Sink invaders 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 potential feedback between local and regional processes in shaping metapopulation dynamics has rarely been tested experimentally. Using nectar microbes as a model system, we examine how a bacterial sink species, 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 bacterial sinks increases resident yeast densities, potentially through the provision of additional resources, and that this benefit is further enhanced when bacterial supply biases dispersal away from bacteria-inoculated patches. We supplemented our experimental results by analyzing a simple two-patch metapopulation model and demonstrated that metapopulation productivity is maximized when patch-specific dispersal rate is lower in the more productive patch (e.g., productivity enhanced by bacterial sink supply). Together, these results underscore the role of dispersal in shaping how a metapopulation experiences density-dependence across heterogeneous landscapes, highlight the relevance of material flows across ecosystem boundaries, and suggest the plausible mechanism in which transient invaders 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 interacting 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 the 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 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). How, then, does the interaction between phoretic organisms and their vectors determine their metapopulation abundance and persistence? What happens when multiple phoretic species share the same vectors? 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. A candidate scenario in which these cryptic interactions could be important is in communities that contain many sink species – species in which their persistence is determined less by local conditions and more by immigration from adjacent habitats. 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 a sink species into a local community, which amplifies the total impact of the sink species despite its otherwise small per-capita effects on residents. For instance, a sink species 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 previous studies assume that sink species impact residents purely

through local interactions. However, knowing that dispersal can shape metapopulations, sink species might also influence residents by altering their dispersal patterns within its metapopulation. Despite evidence 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.

One system in which dispersal vectors modulate species interactions is the floral microbiome. Floral nectar often contains microbial communities (Vannette, 2020) and these microbes are dispersed by pollinators (Belisle et al., 2012; Herrera et al., 2009; Vannette & Fukami, 2017). 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). Furthermore, the microbial activity within nectar can alter pollinator foraging behavior by modifying nectar chemistry or producing volatiles that attract (or repel) pollinators (Chappell et al., 2022; Schaeffer et al., 2019; Vannette et al., 2013), which in turn biases the microbial species that disperse across 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 another path where sink species 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 sink species can impact the metapopulation dynamics of a resident yeast species. Previous work in the system has shown that bacteria reduce nectar pH, which in turn reduces both yeast growth and pollinators' nectar consumption (Chappell et al., 2022). We build upon these findings and 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 sinks. Specifically, we test the hypothesis that reduction of nectar pH by bacterial sinks reduces yeast metapopulation size by modifying nectar pH to the detriment of yeast population growth (*i.e.*, local effects). We also test the hypothesis that pollinator preference that biases dispersal away from low-pH patches alters metapopulation size of yeast by altering its metapopulation connectivity (*i.e.*, local-regional interaction effects). Additionally, we analyze a simple two-patch metapopulation model to verify and supplement the inferences of our experimental results.

METHODS

Overview of study system

To investigate the impact of sink species 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 sets in motion the diverse ecological interactions that occur in these microscopic ecosystems (e.g., competition, priority effects, 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. One caveat, however, is that while the bacterial species *A. nectaris* occurs naturally in *Diplacus* flowers, it was unable to persist on its own under our experimental conditions with artificial nectar (Fig. S3), effectively making it a sink species within our study. The extent to which *A. nectaris* functions as a sink species in *Diplacus* flowers remains to be determined.

Experimental setup

We conducted an experiment that factorially manipulated bacteria population sinks, dispersal bias, and dispersal frequency to test how *A. nectaris*-driven pH changes affect *M. reukaufii* metapopulation by modifying local nectar conditions and metapopulation connectivity through dispersal bias (Fig. 1). Dispersal frequency was manipulated to account for a wider range of effect sizes. Our experimental metapopulations consisted of eight wells (i.e., patches) on a 96-well PCR plate, connected by dispersal. Each metapopulation was assigned to one of 12 treatment groups defined by the fully factorial combination of bacteria sinks (3 levels: 0, 3, or 6), dispersal bias (two levels: random or bias), and dispersal frequency (two levels: 3 or 6), with each treatment replicated six times (12 treatments x 6 replicates = 72 metapopulations). Each replicate metapopulation was initiated by seeding patches with approximately 100-150 viable cells of *M. reukaufii* (see Supplementary Methods) and 100 µl of sterile artificial nectar. Artificial nectar was prepared as specified by Chappell et al. (2022). Plates were sealed with a sterilized air-permeable membrane and incubated at 26°C for two days before beginning the experiment. After initiation, each metapopulation underwent a total of five two-day growth (*i.e.*, dilution) cycles where each cycle included the following order of events: 1) pH sampling + dispersal, 2) resource replenishment, 3) community census, 4) bacteria sinks, and 5) a two-day incubation period:

