Dispersal increases ecological selection by increasing effective community size

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Selection and drift are universally accepted as the cornerstones of evolutionary changes. Recent theories extend this view to ecological changes, arguing that any change in species composition is driven by deterministic fitness differences among species (enhancing selection) and/or stochasticity in birth and death rates of individuals within species (enhancing drift). These forces have contrasting effects on the predictability of ecological dynamics, and thus understanding the factors affecting their relative importance is crucial for understanding ecological dynamics. Here we test the hypothesis that dispersal increases the relative importance of ecological selection by increasing the effective size of the community (i.e., the size relevant for competitive interactions and drift). According to our hypothesis, dispersal increases the effective size of the community by mixing individuals from different localities. This effect diminishes the relative importance of demographic stochasticity, thereby reducing drift and increasing the relative importance of selective forces as drivers of species composition. We tested our hypothesis, which we term the "effective community size" hypothesis, using two independent experiments focusing on annual plants: a field experiment in which we manipulated the magnitude of dispersal and a mesocosm experiment in which we directly manipulated the effective size of the communities. Both experiments, as well as related model simulations, were consistent with the hypothesis that increasing dispersal increases the role of selective forces as drivers of species composition. This finding has important implications for our understanding of the fundamental forces affecting community dynamics, as well as the management of species diversity, particularly in patchy and fragmented environments.

annual plants | dispersal | metacommunity dynamics | selection vs. drift | mesocosm experiment

A major goal of ecology is to understand the mechanisms and interactions that determine the diversity and composition of ecological communities. Traditional ecological theory (commonly referred to as "niche theory") has emphasized deterministic interactions among functionally distinct species that lead to equilibrial and predictable species compositions (1–4). This view emphasizes the role of ecological selection as the main driver of community assembly. In contrast to this deterministic view, "neutral" theories of species diversity (5, 6) totally neglect species niches and assume that all individuals of all species are functionally identical (7). According to such theories, the main force structuring communities is ecological drift, caused by demographic stochasticity.

Over the last decade, various attempts have been made to synthesize these conflicting views, thereby providing a unifying framework for studying ecological communities (8–13). The most recent attempt, the "theory of ecological communities" (14), proposes that community ecology relies on four fundamental elements: selection, drift, dispersal, and speciation. Selection, drift, and dispersal refer to processes operating at the ecological time scale, while speciation operates at the evolutionary scale. According to the theory, any process affecting the dynamics or structure of ecological communities operates through one or more of these "high-level" processes (14).

Here we test the hypothesis that dispersal, one of the three ecological elements of the theory, mediates the relative importance of the other two elements (selection vs. drift), through a mechanism we call the "effective community size" hypothesis. It has previously been recognized that the relative importance of ecological drift decreases with an increasing number of individuals in the community (i.e., community size) due to the law of large numbers (15, 16). This prediction, rooted in population genetics (17), has recently gained experimental support (18). Here we extend this idea and predict (again based on classical population genetics; ref. 19) that dispersal may lead to a similar effect by connecting local communities that would otherwise exhibit independent drift. In other words, even if dispersal does not change the community's actual size, it may increase its effective size (i.e., the size relevant for competitive interactions and ecological drift) by mixing individuals from different localities. As with the actual size, this mechanism, termed the effective community size hypothesis, is expected to diminish the relative importance of demographic stochasticity, thereby reducing drift and increasing the relative importance of selective forces as drivers of community assembly.

The effective community size hypothesis can be best tested using a metacommunity framework (8). According to this hypothesis, increasing dispersal among local communities within a metacommunity should reduce the magnitude of drift at the level of the metacommunity. Therefore, increasing dispersal among local communities within replicated metacommunities (i.e., independent

Significance

A basic challenge of ecology is to understand the mechanisms that generate changes in the composition of ecological communities. At the most fundamental level, any change in species composition results from the interplay between two contrasting forces: selection (representing deterministic forces) and drift (representing stochastic forces). Here we provide experimental evidence that the relative importance of these two forces depends on the magnitude of dispersal. Specifically, increasing dispersal increases the effective size of the communities, thereby diminishing the relative importance of demographic stochasticity and increasing the relative importance of selective forces as drivers of community assembly. Our findings, supported by computer simulations, have important implications for understanding the ecological consequences of dispersal.

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metacommunities starting from a similar species composition and experiencing similar ecological conditions) can be expected to increase the degree of compositional similarity among the metacommunities. Furthermore, if competitive interactions are important drivers of community dynamics, then increasing dispersal among local communities should increase the relative abundance of competitively superior species by increasing the deterministic component of such interactions. Importantly, these predictions refer to spatially uniform competitive environments (20) in which all local and metacommunities experience similar environmental conditions.

We tested the predictions of the effective community size hypothesis and their underlying mechanisms using a combination of a field experiment and a mesocosm experiment focusing on annual plants. The field experiment was designed to test the two predictions under field conditions, whereas the mesocosm experiment was designed to validate the mechanisms underlying the two predictions under more controlled conditions.

