

Neutral theory in macroecology and population genetics

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Current neutral theory in macroecology has many parallels with neutral theory in population genetics, but it also has many distinct features that arise because it focuses mainly on questions at the community level rather than at the population level. Here we highlight the similarities and differences between these two bodies of theories from the aspects of the operational units, definitions of neutrality, basic parameters, driving forces, spatial structure and community assembly rules. Compared with neutral theory in population genetics, whose development spans more than 40 years, neutral theory in ecology, which is only a few years old, is still immature and under-developed. There are many opportunities for major theoretical contributions, some of which can be adopted directly from population genetics, while others will require new theoretical work. We critically discuss these opportunities and theoretical challenges in neutral macroecology, particularly in regard to effective community size, ecological drift, community differentiation and ecological dominance.

The recent development of neutral theory in macroecology provides a tractable null hypothesis for testing community assembly rules (Caswell 1976, Bell 2001, Hubbell 2001). As happened early on to neutral theory in population genetics (Ohta and Gillespie 1996), neutral macroecology has also had its critics (Zhang and Lin 1997, Yu et al. 1998, Clark and McLachlan 2003, McGill 2003, Ricklefs 2003, Chase 2005, Nee 2005). However, neutral theory in macroecology is still very much a work in progress and advances in the theory are just starting to appear (Chave and Leigh 2002, Condit et al. 2002, Vallade and Houchmandzadeh 2003, Volkov et al. 2003, 2005, Alonso and McKane 2004, Etienne and Olff 2004, Etienne 2005, He 2005, He and Hu 2005, Nee 2005). The neutral theory should facilitate the development of quantita-

tive, testable null hypotheses in community ecology, biogeography and conservation biology, particularly in communities whose explicit spatial characteristics or physical barriers play a role. The neutral theory is a null hypothesis because it assumes there are no differences among individuals in terms of per capita vital rates or in their responses to the basic forces acting on a community. Neutral macroecology provides insights into the ecological and evolutionary processes that control the assembly and dynamics of the metacommunity and of local communities, including the roles of dispersal, ecological drift, and speciation. The metacommunity is the evolutionary biogeographic unit in which member species originate, live and eventually go extinct. The metacommunity can be subdivided into “a set of local communities that are linked by dispersal of multiple potentially interacting species.” (Leibold et al. 2004) or a network of communities linked by the exchange of migrants (Mouquet and Loreau 2002). Like the dynamics of a subpopulation in metapopulation (Hanski 1998), a local community in metacommunity has a probability of extinction and can be recolonized by the dispersing individuals from neighbour communities. Member species in a community are sympatric and trophically similar and they actually or potentially compete for the same or similar resources (Hubbell 2001).

The basic assumption of neutral theory in macroecology is that all individuals in the community have equal vital rates of death, birth, immigration, emigration, and even an equal probability of becoming a new

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species (Hubbell 2001). By making the neutrality assumption at the individual level rather than at the species level, a neutral theory of relative species abundance becomes possible within the context of the theory of island biogeography, which originally defined neutrality at the species level (MacArthur and Wilson 1967, Hubbell 2001). The central themes of community ecology could then be reinterpreted, resulting in new explanations for the origin of a variety of macroecological patterns, including species richness, relative species abundance, species-area relationships, β -diversity and phylogeny (Caswell 1976, Bell 2001, Hubbell 2001, Chave and Leigh 2002, Condit et al. 2002, Zillio et al. 2005).

Population genetics and macroecology share a common goal to understand how the spatial and temporal patterns of diversity (alleles and species) are formed and maintained. The development of neutral macroecology is inspired by population genetics; Hubbell (2001) explicitly adopted the analytical strategy used by Ewens (1972), i.e. the “infinite allele model”, to derive the relative species abundance and species–area relationships at the speciation (mutation)–extinction equilibrium. However, with the exception of this theoretical link, the broader theoretical connection of neutral macroecology to existing neutral theory in population genetics remains largely unexplored. Several major conceptual connections between these two bodies of theory can be made that are of central importance to

both ecologists and population geneticists. These connections lead to an appreciation of how current neutral macroecology can gain from insights derived from the classical neutral theory in population genetics. Neutral theory in macro-ecology has already generated a rich array of null hypotheses, but the unexplored connections to theory in population genetics promise to generate even more, and stimulate discussion on new theoretical directions in macroecology.

