The Community-Level Consequences of Seed Dispersal Patterns

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■ **Abstract**   Because it lays the template from which communities develop, the pattern of dispersed seed is commonly believed to influence community structure. To test the validity of this notion, we evaluated theoretical and empirical work linking dispersal kernels to the relative abundance, distribution, dispersion, and coexistence of species. We found considerable theoretical evidence that seed dispersal affects species coexistence by slowing down exclusion through local dispersal and a competition-dispersal trade-off, yet empirical support was scant. Instead, most empirical investigations examined how dispersal affects species distribution and dispersion, subjects with little theory. This work also relied heavily on dispersal proxies and correlational analyses of community patterns, methods unable to exclude alternative hypotheses. Owing to the overall dichotomy between theory and empirical results, we argue that the importance of dispersal cannot be taken for granted. We conclude by advocating experiments that manipulate the seed dispersal pattern, and models that incorporate empirically documented dispersal kernels.

INTRODUCTION

Although ecologists have long appreciated the importance of dispersal for the spread and persistence of populations (Harper 1977, Howe & Smallwood 1982, Skellam 1951), the last decade has witnessed a surge of interest in how this phase of the life cycle influences community structure (Bullock et al. 2002, Cain et al. 2000, Clobert et al. 2001, Nathan 2003, Nathan & Muller-Landau 2000, Wang & Smith 2002). Theoretical models have been an important motivating force, with numerous studies emphasizing the importance of spatial structure in influencing species interactions. Particularly tantalizing are results suggesting that local seed dispersal or competition colonization trade-offs favor the coexistence of competitors (Murrell et al. 2001, Pacala 1997, Rees et al. 1996, Tilman 1994). Results such as these are mirrored in the tropical forest literature, where theories emphasizing the importance of limited dispersal have gained prominence (Hubbell

2001). Meanwhile, empirical ecology is increasingly implicating dispersal as an important control over species diversity. Numerous recent experimental and observational results suggest that local communities are seed limited, with diversity limited largely by the regional species pool (Cornell 1993, Srivastava 1999, Turnbull et al. 2000). Interest has also been heightened by dispersal-mediated processes in conservation biology, including habitat fragmentation (Hanski & Gilpin 1997), species ability to migrate with climate change (Clark 1998), and the spread of biological invasions (Drake et al. 1989).

Although the influence of dispersal on community structure is only beginning to be rigorously examined, ecologists seem to expect an important causal relationship. This is likely because dispersal is believed to set the template from which community patterns develop, and is well documented to influence population spread and persistence (Hanski & Gilpin 1997, Harper 1977, Skellam 1951). However, spread and persistence are very different response variables from most measures of community structure, including patterns of abundance, distribution, and coexistence. More importantly, the template laid by dispersal, often referred to as the seed rain, is influenced by other potentially more important factors, including the distribution, density, and fecundity of parent plants (Clark et al. 1998, Platt 1975), as well as landscape features that trap seeds (Schneider & Sharitz 1988) (Figure 1). Moreover, as noted by several authors (Nathan & Muller-Landau 2000, Schupp & Fuentes 1995, Wang & Smith 2002), a number of important life history processes occur between dispersal and the progression to adult plants. Species interactions and environmental factors strongly influence these transitions and can significantly change the template laid by dispersal (Figure 1). Thus, unless populations are substantially seed limited, the importance of the dispersal kernel for the abundance, distribution, and diversity of species should not be assumed a priori.

In this paper, we critically review theoretical and empirical work relating patterns of dispersal to spatial patterns in communities in an attempt to provide a critical framework for research in this area. More specifically, we ask how important the specific seed dispersal kernel or seed shadow is for explaining relative abundance, distributions, and coexistence in natural communities. By dispersal kernel, we mean the probability density function describing the probability of seed transport to various distances from the parent plant. Although both theoretical and empirical approaches address the importance of seed dispersal for community structure, a large gap exists in the coverage and motivation behind the different methods. As we demonstrate, the modeling work is focused largely on coexistence, motivated by interest in how incorporating spatial processes changes the predictions of earlier nonspatial models. Meanwhile, the empirical work focuses largely on dispersal's effect on species distributions, motivated by natural history observations related to dispersal kernels, the movement of animal vectors, seed trapping patterns, or the clumping of parent plants. Thus, of primary interest in our review is how empirical results match the predictions of theory.

To encourage a greater exchange of ideas and questions between empirical and theoretical approaches, we organize our review around the influence of dispersal kernels on four key features of community structure: patterns of relative
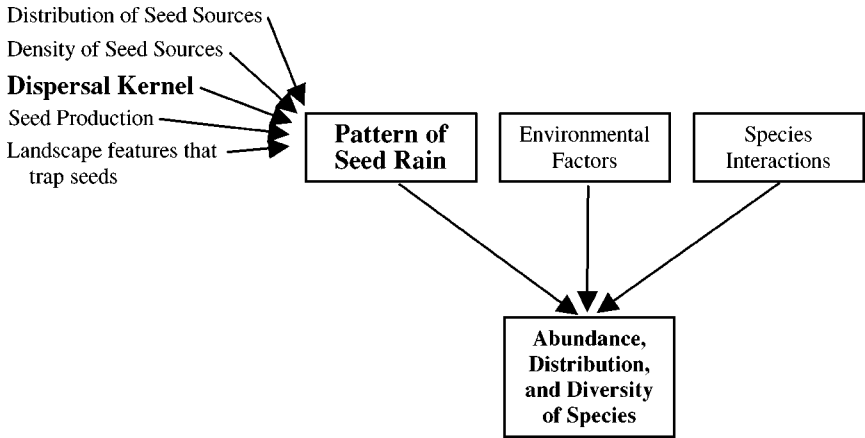
Figure 1 Pathway by which the shape of species dispersal kernels can influence the abundance, distribution, and diversity of species. Shown in bold is the link between dispersal kernals and community patterns that we examine in this review. We emphasize the multitude of factors other than dispersal kernels influencing the seed rain, and the multitude of factors other than seed rain influencing the abundance, distribution, and diversity of species.

abundance, distribution, dispersion, and coexistence. For each of these features, we first chart theoretical predictions on the importance of dispersal and then review evidence for these predictions in the empirical literature. We located our papers by electronically searching the Science Citation Index and examining references therein. Because of the large body of theoretical work on coexistence, we divide this literature into two sections, one describing the effects of local dispersal, the other focused on competition-dispersal trade-offs. For similar reasons, we review the work examining dispersal effects on dispersion separately from work on other types of distribution patterns. We do not review dispersal effects on persistence and spread (Hanski & Gilpin 1997, Howe & Smallwood 1982, Shigesada & Kawasaki 2002, Skellam 1951), the evolution of dispersal (Clobert et al. 2001), or the effects of colonization on community patterns achieved through dormancy or high fecundity. Still, it should be noted that both dormancy and fecundity combine with dispersal to influence colonization (Harper 1977).