Field Experiment

Thirty metacommunities, each consisting of four local communities, were established in a spatially uniform annual grassland by sowing soil samples representing the regional species pool in plots of 25 × 25 cm that were disposed of their natural seed banks. Each plot represented a local community (*Materials and Methods* and Fig. 1*A*). Following their establishment, the metacommunities were assigned at random into three dispersal treatments: no dispersal among local communities, moderate dispersal (50% of the seeds produced in each local community are dispersed uniformly among the four local communities), and

Fig. 1. Schematic illustration of the experimental design. (*A*) A single metacommunity in the field experiment showing the arrangement of the four local communities. (*B*) A set of metacommunities in the field experiment showing the three dispersal treatments. Arrow weights indicate the level of dispersal. (*C*) Design of the mesocosm experiment showing containers of different sizes, with the focal communities marked by dots. Values on the right indicate the number of replicates.

high dispersal (100% of the seeds produced within each local community are dispersed uniformly among the four local communities) (*Materials and Methods* and Fig. 1*B*). Natural dispersal within and between metacommunities was prevented (*Materials and Methods*). The species emerging in each local community were left to grow and interact without any intervention for four successive years (2011–2014). At the end of the fourth year, we determined the abundance of each species in each local community and tested the effect of the dispersal treatment on (*i*) the degree of species similarity among metacommunities and (*ii*) the relative abundance of *Hordeum spontaneum*. Previous competition experiments have shown that this tall annual grass is the best competitor in the study community (21). Therefore, we predicted that our dispersal treatment should increase the degree of compositional similarity among metacommunities, and that this effect would be associated with an increase in the relative abundance of *H. spontaneum*.

Mesocosm Experiment

While having the advantage of directly testing the effect of dispersal on compositional similarity, our field experiment had some notable limitations. First, although all local communities were established using samples from the same species pool, the initial compositions were not fully identical due to sampling effects. Moreover, although the experiment was conducted under uniform habitat conditions, fine-scale, unrecognized heterogeneity in soil properties could potentially affect the observed patterns of compositional similarity. Finally, even under highly controlled manipulations, dispersal effects on metacommunity diversity are highly complex and involve different mechanisms that operate simultaneously, thereby complicating interpretation of the mechanisms responsible for the observed patterns (22).

To overcome these problems, we ran a parallel mesocosm experiment in which we directly manipulated the effective size of the communities (rather than dispersal rates) under controlled abiotic and biotic conditions, with homogeneous soil and identical initial conditions in terms of species composition and abundance (*Materials and Methods*). This experiment was based on a subset of 51 species from the field experiment (*SI Appendix*, Table S1) that were sown in containers of three different sizes: 25 × 25 cm, 50 × 50 cm, and 100 × 100 cm (Fig. 1*C*). All containers were sown using the same species composition, same seed densities, and same soil (55 cm depth, mimicking the field experiment). The mesocosm communities were left to germinate, grow, and interact for 3 y (2012–2015), during which they were blocked for immigration and emigration. After 3 y of spontaneous dispersal within the containers, we determined the abundance of each species in a focal community of a fixed area (25 × 25 cm) located at the center of each container (Fig. 1*C*). Thus, focal communities representing different treatments had the same area (25 × 25 cm) but differed in terms of effective community size. Based on the effective community size hypothesis, we expected that increasing container size would increase the compositional similarity among independent focal communities (i.e., focal communities in different containers), and that this effect would be associated with a corresponding increase in the relative abundance of *H. spontaneum*.

Computer Simulations

To complement our experiments, we analyzed the effect of dispersal on compositional similarity using computer simulations. We simulated the dynamics of metacommunities with main elements qualitatively similar to those of our field experiment (i.e., four local communities, uniform competitive environment, annual life cycle, differences among species in competitive ability but no differences in dispersal rates). Two basic scenarios of competitive hierarchies were examined in these simulations (*Materials and Methods*): a "gradual" hierarchy, involving an arithmetic sequence of competitive abilities in which each species
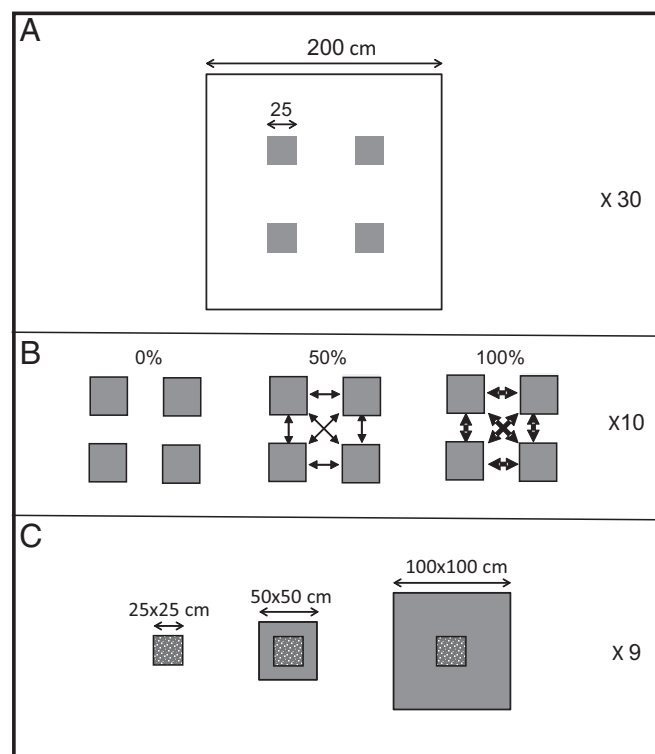
had a constant advantage over the lower species in the hierarchy, and a "dominance" hierarchy, in which one competitively superior species had an equal advantage over all other species in the community. The size of the local communities was kept constant in the model to make the absolute size of the communities independent of the magnitude of dispersal (*Materials and Methods*). To enhance the realism, we also introduced immigration from an external species pool to the overall metacommunity. We expected that increasing the dispersal among local communities would increase the similarity among the modeled metacommunities, and that this effect would be most effective under a dominance hierarchy (due to larger fitness differences among superior and inferior competitors) and under low immigration from the external species pool (since immigration works against local selection).

