Knight 1996) may underlie the *rule* that the proportion of available resources consumed increases as species invade (Diamond 1975). One *pattern* resulting from this rule is that invading species are likely to be drawn from different functional groups until each group is represented, before the pattern repeats (Fox 1987). We think it important to state explicitly the underlying mechanisms from which a rule emerges, as well as to describe the patterns in community structure which are the expression of these rules. The distinction between rule and pattern separates formally cause and effect, and avoids confusion of general principles with site- or taxon-specific patterns (see also Keddy 1992). The challenges are to identify what (if any) rules operate within communities, and to apply these general principles to particular situations.
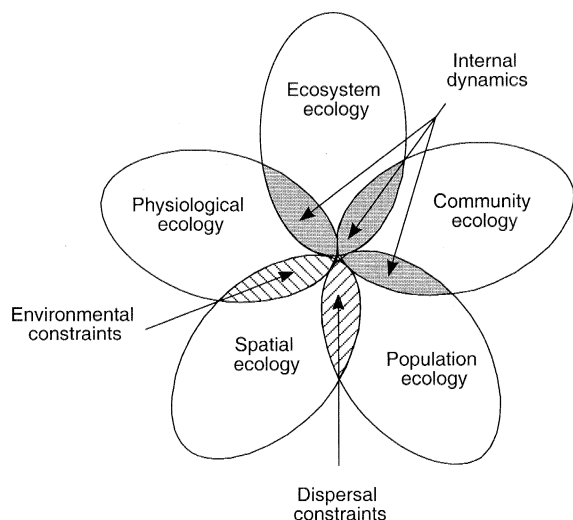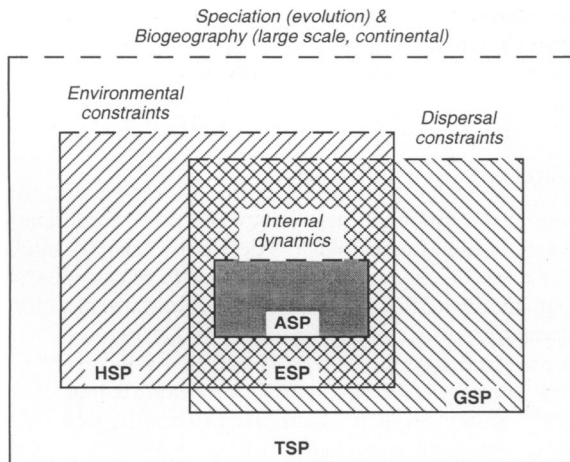
Fig. 2. Illustration of the relationships among species pools, and the processes that determine membership of each pool. Terminology for species pools follows Kelt et al. (1995). TSP: total species pool; GSP: geographical species pool; HSP: habitat species pool; ESP: ecological species pool. Both the GSP and HSP are subsets of the TSP, and their intersection set defines the ESP. We define ASP, the actual species pool of a community, as the subset of the ESP that results from internal dynamics.

At least two authors have attempted to identify distinct types of assembly rules that shape community structure. Brown (1981) differentiated external, physical factors from internal species interactions. He also suggested a potential mechanism underlying some assembly rules in his reference to the allocation of limited resources among coexisting species. His scheme did not, however, separate the factors that determine the potential colonists from those which actually colonise a site. In contrast, Keddy (1992) differentiated the availability of potential colonists from the ability of those species to survive in a particular habitat. His distinction between assembly and response rules alluded also to the idea that *patterns* of community change may differ according to the *direction* of community change. Unlike Brown, however, Keddy did not distinguish between external factors and internal processes. The two classifications highlight different determinants of community change, and a more fruitful scheme might combine the strengths of both.

We propose a terminology that groups the agents and factors of community assembly into three principal determinants: dispersal constraints, environmental constraints, and internal dynamics. Factors external to the community (dispersal and environmental constraints) are separated from internal processes (internal dynamics) and all three determinants define which subset of the total possible species pool actually occurs at a site (Fig. 2). In the terminology of Kelt et al. (1995), the *total species pool (TSP)* of a focal site is determined by evolutionary and large-scale biogeographical processes. A subset of the TSP, the *geo-*

graphical species pool (GSP) is able to disperse to the focal site and hence is available to colonise. A different subset of the TSP, the *habitat species pool (HSP)*, possesses traits which allow establishment and development under the environmental conditions at the focal site. In our scheme, the GSP is determined by dispersal constraints, whereas the HSP is determined by environmental constraints. Both the GSP and the HSP contain potential colonists, but only species which belong to both subsets will be available and capable of colonising the focal site. According to Kelt et al. (1995), the *ecological species pool (ESP)* is the intersection set of the GSP and the HSP. We define further an *actual species pool (ASP)* that is the subset of the ESP constrained by internal dynamics, and which constitutes the observable community (see also Zobel 1992). Species found alive at the focal site must belong to all five species pools, and hence only these species belong to the ASP. Differentiation of species pools based on the ecological processes that define membership allows the relative importance of the determinants to be assessed quantitatively (Kelt et al. 1995). Defining species pools, especially the GSP, is non-trivial in practice (e.g., Srivastava 1999). Comparisons among studies will be facilitated if pools are defined by ecological processes and scaled with reference to the organisms' dispersal abilities, lifespan, and the temporal and spatial extent of the study (e.g., Lancaster and Belyea 1997). Both Brown (1981) and Keddy (1992) disregarded dispersal constraints, but classified environmental constraints as "rules". We propose that the external constraints which limit membership of a community are fundamentally different from assembly rules that emerge from internal dynamics.

In the following sections, we summarise the evidence for assembly rules at various levels of community organisation, and then we examine how these rules interact with environmental and dispersal constraints. Illustrative examples have been selected from empirical and theoretical studies to emphasise the strengths of a multidisciplinary approach, and from a wide range of ecosystems and taxonomic groups to emphasise the broad ecological relevance of community assembly. Not all assembly rules covered in this review will necessarily apply to all communities, some rules may be redundant and others may not have been hypothesised yet. Environmental and dispersal constraints set the boundary conditions within which deterministic assembly rules must operate and these external processes should not be considered an alternative to, or independently of, internal dynamics. The challenge is to determine which assembly rules operate under different constraints, and how the characteristics of the organisms influence the expression of these rules.

