AN INORDINATE FONDNESS FOR SPECIES WITH INTERMEDIATE DISPERSAL ABILITIES

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ABSTRACT

JBS Haldane is widely quoted to have quipped that the Creator, if one exists, has an inordinate fondness for beetles. Although Coleoptera may not be the most speciose order once Hymenopteran diversity is fully accounted for, as a whole the very clear differences in species diversity among taxa require an explanation. Here we show both analytically and through stochastic simulations that dispersal has eco-evolutionary effects that predict taxa to become particularly species-rich when dispersal is neither too low nor too high. Our models combine recent advances in understanding coexistence in niche space with previously verbally expressed ideas, where too low dispersal imposes biogeographic constraints that prevent a lineage from finding new areas to colonize (reducing opportunities for allopatric speciation), while too high dispersal impedes population divergence, leading to few but widely distributed species. We show that this logic holds for species richness and is robust to a variety of model assumptions, but peak speciation rate is instead predicted to increase with dispersal. Our work unifies findings of increasing and decreasing effects of dispersal rate on speciation, and explains why organisms with moderate dispersal abilities have the best prospects for high global species richness.

INTRODUCTION

Dispersal can influence biodiversity through both ecological and evolutionary processes. Ecologically, dispersal can enhance colonization, which increases local diversity if all else is equal [1]. Yet all else is typically not equal: increased movement, by increasing contact with similar species, can limit diversity through competitive exclusion [2]. When multiple processes interact, the outcome can be scale-dependent: theory suggests that regional diversity should decrease with increasing dispersal [3,4], while local diversity is often maximized at intermediate dispersal (unimodal pattern) [4,5]. In some cases this relationship can also become monotonic or multimodal [6]. Experimental studies that manipulate dispersal have typically found a unimodal relationship between dispersal and diversity maintenance, such that diversity peaks at intermediate dispersal [7–9].

Evolutionarily, dispersal can influence the speciation process itself. Increased dispersal ability can increase the extent of species ranges [10], allow individuals to colonize new areas, and thus lead to allopatric speciation. However, by increasing population mixing, dispersal can also erode local adaptation and prevent speciation [11]. Empirical patterns relating dispersal to speciation rates (or species richness, often interpreted as evidence of speciation rates) are mixed [12]. Marine invertebrates typically show higher speciation rates associated with lower dispersal [10,13], while avian studies have found speciation rates to peak at high [14,15], low [16–18], or intermediate dispersal ('short-distance colonists' *sensu* [19]). In angiosperms, speciation rate is related to the dispersal mechanism: lineages with biotic dispersal (e.g. bird-dispersed fruits) tend to have higher diversity than those that rely on abiotic methods such as wind [20–22]. This pattern may partly reflect biotic dispersers

achieving higher dispersal distances, but the interpretation is complex because biotic dispersers can also have an improved likelihood of arriving in a suitable location.

The evolutionary role of dispersal in speciation has received much less theoretical attention than the ecological role of dispersal in biodiversity maintenance. In broad agreement with Mayr's ideas [23], recent theoretical work has shown that increased dispersal rate can, by promoting gene flow, increase the time to a first speciation event [24], and reduce speciation rates for species that, as a result of good dispersal ability, occupy large geographic areas [25]. These unidirectional predictions conflict with a number of recent empirical studies, which instead employ a verbal model arguing that speciation rates should be highest at intermediate dispersal distances [16,20,26,27] (Fig. 1). The core of this idea is expressed succinctly by Price and Wagner [20]: 'Species-rich lineages may have moderate dispersability that is effective enough to extend the geographic range of whole lineages, yet infrequent enough to depress levels of gene flow' (see also [28,29]). Especially if habitable environments are patchy (e.g. Hawaiian islands for angiosperms, [20]), too little movement will lead to much of the world remaining undiscovered by many of the potential lineages that could persist there, while too much movement maintains gene flow at a level that constrains speciation. Diversity remains low for different reasons at either end: it remains limited in the first case as species stay put in narrow-range sympatry, and in the latter case low diversity exists in a pattern of few species each occupying a very large range.