Compared with the development of neutral theory in population genetics, which has a 40-year history, the application of the much younger neutral theory in ecology has only just begun and some areas remain largely or wholly undeveloped. While the linkage between these two bodies of theories has been recognized (Caswell 1976, Bell 2001, Hubbell 2001, Chave 2004, Etienne and Alonso 2005, Vellend and Geber 2005) and some aspects of differences are also discussed (Nee 2005), a more detailed comparison has not yet been made. Here we summarize the similarities and differences between these two neutral theories, as shown in Table 1. Since most of the items in Table 1 are self-explanatory, here we focus on comparing two critical items relevant to driving forces and spatial structure that have not been much discussed so far but are important to understanding community assemblage. We then highlight some fundamental challenges and new directions in applying the neutral theory to macroecology.

Table 1. A comparison between population genetics and neutral macroecology.

Items	Population genetics	Macroecology
Operational units subdivision focal unit observed data Neutral definition	Population Subpopulations Gene Allele frequency Alleles are selectively neutral, selection coefficient ≈ 0 , or $< 1/2N_e$	Metacommunity Local communities Species Species abundance Individuals have equal vital rates
Driving forces	Genetic drift ($1/2N_e$) Mutation Gene flow among subpopulations	Ecological drift ($1/J_M$ or $1/J_L$) Speciation
Spatial structure model	Population genetic structure Island model Stepping stone model Isolation by distance Mainland -island Cline pattern (speciation phases)	Dispersal among local communities Species distribution and abundance variation among local communities Island biogeography
measurement	$1 - F_{is}$ F_{st} Spatial autocorrelation	α -diversity β -diversity
Parameters	$\theta = 4N_e v$ Average number of migrants ($N_e m$) Effective population size (N_e) Distribution of allele frequency Fixed (extinct) probability of an allele Times to equilibrium or extinction for a mutant	Dispersal limitation Metacommunity-local community $\theta = 2J_{Mv}$ or $2J_{Lv}$ Average number of migrants (J_{Lm}) Effective community size (J_M or J_L) Distribution of species abundance Fixed (extinct) probability of a species Times to equilibrium or extinction of a species
Assembly rules	Genetic drift/mutation Genetic drift/migration Genetic drift/migration/mutation	Ecological drift/speciation Ecological drift/dispersal Ecological drift/dispersal/speciation

Similarities and differences

Driving forces

The dynamics of a neutral allele in a population without subdivision is governed by mutation and genetic drift. In the infinite allele model, old alleles are replaced by new alleles as time goes on and this process occurs continuously in the population (continuous influx of new mutations). For a given allele, a balance between mutation and drift cannot be achieved. The distributions of the allele frequency mainly refer to those attained within a certain period of time (Kimura 1983). Eventually, an equilibrium or steady-state distribution of allele frequency is reached between mutation and genetic drift although all these alleles are transient.

The efficacy of genetic drift in changing allele frequencies decreases with the increasing effective population size. This is the number of reproducing adults in an ideal population that would lose genetic variation due to genetic drift or inbreeding at the same rate as the number of reproducing adults in the real population under study. From a statistical point of view, genetic drift is a sampling process wherein some alleles are successfully transmitted into gametes and offspring and others are not. When the population is subdivided, the fate of a neutral allele in a subpopulation is affected by the immigration from neighboring subpopulations. Migration (referring to random migration) counteracts genetic drift and drives the allele frequency distribution toward a steady state if migration is of the same order of magnitude as mutation and genetic drift.

The question of what are the driving forces in neutral macroecology is fundamental, but the definition of ecological drift remains to be more thoroughly developed. From Hubbell's definition (2001), the concept of ecological drift is identical to the demographic stochasticity, assuming that each individual has the same demographic characteristics (probability of reproducing, dying, etc.) from generation to generation. The abundance of any given species in a local community is governed by ecological drift and dispersal and, to a much lesser extent, by speciation. Like the process of genetic drift, ecological drift is equivalent to the sampling process in a community, whereby differences in the realized birth and death rates among species arise due to random chance. Likewise, the magnitude of the effect of ecological drift becomes smaller as the community size increases. As in the infinite allele model, neutral macroecology assumes an infinite species model. This does not mean that there are an infinite number of species present at any given time in the metacommunity, only that there is no limit to species turnover as previous species are replaced by newly evolving species as time goes on. Similarly, an equilibrium for the distribution of species abundance (or relative abundance) in the metacommunity is reached between speciation and ecological drift. This is a basic theoretical

assumption or a mathematical condition for a stable distribution of species abundance (Hubbell 2001). Note that the sampling process is assumed to be based on the total number of individuals, not on the number of species, in communities. Hence species having low abundances are more likely to go extinct.

In contrast to the metacommunity, immigration is a primary force to maintain diversity in a local community under neutrality. Both the number of species and their abundances are affected by immigration from neighbouring local communities, similar to the abundance of a given allele in a subdivided population. The frequency of a given species in a local community is equivalent to the frequency of an allele in a population and is governed by speciation, dispersal and ecological drift.

