

Different dispersal abilities allow reef fish to coexist

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The coexistence of multiple species on a smaller number of limiting resources is an enduring ecological paradox. The mechanisms that maintain such biodiversity are of great interest to ecology and of central importance to conservation. We describe and prove a unique and robust mechanism for coexistence: Species that differ only in their dispersal abilities can coexist, if habitat patches are distributed at irregular distances. This mechanism is straightforward and ecologically intuitive, but can nevertheless create complex coexistence patterns that are robust to substantial environmental stochasticity. The Great Barrier Reef (GBR) is noted for its diversity of reef fish species and its complex arrangement of reef habitat. We demonstrate that this mechanism can allow fish species with different pelagic larval durations to stably coexist in the GBR. Further, coexisting species on the GBR often dominate different subregions, defined primarily by cross-shelf position. Interspecific differences in dispersal ability generate similar coexistence patterns when dispersal is influenced by larval behavior and variable oceanographic conditions. Many marine and terrestrial ecosystems are characterized by patchy habitat distributions and contain coexisting species that have different dispersal abilities. This coexistence mechanism is therefore likely to have ecological relevance beyond reef fish.

connectivity matrices | metacommunity dynamics | metapopulations | biophysical dispersal

The “paradox” of multiple species coexisting without apparent ecological differentiation has been observed across a range of ecological contexts (1). It has been variously ascribed to subtle partitioning of resource niches (2, 3); the mediating effects of predators, parasites, and infectious diseases (4, 5); conspecific aggregation (6, 7); and temporal variation, both in environmental conditions and resource dynamics (8–12). In metacommunities where suitable habitat has a patchy spatial distribution, the process of dispersal can allow species to coexist locally if each has a competitive advantage on a different patch (13) or when superior dispersal abilities allow the fugitive persistence of competitively subordinate species (14). However, recent theoretical studies have shown that dispersal differences between species are by themselves sufficient to allow coexistence, through a range of mechanisms. Interspecific dispersal differences can create ephemeral spatial niches in stochastic environments, and these are enough to allow species to coexist if their dispersal patterns are sufficiently uncorrelated (11). Alternatively, if two competing species have contrasting and asymmetric dispersal patterns, elevated levels of within-species competition can encourage the coexistence of the subordinate competitor (15). Finally, patchy dispersal behavior can increase the variety of coexisting species by decoupling the degree of spatial aggregation from the average dispersal distance (6, 7). Recognizing that dispersal differences alone can allow species coexistence has substantial implications for community ecology, because interspecific variations in dispersal abilities, timing, and behavior are common ecological phenomena (7, 16–19).

Dispersal-focused coexistence theory typically represents the distribution of habitat patches either nonspatially (10, 13, 15) or as uniformly spaced linear or grid arrangements (6, 10, 11). In real ecosystems, however, patches are distributed irregularly through the landscape. Some subregions contain dense patch aggrega-

tions, whereas in others patches are sparsely distributed. When species have different dispersal abilities, an irregular patch distribution means that different species are suited to particular subregions. Successful dispersal, and thus survivorship, depends on an interaction between a species’ dispersal ability and the spatial distribution of habitat. For example, a species that disperses effectively over short distances will be most successful in subregions with densely aggregated patches. In contrast, a species with longer-distance dispersal will disperse more effectively in subregions with widely spaced patches. If the distribution of patches varies in different locations, species with particular dispersal abilities will reproduce more effectively in some regions than in others. This simple fact creates a robust and general mechanism for local and regional coexistence.

