Transient species can increase resident metapopulation size by modifying local conditions and regional connectivity

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Abstract

Populations are regulated by processes operating at both local and regional scales. As a result, species can interact not only within local communities but also through regional-scale processes. However, the feedback between local and regional processes of species interactions in shaping metapopulation dynamics have rarely been tested experimentally. Using nectar microbes as a model system, we examine how a bacterial species dispersing to a sink habitat, sustained by external supply, can interact with a resident yeast species directly by modifying local nectar chemistry and indirectly by altering metapopulation connectivity. We show that the external supply of bacteria increases resident yeast densities, potentially through the provision of resource subsidies, and that this benefit is enhanced when the dispersal rate of yeast is reduced in patches supplied with bacteria. Analysis of a metapopulation model indicates that the benefit of dispersal modification on metapopulation size occurs only when resource availability differs across patches–supporting our interpretation that bacterial supply provides resource subsidies. Taken together, our results underscore the role of dispersal in shaping how metapopulations experience density-dependence across heterogeneous landscapes, highlight the relevance of material flows across ecosystem boundaries, and suggest a plausible mechanism in which transient species may leave lasting impacts on ecological communities.

INTRODUCTION

Many natural populations are spatially subdivided into a network of local populations connected by dispersal, *i.e.*, a metapopulation. Although originally introduced as a spatially implicit model that tracks the number (or fraction) of patches occupied by a single species, metapopulation theory has developed into a more general theory that can accommodate multiple species, explicit local dynamics, and spatial structure (e.g., Hanski, 1998; Tilman, 1994; Leibold et al. 2004). Decades of theoretical work has shown that dispersal does more than merely shuffle individuals across space (Hastings, 1982; Holt, 1985; Karlin & McGregor, 1972; Levin, 1974; Levins, 1969). Even under the simplest scenarios, dispersal of organisms can have non-intuitive effects on local and regional patterns of biodiversity (Hanski, 1998; Huffaker, 1958; Levin, 1974; Levins, 1969). For instance, dispersal allows metapopulations to persist through patch dynamics even when local populations are certain to go extinct (Brown & Kodric-Brown, 1977). Dispersal can even enable metapopulations to persist when average local growth rates are negative, as occasional periods of positive growth inflate overall population size (Kortessis et al., 2025; Matthews & Gonzalez, 2007). Furthermore, dispersal can stabilize or destabilize local populations (Bascompte & Solé, 1994; Doebeli, 1995; Huffaker, 1958; Pascual, 1993) or allow intePracting species (or genotypes) to coexist (Hassell et al., 1991; Karlin & McGregor, 1972; Levin, 1974; Solé et al., 1992). Recent work demonstrates that dispersal can even increase the total number of individuals across the metapopulation (i.e., metapopulation size) relative to the sum of its local carrying capacities without dispersal if local conditions are spatially heterogeneous (Arditi et al., 2015; DeAngelis et al., 2016; He et al., 2025; Zhang et al., 2017). In sum, these results indicate that the dynamics of a regional metapopulation are rarely the simple sum of its constituent populations' dynamics considered in isolation and instead often depend on how dispersal links them.

Despite progress made in understanding how dispersal structures ecological communities, relatively less is known about the ecological consequences when the dynamics of dispersal is itself

coupled to local dynamics. In natural ecological settings, non-random (directed or biased) dispersal is more likely the norm than the exception (Amarasekare, 2010; Clobert et al., 2009; McPeek et al., 2024; Vuilleumier & Possingham, 2006). While directionality in movement can arise naturally via physical forces such as wind, currents, and gravity (Germain et al., 2019; Mari et al., 2014; Okubo & Levin, 2001), it can also result from biotic mechanisms such as habitat selection (Clobert et al., 2009). Although it might seem that directed dispersal via habitat selection is unique to mobile animals with cognitive capacities, organisms with limited motility can also disperse non-randomly via mechanisms such as phoresy (or zoochory in plants), where their interactions with animal dispersal vectors can dictate both the rate and direction of movement (Bartlow & Agosta, 2021).Given that dispersal can modify population size and that species can influence each other's dispersal, a natural question to ask is whether species interactions can be mediated from purely regional processes. For example, what happens when multiple phoretic species share the same vectors? Could shared dispersal vectors mediate interactions between phoretic organisms? If vectors are limited, could competition for them shape the relative abundances of phoretic species at the metapopulation level (Nell et al., 2025)? To date, few studies have tackled these questions, even though doing so could yield important insights into metapopulation dynamics in natural ecological settings.

Recognizing that dispersal can be an integral component of how species interact could reveal cryptic interactions that shape ecological communities. This possibility is particularly relevant for species that form sink populations—species whose persistence is determined less by local conditions than by immigration from adjacent habitats. Because such species cannot maintain growth locally, their potential impacts on 'resident' species—i.e., species capable of persisting without immigration—are often overlooked (Amor et al., 2020; Mallon et al., 2018). However, previous studies suggest that sink populations are not only prevalent but can also impact resident species (Amarasekare & Nisbet, 2001; Holt et al., 2003; Long et al., 2007; Mallon et al., 2018; Pulliam, 1988). The primary mechanism by

which this impact occurs is through the sheer abundance by which immigration introduces the species into a local community, amplifying their total impact despite their otherwise small per-capita effects on residents. For instance, a species occupying a sink habitat can reach sufficiently high densities via immigration and deplete resources to levels that depress the abundance of, or even competitively exclude, an otherwise locally superior competitor (Amarasekare & Nisbet, 2001; Long et al., 2007). Notably, these studies assume that sink populations impact residents purely through local interactions. However, if dispersal can be shaped by other species, sink populations may also influence residents by altering their dispersal patterns across the metapopulation. Despite evidence showing that shared dispersal vectors can reshape dispersal patterns among competing species (e.g., Muller-Landau et al., 2008; Xiao & Zhang, 2016), their long-term demographic consequences remain unknown.

