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Genetic assembly rules and community phenotypes

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Abstract We present a conceptual construct for a genetic based community assembly rule where the genetic composition of a host plant, or resource, affects the structure of the dependent community. This is related to a genetic similarity rule that states that host plants with similar genetic compositions are hosts to similar arthropod communities. We present preliminary data from the *Populus* system to support this concept. We review the recent literature to evaluate the current state of the assembly rule concept and interpret a set of previous studies in the context of a genetic assembly rule. We suggest that by incorporating this concept into community ecology we can begin to bring an evolutionary perspective to this discipline.

Keywords Assembly rules · Community ecology · Genetic-based traits · *Populus*

Introduction

The assembly rule concept has been around since early in the history of modern ecology (Forbes 1887; Cowles 1899; Clements 1936; Gleason 1926; Booth and Larson 1999), but the term was not introduced until Diamond's infamous chapter in 1975. The importance of a workable assembly rule lies in its potential for predicting the composition of species from the species pool. Should such an assembly rule exist, it would have important consequences for basic ecological theory and conservation biology (Keddy and Weiher 1999; Temperton et al. 2004). While the specific term ‘‘assembly rules’’ was not in use, early ecologists described community structure and composition in terms of organizing biotic factors such as competition, predation, and environmental factors (Forbes 1887; Cowles 1899; Clements 1936; Gleason 1926).

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As ecology matured, the formulation of the factors responsible for community organization became more mechanistic. For example, Lindeman (1942) has shown that trophic organization was linked to the abiotic environment. However, when Diamond (1975) introduced the term ‘‘assembly rules’’ he was describing avian community patterns where certain allowable, or forbidden, species combinations were a putative function of competition. This triggered a strong debate among community ecologists, many of which felt that there were no rules in operation (Simberloff et al. 1999) and that the observed patterns were not different than patterns generated by random processes (*see* Strong et al. 1984).

Research on assembly rules continues (Weiher and Keddy 1999a; Temperton et al. 2004) and community studies have became more rigorous, experimental, and long-term (Cody and Smallwood 1996; Brown et al. 2001), although still contentious (Wilson 1995; Fox 1995; Simberloff et al. 1999; Kelt and Brown 1999; Stone et al. 2000; Brown et al. 2002). For example, Fox (1999) summarized an assembly rule for Australian small desert rodents where species from different guilds were added to the community sequentially; a species could not be added to the community until each guild was proportionally represented. Fox and Brown (1993) tested this rule on a community of North American small desert rodents and determined that this rule was also in operation in this group, thus concluding that this was a general rule applicable to desert rodent community structure. Although competition within and among guilds is thought to be the mechanism driving this rule, ultimately resources provide the bottom-up basis for this rule. Consequently, the development of assembly rules is important (Keddy and Weiher 1999) and a bottom-up perspective (e.g., leaf quality), i.e., a genetic approach might prove useful because top–down and lateral effects ultimately depend on bottom–up processes (Hunter and Price 1992). We argue here that genetics is the ultimate foundation for assembly rules with both ecological and evolutionary significance.

The assembly rule concept has evolved to the stage where it has the potential to be a useful construct for understanding and predicting community structure. For example, restoration ecology has embraced assembly rule theory as a basis for rebuilding communities in reclamation and restoration efforts (Keddy 1999; Temperton et al. 2004). To begin, the first stage of assembly rule research is to identify non-random patterns of community structure (Kelt and Brown 1999), but once patterns are identified specific mechanisms need to be stated and tested (Keddy and Weiher 1999; Weiher and Keddy 1999a). It may be useful to state rules as ‘‘if-then’’ statements (Knapp et al. 2004). For example, *if* a specific category of a host plant is sampled *then* a particular chemical composition is predicted. Furthermore, *if* a particular chemical composition is observed *then* an arthropod community phenotype may be predicted (Bangert et al. 2006a). Diamond (1975) accomplished the first step, but only partially finished the second step. Because the mechanism of competition was not tested, the dispute over mechanism and method has continued for over two decades (Stone et al. 2000; Brown et al. 2002).