Theoretical Model

Using a simple theoretical model, we can prove that an irregular patch distribution allows the stable coexistence of species that differ only in their dispersal abilities. We construct a two-species lottery metacommunity model containing three identical patches in a linear arrangement, located at $x = 0, 1$ and $1 + d$ (where $d \geq 1$; Fig. 1A). Both species have two-stage life histories: Sedentary adults are associated with discrete habitat patches, whereas juveniles move between patches during an obligate dispersing stage. Species differ only in their dispersal abilities; at the local patch scale, they are competitively identical. The number of species k juveniles from patch i that disperse and settle on patch j is denoted c_{ij}^k and depends on the distance between the patches (d_{ij}), and each species’ dispersal ability (α_k). We define the amount of dispersal between patches as

$$c_{ij}^k = e^{-d_{ij}/\alpha_k} / \alpha_k, \quad [1]$$

which implies that both species produce the same number of offspring, but those belonging to the species with larger α_k values disperse over greater distances. The resulting dispersal is isotropic and symmetric ($c_{ij}^k = c_{ji}^k$). To provide analytic results on coexistence, we assume that there is no direct dispersal between patches 1 and 3, there is no self-recruitment, and generations are nonoverlapping. However, we still observe coexistence when each of these assumptions is relaxed (SI Text and Figs. S1 and S2).

On each patch in a two-species lottery metacommunity, the abundance of the second species is the complement of the first (i.e., $n_i(t)$ and $[1 - n_i(t)]$ are the relative abundances of species 1 and 2 on patch i). Local patch dynamics follow the deterministic lottery model:

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$$\begin{aligned}
 n_1(t+1) &= \frac{c_{21}^1 n_2(t)}{c_{21}^1 n_2(t) + c_{21}^2 [1 - n_2(t)]}, \\
 n_2(t+1) &= \frac{c_{12}^1 n_1(t) + c_{32}^1 n_3(t)}{c_{12}^1 n_1(t) + c_{32}^1 n_3(t) + c_{12}^2 [1 - n_1(t)] + c_{32}^2 [1 - n_3(t)]}, \\
 n_3(t+1) &= \frac{c_{23}^1 n_2(t)}{c_{23}^1 n_2(t) + c_{23}^2 [1 - n_2(t)]}.
 \end{aligned}
 \tag{2}$$

To determine whether these two species can coexist, we consider standard invasibility criteria (20) to assess the stability of the two extinction equilibria ($n_i = 0$, or $n_i = 1, \forall i$). We find that the two species can coexist if the following conditions hold:

$$\begin{aligned}
 e^{\left[\frac{d}{a_1} - \frac{2d}{a_2}\right]} + e^{\left[\frac{1}{a_1} - \frac{2}{a_2}\right]} &> \left(\frac{\alpha_2}{\alpha_1}\right)^2 \left\{e^{-\frac{1}{a_1}} + e^{-\frac{d}{a_1}}\right\}, \\
 e^{\left[\frac{d}{a_2} - \frac{2d}{a_1}\right]} + e^{\left[\frac{1}{a_2} - \frac{2}{a_1}\right]} &> \left(\frac{\alpha_1}{\alpha_2}\right)^2 \left\{e^{-\frac{1}{a_2}} + e^{-\frac{d}{a_2}}\right\}.
 \end{aligned}
 \tag{3}$$

These conditions imply that for coexistence to be possible, habitat must have an irregular distribution ($d \neq 1$) and the species must have different dispersal abilities ($a_1 \neq a_2$; *SI Text*). Population simulations verify the existence of stable coexistence and show that for a given patch landscape, many different combinations of a_1 and a_2 create a globally attracting stable coexistence state (Fig. 1B). Although relative abundance varies between patches, neither species is able to completely exclude the other from any patch (Fig. 1A). The long-distance disperser is the most abundant species on patch 3, as it disperses most effectively between patches 2 and 3. The short-distance disperser dominates patch 1, as it disperses more effectively between patches 1 and 2. Patch 2 is more evenly shared between the species. If this linear landscape is extended to contain P patches spaced at different distances, we can observe $P - 1$ coexisting species (*SI Text* and Fig. S3).

Dispersal causes mortality, and coexistence is possible because each species experiences lower mortality across a different inter-patch distance. Alternatively, in ecosystems where species disperse with varying success through different vegetation types (19), the nature of the interpatch landscape may play a comparable role to distance in determining species' relative dispersal ability between particular patches. In contrast to competitive advantages at the local patch scale, an irregular patch distribution effectively creates niches at a regional scale, which can be exploited by species with well-suited dispersal abilities. Because these advantages are manifest only at broader spatial scales, adult life stages would appear competitively neutral if studied at a single patch. This coexistence is not specific to the lottery model, but can also be observed with recruitment-limited dynamics and for species with unequal competitive abilities (*SI Text* and Fig. S1). In the latter case, a competitively inferior species can coexist alongside a dominant—and can even exclude the dominant—if its dispersal ability is sufficiently better suited to one or both of the inter-patch distances.