RELATIVE ABUNDANCE

Theoretical Background

Over the past decade, it has become increasingly common to regard local populations as embedded within a larger metapopulation structure. In classic (Levins 1969) and contemporary (Hanski & Gilpin 1997) metapopulation models, species abundance at the metapopulation scale is a function of the colonization and

extinction of individual subpopulations or patches. Thus, species ability to disperse may be an important determinant of relative abundance—which species are common and which are rare.

The expectation that dispersal is positively related to abundance also emerges in several other types of models (Turnbull et al. 2000). In spatial mass effect models (Shmida & Ellner 1984), species occupy marginally unfavorable habitats because of seed input from other, more favorable, locations. Greater input caused by increased dispersal can enhance abundance in these systems. Similarly, if community dynamics can be conceived as a competitive lottery (Chesson & Warner 1981), species can dominate systems by having high colonization rates, achievable through effective dispersal or high fecundity. Greater abundance of better-dispersing species is also predicted under the Janzen-Connell hypothesis (Connell 1971, Howe 1989, Janzen 1970, Schupp & Fuentes 1995), where dispersal away from the parent plant confers greatly reduced density-dependent mortality (Ellner 2001, Law et al. 2003, Pacala & Silander 1985). Although similar predictions emerge from these models collectively, it is the metapopulation predictions that have been most influential in motivating empirical tests of how abundance at the metapopulation scale relates to dispersal ability (Eriksson 1997, Eriksson & Jakobsson 1998).

These tests, however, may not have considered that long-range dispersal is sometimes disadvantageous in models. For example, if the landscape is variable in (abiotic) quality, depending on the spatial scale of favorable and unfavorable patches, short-range dispersal may lead to higher abundance than long-range dispersal (Bolker 2003, Dockery et al. 1998, Travis & Dytham 1999). In these cases the importance of remaining in a good patch more than outweighs the increased intraspecific competition often resulting from short-range dispersal.

Empirical Evidence for a Relationship Between Dispersal and Abundance

In addition to theoretical predictions, empirical work at the population level would seem to suggest that species ability to disperse is an important predictor of relative abundance, at least in some systems. A number of seed addition experiments (see Turnbull et al. 2000 for review) suggest that for early successional systems in particular, seed limitation is common, and thus greater dispersal should confer greater abundance. Nonetheless, in our review of empirical evidence, we found little support for the expectation that relative abundance was controlled by dispersal patterns. For example, Rabinowitz & Rapp (1981) found no relationship between abundance and dispersal under field conditions in a Missouri prairie. Similarly, Eriksson & Jakobsson (1998) found that dispersal mode was unrelated to abundance and geographic range size for over 80 grassland plant species in Sweden. Also in Sweden, the ability of 17 species to disperse on the fur of animals was unrelated to their occupancy rates in seminatural grasslands (Kiviniemi & Eriksson 1999). In the herbaceous flora of central England, seed dispersal as

estimated through terminal velocity was very weakly related to species abundance as assessed by their UK range (Thompson et al. 1999). Thompson et al. (1999) and Eriksson & Jakobsson (1998) reviewed the literature relating dispersal mode to geographic range size more generally and found similarly ambiguous results.

Support for the notion that dispersal dictates commonness and rarity might seem to come from annual plant communities. It is often found that common species are small seeded, whereas large-seeded species are consistently rare (Guo et al. 2000, Levine & Rees 2002, Maranon & Grubb 1993, Rees 1995, Rees et al. 1996). However, although small-seeded species may be better colonizers, this is more likely the result of a relationship between seed size and fecundity rather than seed size and dispersal. Small-seeded species consistently produce more seeds (Jakobsson & Eriksson 2000, Leishman 2001, Rees 1995, Shipley & Dion 1992, Turnbull et al. 1999), yet seed size is very poorly related to dispersal (Carey & Watkinson 1993, Westoby et al. 1996).

How can we explain the absence of a relationship between abundance and seed dispersal when experiments often show seed-limited populations? One likely possibility is that the evidence for seed limitation is more a product of low seed production or a low density of adult plants than of poor dispersal. In addition, numerous other processes, such as competition, dormancy, and habitat variation, may simply be more important than dispersal in controlling relative abundance patterns in communities (Figure 1). Because dispersal can clearly influence the rate of species arrival, it may be more important in controlling temporal patterns of abundance after disturbance. In a simulation study, Hovestadt et al. (2000) showed that long-range dispersers were more abundant in the colonization phase immediately after disturbance, but depending on model details, short-range dispersers subsequently obtained a higher relative abundance. Indeed, on lake islands in Sweden, species lacking traits for water, wind, or animal dispersal are rare or absent early in succession (Rydin & Borgegard 1991), but become abundant years later. Despite these temporal patterns, we conclude that little empirical evidence supports the expectation that interspecific differences in dispersal control commonness and rarity at metapopulation scales.

SPATIAL DISTRIBUTION

Theoretical Background

The distance and direction a plant disperses its seeds should play an important role in the distribution of that species. However, as illustrated in Figure 1 (left), the influence of the dispersal kernel will depend strongly on the importance of other factors influencing the seed rain. For example, Levine (2003) modeled a streamside plant assemblage where species occur in discrete habitat patches linearly arrayed along the channel. Species dispersed 60% of their seeds to other patches and 95% of those seeds to patches downstream. In such a system, one

naturally expects greater deposition downstream than upstream. However, Levine demonstrated that with a uniform distribution of parent plants throughout the system and a reasonable dispersal kernel, most seed input comes from the one or two patches upstream of the target patch. Thus, downstream of the first few patches in the system, seed input increases only marginally. Still, this relatively small downstream variation in seed deposition could drive downstream increases in population size and diversity, but only if the component populations are highly seed limited, as resulting from very low fecundity or recent disturbance. This result demonstrates two points introduced by Figure 1. First, the relationship between the seed-dispersal kernel and the seed rain can be complicated, deserving significantly more attention from both theoreticians and empiricists. Second, for patterns of seed rain to influence species distributions, the component populations must be constrained by seed availability and not species interactions or environmental factors.