Here we investigate if and when intermediate dispersal leads to the best prospects for speciation, as suggested by some of the verbal models, or whether the negative effect of

dispersal on speciation is bound to dominate the outcome, as suggested by the two theoretical contributions mentioned above [24,25]. We use a combination of deterministic and stochastic metapopulation models to explore the relationship between dispersal and speciation, showing: (1) analytically that species richness peaks at intermediate dispersal when dispersal increases colonization and the correlation between patches, and (2) how the nature of resource competition interacts with dispersal to influence the peak speciation rate, species richness, and the proportion of the potential niche space that is filled.

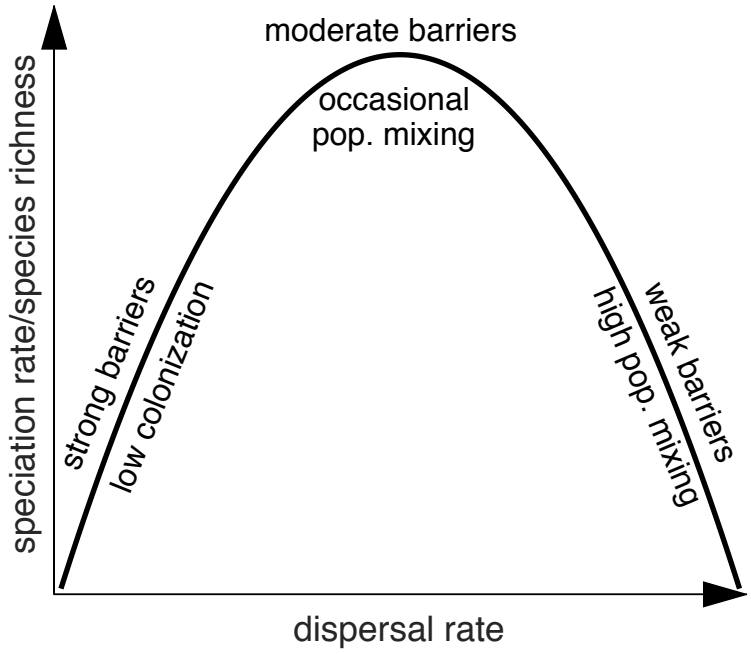

Figure 1 – The 'intermediate dispersal model' of speciation/species richness. When dispersal is rare colonization is too low and when dispersal is high the metapopulation behaves similarly to a single population. Speciation rates and species richness are therefore predicted to peak at intermediate dispersal rates [16,20,26].

RESULTS

DETERMINISTIC TOY MODEL

To illustrate the argument, we first propose the following toy model of dispersal and speciation with a large number of possible species and patches, which tracks the proportion of patches that are occupied, $p(t)$, and the average proportion of species that are unique to occupied patches, $u(t)$:

$$\frac{dp}{dt} = \rho_d p(1-p) - \epsilon_d p \tag{1}$$

$$\frac{du}{dt} = \mu_d u(1-u) - \rho_d p u \tag{2}$$

The parameter ρ_d is the dispersal rate per occupied patch, ϵ_d is the patch extinction rate (i.e. the rate at which patches become unoccupied due to environmental catastrophes) and μ_d is the speciation rate per patch. This model's take on dispersal and speciation is simplistic, but it mathematically captures the essential features of the verbal model: (1) patch colonisation increases with dispersal; and (2) dispersal reduces the differences in species distributions between patches. Total species richness (as a proportion of the theoretical maximum), is given by the product of $p(t)$ and $u(t)$.

At the non-trivial equilibrium, we have $p^* = 1 - \frac{\epsilon_d}{\rho_d}$ and $u^* = 1 - \frac{\rho_d - \epsilon_d}{\mu_d}$ for $\rho_d > \epsilon_d$ and $\mu_d > \rho_d - \epsilon_d$, with species richness (as a proportion of the theoretical maximum) equal to the product of p^* and u^*. Given that the proportion of occupied patches (p^*) increases with dispersal (ρ_d) and the average proportion of species that are unique within each occupied

patch (u^*) decreases with dispersal, species richness is maximised at intermediate dispersal (Fig. 2), showing analytically that the core principles of the verbal model are mathematically sound (Fig. 1).

While this toy model provides some insights into the validity of the verbal model, it lacks important features of real populations such as resource competition, it views dispersal and speciation in a very simplified manner, and it does not predict speciation rates. Furthermore, it views extinction as a patch-level process, whereby if species do not disperse at a sufficient rate then they will eventually be driven extinct due to a localized catastrophe. This assumption suffices for the purposes of our toy model, but understanding species diversification requires considering a species-level rather than patch-level extinction process. We therefore switch our focus to a stochastic metapopulation model with dispersal between a finite number of patches, local resource competition, and species-level extinctions.

