Intermediate abundance promotes speciation when dispersal is limited

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Abstract

Stub

Introduction

A fundamental question in evolutionary ecology concerns why some clades are diverse while others are not. Are there properties of species and lineages that promote speciation? One line of inquiry with a long and convoluted history is the role of rarity and commonness is driving diversification. Going back over 150 years, Darwin (1859) argued that widespread, abundant species should be superior competitors and thus more likely to give rise to new species.

This line of thinking carried forward to macroecologists who attempted to model, with some empirical support, the presumed positive association between commonness, fitness, and speciation (Maurer 1999). Paleontologists searched for relationships between commonness and diversification, alternately finding evidence for a positive relationship (Krug et al. 2008) but also a negative relationship [stanley1986; Jablonski and Roy (2003)]. Empirical studies of modern taxa have largely found that commonness is negatively or inconclusively related to measures of diversification (Jablonski and Roy 2003, Makarieva and Gorshkov 2004, Greenberg and Mooers 2017, Smyčka et al. 2023, Afonso Silva et al. 2025, but see Hay et al. 2022). While some of these studies focus specifically on average abundance, others on range size, and some on both, the two macroecological properties are most often strongly correlated (Brown 1995, Gaston 2003) and for now we will treat both as existing on a continuum between rarity and commonness.

More recent theoretical and modeling work has largely assumed a positive relationship between commonness and diversification. Hubbell (2001) perhaps started this trend with the inclusion of "point mutation" speciation in the Unified Neutral Theory of Biodiversity (UNTB). Because point mutation speciation assumes a constant probability of specaition for every individual,

lineages with more individuals will experience more speciation events in the UNTB [Hubbell (2001); etienne2007modes]. The speciation mechanism first proposed by Hubbell (2001) was never an accurate model of real diversification, but even later attempts to increase the realism of speciation in the UNTB retain the emergent property that more abundant lineages will undergo more specaition: protracted speciation (Rosindell et al. 2010) again assumes that incipient speciation is constant across individuals and thus full speciation will scale positively with lineage abundance; fission speciation (Etienne and Haegeman 2011) also assumes the probability of fission (the event that leads to speciation) increases with the number of individuals in a species. Largely independently from UNTB and its descendants, phylogenetic models of geographic change and diversification also explicitly assume that more widespread species have greater opportunity for speciation (Goldberg et al. 2011).

However, another process underlies speciation itself, the study of speciation in relation to commonness, and the relationship between abundance and range size: dispersal. Dispersal is a key mechanism by which populations can become isolated or connected, potentially leading to specaition or admixture (Yamaguchi 2022); it is a key process in phylogenetic models of geographic change and diversification (Matzke 2014); it is necessary to maintain biodiversity in the UNTB (Hubbell 2001); and it is the mechanism connecting abundance to range size in both neutral (Hubbell 2001) and non-neutral (Brown 1995) macroecological models.

Due to the potential for dispersal to create population isolates but also swamp out regional differences that could have led to specaition, it remains an intriguing question what the connection is between dispersal ability as a biological trait and speciation as an evolutionary outcome (Yamaguchi 2022). Some empirical studies have found that measures of diversification have a hump-shaped or negative relationship with morphological proxies for dispersal ability (Price and Wagner 2004, Claramunt et al. 2012, Czekanski-Moir and Rundell 2019) while others have found a positive to flat relationship between dispersal ability and diversification (Claramunt et al. 2025). Agent-based model simulations have supported the idea of a trade-off between too little dispersal leading to population instability and too much dispersal leading to admixture with intermediate dispersal balancing the two extremes allowing for speciation (Birand et al. 2012, Ashby et al. 2020, Ciccheto et al. 2024).

But dispersal is not just a trait connected to morphology or imposed in a simulation, it emerges from population dynamics: each individual carries some probability of dispersing, thus species with more individuals will present with higher dispersal. This is the assumption, a realistic one, in birth-death-immigration models (Kendall 1948) of which the UNTB is one [Hubbell (2001); alonso2004]. Therefore, commonness and dispersal are interconnected and interdependent in their effects on speciation if they indeed have any consistent effects. It also remains an open debate whether their effects result from the determinism of adaptive evolution as Darwin (1859) believed or instead emerge from chance.

Here we develop a birth-death-immigration model with protracted specaition embedded in a landscape of multiple local populations connected with limited dispersal to investigate the role of abundance and chance in modulating the probability of speciation. Contrary to Darwin (1859) and UNTB (Hubbell 2001, Etienne et al. 2007, Rosindell et al. 2010, Etienne and

Haegeman 2011), we find that intermediate abundances lead to the greatest probability for dispersal. Critically, this result does not depend in any way on whether populations are more or less adaptively fit, it only depends on a balance between large enough population sizes to accrue sufficient probability of incipient speciation but small enough population sizes to not loose regional differentiation due to increased dispersal. We also analyze real data on the species richness and abundance of endemic arthropods in the pae āina Hawai i finding empirical evidence for intermediate abundance promoting speciation.