The Importance of Seed-Trapping Agents

In contrast to theory, numerous empirical studies have related seed deposition to species distributions, yet in most of the work, spatial variation in deposition is not easily related to the dispersal kernels. Instead, it is driven largely by landscape elements that trap seeds or propagules. Differences in seed morphology still influence deposition patterns but do so largely through their interaction with the trapping agents. For example, Schneider & Sharitz (1988) tracked the dispersal of tree seeds in a swamp forest in the southeastern United States. Seeds were initially gravity dispersed, but then as water levels rose, they were redistributed by hydrochory to locations against emergent structures including twigs, trees, logs, branches, knees, and stumps. Some of these substrates, such as trees and tree knees, provided elevated stable microsites, and tree seedlings were disproportionately found in these locations. Importantly, seed morphology influenced deposition and seedling patterns across species. The small, angular cypress seeds were more frequently trapped by knees than the larger ellipsoid tupelo fruits. Consequently, 45% of the cypress seedlings occurred on knees in comparison to only 27% of tupelo seedlings.

Several studies conducted in northern Swedish rivers have experimentally released propagules or propagule mimics and correlated their deposition with species distributions and diversity. Although not a seed-dispersal study, Johansson & Nilsson (1993) tagged uniformly sized ramets of the vegetatively dispersing *Ranunculus lingua* and correlated their deposition with the presence of established plants. They found that ramet deposition was disproportionately high in curves and at obstacles along the river, also the locations where established stands tended to be found (see Andersson et al. 2000 for a similar approach focusing on diversity). Patterns such as these may relate to propagule characteristics. Nilsson et al. (1991) found that long-floating species tended to be more abundant in areas that trapped floating seed mimics, whereas the distribution of short-floating species

was unrelated to trapping patterns. Danvind & Nilsson (1997) found no correlation between floating time and distribution patterns along an alpine Swedish river.

Seed deposition driven by trapping has also been correlated with species distributions in nonriverine studies. Rabinowitz (1978) hypothesized that the different sized seeds of the three mangrove dominants in Panama were trapped at different points along the tidal elevation gradient, matching the elevational distribution of adult trees. Support was provided by the experimental transport of mangrove propagules outside their tidal zone, which showed survivorship across the elevation gradient. Nonetheless, recent work (W. Sousa & B. Mitchell, manuscript in review) estimating the dispersal kernels in the same mangrove forests has found no evidence for tidal sorting of propagules. In a similar system, Rand (2000) found that the restricted distribution of several salt marsh species to particular tidal elevations was more a function of competition and physiological stresses than seed deposition patterns. In contrast, in the Negev desert of Israel, *Anastica hierochuntica* forms reticulate distribution patterns that relate to seed deposition in the cracks that form with the wetting and drying of the soil (Friedman & Stein 1980). Peart & Clifford (1987) attributed the segregation of grass species across different soil types to the interaction of the soil texture and cracking with the different awn types of the various species.

In these studies, patterns of seed deposition result from structures or topography that traps or sorts propagules. Seed morphology then influences not only how seeds move, but maybe more importantly, where seeds stop, a less appreciated and more difficult to predict component of the dispersal kernel. The realized distribution of seeds may therefore be very different than the potential distribution predicted by the dispersal kernel alone. In addition, the local community surrounding a dispersing individual may strongly influence the dispersal kernel by trapping seeds and influencing the size of the disperser through competition. Consequently, further work clarifying the relationship between dispersal kernels and patterns of deposition (Figure 1, left) is particularly important for clarifying its influence on distributions (Alcantara et al. 2000).

Distributions Driven by Dispersal Kernels

Relatively few studies related seed-dispersal kernels to distribution patterns. In one of the only studies relating dispersal to the seed rain, Dalling et al. (2002) demonstrated that spatial patterns of seed rain for many neotropical pioneer trees were driven largely by limited dispersal. The resulting seed rain patterns were an important predictor of seedling abundance in forest gaps. Similarly, Platt & Weiss (1977) examined field-derived dispersal kernels and competitive traits of fugitive plants living on badger mounds in an Iowa prairie. The species segregate across a habitat gradient in mound density such that the more poorly dispersing species dominate the portion of habitat with closely spaced mounds, whereas better-dispersing species dominate the area with distantly spaced mounds. Parallel

gradients in soil moisture and interspecific differences in physiological tolerance maintain the species segregation.

Several riverine studies begin with the assumption that asymmetric downstream dispersal drives longitudinal variation in seed deposition in these systems (but see Levine 2003). They then attribute downstream increases in diversity to dispersal. Nilsson et al. (1994) found that tributaries of the Vindel river in Sweden contained only a subset of those species found in the main stem, a result they attributed to the downstream transport and accumulation of seeds. Honnay et al. (2001) analyzed spatial patterns of diversity in plant communities along dendritic networks of small forest streams and came to similar conclusions (also see Friedman & Stein 1980). These studies, however, are simply correlational analyses of community patterns. No measurements of seed dispersal, deposition, or limitation are made, and thus as Nilsson et al. (1994) acknowledge, other processes, particularly changing environmental conditions along the downstream gradient, could also explain the diversity pattern. A more manipulative approach was taken by Levine (2001), who documented downstream increases in diversity and individual plant abundance along the Eel river in California. Experimentally released propagule mimics successfully dispersed to suitable microsites downstream, and the streambed assemblages were seed limited. Most importantly, when seed supply was experimentally equalized across the downstream gradient, there was no greater colonization of the most downstream habitats as compared with those 5 km upstream. Nonetheless, even with all this evidence, whether downstream dispersal is sufficient to drive downstream increases in seed deposition remains untested in this and other work.

Considering the relative rarity of hydrochory in nature, our review documented a disproportionate number of studies where water dispersal influenced species distributions. In part, this can be attributed to the obvious directional movement of water in many systems. In addition, the plant communities that line rivers and lakeshores are readily disturbed, likely preventing processes such as competition from exerting their full impacts. Last, the flooding that occurs in these habitats can export most of the seed, favoring seed limitation (Levine 2001). Despite the apparent importance of dispersal for distributions in systems with hydrochory, few empirical studies in these or other habitats tested for seed limitation or examined the processes occurring between seed arrival and the progression to adult plants. Thus, regardless of whether the distribution patterns are argued to result from trapping agents or dispersal kernels, the empirical evidence as a whole is highly correlational, often unable to exclude alternative explanations for the putative dispersal-driven distribution patterns.