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Internal dynamics

Internal dynamics encompass most of the existing assembly rules. Hitherto, most studies have examined rules operating within a trophic level; we also examine assembly rules operating across trophic levels and whole systems. We believe this approach is consistent with the broadest ecological definition of "community". In Table 1, we present some possible rules, their underlying mechanisms and resultant patterns of community structure as we have gleaned them from the literature. The astute reader will notice that we have classified the "rules" of some authors as patterns. Statement of a rule as the outcome of processes operating within the community emphasises the dynamic nature of community assembly, rather than static patterns of community structure. Further, this statement requires knowledge of underlying mechanisms, any one of which may lead to several community-level patterns. The patterns observed in community structure can provide clues to assembly rules, but cause-and-effect can be inferred only once the underlying mechanisms and their consequences are understood.

Table 1. Assembly rules, underlying mechanisms, and resulting patterns in communities, as stated in or implied by literature sources.

Rule and mechanism	Resulting pattern(s)	References
A community assembles such that:		
1. Resource utilisation within guilds tends to increase due to interspecific competition	1. Traits associated with resource competition are overdispersed; niche overlap is minimised	Diamond 1975, M'Closkey 1978, Hanski and Cambefort 1991a, Pacala and Tilman 1994
2. Resource utilisation across guilds or functional groups tends to increase due to interspecific competition	2a. Species tend to be drawn from a different functional group until each group is represented, and then the pattern repeats 2b. The proportion of species from different guilds remains constant	Fox 1987, Fox and Brown 1993, Wilson and Roxburgh 1994, Morris and Knight 1996
3. Spatial or temporal variance/co-variance tends to increase within guilds through mechanisms operating at establishment	3a. Intraspecific aggregation is greater than interspecific aggregation within guilds 3b. Traits associated with resource competition are underdispersed	Hanski and Cambefort 1991a, Frelich et al. 1993, Shorrocks and Sevenster 1995, Durant 1998
4. Per capita predation risk tends to decrease due to apparent competition among prey for predator refuges	4a. The surviving prey species is that which supports the largest population of generalist predator; traits associated with competition for predator refuges are overdispersed among prey 4b. Less competitive prey species can invade if the population of a superior competitor has been depleted by a specialist predator	Holt et al. 1994, Grover 1994
5. Total predation pressure tends to increase and per capita predation risk to decrease, through exploitation competition among predators for prey and apparent competition among prey	5. Predator-prey ratios remain constant	Holt 1977, 1984, Jeffries and Lawton 1984, 1985, Mithen and Lawton 1986
6. ?	6a. The proportion of species in each trophic level changes non-randomly 6b. The proportion of species in each trophic level remains constant	Heatwole and Levins 1972, Hanski and Koskela 1977, Koskela and Hanski 1977, Mikkelson 1993, Wardle et al. 1995
7. Spatial aggregation of prey (or host) populations tends to increase due to localised predation (or parasitism)	7. Prey (or host) populations are spatially aggregated, and predator-prey ratios are highest around the margins of these patches	Hassell et al. 1994, Maron and Harrison 1997
8. A greater proportion of available energy and nutrients is retained in the biomass, due to selection of species which cycle energy and nutrients most efficiently	8a. Generalist species tend to be replaced by specialist species 8b. Small, short-lived species tend to be replaced by larger, longer-lived species	Ulanowicz and Abarca-Arenas 1997, Loreau 1998
9. Non-random spatial patterns of communities tend to develop due to positive feedback involving local alteration of environmental constraints	9. Communities are spatially organised in a non-random pattern	Swanson and Grigal 1988, Wilson and Agnew 1992, Jones et al. 1994, 1997

Within trophic levels

Most studies on community assembly have considered coexistence of species restricted to one trophic level or taxonomic group. Much of this work was reviewed recently by Weiher and Keddy (1995b), and we will not review these studies in depth. Weiher and Keddy identified two major approaches to community pattern detection: species-based and trait-based approaches. They concluded that testing for non-randomness of species associations helps to detect community patterns, but is of little value in defining the rules that generate those patterns. In contrast, trait-based and functional group approaches facilitate generalisations and give clues to the mechanisms that underlie rules. Weiher and Keddy (1995b) proposed a qualitative model for trait patterns, in which traits related to interspecific competition for space or resources (internal dynamics) become overdispersed during assembly (i.e., become less similar than expected by chance), while traits subject to environmental constraints become underdispersed (i.e., become more similar than expected by chance). Their model suggests also that the prevalence of trait overdispersion decreases as the spatial scale of the investigation increases. Note, however, that analyses of trait patterns should control for phylogeny, which may influence trait dispersion independently of any functional community explanation (Silvertown and Dodd 1996). The scaling phenomenon arises from the size, and perhaps taxonomic diversity, of the TSP (Weiher and Keddy 1995b). Both the GSP and the HSP also increase in size with the scale of the investigation, but coincidentally become more spatially heterogeneous. We would expect, therefore, that both the prevalence of historical effects (dispersal constraints) and the coarseness of environmental filters (environmental constraints) will increase with the scale of the investigation.