A system in which dispersal vectors modulate species interactions is the floral microbiome, making it an excellent model system for examining the potential feedback between local and regional processes. Floral nectar often contains microbial communities (Vannette, 2020) that are dispersed by pollinators (Belisle et al., 2012; Herrera et al., 2009; Vannette & Fukami, 2017). The identity of pollinators can be a strong determinant of microbial composition, suggesting that their abundance and foraging patterns can shape the spatial distribution of microbial communities in floral nectar (Belisle et al., 2012; Morris et al., 2020; Vannette et al., 2021; Vannette & Fukami, 2017). As is true for many microbial systems (Mallon et al., 2018), floral nectar is likely to contain many transient invaders given that nectar microbes are often a subset of the microbial communities found on pollinators (Belisle et al., 2012; Herrera et al., 2009; Vannette & Fukami, 2017). Importantly, the microbial activity within nectar can alter pollinator foraging behavior by modifying nectar chemistry or producing volatiles that attract or repel certain pollinators (Chappell et al., 2022; Schaeffer et al., 2019; Vannette et al., 2013). Local modification of nectar chemistry may thus bias dispersal towards or away from certain flowers. In other words, these microbes participate in their own dispersal despite not being able to move on their own.

Considered together, these processes create a feedback loop between local dynamics and regional dispersal via pollinator foraging (Nell et al., 2025), providing an additional pathway in which sink populations could interact with residents at the metapopulation level.

Here, using nectar microbes isolated from the hummingbird-pollinated sticky monkeyflower in California (*Diplacus aurantiacus*), we conducted a laboratory experiment to investigate how a bacterial species invading a sink habitat can impact the metapopulation dynamics of a resident yeast species. To avoid ambiguity, we refer to dispersal from external sources as invasion (or supply) and reserve dispersal for movement among patches within the metapopulation (external vs. internal dispersal sensu Fukami 2005). Previous work in this system has shown that the bacteria species reduces nectar pH, which in turn suppresses yeast growth and reduces pollinators' nectar consumption (Chappell et al., 2022). In a pilot experiment, we found that the bacteria species cannot sustain a viable population under our experimental conditions but can nevertheless reduce nectar pH, making it well suited for examining the effects of species invading a sink habitat on resident yeast species. Specifically, we ask how the yeast metapopulation responds to changes in local nectar chemistry (i.e., reduced pH) and patch (*i.e.*, local population) connectivity mediated by pollinator foraging preferences in the presence of bacterial sink populations. First, we test the hypothesis that reduction of nectar pH by the external supply of bacteria reduces yeast metapopulation size by modifying nectar pH to the detriment of yeast population growth (*i.e.*, local effects). Second, we test the hypothesis that pollinator preference biases dispersal away from low-pH patches, thus altering metapopulation size of yeast by altering its metapopulation connectivity (*i.e.*, local-regional interaction effects). Finally, we analyze a simple two-patch metapopulation model to verify and complement inferences drawn from our experimental results.

METHODS

Overview of study system

To investigate the impact of a species invading a sink habitat on the metapopulation dynamics of a resident species, we conducted experiments using two nectar microbes: the bacterium *Acinetobacter nectaris* (strain FNA17) and the yeast *Metschnikowia reukaufii* (strain MR1). These microbes naturally inhabit the floral nectar of the sticky monkeyflower, *Diplacus aurantiacus,* and the specific strains we used were isolated from flowers in Jasper Ridge Biological Preserve ('Ootchamin 'Ooyakma) located in the Santa Cruz Mountains of California. *Diplacus aurantaicaus* is a shrub native to coastal Oregon and California and is commonly pollinated by hummingbirds (Belisle et al., 2012). Instead of dispersing between flowers themselves, these microbes "hitchhike" onto pollinators to move between flowers. When microbes arrive at a new flower, they proliferate by metabolising nectar resources and in so doing, modify nectar chemistry and set in motion the diverse ecological interactions that occur in these microscopic ecosystems (e.g., microbe-microbe interactions, plant-pollinator mutualisms; Chappell & Fukami, 2018; Quevedo-Caraballo et al., 2025). Its relative simplicity and tractability allows this study system to be replicated in laboratory settings with artificial nectar in microwell plates as flowers and pipettes to simulate pollinator-assisted dispersal (Chappell et al., 2022; Grainger et al., 2019; Letten et al., 2018; Tucker & Fukami, 2014; Vannette & Fukami, 2014). Following these prior studies, we adapted this experimental microcosm for the purpose of our study.

Experimental setup

We conducted an experiment that factorially manipulated 'bacterial supply' (i.e., the number of habitat patches in each metapopulation that would receive bacteria from an external source, dispersal bias, and dispersal frequency (i.e., the number of dispersal events within a growth cycle) to test how *A. nectaris* bacteria-driven pH changes affect *M. reukaufii* yeast metapopulation by modifying local nectar conditions

150 and metapopulation connectivity through dispersal bias (Fig. 1). Note that our hypothesis is concerned
151 with how patches are wired (*i.e.*, dispersal bias) and not the overall frequency of dispersal events *per se.*
152 Thus, we included two levels of dispersal frequency to ensure a meaningful difference between the levels
153 of the dispersal bias treatment is realized, rather than being a variable that is itself of interest. Our
154 experimental metapopulations consisted of eight wells (i.e., patches) on a 96-well PCR plate, connected
155 by dispersal. Each metapopulation was assigned to one of 12 treatment groups defined by the fully
156 factorial combination (Fig. 1A) of bacterial supply (three levels: 0, 3, or 6), dispersal bias (two levels:
157 random or bias), and dispersal frequency (two levels: 3 or 6), with each treatment replicated six times (12
158 treatments x 6 replicates = 72 metapopulations). Each replicate metapopulation was initiated by seeding
159 patches with approximately 100-150 viable cells of *M. reukaufii* (see Supplementary Methods) and 100 µl
160 of sterile artificial nectar. Artificial nectar was prepared as specified by Chappell et al. (2022) and the full
161 recipe is provided in Supplementary Methods. Plates were sealed with a sterilized air-permeable
162 membrane and incubated at 26°C for two days before beginning the experiment. After initiation, each
163 metapopulation underwent a total of five two-day growth-dilution-cycles where each cycle included the
164 following order of events: 1) pH sampling + dispersal, 2) resource replenishment, 3) community census,
165 4) bacterial supply, and 5) a two-day incubation period (Fig. 1B):

166

167 **Event 1: Dispersal.** To simulate pollinator-assisted dispersal, we first sampled the pH of local patches,
168 generated a sequence of dispersal events, then pipetted nectar between patches according to the order of
169 generated sequences. Specifically, for the bias treatment, 10 µl of nectar from each patch were pipetted
170 onto pH indicator strips. Once pH readings developed, we recorded the pH values and used them as
171 weights (representing pollinator preferences) to generate a new sequence of dispersal events between
172 donor-recipient pairs. Specifically, donor and recipient patches were selected by sampling two patches
173 without replacement, with a weighted distribution over the eight patches (A–H), where selection
174 probabilities are proportional to their respective pH values. The weight of each patch (ω_i) was calculated