DISPERSION

The aggregation of species in communities can influence the rate of competitive displacement (Stoll & Prati 2001), patterns of resource availability (Pastor et al. 1999), and macroecological patterns including species-area curves and species-abundance distributions (Chave et al. 2002). Because local dispersal is an obvious

source of clumping, numerous studies attribute adult aggregation to restricted seed transport. However, as is true with distribution patterns more generally, a number of conditions have to be met before dispersal controls dispersion patterns (Schupp & Fuentes 1995). Not only must the component populations be so sparsely arrayed that local dispersal drives clumping of dispersed seeds, but density-dependent mortality cannot be so severe as to eliminate the aggregation of seedlings.

Models Where Local Dispersal Generates Aggregation

Bleher et al. (2002) used simulation models to show that local dispersal and, to a lesser degree, low adult density strongly influenced the clumping of forest trees. Bleher et al. accomplished this by constraining fecundity such that all species effectively produce one offspring, but the relevance of such growth rates to natural systems is unclear. Presumably, with different fecundity across species, some populations would grow and their patches would coalesce, whereas others would decline and their clumps contract. Like Bleher et al., Chave et al. (2002) examined clumping patterns in neutral models (where birth rates just balance death rates), and showed greater clumping with increased local dispersal. Chave et al. also explored the influence of local dispersal in models where stable coexistence is achieved through a competition-fecundity trade-off and density dependence. They showed that when these other processes generate coexistence, local dispersal can strongly influence clumping, which causes the species-area curve to rise more gradually than when species are more diffusely spread through the habitat. Dispersal-generated clumping can also influence ecosystem processes. In a simulation model of boreal forest where species differ in decomposability, Pastor et al. (1999) showed how local dispersal generates species aggregation that alters the spatial pattern of nitrogen availability.

Further support for the influence of local dispersal on clumping is explicitly or implicitly provided by studies demonstrating its impact on coexistence (reviewed below). Still, it is important to remember that dispersal is just one of several spatial processes that shape the pattern of individuals across the landscape (Figure 1) (Schupp & Fuentes 1995). For example, because interactions between individuals also tend to be localized in space, offspring experience intense kin competition with local dispersal. Theory shows that local interactions can cause the realized pattern of adults to be random, overdispersed (spatially segregated or evenly spaced) or clumped (Ellner 2001, Law et al. 2003, Molofsky et al 2002, Pacala & Silander 1985). Generally, to achieve aggregation in homogeneous space with local dispersal, interactions must occur on a spatial scale similar to that of the dispersal kernel (Ellner 2001, Law et al. 2003, Pacala & Silander 1985). If dispersal occurs over much larger scales than neighborhood interactions then an even spacing of conspecific individuals is expected (Law et al. 2003). Alternatively, processes other than dispersal (Figure 1), such as spatial heterogeneity in the external environment, or reduced pollination of isolated individuals, may also generate aggregation. In sum, theory suggests that depending on the spatial scale of density dependence, local

dispersal can drive a wide range of dispersion patterns, patterns that can also be explained by variation in environment.

Empirical Evidence

A large body of empirical work documents local seed dispersal and an aggregated distribution of adults, and suggests a causal link between the two (e.g., Bleher & Bohning-Gaese 2001, Fragaso 1997, Westelaken & Maun 1985). However, as argued by Schupp & Fuentes (1995) and put forth by theoretical work more generally, because of the primacy of processes occurring between seed arrival and maturity to adult plants, this correlative evidence is insufficient to demonstrate dispersal-driven patterns. Indeed, Overton (1996) documented local dispersal of mistletoe, but this had no effect on the spatial autocorrelation in the number of mistletoe per tree. More generally, numerous studies have found that the aggregated distribution of seeds and seedlings following local dispersal tends to disappear as the seedlings mature (Barot et al. 1999, Houle 1995, Rey & Alcantara 2000, Schupp & Fuentes 1995). We thus concentrate our review on several more quantitative and comparative approaches to assessing the importance of dispersal for aggregation patterns.

Because the major alternative to dispersal for explaining a clumped species distribution involves patchy environmental variables, one approach for testing the importance of local dispersal is to use multiple regression to ask whether species are more clumped than can be explained by spatial variation in the environment alone. Svenning (2001) found that aggregation of four palm species in an Andean rainforest could not be explained by variation in forest structure, topographic-edaphic conditions, altitude, or aspect. This, coupled with greater densities of seedlings near adult plants, caused the investigator to implicate dispersal as a control over the clumped distribution of these species. With a similar approach, Svenning & Skov (2002) found that in a managed forest in Denmark, 20 of 60 understorey plant species exhibited aggregation unexplainable by environmental parameters and thus attributable to dispersal. Moreover, animal- and wind-dispersed species showed less clumping than species with less-efficient dispersal modes. In contrast to these results, the predominance of environmental variables in influencing tree clumping patterns was suggested for the palm *Borassa aethiopum* in an African savanna (Barot et al. 1999) and for species occupying South Pacific island (Webb & Fa'aumu 1999) and Malaysian (Plotkin et al. 2002) forest.

Similar approaches have been used to attribute species turnover through space to dispersal. Tuomisto et al. (2003) found that decreasing floristic similarity with distance in Amazonian rainforests could not be entirely explained by changing environments with distance, pointing to the potential importance of local dispersal. Moreover, the importance of geographic distance alone (a proxy for local dispersal) versus environmental factors was comparatively less important in pteridophytes than in the more poorly dispersed Melastome shrubs, further supporting the role of dispersal. Similarly, Condit et al. (2002) used predictions of Hubbell's (2001)

neutral model to argue that local dispersal could explain patterns of species turnover in tropical rainforests over the scale of 0.2 to 50 km.