Trait overdispersion has been documented directly through analysis of traits and indirectly through analysis of guilds or functional groups. Authors differ in their use of the terms guild and functional group (see Simberloff and Dayan 1991, Kelt et al. 1995), but all assume implicitly that species potentially compete for the same resources within but not between functional groups. Members of different groups are unlikely to prey upon one another, as is implicit in our discussion of across trophic level processes, below. The concept of limiting similarity supposes that, to coexist, species must differ by some minimum amount (e.g., MacArthur and Levins 1967). For example, Armbruster (1986) examined the pollination ecology and floral morphology in the genus *Dalechampia* and found that coexisting species were less similar than expected by null models, suggesting that competition for pollinator services was minimised. Diamond (1975) proposed that, within a guild of fruit-eating birds, the combination of species present in a community at any time will max-

imise resource utilisation, yet allow each species to persist and reproduce (Table 1, Rule 1). Although this formulation of the rule is for static communities, a temporal component is implicit. M'Closkey (1978) extended Diamond's proposal to seed-eating rodents, and concluded that assembly sequences "maximally saturate the resource space". The corresponding pattern through time would be an assembly trajectory in which niche overlap is always minimised, e.g., by drawing species from different body size classes (Table 1, Pattern 1) as suggested in communities of fruit-eating pigeons (Diamond 1975) and dung beetles (Hanski and Cambefort 1991a). Fox (1987) proposed that each species entering a community is likely be drawn from a different functional group until each group is represented, and then the rule repeats (Table 1, Pattern 2a). This is more general than Diamond's species-specific pattern in that it specifies the functional group from which the species should come, rather than the identity of the species in the assembly (Fox and Brown 1993). This "favoured states" rule is similar to the "guild proportionality" rule of Wilson and co-workers (e.g., Wilson and Whittaker 1995) (Table 1, Pattern 2b); whereas Fox's rule is based on numbers of species, Wilson's is based on proportions. Empirical evidence for selection of different guilds includes communities of granivorous rodents (Fox and Brown 1993) (but see Stone et al. 1996) and plant communities of grasslands (Wilson and Roxburgh 1994) and salt-marshes (Wilson and Whittaker 1995).

Patterns of trait overdispersion, such as limiting similarity and favoured states, can be explained theoretically by resource dynamics (Pacala and Tilman 1994, Morris and Knight 1996). According to the R^* rule of resource competition (Tilman 1985), a species can invade only if it depletes resources to a lower equilibrium concentration than that maintained by the resident species. The logical outcome of the R^* rule is that a greater proportion of available resources is consumed or monopolised with the invasion of each new species (Table 1, Rules 1 and 2). In a homogeneous environment, the R^* rule inevitably results in competitive exclusion. In a heterogeneous landscape, in which environmental constraints (but not the HSP) vary across space and time, the theory predicts that coexisting species exhibit overdispersion of traits associated with competition for resources (Table 1, Pattern 1), a pattern consistent with limiting similarity (Pacala and Tilman 1994). For example, a large fruit pigeon is more likely to be joined by a smaller member of the same guild, rather than by one which feeds on the same size fruits and perches on the same size branches (Diamond 1975). The theory has received some empirical support from studies of animals using distinctly different resources and less support from studies of plants competing for the same inorganic resources. A community that consists of one species from each guild fills a greater proportion of resource space than does a community

that consists of two or more species from the same guild (Morris and Knight 1996). Each successful invader depletes its favoured resource to a lower equilibrium concentration, so that the next invader will probably come from a guild that favours a different resource (Morris and Knight 1996). If species are distributed equally among guilds, the outcome is a pattern of favoured states in which each guild is represented equally in the ASP (Table 1, Pattern 2a). For example, a community of small mammals is more likely to include a granivore, a herbivore, and an insectivore rather than two or more species from any one of these guilds. The mechanistic approach of resource dynamics makes explicit the relation of specific traits to competitive ability, so predictions can be made about whether the rule will operate for particular species under particular environmental constraints. We will return to this question of environmental contingency in later sections.

An alternative mechanism for coexistence of members of the same guild is spatial (or temporal) aggregation into patches dominated by single species (Atkinson and Shorrocks 1981, Hanski 1981, Shorrocks and Rosewell 1987, Ives 1988, Frelich et al. 1993). A Markov simulation model of temperate forest development showed that an initially random, mixed distribution of *Acer saccharum* Marsh. and *Tsuga canadensis* (L.) Carr. could evolve to a patchy distribution of single-species stands, without invoking any underlying differences in soils, topography, or disturbance (Frelich et al. 1993). The formation of these persistent spatial patterns, also observed in the authors' Michigan study area, depended on the chance or edaphic juxtaposition of more than one tree of the same species, and a subsequent negative effect on establishment of the competitor species. Potentially competitive insect species that live on patchy and ephemeral resources, such as fungal fruiting bodies or dung pats, can coexist because the adult female deposits her eggs in high density masses (Hanski and Cambefort 1991b, Shorrocks and Sevenster 1995). The resulting pattern of spatial variance/covariance (Table 1, Pattern 3a) ensures that an individual is more likely to experience competition from a sibling than from an individual of another species (Shorrocks and Sevenster 1995). Potential competitors may also coexist by partitioning resources in time as well as in space. Durant (1998) suggests that the competitively inferior cheetah is able to coexist with other carnivores on the Serengeti plains by seeking spatiotemporal refuges in an environment in which the distribution of superior competitors is dynamic. Theoretically, a low degree of temporal overlap favours the coexistence of species that use resources efficiently and exhibit a high degree of similarity (Loreau 1992). Hence, in contrast with patterns predicted from resource competition (Table 1, Patterns 1, 2a and 2b), temporal segregation of resource use should lead to underdispersion of traits among species (Table 1, Pattern 3b). We tentatively propose a new assembly rule that spatial and temporal variance/covariance tends to increase with the invasion of each new species within a guild (Table 1, Rule 3). The resulting patterns observed within guilds are greater relative strength of intraversus inter-specific aggregation in time or space (Table 1, Pattern 3a), and trait underdispersion (Table 1, Pattern 3b).

Across trophic levels

How does the trophic structure of the community develop? In multi-trophic level systems, a temporal element is clear in that resources or prey must become established or make frequent colonisation attempts before their predators can invade successfully (unless the predator is also cannibalistic, e.g., Blaustein et al. 1996). Note that we define predators and prey in the broadest ecological sense to include representatives of two or more trophic levels, such that energy flows between trophic levels. Predators could be carnivores or herbivores, true predators, parasites, parasitoids or grazers; prey are any organisms that are alive when the predator attacks. Other consumers include saprophytes and detritivores which consume inanimate resources such as detritus. When interactions occur across trophic levels, more than one rule may apply simultaneously or different rules may apply in different situations. These contingencies make it difficult to unravel a posteriori what assembly rules formed extant communities. Some progress has been made on the theoretical front.

