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FORUM is intended for new ideas or new ways of interpreting existing information. It provides a chance for suggesting hypotheses and for challenging current thinking on ecological issues. A lighter prose, designed to attract readers, will be permitted. Formal research reports, albeit short, will not be accepted, and all contributions should be concise with a relatively short list of references. A summary is not required.

Assembly rules, null models, and trait dispersion: new questions from old patterns

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> "... the same environments are repeated in the same region, their selective action upon the plant immigrants leads to an essentially similar flora in each, and a similar flora produces similar reactions. These conditions produce the well known phenomena of plant associations of recognizable extent and their repetition with great fidelity in many areas of the same region, but they also produce the variable vegetation of our sand dunes and small pools, the fragmentary associations of areas of small size, and the broad transition zones where different types of vegetation are mixed."
>
> H. A. Gleason (1926)

While studying assemblages of birds on and around the island of New Guinea, Diamond (1975) posed a simple question – what do we need to know in order to predict how communities are assembled from a common species pool? This is the central question of community ecology, but Diamond skipped an important step: he failed to first show that the bird assemblages were structured as opposed to random (Connor and Simberloff 1979). So for about twenty years ecologists have been asking whether non-random patterns exist.

Table 1 shows that it is time to conclude that non-random communities do indeed exist. It is therefore time to move to newer questions: (1) What kinds of patterns exist in species assemblages and in the traits they possess? (2) How do these patterns change in space, in time, and among taxa? (3) What do we need to know in order to predict how communities are assembled from a common species pool?

Our objectives in this paper are both strategic and tactical. To some extent, the field of assembly rules is mired by the search for non-randomness in species composition. At the strategic scale, we argue that the early (first order) questions are answered, and we try to stimulate the transition to newer questions. At the tactical scale, we suggest some means for addressing the newer (second order) questions and present a phase space diagram that illustrates one possible playing field.

The search for species patterns

Most ecologists are used to thinking in terms of lists of species that occur in certain places, and in making comparisons among those places. The idea of assembly rules seems well rooted in this substrate. Although one is given the impression that null models must be new and sophisticated, the simplest test for non-randomness is the well-known chi-square test for association between pairs of species (e.g. Kershaw 1964, Sokal and Rohlf 1981). This test simply determines whether or not the occurrences of two species are independent. Rejection of the null hypothesis (that they are not independent) allows for two possible results: the species may co-occur more often than expected by chance (positive association) or they may co-occur less often than expected (negative association). Many of the early "null models" for detecting species patterns tested for such patterns (the missing species combinations of Connor and Simberloff 1979, and "checkerboardness" of Gilpin and Diamond 1984). More recently, tests for other types of species patterns, such as nestedness have been developed (Patterson 1987, Wright and Reeves 1992).

The assumptions and constraints built into null models and their test statistics have been an area of heated debate, and this has given rise to some of the contradictory results (e.g. birds, Connor and Simberloff vs Gilpin and Diamond; marine intertidal species, Underwood vs Dale; desert rodents, Fox and Brown vs Wilson, Table 1). More recently consensus has been growing regarding the methodological constraints and tradeoffs (cf. Jackson et al. 1992, Silvertown and Wilson 1994), and this has led to

Table 1. The search for pattern in ecological communities. Some definitions are provided in Appendix 1.