An alternative approach for assessing how seed transport influences patterns of aggregation assumes that dispersal mode is a predictor of dispersal kernels (Willson 1993), and compares clumping across species differing in dispersal mode. Working in a Costa Rican dry forest, Hubbell (1979) found that the rate at which density declined with distance from adults was steepest for species dispersed by mammals, followed by wind, and then by birds and bats. Condit et al. (2000) found that wind- or explosively dispersed species were less clumped than animal-dispersed species in a Panamanian forest, but this difference was nonsignificant. Nonetheless, in a Malaysian forest, dipterocarps, with their poorly dispersed seeds were more aggregated than nondipterocarps (Condit et al. 2000). Also studying Malaysian rain forest trees, Plotkin et al. (2002) described how seed-dispersal mode influences the spatial distribution of large and small individuals within a cluster. In earlier work, Plotkin et al. (2000) showed clustering of individuals independent of topography, suggestive of dispersal driven aggregation.

Results for species other than tropical trees are more equivocal. Nieder et al. (2000) found that whether epiphytes were dispersed via wind or animals was unrelated to their degree of clumping. In contrast to the Hubbell (1979) results, but at a much smaller scale (2 m × 0.5 m plots), Myster & Picket (1992) found that bird-dispersed trees invading an old field were more clumped than those dispersed by wind or mammals. The perching behavior of birds presumably generates clumps of seed at this smaller spatial scale. A number of other studies have demonstrated that animal dispersal causes very local aggregation of seeds (Howe 1989).

Limitations of Current Approaches

One very important limitation of the work relating aggregation to dispersal is that nearly all of the evidence is correlational or indirect. These results are thus best regarded as patterns that generate hypotheses, rather than definitive support for the importance of dispersal. A number of key assumptions are implicit when dispersal is assessed as the residual clumping unexplained by environmental variables (as in Svenning 2001, Svenning & Skov 2002, Tuomisto et al. 2003). Most significantly, we must assume that all potentially important environmental variables, past or present, are accounted for in the statistical model. Any unmeasured variables must at least be correlated with those that are quantified. This is probably an unreasonable assumption because an historical process such as a forest gap four decades ago could easily influence clumping patterns today, yet unless it left a signature in currently measured environmental variables, such an effect would be incorrectly attributed to dispersal. In addition, these studies assume that positive density dependence, as might arise though pollination or shared soil mutualists, is not important.

Other concerns exist for studies using dispersal mode as a proxy for the dispersal kernel or mean dispersal distance. Dispersal mode is often shared across members of a family, such as wind dispersal in the Asteraceae, and is thus likely to be

correlated with other factors that could influence clumping, such as seed production or competitive ability. Indeed, Horvitz & LeCorff (1993) found that within the tropical understorey herbs of the Marantaceae, ant- versus bird-dispersed plants did not differ in their degree of clumping. The potential power of alternative experimental approaches for assessing the influence of dispersal patterns on aggregation is emphasized by Turnbull et al. (1999). When annual species of limestone grassland were dispersed randomly by the investigators, the community that developed still showed strong aggregation, indicating that environmental variables exert important controls over dispersion patterns in the system.

A more general problem in this work is that aggregation is a scale-dependent measure, and thus species clumped at one scale may be randomly distributed at another. Thus, if the question is whether dispersal is important to the degree of aggregation, then the measurement of aggregation needs to be made over scales similar to the spatial scale of dispersal. Aggregations at scales larger than dispersal may indicate the importance of larger-scale processes such as environmental heterogeneity. For example, Peres & Baider's (1997) hypothesis that clumping in Brazilnut trees is dispersal driven may seem reasonable considering that the spatial scale of the seed-dispersal kernel generated by agoutis matches the scale of tree clumping. By contrast, it is not surprising that dispersal mode does not influence plant clumping at the scale of 10×10 km grid cells dividing the United Kingdom (Quinn et al. 1994).

COEXISTENCE THROUGH LOCAL DISPERSAL, AGGREGATION, AND SEGREGATION

Classic Lotka-Volterra competition models assume that dispersal and species interactions are spatially unrestricted. Much of the recent interest in the influence of species dispersal on community structure has been motivated by theoretical work relaxing this assumption. Results suggest that local dispersal often slows rates of competitive displacement (Bolker & Pacala 1999, Law et al. 2003, Murrell & Law 2003). This, along with coexistence achieved through a competition-colonization trade-off has generated a surge of interest in spatial processes in plant communities (Murrell et al. 2001, Murrell & Law 2003). However, as we explain below, the literature relating local dispersal to coexistence is plagued by ambiguity over the temporal scales over which local dispersal influences coexistence.

Models Showing Local Dispersal Effects on Coexistence

An increasingly popular perception among ecologists has been that local dispersal promotes coexistence by causing the spatial segregation of heterospecific individuals across a landscape (e.g., Green 1989, Murrell et al. 2001, Pacala 1997, Pacala & Levin 1997, Weiner & Conte 1981). In homogeneous environments (as assumed in most community theory), mathematical models for two-species

competition show that local dispersal contributes more to the aggregation of conspecifics through parent-offspring proximity than it does to aggregation of heterospecifics (Murrell & Law 2003). This segregation of species reduces the relative frequency of inter-versus intraspecific interactions (Pacala 1997); more generally, weaker inter-versus intraspecific competition favors coexistence (Chesson 2000). Local interactions are also key in these models (Bolker & Pacala 1997, 1999; Dieckmann et al. 2000; Law et al. 2001, 2003; Murrell & Law 2003). If species interact with other individuals in a system over a sufficiently large spatial scale, local dispersal will have little effect on the frequency of heterospecific versus conspecific interactions.

However, the importance of such spatial segregation for long-term coexistence has recently been challenged on several counts. First, it is apparent that inequality in dispersal kernels between otherwise similar species will lead to the exclusion of the more aggregated species (the shortest disperser, all else being equal) (Bolker & Pacala 1999, Durrett & Levin 1998, Murrell & Law 2003, Pacala 1986). Second, even if dispersal is symmetric, segregation on its own is not enough to prevent exclusion where it is predicted in the nonspatial case (Chesson & Neuhauser 2002, Durrett & Levin 1998, Ghandi et al. 1998, Neuhauser & Pacala 1999, Takenaka et al. 1997). In these models, the dynamics may be thought of as having two phases: the initial phase where monospecific clusters build up owing to local dispersal, and the second phase where these clusters start to interact. It is the second phase that is most important for determining the long-term (equilibrium) outcome of competition, and in particular it is the interactions at the cluster boundaries that are of greatest importance (Chesson & Neuhauser 2002, Ghandi et al. 1998). Here, heterospecific interactions are relatively frequent and the stronger competitor wins. Thus, clusters of the stronger species will slowly but surely overwhelm the clusters of the weaker species. It is notable that the speed with which this occurs is dependent on the geometry of the cluster boundary; the larger the curvature of the cluster interface the faster the rate of exclusion (Ghandi et al. 1998). The curvature of the clusters is greatly dependent on the dispersal kernel, providing a mechanistic link between the dispersal distance and the rate of exclusion.