A theoretical rule analogous to the R^* rule (Tilman 1985) applies specifically to predation (Holt et al. 1994). The mechanism underlying this so-called P^* rule (Table 1, Rule 4) is apparent competition among prey for predator-free refuges. Among prey limited by a common, generalist predator, the winning species should be that which can support the largest population of predators (Table 1, Pattern 4a). As with the R^* rule, empirical support for the P^* rule is equivocal (Bonsall and Hassell 1998). When prey are both limited by a resource and subject to predation, theory predicts that Rules 1, 2, and 4 do not apply universally, but have limited domains of applicability (Grover 1994, Holt et al. 1994). Resource-limited prey subject to apparent competition via a shared predator may coexist, or either prey species may exclude the other, depending on the interaction between assembly rules, resource supply, and the invasion sequence (Holt et al. 1994). In the special case of specialist herbivores feeding on nutrient-limited plants, the theory predicts that less competitive plants can enter the community (Table 1, Pattern 4b) only if the population of the resident, superior competitor has been depleted by prior invasion of its specialist herbivore (Grover 1994). In this case, species composition and food web structure depend on the interaction

of assembly rules with the order of species invasion (Grover 1994). We are unaware of any empirical studies that have tested these predictions explicitly. We defer to following sections further discussion of the interaction of assembly rules with environmental and dispersal constraints. The salient point here is that the interaction of an assembly rule operating at one level of community organisation (say, within a guild) with a rule operating at another level of organisation (say, across trophic levels) may lead to patterns of community structure which could not be predicted from either rule working independently.

Interaction between rules operating at different levels of community organisation can, in theory, explain some reported patterns of predator-prey ratios. Studies in which species are classified either as predators or as prey report that the ratio of predators to prey is roughly constant across communities (e.g., Briand and Cohen 1984, Jeffries and Lawton 1985). The veracity of constant predator-prey ratios (Table 1, Pattern 5) has been challenged on the basis that lumping of species into such broad categories is inappropriate (Pimm et al. 1991, Hall and Raffaelli 1993), and that appropriate null models are difficult or impossible to construct (Wilson 1996) when only part of the ESP is known (e.g., Colwell and Winkler 1984). We suspect that irrefutable evidence for or against constant predator-prey ratios requires direct observations of communities over time. Despite the ongoing controversy over their existence, if such patterns do exist, they could arise through a mechanism involving apparent competition (Holt 1977, 1984). Jeffries and Lawton (1984, 1985) argue that the number of prey species able to coexist with a set of generalist predators is constrained by competition amongst prey for predator refuges (enemy free space). If predator richness is determined by prey richness, the result will be a broadly constant ratio of predators to prey (Table 1, Pattern 5). Invasion and stable coexistence of prey are favoured if species differ in traits such as body size, feeding habits, movement patterns, and anti-predator defences. As with Pattern 1, prey species exhibit overdispersion of traits (Table 1, Pattern 4a), but in this case the traits are associated with competition for predator refuges rather than resources. A computer simulation model of food web development (Mithen and Lawton 1986) based on apparent competition produced webs that converged on an approximately constant ratio of predator to prey species and the frequency distribution of particular values was similar to that reported for real food webs. How the mechanisms underlying this pattern should be stated formally as an assembly rule is unclear, but may involve a balance between increased resource use by predators and reduced predation risk to prey via competition among prey for predator refuges (Table 1, Rule 5). For this rule to work in nature, the whole prey trophic level must be predator-limited (Hairston et al.

1960, Holt 1977, 1984, Mithen and Lawton 1986) so patterns in communities that deviate from the expected do not necessarily refute the rule.

Two general patterns in the relative abundance of different trophic levels may exist (Table 1, Patterns 6a and 6b). In the first pattern, the proportion of different species in each trophic level changes non-randomly, i.e. some trophic categories always have a greater-than-average probability of being added to, or removed from, a community (Table 1, Pattern 6a). Empirical evidence comes from a variety of sources: During the short-term assembly of insect communities in dung pats, the proportion of predatory species is low initially, but increases over time (Hanski and Koskela 1977, Koskela and Hanski 1977). A decomposer food web in sawdust assembled by the sequential addition of species along different food chains: bacterial feeders first, then fungal feeders, saprophages, and their predators (Wardle et al. 1995). On longer and larger scales, after the volcanic eruption and subsequent devastation of Krakatau, the first animal colonists of the new islands were scavengers feeding on debris washed up by the sea, then followed omnivores, later herbivores, and lastly predators and parasites (Dammerman 1948, cited in Heatwole and Levins 1972). The sequences differ among studies, adding to the difficulty of predicting which particular trophic levels have the highest (or lowest) probability of addition to, or removal from, the community. In the second pattern of food web assembly, the proportion of different species in each trophic level may remain constant (Table 1, Pattern 6b). Using five different data sets of inferred temporal sequences based on biogeographic distributions, Mikkelson (1993) concluded that a homogeneous trophic distribution was the most likely temporal sequence. These studies (and others) describe changes in trophic structure over ecologically meaningful time scales, but none provides insight into what assembly rules and underlying mechanisms might produce these patterns (Table 1, Rule 6). The difficulty may lie in teasing apart the relative importance of dispersal constraints versus internal dynamics. The temporal pattern in trophic structure may reflect the order of species arrival and changes in the GSP more strongly than assembly rules operating across trophic levels. Mathematical modelling is a potentially powerful method of exploring the patterns generated by mechanistic rules in multi-trophic level communities (e.g., Post and Pimm 1983, Drake 1990, Law and Blackford 1992, Luh and Pimm 1993, Morton et al. 1996), but theoretical predictions about the development of trophic structure in communities are lacking. New examples, or re-analysis of old examples, in which membership of the GSP is constant, or any changes known, will help to elucidate the rules and mechanisms underlying temporal patterns in trophic structure (e.g., Spencer and Warren 1996, Warren 1996). We will return to the question of dispersal contingency in later sections.

