

# Intermediate abundance promotes speciation when dispersal is limited

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## Abstract

Foo foo foo

## Introduction

- Jablonski and Roy (2003): “Late Cretaceous gastropod genera exhibit a strong negative relation between the geographical ranges of constituent species and speciation rate per species per million years...These results support the view that the factors promoting broad geographical ranges also tend to damp speciation rates” analysis of modern only might not reveal this pattern—why Hawai'i could be a good place to look
- Krug et al. (2008): uses spp:gen ratio. widespread bival genera have more species. “Species within these cosmopolitan genera may have life-history traits or other attributes that allow for rapid adaptation to new environments, promoting both speciation and range expansion of a lineage”
- Birand et al. (2012): ABM, but about range and pixels are agents. found increased dispersal decreases speciation
- Hay et al. (2022): Provides good background on range size +/- corr with speciation. “Honeyeater speciation rate differs considerably between islands and the continental setting across the clade’s distribution, with range size contributing positively in the continental setting, while dispersal ability influences speciation regardless of setting. These outcomes support Darwin’s original proposal for a positive relationship between range size and speciation likelihood, while extending the evidence for the contribution of dispersal ability to speciation.”
- Goldberg et al. (2011): GeoSSE model assumes speciation increases with range size, extinction decreases with it
- Smyčka et al. (2023): hard to say if range size is + or - corr with speciation (could be impacted by change in range size with speciation)

- Kisel and Barraclough (2010): gene flow important for speciation; islands good for studying speciation
- Gaston (2003): classic reference on range size + corr with speciation
- Pigot et al. (2010): model of range size and diversification: finds larger ranges produce more speciation, but with speciation, ranges shrink, causing speciation slow down
- Ashby et al. (2020): ABM showing intermediate dispersal produces most speciation
- Price and Wagner (2004): speciation in Hawai'i plants; intermediate dispersal hypothesis; should check for possible data usability on lineage designation
- Claramunt et al. (2012): “Using a surrogate for flight performance and a species-level DNA-based phylogeny of a large South American bird radiation (the Furnariidae), we found that lineages with higher dispersal ability experienced lower speciation rates.”
- Ciccheto et al. (2024): model shows intermediate dispersal is optimum for diversification
- Casey et al. (2021): extinction up with decreasing abundance (range size also, but less predictive)
- Claramunt et al. (2025): “we found mixed evidence for the effect of dispersal on diversification rates: dispersive lineages show either slightly higher speciation rates or higher extinction rates. Our results therefore suggest that high dispersal ability increases range expansion and turnover, perhaps because dispersive lineages expand into islands or other geographically restricted environments and have lower population sizes...even though per capita dispersal rates may be high for highly dispersive species, levels of gene flow may be relatively low due to lower population size. This effect may explain why population genetic studies have not consistently found the expected negative relationship between dispersal ability and genetic differentiation<sup>71,72,73</sup> and why rates of speciation remain relatively stable across a wide range of dispersal capabilities”
- Makarieva and Gorshkov (2004): relationship between abundance and speciation open question. they go into neutral pop gen which we should too
- Afonso Silva et al. (2025): negative relationship between gen div and diversification. go into how low gen div, and thus Ne, could drive speciation
- Rosindell et al. (2010): protracted speciation; still most abundant is speciator
- Etienne and Haegeman (2011): fission speciation; still most abundant is speciator
- Etienne et al. (2007): makes explicit “the speciation rate of a species is directly proportional to its abundance in the metacommunity.” Find abundance-independent speciation is poor fit to data, indicates speciation matters
- Stanley (1990): speciation and extinction are correlated; could be abundance driven, dispersal driven, specialization driven
- Stanley (1986): speciation, extinction correlated in Neogene bivalves he was looking at; proposed a model for humped speciation across abundance
- Darwin (1859): widespread, more common leads to more speciation because of superiority
- Maurer (1999): organizes darwin's argument about widespread species being greater speciators
- Brown (1995): abundance range size correlation
- Czekanski-Moir and Rundell (2019): review finding that poor dispersal is key in producing “nonadaptive” radiations

- Greenberg and Mooers (2017): link between extant species diversity and extinction risk (arguing for correlation between etinciton and 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 a 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 enough” is determined by a waiting time parameter  $\tau$ —the larger  $\tau$ , 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  $\tau$  time (in the absence of immigration) until it is a full species, each immigration event adds an increment to  $\tau$  of  $\xi/n_i$  where  $\xi$  is a parameter we can set and  $n_i$  is the population size of the incipient species
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

These processes are governed by the following parameters:

- $\lambda$  (**la**): local birth rate
- $\mu$  (**mu**): local death rate
- $\gamma$  (**g**): dispersal rate from the global source pool to one local population
- $m_p$  (**m\_prop**): proportional dispersal rate between local populations relative to global rate; immigration rate  $m = \gamma \times m_p$
- $\nu$  (**nu**): incipient speciation rate
- $\tau$  (**tau**): wait time to full speciation in the absence of dispersal
- $\xi$  (**xi**): amount each dispersal event sets back the progression toward speciation
- $n_p$  (**np**): number of local populations
- $n_{\text{step}}$  (**nstep**): number of iterations to run the simulation for

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

### 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

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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

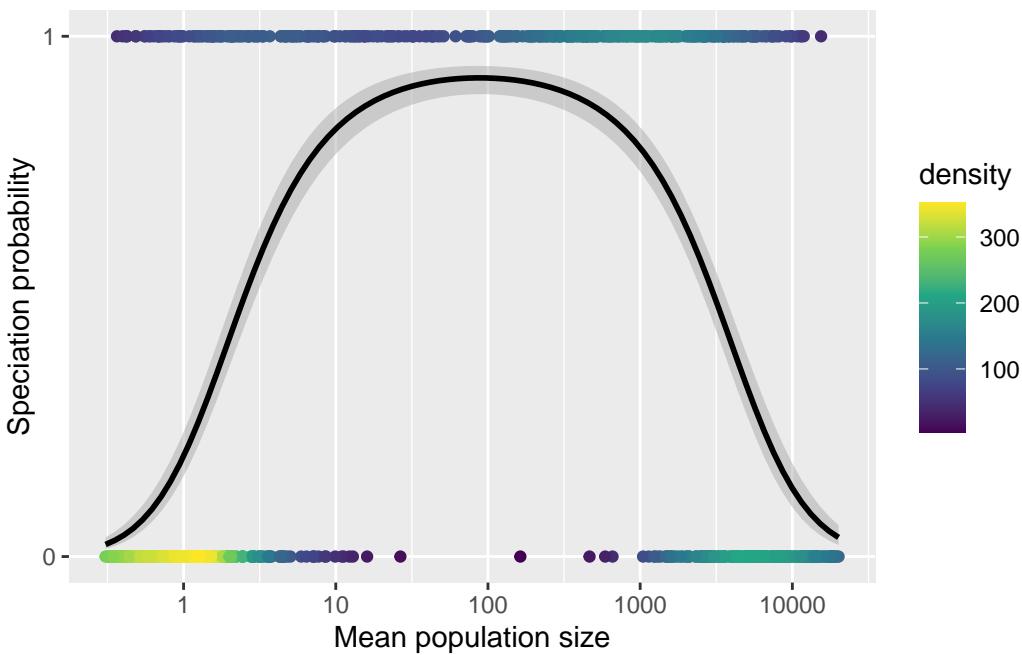


Figure 1

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