Thus, rather than a stabilizing force for coexistence, localized dispersal may be thought of as an equalizing process because it slows down the dynamics without changing the expected equilibrium (Chesson 2000, Ghandi et al. 1998). Nonetheless, by slowing exclusion to such long timescales, other processes such as immigration (Hubbell 2001) and selection (Aarssen 1984, Park & Lloyd 1955, Pimentel 1968) may act to maintain diversity. In neutral models explored by Hubbell (2001) and Chave et al. (2002), local dispersal slows the rate at which species drift to extinction. Because these models also incorporate external immigration or speciation, this slowing of displacement increases species richness by changing the balance between extinction and speciation (or colonization). In doing so, local dispersal also changes the species-abundance distribution (Chave et al. 2002). Similar results are achieved when species coexist through density dependence or fecundity-competition trade-offs.

In a comparatively rare example of theory examining the effects of local dispersal in spatially heterogeneous environments, Snyder & Chesson (2003) found that local dispersal increased the degree of coexistence as compared with that achieved under global dispersal. This result requires niche differentiation among species and dispersal occurring over smaller spatial scales than the environmental autocorrelation. However, in the model, environmental heterogeneity is fixed, and as the authors caution, longer-range dispersal may be more important in temporally heterogeneous environments.

A possibly more surprising result of segregation is that, at least in discrete-space models where interactions occur in very small neighborhoods (nearest neighbor on a grid), local dispersal can hinder coexistence (Bolker et al. 2003, Neuhauser & Pacala 1999). This occurs when species are competitively unequal but intra- is greater than interspecific competition, allowing coexistence in the nonspatial analog. Nonetheless, this effect only serves to reduce the amount of coexistence where it is marginal in the first place.

Much of the above theory is based on the well known Lotka-Volterra competition equations, which are extended to include local interactions and local dispersal. Clark & Ji (1995) used a more mechanistic, patch-based model to show that local dispersal between neighboring patches and a disturbance regime that reset patches periodically could aid coexistence as long as there was spatial variation in seed deposition (caused by both seed limitation and local dispersal), and a nonlinear relationship between fecundity and patch density. As in a spatial-storage effect (Chesson 2000), high seed production in relatively uncrowded patches more than outweighs the poor seed production in crowded patches, allowing stable coexistence. Incorporating a more mechanistic approach, such as that used by Clark & Ji, while still including local interactions and local dispersal, would be of much value in extending the theory on dispersal and coexistence.

Field Evidence that Local Dispersal Influences Coexistence

Motivated by the results of recent theory, a large number of empirical studies now speculate that local interactions favor coexistence (e.g., Hubbell et al. 1999, Tuomisto et al. 2003). However, largely owing to the only recent development of the models, the rigorous empirical tests required to justify such claims have yet to be completed. Rees et al. (1996) used models fit to monitoring data of sand dune annuals in Britain to show that species suffered intense intraspecific competition but little interspecific competition in the field. They attributed this result to the high degree of intraspecific aggregation found in the system. The degree to which this clumping resulted from local dispersal versus species specialization on different habitat types was unclear. Stoll & Prati (2001) examined competitive interactions among species experimentally planted in clumped versus random distributions. Consistent with aggregation enhancing the impacts of intra-versus interspecific interactions, competitively inferior species performed better, and competitively superior species performed worse in the aggregated treatment. These results are similar to those in a longer-term study by Schmidt (Rejmanek 2002, Schmidt 1981),

which showed that over a period of three years, intraspecific aggregation allowed the exotic *Solidago canadensis* to coexist with the native *Urtica dioica*, whereas without the aggregation, *S. canadensis* was quickly excluded. Both studies follow from a history of applied research examining how spatial patterning influences the impacts of weeds on crops (Garrett & Dixon 1998). We emphasize, however, that local dispersal need not always be important. Webb & Peart (2001) used models parameterized with field data to suggest that local dispersal was relatively unimportant for tree coexistence in a Bornean tropical forest.

We conclude from published work that local dispersal does not favor the long-term coexistence of species but instead simply slows the rate of displacement. Thus, if we want to attribute the coexistence of species in a natural community to the local nature of dispersal, we need to first clarify the timescales over which we are attempting to explain coexistence and then demonstrate that local dispersal is sufficient to explain coexistence over those timescales. This is very different than demonstrating the almost trivial result that local dispersal slows down displacement. Incorporating timescales will almost undoubtedly require the use of models parameterized with field data, as advocated in our conclusions.

COEXISTENCE THROUGH COMPETITION-DISPERSAL TRADE-OFFS

Ecologists have long known that a superior competitor and superior colonizer can coexist in homogeneous model systems (Hastings 1980, Holmes & Wilson 1998, Horn & MacArthur 1972, Hutchinson 1951, Levins & Culver 1971, Tilman 1994). However, the recent demonstration that this mechanism of coexistence extends to any number of species (Tilman 1994) has generated a surge of interest in this area. Coexistence occurs because the superior competitor lacks the colonization ability to fill all available habitats, leaving space for more poorly competing but better-colonizing species. Although colonization is a function of both fecundity and dispersal ability, most theory has assumed a competition-fecundity trade-off (Hastings 1980, Tilman 1994); only more recently has dispersal distance been considered explicitly (Bolker & Pacala 1999, Dytham 1994, Holmes & Wilson 1998, Murrell & Law 2003). Although our primary interest is coexistence through competition-dispersal trade-offs, we also review relevant theoretical results incorporating competition-fecundity trade-offs.

Assumptions Underlying Theoretical Results

The result that numerous species can coexist through a competition-colonization trade-off (Tilman 1994) depends on several questionable assumptions. First, there must be a strict hierarchy of competition inversely related to colonization. Second, the colonization of a stronger competitor must always eliminate any established weaker competitor from its location, and do so prior to its reproduction (Tilman 1994, Yu & Wilson 2001). This rapid displacement assumption seems particularly unrealistic for many plants (Levine & Rees 2002, Yu & Wilson 2001)

because seedlings are unlikely to outcompete established individuals. Relaxing this assumption recovers so-called lottery models, where competition for empty sites occurs at the juvenile stage (Yu & Wilson 2001). In such lottery models, the competition-colonization trade-off is insufficient to produce coexistence, although coexistence can be achieved with environmental heterogeneity, fecundity-dispersal trade-offs, or stochastic variation in seed arrival (Chesson & Warner 1981, Comins & Noble 1985, Kisdi & Geritz 2003, Kohyama 1993, Yu & Wilson 2001).