	General pattern	Extra terminology	Taxon	Reference
A. No patterns				
1. Species patterns	Random	Clustered boundaries	intertidal organisms	Underwood (1978), Auerbach and Shmida (1993)
		Missing species combinations	birds	Connor and Simberloff (1979, 1984)
		Niche limitation	plants	Wilson et al. (1987)
		Checkerboard, nested	rock pool algae	Wilson et al. (1992)
2. Trait patterns	Random –		bumblebees	Hanski (1982), Ranta (1982),
	(not more different than expected by chance[1])		birds	James and Boecklen (1984), Simberloff (1984)
			lizards	Ricklefs et al. (1981), Scheibe (1987)
			swamp plants	Rathcke (1984)
			forest birds	Hopf and Brown (1986)
			forest plants	Wilson (1989)
			desert rodents	Wilson (1995)
B. Patterns				
1. Species patterns	Non-random	Clustered boundaries	saltmarsh plants	Pielou (1975), Pielou and Routledge (1976)
			wetland plants	Keddy (1983), Shipley and Keddy (1987)
			intertidal algae	Dale (1984)
		Checkerboard patterns	birds	Gilpin and Diamond (1984)
			birds, bats	Stone and Roberts (1990)
		Niche limitation	lawn plants	Watkins and Wilson (1992)
			forest plants	Zobel et al. (1993)
		Nonrandom patterns	fish	Jackson et al. (1992)
		Nestedness	various (23)	Wright and Reeves (1992)
			birds, mammals	Atmar and Patterson (1993)
		Various	desert perennials	Silvertown and Wilson (1994)
		Disassembly rules	3 trophic levels	Mikkelson (1993)
	Historical effects	Priority effects	frogs	Wilbur and Alford (1985)
		Alternative endpoints	plankton	Robinson and Edgemon (1988), Drake (1991)
2. Trait patterns	Species more different than expected			
		Limiting similarity	birds, mammals	MacArthur (1958), Hutchinson (1959), Brown and Bowers (1984)
			birds	Ricklefs and Travis (1980), Hendrickson (1981), Travis and Ricklefs (1983), Schoener (1984), Simberloff (1984)
			rodents	Bowers and Brown (1982), Hopf and Brown (1986), Dayan and Simberloff (1994)
			plants	Armbruster (1986), Cody (1991), Armbruster et al. (1994)
			theoretical plants	Pacala and Tilman (1994)
		Narcissus effect, others	theoretical animals	Colwell and Winkler (1984)
		Guild favored states	rodents	Fox and Brown (1993, 1995)
		Guild proportionality	lawn plants	Wilson and Watkins (1994), Wilson and Roxburgh (1994)
		Trait overdispersion	birds	Moulton and Pimm (1987), Lockwood et al. (1993)
	Species less different than expected			
		Genus:species ratio	plants, insects, birds	Williams (1964)[2]
		Regeneration niche	herbs	Grubb (1977)
		Templets		Southwood (1977, 1988)
			aquatic organisms	Townsend and Hildrew (1994)
		Vital Attributes	trees	Noble and Slatyer (1980)
		Sieves	wetland plants	van der Valk (1981)
		–	plants worldwide	Box (1981)
		Filters	theoretical plants	Keddy (1992)
		Trait convergence	swamp plants	Rathcke (1984)

note – community/texture convergence was not considered here because it is tangential to the issue of assembly from a common species pool.

1. alternative hypotheses were not usually tested.
2. there are more species per genus than expected by chance and congeners are assumed to be more similar to each other than to other species.

an increasing number of cases where patterns have been detected. This is no suprise to botanists, who have documented positive and negative associations of species for decades (e.g. Kershaw 1964, Pielou 1974). It is time to conclude that in some places, at some times, with some taxa, communities exist.

We need to restrict the use of the term assembly rules. Merely demonstrating that a pattern exists does not in and of itself qualify for the appellation "assembly rule". This term should be reserved for the rules, or constraints, that govern the patterns. Past studies have tended to emphasize the search for patterns themselves and have often done little more than detect non-randomness, rather than defining the underlying assembly rules. Assembly rules are explicitly defined constraints that can be used to predict community structure.

Trait patterns

As an alternative to considering lists of species names, one can use the traits they possess and seek patterns in them. For example, the principle of limiting similarity suggests that coexisting species should exhibit trait differences greater than that expected by chance. The assumed mechanism is that coexistence of two species is not possible if niche overlap is too great (e.g. MacArthur 1958, MacArthur and Levins 1967). Community-wide patterns of limiting similarity have been called trait overdispersion (Moulton and Pimm 1987). For example, Mac Arthur (1958) showed that a group of very similar birds which coexist have markedly different foraging strategies. Other examples include the *Opuntia* cacti where morphologically similar congeners do not coexist (Cody 1991), and passeriform birds introduced to Pacific islands where the successful immigrants were morphologically more different than expected (Lockwood et al. 1993). Table 1 shows that there are many examples of significant trait patterns. Indeed, patterns of limiting similarity appear to be quite common, particularly for animals.