In addition to the above parallel relationships between neutral theories in macroecology and population genetics, the patterns in allele frequencies and relative abundance of species also exhibit parallelisms, but, more important, they are not independent. Demographic stochasticity (ecological drift) will affect population sizes and relative species abundance in the community, but changes in population size will in turn affect the process of genetic drift on allele frequencies within populations. Thus, effects of these shared forces create linkages between these three organizational levels (gene frequencies, population size, and community relative species abundance) and the linkage can give deep insights into the connection between these bodies of neutral theory. Discussions for each of three forces in the sections below further elucidate these linkages.

(i) Genetic drift versus ecological drift

Two distinct points concerning the relationship between genetic drift and ecological drift deserve attention. First, species abundances in a community are not evenly distributed and are crucial in determining genetic drift of individual species. In a given community, the abundances of some species are equal to or larger than their effective population sizes, defined genetically, whereas the abundances of many other species are smaller than their effective population sizes. This occurs because of random variation in population size. Thus, in the same community the effect of genetic drift will be greater in species with small abundances than in those with large abundances. The extinction rate for a species with large abundance is smaller than that in the ideal population of the same species. Thus, an unequal rate of genetic drift exists among species in the same community. Similarly, the rate and effect of ecological drift are greater on rare species than on common species and an unequal rate of ecological drift exists among species as well. The current theory of ecological drift has not yet been explicitly linked to that of genetic drift, however.

Second, ecological drift can simultaneously influence population size of each species, which in turn influences the strength of genetic drift of each species. However, the effects of ecological drift on genetic drift are not linearly additive. In contrast, genetic drift should have no effect on ecological drift if alleles are selectively neutral. If alleles are not selectively neutral, then fixation of non-neutral alleles can have population consequences that affect the results of demographic stochasticity.

(ii) Gene migration versus individual dispersal

Dispersal in both macroecology and population genetics refers to the process in which individuals spread out geographically. The only difference is that migrating individuals in population genetics contain two alleles per individual for a diploid neutral nuclear gene, but one allele per individual for a haploid neutral organelle gene. In addition, gene migration in plant species can be mediated through haploid pollen grains, which is different from the diploid seed movement. Dispersal in neutral macroecology is basically the same as the migration of haploid genes in population genetics. Taken together, the total migration rate of genes to a community (the sum of migration rates of each species in a community) is no smaller than the dispersal rate (the proportion of immigrating individuals in a community) in neutral macroecology.

(iii) Neutral gene mutation versus speciation

There is no obvious relationship between the processes of speciation in neutral macroecology and mutation in population genetics. Because there is no generally accepted genetic theory of speciation at the moment, population genetics is largely silent about speciation and neutral macroecology is similarly silent about speciation mechanisms. Neutral mutations are not involved in speciation because they are mutations without functional effects. Presumably, speciation processes involve mutations of functional, non-neutral loci, where the average mutation rate is generally lower due to natural selection than it is at neutral loci, even though the underlying mechanisms are generally not yet known. Thus, the average speciation rate should be smaller than the average mutation rate at neutral loci. Also, speciation rate should be smaller than the mutation rate at individual non-neutral loci if many genes are involved in speciation, even though it is far from clear how many functional mutations are required for creating a new species.

Empirical data indicate that mutation and speciation rates are not constant. Mutation rate varies from locus to locus and different phylogenetic clades have different rates of speciation (Coyne and Orr 2004). However, neutral theories in both population genetics and macroecology assume a constant rate of mutation and speciation (clock-like assumption), or they characterize the

average mutation and speciation rate, respectively. More studies on stochastic models with variable rates of mutation or speciation are needed in both theories.

Spatial structure

We now discuss the similarity and differences relevant to the spatial structure between the two neutral theories. The similarity can be seen from the conceptual framework for modelling spatial structure. In population genetics, the models for discretely distributed populations include the island model, the stepping-stone model, the island-mainland, clines and the metapopulation structure (Wright 1969). Other models are more suitable for continuously distributed populations and more useful for studying isolation by distance (Slatkin 1993). Correspondingly, the spatial structure of a neutral metacommunity is mainly described by the theory of island biogeography (MacArthur and Wilson 1967) and other models of community structure (Chave et al. 2004). The parallel between the island biogeography theory and the island model of Wright (1969) is obvious, and a similar parallel can also be drawn between community ecology and population genetics (Table 1).