Although the above assumptions pertain to competition-colonization trade-offs generally, the nature of competition is also key to coexistence produced specifically by a competition-dispersal trade-off. Species with longer-range dispersal can coexist with superior competitors (Bolker & Pacala 1999, Law & Dieckmann 2000, Murrell & Law 2003), but this requires a relatively large asymmetry in competition (Murrell & Law 2003). Without strongly asymmetric competition, the species possessing an optimal combination of competition and colonization dominates the system. A similar competitive hierarchy is required in competition-fecundity trade-off models (Adler & Mosquera 2000, Geritz et al. 1999). If this assumption is met, Holmes & Wilson (1998) show that species with greater dispersal can also coexist with those that are simultaneously better competitors and more fecund. Nonetheless, this result was only found for a small set of parameter combinations.

The ability of the competition-colonization trade-off to generate coexistence is also sensitive to the density and fecundity of the superior competitor. If the superior competitor has fecundity high enough that it leaves only a small fraction of unoccupied patches, the inferior competitor is unlikely to persist (Bolker et al. 2003). High density can also be achieved through high dispersal, which reduces parent-offspring competition, favoring a more even distribution of individuals across space (Bolker & Pacala 1997, Ellner 2001, Law et al. 2003). However, this more diffuse distribution of individuals may still leave temporary gaps that the weaker competitor can exploit as long as it more rapidly completes its life cycle. In fact, short-range-dispersing weaker competitors can coexist with a long-range-dispersing dominant by having a higher turnover rate (Bolker & Pacala 1999). In sum, the main conclusion from the theory is that while competition dispersal trade-offs favor coexistence, this requires several assumptions that may not apply to real systems.

Empirical Support

Like the theoretical work, most of the empirical studies examining competition-colonization trade-offs and their implications for coexistence examine fecundity-competition trade-offs (Levine & Rees 2002). Evidence for a dispersal-competition trade-off is sparse and comes largely from systems with regular disturbance. Brewer et al. (1998) found only weak evidence for a competition-dispersal trade-off among clonal grasses coexisting in a regularly disturbed salt marsh habitat. Instead they attributed coexistence to interspecific differences in physiological tolerance of gap conditions. Yeaton & Bond (1991) showed that ant dispersal gives a competitively inferior South African fynbos shrub an advantage in colonizing the

open areas after disturbance. However, Markov chain models suggested that this dispersal advantage was not sufficient to explain long-term coexistence with the competitive dominant shrub in the system. In some of the best support for coexistence achieved through a competition dispersal trade-off, Platt (1975) showed that the species occupying mature Iowa prairie (the competitive dominants) tended to disperse more poorly than "fugitive" species living primarily on badger mound disturbances. However, dispersal capacity and propagule production were positively correlated; thus, the source of the colonization advantage is unclear.

The best support for coexistence achieved through a competition-dispersal trade-off comes from models parameterized with field data, although even here evidence is not definitive. Working in temperate forest with two codominant tree species, Nanami et al. (1999) documented clumping in the gravity-dispersed and dioecious-competitive dominant, which they hypothesize favored the persistence of the bird-dispersed competitive inferior. Although this is simply a pattern analysis, they followed the work with mathematical models testing the suitability of a competition-dispersal trade-off as a coexistence mechanism in the system (Nanami et al. 2000). Results indicated that because male trees of the competitive dominant do not drop seeds below the parent canopy, this creates gaps that are differentially colonized by the better-dispersing competitive inferior. Still, this result depends strongly on the dioecy, restricting its generality to other systems.

In Pacala et al.'s (1993) analysis of their SORTIE forest simulation model, which they parameterized with field-derived measures of vital rates, coexistence in Eastern U.S. forest trees is achieved in part through a documented trade-off between dispersal and the ability to cast and survive shade. Although other trade-offs are also important to coexistence in their simulation, Ribbens et al. (1994) show a tremendous impact of changing mean dispersal distance on coexistence and dominance. Still, although a number of studies implicitly or explicitly invoke competition-colonization trade-offs, relatively little definitive empirical evidence exists to support coexistence achieved through this mechanism.

CONCLUSIONS

Our review of the literature uncovered a dichotomy of support for the importance of seed dispersal for community patterns. Although we found an ever expanding body of theory suggesting that seed dispersal affects species coexistence through local dispersal and a competition-dispersal trade-off, empirical support was scant. Instead, most empirical investigations examined how dispersal and seed-trapping agents affect species distribution and dispersion, subjects with little theory. In addition, this work relied heavily on dispersal proxies and correlational analyses of community patterns, methods unable to exclude alternative hypotheses. Interestingly, this relatively tepid support for dispersal's influence on community patterns is in contrast to work at the population level, where dispersal is well appreciated to strongly influence fitness, colonization, spread, and persistence (Harper 1977, Howe & Smallwood 1982, Skellam 1951).

Thus, the main conclusion of our review is that it may be premature to expect that patterns of seed dispersal strongly influence community structure. Of course, species without any dispersal could not spread beyond a founding individual, but it remains unclear whether the specific pattern of dispersed seed is a strong determinant of relative abundance, distribution, dispersion, and coexistence in natural systems. Although this lack of clarity stems from the weak empirical support in the literature, this weak support could be interpreted in several ways. It may be that the shape of the dispersal kernel is important, but current methodological approaches are too correlational to definitively demonstrate its impacts on patterns in the field. Alternatively, dispersal may be less important than we commonly believe. Resolution of these alternatives requires more rigorous approaches to understanding the importance of dispersal.