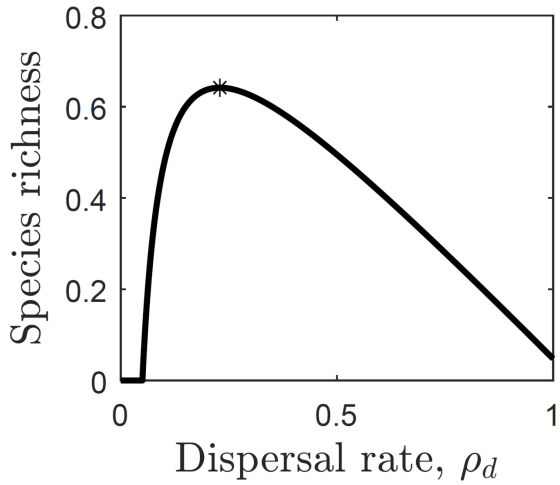

Fig. 2 – Results for the deterministic toy model. Species richness peaks at intermediate dispersal (star): $\rho_d = \sqrt{\epsilon_d(\epsilon_d + \mu_d)}$. Illustrative parameters: $\epsilon_d = 0.05$, $\mu_d = 1$.

STOCHASTIC METAPOPULATION MODEL

We adapt the multidimensional niche model described by Ashby et al. [30] to allow for (1) multiple patches with dispersal and (2) neutral traits to distinguish between species that evolve independently in different patches. A total of L patches are arranged in a ring (to remove boundary effects) with dispersal occurring between adjacent patches (Fig. 3A). Individuals compete locally over y 'substitutable' or 'non-substitutable' resource types (*sensu* [30]). It is assumed that organisms can replace one type of substitutable resource with another (e.g. different food sources), but cannot do so with resources that are non-substitutable (e.g. food and nest sites). In practise this means that the competition kernels (see below, equations 3-4) are determined multiplicatively for substitutable resources and additively for non-substitutable resources (see [30] for a more detailed discussion of this distinction). We assume each resource type is subdivided into c_k resources $(k = 1, \dots, y)$ giving a maximum of $n = \prod_{k=1}^{y} c_k$ potential niches, which may be filled or unfilled by organisms in each patch (*sensu* [30]). In other words, each niche is defined by a unique set of niche traits which a species may potentially possess, regardless of whether a species currently exists with those traits. We define $z_i^k \in \{1, \dots, c_k\}$ to be the preferred resource within resource type k for species i (each resource type is also arranged in a ring to remove boundary effects). Species are defined by their set of niche traits, $\{z_i^k | k = 1, \dots, y\}$, combined with a neutral trait, v_i. In our preliminary simulations we allowed the neutral trait to mutate at a given rate, but we found this to be more computationally intensive and to produce qualitatively similar results to a simpler method. We instead set the neutral trait for each species to correspond to the patch in which the species first arose, $v_i \in \{1, \dots, L\}$, giving a maximum of $s = Ln$ potential species. We include a neutral trait so

that two lineages in different patches which independently evolve to occupy the same niche are classed as distinct species (detectable as their neutral traits having different values).

We define E_{ij}^{k} to be the minimum distance between the preferred resources of species i and j within resource type k (Fig. 3B) and the strength of competition between species i and j to be:

$$\alpha_{ij} = \prod_{k=1}^{y} e^{-g_k {E_{ij}^{k}}^2} \tag{3}$$

for substitutable resources (Fig. 3C) and

$$\alpha_{ij} = \sum_{k=1}^{y} w_k e^{-g_k {E_{ij}^{k}}^2} \tag{4}$$

for non-substitutable resources (Fig. 3D), where $g_k > 0$ mediates the niche breadth for resource type k (i.e. the extent to which species consume resources similar to their preferred resource) and w_k is the relative importance of the resource type when resources are non-substitutable $\left(\sum_{k=1}^{y} w_k = 1\right)$.