There have been recent instructive reviews and critiques of the assembly rule concept in order to make it a useful heuristic for understanding community ecology (Belyea and Lancaster 1999; Booth and Larson 1999; Weiher and Keddy 1999a), but assembly rules are often invoked, but not explicitly stated or tested (Keddy and Weiher 1999), i.e., the recommendations of these assembly rule researchers has generally not been put into practice. We conducted a review of the primary literature on assembly rules subsequent to these published reviews. In papers that had the phrase "assembly rules" in their title or abstract, we found that 48% (16/33) did not explicitly state or test an assembly rule but rather suggested that assembly rules may be responsible for the observed patterns, while only 21% (7/33) were explicit. The remaining papers were concerned with the statistical properties of null model analysis used to detect significant patterns (12%; 4/33), reanalyzed previous studies (3%; 1/33), or were conceptual (6%; 2/33). Ironically, when assembly rules have been explicitly stated and tested (9%; 3/33) old controversies have continued, in large part based on methodology for detecting significant patterns (e.g., Brown et al. 2000; Stone et al. 2000).

If the assembly rule construct is to be useful and predictive in community ecology, ecologists must explicitly state, then test rules. Rules range from being stated in general terms of how a community is structured (e.g., Fox 1999) to explicit statements of which species are predicted to be present. These rules may be fundamentally different for plant and animal communities. For example, plant communities may be primarily structured by abiotic factors first and then competition second (Weiher and Keddy 1999b), whereas animal communities may be more strongly influenced by biotic mechanisms such as species interactions (e.g., competition or predation). For example, a habitat filter may initially structure a plant community and the associated animal community may be structured by interspecific competition for those plant resources (Weiher and Keddy 1999b). In our research we primarily focus on the dependent animal community. The current perspective relies on ecological explanations that can be highly contingent (*sensu* Lawton, 1999), while an approach based on genetics will eventually incorporate evolution and natural selection and might increase the efficacy of the concept.

A genetic assembly rule for dependent communities

We propose a third phase to assembly rule research that should increase our ability to predict community composition. We suggest a genetically based assembly rule where the genetic composition of the resource (e.g., leaf quality, photochemical composition) affects community structure. For example, *if* the genotypic class (e.g., subspecies: Floate et al. 1996; or cross type: Bangert et al. 2006a) of the host were known, *then* the community phenotype of dependent species might be predicted. This construct is complimentary to the extended phenotype (*sensu* Dawkins 1982) recently suggested by Whitham et al. (2003) in the development of community genetics and is defined as the effects of genetic variability that extend beyond the individual or population (Whitham et al. 2003; Wimp et al. 2005; Shuster et al. 2006; Whitham et al. 2006), i.e., the effects of genes cascade up (*sensu* Hunter and Price 1992) to affect community properties in which the individual is embedded.

We predict that dependent mutualistic, predatory, and parasitic communities will be partially structured by the genetic composition of the underlying resource when genetic variability is high. Conversely, a genetic assembly rule would predict that environmental factors would become increasingly more important as genetic diversity diminishes (Bangert et al. 2006b, c). Here we use the term predator to include herbivores and granivores. For example, greater habitat diversity, or a more complex set of habitat filters should result in greater plant genetic diversity, which will result in a more diverse animal community (see Wimp et al. 2004).

Our own work suggests that we are better able to predict arthropod herbivore community structure associated with different genotypic classes of cottonwood host plants based on indicator-species-value analysis (IndVal; Dufrêne and Legendre 1997). If there is a genetic basis to community structure there is the added value of placing community ecology into an evolutionary framework (Whitham et al. 2003; Wimp et al. 2005; Bangert et al. 2006b; Shuster et al. 2006; Whitham et al. 2006). Our work has focused on hybridizing complexes of plants because genetic diversity is maximized in hybrid systems (Grant and Grant 1994; Whitham et al. 1999) and has been shown to be important in species formation (Grant 1981; Stace 1987; Smith and Sytsma 1990; Arnold 1997). These attributes provide us with a model system in which to study genetic assembly rules. In a system of hybridizing *Eucalyptus* species in Australia, the dependent arthropod community is different among genotypic classes, or crosstypes, (i.e., parental species, F_1 hybrids, and backcross hybrids) and is strongly correlated with the chemical composition of their hosts (Dungey et al. 2000). In North America, both the arthropod community and tannin concentrations are strongly correlated with the genetic composition of hosts in a naturally hybridizing complex of cottonwoods (Schweitzer et al. 2004; Bangert et al. 2006a). Furthermore, in two studies, 31–54% of the leaf-modifying arthropod community members were significant indicators of four cottonwood cross types (Bangert et al. 2005; Wimp et al. 2005).

The previous findings also suggest that a genetic approach to community assembly may be useful because plant–animal interactions are exceedingly common, and the bottom-up consideration of the genetic composition of producers puts community ecology into an evolutionary framework. For example, a genetic assembly rule suggests that selective pressures operating on a host plant population may become selective pressures on the dependent community.