Great Barrier Reef Landscape

The model in Fig. 1 captures the essence of irregular patch landscapes, but not their full complexity. A large landscape can contain subregions with a range of different patch densities and can thereby potentially support a substantial number of coexisting species. We demonstrate this by simulating reef fish metacommunities on the Great Barrier Reef (GBR) in northern Australia. Reef fish metacommunities on the GBR provide an appropriate test case for this coexistence mechanism. The GBR is an archipelagic system of 5,000 reefs and shoals, distributed in complex spatial patterns. In

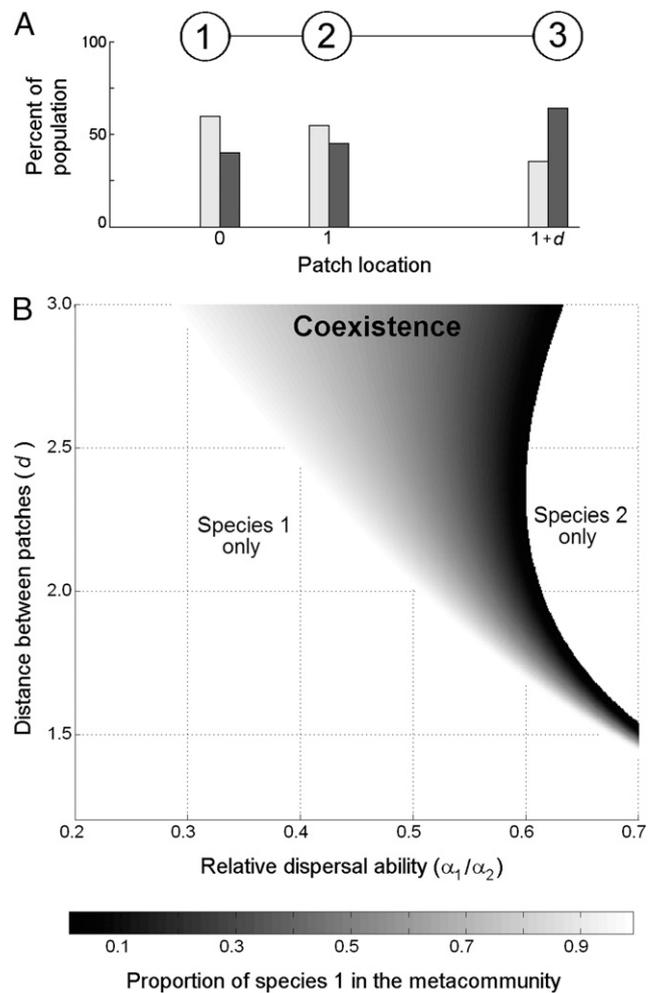


Fig. 1. (A) Schematic representation of the equilibrium three-patch system when $\alpha_1 = 1$, $\alpha_2 = 2$, and $d = 3$. Bars with dark shading represent the proportion of each patch occupied by the long-distance disperser; bars with light shading represent the short-distance disperser. (B) Equilibrium metacommunity composition for the three-patch system as a function of species' relative dispersal abilities, α_1/α_2 , and d . The shaded region indicates parameter combinations that allow coexistence, with the gradations indicating the relative equilibrium abundance of species 1 in the metacommunity; in the unshaded regions, one species is excluded by the other as indicated ($\alpha_1 = 1$).

certain trophic guilds, community dynamics can be described using lottery models, as multiple species have indistinguishable competitive abilities, resource needs, and habitat preferences (8, 21, 22). Adults remain resident on single reefs, but their larvae disperse between reefs during a nearly ubiquitous planktonic larval stage (23). The length of time spent dispersing (the pelagic larval duration, PLD) partly determines their average dispersal distance, and this PLD varies considerably among species (23, 24).