The number of individuals belonging to species i in patch p at time step t is given by $N_i^p(t)$. Each time step is assumed to encompass many generations implying a timescale over which species distributions change due to niche overlap. The change in population size between time steps due to ecological processes (births, deaths, resource competition) is given by

$$\Delta N_i^p(t) = P\left[g_i^p(t) N_i^p(t)\right] - N_i^p(t) \tag{5}$$

where $P[\lambda]$ is a Poisson distributed random variable with mean λ. The growth function, $g_i^p(t)$, is the expected proportional change in population size due to competition with other organisms in the same patch and is equal to:

$$g_i^p(t) = 1 + r\left(1 - \frac{1}{K_i}\sum_{j=1}^{s} \alpha_{ij} N_j^p(t)\right) \tag{6}$$

where r scales the rate of the within-patch dynamics, $\alpha_{ij} \in [0,1]$ is the degree of niche overlap (i.e. strength of competition) between species i and j, and K_i is the baseline carrying capacity of species i, which is drawn from a normal distribution with mean K_{mean} and standard deviation K_{std}.

Once the within-patch dynamics have been updated we allow speciation, dispersal, and random extinctions to occur. The total number of speciation events from species j to i is

$$M_{ij}^p(t) = P\left[\mu_s m_{ij}^p \left(N_i^p(t) + \Delta N_i^p(t)\right)\right] \tag{7}$$

where μ_s is the speciation rate and m_{ij}^p determines if species j can mutate to species i: $m_{ij}^p = 1$ if the species are exactly one niche trait apart from each other $\left(\sum_{k=1}^{y} E_{ij}^k = 1\right)$ and if $v_i = p$ so that the new species' neutral trait corresponds to the patch in which it arises (to

distinguish it from other species that evolve in other patches to occupy the same niche). The number of dispersal events from patch p to patch u for species i is given by:

$$S_i^{up}(t) = P\left[\rho_s A_{up}\left(N_i^p(t) + \Delta N_i^p(t)\right)\right] \tag{8}$$

where ρ_s is the dispersal rate and A_{up} is the adjacency matrix, such that $A_{up} = 1$ if patches u and p are adjacent and $A_{up} = 0$ otherwise. The total change in species i in patch p due to dispersal is therefore:

$$D_i^p(t) = \sum_{u=1}^{L}\left(S_i^{pu}(t) - S_i^{up}(t)\right) \tag{9}$$

Finally, we allow random extinction events to occur with probability ϵ_s per species per patch at each time step.

We focus our analysis on the dispersal rate (ρ_s) and the type of resource competition (substitutable or non-substitutable resources), carrying out 1,000 simulations per parameter set (source code available in the *Supplementary material*). We initially seed one patch with a single species, then simulate the dynamics for $T = 10^4$ time steps. The duration was chosen based on preliminary simulations, which typically reached quasi-equilibrium within this time period (longer simulations do not qualitatively change the results, as shown in the *Supporting Information*).

We measure species richness at time t, $R(t)$, by pooling all patches together and counting species that are above a threshold of $\delta = 10$ individuals. We calculate the quasi-equilibrium species richness, R^*, by taking the mean of $R(t)$ over the final 1,000 time steps of the simulation. To help understand the process that leads to changes in species richness, we calculate the maximum speciation rate, σ, by sampling the population every 100 time steps and counting the difference in the total number of extant species across the entire metapopulation between sampling points. This allows us to determine the conditions that lead to rapid increases in species richness. Finally, to understand the relationship between species richness and resource competition, we calculate the proportion of potential niches that are filled at the quasi-equilibrium. This allows us to determine how species patterns are driven by the total number of distinct niches discovered by the globally diversifying taxon.