Genetic assembly rule predictions

If genetic assembly rules are generally applicable, several hypotheses follow. First, organisms respond to each other at levels finer than the species level and species will discriminate among different genotypes. For example, McIntyre and Whitham (2003) found that the bud-galling mite, *Aceria parapopuli*, was found almost exclusively on natural F_1 hybrid cottonwoods growing in a common garden and in the wild. Within this cross type mites were highly discriminatory among individual F_1 genotypes where their intrinsic rates of increase varied from $r = 0.0$–1.5. These differences translate into large differences in population growth rates and extinction probabilities on individual genotypes. Similarly, Wimp et al. (2005) found that three different arthropod species distinguished between complex backcross hybrids and narrowleaf cottonwoods that were so similar in appearance that molecular genetic analysis was required to differentiate their pure or hybrid status.

Thus, if single species show strong responses to host plant genotypes or a subset of a host species genome, we predict that dependent communities will also show strong responses to the underlying genetic variation in the plant population. Moreover, we predict that hosts that are similar genetically will support similar communities and community composition will change with a change in the genetic composition of the host (Bangert et al. 2006a; Fig. 1). In two different systems of plant–animal

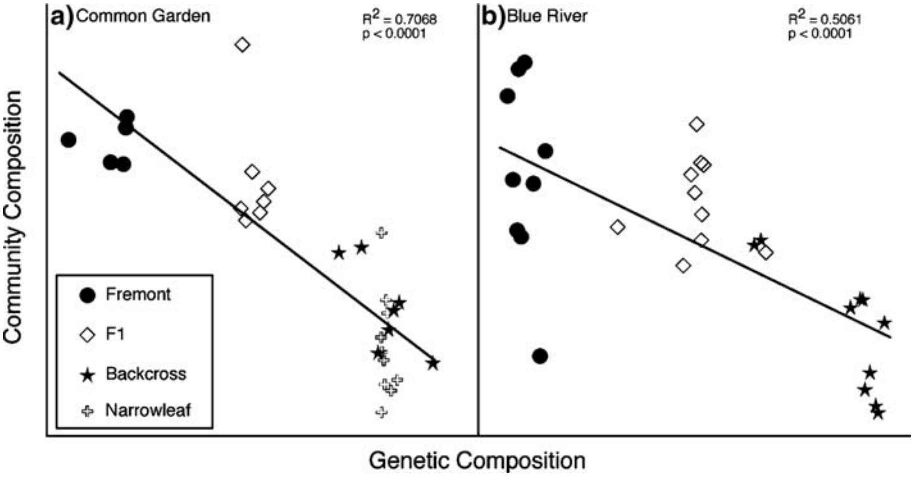

Fig. 1 The relationship between arthropod community and genetic compositions from cottonwood trees in (**a**) the common garden in Ogden, Utah, USA, and (**b**) trees growing in the wild along the Blue River, Arizona, USA. The genetic data from the common garden is based on RFLP data, the Blue River is based on AFLP data, and arthropod community composition is based on the Bray–Curtis similarity coefficient. These data show that the associated arthropod community structure changes with the change in the genetic composition of cottonwoods. This analysis is conducted on the one-dimensional scores from non-metric multidimensional scaling (NMDS). There is no a priori expectation for the sign of the slope, but the a priori expectation is that a significant relationship exists between cottonwood genes and the arthropod community

interactions, Floate and Whitham (1995) and Floate et al. (1996) showed that different cross types in cottonwoods (Salicaceae: *Populus* complex), and subspecies of rabbitbrush (Compositeae: *Chrysothamnus nauseosus*), each supported very different insect faunas. Furthermore, this level of herbivore specificity among cross types was consistent both in the wild and in a common garden where environmental factors were minimized (Wimp et al. 2005).

In support of a genetic assembly rule approach, a study by Hochwender and Fritz (2004) showed similar results from synthetically generated willow hybrids in a common garden. Canonical discriminant analysis of the multivariate community indicated which arthropod species were responsible for the observed patterns. They also found that the communities between different hybrid cross types were more dissimilar than the communities between the two parental hosts, and these communities were located outside of the parental communities in multivariate space suggesting that this dependent community was structured by non-additive genetic effects.