Improving the Empirical Evidence

Because estimating and manipulating seed-dispersal kernels in the field is difficult, testing the importance of dispersal kernels for community structure can be challenging. In principle, the ideal empirical study would (*a*) document seed shadows and dispersion patterns, (*b*) correlate these with patterns of community structure, and then (*c*) demonstrate that experimentally manipulating the seed shadow changes population or community structure (Schupp & Fuentes 1995). Although examples of each of these steps can be found in the literature, we found no single study that performed all of them. Instead, most of the empirical work relating dispersal to community properties tended to be correlational, often involving proxies for dispersal kernels, such as dispersal mode. These studies thus relied heavily on several potentially precarious assumptions, including the fact that dispersal mode is a reasonable predictor of dispersal kernels and that aggregation unrelated to current environmental variables is attributable to dispersal. These assumptions may be valid in much of the work (Willson 1993), but without further support some conclusions may be incorrect. This is illustrated by the often-cited example where dispersal influences patterns of mangrove tree zonation through the tidal sorting of propagules (Rabinowitz 1978). Although Rabinowitz's hypothesis has intuitive appeal, recent work actually quantifying the seed-dispersal kernels of mangrove trees in the same forests suggests the tidal sorting of propagules is unlikely to generate the zonation (W. Sousa & B. Mitchell, unpublished data).

How can we more definitively demonstrate that dispersal influences relative abundance, distribution, dispersion, and coexistence? To this end, we strongly encourage experiments that directly manipulate the seed-dispersal kernel, as advocated in more specific cases by Bolker & Pacala (1999), Pacala & Rees (1998), and Schupp & Fuentes (1995). Such experiments are not substitutes for quantifying dispersal kernels and community patterns, but they are complementary and uniquely poised to definitively test the mechanisms suggested by the patterns. The basic methodology involves manipulating the seed-dispersal kernel in replicate

plots and comparing the resulting community pattern (relative abundance, distribution, coexistence) to that in an unmanipulated control. The kernel is manipulated by first collecting all seed produced in a plot and then depending on the research question, dispersing it randomly or locally. Community patterns in an additional treatment, where seed is dispersed following the estimated natural kernels, can be compared with the unmanipulated control to test for any artifacts associated with seed handling. This basic approach has been successfully used to examine the population-level consequences of the dispersal kernel in a tropical forest tree (Augspurger & Kitajima 1992).

If dispersal controls commonness and rarity, then forcing all species' dispersal to follow the across-species mean or median kernel should cause the more common species to decline and the rarer species to increase relative to controls. If dispersal kernels control aggregation or other distribution patterns, then dispersing all seed globally should eliminate, or at least begin to homogenize, the distribution or aggregation patterns (e.g., Levine 2001, Turnbull et al. 1999). If species coexist through local dispersal, then dispersing seeds globally should enhance competitive displacement (Bolker & Pacala 1999). Lastly, if species coexist through a competition-dispersal trade-off, then equalizing the dispersal kernel across species should result in the displacement of species (Pacala & Rees 1998).

The experiments will be most tractable with communities of annual or short-lived perennial plants where dispersal occurs over relatively small spatial scales. Still, even with longer-lived organisms, trends in the predicted direction with early life stages (Augspurger & Kitajima 1992) can be used to bolster correlational evidence. In addition, seed addition experiments located at different locations relative to existing distributions could follow the rationale of the experiments above but be conducted over larger spatial scales. For example, in studies attributing adult clumping to local dispersal, experiments should show seed limitation away from the clump. In other words, if seeds did travel further, adults could establish. Last, we encourage experiments conducted in real ecological habitats where other potentially important factors are free to exert their impacts. Our review does not question whether dispersal has any effect on abundance, distribution, and diversity, but rather questions the importance of such an effect in comparison to other factors (Figure 1).

Future Directions for Theory

Theory has shown that without interspecific trade-offs, aggregation does not lead to stable coexistence (Bolker & Pacala 1999, Durrett & Levin 1998, Murrell & Law 2003, Neuhauser & Pacala 1999, Takenaka et al. 1997). Yet the models used to produce this result are based largely on the Lotka-Volterra competition equations, and most incorporate linear density dependence. Incorporating more complex processes such as nonlinear competition may change some of these predictions or at the very least lead to new strategies for coexistence (Bolker & Pacala 1999).

However, few models have taken this approach (see Pacala 1986 for a rare exception). Incorporating processes such as nonlinear effects of density may be at the expense of analytical tractability, but the techniques available to spatial theory are sophisticated enough to make it possible (Dieckmann et al. 2000, Tilman & Kareiva 1997).

Theory has also focused largely on the question of coexistence. Yet other community dynamics require closer attention from theoretical ecologists. For example, the work of Chave et al. (2002) showed that the scale of dispersal is the most important influence on many measures of community structure. Still, it is not known if these results are robust to inequality in dispersal ability across species. Although it is often assumed that longer-range dispersers are the more abundant, this prediction might change when the landscape is spatially heterogeneous, favoring short-range dispersal (Bolker 2003, Travis & Dytham 1999).

Last, empirical work should motivate interesting modeling questions. Most notably, we found a surprising number of empirical studies that documented the importance of trapping agents in controlling patterns of seed arrival. Interestingly, whereas clumping that results from local dispersal should enhance intraspecific aggregation and thus slow displacement, clumping that results from general trapping agents could increase heterospecific contact. Alternatively, trapping may segregate species if seed morphology influences trapping patterns, as in Schneider & Sharitz (1988). How trapping agents, their species specificity, and their spatial arrangement influence abundance, distribution, and coexistence are issues ripe for theoretical exploration.

Closing the Gap Between Theory and Empirical Work

We documented a clear dichotomy between the empirical and theoretical literature relating dispersal kernels to community patterns. Closing this gap is essential to clarifying the importance of dispersal. To this end, we strongly advocate the development of mathematical models parameterized with empirically documented seed-dispersal kernels and other realistic demographic parameters (as in Wu & Levin 1994). Such approaches can uniquely address whether the predictions of the mathematical models reasonably describe the dynamics of real ecological communities. Such approaches will also force investigators to ask the key long-term questions such as what maintains the dispersal-driven patterns, or what creates seed limitation. Models should also prove particularly informative for exploring the influence of seed-dispersal kernels, parent plant density, and seed production on seed deposition across the landscape. The relationship between dispersal kernels and seed rain is an underexplored, but critical, linkage between dispersal and community patterns.

The potential importance of seed dispersal for community dynamics has long been acknowledged, and recent theoretical results support this expectation. However, the results of our review suggest that the importance of dispersal cannot be taken for granted; empirical support for the theoretical predictions is largely

lacking. A firmer understanding of the role of dispersal in community structure is achievable if we begin with more rigorous field approaches directly manipulating seed-dispersal kernels. These results must then by coupled with the predictions of models incorporating empirically derived dispersal kernels.

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