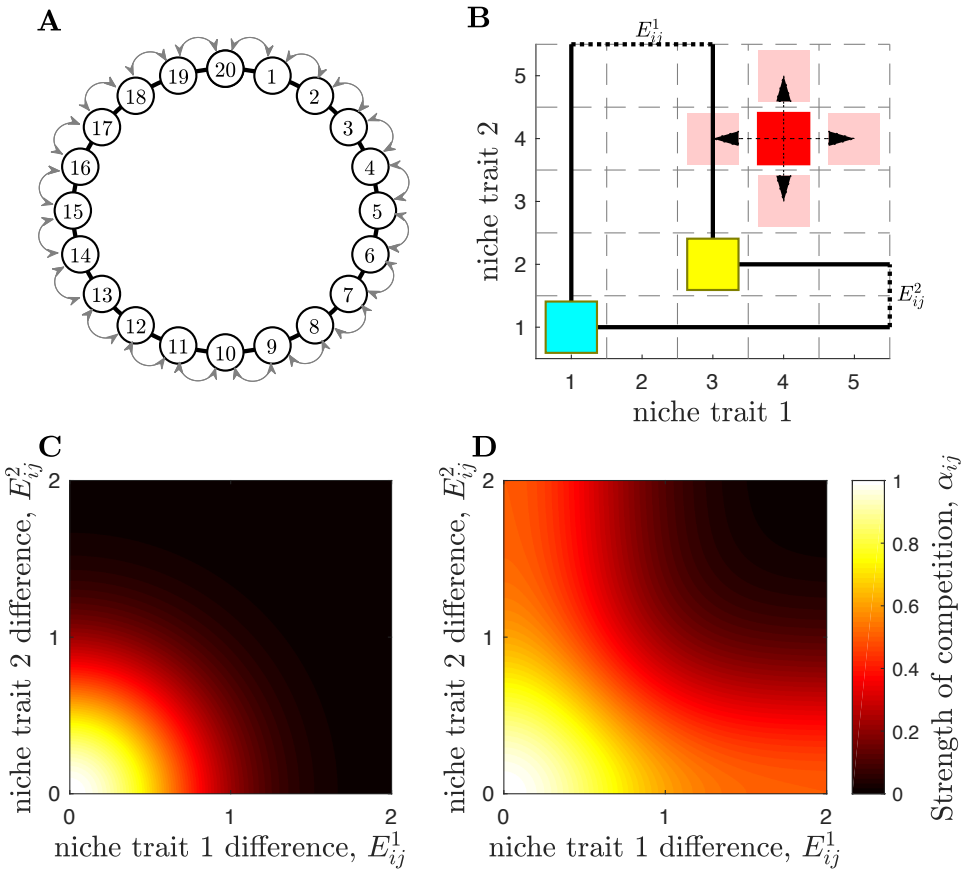

Figure 3 – Stochastic metapopulation model overview. (A) The environment is split into $L = 20$ patches arranged in a ring to remove boundary effects. Competition occurs within patches and dispersal between adjacent patches (arrows). (B) Each species occupies a position in the niche space corresponding to its preferred resources/traits. Speciation (red) occurs at rate μ_s causing a change in one niche dimension (arrows). The strength of competition, α_{ij}, between two species (yellow and blue) is based on the distance between species in each dimension of the niche space, E^k_{ij}, and whether the resources/traits are: (C) 'substitutable' (e.g. different food sources), or (D) 'non-substitutable' (e.g. food source and nest sites), as described in [30].

We separate our analysis into two parts, considering the effects of dispersal first on the quasi-equilibrium (QE) species richness, R^*, and niche space, and then on the maximum speciation rate, σ, that underlies and partially explains the emerging species richness. In line with both the verbal and deterministic models, we find that species richness is typically maximised at intermediate dispersal (Fig. 4A), a finding that is extraordinarily robust across different modes of resource competition (i.e. substitutable or non-substitutable resources), a wide range of model parameter values (Fig. S1-S7), and over longer time scales (Fig. S8).

The pattern for species richness is qualitatively similar for substitutable and non-substitutable resources, but we find that the extent to which potential niches are filled at the global level depends both on dispersal and resource type. Specifically, the proportion of potential niches that are filled peaks at intermediate dispersal when resources are non-substitutable (e.g. food source and nest sites), but is either roughly constant or increasing when resources are substitutable (e.g. different food sources; Fig. 4B, S1-S8). The reason for this difference lies in the way species are distributed within each patch (Fig. 5). Competition for substitutable resources tends to lead to most niches being occupied within each patch, thus dispersal is not a strong predictor of how much of niche space is filled globally. In some cases, within-patch niche diversity may remain lower when dispersal is rare (due to extinctions that are not compensated for by frequent colonization, Fig. S1B-S8B), while all other dispersal values simply allow maximal niche diversity to be reached (Fig. 4B).