We consider whether different dispersal abilities can allow species to coexist in a subsection of the GBR, comprising 110 reefs that span $>2^\circ$ of latitude (Fig. 2A). The lottery dynamics of a P -patch, S -species metacommunity are defined by the equation

$$n_i^k(t+1) = \frac{\sum_{j=1}^P c_{ji}^k n_j^k(t)}{\sum_{k=1}^S \sum_{j=1}^P c_{ji}^k n_j^k(t)},
 \tag{4}$$

where k enumerates the species, and i and j the patches. For reef fish, the relationship between dispersal strength and distance is

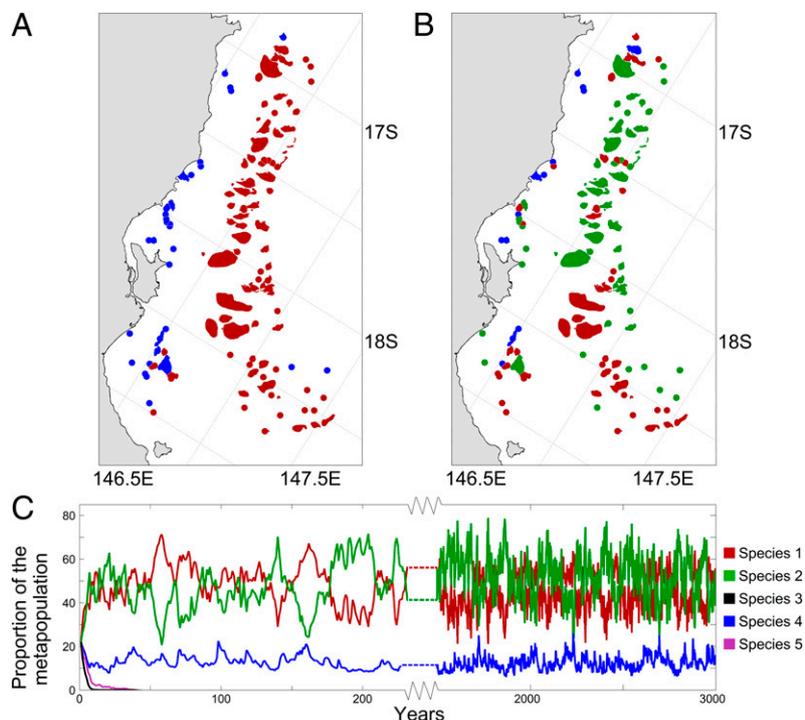


Fig. 2. (A) Spatial dominance pattern with static biophysical dispersal. Color indicates the most abundant species on each reef at equilibrium. (B) Spatial dominance pattern with temporally variable biophysical dispersal after 500 y have elapsed. (C) Relative abundance of the five species when biophysical dispersal varies annually, averaged across all reefs.

commonly described using normalized Gaussian functions that are deterministic, isotropic, and symmetric (25):

$$c_{ij}^k = e^{-d_{ij}^2/\alpha_k} / \alpha_k. \quad [5]$$

We seed each of the reefs with an equal proportion of 500 different fish species, each of which has a different dispersal ability, defined by α_k (SI Text). The community dynamics described in Eq. 4 are repeatedly applied until equilibrium is reached. When metacommunity dynamics stabilize, 27 species from the original 500 coexist, with a wide range of dispersal abilities. At equilibrium, persistent species dominate small clusters of reefs in regions where the reef spacing is frequently close to their favored dispersal distance. However, although these dominant species are the most abundant on a given reef, they cannot exclude all other species.