Event 1: Dispersal. To simulate pollinator-assisted dispersal, we first sampled the pH of local patches, generated a sequence of dispersal events, then pipetted nectar between patches according to the order of generated sequences. Specifically, 10 µl of nectar from each patch were pipetted onto pH indicator strips in the bias treatment, whereas in the random treatment the samples were discarded because dispersal did not depend on pH. While waiting for pH readings, we conducted three background dispersal events by

pipetting 3 µl of nectar from a donor patch to a recipient patch, following a random sequence of donor-recipient pairs that we pre-generated prior to the experiment by sampling two patches (from eight) without replacement sequentially in R (see scripts). The sequence for background dispersal was identical for all 72 metapopulations. Background dispersal was conducted to give the bacteria some opportunity to disperse in the system and to account for other vectors that disperse microbes non-preferentially such as by wind and thrips (Chappel & Fukami 2018). Once pH readings developed, we recorded the pH values and used them as weights (representing pollinator preferences) to generate a new sequence of dispersal events between donor-recipient pairs. Specifically, donor and recipient patches were selected by sampling two patches without replacement, with a weighted distribution over the eight patches (A–H), where selection probabilities are proportional to their respective pH values. The weight of each patch (ω_i) was calculated using the Monod equation with a half-saturation constant set at 3, which is a pH value that lies between nectar conditioned by bacteria (pH = 2) and yeast (pH = 4; Chappel et al 2022). More precisely, the weight of patch *i* is $\omega_i = pH_i / (3 + pH_i)$ and the probability of selecting it is obtained by normalizing these weights, $P_i = \omega_i / \sum_{j=1}^{8} \omega_j$. This setup reflects the field observation that low-pH patches are less likely to be visited by pollinators and, consequently, microbes are less likely to disperse into or out of them (Vannette et al. 2013; Chappell et al. 2022). Dispersal sequences from random dispersal treatments were done in a similar manner except that the probabilities were always equal across patches (*i.e.*, does not depend on pH). The number of dispersal events per growth cycle is determined by the dispersal frequency treatment, either 3 or 6, which was manipulated factorially with dispersal bias. In other words, each replicate undergoes 3 or 6 sequential dispersal events within a growth cycle.

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

Event 3: Sampling. Immediately after dilution, we sampled each local community by plating 5 µl of the newly diluted nectar onto yeast malt agar (YMA) for yeast and 5 µl onto tryptic soy agar (TSA) for bacteria, and then enumerated the resulting colony-forming units (CFUs) after >3 days of incubation at room temperature as a measure of microbial density (following Peay et al., 2012 and Vannette et al., 2013). Due to time constraints associated with simultaneously conducting the experiment and counting CFUs, we took images of the agar plates and enumerated CFUs after completion of the experiment (see Appendix for sample images).

Event 4: Bacterial sinks. Following sampling, bacterial cells were added to patches according to the sink treatment. Specifically, bacterial cells were either added to no patches (sink = 0), patches A to C (sinks = 3), or patches A to F (sink = 6). We chose to add bacteria to only a subset of patches within the metapopulation because this allows spatial heterogeneities in nectar pH and thus creates variation in dispersal probabilities under the dispersal bias treatment. Although it is not required, we chose to fix the patches in which bacteria were added (as opposed to randomly selecting patches to inoculate) to minimize experimental error. Approximately 20,000 bacterial cells were inoculated to each designated patch (see Supplementary Methods). Sink supplements of bacteria were done after sampling because in our pilot trials, this amount of bacteria was necessary to reduce pH (after 2 days) but would be too dense to count if plated directly after inoculation. Thus, the bacteria that we sampled came from the remaining bacteria inoculated two days prior.