The exact opposite pattern is also possible: coexisting species can be more similar than expected by chance. Because this type of pattern is the converse of trait overdispersion, we call it trait underdispersion. Most of the recent trait-based studies have omitted this alternative hypothesis, and have not tested for underdispersion. Plant ecologists, ecophysiologists, and biogeographers have had a keen interest in finding traits that are required for existence in a particular site (e.g. Du Rietz 1931, Raunkiaer 1934, Lieth 1956). Although rarely explicitly tested, trait underdispersion represents a constraint on membership in a community, and therefore it also represents a type of non-random pattern that communities may show. While looking for evidence of limiting similarity, Rathcke (1984) found instead that flowering phenology in one of two swamp sites was more similar than expected by chance. Williams (1964) found that there tend to be more species per genus in a community than would be expected by chance alone (Table 1). If we accept the idea that congeners are generally more similar to each other than to other species, then coexisting species have trait differences that are less than expected by chance. Other examples range from the prediction of plant growth form from climate (Box 1981) to traits associated with establishment requirements for plants in wetlands (van der Valk 1981). In general, the trait-filter model of assembly rules (Keddy 1992) should produce underdispersion.

There are several reasons why the value of assembly rules increases when they are based on traits. First, when rules are based on species names and a local species pool, they will be specific to one area and they will not be easily comparable to other sites or habitat types. Assembly rules will be generalizable only if based upon traits or upon trait-based functional groups (Keddy 1992). Second, focusing on traits will help alleviate reliance on often murky taxonomy. Third, species that are nearly identical or function as interchangeable or equivalent species will also pose no special problem if emphasis is put on traits. Gleason (1926) wrote, "much of the structural variation in an association [community type] would disappear if those taxonomic units which have the same vegetational form and behavior could be considered as a single ecological unit." Fourth, trait-based rules provide more information to readers outside any particular area of expertise. Lists of species names have little meaning to most ecologists outside each often narrow speciality. Finally, trait-based rules will usually be simpler to construct, whereas species-based rules will often ramify into a list of complex pairwise interactions. Consider the following:

The species form of "rule" might be: if a community has species A, then it usually will not also have species B or C unless species D or E *and* either species F or G are present, while if a community has species D, then it will not also have species E unless species F or G *and* either species A, B, or C are also present, etc.

While a more trait-based rule is clearer: the proportion of species from each functional group will tend to remain constant for each observation (cf. Wilson 1989, Fox and Brown 1993, but see also Wilson 1995, Wilson and Roxburgh 1994).

A summary model for trait patterns

At first one might imagine that coexisting species have traits that are either overdispersed or not. But the pattern probably depends on what traits are chosen, what the scale of the species pool is, and what type of habitat is being examined. In contrast, it is more probable that some traits will be overdispersed (perhaps those associated with competition) while others, will be underdispersed (perhaps those affected by abiotic filters). Thus the more

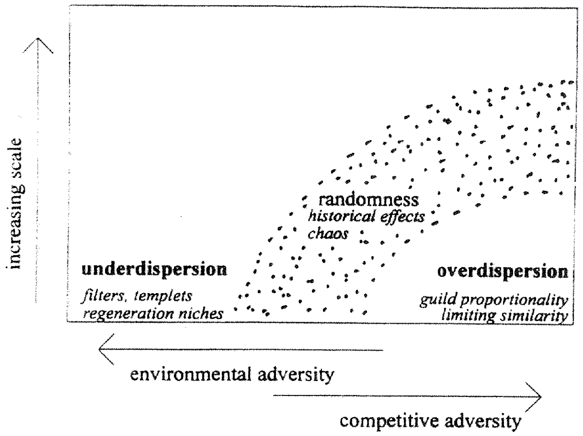

Fig. 1. A qualitative model for trait dispersion.

fundamental questions include: (1) which traits show which pattern, (2) how do the patterns vary in space, (3) how does the size of the species pool (or the range of species considered) affect the type of pattern, and (4) are the patterns consistent among habitats?

