

## **DISTINGUISHING THE ROLES OF DISPERSAL IN DIVERSITY MAINTENANCE AND IN DIVERSITY LIMITATION**

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**Abstract:** Considerable recent research effort has gone into studying how dispersal might affect the diversity of local communities. While this general topic has received attention from theoretical and empirical ecologists alike, the research focus has differed between the two groups; theoretical ecologists have explored the role of dispersal in the maintenance of diversity within local communities, whereas empirical ecologists have sought to quantify the role of dispersal in limiting local diversity.

We argue that there is no necessary relationship between these two components of diversity and we therefore need to develop empirical approaches to quantify the dispersal-maintained component of diversity, as well as the dispersal-limited component. We develop one such approach in this paper, based on a quantitative partitioning of the natural regeneration within intact communities onto different sources of recruits (local community vs. dispersal across different spatial or temporal scales).

**Keywords:** Community diversity, Components of diversity, Local diversity, Seed addition

### **INTRODUCTION**

Over the past decade, ecological studies have increasingly suggested that dispersal plays an important role in controlling the diversity and structure of local communities (e.g., HARRISON 1997, HUBBELL et al. 1999, SNÄLL et al. 2003, WEHNCKE et al. 2003). This focus on the community-level effects of dispersal has been motivated by a growing body of theory demonstrating that limited dispersal may modify the outcome of ecological processes, such as competition (TILMAN 1994, HURTT & PACALA 1995, LOREAU & MOUQUET 1999, STOLL & PRATI 2001, BOLKER et al. 2003, AMARASEKARE 2003) and disturbance (MOLONEY & LEVIN 1996, SEABLOOM & RICHARDS 2003), and that limited dispersal alone might even account for many of the patterns in abundance and diversity that we observe in nature (BELL 2001, HUBBELL 2001). ZOBEL & KALAMEES (2005) call for experimental approaches to assess the role of dispersal in communities is very timely in that it points to the growing lag between the rapidly developing theory and the actual empirical evidence (see also LEVINE & MURRELL 2003, LEIBOLD et al. 2004); we still do not know, in any quantitative way, to what extent, and under what conditions, dispersal actually contributes to the diversity of natural communities.

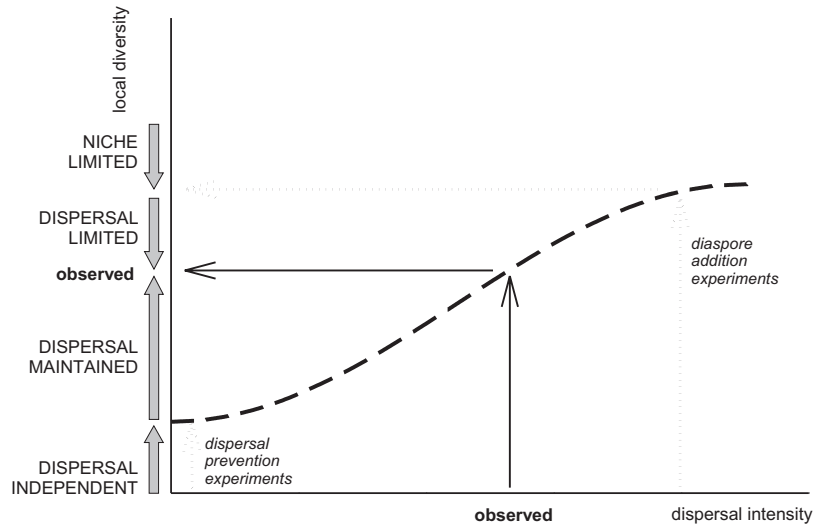


Fig 1. Relationship between dispersal and local diversity within a hypothetical community (dashed line). Dotted lines reflect some possible outcomes of different experimental approaches to study the role of dispersal in diversity limitation and diversity maintenance. Grey arrows are different components of diversity.

Unlike ZOBEL & KALAMEES (2005), however, we do not believe that seed addition experiments can provide the data needed to assess the importance of dispersal for the structure and diversity of natural communities. This is because such experiments address only whether increased dispersal could potentially lead to higher diversity, and not to what extent dispersal actually contributes to the observed diversity of communities. The distinction between these two questions is important because they incorporate quite different, and potentially independent, components of community diversity.

To illustrate this point, consider the relationship between dispersal and local diversity within a hypothetical community (Fig. 1). In this figure, the x-axis reflects some quantitative measure of dispersal, such as seed rain density or average dispersal distances traveled by seeds, and the y-axis reflects local diversity; the number of species present at the (arbitrarily chosen) spatial scale used for sampling a given community. This number is the net outcome (at the time of sampling) of both dispersal and local extinction and so represents the balance of colonization-extinction dynamics. The dashed curve describes the relationship between dispersal and local diversity in our hypothetical example. Fig. 1 illustrates how such a function divides the total pool of available species (*sensu* ZOBEL 1997) into four distinct components at any particular level of dispersal.