Results

In the field experiment, dispersal between local communities within metacommunities significantly increased the degree of compositional similarity among the metacommunities (Fig. 2*A*). Importantly, the corresponding effect of dispersal on the actual size of the metacommunities (total abundance of individuals of all species) was not significant, ruling out the possibility that the mechanism underlying the positive effect of dispersal on compositional
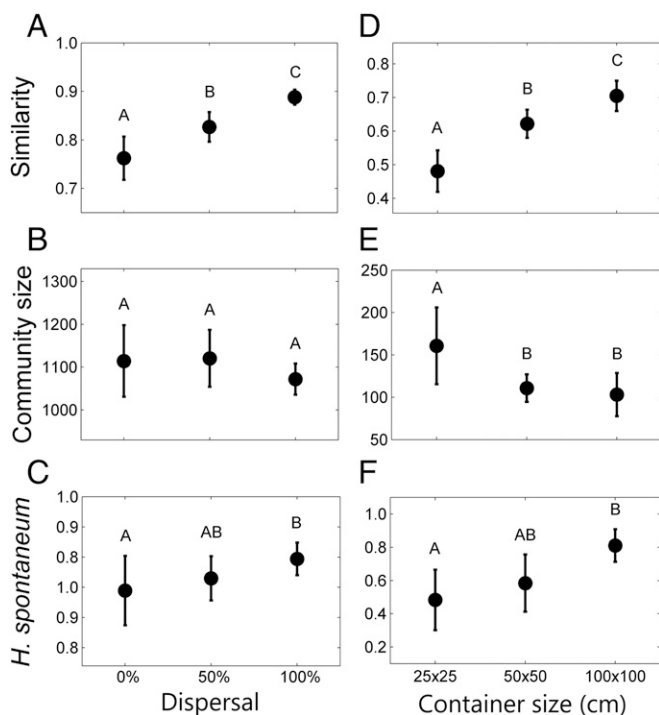

Fig. 2. Experimental support for the effective community size hypothesis. (*A–C*) Results of the field experiment showing the effect of dispersal among local communities on compositional similarity among replicated metacommunities (expressed by the Bray–Curtis measure of similarity) (*A*), absolute size of the metacommunity (total abundance of all individuals of all species in the metacommunity) (*B*), and relative abundance of *H. spontaneum* (*C*). (*D–F*) Results of the mesocosm experiment showing the effect of container size (a surrogate for effective community size) on compositional similarity among replicated focal communities (expressed by the Bray–Curtis measure of similarity) (*D*), absolute size of the focal community (total abundance of all individuals of all species) (*E*), and relative abundance of *H. spontaneum* (*F*). Error bars indicate 95% CI; common letters indicate treatments that do not differ significantly from one another (*P* > 0.05, Tukey test for multiple comparisons). Significance of differences among treatments in compositional similarity were determined using the distance-based test for homogeneity of multivariate dispersions.

similarity was an increase in the absolute size of the communities (Fig. 2*B*).

Another striking result was a dramatic increase in the relative abundance of *H. spontaneum*, from 4.5% following emergence in the first year of the experiment to 91.7% at the end of the experiment (average of all dispersal treatments). However, the magnitude of this increase was significantly influenced by the magnitude of dispersal and was greatest under the 100% dispersal treatment (Fig. 2*C*). Thus, both predictions of the effective community size hypothesis were supported by the field experiment.

The mesocosm experiment provided further support for the effective community size hypothesis, showing that increasing container size increased the compositional similarity among independent focal communities (Fig. 2*D*). This increase was associated with a decrease in the total abundance of all species (Fig. 2*E*), and an increase in the relative abundance of *H. spontaneum* (Fig. 2*F*). As with the field experiment, the relative abundance of *H. spontaneum* showed a remarkable increase during the course of the experiment (from 1.96% at the beginning of the experiment to an average of 62% in all focal communities), providing further and independent support for the competitive superiority of this species. Thus, increasing dispersal in the field experiment and increasing effective community size in the mesocosm experiment produced fully compatible results in support of the effective community size hypothesis.