The similarity and differences are also manifest from the parameters for describing spatial structure. In macroecology, diversity can be described by parameters such α - and β -diversity. The α -diversity is equivalent to single-locus $1 - F_{is}$ in population genetics. The former describes the species diversity within a community and the later describes the genetic diversity within populations. β -diversity for describing community differentiation is equivalent to single-locus F_{st} in population genetics. β -diversity represents the turnover in species among communities over landscapes. The difference between F -statistics and α - and β -diversities is that the former is a linear partition of gene frequency variances (Weir 1996) but the latter may or may not be a linear partition of variances (Lande et al. 2003). α -diversity may be positively correlated with β -diversity although these two diversity indices represent species diversity within and between communities, respectively. This is because a high α -diversity usually reflects the presence of many locally rare species and a high turnover of these rare species from one local community to another, leading to a high β -diversity. This is similar to the relationship between $1 - F_{is}$ and F_{st} , which also shows a positive correlation inferred from the relationship of $1 - F_{it} = (1 - F_{st})(1 - F_{is})$ when F_{it} in the whole population is fixed (Wright 1969).

When the spatial structure is linked to spatial distance, a common observation is that the similarity between neighbouring individuals or populations or local communities gradually decays with distance, in terms of both the genetic correlation of allele frequency in population genetics and the correlation of species relative abundance

in neutral macroecology. The biological basis for creating such a pattern is for the separation distance to act as a barrier to dispersal (Wright 1943, Hubbell 2001). In population genetics, Nagylaki (1974) examined the probability that two homologous genes separated by a given distance in space are the same allele in geographically structured populations. This idea is in parallel to the spatial version of Simpson's index (Chave and Leigh 2002), describing the change in β -diversity with spatial distance. A negative exponential function often provides a good approximation to such naturally occurring pattern in both population genetics and neutral macroecology (Malécot 1969, Chave and Leigh 2002, Condit et al. 2002), although more complex functions have been proposed (Zillio et al. 2005).

Finally, a deeper insight into the similarity and differences of the two bodies of theory comes from considering dispersal: dispersing individuals among communities in macroecology or among populations in population genetics. In neutral macroecology, when species diversity in metacommunity is taken into account, the inter-community exchange can have different consequences (Hubbell 2001, Cadotte and Fukami 2005, Gray et al. 2005). First, high rates of dispersal can enhance local diversity but reduce metacommunity diversity, whereas low rates of dispersal may not effectively counteract the effect of ecological drift, but may enhance metacommunity diversity. This result is congruent with the situation in population genetics in which a population is subdivided into a finite number of subpopulations and each subpopulation is influenced by drift and migration, and has the same effective population size. The effective size of a whole population reduces with an increase in the inter-population migration rate (Wright 1943), $N_{e(\text{total})} = nN_{e(\text{local})}/(1 - F_{st})$, where n is the number of subpopulations. An increase in migration rate can reduce population differentiation (F_{st}) and hence reduce the effective size of the whole population. Second, if migration rates are the same among all species on a per capita basis, common species have more migrants than rare species due to sampling. The result is that there is a mass effect that causes an increased loss of rare species from the metacommunity and so metacommunity diversity actually decreases with increasing migration. However, in local communities an increasing in migration rate can cause an increase in local community diversity because migration brings species from metacommunity into local communities.

Perspectives in neutral macroecology

Is there an effective community size?

The difference between the actual population size and the effective population size has been long appreciated in population genetics. The reasons for making such a

distinction have been widely documented in the literature (Wright 1969). The concept of effective population size is useful for comparing the effects of genetic drift among populations of the same species, irrespective of the complicating effects of mating system and age structure. Its equivalence in macroecology has recently been considered (Lande et al. 2003, Orrock and Fletcher 2005).

Just as population size varies over time in population genetics, so does the size of a real community. Considering variable community size is similar to considering the problem of fluctuating drift in population genetics. In the original development of neutral macroecology by Hubbell (2001), community size was treated as a constant because of the assumption of zero-sum dynamics. In the subsequent development of the theory, this assumption has been relaxed (Volkov et al. 2003, He 2005) and community size is allowed to vary although many theoretical questions from this relaxation remain to be answered. However, even if zero-sum dynamics applies, one can still suppose that the total carrying capacity for all species in a community could vary through time. If community size can vary, which often takes place in natural communities, the concept of "effective community size" may be biologically significant. In this case, the effect of ecological drift can vary, not only because of variation in the population size of individual species, but also because of variation in community size. One typical situation is that a local community suffers a "bottleneck" event, then rare species are of a greater risk of local extinction than the expected species of their average abundance and the diversity of species may decrease more than expected from the immigration-extinction equilibrium. The importance of such effects depends upon how variable a community size really is. Large fluctuations in community size can be caused by severe disturbances, habitat fragmentation, or other natural or anthropogenic causes.