To illustrate this, we have developed a qualitative model for trait dispersion which illustrates the three principal patterns which a trait (or a group of traits) can exhibit in communities (Fig. 1). The model was developed in order to make sense of the different and apparently contradictory results outlined in Table 1.

The primary axis (the abscissa) represents the gradient from environmentally enforced adversity to competitively induced adversity. At one end, environmental adversity includes factors such as abiotic stress (drought, salinity), disturbance (fire, ice scour), or predation. At the other, resources or space are limited owing to competitive adversity (cf. Southwood 1977, Grime 1979). We assume, for simplicity, that as environmental adversity decreases, the relative importance of competitive adversity increases. (We have used this shorthand to reduce the number of axes in our model and increase clarity, but if necessary these two gradients could be separated.) Along this axis we would expect two regions of non-randomness. At one extreme (Fig. 1, right), traits associated with meeting the challenges of competitive adversity will be overdispersed. At the other extreme (Fig. 1, left), traits that are associated with meeting the challenges of environmental adversity will be underdispersed because species will have converged upon successful adaptations. Traits that are associated with neither of these selective pressures will likely be randomly distributed among species in a community.

Between the two areas of significant pattern is a zone of randomness. Apparent randomness could be due to stochasticity, or it could be due to deterministic factors which are keenly sensitive to initial conditions. This latter possibility corresponds to the idea of overriding importance of history in determining community composition, and it is suggestive of chaotic assembly rules (cf. Drake 1991). If several traits are grouped using some multivariate technique such as principal components analysis, a pattern could be diluted to randomness due to mixing over- and under-dispersed traits.

A second axis corresponds to the scale of the investigation, most notably as it affects the size of the species pool that is being considered. Most ecologists looking for evidence of limiting similarity have used congeners or members of a single guild (e.g., warblers, MacArthur 1958; *Opuntia* cacti, Cody 1991, granivorous rodents, Fox and Brown 1993, passeriform birds, Lockwood et al. 1993). This approach uses a restricted and small scale species pool. Conversely, studies that have looked for trait-environment linkages have used large species pools to find evidence of underdispersion (e.g., east African birds, Williams 1964; world-wide plant growth form, Box 1981). We therefore suggest that dispersion decreases as the scale of the investigation increases. At large enough scales the patterns are virtually obvious: for deserts compared to wetlands, most traits will be underdispersed. Overdispersion is therefore a phenomenon likely restricted to small-scale deterministic situations where competitive adversity predominates (cf. Wilson and Roxburgh 1994). Indeed, Colwell and Winkler (1984) showed that as the taxonomic scale of the species pool is increased, the likelihood of finding significant overdispersion decreases.

Conclusion

Consider the opening question. Are there non-random patterns in species assemblages? We have argued that the answer is yes and it is time to move on to newer questions: (1) What kinds of patterns exist in species assemblages and in the traits they possess? (2) How do these patterns change in space, in time, and among taxa? (3) What do we need to know in order to predict how communities are assembled from a common species pool?

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Appendix 1. Some definitions of terms.

limiting similarity	when coexisting species partition resources and have minimal niche overlap; this is often reflected in morphological differences among the species (see also MacArthur 1958, usually applied to congeners)
guild proportionality	when the proportion of species in a community that belong to a particular guild(s) is more constant than expected by chance (see also Wilson 1989), this is consistent with limiting similarity – not all species can come from one guild and guilds show limiting similarity
trait overdispersion	when species in a community are more different for a particular trait than expected if species were randomly chosen from a species pool, a community-wide manifestation of limiting similarity (see also Lockwood et al. 1993)
trait underdispersion	when species in a community are more similar for a particular trait than expected if species were randomly chosen from a species pool
clustered boundaries	when the edges of species occurrences coincide along a zonation gradient (see also Underwood 1978, Dale 1984)