In contrast, competition for non-substitutable resources leads to non-overlapping and potentially arbitrary associations between resources in different patches as an emergent

property of the system (Fig. 5). At low or high dispersal, most of niche space remains unfilled since few patches are occupied or there is high mixing between patches eroding variation in niche diversity, respectively. At intermediate dispersal, however, many patches are occupied and the occupied niches between patches are unlikely to be the same due to the arbitrary nature of the non-overlapping distributions. This leads to a peak in the proportion of potential niches that are occupied. In summary, competition for substitutable resources leads to complete saturation of all potential niches whenever a patch is occupied, with no differences between occupied patches, whereas competition for non-substitutable resources leads to arbitrary non-overlapping niches filled within each patch and a peak in occupied niches at the global level for intermediate dispersal.

While the verbal model is well-supported in terms of species richness (and in terms of occupied niches when resources are non-substitutable), we find that the peak speciation rate increases with dispersal (Fig. 4C). This is because the speciation rate depends on both the total number of species across the system and the local availability of new niches (Fig. 6). When dispersal is low, the speciation rate is highly constrained: few patches are occupied, thus few speciation events can occur due to the limited number of extant species and available niches. As dispersal increases, more patches become colonized and so there are more niches available locally, causing the initial speciation rate to increase. When dispersal is high, all patches rapidly become occupied, and so the number of available niches increases very quickly, leading to a high speciation rate. In fact, the explosion of diversity can initially outpace local resource competition before less-fit species are gradually driven extinct.

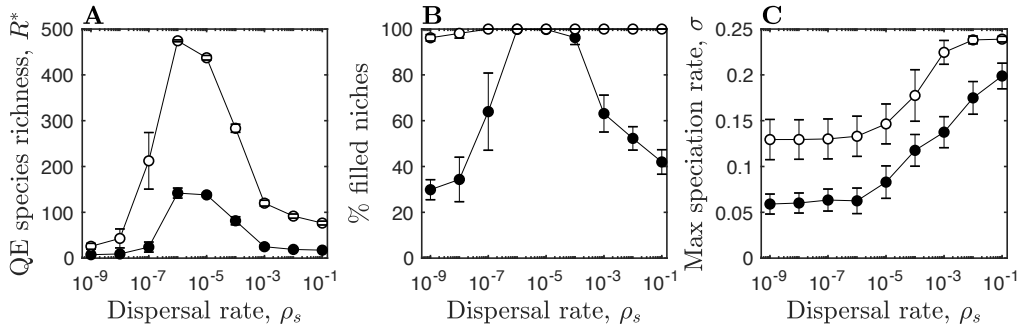

Figure 4 – Simulation results. Panels show results for substitutable (white) and non-substitutable resources (black) as a function of the dispersal rate, ρ_s. Markers correspond to mean values from 1,000 simulations, with error bars showing one standard deviation. (A) Quasi-equilibrium (QE) species richness, R^*; (B) percentage of potential niches that are filled in at least one patch. (C) Maximum speciation rate, σ. Parameters: $g_1, g_2 = 1.5$, $K_{mean} = 1000$, $K_{std} = 10$, $L = 20$, $m_1, m_2 = 5$, $n = 2$, $w_1, w_2 = 1/2$, $\epsilon_s = 10^{-3}$, $\mu_s = 10^{-4}$.