The challenge is how to mathematically and biologically define the effective community size. Lande et al. (2003) suggested that "the effective size of a neutral community with changing size and geographic structure is the size of an ideal neutral community of constant size that would produce the same expected rate of loss of Simpson diversity." A next question is how the ideal community size may be defined in analogue to the concept of ideal population size. The crucial difference between these two concepts is that mating affects effective population size in genetics but does not affect species diversity in neutral macroecology (because the dynamics of species abundance is equivalent to the dynamics of haploid genes in populations).

Hubbell's (2001) originally fixed community size J actually refers to the effective community size. This can be seen from the similarity between community size J in

neutral macroecology and effective population size in population genetics, evident from the similar diversity measures: $\theta = 4N_e v$ in neutral population genetics and $\theta = 2Jv$ in macroecology (Table 1). Because of the monotonic relationship between the Simpson index and θ (He and Hu 2005), the effective community size so defined is in essence the fixed community size J of Hubbell. Thus, like allele frequency that can vary within a population but the effective population size does not, species frequency can vary within a community but the community size J does not have to. This effective community size maintains a certain level of diversity, measured by the Simpson index or θ , for a community. The emerging question now is how much variation in J is allowed in order to maintain the same level of diversity.

It is important to be aware that although there is an equivalent role for J and N_e from the drift point of view and the effective community size can be defined as in the above, the utility of the concept of effective community size remains to be explored.

Elucidating community assembly rules

Communities are not generally governed by purely neutral processes, but are structured by the joint effect of multiple processes, some stochastic, some deterministic. Neutral theory characterizes the behaviour of communities as if all species exhibit the mean per capita demographic stochasticity in the community. In this sense, it is a "mean field" theory that describes what communities are expected to be like if all species obeyed the mean. However, to the extent that the dynamics of actual communities requires niche differences or species asymmetries to be specified, then more complex, non-neutral hypotheses have to be considered. The importance of the neutral theory is that, although simple, it embodies all of the classical demographic processes of population biology: birth, death, emigration, immigration, as well as speciation and these processes are the same among individuals. In this sense the neutral theory is mechanistic, although the biological mechanism it uses to explain the relative species abundance distribution in communities is very simple. It is currently the only theory in ecology to offer an explanation from population biology for Fisher's log series distribution. This distribution arises from density independent population growth in the metacommunity at the steady state between speciation and extinction (Volkov et al. 2003).

In population genetics, random changes in gene frequency can be induced either by genetic drift or by random fluctuation in selection intensity (Wright 1969). The two dominating processes (drift and random selection) can lead to a similar gene frequency distribution. In macroecology, the analogue to selection is

interspecific competition, both direct and indirect, leading to different relative fitnesses. Species may differ in their use and ability to sequester limiting resources (Tilman 1988) resulting in direct competition, or they may differ in their responses to predators, pathogens, or mutualists, leading to indirect competitive effects (Holt 1977, Chase and Leibold 2003). Chave et al. (2002) and Tilman (2004) have shown that incorporating such effects along with stochasticity can generate patterns of relative species abundance that qualitatively resemble those arising under purely neutral dynamics. However, neither Chave et al. (2002) nor Tilman (2004) actually confronted their more complex, alternative theories with data. Such quantitative comparisons are needed, using evaluation methods such as the Akaike Information Criterion that penalize models for fitting large numbers of free parameters. However, the most important point to make here is that ecological drift and competition are not mutually exclusive phenomena, just as genetic drift and selection are not mutually exclusive processes in population genetics. In both cases, however, additional information is required to evaluate their relative quantitative contribution to observed patterns of species abundances in communities.

Estimating the exchange of individuals between communities

The problem of estimating the number of migrants has been studied extensively with molecular markers in population genetics (Avice 1994) but is not so much studied in neutral macroecology. One of the major contributions of the neutral theory of biodiversity is to recognize the importance of dispersal limitation in structuring communities. The effects of dispersal on patterns of relative species abundance were initially obtained through simulation because the analytical form of the species–abundance model – the zero-sum multinomial distribution – was not available (Hubbell 2001). Recent advances in the field have led to several analytical forms of species–abundance models (Vallade and Houchmandzadeh 2003, Volkov et al. 2003, Alonso and McKane 2004, Etienne and Olff 2004, and particularly Etienne 2005), whose sampling formula explicitly incorporates immigration rate. This general formula has shown the usefulness of species–abundance models for estimating immigration rate in local communities. However, Volkov et al. (2005) have recently argued that observed patterns of relative species abundance do not contain sufficient information to determine whether they arise from dispersal limitation, or some other process, such as density dependence.