Methods

Simulating a birth-death-immigration process with speciation

We simulate a birth-death-immigration process (BDI) with speciation (BDIS) in a modified metapopulation (Hanski 1998) setting. In this setting there are a number of local populations connected by dispersal as well as an global source pool connected to each local population by dispersal. The global source pool is considered extremely large relative to local populations such that extinction of the global source pool is unlikely on the time scale of local dynamics (we approximate this assumption by never allowing the source pool to go extinct). Local populations grow and shrink according to local births and deaths, dispersal between local populations, and dispersal from the source pool. New species arise via a modified protracted speciation process (Rosindell et al. 2010) similar to the model of Tao et al. (2021). Our simulation model is consistent with other models derived from the Unified Neutral Theory of Biodiversity [UNTB; Hubbell (2001)], but unlike those models' multi-species perspectives, we only concern ourselves with a single species and whether that one species undergoes a speciation event. In that way we do not in fact make the assumption of per capita neutrality across species, meaning our results could be generalization to multi-species eco-evolutionary models based on niche theories (**niche-stuff?**).

Our simulation proceeds according to these rules:

1. Birth, death, immigration, and speciation all happen independently and are determined by their own respective rates
2. Speciation has 2 steps:
    i. incipient speciation happens by turning one local population into an incipient new species
    ii. if the incipient species lasts long enough it becomes a new species; "long engough" is determined by a waiting time parameter τ—the larger τ, the longer an incipient species must wait before becoming a genuinely new species
3. Immigration between local communities and from the global source pool slows the progress toward speciation; if an incipient species has to wait τ time (in the absence of immigration) until it is a full species, each immigration event adds an increment to τ of ξ/n_i where ξ is a parameter we can set and n_i is the population size of the incipient species

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Table 1: Parameters govering the simulation and their ranges over the simulation experiment. Mathematical parameter names are given first followed by their name in the simulation code. Note `np` and `nstep` were fixed throughout the course of the simulation experiment

parameter		range		description
λ	(`la`)	1.0	10.000	local birth rate
μ	(`mu`)	1.0	10.000	local death rate
γ	(`g`)	0.0	0.100	dispersal rate from the global source pool to one local population
m_{prop}	(`m_prop`)	0.0	0.100	proportional dispersal rate between local populations relative to global rate
ν	(`nu`)	0.0	0.001	incipient speciation rate
τ	(`tau`)	0.0	4.000	wait time to full speciation in the absence of dispersal
ξ	(`xi`)	0.5	2.000	amount each dispersal event sets back the progression toward speciation
n_p	(`np`)	2.0	2.000	number of local populations
n_{step}	(`nstep`)	10,000.0	10,000.000	number of simulation iterations

4. Once full speciation occurs the simulation is stopped; if the simulation reaches the maximum designated number of iterations without full speciation, then the simulation stops anyway

Full details of the simulation are provided in Supplementary Section S2. Underlying C++ and R source code is available in the R package *abondolism* (Rominger 2026) accompanying this paper.

Simulation experiment

Table 1 summarizes the simulation parameters in our model and the range of values we use in our simulation experiment. In all cases parameter values are drawn from a uniform distribution. A total of 10,000 simulations were run, each with a unique set of randomly sampled parameters.

Parameter values were chosen as a balance between biological realism and computational efficiency: rates are sufficiently fast to allow for abundances to reach levels often found in survey data (e.g. the arthropod survey data we analyze here) within

Analysis of arthropod richness and abundance from the pae ̄āina Hawai i

Gruner abundance: calculate mean across sites

Bishop checklist: *generally* each native genus got here once and radiated
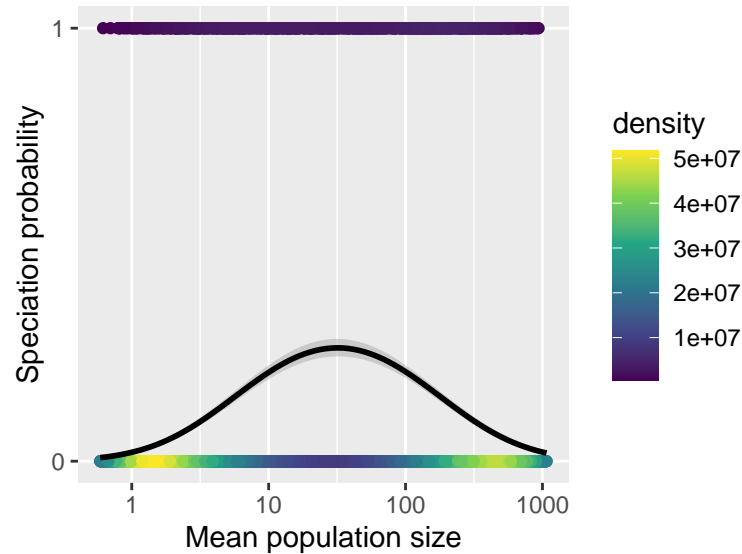
Results

Figure 1: Relationship across simulation runs between average abundance over local populations and speciation. Curve is a quadratic binomial generalize linear model and gray region shows 95% confidence envelope

So we see there is a sweet spot of intermediate abundance where speciation is most likely to take place!