Event 5: Incubation. Following the inoculation of bacterial sinks, 96-well plates were sealed with sterilized, air-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 sinks 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 study objectives and excluded the three-way interaction term because including it did not improve model fit. In addition, we also tested treatment effects on the variance of yeast metapopulation size as a measure of metapopulation stability by including them as predictors in `dispformula` of the `glmmTMB` function in R. To prevent overfitting, we implemented a forward model selection process that sequentially added terms as predictors of the dispersion component of the model, which significantly improved model fit (as evaluated by χ^2 tests). Accounting for potential variance structure in our data can provide more robust tests of our fixed effect estimates, but we also examined this structure for ecological reasons: more stable systems tend to return to their attractor faster, resulting in less variation across probabilistic realizations. Therefore, if our treatments influenced stability (not just metapopulation size), we expected this treatment effect to be reflected in changes in variance across treatment levels.

Potential artefacts of experimental design

We conducted additional tests to confirm that our experimental results were not contingent on the choices of our experimental design. In particular, we verified the degree to which dispersal patterns in the bias treatment deviated from the random treatment and that the position of the microplate wells had no effect on yeast densities. In brief, we tested these two possibilities by measuring the deviance in patch-specific dispersal propensities between the bias and random treatment groups and tested for differences in yeast densities among microplate wells after partialing out treatment effects. We provide a more thorough

242 description of these additional tests in the Supplementary methods and provide the results in Fig. S1 and
243 Fig. S4.
244

245 *Metapopulation model*

246

247 We supplemented our experimental results with the analysis of a two-patch metapopulation model. As
248 described in our Results, we unexpectedly found that the densities of the resident species *M. reukaufii*
249 were positively correlated with the densities of the sink species, *A. nectaris* (Fig. 3). Given this finding,
250 we explored the possibility that, in addition to affecting regional connectivity by modifying nectar pH,
251 immigration of *A. nectaris* could also impact the resident species locally by bringing in additional
252 resources that increase local carrying capacity. Because metapopulation studies are typically competitive
253 (as in most areas of ecology; James et al 2025), it remains unknown how positive local effects of sink
254 populations can cascade to affect the metapopulation of a resident species. To address this knowledge
255 gap, we asked: what would be the combined effects of dispersal bias (i.e. dispersal heterogeneity) and
256 resource heterogeneity? To ask this question, we constructed a two-patch metapopulation model and
257 examined how regional equilibrium densities would change as a function of the asymmetry in carrying
258 capacities (mimicking asymmetries that would arise when bacterial sinks increase local resource
259 availability) and dispersal rates between the two patches.
260

261 To simplify analysis, we did not explicitly model the densities of the bacterial sink species and simply
262 assumed that its effects are reflected in the magnitude of asymmetries in patch-specific carrying capacities
263 and dispersal rates. Specifically, asymmetry in carrying capacity means that one patch has a higher
264 resource availability and is able to sustain a larger local population, whereas asymmetry in dispersal rates
265 means that there is a net flow of individuals from one patch to the other. Our general model takes the
266 form:

$$\frac{dB}{dt} = rB\left(1 - \frac{B}{\beta K}\right) - D(1 + \delta)B + D(1 - \delta)N$$