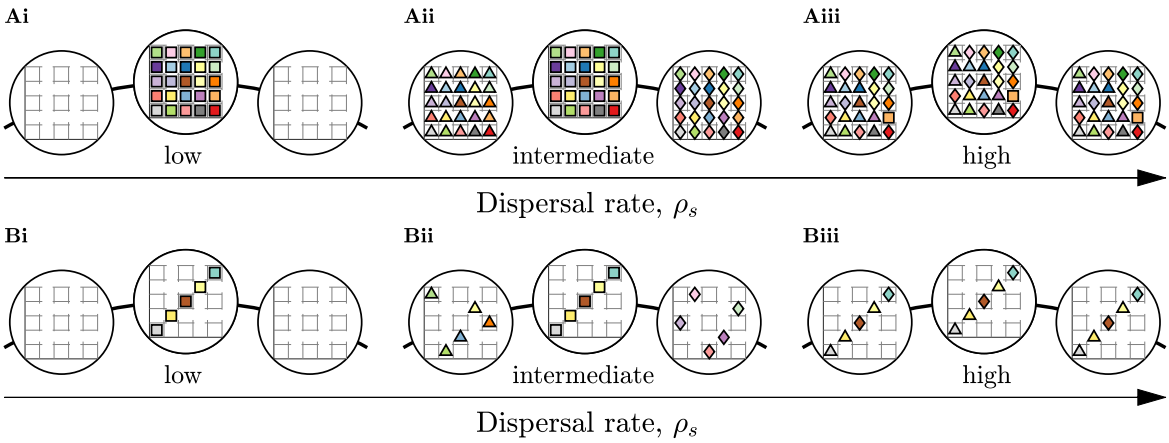

Figure 5 – Interactions between resource type and dispersal. Patches are represented by large connected circles, and markers represent species in a 2-dimensional niche space, with colors corresponding to the niche and shapes to the neutral trait of that species. (A) When resources are substitutable (e.g. different food sources), all potential niches are filled within each patch and so dispersal does not affect the global distribution of occupied niches in this example. (B) When resources are non-substitutable (e.g. food source and nest sites), species separate into non-overlapping distributions within each patch. However, due to the arbitrary nature of the non-overlapping distributions, different species distributions can evolve in each patch at intermediate dispersal, leading to a corresponding peak in the proportion of potential niches that are filled at the global level.

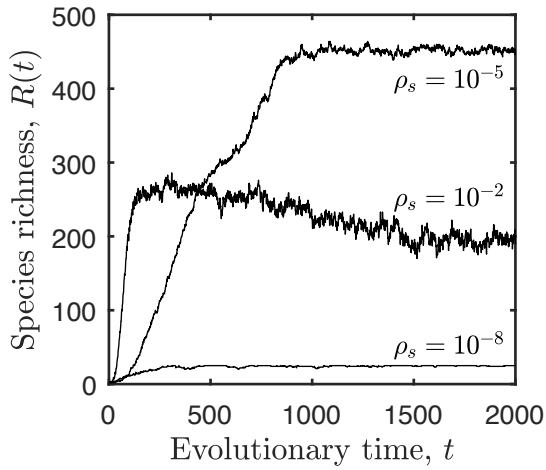

Figure 6 – Example simulation dynamics for different dispersal rates, ρ_s. When dispersal is low ($\rho_s = 10^{-8}$), both the maximum speciation rate, σ, and the quasi-equilibrium species richness, R^*, are low. When dispersal is intermediate ($\rho_s = 10^{-5}$), the maximum speciation rate is moderate and the quasi-equilibrium species richness is high. When dispersal is high ($\rho_s = 10^{-2}$), the maximum speciation rate is initially very high, but once all patches are occupied the species richness begins to fall due to competition among species that overlap in niche space, leading to lower quasi-equilibrium species richness. Parameters as in Fig. 4, with substitutable resources.

DISCUSSION

Our models confirm the intuitive prediction (Fig. 1) that maximal species richness should typically occur among organisms with intermediate dispersal (Fig. 2, 4). If dispersal rates are too low, then relatively little of the globally available area is found and occupied by the taxon, and the total number of unique species remains low. If dispersal rates are high, then this limitation on range spread ceases to be relevant, but now strong population mixing prevents divergence between habitat patches; again, the total number of unique species remains low. It is therefore only at intermediate dispersal that most patches are occupied at a global scale, but the exchange of migrants remains low enough to permit divergence of resource use between patches. This pattern is qualitatively robust to a wide range of parameters, including variation in niche breadth, the number of available niches, carrying capacities, the number of patches, the relative speed of the ecological dynamics, baseline speciation rate, and time scales (Fig. S1-S8); it is therefore likely to be very general.

Notably, we find that global niche diversity can also peak at intermediate dispersal, but only when competition is for non-substitutable resources (e.g. food source and nest sites) as this leads to arbitrary non-overlapping associations between niche traits within each patch [30]; intermediate dispersal therefore produces different combinations of filled niches across patches, leading to high global niche diversity. Even though species sometimes disperse to other patches or new species arise locally, a priority effect tends to maintain established patterns within a patch and prevents the invasion of new species. Once the maximum number of species with non-overlapping traits has become locally established, any new or invading species will have to compete on multiple fronts, and will therefore be at a