Principal component analysis (PCA) ordinations of the data provided further support for the robustness of the results. Increasing dispersal reduced the convex envelope (hull) of the metacommunities in the field experiment (Fig. 3*A*), and increasing the container size decreased the convex hull of the focal communities in the mesocosm experiment (Fig. 3*B*). These results indicate that both treatments reduced the magnitude of compositional differences among replicated communities. Moreover, in both experiments, the shrink in the size of the convex hulls was associated with a shift in their center of gravity, indicating a directional (deterministic) shift in species composition. All the foregoing results are consistent with expectations based on the effective community size hypothesis.

In our simulations, increasing dispersal among local communities increased the degree of compositional similarity among replicated metacommunities (Fig. 4). However, there were strong interactions between the effects of dispersal, immigration, and the type of competitive hierarchy on compositional similarity (Fig. 4). As expected, metacommunities with a dominant competitive hierarchy (Fig. 4, Lower) showed higher levels of selection (i.e., higher compositional similarity) than metacommunities with a gradual hierarchy. Within a given category of competitive hierarchy, increasing immigration from the regional species pool reduced the levels of compositional similarity (Fig. 4).

Discussion

Our results provide three independent lines of support for the effective community size hypothesis. The increase in compositional similarity among replicated metacommunities with increasing dispersal (Fig. 2*A*) indicates that dispersal reduced the magnitude of ecological drift among independent metacommunities. The corresponding increase in the relative abundance of the best competitor (*H. spontaneum*) with increasing dispersal (Fig. 2*C*) indicates that dispersal increased the deterministic component of competitive interactions. Both patterns are indicative of an increase in the strength of selective forces as drivers of community assembly. Importantly, the actual size of the communities was not affected by dispersal (Fig. 2*B*). Thus, we attribute these results to a positive effect of dispersal on the effective size of the communities.

The results of the mesocosm experiment are fully consistent with this interpretation. In this experiment, we directly manipulated the effective size of the communities by sowing seeds of 51
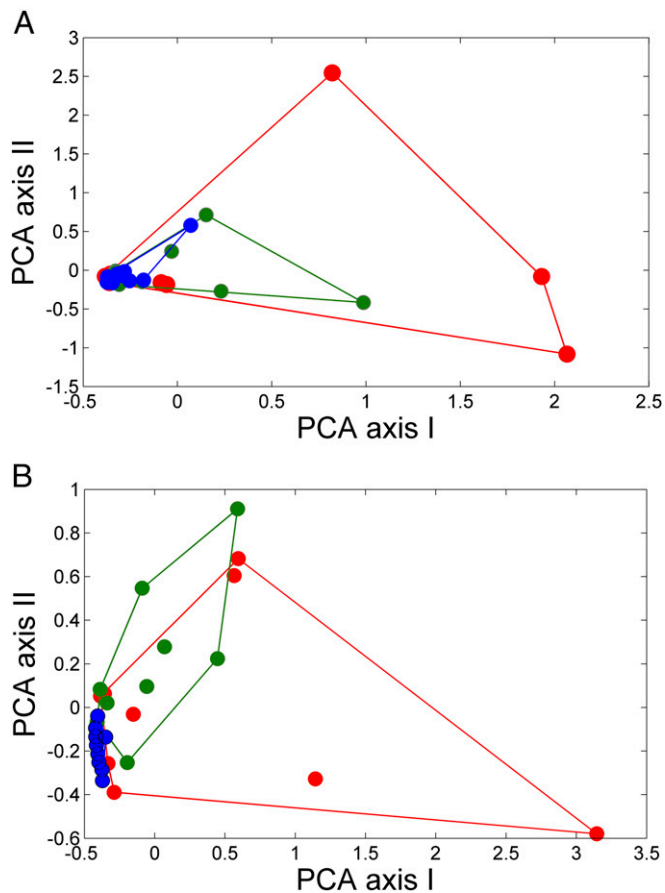
Fig. 3. PCA ordinations of the data obtained from the field experiment (*A*) and the mesocosm experiment (*B*). Each point represents a community (metacommunity in the field experiment, focal community in the mesocosm experiment). Colors indicate dispersal treatment in the field experiment (red, 0%; green, 50%; blue, 100%) and container size in the mesocosm experiment (red, small; green, medium; blue, large). The size of the convex polygon of each treatment represents the degree of dissimilarity among communities subjected to the relevant treatment.

species representing the regional species pool in containers of different sizes. The finding that increasing container size increased the compositional similarity among replicated focal communities (Fig. 2*D*), along with the corresponding increase in the relative abundance of *H. spontaneum* (Fig. 2*F*), are consistent with the results of the field experiment and provide further and independent support for the effective community size hypothesis.