The identity of the most abundant species on any given reef at equilibrium can be predicted by considering the distance to surrounding reefs. For the dispersal functions described in Eq. 5, a species with ability α_k is the most effective disperser over a distance of $d_{ij} = \sqrt{\alpha_k}$. If a particular reef is surrounded by other reefs at distance $\sqrt{\alpha_k}$, we would consequently expect that reef to be dominated by species k . We therefore predict that on a given reef, the most abundant species will be the most effective disperser in the neighborhood of that reef. That is, the dominant species on patch i will maximize:

$$\max_{\alpha} \sum_{j=1}^P e^{-d_{ij}^2/\alpha} / \alpha. \quad [6]$$

Compared with the simulated metacommunity equilibrium, the α_k of the most abundant species on each reef has a high positive correlation with the α -value that maximizes Eq. 6 (Pearson's $r = 0.89$; SI Text and Fig. S4). The predictive power of a reef's neighborhood is high, given that this approach does not consider

broader-scale characteristics of the reef distribution. These include factors such as the number of other reefs in the system where the same species is dominant and whether those sympatric reefs are aggregated or fragmented through the landscape.

Biophysical Dispersal Patterns

Although dispersal is commonly modeled with Gaussian kernels, reef fish larval dispersal is in fact “biophysical”, that is, governed by both hydrodynamics and biological factors. These factors include tidal patterns and oceanic currents (26–28) and the larvae's developing locomotive and sensory capabilities (23, 26–28). Dispersal is therefore highly variable, and both spatial (13, 15) and temporal (9, 11, 28) variabilities interact to determine metacommunity dynamics and coexistence. In the second GBR example, we investigate whether species with different dispersal abilities can coexist in the presence of stochastic biophysical factors. We simulated the dispersal of five different species in the region of the GBR shown in Fig. 2, for each year between 1967 and 1998 (27). Each of the five species has a unique set of traits that determines their behavior during the pelagic larval phase and its duration (Table S1). The traits are chosen from plausible estimates of larval behavior, but are not intended to replicate any species in particular. Regional hydrodynamics were numerically modeled using a high-resolution current field for the reef–shelf complex that is calibrated by extensive current, wind, and tide measurements for the Coral Sea throughout the modeled years (SI Text). The modeled hydrodynamics were used to create an individual-based model of larval dispersal that estimates both self-recruitment and interpatch connectivities. The results are stored in a set of “connectivity matrices” containing elements $c_{ij}^k(t)$, where $k = 1, \dots, 5$; $i, j = 1, \dots, 110$; and $t = 1967, \dots, 1998$.

We model metacommunity dynamics using Eq. 4 and the $c_{ij}^k(t)$ values provided by the biophysical dispersal model. To assess whether this coexistence mechanism is robust to the effects of (a) biophysical dispersal and (b) temporal variability, we successively

add these two factors to the metacommunity simulation. We begin with a null scenario, where the interreef dispersal of five species is described using Gaussian functions (Eq. 5) and is therefore influenced by neither hydrodynamics nor stochasticity. The dispersal characteristics for the five species are chosen to correspond to each of the species in the biophysical dispersal data. The parameter α_k is chosen so that the mean dispersal distance in each of the five Gaussian species is the same as that of one of the species in the biophysical dispersal dataset (Table S2). When this null scenario is simulated to equilibrium, a single species (species 1) excludes all competitors. Species 1 is the most effective disperser across 75% of the 11,990 interreef distances in the region and dominates the neighborhood of all reefs in the system according to Eq. 6. Its exclusion of the other species in the metacommunity is therefore unsurprising.

In the second scenario, we replace the Gaussian functions with the biophysical dispersal datasets. To remove stochasticity, we define the amount of dispersal between each reef in the system using the average across the 32-y dataset [i.e., $\bar{c}_{ij}^k = \sum_{t=1967}^{1998} c_{ij}^k(t)/32$]. The resulting equilibrium reveals a metacommunity that is very different from the first scenario, with two additional species (denoted 2 and 4) coexisting alongside species 1. Although all three species are found throughout the system, each is most abundant in a subregion roughly defined by cross-shelf location (Fig. 24). The shortest-distance disperser (species 1) continues to dominate the outer shelf, but is largely displaced from the inner shelf by a long-distance disperser (species 4). A species that disperses over intermediate distances (species 2) persists at low levels (<5%) throughout the system. Interestingly, species dominance patterns observed on the GBR also exhibit cross-shelf structure that has been maintained over decades (2, 29, 30). Dispersal in the GBR lagoon is dominated by longshore, rather than cross-shelf larval transport (31). By reducing cross-shelf dispersal, the GBR's hydrodynamics may impede the invasion of different species from adjacent, cross-shelf locations (30). This bias towards longshore dispersal may allow species to exploit differences in the reef distribution between the inner and outer shelf that are too small to allow coexistence when dispersal is isotropic.