disadvantage compared to resident (non-overlapping) species. In contrast, competition for substitutable resources ultimately leads to high saturation of potential niches whenever a patch is occupied, even for very low dispersal. Although increasing dispersal leads to the colonization of new patches, it may not lead to a corresponding increase in niche diversity because the same set of niches can be filled in each patch. Our model assumed there were only two niche dimensions, but our findings will likely apply whenever there are multiple niche dimensions due to the overlapping/non-overlapping patterns that these different resource competitions are known to produce [30]. Finally, rather than peaking at intermediate dispersal, we found that the maximum speciation rate increased with dispersal. This is because high dispersal leads to rapid colonization of all patches and hence a high number of locally-available niches for species to fill. Indeed, when a patch is newly colonized, there is likely to be a short period of rapid diversification (i.e. an adaptive radiation) as species partition the available niches, followed by a reduction in the speciation rate [31].

As a whole, our model has potential to unify previous findings, as it shows why it is possible to find both increasing [14] and decreasing [10] effects of dispersal rate on speciation. These findings may reflect distinct but often co-occurring processes, visually depicted as taxa potentially residing on different slopes of a unimodal (humped) shape. On the left slope (Fig. 1), more dispersal leads to higher regional species richness, as speciation is limited by the rate at which lineages spread to new areas in which speciation can occur. On the right slope, dispersal has surpassed the point where it leads to maximum speciation; further increases in dispersal lead to dynamics where frequent exchange of migrants maintains few but very

widely distributed species. Note that global species richness, being the outcome of speciation rates that operate over various areas, is not equivalent to speciation rate itself; if the same rate operates in a geographically restricted taxon, the outcome is fewer species than if the same rate applies over multiple geographic locations, thus the effect of dispersal definitely should be taken into account as it modifies the importance of regional versus global diversification (for a discussion of allopatric and sympatric speciation in a biogeographic context see [27]).

Haldane's apocryphal quip [32] might therefore be complemented by speculating on a potential causality: beetles have wings but they use them relatively infrequently, and over shorter distances, compared with many other volant organisms. Obviously, we do not claim this to be the sole causality. Additional drivers of species richness in this taxon have been identified from feeding on angiosperms, [32] to variation in the ability to resist extinction, [33], and it should also be noted that Hymenoptera may challenge the status of Coleoptera as the most speciose order [34]. Nevertheless, it is intriguing that beetle speciation appears to be particularly sped up in cases where lineages that first dispersed to new areas subsequently lost the ability to fly [35] (for evidence that colonization ability of beetles covaries with flight ability see [36]).

While the theory of speciation has made great strides, quantitative predictions regarding the conditions that predispose taxa to speciate rapidly or less rapidly are surprisingly rare. Like any model of evolutionary ecology, ours makes a compromise between generality (with its messages hopefully applying across many taxa) and the precision and inclusiveness

regarding many phenomena that might vary in their taxon-specific importance. By leaving much detail (regarding e.g. biogeography or genetic architecture) outside the model, we have conducted a very general investigation of the core principles underlying the dispersal-speciation paradigm. Our chosen focus is on how resource competition can lead to contrasting distributions of niches as a function of dispersal, and in turn the likely consequences for species richness and speciation rates.

One potential model limitation is that we used an 'all else being equal' assumption structure by envisaging all lineages to have constant and random dispersal abilities. Further work could usefully relax such assumptions, as dispersal is unlikely to be a truly random process and it is known that post-colonization reductions in flight ability [37] can promote speciation [35,38] while also potentially increasing extinction rates [39]. The motivation for our work was the curious lack of theoretical models testing the prediction of a hump-shaped relationship between dispersal and speciation. We have shown this relationship to be robust to a wide range of modelling assumptions, which suggests the fundamental concept is likely to be fairly general. Future, more complex models of the dispersal and speciation processes can add nuance to the relationship we found, hopefully exploring whether the verbal model of dispersal and speciation remain as mathematically sound as our work, as a first step in this direction, shows them to be. Our work therefore sets the stage for further theoretical work on more complex speciation processes and temporal (evolutionary) changes in dispersal ability, taking into account the potentially contrasting [4] effects of dispersal on local, regional and global diversity patterns.

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AUTHOR CONTRIBUTIONS

A.K.S. and H.K. conceived the study and B.A. carried out the modelling work. All authors contributed equally to writing the manuscript. The authors declare no conflicts of interest.

DATA ACCESSIBILITY

Simulation code is available in the *Supplementary material*.

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