$$\frac{dN}{dt} = rN(1 - \frac{N}{K}) - D(1 - \delta)N + D(1 + \delta)B$$

where ***B*** and ***N*** are the densities of the resident (e.g. yeast) species in the bacterial-sink (B) and the no-bacteria (**N**) patch, respectively. The parameters ***r*** and ***K*** represent the local intrinsic growth rate and carrying capacity, while ***D*** denotes the average per-capita dispersal rate across the metapopulation. The parameters $\boldsymbol{\beta}$ and $\boldsymbol{\delta}$ control the asymmetries in carrying capacity and dispersal rate between the two patches. Specifically, the carrying capacity of patch B is a factor of $\boldsymbol{\beta}$ greater than that of patch N, and its dispersal rate is a factor of $1 + \boldsymbol{\delta}$ greater. We assume $\boldsymbol{r} = \boldsymbol{K} = 1$ (following nondimensionalization of the system), which reduces the number of free parameters to the three that are most aligned with our experimental treatments: dispersal frequency (***D***), bacterial sinks ($\boldsymbol{\beta}$), dispersal bias ($\boldsymbol{\delta}$). Note that dispersal bias in our experiment corresponds to $\boldsymbol{\delta} < 0$ in the model, where patches with bacterial sinks (i.e., patch B) are *less* likely to be visited by pollinators. With this model, we solved for its steady-state solutions numerically using the Newton-Raphson method from the rootSolve package in R.

RESULTS

Effects of sink populations, dispersal bias, and frequency on yeast metapopulation size

Bacterial sinks 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, sinks 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 sinks 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 sinks are present (i.e., when Sinks > 0). Only under these conditions would pH values differ between patches, leading to asymmetries under dispersal bias. Thus, the non-significant effect of dispersal bias in isolation reflects a sensible experimental setup.

Sinks also significantly influenced the *variance* of yeast metapopulation size, independent of its effect on the mean (Fig. 2 & 3b; Tables 1 & S2). As a reminder, count data (*e.g.*, colony counts) often exhibit a mean–variance relationship where $\mu \propto \mathrm{Var(X)}$, meaning that larger populations exhibit greater variance. Our use of a negative binomial GLMM allows for more flexibility, by modeling variance as $\mathrm{Var(X)} = \mu(1 + \alpha)$. Here, larger values of α indicate greater overdispersion relative to what is expected from a Poisson distribution. Because we had no strong *a priori* expectation for how α might vary across treatments, we implemented a forward model selection approach to identify candidate factors that contribute to the dispersion of yeast metapopulation size (i.e., whether α covaries with treatments). We found that sinks were the only factor that significantly improved model fit over an intercept-only model (ΔAIC = -34.8, P < 0.001), and that sinks significantly reduced the variance in yeast metapopulation size (estimate = -0.109; χ^2=4.2, P=0.04; Tables 1 & S2; Figs. 2 & 3b).

Theoretical predictions of metapopulation model

Motivated by our experimental results and the unexpected finding that patches with a higher number of bacteria tended to contain a slightly higher number of yeast (ρ =0.149, P<0.01; Fig. 5), we analyzed the equilibrium conditions of an idealized two-patch metapopulation model to examine whether our results could be explained by the changes in local carrying capacities due to bacterial sinks. Model predictions generally agree with our experimental results. Specifically, increasing the carrying capacity of the sink patch relative to the non-sink patch ($\beta > 1$) increases the overall metapopulation size (Fig. 4), similar to how sinks tended to have a positive effect within most of our treatment levels (Fig. 3c). Furthermore, higher relative dispersal rate in the patch with lower carrying capacity (*i.e.*, δ < 0; dispersal bias in our

experiment) also has an increasingly positive effect relative to symmetric dispersal (*i.e.*, random) on metapopulation size as the difference in carrying capacities become larger (*i.e.*, positive interaction between β and δ; Fig. 4b). In other words, the effect of dispersal bias is only apparent when resource availability is spatially heterogeneous.

DISCUSSION

Our study demonstrated that sink populations could influence a resident metapopulation through both local environmental modification and changes in regional connectivity. In particular, we found that the addition of bacterial sink populations increased yeast densities within local patches (Fig. 3), consequently increasing metapopulation size (Figs. 3–4). Moreover, the positive effects of sink supply were strongest when dispersal was biased away from bacteria-inoculated patches (Fig. 3c). Taken together, these results demonstrate that transient invaders can impose demographic consequences to resident species through 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 experimental limitations and opportunities for future research.

