



# Deterministic insights from stochastic interactions

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Theodosius Dobzhansky once famously noted that “nothing in biology makes sense except in the light of evolution.” Given their profound influence (1, 2), it may also be safe to wager that nothing in community ecology makes sense except in the light of area and heterogeneity. In PNAS, Ben-Hur and Kadmon (3) demonstrate that area and heterogeneity may themselves be fundamentally entwined, creating unappreciated, yet potentially ubiquitous thresholds in how species diversity accrues. These results have exciting implications for predicting and preserving species diversity.

Two maxims in community ecology are that area and heterogeneity are positively related to species diversity (2): As area and heterogeneity increase, theory predicts that the number of species in an ecological community generally increase, too. For a given amount of total area, a geometric certainty is that increasing the number of habitats in that area (i.e., increasing heterogeneity) means that the average area of each habitat must decrease. Since this area–heterogeneity tradeoff (AHTO) arises due to a fundamental geometrical constraint (4, 5), it is theoretically ubiquitous in ecological systems. Furthermore, because conservation decisions center on the size and heterogeneity of habitats to target for protection (6, 7), the AHTO could also be an important tool for guiding conservation around the globe. In their paper, Ben-Hur and Kadmon (3) use multispecies plant communities and multiple years of data to provide an important experimental test of the predictions of the AHTO. Their study is compelling not only for what they find but also because of what they do not find.

The AHTO is predicted to generate a hump-shaped (i.e., unimodal) relationship between richness and heterogeneity (4, 5) (Fig. 1). At one extreme, if the area consists of one or a few habitats, only a small subset of species that are well suited to these habitats will colonize and become established. As the number of habitats (heterogeneity) increases, more species find opportunities to persist in habitats where they are well suited. However, once the number of habitats becomes very large, and the average size of the habitat

is smaller as a result, the small populations supported in the small habitats become more likely to go locally extinct due to stochastic events, leading to a reduction in species richness at high heterogeneity (Fig. 1). The joint action of these forces leads to the greatest species richness at an intermediate level of the AHTO.

As predicted, the authors’ data support the positive relationship between richness and heterogeneity at the low-heterogeneity end of the AHTO gradient (3). However, rather than finding that richness started to decrease as the heterogeneity increased and habitat area dropped, the authors find that richness continued to increase (3). This unpredicted result reveals the importance of a process predicted to play an especially important role in small patches: stochastic determination of victory in competition (8, 9).

How might small habitats promote species diversity, when these are places where populations are small and persistence is threatened by unpredictable environmental forces? Although small populations are more likely to experience extinction due to external forces, small populations can also be greatly affected by chance events in individual survival and reproduction (i.e., demographic stochasticity; ref. 10). A change in the frequency of a species in a community due to chance events is termed ecological drift, and comes from theory pioneered in population genetics, where changes in gene frequency due to random events are termed genetic drift (11). While ecological drift can lead to the local extinction of either superior or inferior competitors, it can also benefit inferior competitors as it is their only route to victory. The key to this paradoxical prediction where small habitats promote diversity is that ecological drift is a more formidable force in small communities, so inferior competitors are more likely to achieve victory by chance in small habitats (8). As Ben-Hur and Kadmon (3) find, ecological drift can arise in the AHTO because increasing heterogeneity creates small communities (i.e., those where interactions are confined to a few individuals in small habitats) where stochastic forces may overwhelm competitive superiority (8, 9).

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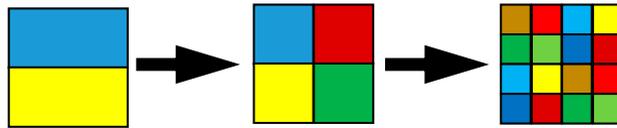
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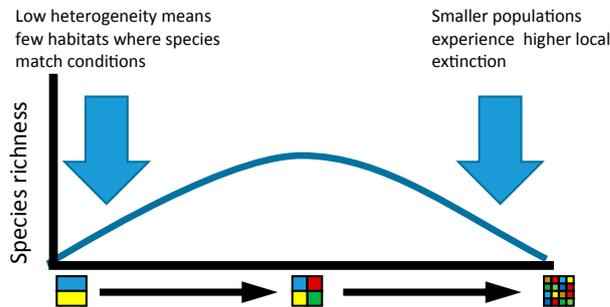
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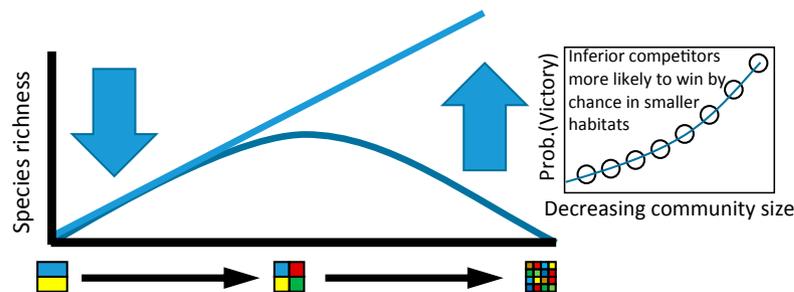
**A** The Area–Heterogeneity Tradeoff (AHTO): Increasing heterogeneity decreases average habitat size



**B** AHTO may have unimodal relationship with richness because habitat availability is important on one end of the gradient but extinctions are important on the other



**C** AHTO may have positive relationship with richness because inferior competitors are more likely to win by chance in smaller habitats