175 using the Monod equation with a half-saturation constant set at 3, which is a pH value that lies between
176 nectar conditioned by bacteria (pH = 2) and yeast (pH = 4; Chappell et al 2022). More precisely, the
177 weight of patch *i* is $\omega_i = pH_i / (3 + pH_i)$ and the probability of selecting it is obtained by normalizing
178 these weights, $P_i = \omega_i / \sum_{j=1}^{8} \omega_j$. This setup reflects the field observation that low-pH patches are
179 less likely to be visited by pollinators and, consequently, microbes are less likely to disperse into or out of
180 them (Vannette et al. 2013; Chappell et al. 2022). For the random treatment, the pH sampling step was
181 skipped (but still discarding 10 µl of nectar from each patch) because dispersal did not depend on pH.
182 Instead, dispersal sequences from random dispersal treatments were done in a similar manner except that
183 the probabilities were always equal across patches (*i.e.*, independent of pH); the sequence for background
184 dispersal was identical for all 72 metapopulations in the random dispersal treatment. For both the biased
185 and random dispersal treatment, each dispersal event was achieved by pipetting 3 µl of nectar from a
186 donor patch to a recipient patch. Background dispersal was conducted to ensure that patches within a
187 replicate metapopulation are connected within the experimental duration. The number of dispersal events
188 per growth cycle was determined by the dispersal frequency treatment, either 3 or 6, which was
189 manipulated factorially with dispersal bias. In other words, each replicate underwent 3 or 6 sequential
190 dispersal events (in addition to background dispersal) within a growth-dilution cycle.

191

192 **Event 2: Resource replenishment.** Once the dispersal events were completed, all patches were diluted
193 by transferring 5 µl of nectar into 95 µl of fresh, sterilized media on new 96-well plates to simulate
194 resource replenishment (i.e., nectar production in flowers). We used new sterile 96-well plates, instead of
195 removing and adding nectar from the original, to minimize contamination.

196

197 **Event 3: Sampling.** Immediately after dilution, we sampled each local community by plating 5 µl of the
198 newly diluted nectar onto yeast malt agar (YMA) for yeast and 5 µl onto tryptic soy agar (TSA) for

199 bacteria, and then enumerated the resulting colony-forming units (CFUs) after >3 days of incubation at
200 room temperature as a measure of microbial density (following Peay et al., 2012 and Vannette et al.,
201 2013). Due to time constraints associated with simultaneously conducting the experiment and counting
202 CFUs, we took images of the agar plates and enumerated CFUs after completion of the experiment (see
203 Appendix for sample images). In a few cases, colonies were too numerous to count so we set their counts
204 to 200, a value just above the maximum from samples that were countable. To ensure this artificial cutoff
205 did not qualitatively affect our results, we repeated our analyses with these samples removed (see
206 'Potential artifacts of experimental design' below).

207

208 **Event 4: Bacterial supply.** Following sampling, bacterial cells were added to patches according to the
209 bacterial supply treatment. Specifically, bacterial cells were either added to no patches (bacterial supply =
210 0), patches A to C (bacterial supply = 3), or patches A to F (bacterial supply = 6). We chose to add
211 bacteria to only a subset of patches within the metapopulation because this allows spatial heterogeneities
212 in nectar pH and thus creates variation in dispersal probabilities under the dispersal bias treatment.
213 Although doing so is not required, we chose to fix the patches in which bacteria were added (as opposed
214 to randomly selecting patches to inoculate) to minimize experimental error. Approximately 20,000
215 bacterial cells (~200 cells/µl nectar) were inoculated to each recipient patch (see Supplementary
216 Methods). Bacterial cells were supplied after sampling because in our pilot trials, this amount of bacteria
217 was necessary to reduce pH (after 2 days) but would be too dense to count if plated directly after
218 inoculation. Thus, the bacteria that we sampled came from the remaining bacteria inoculated two days
219 prior.

220

221 **Event 5: Incubation.** Following bacterial supply, 96-well plates were sealed with sterilized, air-
222 permeable membranes and incubated at 26°C for 48 hours before beginning the next cycle.

Data analysis

Yeast metapopulation size

To assess treatment effects on yeast metapopulation size, we defined metapopulation size as the sum of local patch densities within a metapopulation replicate and modelled it as a response variable in a negative binomial generalized linear mixed model (GLMM). This model included dispersal frequency and bacterial supply as continuous predictors, dispersal bias as a categorical variable, and all two-way interactions as fixed effects, with replicate and time as random effects. We included all two-way interactions because they aligned with our hypotheses and excluded the three-way interaction term because including it did not improve model fit. Because initial statistical fits with Poisson-distributed errors showed violation of homoscedasticity, we implemented a forward model selection to account for potential variance structure in our data. Specifically, we sequentially added treatment terms as predictors to the dispersion component of the negative binomial GLMM and only kept terms that significantly improved model fit (as evaluated by χ^2 tests; Table S1). This led to the selection of a model that included bacterial supply as a significant predictor of the variance in yeast metapopulation size (Table 1; ΔAIC = -34.8, $P < 0.001$) which satisfied the assumption of residual homoscedasticity. Furthermore, we also assessed the correlation between local densities of yeast and bacteria to provide additional evidence for the local effects of bacteria supply on yeast population size using the `cor.test()` function in base R. Statistical models were fitted in R using the 'glmmTMB' and model assumptions were evaluated using the 'DHARMa' package.

Potential artefacts of experimental design

246 We conducted additional tests to confirm that our experimental results were not contingent on the choices
247 of our experimental design. We describe three specific tests here in brief, and provide more detailed
248 descriptions in the Supplementary Methods, with results shown in Fig. S3 and Fig. S4. First, because a
249 few samples formed colonies that were too dense to count (35 samples out of 354 total; denoted 'Inf' in
250 our raw data), we included them in our statistical analyses by setting their counts to 200. To ensure that
251 this decision did not artificially bias our results, we refitted the same statistical models with these samples
252 removed and found no qualitative differences (Table S1-2; Fig. S2). Second, we verified the extent to
253 which our experimental treatments modified the dispersal in patches supplied with bacteria relative to
254 those without. For example, if treatments were successful, then bacteria supplied patches should be less
255 likely to be selected for dispersal relative to patches with no supply under the dispersal bias treatment. To
256 test this, we measured the differences in dispersal propensities (i.e., frequency that a patch type is selected
257 for dispersal) between dispersal treatments and tested whether these differences differed by patch type. A
258 GLMM revealed marginally significant difference in the dispersal propensities between patch types (P =
259 0.05; Fig S3). Lastly, we confirmed that the position of microplate wells had no effect on yeast densities
260 by comparing the densities between wells within replicate after controlling for treatment effects via
261 bootstrapping.