Two methods that originate from neutral population genetics are potentially useful in neutral macroecology, provided that the speciation rate is very small (ignorable)

in comparison with the rate of exchange of individuals among local communities. The first method is based on species turnover rate over landscape (i.e. β -diversity). The use of β -diversity to estimate the number of intercommunity migrants is analogous to the use of F_{st} to estimate the number of inter-population migrants in discretely distributed populations. The presence of migration among communities can be statistically detected using methods such as bootstrapping to find the density distribution for the number of inter-community migrants under the neutral hypothesis. The probability of observing the number of exchanging individuals can be calculated. In the case of continuous landscapes, dispersal variance instead of the number of intercommunity migrants is to be estimated. This approach focuses on the dispersal behaviour within a continuous community rather than between disjunctive communities or islands. A recent example of such an approach is the paper by Condit et al. (2002) which estimated the probability that two trees in tropical forests separated by distance r are of the same species, assuming a Gaussian diffusion dispersal process and ecological drift. However, dispersal in many cases may not be well described by Gaussian diffusion (Kot et al. 1996). This approach relies on the neutral assumption that individuals are demographically equivalent in their dispersal abilities, unlike the case of using F_{st} to estimate the number of migrants with the commonly accepted neutral markers, which make no assumptions about ecological equivalence. Thus, the estimate of the number of inter-community migrants is likely biased when the neutral hypothesis is violated.

The second approach to estimating the number of inter-community migrants is based on the distribution of locally endemic species. This approach is similar to the method that uses the distribution of private alleles to estimate the number of migrants in population genetics (Barton and Slatkin 1986). This method is based on the conditional average frequency of rare alleles calculated from the density distribution of allele frequencies. The population genetics theory is developed from the assumptions of the island model and is applicable to neutral macroecology in the case of island communities. Wright's island model can be extended to a metacommunity that is subdivided into many discrete local communities (islands). This approach should be applied to neutral macroecology with some caution, however (and they also are caveats for using the method in population genetics). The first reason for caution is the complicating effect of variable local community size. As community size increases, both the number of endemic species and their proportion increase in the community. This issue needs to be addressed for archipelagos of islands or local communities of unequal sizes. The second reason for caution is heterogeneity in migration distances

among islands that are close together or far apart. The simple version of the theory assumes all islands (or populations) are effectively equidistant from one another. This assumption needs to be relaxed in establishing an island community model in which more distant communities share fewer migrants than nearby communities. The stepping-stone model in which both short and long distance migration are considered is probably a more realistic approach for macroecology. Finally, each local community is assumed to be demographically stable (no extinction), but in reality, the potential extinction of some local communities may occur (Hanski 1998).

Testing neutrality

Understanding the relative importance of ecological drift versus non-neutral ecological processes is crucial in understanding the structure of individual communities and differences among communities. A major challenge is how to test whether the structure of communities is dominated by processes such as competition and predation or by migration and ecological drift. The answer to this question will undoubtedly partly be a function of scale. Population genetic methods are available to test if selection is involved in spatial population structure (Ohta 1982), but approaches that test for linkage disequilibrium are not readily applicable to ecological drift in a subdivided metacommunity. The use of β -diversity for testing the neutral hypothesis seems more effective since violation of any neutral assumption may cause a significant departure from the expectation under null neutral hypothesis. However, in this case, how dispersal is modelled may matter to the outcome of the test (Boreada de Agua et al. 2006). Statistical test can also be conducted using the bootstrapping method. This is similar to testing the deviation of Q_{st} (the F_{st} version in quantitative traits) from F_{st} (neutral markers) (Merilä and Crnokrak 2001).

Another challenge is to test whether the species abundance distribution is consistent with theoretical neutral predictions. There is a possibility that the species abundance distribution in a local community may depart from neutral predictions even though the metacommunity in which the local communities are embedded behaves neutrally. The departure may be caused by a phenomenon called ecological dominance in a local community. Hubbell (2001) defines the ecological dominance as an excess or deficit of abundance of a species that lies outside the 95% confidence limits of its expected stochastic mean abundance in the local community at equilibrium between immigration and local extinction. This definition differs from the classical definition based on the deviation of species

abundance from perfectly even abundance. The new definition explicitly recognizes that differing relative abundances of species are expected to arise from neutrality. Accordingly, the tests are modified to incorporate the null relative abundance distribution expected under neutrality. This is similar to testing an excess or deficit of heterozygotes. Genetic neutrality test using allele frequency or genetic marker data, such as Ewens-Watterson test (Manly 1985), may be applicable to neutral macroecology. However, the neutrality test for DNA sequence data, such as the method introduced by Tajima (1989) for testing whole DNA sample and the McDonald-Kreitman method (1991) for testing local-region sequence, seems difficult to adapt to neutral macroecology. Thus, new statistical methods to test ecological dominance are still needed.