First, a part of the local diversity may be independent of dispersal. This is the number of species that would persist within a sampling unit in the absence of any dispersal, represented by the lower bound (y-intercept) of the function in Fig. 1. The size of this component may differ among communities, but should generally increase with the degree of niche partitioning and/or the fine-scale (within-patch) environmental heterogeneity of the particular communities (GRUBB 1977, TILMAN 1982, PACALA & TILMAN 1994). This is the component

of diversity specifically addressed by the classical models of closed communities at equilibrium (MACARTHUR & LEVINS 1967, MAY 1973, TILMAN 1982).

Second, dispersal among patches within the community, or from outside the community, may increase species richness above the dispersal-independent component, as exemplified by the observed local diversity in Fig. 1 (i.e., there is a positive net effect of among-patch colonization-extinction dynamics). If this is the case, then the local diversity is, in part, maintained by dispersal. This role of dispersal in diversity maintenance is addressed by theories that incorporate spatial dynamics into models of coexistence (see LEVINE & MURRELL 2003, LEIBOLD et al. 2004 for reviews). The outcomes under different modeling scenarios, from neutral (HUBBELL 2001) to patch dynamics (TILMAN 1994, YU & WILSON 2001) and mass effects (AMARASEKARE & NISBET 2001, MOUQUET & LOREAU 2003) suggest that dispersal may play an important role in the maintenance of local diversity under a wide range of conditions.

Third, in most communities, replicate sampling units are not identical in composition; there is species turnover, or beta-diversity, among patches within the community as well as among communities. Parts of this turnover may occur because propagules of all species do not reach all patches in every generation. In this case, the observed local diversity of any patch in the community is limited by dispersal if higher diversity could potentially be maintained under higher rates of dispersal than currently occur (ultimately; globalized). An upper bound to this component, as indicated in Fig. 1, would be expected due to the finite number of individuals that can be fitted into individual plots, or, for larger sampling units, due to the limited number of species in the available pool. This role of dispersal as a diversity-limiting factor is the one specifically addressed by diaspore addition experiments, with different variants of this question addressed by the addition of propagules from different pools, and at different densities (see ZOBEL & KALAMEES 2005). The key question addressed by these diaspore addition experiments is to what extent communities are open to immigration; this is quite distinct from the question of whether the observed diversity of a community is maintained by dispersal (Fig. 1).

Finally, part of the species turnover may be due to species being absent from patches and local communities where their environmental requirements are not met. In this case, local diversity is also limited by niche availability in which case the upper bound to diversity in Figure 1 would be affected by the environmental heterogeneity among patches and/or the niche width of the species.

Clearly, the relative magnitude of these four components of diversity within a given system will depend on the scale of measurement; all else being equal, an increase in sampling unit size should increase the number of dispersal-independent species and decrease the number of dispersal-limited and niche-limited species. Predictions about changes in the number of dispersal-maintained species are less obvious.

The relative magnitude of these components will also depend on the life history stage of organisms being examined. For example, if species sorting through mortality is an important process structuring the community, the dispersal-maintained component of diversity is likely to decline from juveniles to mature adults.

Why is it important to distinguish between these four components of diversity? To date, empirical studies have focused mainly on the role of dispersal in limiting local diversity; through diaspore addition experiments (see TURNBULL et al. 2000, ZOBEL & KALAMEES 2005). However, these experiments are often interpreted as tests of theory that, in contrast, address dispersal as potentially maintaining local diversity. This interpretation is based on a general assumption of symmetry; that if an input limits an output, increased input will lead to increased output, and decreased input will lead to decreased output. One observation from Fig. 1, however, is that this is not necessarily the case for a relationship between dispersal and diversity. This is because other factors, such as competition and niche availability, may introduce an upper bound to local diversity. The two general experimental approaches of adding diaspores to plots and preventing diaspores from entering plots are therefore not symmetrical; they quantify different, and potentially independent, components of diversity. This becomes especially obvious if we consider a hypothetical community near such an upper bound; here adding diaspores might not increase diversity significantly (e.g., due to niche limitation), but dispersal could still be a major factor contributing to the observed diversity of that community. HAIG & WESTOBY (1988) made a similar argument for the relationship between pollen limitation and seed set; they argue that results of pollen addition experiments are not necessarily indicative of the importance of pollen rain for seed set if the latter is also limited by other factors such as resource availability.

Our next step should therefore be to quantify all four components of diversity for different systems, especially focusing on dispersal-independent and dispersal-maintained diversity, which have been largely ignored empirically. This would provide the empirical data to test and parameterize theoretical models, and enable us to answer a number of important questions, such as: What are the absolute contributions of these two components of diversity to observed community diversity, and how is their relative importance affected by e.g., the size of the local or regional species pools, the spatial scale of measurement, the successional status of the local community, or environmental characteristics such as productivity or disturbance? What is the variability in dispersal-independent and dispersal-maintained diversity within and among communities? Do these components differ in the traits of their constituent species?