These examples show that dependent communities respond to their hosts at the categorical scale, but the prediction also suggests that communities should respond to a continuum of genotypes in the host plant. In a common garden, Bangert et al. (2006a) found that trees with similar genetic compositions had similar arthropod communities and this relationship is consistent at both the river and regional scales encompassing 720,000 km^2 (i.e., Arizona, New Mexico, Colorado, and Utah; Bangert et al. 2006b). Furthermore, this relationship was expressed in two different naturally hybridizing cottonwood (*Populus* spp.) systems. Another study showed that the community changes along the genetic continuum within the F$_1$ and backcross classes, and at a finer scale within the Fremont cottonwood and thus was not driven by the pure parental species (Bangert et al. 2006b). These results suggest that the effects of genetic variability extend beyond the host plant. Most of the studies outside of the cottonwood system did not state predictions of community structure based on the genetic composition of the plant. However, these studies do support the prediction that community composition may be predictable based on plant cross type, and conversely, cross type can be predicted from the observed community (Floate and Whitham 1995; Floate et al. 1996).

A second hypothesis states that as genetic diversity of a plant population increases, the diversity of the dependent community will increase. At the stand level, Wimp et al. (2004; Fig. 2) found a positive relationship between cottonwood genetic diversity and arthropod community diversity. In this study, plant genetic diversity explained nearly 60% of the variability of the associated arthropod community. Even though mean richness among cross types may not be different, beta diversity, i.e., changes in community composition, can be very different along a genetic gradient resulting in an increase in total richness (gamma diversity) when greater plant genetic diversity is present (Bangert et al. 2005; Wimp et al. 2005). A similar study by Tovar-Sánchez and Oyama (2006) found that genetic diversity at the stand level explained nearly 78% of insect community diversity in a hybridizing oak system across seven oak hybrid zones.

A third hypothesis states that genetic assembly rules will scale up from local to regional levels. First, at a regional scale of 18 rivers (i.e., 720,000 km^2), we found that rivers with similar plant cross type compositions had similar arthropod community compositions (Bangert et al. 2006b) and this prediction held when spatial autocorrelation was factored out (Legendre, 1993). Second, at the smallest scale of a common garden (m^2) in which environmental effects are largely eliminated, we also found that the arthropod community discriminated among Fremont (*Populus fremontii*) and narrowleaf cottonwoods (*P. angustifolia*), and their F_1 and backcross hybrids (Bangert et al. 2006a). Furthermore, in a river scale analysis, the arthropod community was different among these cross types involving 258 trees in 10 rivers

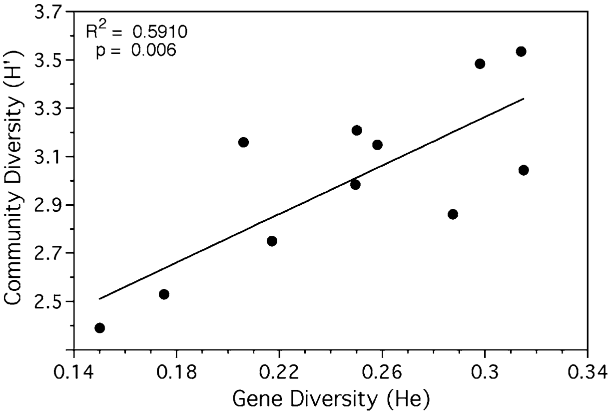

Fig. 2 Arthropod community diversity (H′) increases as cottonwood genetic diversity (He) increases. Genetic diversity was assessed using an AFLP marker system. Diversity for both factors was calculated at the stand level for 11 replicate cottonwood stands with varying amounts of genetic diversity. Modified from Wimp et al. (2004)

representing two different naturally hybridizing cottonwood systems (*P. fremontii* × *P. angustifolia* and *P. deltoids* × *P. angustifolia*; Fig. 3: river scale). The same pattern was observed in the regional scale analysis of 264 trees representing 18 river systems and these same two hybridizing complexes (Fig. 3: regional scale). Finally, a third study of six rivers showed that trees with similar genetic compositions also had similar arthropod communities (Bangert et al. 2006b). Moreover, these relationships were detectable at the stand, river, and regional scales arguing that patterns at small scales also emerge at much larger scales resulting in genetically based patterns that are repeatable across the landscape. These studies suggest that a genetic approach to community structure is a useful tool for understanding dependent communities. Importantly, these three hypotheses are based upon an underlying genetic assembly rule where hosts that are more closely related host more similar communities.