Concluding remarks

Population genetics, community ecology and biogeography have largely been disconnected disciplines, although they share a common goal of understanding how the spatial and temporal patterns of diversity are formed and maintained over several orders of magnitude in scale. The newly developed neutral macroecology has renewed interest in developing a better theoretical understanding of patterns of relative species abundance from local to biogeographic scales. It also provides a theoretical framework within which to link ecological diversity with genetic diversity. Although population genetics and macroecology deal with problems on different hierarchical levels of the biotic realm, the neutral theories of genetics and macroecology unsurprisingly share many similarities, including driving forces, community/population assembly rules, and in some of their critical parameters. A species in neutral macroecology (infinite species model) is equivalent to an allele in population genetics (infinite allele model), and the dynamics of a species in a neutral community is equivalent to the dynamics of a haploid gene in a natural population. Differences between these two bodies of theories are also significant because the neutral macroecology focuses on the community level, whereas population genetics focuses on the population level. There is considerable room for new theoretical explorations in neutral macroecology, some of which can take advantage of previously developed theory in population genetics with little modification while some of which will require the development of new theories, as seen in the major issues discussed in this paper. These theories will doubtless contribute to better understanding, ultimately conservation, of spatial and temporal dynamics of biodiversity.

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References

- Alonso, D. and McKane, A.J. 2004. Sampling Hubbell's neutral theory of biodiversity. – *Ecol. Lett.* 7: 901–910.
- Awise, J. C. 1994. Molecular markers, natural history and evolution. – Chapman and Hall.
- Barton, N. H. and Slatkin, M. 1986. A quasi-equilibrium theory of the distribution of rare alleles in a subdivided population. – *Heredity* 56: 409–415.
- Bell, G. 2001. Neutral macroecology. – *Science* 293: 2413–2418.
- Borda de Agua, L., Hubbell, S. P. and He, F. 2006. Biodiversity scaling under neutrality. – In: Storch, D. and Sizing, A. L. (eds), *Biodiversity scaling*. Oxford Univ. Press.
- Cadotte, M.W. and Fukami, T. 2005. Dispersal, spatial scale, and species diversity in a hierarchically structured experimental landscape. – *Ecol. Lett.* 8: 548–557.
- Caswell, H. 1976. Community structure: a neutral model analysis. – *Ecol. Monogr.* 46: 327–354.
- Chase, J. M. and Leibold, M. A. 2003. *Ecological niches: linking classical and contemporary approaches*. – Univ. of Chicago Press.
- Chase, J. M. 2005. Towards a really unified theory for metacommunities. – *Funct. Ecol.* 19: 182–186.
- Chave, J. 2004. Neutral theory and community ecology. – *Ecol. Lett.* 7: 241–253.
- Chave, J. and Leigh, E.G. 2002. A spatially explicit neutral model of β -diversity in tropical forests. – *Theor. Popul. Biol.* 62: 153–168.
- Clark, J. S. and McLachlan, J.S. 2003. Stability of forest diversity. – *Nature* 423: 635–638.
- Condit, R., Pitman, N. C. A., Leigh, E. G. et al. 2002. Beta-diversity in tropical forest trees. – *Science* 295: 666–669.
- Coyne, J. A. and Orr, H. A. 2004. *Speciation*. – Sinauer Ass.
- Etienne, R. S. 2005. A new sampling formula for neutral biodiversity. – *Ecol. Lett.* 8: 253–260.
- Etienne, R. S. and Olff, H. 2004. A novel genealogical approach to neutral biodiversity theory. – *Ecol. Lett.* 7: 170–175.
- Etienne, R. S. and Alonso, D. 2005. A dispersal-limited sampling theory for species and alleles. – *Ecol. Lett.* 8: 1147–1156.
- Ewens, W. 1972. The sampling theory of selectively neutral alleles. – *Theor. Popul. Biol.* 3: 87–112.
- Gray, J. S., Björger, A. and Ugland, K. I. 2005. The impact of rare species on natural assemblages. – *J. Anim. Ecol.* 74: 1131–1139.
- Hanski, I. 1998. Metapopulation dynamics. – *Nature* 395: 41–49.
- He, F. 2005. Deriving a neutral model of species abundance from fundamental mechanisms of population dynamics. – *Funct. Ecol.* 19: 187–193.
- He, F. and Hu, X. S. 2005. Hubbell's fundamental biodiversity parameter and the Simpson diversity index. – *Ecol. Lett.* 5: 386–390.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. – *Theor. Popul. Biol.* 12: 197–229.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. – Princeton Univ. Press.
- Kimura, M. 1983. *The neutral theory of molecular evolution*. – Cambridge Univ. Press.
- Kot, M., Lewis, M. A. and van den Driessche, P. 1996. Dispersal data and the spread of invading organisms. – *Ecology* 77: 2027–2042.
- Lande, R., Engen, S. and Sæther, B. E. 2003. *Stochastic population dynamics in ecology and conservation*. – Oxford Univ. Press.