Our model simulations strengthen the experimental results, showing that increasing dispersal increases compositional similarity among replicated metacommunities (Fig. 4). Importantly, our model lacks stabilizing mechanisms and assumes that species can be ranked along a single axis of competitive ability. This one-dimensional competitive hierarchy was applied following previous studies showing that competition for light is the main determinant of community structure in our study system, and that a single species (*H. spontaneum*) has a strong competitive advantage over all other species in the community due to its greater stature (21). Thus, we believe that the assumption of one-dimensional, dominant competitive hierarchy (Fig. 4*B*) provides a reasonable representation of the competitive regime in our study system. It should also be noted that stabilizing forces, such as spatial niche partitioning or competition-colonization trade-offs, could be ruled out by the setup and scale of our experiment.

Theoretical Implications. Dispersal is known to be a key driver of community dynamics, and its role in structuring ecological communities has been demonstrated in numerous theoretical (9, 23, 24–28) and empirical studies (22, 29). Studies focusing on spatially heterogeneous environments have emphasized the role of dispersal as a "homogenization" mechanism that may lead to a reduction in species richness, particularly at high levels of dispersal (30, 31). Studies focusing on uniform competitive environments have shown that dispersal may have both a positive effect on species richness, by allowing a competition-colonization trade-off (23, 32), or a negative effect, by reducing opportunities for competitive refuges (33). The effective community size hypothesis adds a new dimension to the role of dispersal as a process affecting community dynamics and suggests that disentangling the mechanisms by which it affects the dynamics and structure of ecological communities might be more challenging than has been proposed previously (22).

Moreover, the most recent synthesis of community ecology (14) considers dispersal one of the four most fundamental forces structuring ecological communities (selection, drift, dispersal, and speciation). These forces are considered high-level processes in the sense that, any process affecting community dynamics involves one or more of them. The effective community size
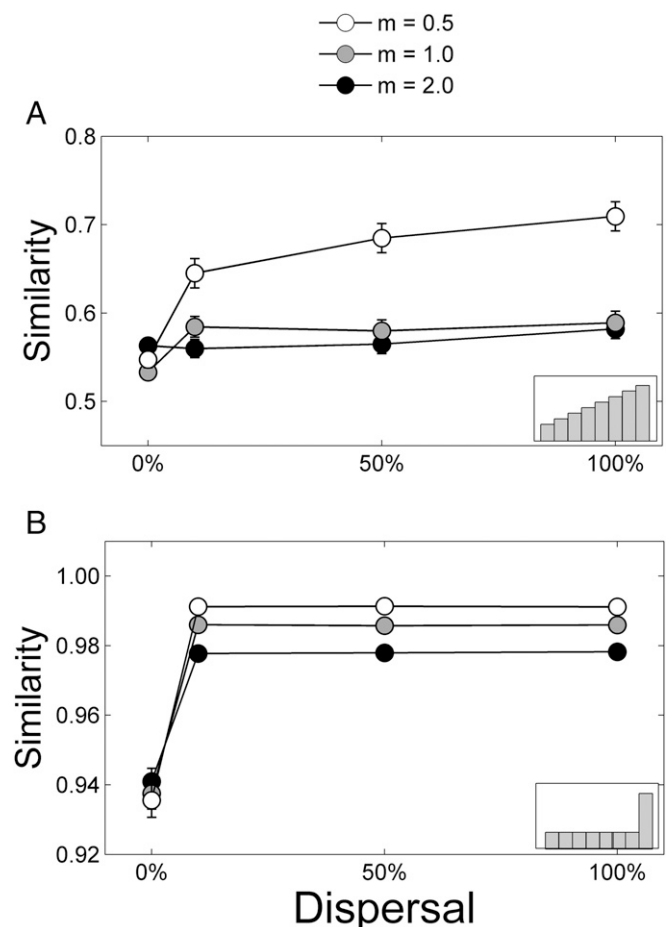

Fig. 4. Results of model simulations showing the effect of dispersal among local communities on compositional similarity among replicated metacommunities. Compositional similarity is quantified using the Bray–Curtis measure of similarity. (*A*) Gradual competitive hierarchy. (*B*) Dominance competitive hierarchy. (*Insets*) Visualization of the two types of competitive hierarchies. Gray levels indicate different levels of immigration (*m*) to the metacommunity.

hypothesis directly links three of these forces (all processes operating at the ecological time scale) and proposes a mechanism by which one of them (dispersal) determines the balance between the other two (selection and drift).

The effective community size hypothesis is highly relevant for the current debate concerning the role of niche-based vs. neutral processes of community assembly (10, 34–37). The fact that both types of processes receive considerable empirical support has led to the recognition that ecological communities can be positioned along a continuum ranging from purely neutral to entirely deterministic interactions (9). Our experimental results demonstrate that dispersal might influence the position of ecological communities along this continuum by mediating the effective size of the community. Our simulations confirm this result and provide additional insights into the conditions under which this mechanism is expected to be important.