Internal dynamics that operate across trophic levels, as with guilds, can lead to the formation of spatial patterns even across continuous habitats. Variance-covariance dynamics can be important in communities where non-random spatial searches of aggregated prey by predators or parasitoids leads to frequency-dependent predation and maintains high diversity of prey species (Murdoch and Oaten 1975, Hanski 1981). Reaction-diffusion models have been used to explore spatial pattern formation of predator-prey and host-parasitoid systems (Hassell et al. 1994), but until recently few empirical studies have explored the consequences in natural communities. In a field experiment where experimental populations of tussock moth larvae were created, Maron and Harrison (1997) showed that parasitoids could suppress moth outbreaks, but the suppressive effect decreased with increasing distance from the source of the outbreak. The results support theoretical predictions that a strong predator which ranges slightly further than its prey will prevent spread of the prey beyond a sharply defined patch of high density. The implications of spatial pattern formation for the trophic relationships of natural communities are just beginning to be explored so, again, no assembly rules have been formulated. We propose tentatively that during an assembly sequence, distributions of prey (or hosts) will become more clumped with invasion of predators (or parasitoids) having a larger home range (Table 1, Rule 7). The resulting pattern observed in a community would be high intra-specific aggregation of the prey or host (Table 1, Pattern 7). Whether the predator (or parasitoid) also becomes aggregated depends on its range size relative to that of the prey (or host).

Within ecosystems

Do assembly rules act at the ecosystem level? This question takes community assembly beyond the more traditional subdisciplines into the realm of ecosystem ecology (Fig. 1). Part of the answer can be gleaned from consumer-resource based rules, similar to those that apply within and across trophic levels (Table 1, Rules 1, 2, and 4). Loreau (1995) analysed the whole-system effect of adding consumers to food webs and concluded that energy and matter flow through the system increase if consumers reduce nutrient recycling times. Ulanowicz and Abarca-Arenas (1997) suggest that selection of species which use resources more efficiently than existing species channels matter and energy flow along the most efficient routes and increases the proportion of available energy and nutrients retained in the biomass (Table 1, Rule 8). For example, the carnivorous macrophyte *Utricularia* supplements marginal or insufficient uptake of dissolved inorganic nitrogen by preying on zooplankton, which

in turn feed on periphyton growing on the macrophyte. An increase in the biomass of *Utricularia* provides more substrate for the periphyton, which provides more food for the zooplankton, which supplements the nitrogen intake of *Utricularia* (Ulanowicz 1995). The system of flows across trophic levels results in a positive feedback that tends to promote the coexistence of the three species when nutrient-limited. In a broader context, the patterns resulting from Rule 8 might include temporal shifts from generalist to specialist species (Table 1, Pattern 8a) and from small to large species (Table 1, Pattern 8b, Ulanowicz and Abarca-Arenas 1997).

Resource-based rules, when applied to abiotic resources such as inorganic nutrients or space, imply an autogenic alteration of environmental constraints: according to the R^* rule, the winner is that species which can deplete the abiotic resource to the lowest level. There are other ways, however, in which an organism may alter its local environment, thereby promoting certain trajectories of community change. In many boreal mires, terrestrial and aquatic communities form a regular, alternating sequence of ridges and pools, oriented perpendicular to the line of water flow. These distinctive patterns apparently do not originate from any underlying geological pattern, but arise as peat accumulates. Swanson and Grigal (1988) proposed a mechanism that depends on an inherent difference in hydrological properties, such that water tends to pond behind ridges and to be transmitted through pools. Positive feedback ensues because the plant species which form ridges tend to spread from existing centres preferentially across the line of water flow and on to patches that are free of ponded water. Under certain conditions, this feedback between hydrology and plant community leads to the formation of distinct ridge-and-pool patterning (Swanson and Grigal 1988). Wilson and Agnew (1992) give several other examples of how certain plants alter the local environment to their own benefit, creating sharp boundaries in the abiotic environment as well as in species composition. Ecosystem engineers of all taxonomic persuasions (Jones et al. 1994, 1997) change the environmental constraints, with marked consequences for physical conditions, coexisting species, and future colonists. Any assembly rule at this level must be highly speculative, but we propose that distinct communities tend to develop in non-random spatial patterns, due to positive feedback involving local and autogenic alteration of environmental constraints (Table 1, Rule 9). The resulting pattern is spatial organisation of communities (Table 1, Pattern 9). We will return in a later section to the question of how a rule that emerges from internal dynamics can involve environmental constraints.

Table 2. Level of organisation and underlying mechanisms of hypothesised assembly rules. See Table 1 for statements and patterns corresponding to rule numbers.

Level of organisa-tion	Underlying mechanism	
	Resource dynam-ics	Spatial organisa-tion
Within trophic levels	1, 2	3
Across trophic levels	4, 5, 6	7
Within ecosystems	8	9

Why are there so many assembly rules?

"So it follows that productivity is increased, the quality of the products is improved, and the process is simplified when an individual sets aside his other pursuits, does the one thing for which he is naturally suited, and does it at the opportune moment." – (Plato: 60)

In the preceding section, we identified two classes of mechanism, resource dynamics and spatial organisation, that underlie assembly rules operating at all three levels of community organisation (Table 2). Of the rules listed in Table 1, those that implicitly or explicitly invoke resource dynamics as the underlying mechanism have received the most attention. Indeed, when formulated in a general way, resource-based rules recall Plato's Principle of Specialisation. The emphasis on resources may reflect the prevailing and historical bias in community ecology and is not necessarily a true representation of the general principles operating in communities. Alternatively, resource dynamics may indeed be fundamental to the way in which communities assemble, and many of the assembly rules outlined in Table 1 may be simple corollaries of a more general principle expressed at different levels of organisation, e.g., within versus across trophic levels. Hence, the same principle based on resource dynamics might lead to niche heterogeneity within a guild where resources are limiting (Table 1, Rule 1), and might lead to constant predator-prey ratios where prey are predator-limited (Table 1, Rule 5). Taken independently, the $R*$ and $P*$ rules (Table 1, Rules 1, 2, and 4) imply that the community will use resources more efficiently, and accumulate more biomass as new species invade: the winning prey capture the most resource, or they support the highest number of predators. These outcomes appear to be consistent with maximal principles which apply to whole systems (Table 1, Rule 8), but when species from different trophic levels enter the community sequentially, resource utilisation may alternately increase and decrease (Grover 1994). The potential interaction of rules operating at different organisational levels highlights the importance of indirect effects and the need to look at community patterns across trophic levels and whole systems. Studies which search for a particular rule by looking at species composition at one level only may miss a crucial interaction.