Because cottonwoods are a dominant tree of a major riparian vegetation type that is a hot spot of biodiversity (Finch and Ruggerio 1993; Bangert et al. 2005), the preservation of genetic variation in this species has important community and ecosystem consequences (e.g., McIntyre and Whitham 2003; Whitham et al. 2003; Bangert et al. 2005). To the extent that these findings are found to apply to other dominate species (*see* Crutsinger et al. 2006; Reusch et al. 2005), the importance of conserving genetic diversity in common or dominant species takes on new importance (Wimp et al. 2004). For example, if different arthropod species are dependent

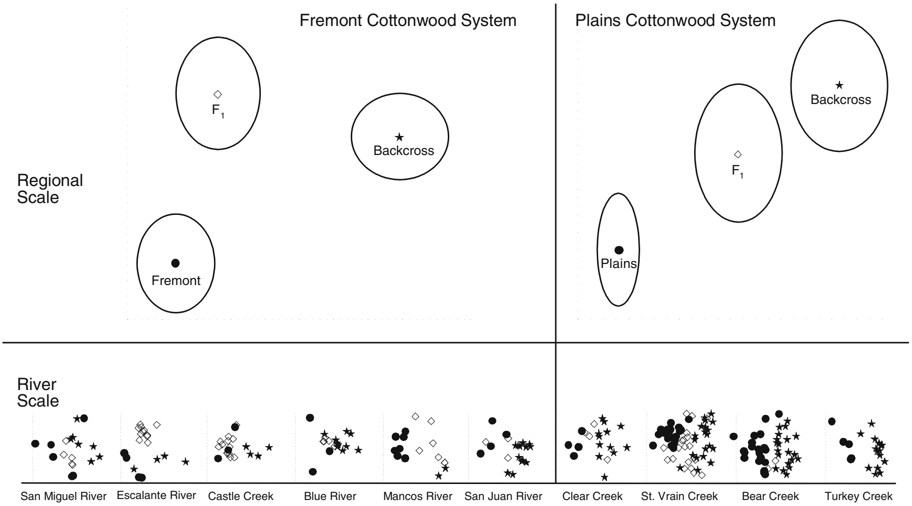

Fig. 3 NMDS ordinations of arthropod community composition exhibit similar patterns at the individual river scale representing 10's of km (lower panel) and at the regional scale representing720,000 km^2 (upper panel). At the river scale, Fremont (*P. fremontii*) and plains (*P. deltoides*) cottonwoods ((●) exhibit extremely little overlap with the backcross to narrowleaf cross type (★). The communities on the F_1 cross type (◇) are always intermediate but show some similarity with the other two cross types as predicted if the community is structured by host plant additive genetic heritability. At the regional scale 149 trees from seven rivers were surveyed from the Fremont cottonwood hybridizing system and 115 trees from 12 rivers were surveyed in the plains cottonwood hybridizing system resulting in similar patterns (upper section). Axes are unit-less where the NMDS procedure places multivariate compositions as points into Euclidean space relative to all other points; points that are close are more similar than points that are further apart. Regional data are presented as community centroids with 95% confidence ellipsoids

on different subsets of the cottonwood genome, as our findings argue, then it is not enough to preserve cottonwoods in general; the entire genome should be preserved for the survival of the entire dependent community.

Examples from the literature

Many previous studies on community structure have not been discussed in the context of genetic assembly rules, but discussion based on these rules may unify our understanding and prediction of community structure. For example, Fritz and Price (1988) have shown that a galling sawfly community was different among different replicated willow clones across 2 years grown in a common garden. By knowing the genetic composition of these clones, prediction of community structure may be possible. Maddox and Root (1990) have shown that different arthropod species are correlated on *Solidago altissima* across multiple genotypes. Some species are positively, and others, negatively correlated. The aggregate pattern of these pair-wise correlations suggests that the entire community is structured by the genetic composition of the host plant and that communities are different on different genotypes within the same host species. By knowing these relationships, community structure may be predictable based on the genetic composition of the host.

In two studies of galling arthropods on oaks (*Quercus* spp.) Boecklen and Spellenburg (1990) and Aguilar and Boecklen (1992) showed that the arthropod community was structured differently among parental species and their hybrids. When different genotypic classes of oak are sampled, we should be able to predict the community structure of the sample. Their studies suggest that plant genetics structure the associated arthropod community. A genetic assembly rule approach might provide predictability based on genotypic class or even genotype. Moreover, plant QTL's (quantitative trait loci) may be developed for associated dependent species or suites of species (*sensu* Maddox and Root 1990). These studies support the hypothesis that dependent communities respond to their host at levels finer than species.