The effective community size hypothesis has direct implications for habitat fragmentation, one of the main threats to global biodiversity (38–43). According to this hypothesis, fragmentation may influence the magnitude of drift in fragmented communities by two distinct mechanisms (Fig. 5). The decrease in the size of habitat patches reduces the actual size of local communities, while the decrease in patch connectivity reduces the effective size of the communities. Both mechanisms are expected to increase the relative importance of drift as a driver of species diversity. The first mechanism has been recognized for decades (44), while the second mechanism is the prediction of the effective community size hypothesis. At present, we lack a theoretical or empirical basis for evaluating the relative importance of the latter mechanism and the degree to which it affects the response of ecological communities to habitat fragmentation. A better understanding of the causal relationships among dispersal, effective community size, selection, and drift is particularly important for biodiversity conservation, since conservation efforts often focus on small and isolated populations in which demographic stochasticity is an important driver of population dynamics.

Summary. Dispersal is a crucial ecological process, and numerous experimental studies have demonstrated its importance in structuring ecological communities. Here we show that dispersal affects the relative importance of selection vs. drift by increasing the effective size of the community (i.e., the effective community size hypothesis). This finding has important implications for community ecology and conservation and highlights the need for a more comprehensive treatment of the complex interactions among selection, drift, and dispersal in future studies of community ecology and conservation.

Materials and Methods

Field Experiment. The field experiment was conducted in an annual grassland located in Beit Guvrin National Park, Israel over a 4-y period (2011–2015); details are provided in *SI Appendix*. The seeds required for establishing the metacommunities were collected by scraping the top 1-cm layer of soil in randomly stratified patches scattered over the entire study area. The seed bank samples were well mixed to attain a homogenous mixture, and a random sample of 1,250 mL from this homogenized regional seed pool was used to establish each local community. Each metacommunity consisted of four adjacent plots of 25×25 cm (e.g., local communities) that were positioned at the corners of a 1×1 m square by sowing 1,250-mL samples from the common seed pool (Fig. 1A). Each metacommunity was assigned at random to one of three dispersal treatments (Fig. 1B): control (no dispersal among the four local communities), intermediate dispersal (50% of the seeds produced in each local community are randomly and uniformly dispersed among the four local communities), and global dispersal (100% of the seeds produced in each local community are dispersed randomly and uniformly among the four local communities). These dispersal treatments were repeated each summer over a 3-y period. Natural dispersal among the local communities was prevented by positioning a 50-mesh vertical nylon net around each local community during the period of natural seed dispersal. The species emerging in each local community were allowed to grow and interact without any intervention until the dispersal treatment of the successive year.

The response of the metacommunities to the dispersal treatment was tested by counting the number of individuals of each species in each of the 120 local communities during peak flowering of the fourth year of the experiment. These data were used to quantify the Bray–Curtis measure of compositional similarity among all metacommunities within each dispersal category. The statistical significance of differences in compositional similarity among dispersal treatments was determined using the distance-based test for homogeneity of multivariate dispersions (45). We also performed PCA ordination of all metacommunities to evaluate the robustness of the patterns obtained using the Bray–Curtis measure of similarity. For each metacommunity, we also calculated the relative abundance of *H. spontaneum*, and the absolute size of the community (total abundance of all individuals of all species).

Mesocosm Experiment. The mesocosm experiment was based on artificial plant communities that were established by sowing seeds collected in the study area within metal containers of three sizes: 25×25 cm (small), 50×50 cm (medium), and 100×100 cm (large). All containers had the same depth (55 cm), and each size was replicated nine times. The experiment was conducted at the botanical garden of the Hebrew University of Jerusalem over a 3-y period (2011–2014); more details are provided in *SI Appendix*. Each container was filled by alluvium soil mixed with fine volcanic tuff. Seeds of the selected species were sown at a constant density of 200 seeds/m² per species. During the dispersal period, each container was surrounded by a 50-mesh vertical nylon net to prevent seed loss and contamination by seeds from surrounding vegetation. An area of 25×25 cm located at the center of each container was defined as a "focal" community, and all measurements were performed within this area (Fig. 1C). Thus, while all focal communities had the same area, their effective area had three levels: 25×25, 50×50, and 100×100 cm. During peak flowering of the third growing season, all individuals of all species were counted in each focal community, and the effects of container size on compositional similarity among replicated focal communities, the size of the focal communities, and the relative abundance of *H. spontaneum* were tested using the same procedures used to test the effect of the dispersal treatment in the field experiment, but with container size (small, medium, large) rather than dispersal treatment as the fixed effect.
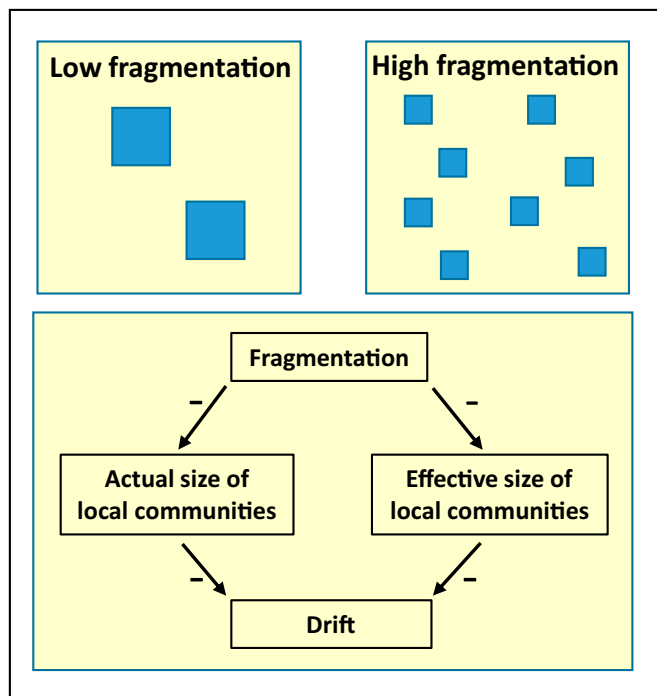