262

263 *Metapopulation model*

264 We complemented our experiment with the analysis of a two-patch metapopulation model. As described
265 in our Results, we unexpectedly found that the densities of the resident species *M. reukaufii* were
266 positively correlated with the densities of the bacterial species, *A. nectaris* (Fig. 3). Given this finding, we
267 explored the possibility that, in addition to affecting regional connectivity by modifying nectar pH,
268 immigration of *A. nectaris* could also impact the resident species locally by bringing in resource subsidies
269 that increase the local carrying capacity of yeast. To explore this possibility in a model and see if patterns

resemble those seen in our experiment, we analyzed a two-patch metapopulation model and asked how dispersal bias (induced by pH modification) and local resource subsidies (via external supply of bacteria) jointly affect yeast metapopulation size.

To simplify analysis, we did not explicitly model the densities of the bacterial species and simply assumed that its effects are reflected in demographic and dispersal parameters of the resident yeast. Our general model takes the form:

$$\frac{dN_B}{dt} = rN_B\left(1 - \frac{N_B}{\beta K}\right) - D(1 + \delta)N_B + D(1 - \delta)N_N$$

$$\frac{dN_N}{dt} = rN_N\left(1 - \frac{N_N}{K}\right) - D(1 - \delta)N_N + D(1 + \delta)N_B$$

where N_B and N_N are the densities of the resident yeast in patch B (bacteria-containing) and patch N (no-bacteria), respectively. The parameters *r* and *K* represent the local intrinsic growth rate and baseline carrying capacity (*i.e.*, the carrying capacity in the absence of enhancement by bacterial subsidies), while *D* denotes the average per-capita dispersal rate across the metapopulation. The parameters $\boldsymbol{\beta}$ and $\boldsymbol{\delta}$ control asymmetries in carrying capacity and per-capita dispersal rate between the two types of patches. Specifically, $\boldsymbol{\beta}$ represents the enhancement of carrying capacity in the bacteria-containing patch, whereas $\boldsymbol{\delta}$ represents asymmetry in per-capita dispersal rates between patches, with $\boldsymbol{\delta < 0}$ indicating reduced patch B per-capita dispersal rate relative to patch N (*i.e.*, dispersal bias treatment in experiment). Importantly, $\boldsymbol{\beta}$ introduces asymmetry in carrying capacity between local patches while also increasing the total carrying

290 capacity at the metapopulation-level, whereas $\boldsymbol{\delta}$ modifies the difference (or asymmetry) in per-capita
291 dispersal rates between patches without altering average per-capita dispersal rate across patches.

292

293 This parameterization mirrors our experimental setup. In the experiment, bacterial supply
294 increases the resources available in bacteria-containing patches (and therefore the metapopulation as a
295 whole) and thereby increases yeast density through demographic feedback. In contrast, the dispersal bias
296 treatment controls the likelihood that a bacteria-containing patch is selected for dispersal relative to a no-
297 bacteria patch. Specifically, because each bacteria-containing patch is sampled with weight determined by
298 its pH (*i.e.*, ω_B), the probability of sampling a bacteria-containing patch from the experimental
299 metapopulation is proportional to ω_B times the number of bacteria-containing patches (i.e., $\omega_B * n_B$),
300 which aligns with the $D(1+\delta) * N_B$ term in the model. Accordingly, if bacteria do not reduce pH, then
301 $\omega_B = \omega_N$ (equivalent to the random dispersal treatment) and the probability of selecting a given patch
302 type for dispersal is proportional to the frequency of that type in the metapopulation (*i.e.*, determined
303 strictly by bacterial supply). By reducing the system to two patches, the model assumes that
304 metapopulation differences arise primarily from dispersal between patch types ($N_B \rightarrow N_N$ or $N_N \rightarrow N_B$) and
305 not within ($N_B \rightarrow N_B$ or $N_N \rightarrow N_N$) (see Discussion for limitations).

306

307 With this model, we evaluated how and examined why metapopulation size varies as a function
308 of parameter values. For simplicity and given the non-significant effect of dispersal frequency (see
309 Results), we assume $\boldsymbol{r} = \boldsymbol{K} = \boldsymbol{D} = 1$, which reduces the number of free parameters to the two aligned with
310 our hypotheses: bacterial supply ($\boldsymbol{\beta}$) and dispersal bias ($\boldsymbol{\delta}$). With this reduced model, we computed the
311 metapopulation size at varying levels of β *and* δ by solving for its steady-state solution numerically in R
312 and taking the sum of equilibrium densities (denoted N_B^* and N_N^*) across both patches. To obtain a

heuristic understanding of why metapopulation size varies at all, we derived analytically the condition under which metapopulation size would be maximized under our model, as predicted by the theory of ideal free distribution (IFD; (Fretwell & Lucas, 1969; Holt 1985). In brief, IFD predicts that mean fitness (or average per-capita growth rate) is maximized when individuals distribute themselves such that fitness is equalized across patches. At equilibrium, this corresponds to the condition where the density in each patch equals its local carrying capacity, since any deviation would imply unequal fitness: one patch would be underfilled (positive growth) while the other would be overfilled (negative growth). One trivial case in which this condition holds is when $D = 0$. However, since we assume dispersal ($D = 1$), the remaining condition that satisfies IFD occurs when the number of migrants in each patch cancels out: $(1+\delta)N_B^* = (1-\delta)N_N^*$. By substituting the local carrying capacities $\boldsymbol{\beta}$ and 1 for the equilibrium densities N_B^* and N_N^*, respectively, and re-arranging yields the condition: $\delta = (1-\beta) / (1+\beta)$. We verify that this condition corresponds to the maximization of metapopulation size by comparing it to simulations.