**Fig. 1.** (A) The area–heterogeneity tradeoff (AHTO) arises because, assuming total area remains constant, any increase in heterogeneity (e.g., the creation of a new habitat) entails a reduction in the average habitat size (4). (B) Original predictions of the relationship between AHTO and species richness. At one extreme, if an area consists of one or a few habitats (i.e., low heterogeneity), only a small subset of species from the regional pool of species that are well suited to these habitats will colonize them and become established. As the number of habitats (heterogeneity) increases, more species find opportunities to persist in habitats where they are well suited. However, once the number of habitats becomes very large (and the average size of the habitat is smaller as a result), the small populations supported in the small habitats would become more likely to go locally extinct due to stochastic events, leading to a reduction in species richness at high heterogeneity. The joint action of these forces would lead to the greatest species richness at an intermediate level of the AHTO (4). (C) In contrast to a unimodal relationship, a positive linear relationship might exist between richness and the AHTO because smaller habitats are areas where inferior competitors are more likely to achieve victory by chance alone. Ben-Hur and Kadmon (3) find evidence of this intriguing possibility in their multispecies, multiyear experimental test of the AHTO.

Importantly, examining only patterns of species richness cannot unambiguously reveal the action of diversity determined by stochasticity, because knowing the number of species in a community provides no information about the traits of the species (i.e., are they strong or weak competitors?). Instead, revealing the signature of stochastic victory often requires examining patterns in the identity of species among patches (9, 12, 13). This approach is most powerful if it incorporates competitive ability, because theory predicts the disproportionate loss of good competitors from small habitats (9). In their study, Ben-Hur and Kadmon (3) applied this logic to their data and evaluated how heterogeneity modified the frequency of a species that is a competitive dominant in their system (*Hordeum spontaneum*). Consistent with predictions of community-size theory, they observed that the dominant competitor

was less common in communities where heterogeneity was high (and thus the effective size of the community was low).

Ben-Hur and Kadmon (3) also used their data to evaluate the other side of that prediction, i.e., that superior competitors would be particularly effective at outcompeting other species in larger habitats (9). The authors compare small (0.25 m<sup>2</sup>) and large (2 m<sup>2</sup>) areas and suggest that the reduction in richness in larger habitats indicates that deterministic forces are important for driving extinctions observed in them. This pattern is consistent with community size modifying the relative role of stochastic elimination of species, which should have a disproportionate effect on good competitors (9). In larger communities, superior competitors are less likely to go extinct via stochastic forces, and these species then deterministically exclude the inferior competitors.

In testing the predictions of the AHTO, the study by Ben-Hur and Kadmon (3) leads to an important refinement of the AHTO predictions, and adds to a growing body of empirical studies that demonstrate how stochastic and deterministic forces may both be jointly acting in ecological communities (14–16). The results of this work are exciting because, if the AHTO is a fundamental characteristic of ecological systems, this refinement of the AHTO will contribute significantly to a theory that will be a significant addition to the ecological toolbox, helping advance the basic ecological goal of predicting patterns of diversity.

The authors' findings also provide important insights for applied ecology. A critical ecological challenge is to anticipate the effects of anthropogenic habitat destruction and modification on ecological communities and to design conservation reserves that provide maximum protection to biodiversity. Area and heterogeneity are essential components of this challenge because anthropogenic activities directly modify area (e.g., habitat destruction; refs. 17 and 18) as well as heterogeneity (e.g., via fragmentation, altered habitat composition, modification of disturbance regimes, and shifts in climatic variation; refs. 17 and 18). Results from the study by Ben-Hur and Kadmon (3), if they prove to be applicable at larger spatial scales, provide a more informed way to characterize the role of small and large patches for conservation and restoration. For example, small habitat patches may be places where populations are more likely to go extinct due to small size (1, 2, 16), where they may be less likely to colonize due to dispersal limitation (1, 2), and where high edge-to-area ratios increase the potentially deleterious effects of neighboring habitats (17). However, in finding empirical support for the role of small habitats in promoting diversity of inferior competitors, the results of the study by Ben-Hur and Kadmon (3) suggest that small habitats might have the theoretically predicted, but empirically unappreciated, benefits for species with particular characteristics. For instance, in situations where species of conservation concern are inferior competitors and competitive exclusion is the primary threat to their viability, smaller habitat patches may provide locations where competitive exclusion is less likely. On the other hand, if species of conservation concern

are good competitors or if populations in small patches are subjected to extinction via environmental variation, then larger patches of habitat are preferable, because they guard against both.

Future empirical and theoretical extensions of the AHTO will be critical for expanding on the findings that Ben-Hur and Kadmon (3) present. Two important future questions are 1) the degree to which the AHTO effects the authors observe in their experiments scale up and 2) whether there are general patterns that provide predictions for species and situations that lead to positive or negative AHTO effects. Because spatial dynamics, temporal dynamics, environmental disturbance, and variation in the distribution of competitive abilities may all alter the dynamics of deterministic vs. stochastic forces of community assembly (12, 13, 19–21), greater integration with existing theory will provide essential guidance for future AHTO experiments and predictive frameworks. While the AHTO model explored by Ben-Hur and Kadmon (3) focuses on competitive interactions, extensions to other trophic levels may also be highly informative. For example, herbivores, predators, and pathogens can all have profound effects on persistence of species and interactions among the species they attack, and the dynamics of these natural enemies can all be affected by patch size and heterogeneity (1, 19). As a result, continued integration of the AHTO with theories that more explicitly consider inherently spatial, temporal, and trophic processes will be important future steps.

Random events are an unavoidable consequence of an unpredictable world. Competition is the unavoidable consequence of living in a world of finite resources. By experimentally demonstrating that the AHTO provides a means to understand variation in the relative role of deterministic and stochastic processes, Ben-Hur and Kadmon (3) provide an important way to understand variation in ecological communities. The uncertain future of diversity may be more predictable as a result.

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