Fig. 5. Schematic illustration of the mechanisms by which fragmentation affects ecological drift according to the effective community size hypothesis. (*Upper*) Two levels of fragmentation. (*Lower*) The mechanisms by which fragmentation affects the magnitude of drift.

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Model Simulations. The model was designed to represent a metacommunity consisting of $n = 4$ local communities with a regional species pool of $S = 20$ species that differed in their competitive ability. Differences in competitive ability were introduced by varying the per capita reproductive rates of the component species, r_i. Two basic types of competitive hierarchies were examined by appropriate parameterization of the reproductive rates: an arithmetic sequence of competitive hierarchy (termed the gradual competitive hierarchy) and a dominance hierarchy in which all species had the same reproductive rate, except for one species (the superior competitor) that had a higher rate. In both cases, the reproductive rates of the best and worst competitors were $r = 9$ and $r = 3$, respectively. Each local community consisted of a constant number of adult individuals ($J = 20$) to make the size of the community independent of the magnitude of dispersal.

Simulations were initiated with a perfectly even and panmictic metacommunity with a single individual of each species in each local community. The initial metacommunity was then repeatedly modified by simulating discrete generations via the following steps:

i) Reproduction. The population of each species i in each local community was multiplied by its per capita growth rate, r_i, to produce a pool of potential recruits for the next generation.

ii) Mortality. All adult individuals were killed (i.e., nonoverlapping generations).

iii) Recruitment. For each local community, $(1-a) \times J$ individuals ($0 \leq a \leq 1$) were recruited by a random drawing of individuals from the locally produced propagules. The remaining propagules of all local communities were then combined to create a pool of propagules, from which a number of $a \times J$ individuals were drawn at random and added to each local community.

iv) Immigration. m immigrants were drawn at random from a regional pool containing all S species with equal proportions to replace m randomly chosen individuals in the whole metacommunity.

This modeling procedure kept the number of individuals in each local community constant to make the actual size of the community independent of dispersal rate. The simulation was terminated when the number of species at both the local community and metacommunity levels reached a steady state (i.e., no further trend of both attributes could be identified), typically after 30–200 generations, depending on model parameters.

To evaluate the effect of dispersal on compositional similarity between metacommunities, we performed 1,000 pairs of simulations under each combination of dispersal level (0%, 10%, 50%, and 100%), competitive hierarchy (gradual vs. dominance hierarchy), and immigration level ($m = 0.5$, 1.0, and 2.0). We then calculated the Bray–Curtis measure of similarity for each of the 1,000 pairs of simulations under each of the 24 parameter combinations (i.e., the degree of similarity between two random metacommunities in each of the 24,000 paired simulations). The results of these simulations allowed us to determine the effect of dispersal on the mean value of compositional similarity, as well as the sensitivity of the resulting patterns to variations in the type of competitive hierarchy and the level of immigration to the metacommunity.