For the third scenario we include the temporal variability found in the dispersal dataset. Each year, dispersal for all species is modeled using the connectivity matrices of a year chosen at random from the dataset. Competitive interactions can be strongly influenced by temporal variation, but its inclusion in this model does not alter the set of coexisting species. Species 3 and 5 quickly decline to extinction, leaving the same three persistent species that coexist with fluctuating relative abundances (Fig. 2C). Stochasticity in the dispersal patterns does equalize the species' populations, drastically increasing the relative abundance of species 2 on the outer shelf to the detriment of species 1 and 4 (Fig. 2B and Table S2). Despite substantial variability in the dispersal patterns, the composition of the metacommunity remains relatively stable through time; the relative abundances of species 1, 2, and 4 have coefficients of variation of 0.18, 0.20, and 0.24, respectively. At a local scale, the dominant species on a given patch also remains relatively constant; on the average reef the same species dominates in 78% of years.

Discussion

In contrast to other dispersal-mediated coexistence mechanisms, our results reproduce two key attributes of the GBR reef fish

metacommunity. First, coexisting species are not found everywhere at the same abundance, but are instead consistently profuse in some subregions and rare in others. Many coexistence models, particularly those that rely on the presence of stochasticity, generate community abundance patterns that exhibit ephemeral local dominance (9–11). The stable dominance patterns generated by this mechanism qualitatively resemble those found in reef fish metacommunities on the GBR and are maintained in the presence of realistic environmental stochasticity (Fig. 2B). Alternative coexistence mechanisms that do create stable patterns of geographic replacement generally require species to possess local competitive advantages in the subregions they dominate (13, 14). However, such local advantages are frequently absent between adult stages of coexisting reef fish species from similar trophic levels (8, 22, 29).

Second, our findings offer an intuitive explanation for why species with both long and short dispersal distances can coexist, in contrast to theories that emphasize the advantages of short-distance dispersal (32). In regions where habitat patches are sparsely distributed, a long dispersal distance (resulting, for example, from a long PLD) provides evident competitive advantages. Across its 2,600-km length, the spatial density of reefs in the GBR exhibits broad variation, driven by changes in the width and depth of the continental shelf, wave exposure, and local geomorphology. Dispersal differences can convert this spatial complexity into biodiversity, by allowing species to exploit regional-scale competitive advantages. Analyses that consider only regular patch distributions therefore overlook a significant source of ecological complexity. In population genetic models with regular patch distributions, dispersal can create stable clines when genotypes disperse in different directions (33) and can reinforce clines created by spatial selection gradients (34). Irregular patch distributions could offer an alternative explanation for the coexistence of alleles that code for dispersal polymorphisms, but are otherwise selectively neutral.

In addition to recreating observed features of reef fish coexistence, the mechanism described in this paper is driven by two widely recognized characteristics of reef fish metacommunities. These characteristics are an irregularly spaced network of habitat patches and species with different dispersal abilities. These two features are shared by a range of other ecological communities, both marine and terrestrial. For example, while studying fugitive grass communities on badger mounds, Platt and Weiss (35) argued that a competition–colonization trade-off could explain species segregation. The observed pattern—short dispersers dominating regions with high mound density, and long dispersers dominating where mounds were more sparsely distributed—is also compatible with our coexistence mechanism. Other examples include Proteaceae species in the South African fynbos (16), rainforest bird species on island archipelagos (18), and invertebrates in intertidal habitats (24) and around deep sea vents (17). This coexistence mechanism may therefore be contributing to the maintenance of biodiversity in a range of ecological contexts beyond reef fish metacommunities.

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