FORUM

Trait-divergence assembly rules have been demonstrated: Limiting similarity lives! A reply to Grime

Wilson, J. Bastow

Botany Department, University of Otago, P.O. Box 56, Dunedin, New Zealand; E-mail bastow@bastow.ac.nz

Abstract

The recent Forum contribution by Grime (2006) contrasts the MacArthur/Diamond assembly-rule approach to studying plant communities with the study of environmental trait gradients. Both are valid and useful. In doing so, Grime declares that the assembly rules model, in which negative interactions between plants act with limiting similarity to cause local trait divergence, is "not supported by empirical study of plant communities". This is, he says, the agony of community ecology. I show that there is now abundant evidence for assembly rules, and no agony.

Keywords: Environmental filter; Environmental trait gradient; Guild proportionality; Texture convergence; Trait convergence.

Grime (2006) discusses trait convergence (the tendency for co-occurring species to have similar traits) and trait divergence (the tendency for them to have different traits). I should like to disagree with one aspect of his otherwise useful commentary.

Grime mentions two research programmes in vegetation science. Diamond (1975) originally stated assembly rules as 'forbidden combinations', but they are now generally seen as the existence of more trait divergence between the species of a local assemblage than expected under a random null model. These are the 'differing traits or trait values' to which Grime refers. The theoretical basis of assembly rules is the competition-based limiting similarity process of MacArthur & Levins (1967), called 'Darwin-Diamond' model by Grime. His use of Diamond in his term for the concept, his citing of Connell's 'ghosts of competition past', his characterising it as "formalized as 'limiting similarity'", and his citation of the major book on assembly rules, Weiher & Keddy (1999), make it absolutely clear that he is addressing the concept of assembly rules: "restrictions on the observed patterns of species presence or abundance that are based on the presence or abundance of one or other species or groups of species (not simply the response of individual species to the environment)" (Wilson 1999).

Before assembly rules can act, there will be environmental filtering leading first to a regional pool determined by the climate and then to a local pool of species filtered also by the habitat. This local pool shows convergence compared to the wider pool available, due to common adaptation to the physical environment. This is the second process that Grime discusses with "roots extending back to the pioneers of plant geography". It clearly happens, and I have no argument with Grime here. He discusses whether trait convergence based on environmental filtering might be less stringent in regenerative traits than in vegetative ones. I shall leave any comment on that idea to others, and discuss only on the issue of assembly rules.

Assembly rules occur in the formation, from the local pool, of a particular assemblage, for example that in a quadrat. According to the limiting-similarity concept of MacArthur & Levins there will be stronger competition between species that are more similar in their resource use, more similar in their functional traits. This would lead to greater variation in traits than expected from a random-based null model, the trait divergence that Grime mentions. The process must be based on negative interactions between plants, i.e. on interference (for example, disturbance could not operate as interference between species, and could therefore not effect limiting-similarity). Grime (2006) quite reasonably mentions competition and this will be the usual type of interference involved, but assembly rules could be based on other types of interference, e.g. allelopathy, red:far-red effects, autogenic disturbance, pollen occlusion, interactions via heterotrophs, etc. It is clear from Grime (2001) that he appreciates that these other types of interference occur and also that competition is often the major one. The term 'assembly rule' was coined by Diamond for the pattern. The pattern must be based on plant interactions but just which process is involved has not been proved even for a single rule. This is a gap in vegetation science.

Grime declares that the existence of trait-divergence assembly rules is "not supported by empirical studies of plant communities", emphasising this by a quote from Lewontin (1974) as "the agony of community ecology", and this is our point of disagreement. In fact, many assembly rules, significant against carefully constructed null models, have been demonstrated.

The assembly rule most directly related to MacArthur's theory, limiting similarity, was demonstrated for a guild of congeneric euphorbiads by Armbruster (1986); it was apparently based on competition for pollinators. The similar rules of Stubbs & Wilson (2004) on a sand dune were attributed to competition for soil water and nutrients. An alternative approach is texture convergence, under which species are sorted, ecologically or in evolution, to fill the range of niches within each community, leading to greater similarity between assemblages on different continents or within an area than expected at random (Smith & Wilson 2002). The texture convergence found by Smith et al. (1994) and Watkins & Wilson (2003) both suggested divergence in light-capture strategy. A closely-related way of analysing within-assemblage trait divergence, and hence betweenassemblage convergence, is guild proportionality, seeking more constant representation of guilds in an assemblage than expected at random. The guild proportionality effect found in a salt marsh by Wilson & Whittaker (1995) appeared to be related to the structure of the canopy, as did that on a much vertical larger scale by Wilson et al. (1995) using rainforest strata. Assembly rules should also be seen as communities come together, and in the succession study of Fukami et al. (2005) the multivariate functional composition of replicates became more similar; they concluded that "deterministic assembly rules governed assembly".

The best evidence has come from a community very close to equilibrium¹, the Botany Lawn of the University of Otago, New Zealand (Roxburgh & Wilson 2000). There is guild proportionality (Wilson & Watkins 1994; Wilson & Roxburgh 1994). Intrinsic guilds were determined by "interviewing the plants" via guild proportionality analysis, not a priori (Wilson & Roxburgh 1994). They seemed to be related to the position of the leaf in the canopy. These guilds were confirmed by experiment (Wilson & Roxburgh 2001) and by trait analysis (Mason & Wilson 2006). Limiting similarity in leaf morphology and local texture convergence in chlorophyll content were demonstrated (Watkins & Wilson 2003; Mason & Wilson 2006). Most of these investigations have pointed to niche differentiation within the canopy and to light harvesting at different times during the mowing cycle, though Mason & Wilson (2006) suggested the effect might be indirect, due to the effect of defoliation on root growth stoppage and hence on competition for nutrients.

Assembly rules have been demonstrated many times. If lack of demonstrated assembly rules really was causing agony to community ecology in 1974, there is certainly no agony now. The challenge for vegetation science is to discover the mechanisms behind the rules.

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Received 18 October 2006; Accepted 1 December 2006; Co-ordinating Editor S. Díaz.

¹ According to the established criteria of Connell & Sousa (1983), i.e. lack of directional change in species composition.