The desert rodent communities that Fox and Brown (1993) studied appeared to be structured by inter- and intraguild competition, such that all guilds must be represented in the community before another species from any guild is added (their assembly rule). A genetic assembly rule for this community would predict that the genetic composition of the resource would influence community assembly. Consequently, if particular resources or phenotypes of resources are selected against then the dependent rodents will also be differentially selected against and community structure will change. Thus, competition is the basis of the Fox and Brown assembly rule, whereas the underlying genetic structure of the plant populations, and/or plant community, would be the alternative genetically based assembly rule for the same patterns. Neither hypotheses are mutually exclusive, but we argue that a genetic based approach is ultimately more proximal and suitable for placing the interactions of the plants and their rodent community within an evolutionary framework. A classic example illustrates this prediction (summarized in Grant and Grant 1993, 1995). On the Galapagos islands during El Niño years large seeds are selected against along with the finches that are dependent on the size structure of the seed resource, resulting in a change in the frequency structure of both seeds and finches, i.e., finch community structure changes.

The fractal dimension of tree architecture is heritable (Bailey et al. 2004) and it has been hypothesized that differences in tree architecture may be responsible for differences in avian nesting patterns and foraging behavior (Martinsen and Whitham 1994). Also, Morse et al. (1985) have shown that arthropod abundances increase with increasing fractal dimension of plant architecture. Thus, a genetic assembly rule may be applied to multiple trophic levels. These studies suggest that there is a genetic component to community structure and that selective forces acting on a dominant plant species may cascade up to affect associated community members.

Finally, several recent studies in community genetics have shown a genetic basis to community attributes. In an experiment with the foundation species, *Zostera marina* a common sea grass, Reusch et al. (2005) found that plots with higher genetic diversity increased resistance to extreme heat events and positively benefited the associated invertebrate fauna. Likewise, in another experiment Crutsinger et al. (2006) found that as the genetic diversity of *Solidago altissima* increased, both arthropod species richness and annual net primary production also increased. In one study Johnson and Agrawal (2005) found the community attributes of abundance, Simpson's diversity index, and species richness to be heritable on the plant *Oenothera biennis*. In another study Johnson et al. (2006) found that "genetically diverse plant patches had 18% more arthropod species and a greater abundance of omnivorous and predacious arthropods compared with monocultures." We suggested that many of the previous studies could be fit into a genetic based assembly rule framework; these four recent studies show the genetic basis of community attributes, which suggests that the synthesis with the assembly rule approach is appropriate.

Summary

Clearly, the genetic composition of resources has effects that extend beyond the individual to influence community processes (Whitham et al. 2003) and operates below the species level. This suggests that ecological processes can be influenced by the indirect selective pressures on the underlying resource, thus placing community ecology into an evolutionary framework with the merging of community assembly rules with community genetics. For example, selective pressures on particular genotypes, or genotypic classes, will indirectly act on the dependent community associated with the trait(s) under selection resulting in differential, among-community selection pressures (Wilson 1997). More recently, arthropod community composition has been shown to be a heritable trait of the cottonwood host (Whitham et al. 2006), however, Shuster et al. (2006) emphasizes that communities do not have fitness, per se, in the classical sense. Does this mean that if communities are heritable they can evolve? Recently the National Science Foundation (NSF) requested a call for proposals to address Frontiers in Integrative Biological Research (FIBR). We suggest that research on the genetic basis of community structure and the evolution of ecological processes qualifies as a biological frontier.

Neither genetic nor assembly rule approaches are new, but genetically based assembly rules are novel. Currently, non-genetic based prediction is difficult and contingent upon multiple ecological factors and their interactions (e.g., Drake 1991; Lawton 1999). A genetically based approach argues that community structure may be partially predicted based on individual genotypes or genotypic classes, thus accounting for more of the variance in community structure. For example, with the advance and application of molecular genomic methods coupled with indicator species analysis and other statistical procedures, we should be able to assign a probability to which species should be present on certain genotypic classes. A corollary to this rule is: when the composition of the dependent community is known, we should be able to predict the genotypic class, or possibly the genotype, of the plant (Floate and Whitham 1995; Floate et al. 1996), thus, a predictable two-way rule becomes operational. This approach should advance community ecology by increasing the level of predictability and introducing an evolutionary perspective, both of which have been weak in this discipline. We have provided just a few examples, but many more examples fall within the genetic assembly rule framework. What is currently lacking is the a priori study of assembly rules, which will increase our ability to make predictions, unify ecological theory, and add generality and evolution to community ecology.

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