RESULTS

Effects of bacterial supply, dispersal bias, and dispersal frequency on yeast metapopulation size

Bacterial supply significantly modified overall yeast metapopulation size (χ^2= 6.103, P = 0.013; Table 1; Fig. 2&3a) and the magnitude of this effect depended on dispersal bias (χ^2 = 6.162, P=0.013; Table 1). Specifically, bacterial supply increased yeast metapopulation size under biased dispersal, but not under random dispersal (Fig. 3c). In contrast, neither dispersal frequency ($\chi^2 = 1.053, P = 0.305$) nor dispersal bias ($\chi^2 = 1.626, P = 0.202$) alone had significant main effects on yeast metapopulation size (Table 1). We also found no significant interaction between bacterial supply and dispersal frequency (χ^2 = 3.419; P = 0.064; Table 1). The non-significant main effect of dispersal bias is expected, as the experimental design ensures that dispersal bias is only functionally consequential when bacterial sink populations are present (i.e., when bacterial supply > 0). Only under these conditions would pH values differ between

patches and asymmetric dispersal be possible under dispersal bias. Thus, the non-significant effect of dispersal bias in isolation reflects a sensible experimental setup. Lastly, local yeast densities also positively correlated with local bacteria densities (ρ =0.149, P<0.01; Fig. 5), an unexpected result that suggests that bacteria have a net positive (rather than purely competitive) effect on yeast.

Theoretical predictions of metapopulation model

Model predictions agree qualitatively with our experimental results that on average, bacterial supply increases metapopulation size and that this effect is greater when per-capita dispersal rate is lower in the bacteria-containing patches (Fig. 5). Note that because we assume $r = K = D = 1$ for analytical tractability, comparisons between model predictions and experiment are thus based on relative effects, as the theoretical and experimental system may differ in their baseline parameter values (*e.g.*, experiment $K \neq 1$). Specifically, our model predicts that increasing the carrying capacity of yeast in the bacteria-containing patch ($\beta > 1$) increases the overall metapopulation size (Fig. 5), similar to how bacterial supply had an overall positive effect on yeast metapopulation size across treatments in our experiment (Fig. 3B; average across treatments). Furthermore, the effect of lowering per-capita dispersal rate in the bacteria-containing patch relative to the no-bacteria patch (*i.e.*, decreasing δ, analogous to dispersal bias in the experiment) reduced metapopulation size when carrying capacities are similar, but increased it as the carrying capacity of the bacteria-containing patch increased ($\beta \gg 1$; Fig. 5a). In other words, dispersal bias increased metapopulation size relative to symmetric random dispersal only when the bacteria-containing patch had sufficiently more resources, consistent with the significant interaction term between bacterial supply and dispersal bias observed experimentally (predicted lines cross in Fig. 3A). Lastly, we found that metapopulation size is maximized when the total number of migrants in each patch are equalized, in accordance with the ideal free distribution (unpacked in Discussion; Fig. 5B).

DISCUSSION

Our study demonstrated that an invader with negative growth rates in all patches could still influence the metapopulation of a resident species by modifying both local habitat conditions and regional connectivity. In particular, we found that addition of an externally-sustained bacterial species increased the resident yeast metapopulation size, and that this effect was larger when they also reduced dispersal rates in the patches in which they occurred. Furthermore, our theoretical results align with experiments, and suggest that the mechanism by which dispersal bias increases yeast metapopulation size is through equalizing per-capita growth rates across patches, thereby bringing the metapopulation size closer to the theoretical maximum defined by the ideal free distribution. Taken together, these results demonstrate that transient invaders can impose demographic consequences on resident species through the interaction between local and regional processes. Below, we connect our results to metapopulation theory, discuss the biological mechanisms that may have generated these patterns, place our findings within broader ecological frameworks, and discuss key study limitations as well as opportunities for future research.

Dispersal and metapopulation size

Our study provides a rare empirical demonstration of how biotically-induced dispersal asymmetries can alter metapopulation size. Furthermore, the analysis of our theoretical model connects our experimental results to well-known effects of dispersal in spatially heterogeneous landscapes. In particular, theory shows that when carrying capacities vary spatially, dispersal typically reduces metapopulation size because productive patches export more migrants than they receive, causing greater overfilling of low-capacity patches than underfilling of high-capacity patches and thus stronger overall density dependence (Holt, 1985; McPeek & Holt, 1992; Pacala & Roughgarden, 1982). This demographic cost of dispersal underlies the “slower disperser wins” phenomenon (Dockery et al., 1998; Hastings, 1983) and explains

384 how a locally inferior competitor can coexist with a competitively superior species with faster dispersal
385 rates (Abrams & Wilson, 2004; Amarasekare & Nisbet, 2001; Pacala & Roughgarden, 1982). With
386 respect to our experiment, the demographic cost of dispersal in a landscape with heterogeneous carrying
387 capacities also explains why the positive effect of bacterial supply on metapopulation size was absent
388 when dispersal was random (Fig. 3A).

389

390 In agreement with McPeek & Holt (1992), our study shows that the detriments of dispersal on
391 metapopulation size can be nullified if differences in local per-capita dispersal rates offset differences in
392 local carrying capacities. The degree of this offset can be interpreted as a deviation from the ideal free
393 distribution, the condition under which local growth rates are equalized and metapopulation size is
394 maximized (Fig. 5B). Our formulation of dispersal slightly differs from that of McPeek & Holt (1992);
395 rather than assigning each patch an independent dispersal parameter, our model contains a single
396 parameter that controls the asymmetry in per-capita dispersal between patches. This formulation reflects
397 dispersal asymmetry arising from the foraging preferences of the dispersal vector (i.e., pollinators), such
398 that a single parameter captures a metapopulation-level process that generates patch-specific differences
399 in per-capita dispersal rates. More broadly, our results also align with empirical studies showing that
400 movement between habitats can modify demographic parameters (Donahue et al., 2003; Fox, 2007),
401 while extending this idea to the modification of dispersal parameters themselves.

402

403 *Biological mechanisms: Why does bacterial supply increase yeast densities?*

404 Our experimental results appear to contradict previous work showing that the reduction in pH by bacteria
405 inhibits yeast growth (Chappell et al., 2022; Figs. 3-4 & S1). We posit that experimental differences may
406 have contributed to the apparent disagreements. In the present experiment, densities of yeast and bacteria

407 were approximately the same at the beginning of each dilution cycle (~100-200 cells/μL; Fig. 1, see
408 Methods). Thus, nectar acidification by the bacteria occurred concurrently with yeast population growth,
409 possibly preventing pH from dropping fast enough to suppress yeast growth. However, this explanation is
410 only partial because it does not explain the observed positive effect of bacterial supply on yeast densities.
411 We posit that the addition of bacterial cells may have also introduced resource subsidies that enabled
412 yeast to reach higher densities. Although each inoculation event contributed only ~1% of the nectar
413 volume, additional inputs may have arisen from metabolites released by bacterial cells or from cell lysis,
414 beyond those present in the nectar medium used to suspend cells prior to inoculation. While this
415 mechanism has not been confirmed experimentally, it is consistent with reports of *Acinetobacter* spp.
416 releasing metabolic by-products in low-nitrogen nectar environments (Álvarez-Pérez et al., 2019; Kato et
417 al., 2025; Morales-Poole et al., 2023). Because many microbes secrete metabolites (Douglas, 2020) and
418 deceased cells can impact local communities (Hao et al., 2026), future work can identify the biochemical
419 pathways mediating these interactions.