Spatial dynamics is another mechanism underlying assembly rules that operate alongside resource dynamics at every level of community organisation (Tables 1 and 2). Is there any interaction between resource-based and spatially based rules? Ulanowicz and Abarca-Arenas (1997) presented an analysis based on information theory which suggests that an ecosystem has an inherent propensity to grow in biomass and develop in information content (which might include non-random spatial and temporal distributions of species). Jorgensen (1992) argues that the tendencies for ecosystem organisation and system biomass to increase over time can be integrated into an "ecological law of thermodynamics", whereby an ecosystem tends to move away from thermodynamic equilibrium in response to a supply of high-quality energy. Such holistic maximal principles have been criticised because they do not provide a mechanism for selection at the community level (Wilson 1997). The paradox can be resolved, however, if communities are organised into spatially aggregated units that differ in lifetime reproductive success (Wilson 1997). Within each unit, genotypes are selected for high resource use intensity; between units, genotypes are selected for basic reproductive rate (Loreau 1998). If between-unit selection is slower than within-unit selection, the combined process can resemble evolution in which resource use is maximised at the community level (Loreau 1998). Hence, selection for resource use at the community level (Table 1, Rule 8) depends on spatial pattern formation of constituent populations (Table 1, Rules 3 and 7) and on resource dynamics within and across trophic levels (Table 1, Rules 1, 2, and 4).

Throughout the discussion of assembly rules, we emphasised functional controls on the composition of the community. Which is the appropriate unit for selection by assembly rules, the species or the functional group? Keddy (1992) has argued that the determinants of community assembly operate on traits rather than species, and one might consider functional groups as collections of traits. A functional approach is appealing, but in multi-generational studies we must also consider population dynamics, i.e., a reproductively isolated population must maintain a minimum size to remain viable. It is difficult to assess in terms of population dynamics the viability of a functional unit, which might include several different, reproductively distinct genotypes. Therefore, it is possible that the functional unit differs from the unit of selection (sensu Wilson 1997). We may be able simply to sum the fitness of all genotypes to estimate the fitness of the functional group as a whole. But at some point it is necessary to deal with genotypes, not functional groups.

Are the rules listed in Table 1 sufficient and complete, and how do they interact with one another? Some

gaps are immediately obvious. For example, Pattern 6a regarding the trophic structure of communities (proportional representation of species in different trophic levels) has empirical support but, as yet, no rules or underlying mechanisms that might produce such a pattern have been proposed. Further, interspecific interactions have been limited to competition and predator-prey dynamics (sensu lato) whereas interactions such as mutualisms and symbioses have not been incorporated into assembly rules. Another challenge is that we do not know under what circumstances rules based on different mechanisms or operating at different levels (Table 2) come into play. One possible way forward is to consider the traits of the species involved. For example, if a group of species all exploit the same type of resource (e.g., inorganic energy and nutrients for plants, fungal fruiting bodies for *Drosophila*), then species might differentiate themselves spatially and temporally (Table 1, Rule 3), rather than functionally (Table 1, Rule 1). As another example, the extent to which environmental constraints are altered autogenically (Table 1, Rule 9) might depend on the mobility and life-history strategy of the organisms. Sessile, long-lived organisms such as trees, for example, are more likely to alter microclimate and soil chemistry than are flying insects. Clearly, the contingencies of environmental and dispersal constraints within which assembly rules operate must also be considered.

Environmental constraints

The abiotic environment influences community assembly by restricting which species can establish at the site (i.e., membership of HSP, Fig. 2), and by constraining the function of successful colonists. The environment may be compared with a filter, or hierarchy of filters, that deletes species by selecting for or against particular traits (e.g., Weiher and Keddy 1995a, Poff 1997), which become underdispersed (sensu Weiher et al. 1998). Change in environmental constraints may be directional (e.g., the exposure of land surfaces with marine regression), or locally catastrophic (e.g., landslides). Either of these types of change may lead to local extinctions and range contractions of previously successful colonists, or invasions and range expansions of species excluded previously. In the case of locally catastrophic change, extinctions are non-selective in that species remaining do not necessarily conform any more closely to the assembly rules than those species that have gone extinct. Even if the same set of rules apply, whether the original community trajectory will be repeated may depend on whether all original species are available for reinvasion (Law and Morton 1996, Samuels and Drake 1997). The preceding discussion of internal dynamics assumed that environmental con-

straints have remained constant (stayed essentially unchanged, sensu Grimm and Wissel 1997) for long enough that communities approach equilibrium. The outcome of many of the resource-based rules listed in Table 1 depend as much on the availability of abiotic resources and space as on species interactions (Tilman 1985, Loreau 1992, Holt et al. 1994, Morris and Knight 1996, Ulanowicz and Abarca-Arenas 1997). Hence, even in systems at equilibrium, environmental constraints influence species interactions and the expression of assembly rules through the availability of space, energy, and nutrients and the consistency of this supply. Correspondence between species traits and the outcome of assembly rules may explain why habitat templets have proved so successful in mapping species composition to habitat type (for a review, see Southwood 1988).