1. Hutchinson GE (1957) Concluding remarks. *Cold Spring Harb Symp Quant Biol* 22: 415–427.
2. Whittaker RH (1975) *Communities and Ecosystems* (Macmillan, New York).
3. Tilman D (1982) *Resource Competition and Community Structure* (Princeton Univ Press, Princeton).
4. Chase JM, Leibold MA (2003) *Ecological Niches: Linking Classical and Contemporary Approaches* (Univ Chicago Press, Chicago).
5. Hubbell SP (2001) *The Unified Neutral Theory of Biodiversity and Biogeography* (Princeton Univ Press, Princeton).
6. Bell G (2001) Neutral macroecology. *Science* 293:2413–2418.
7. Allouche O, Kadmon R (2009) A general framework for neutral models of community dynamics. *Ecol Lett* 12:1287–1297.
8. Leibold MA, et al. (2004) The metacommunity concept: A framework for multi-scale community ecology. *Ecol Lett* 7:601–613.
9. Gravel D, Canham CD, Beaudet M, Messier C (2006) Reconciling niche and neutrality: The continuum hypothesis. *Ecol Lett* 9:399–409.
10. Adler PB, Hillerislambers J, Levine JM (2007) A niche for neutrality. *Ecol Lett* 10: 95–104.
11. Kadmon R, Allouche O (2007) Integrating the effects of area, isolation, and habitat heterogeneity on species diversity: A unification of island biogeography and niche theory. *Am Nat* 170:443–454.
12. Haegeman B, Loreau M (2011) A mathematical synthesis of niche and neutral theories in community ecology. *J Theor Biol* 269:150–165.
13. Kalyuzhny M, Kadmon R, Shnerb NM (2015) A neutral theory with environmental stochasticity explains static and dynamic properties of ecological communities. *Ecol Lett* 18:572–580.
14. Vellend M (2016) *The Theory of Ecological Communities* (Princeton Univ Press, Princeton).
15. Ruokolainen L, Ranta E, Kaitala V, Fowler MS (2009) When can we distinguish between neutral and non-neutral processes in community dynamics under ecological drift? *Ecol Lett* 12:909–919.
16. Orrock JL, Watling JI (2010) Local community size mediates ecological drift and competition in metacommunities. *Proc R Soc B* 277:2185–2191.
17. Kimura M (1962) On the probability of fixation of mutant genes in a population. *Genetics* 47:713–719.
18. Gilbert B, Levine JM (2017) Ecological drift and the distribution of species diversity. *Proc Biol Soc* 284:20170507.
19. Wright S (1940) Breeding structure of populations in relation to speciation. *Am Nat* 74:232–248.
20. Amarasekare P (2003) Competitive coexistence in spatially structured environments: A synthesis. *Ecol Lett* 6:1109–1122.
21. Segre H, et al. (2014) Competitive exclusion, beta diversity, and deterministic vs. stochastic drivers of community assembly. *Ecol Lett* 17:1400–1408.
22. Grainger TN, Gilbert B (2016) Dispersal and diversity in experimental metacommunities: Linking theory and practice. *Oikos* 125:1213–1223.
23. Calcagno V, Mouquet N, Jarne P, David P (2006) Coexistence in a metacommunity: The competition-colonization trade-off is not dead. *Ecol Lett* 9:897–907.
24. Hurtt GC, Pacala SW (1995) The consequences of recruitment limitation: Reconciling chance, history, and competitive differences between plants. *J Theor Biol* 176:1–12.
25. Chave J, Muller-Landau HC, Levin SA (2002) Comparing classical community models: Theoretical consequences for patterns of diversity. *Am Nat* 159:1–23.
26. Bolker BM, Pacala SW, Neuhauser C (2003) Spatial dynamics in model plant communities: What do we really know? *Am Nat* 162:135–148.
27. Amarasekare P, Hoopes MF, Mouquet N, Holyoak M (2004) Mechanisms of coexistence in competitive metacommunities. *Am Nat* 164:310–326.
28. Ai D, Gravel D, Chu C, Wang G (2013) Spatial structures of the environment and of dispersal impact species distribution in competitive metacommunities. *PLoS One* 8: e68927.
29. Levine JM, Murrell DJ (2003) The community-level consequences of seed dispersal patterns. *Annu Rev Ecol Evol Syst* 34:549–574.
30. Mouquet N, Loreau M (2003) Community patterns in source-sink metacommunities. *Am Nat* 162:544–557.
31. Leibold MA, Miller TE (2004) *Ecology, Genetics, and Evolution of Metapopulations*, eds Hanski I, Gaggiotti O (Academic, New York), pp 133–150.
32. Tilman D (1994) Competition and biodiversity in spatially structured habitats. *Ecology* 75:2–16.
33. Amarasekare P, Nisbet RM (2001) Spatial heterogeneity, source-sink dynamics, and the local coexistence of competing species. *Am Nat* 158:572–584.
34. Chase JM (2005) Towards a really unified theory for metacommunities. *Funct Ecol* 19: 182–186.
35. Cadotte MW (2007) Concurrent niche and neutral processes in the competition-colonization model of species coexistence. *Proc R Soc B* 274:2739–2744.
36. Chase JM, Myers JA (2011) Disentangling the importance of ecological niches from stochastic processes across scales. *Philos Trans R Soc B* 366:2351–2363.
37. Carmel Y, et al. (2017) Using exclusion rate to unify niche and neutral perspectives on coexistence. *Oikos* 126:1451–1458.
38. Gilbert B, Laurance WF, Leigh EG, Jr, Nascimento HEM (2006) Can neutral theory predict the responses of Amazonian tree communities to forest fragmentation? *Am Nat* 168:304–317.
39. Lindenmayer DB, Fischer J (2007) Tackling the habitat fragmentation panchreston. *Trends Ecol Evol* 22:127–132.
40. Laurance WF (2008) Theory meets reality: How habitat fragmentation research has transcended island biogeographic theory. *Biol Conserv* 141:1731–1744.
41. Laanisto L, et al. (2013) Microfragmentation concept explains non-positive environmental heterogeneity-diversity relationships. *Oecologia* 171:217–226.
42. Fahrig L (2017) Ecological responses to habitat fragmentation per se. *Annu Rev Ecol Evol Syst* 48:1–23.
43. Fahrig L (2017) Forty years of bias in habitat fragmentation research. *Effective Conservation Science: Data Not Dogma*, eds Kareiva P, Marvier M, Silliman B (Oxford Univ Press, New York), pp 32–38.
44. Lande R (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am Nat* 142:911–927.
45. Anderson MJ (2006) Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62:245–253.