420

421 *Meta-ecosystems and nectar microbiome*

422 The nutrient-subsidy mechanism we propose may reflect an experimental artefact, but the process may be
423 more general and relevant across ecosystems. Our results align with core ideas in meta-ecosystem
424 ecology, which emphasizes how flows of matter and energy shape ecosystem dynamics (Gounand et al.,
425 2018; Loreau et al., 2003; Massol et al., 2017; Polis et al., 1997). By focusing on connections across
426 ecosystem boundaries, this framework considers a broader set of spatial flows than traditional
427 metapopulation approaches would, including the movement of inorganic nutrients, organic matter, and
428 other non-living biotic materials in addition to living organisms. In nectar microbes, for instance, floral
429 nectar represents a primary habitat but not the only one they occupy. Nectar yeast may overwinter in bee
430 nests (Pozo et al., 2018), while soil and plant surfaces can also serve as refugia for other microbes before

they recolonize flowers in the following season (Vannette, 2020). Together, these examples highlight that dispersal moves not just organisms but also the energy and nutrients associated with them from previous places, prompting questions about the extent to which these cross-ecosystem fluxes affect local microbial communities.

Experimental caveats and theoretical assumptions

Our experimental and theoretical approaches necessarily involve several caveats and simplifying assumptions. For tractability, our two-patch model formalism ignores dispersal among identical habitats, implicitly assuming that such movements have negligible effects on metapopulation dynamics. While this may be a reasonable assumption within an idealized experimental setting like ours, movement between identical habitats is likely to be important in real-world systems with extinction-recolonization dynamics (*e.g.*, Brown & Kodric-Brown, 1977). With respect to our experiment, bacterial cells were always inoculated into the same subset of patches, raising the possibility that our results reflect spatial placement (e.g., edge effects on the PCR plate) rather than the effects of experimental treatments. However, supplementary analyses found no evidence for location-specific effects (Appendix S4). Moreover, although the factorial design of our experiment allowed us to isolate the effects of dispersal frequency and dispersal bias, these factors likely covary in nature. For instance, pollinators may reduce visitation to regions dominated by bacteria, thereby also lowering visitation to any yeast-dominated patches within those regions. Lastly, both our experiment and model assumed conservative dispersal, whereas nectar consumption by pollinators implies that only a fraction of microbes and nectar material are transferred among flowers (*i.e.*, dispersal has no fitness costs). Although this assumption is unlikely to hold in natural systems, the rapid life cycles of nectar microbes suggests that even small numbers of immigrants may be sufficient to modify local community structure.

Conclusion

This study experimentally demonstrated that a species invading a sink habitat can influence a resident metapopulation by modifying local conditions and altering metapopulation connectivity. More broadly, our results highlight that dispersing organisms can carry resources and nutrients acquired from previous habitats, allowing them to interact with resident species—even after death—by modifying the resource landscape that those species experience. Our experiments thus demonstrate the possibility that transient invaders may leave lasting ecological effects that persist well beyond their extinction. Given the prevalence of sink populations (Dias, 1996; Pulliam, 1988) in general and of unsuccessful microbial invasions in particular (Amor et al., 2020; Mallon et al., 2018), we suggest that it is worth investigating the extent to which these transient invaders structure local communities and metapopulations in natural ecosystems.

TABLES

Table 1. ANOVA table for the effects of treatments on metapopulation size and variance (n = 354)

Component	Term	χ^2	P
conditional	**Bacterial supply**	**6.10**	**0.01**
conditional	Bias	1.62	0.20
conditional	Frequency	1.02	0.31
conditional	**Bacterial supply:Bias**	**6.22**	**0.01**
conditional	Bacterial supply:Frequency	3.42	0.06
conditional	Bias:Frequency	1.12	0.29
dispersion	**Bacterial supply**	**4.20**	**0.04**

FIGURES

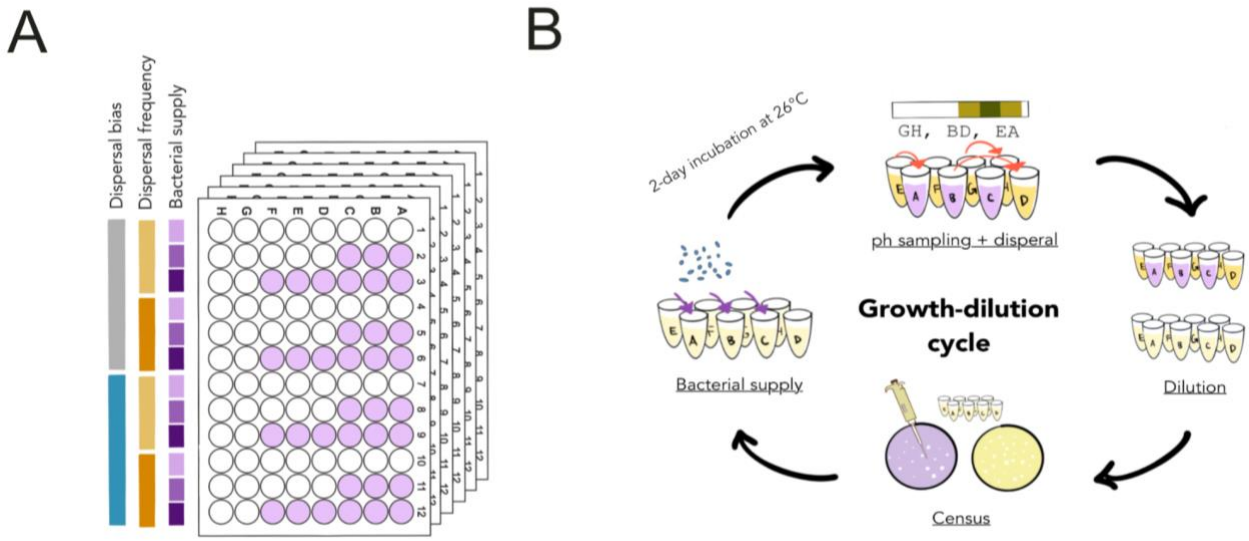


Figure 1. Overview of experimental setup. (**A**) Fully crossed design: dispersal bias (2) × dispersal frequency (2) × bacterial supply (3), each with six replicates. Each metapopulation consisted of 8 patches (PCR plate wells) connected by dispersal and underwent four 2-day growth–dilution cycles. (**B**) At the start of each cycle, patch pH was measured and used to generate donor–recipient pairs (see Methods). Dispersal was performed by transferring 3 µl of nectar from donor to recipient (red arrows). Patches were then diluted (5 µl into 95 µl fresh nectar) to emulate resource renewal, and samples were plated (TSA for bacteria, YMA for yeast) to estimate densities (CFUs). Bacteria (~20,000 cells) were added according to treatment, and plates were sealed and incubated at 26°C for 2 days.