Interaction of environmental constraints with internal dynamics

Habitat templets often include an axis of increasing environmental stress or harshness, and an axis of increasing disturbance (e.g., Grime 1979, Hildrew and Townsend 1987, Southwood 1988). In harsh or variable environments, deterministic processes such as predation and competition traditionally have been considered weak or dynamically trivial compared with abiotic or non-equilibrial processes (Hutchinson 1961, Connell 1975, Menge 1976, Grime 1979, Huston 1979). In highly disturbed habitats, temporal variation is a characteristic feature of the abiotic environment (e.g., streams subject to frequent spates or annual droughts, or grasslands subject to periodic fire), and magnitude and periodicity of change are as important as the average in defining the environmental constraints. The constraints are stable in that only those species which can persist in the variable environment are members of HSP. Distinguishing between catastrophic environmental change and inherent environmental variability is clearly a question of scale and could perhaps be made with reference to the organisms' generation times and the spatial extent of the community (e.g., Lancaster and Belyea 1997). Assembly rules with an underlying competitive mechanism (e.g., Table 1, Rules 1 and 2) may be dynamically trivial in variable environments or the nature of competition may change, e.g., from competition for nutritional resources to competition for space in disturbance-free refugia. Hence, stochastic events may interrupt or weaken species interactions, but need not preclude or diminish the importance of deterministic processes in community structure (Chesson and Huntly 1988, 1997). Exceptions to the harsh-benign rule are also known (e.g., Lancaster 1996) and environmental heterogeneity may allow persistence of competitors through storage effects (Warner and Chesson 1985,

Chesson and Huntly 1997). Assembly rules involving increased efficiency of nutrient cycling (Table 1, Rule 8) may continue to operate in harsh environments. Leonard et al. (1998) provide compelling evidence that the harshness of physical processes dictate whether intertidal communities are structured primarily by top-down or bottom-up forces. Hence, environmental constraints may influence the relative importance and interactive effects of assembly rules, but do not necessarily eliminate their role in structuring communities.

Autogenic alteration of the local environment (Table 1, Rule 9) is another way in which environmental constraints interact with assembly rules. One of the key features of this rule is that changes to environmental constraints are induced by the organisms themselves, not imposed by external forces. In some cases, inherent variability of the abiotic environment may be dampened. Dense beds of riverine macrophytes, for example, can reduce the magnitude of flow variations and increase sedimentation (e.g., Gurnell and Midgley 1994, Sand-Jensen and Mebus 1996). In other cases, the habitat may become increasingly harsh, excluding species which would otherwise compete with the instigator of the change. *Sphagnum* mosses, for example, alter soil chemistry and hydrology to such an extent that many previously extant species are excluded (e.g., van Breemen 1995). Hence, the autogenic alteration of environmental constraints may help to induce a directional change in the community.

Dispersal constraints

It is implicit in our discussion so far that a continuous and unlimited supply of new species is available to invade, or attempt to invade, a community. In reality, that supply of hopeful invaders (the GSP) is only a subset of the TSP (Fig. 2) and is not static over time. Many of the assembly rules listed in Table 1 also assume implicitly that species invasions are independent and are separated by a sufficiently long period of time for the community to reach equilibrium before the next invasion. These simplifying assumptions may facilitate the development of theoretical models, but empirical ecologists must embrace the complexities of real world situations.

Determining membership of the GSP for empirical studies of community assembly is difficult, because regional species checklists (i.e., a sum of ASPs) may over- or under-estimate the true GSP (Srivastava 1999). In addition to the problems of enumeration, there are more subtle difficulties in defining the timing and sequence of species arrival at a site. Dispersal is contingent upon a suite of historical (e.g., Davis 1983) and local (e.g., Johansson and Nilsson 1993) factors and cannot be predicted from species-specific traits alone.

Dispersal of some plants, animals, and fungi may be aided by, or dependent upon, close physical association with other species (e.g., Threlkeld et al. 1993, Chambers and MacMahon 1994, Marshall 1996) so arrival of co-dispersers may not be independent. The constraints of dispersal across space may be avoided by producing banks of dormant propagules that can remain viable for hundreds of years (Thompson 1987, Hairston et al. 1995). Species with such long-lived propagules may remain part of the GSP for long periods in which they have been excluded from the HSP, but a change in environmental constraints may allow rapid establishment. For example, many potential colonists of ephemeral pools, including some Crustacea and Protozoa, have a desiccation-resistant resting stage and may remain dormant in the sediments until seasonal rains fill pool basins (Hildrew 1985, Hairston 1996, McGrady-Steed and Morin 1996). Storage effects may exist also for species which display temporal fluctuations in recruitment success and have long-lived adults (e.g., Warner and Chesson 1985, Chesson 1994). These species may be persistent in the community, but be incapable of dispersal most of the time. Our knowledge of the independent or co-dispersal abilities of many species, and of the longevity of resting stages, is incomplete. So too is our understanding of how species disperse across real landscapes. This ignorance need not preclude advances in community assembly, but the most enlightening empirical studies are likely to be at sites where dispersal constraints are minimal (e.g., Blaustein and Margalit 1996), well-known (e.g., Kelt et al. 1995), or can be controlled directly (e.g., Drake et al. 1993).

Interaction of dispersal constraints with internal dynamics, and priority effects

Variations in the order of species' arrivals, through temporal variations in the membership of GSP or chance events during dispersal, can strongly influence community assembly, as demonstrated in numerous empirical and theoretical studies (Morin 1984, Barkai and McQuaid 1988, Drake et al. 1993, Grover 1994, Blaustein and Margalit 1996, Law and Morton 1996, Wilbur 1997). Some of the earlier modelling studies (Post and Pimm 1983, Drake 1990) suffered from technical flaws which the authors admit may undermine their conclusions (Morton et al. 1996), but studies using robust methods corroborate this phenomenon. We agree with Grover (1994) that historical contingencies, such as priority effects, result from interactions between the order of species invasions (i.e., dispersal constraints) and assembly rules. For example, larval mosquitoes and toads compete for prey in temporary pools, and both species may dominate different pools in the same complex (Blaustein and Margalit 1996). The order of arrival

of the competitors in a particular pool depends on chance, but alternative communities arise because the first colonist prevents the subsequent establishment of its competitor (Table 1, Rule 1). Hence, alternative community structures arise only if more than one invasion sequence is possible, and if early invaders are involved in interactions that promote or prevent the subsequent establishment of another species. We assume implicitly that new potential colonists continue to arrive provided the TSP is not exhausted (Cornell and Lawton 1992), in which case communities will be unsaturated.