The significance of the different components of diversity relative to dispersal clearly depends on the shape of the function relating the two. A wide range of relationships is possible; two obvious examples, in addition to the monotonically increasing relationship suggested in Fig. 1, would be a flat or a hump-shaped relationship. The former is predicted under fully niche-based models of community assembly (e.g., TILMAN 1982), whereas the latter would be expected in the general case where one species (e.g., a natural enemy or a superior competitor) is capable of driving another extinct, for example under competition-colonization trade-offs (TILMAN 1994, BOLKER & PACALA 1997, see LEIBOLD et al. 2004). In this case, inferior competitors would go globally extinct as the dispersal of the superior competitor increases over a certain threshold. Empirically, however, the shapes of these relationships are virtually unknown. We also do not know whether the shapes or slopes of these relationships vary among communities or along gradients in any systematic way.

To answer these and related questions we need to be able to quantify the different components of diversity. Carefully designed seed addition experiments, as advocated by ZOBEL & KALAMEES (2005), are powerful tools for teasing apart the dispersal-limited and niche-limited components, but we also need to develop and expand on methodology to separate the dispersal-independent and dispersal-maintained components of observed diversity. The obvious experimental approach would be to prevent natural dispersal into intact vegetation (Fig. 1), but such experiments have, so far, only been carried out in a few cases (WILLIAMS 1984, PEART 1989, KALAMEES & ZOBEL 2002, see also EDWARDS & CRAWLEY 1999, for a similar approach to investigate the role of seedbanks). This is partly because of methodological constraints: (1) the creation and maintenance of dispersal filters may create artifacts through interfering with abiotic (e.g., light and moisture) and biotic (e.g., grazers) factors, (2) the slow dynamics of many communities could necessitate very long-term studies to actually observe the local extinctions predicted if dispersal contributes to observed diversity, and (3) decreased recruit densities, an expected side-effect of reduced dispersal by experimental manipulation, could change mortality or growth during establishment so that different dispersal treatments would not be directly comparable.

One way to avoid such methodological constraints is to carry out the experiments with synthetic rather than natural communities. Several recent reviews of metacommunity ecology (e.g., LEVINE & MURRELL 2003, BOLKER et al. 2003) point to the lack of empirical data and call for such experiments, but so far, we know of only one experiment that has actually been carried out. MOUQUET et al. (2004) created a synthetic herbaceous community, and subjected it to different dispersal scenarios. They found that diversity increased with increasing seed rain density or under a competition-colonization trade-off scenario. Future studies could expand on this approach in several ways; by including more treatments (e.g. vary not only the density and relative abundance, but also the levels of spatial aggregation in the seed rain, c.f., STOLL & PRATI 2001), by experimenting on different species and environments, and by including a broader range of plant functional types into the experiments. It would be particularly interesting to replicate such experiments along environmental gradients (e.g., productivity, disturbance) to provide empirical data on how the role of dispersal in the maintenance of diversity changes along these gradients (see questions above).

However, not all species and not all communities are suitable for such experiments. It is, for example, likely that they will be less successful in systems characterized by long generation times, complex life cycles, or very specific germination requirements. We therefore need a wider range of methodologies to explore the role of dispersal for the maintenance of diversity under a wider range of conditions. We have recently developed one such technique that enables the quantification of the contribution of dispersal to the observed diversity by using species identities as recruit “tags” (VANDVIK & GOLDBERG, unpubl. data). This is done by combining data from monitoring seedling recruitment into a set of target plots with data on the distances to the nearest possible source of recruits of each species into each of these plots. An advantage of such non-manipulative approaches is that they enable the quantification of the role of dispersal in diversity maintenance of intact communities (i.e., without interfering with other aspects of community dynamics such as density dependent processes, etc.). This opens up the possibility of following local and dispersed recruits beyond

the colonization stage, and hence to assess the relative importance of different processes, such as dispersal into patches and subsequent competitive or other interactions within patches in determining diversity of the adult vegetation (VANDVIK & GOLDBERG, unpubl.data).

The main purpose of this comment has been to point to a major source of confusion in the literature on the community-level consequences of dispersal; the frequent lack of clear distinctions between the role of dispersal as a diversity-limiting process and as a diversity-maintaining process within communities. This is not merely a terminological issue; without this distinction the statement that “dispersal is important” within a given system can actually have two very different meanings; (1) dispersal among patches contributes significantly to maintain local diversity (i.e., the dispersal-maintained component of diversity is large; Fig. 1) or (2) limited dispersal significantly decreases local diversity (i.e., the dispersal-limited component of diversity is large; Fig. 1). Both interpretations are widely used in the literature; and whereas ecological theory has largely focused on the former (e.g., HURTT & PACALA 1995, HUBBELL 2001, AMARASEKARE & NISBET 2001, CHAVE et al. 2002, BOLKER et al. 2003), empirical studies on dispersal have concentrated on the latter (e.g., TURNBULL et al. 2000, FOSTER & TILMAN 2003, GRAAE et al. 2004, MCEUEN & CURRAN 2004). However, the absolute and relative magnitude of the four components of diversity in Fig. 1 are expected to vary within and among communities, depending on factors such as species traits, landscape and habitat structure, environmental heterogeneity, and the spatial scale of measurement. This makes it unlikely that the diversity of particular communities can be understood by considering any of these components in isolation. Therefore, all four components of diversity need to be considered in further empirical and theoretical developments.

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