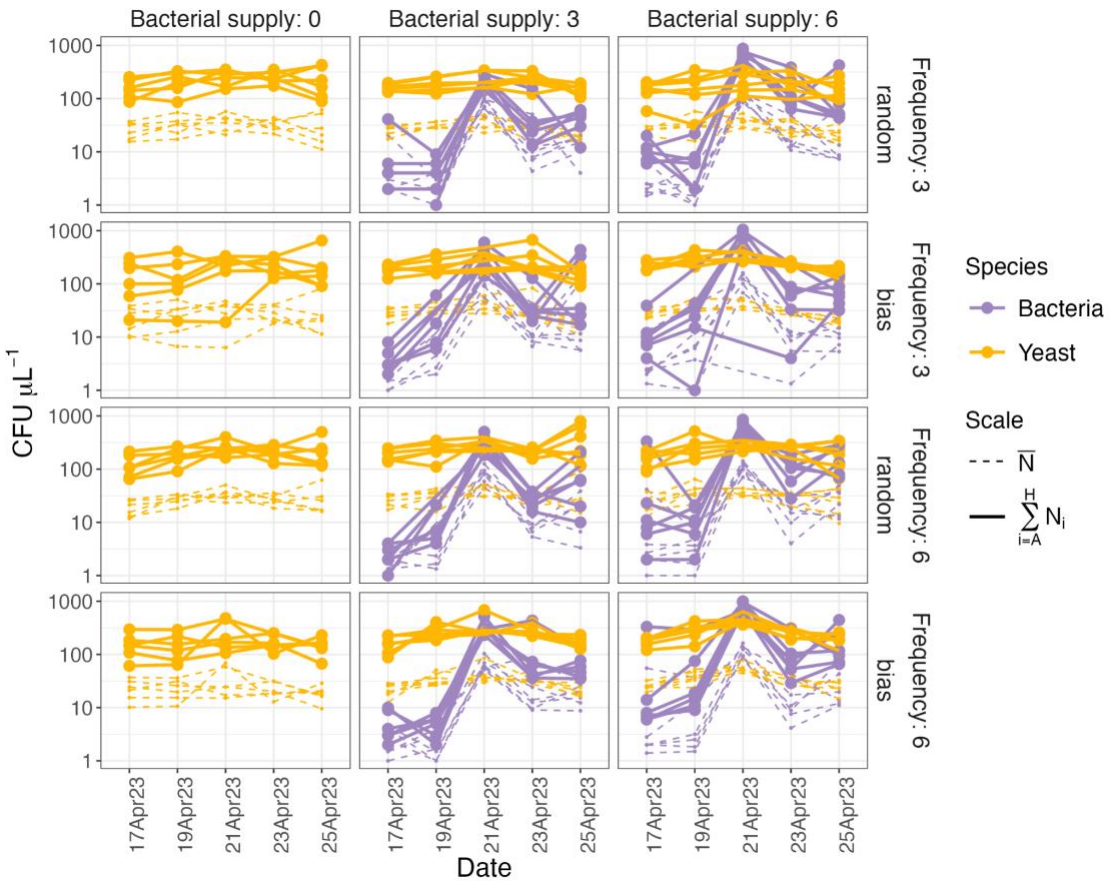


Figure 2. Time-series data of bacteria and yeast densities at local and regional scales. Lines show the time-series of the microbial densities of a single replicate metapopulation. The densities of bacteria (strain: FNA17) and yeast (strain: MR1) are colored in purple and yellow, respectively. Solid lines (with points) show the metapopulation size ($\sum N_i$) while dashed lines show the average density of a single patch ($\bar{N}$) within a replicate metapopulation. Each facet contains the 6 replicates of a single treatment specified by the facet labels.