How many alternative community states can arise from the same set of potential colonists? Modelling studies agree that the number of alternative communities increases with size of the ESP (Luh and Pimm 1993, Law and Morton 1996), but predictions on the maximum number of alternative states range from eight (Luh and Pimm 1993) to four or fewer (Law and Morton 1996). Different predictions may depend on assumptions about the species pool or methods of computation (Morton et al. 1996) and on the assembly rules operating on potential colonists. Luh and Pimm (1993) described results for species combinations arising with or without assembly rules. Other authors provide less insight into the internal dynamics of their models. Internal dynamics are important and assumptions about energetic requirements and the body-size ratios of predators and prey should be treated equally with assumptions about the species pool and mathematical stability, rather than be relegated to an appendix (e.g., Law and Morton 1996). Understanding how rules govern the assembly process is fundamental to understanding the importance of priority effects.

Recent modelling studies suggest that rates of species invasions so high that the system never reaches equilibrium may disrupt the operation of assembly rules. Simulated assembly of communities with a slow invasion rate (one species per 100 years) produced several alternative community states dominated by those species which arrived early in the sequence (Lockwood et al. 1997). Historical effects were reduced and species composition was more labile when invasion rate was increased by two orders of magnitude (one species per year), so that the system failed to reach equilibrium before the next invasion (Lockwood et al. 1997). Interestingly, historical effects which arose during assembly of an aquatic mesocosm community appeared even though equilibrium was never reached (Drake et al. 1993, 1994). Are theory and empirical results incompatible? Part of the answer may lie in the match between the rate of invasion and the rate at which species are selected by assembly rules. Hraber and Milne (1997) developed an individual-based, genetically explicit model in which the influx of new species is analogous to genetic mutation, and the outcome of species interactions (predation, competition, mutualism) is analogous

to selection of genotypes with particular traits. Simulation results suggest that guilds can assemble only if new species are added more slowly than species are selected or excluded by interspecific interactions. Hence, there is a threshold invasion rate below which species are selected and communities evolve to an orderly state, and above which alternative species occur with equal likelihood and communities collapse to a disorderly state. These results suggest that simultaneous invasions, e.g., when two or more species co-disperse or are released from dormancy simultaneously, may weaken the assembly rules. The implications of these modelling studies are fascinating, but testing these ideas empirically is daunting (though perhaps not impossible).

Dispersal constraints may restrict the rate at which conspecifics arrive in a community and this may also influence the expression of assembly rules. In marine intertidal systems, for example, settlement rates of barnacle larvae are determined by the effect of oceanic circulation patterns on onshore transport and the density of kelp beds that harbour predators of zooplankton. Communities with very high settlement rates of barnacles may be structured by predators, whereas low settlement rates themselves can limit community structure and dynamics in other habitats (Roughgarden et al. 1987). The idea that communities are continuously invaded by potential colonists and that this invasion rate itself might influence community assembly has not been explored in detail.

Interactions amongst internal dynamics, environmental and dispersal constraints

Can assembly rules operate under all conditions? So far, we have portrayed community assembly as a progressive change in community structure, reliant on the introduction of new species and subsequent selection of those species able to establish and coexist. The trajectory has direction: as time passes, the total biomass and the spatial organisation of the community tend to increase (Table 1, Patterns 8 and 9). In contrast, species richness might increase or decrease because the invasion of particular species may comply with the assembly rules yet cause the extinction of several extant species. Directionality in community assembly may be lost if the invasion rate exceeds the rate of species selection (Hraber and Milne 1997, Lockwood et al. 1997). An analogous loss of directionality may occur if the rate of non-selective species extinction exceeds the rate of selection by assembly rules, as might occur with catastrophic change in environmental constraints. We might speculate that assembly rules occur only if the selective process occurs at a rate greater than that at which species are added to the community, and less than that at which species are deleted non-selectively.

Do different determinants predominate at different stages of community assembly or disassembly? By "disassembly" we mean a break-down of the interactions amongst constituent species, rather than a simple decrease in species richness (although the two patterns may be coincident). Holling (1992) suggested a four-stage cycle of terrestrial succession that includes both assembly and disassembly: (1) *Exploitation*, pioneer species rapidly colonise a recently disturbed patch, (2) *Conservation*, total biomass and community organisation increase, (3) *Release*, biomass is suddenly released by agents either internal (e.g., insect pests) or external (e.g., fire) to the community, and (4) *Reorganisation*, nutrients bound in organic detritus from the collapsed community are made available for exploitation by pioneers in the next cycle. We would expect that most assembly rules operate primarily during Exploitation and Conservation, and account for the slow increase, for example, in system biomass and non-random spatial distributions (e.g., Table 1, Rules 3, 7 and 8). Rules may operate also during Reorganisation, but predominantly on the decomposer or microbial parts of the food web. Exploitation and Conservation stages may be characterised by increased resistance to invasion, as suggested theoretically by Lotka-Volterra models (Law and Morton 1996) and empirically by palaeoecological evidence that forest communities develop an "inertia" causing vegetation changes to lag behind environmental changes (Smith 1965). We might speculate that the Exploitation stage, where inertia is weak, is most sensitive to interactions between the invasion sequence (dispersal constraints) and assembly rules, so that priority effects and alternative stable states may arise. We might speculate also that the extent to which a community increases in spatial organisation and energy and nutrient storage depends on the length of Conservation relative to other stages. In a comparative study of islands of equal age but different fire frequency, the amount of carbon and nitrogen stored in soil humus increased with the length of time since disturbance (Wardle et al. 1997). Total or partial collapse of the community during Release i.e., disassembly, is likely to be a transient, rapid event. Empirical data on disassembly are rare, but suggest that the proportion of species in different trophic levels remains constant (Mikkelson 1993), whereas it varies non-randomly during assembly (Table 1, Patterns 6a and 6b). The evidence for disassembly is rather weak and based on inference of present distributions whereas the evidence for assembly is confounded by lack of knowledge of the history of invasion. Given the hysteretic effects of increased invasion resistance and inertia that may accompany Exploitation and Conservation (Smith 1965, Law and Morton 1996), the possibility seems exceedingly remote that a community would disassemble by species being deleted in the reverse order in which they were added. In this sense, community assembly may be irreversible. Any predic-

tions, however, are entirely speculative and we await empirical evidence with interest.

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