- Leibold, M. A., Holyoak, M. et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. – *Ecol. Lett.* 7: 601–613.
- Manly, B. F. J. 1985. The statistics of natural selection. – Chapman and Hall.
- MacArthur, R. H. and Wilson, E. O. 1967. The theory of island biogeography. – Princeton Univ. Press.
- Malécot, G. 1969. The mathematics of heredity. Revised, edited and translated by D. M. Yermanos. – W. H. Freeman and Co.
- McDonald, J. F. and Kreitman, M. 1991. Adaptive protein evolution at *adh* locus in *Drosophila*. – *Nature* 351: 652–654.
- McGill, B. J. 2003. A test of the unified neutral theory of biodiversity. – *Nature* 422: 881–885.
- Merilä, J. and Crnokrak, P. 2001. Comparison of genetic differentiation at marker loci and quantitative traits. – *J. Evol. Biol.* 14: 892–903.
- Mouquet, N. and Loreau, M. 2002. Coexistence in metacommunities: the regional similarity hypothesis. – *Am. Nat.* 159: 420–426.
- Nagylaki, T. 1974. The decay of genetic variability in geographically structured populations. – *Proc. Natl Acad. Sci. USA* 71: 2932–2936.
- Nee, S. 2005. The neutral theory of biodiversity: do the numbers add up? – *Funct. Ecol.* 19: 173–176.
- Ohta, T. 1982. Linkage disequilibrium due to random genetic drift in finite subdivided populations. – *Proc. Natl Acad. Sci. USA* 79: 1940–1944.
- Ohta, T. and Gillespie, J. H. 1996. Development of neutral and nearly neutral theories. – *Theor. Popul. Biol.* 49: 128–142.
- Orrock, J. L. and Fletcher, R. J. 2005. Changes in community size affect the outcome of competition. – *Am. Nat.* 166: 107–111.
- Ricklefs, R. E. 2003. A comment on Hubbell's zero-sum, ecological drift model. – *Oikos* 100: 185–191.
- Slatkin, M. 1993. Isolation by distance in equilibrium and non-equilibrium populations. – *Evolution* 47: 264–279.
- Tajima, F. 1989. Statistical method for testing the neutral mutation hypothesis by DNA polymorphism. – *Genetics* 123: 585–595.
- Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. – Princeton Univ. Press.
- Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. – *Proc. Natl Acad. Sci. USA* 101: 10854–10861.
- Vallade, M. and Houchmandzadeh, B. 2003. Analytical solution of a neutral model of biodiversity. – *Phys. Rev. E* 68: 061902–061905.
- Vellend, M. and Geber, M. A. 2005. Connections between species diversity and genetic diversity. – *Ecol. Lett.* 8: 767–781.
- Volkov, I., Banavar, J. R., Hubbell, S. P. et al. 2003. Neutral theory and relative species abundance in ecology. – *Nature* 424: 1035–1037.
- Volkov, I., Banavar, J. R., He, F. et al. 2005. Density dependence explains tree species abundance and diversity in tropical forests. – *Nature* 438: 658–661.
- Weir, B. S. 1996. Genetic data analysis II. – Sinauer Ass.
- Wright, S. 1943. Isolation by distance. – *Genetics* 28: 114–138.
- Wright, S. 1969. Evolution and the genetics of populations. Vol. 2. The theory of gene frequencies. – Univ. of Chicago Press.
- Yu, D. W., Terborgh, J. W. and Potts, M. D. 1998. Can high tree species richness be explained by Hubbell's null model? – *Ecol. Lett.* 1: 193–199.
- Zhang, D. Y. and Lin, K. 1997. The effects of competitive asymmetry on the rate of competitive displacement: how robust is Hubbell's community drift model? – *J. Theor. Biol.* 188: 361–367.
- Zillio, T., Volkov, I., Hubbell, S. P. et al. 2005. Spatial scaling relationships in ecology. – *Phys. Rev. Lett.* 95: 098101: 1–4.