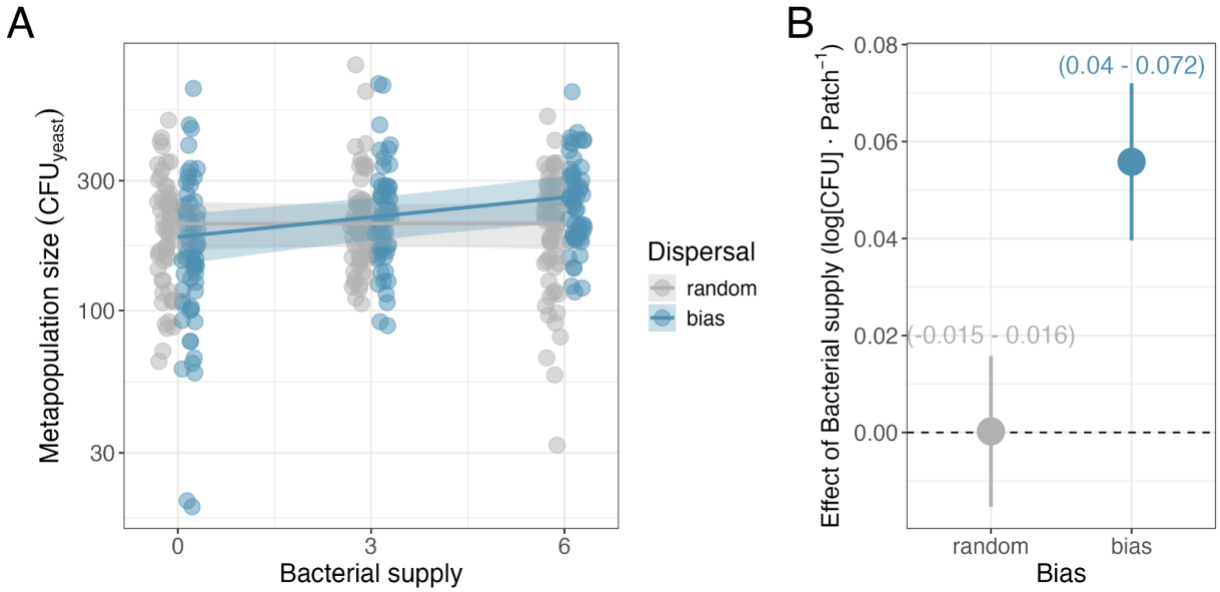
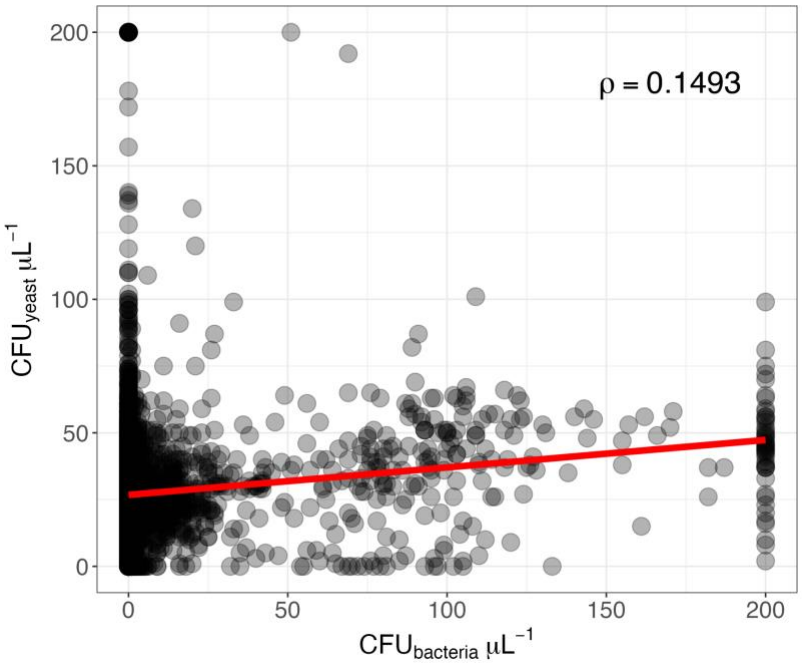


Figure 3. Effects of bacterial supply and dispersal bias on yeast metapopulation size and variance. (**A**) Estimated treatment effects on the metapopulation-level colony forming units of yeast per μl, while fitted lines and 95% confidence intervals are from GLMM estimates. Points in (**B**) show the estimated marginal effect of bacterial supply on yeast CFUs at different levels of dispersal bias and evaluated at the mean dispersal frequency (4.5) with error bars indicating SE.



508

509 **Figure 4. Association between patch-level yeast and bacteria densities.** Points indicate the
510 number of colony forming units (CFU) of bacteria and yeast per μl in a single patch of a
511 metapopulation. Line of best fit was drawn to aid visualization and ρ is the Pearson correlation
512 coefficient ($p < 0.01$). Points clustered around 200 CFUs represent cases where CFUs were too
513 dense to count; see Methods.

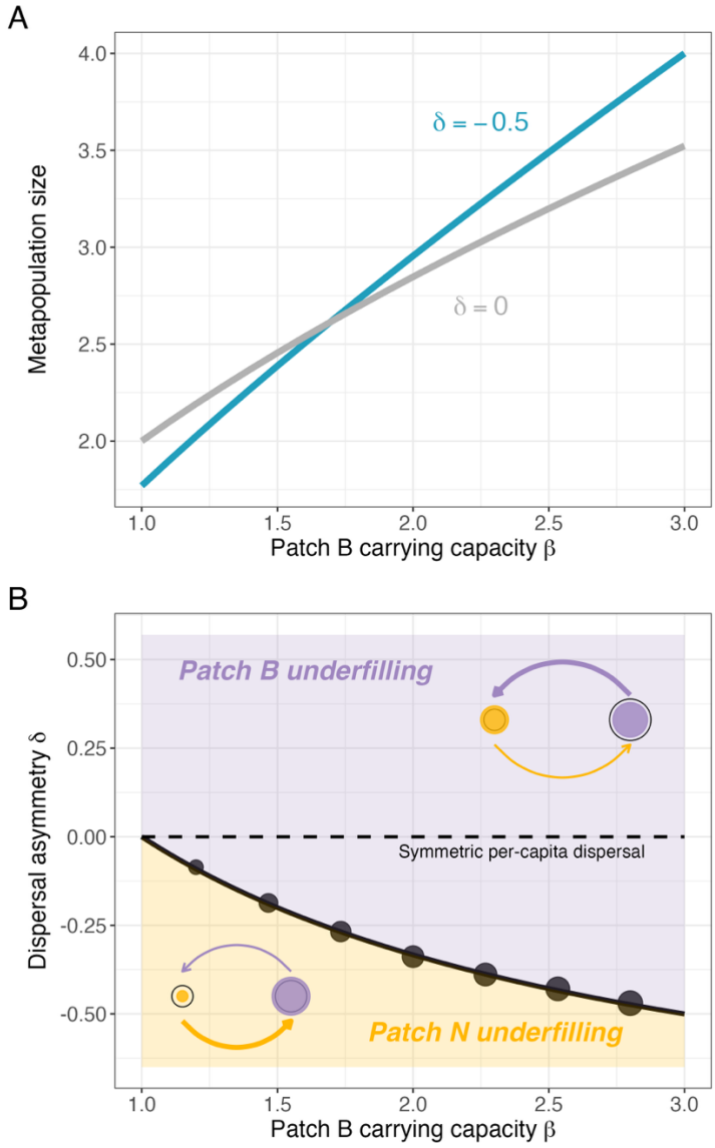


Figure 5. Theoretical predictions of metapopulation size with heterogeneous per-capita dispersal rates and carrying capacities. Metapopulation size is the total equilibrium density across both patches ($N_B^* + N_N^*$). (**A**) Metapopulation size increases with patch B carrying capacity (β), but more strongly when per-capita dispersal from patch B is lower (blue relative to grey curve). (**B**) As β increases, equalizing total migrants between patches requires lower per-capita dispersal from patch B ($\delta < 0$). The black curve shows the condition $(1+\delta)N_B^* = (1-\delta)N_N^*$). Above and below the curve, patch B and patch N, respectively, contribute more migrants at equilibrium. Points indicate the value of δ that maximizes metapopulation size for a given β (point size proportional to metapopulation size). In both panels, $r = K = D = 1$.

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