Intermediate abundance promotes speciation

Abstract

Foo foo foo

Introduction

```
print(Sys.time())
```

```
[1] "2026-01-28 16:19:56 HST"
```

```
quarto::quarto_render("ab_supp.qmd", quiet = TRUE)
tinytex::xelatex("ab_supp.tex", clean = FALSE)
```

```
[1] "ab_supp.pdf"
```

WTF Supplementary Figure S1

OMG Supplementary Section S2

- 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 Hawawi'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 pixles 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 specaition, ranges shrink, causing specaition slow down
- Ashby et al. (2020): ABM showing itermediate dispersal produces most speciation
- Price and Wagner (2004): speciation in Hawai'i plants; intermediate disperal 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[71,72,73] 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 bivalvs 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 "nonadatpive" radiations
- Greenberg and Mooers (2017): link between extant species diversity and extinction risk (arguing for correlation between etinciton and speciation)

Birth-death-immigration model with speciation

We simulate a birth-death-immigration model (BDI) with speciation (BDIS) in a metapopulation setting. This is the set-up

- There are `np` number of local populations in the metapopulation
- There is a global source pool

Here are the biological process steps:

1. Birth, death, immigration, and speciation all happen indipendently and are determined by respective rates (see params below)
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

3. Immigration between local communities and from the global source pool slows the progress toward speciation (technically if an incipient species has to wait τ time (in the absence of immigration) until it's 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)
4. Once full speciation occurs the simulation is stopped; if the simulation reaches the maximum designated number of iterations (`nstep`) without full speciation, then the simulation stops anyway

Here are the parameters:

- λ (`la`): birth rate
- μ (`mu`): death rate
- γ (`g`): immigration rate from global source pool
- m_p (`m_prop`): proportional immigration rate between local populations; immigration rate $m = \gamma \times m_p$
- ν (`nu`): incipient speciation rate
- τ (`tau`): wait time to full speciation in the absence of immigration
- ξ (`xi`): amount each immigrant sets back the progression toward speciation
- (`np`): number of local populations
- (`nstep`): number of iterations to run simulation for

And we can now actually run this thing and see what happens

```
library(abundolism)

nrep <- 1000 # number of different parameter combos to look at
la <- runif(nrep, 1, 10)
mu <- runif(nrep, 1, 10)
g <- la * runif(nrep, 0, 0.1)
m_prop <- runif(nrep, 0, 0.1)
nu <- runif(nrep, 0, 0.001)
tau <- runif(nrep, 0, 4) #10 / (la + mu + runif(nrep, 0, 1))
xi <- rep(1, nrep)
np <- 4
nstep <- 100000


# `sim_BDI_spec` is the workhorse function
sim_dat <- sim_BDI_spec(la = la, mu = mu, g = g, m_prop = m_prop,
                        nu = nu, tau = tau, xi = xi, np = np,
                        nstep = nstep)

ggplot(sim_dat,
       aes(x = tau, speciation)) +
    geom_pointdensity(method = "kde2d") +
    scale_shape_binned() +
    scale_color_viridis_c() +
    # scale_x_log10() +
    geom_smooth(method = "glm",
                method.args = list(family = "binomial"),
                color = "black")

ggplot(sim_dat, aes(time, mean_pop_size)) +
```

```
    geom_point(data = select(sim_dat, !speciation),
               mapping = aes(time, mean_pop_size), color = "gray50") +
    geom_pointdensity() +
    facet_wrap(vars(speciation)) +
    scale_x_log10() +
    scale_y_log10() +
    scale_color_viridis_c(trans = "log10")

ggplot(sim_dat, aes(mean_pop_size)) +
    geom_histogram() +
    scale_x_log10()
```

Now we can plot the results and find out how abundance relates to speciation in this model

```
library(ggplot2)
library(ggpointdensity)

# make a quadratic logistic model
sim_dat$log_pop <- log(sim_dat$mean_pop_size, 10)
mod <- glm(speciation ~ log_pop + I(log_pop^2), data = sim_dat,
           family = "binomial")

# add to data
sim_dat$mod_pred <- predict(mod, type = "response")

ggplot(sim_dat,
       aes(x = mean_pop_size, y = speciation)) +
    geom_pointdensity() +
    scale_color_viridis_c() +
    scale_x_log10() +
    scale_y_continuous(breaks = c(0, 1)) +
    xlab("Mean population size") +
    ylab("Speciation probability") +
    theme(panel.grid.minor.y = element_blank()) +
    geom_smooth(method = glm, formula = y ~ x + I(x^2),
                method.args = list(family = "binomial"), color = "black")



ggplot(sim_dat, aes(x = mean_pop_size)) +
    geom_histogram() +
    scale_x_continuous(transform = "log10")
```

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

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.

Casey, M. M., Saupe, E. E. and Lieberman, B. S. 2021. The effects of geographic range size and abundance on extinction during a time of "sluggish"'evolution. - Paleobiology 47: 54–67.

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.

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

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.

Kisel, Y. and Barraclough, T. G. 2010. Speciation has a spatial scale that depends on levels of gene flow. - The American Naturalist 175: 316–334.

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.

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

Pigot, A. L., Phillimore, A. B., Owens, I. P. and Orme, C. D. L. 2010. The shape and temporal dynamics of phylogenetic trees arising from geographic speciation. - Systematic biology 59: 660–673.

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

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.

Stanley, S. M. 1986. Population size, extinction, and speciation: The fission effect in neogene bivalvia. - Paleobiology 12: 89–110.

Stanley, S. M. 1990. The general correlation between rate of speciation and rate of extinction: Fortuitous causal linkages. - Causes of evolution: a paleontological perspective: 103.