To-do

- intro
- bring in HI arth data
- figure out if want to model arth data with stan
- if yes, connect prob(speciation) to rate (r = delta_t p o(delta_t)) and connect that to neg binom regression

References

Afonso Silva, A. C., Maliet, O., Aristide, L., Nogués-Bravo, D., Upham, N., Jetz, W. and Morlon, H. 2025. Negative global-scale association between genetic diversity and speciation rates in mammals. - Nature communications 16: 1796.

Ashby, B., Shaw, A. K. and Kokko, H. 2020. An inordinate fondness for species with intermediate dispersal abilities. - Oikos 129: 311–319.

Birand, A., Vose, A. and Gavrilets, S. 2012. Patterns of species ranges, speciation, and extinction. - The American Naturalist 179: 1–21.

Brown, J. H. 1995. Macroecology. - University of Chicago Press.

Ciccheto, J. R. M., Carnaval, A. C. and Araujo, S. B. L. 2024. The influence of fragmented landscapes on speciation. - Journal of Evolutionary Biology 37: 1499–1509.

Claramunt, S., Derryberry, E. P., Remsen Jr, J. and Brumfield, R. T. 2012. High dispersal ability inhibits speciation in a continental radiation of passerine birds. - Proceedings of the Royal Society B: Biological Sciences 279: 1567–1574.

Claramunt, S., Sheard, C., Brown, J. W., Cortés-Ramírez, G., Cracraft, J., Su, M. M., Weeks, B. C. and Tobias, J. A. 2025. A new time tree of birds reveals the interplay between dispersal, geographic range size, and diversification. - Current Biology 35: 3883–3895.

Czekanski-Moir, J. E. and Rundell, R. J. 2019. The ecology of nonecological speciation and nonadaptive radiations. - Trends in Ecology & Evolution 34: 400–415.

Darwin, C. 1859. On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life. - John Murray.

Etienne, R. S. and Haegeman, B. 2011. The neutral theory of biodiversity with random fission speciation. - Theoretical Ecology 4: 87–109.

Etienne, R. S., Apol, M. E. F., Olff, H. and Weissing, F. J. 2007. Modes of speciation and the neutral theory of biodiversity. - Oikos 116: 241–258.

Gaston, K. J. 2003. The structure and dynamics of geographic ranges. - Oxford University Press.

Goldberg, E. E., Lancaster, L. T. and Ree, R. H. 2011. Phylogenetic inference of reciprocal effects between geographic range evolution and diversification. - Systematic biology 60: 451–465.

Greenberg, D. A. and Mooers, A. Ø. 2017. Linking speciation to extinction: Diversification raises contemporary extinction risk in amphibians. - Evolution Letters 1: 40–48.

Hanski, I. 1998. Metapopulation dynamics. - Nature 396: 41–49.

Hay, E. M., McGee, M. D. and Chown, S. L. 2022. Geographic range size and speciation in honeyeaters. - BMC Ecology and Evolution 22: 86.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. - Princeton University Press.

Jablonski, D. and Roy, K. 2003. Geographical range and speciation in fossil and living molluscs. - Proceedings of the Royal Society of London. Series B: Biological Sciences 270: 401–406.

Kendall, D. G. 1948. On some modes of population growth leading to RA fisher's logarithmic series distribution. - Biometrika 35: 6–15.

Krug, A. Z., Jablonski, D. and Valentine, J. W. 2008. Species–genus ratios reflect a global history of diversification and range expansion in marine bivalves. - Proceedings of the Royal Society B: Biological Sciences 275: 1117–1123.

Makarieva, A. M. and Gorshkov, V. G. 2004. On the dependence of speciation rates on species abundance and characteristic population size. - Journal of Biosciences 29: 119–128.

Matzke, N. J. 2014. Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. - Systematic biology 63: 951–970.

Maurer, B. A. 1999. Untangling ecological complexity: The macroscopic perspective. - University of Chicago Press.

Price, J. P. and Wagner, W. L. 2004. Speciation in hawaiian angiosperm lineages: Cause, consequence, and mode. - Evolution 58: 2185–2200.

Rominger, A. J. 2026. abundolism.

Rosindell, J., Cornell, S. J., Hubbell, S. P. and Etienne, R. S. 2010. Protracted speciation revitalizes the neutral theory of biodiversity. - Ecology Letters 13: 716–727.

Smyčka, J., Toszogyova, A. and Storch, D. 2023. The relationship between geographic range size and rates of species diversification. - Nature Communications 14: 5559.

Tao, R., Sack, L. and Rosindell, J. 2021. Biogeographic drivers of evolutionary radiations. - Frontiers in Ecology and Evolution 9: 644328.

Yamaguchi, R. 2022. Intermediate dispersal hypothesis of species diversity: New insights. - Ecological Research 37: 301–315.