Dispersal and metapopulation size

Our study offers a rare empirical test of asymmetric dispersal modifying metapopulation size. It is often assumed that population sizes are bounded by their carrying capacities. However, once populations are spatially replicated (e.g., metapopulation), spatial variance in carrying capacity can change independently of the mean, enabling regional abundance to exceed this expected limit. This is not a new result, as previous studies has proven rigorously that a positive ***r***–***K*** correlation can inflate metapopulation size by allowing low-productivity sites to be overfilled more than high-productivity sites are underfilled (DeAngelis et al., 2016; Lou, 2006; Zhang et al., 2017). However, our theoretical results extend this insight by demonstrating that inflation can also arise without a positive ***r***–***K*** correlation, emerging instead from a negative correlation between ***K*** and patch-specific dispersal rates (***d***) while holding ***r*** fixed.

339 Furthermore, our experimental results showed that adding bacterial sinks reduced the variance in
340 metapopulation size among replicates. This outcome is neither captured in previous, or our present,
341 models, and suggests that sinks may influence not only ***K*** but potentially ***r*** as well. We posit that because
342 the stability of logistic growth depends on ***r***, even small increases in stability can dampen stochastic
343 fluctuations around the equilibrium, reducing variance and increasing the expected population size
344 through nonlinear averaging (Levins, 1969). Our study provides an initial step toward understanding this
345 joint ***r***–***K***–***d*** geometry and motivates future work on how these interactions shape metapopulation size,
346 stability, and responses to stochastic perturbations in metapopulation size.

347 *Biological mechanisms: Why do bacterial sinks increase yeast densities?*

348 Although acidic nectar can inhibit *M. reukaufii* (Chappell et al., 2022), our results show that immigration
349 of *A. nectaris* may instead enhance yeast growth despite also lowering nectar pH (Fig. 3 & S1). In our
350 experiment, densities of yeast and bacteria were approximately the same at the beginning of each dilution
351 cycle (~100-200 cells/μL; Fig.1, see Methods). Thus, nectar acidification by *A. nectaris* occurred
352 concurrently with *M. reukaufii* population growth, possibly preventing pH from dropping early enough to
353 suppress yeast growth. However, this explanation must only be partial because it does not explain the
354 observed positive effect of sink addition on yeast densities. We posit that the addition of bacterial sinks
355 may have also introduced resource subsidies that enabled yeast to reach higher densities. Although each
356 inoculation event contributed only ~1% of nectar volume, additional inputs may have arisen from
357 metabolites released by bacterial cells or from cell lysis. While this mechanism has not been confirmed
358 experimentally, it is consistent with reports of *Acinetobacter* spp. releasing metabolic by-products in low-
359 nitrogen nectar environments (Álvarez-Pérez et al., 2019; Kato et al., 2025; Morales-Poole et al., 2023).
360 As many microbes secrete metabolites (Douglas, 2020), future work can identify the biochemical
361 pathways mediating these interactions.

362 *Meta-ecosystems and nectar microbiome*

363 The nutrient-subsidy mechanism we propose may reflect an experimental artifact, but the process may be
364 more general and relevant across ecosystems. Our results align with core ideas in meta-ecosystem
365 ecology, which emphasizes how flows of matter and energy shape ecosystem dynamics (Gounand et al.,
366 2018; Loreau et al., 2003; Massol et al., 2017). By focusing on connections across ecosystem boundaries,
367 this framework considers a broader set of spatial flows than traditional metapopulation approaches would,
368 including the movement of inorganic nutrients, organic matter, and other non-living biotic materials in
369 addition to living organisms. In the case of nectar microbes, for instance, floral nectar represents a
370 primary habitat, but not the only one they occupy. For example, nectar yeast may overwinter in bee nests
371 (Pozo et al., 2018), while some species may seek refuge in soil and plant surfaces (Vannette, 2020) before
372 recolonizing flowers in the following season. Together, these examples highlight that dispersal moves not
373 just organisms but also the energy and nutrients associated with them from previous places, prompting
374 questions about the extent to which these cross-ecosystem fluxes affect local microbial communities.

375 *Experimental caveats and theoretical assumptions*

376 Our experimental and theoretical approaches necessarily involve several caveats and simplifying
377 assumptions. For tractability, the two-patch formalism ignores dispersal among identical habitats which
378 therefore assumes that such movements have negligible impacts on metapopulation dynamics. With
379 respect to our experiment, bacterial sink populations were always inoculated into the same subset of
380 patches, raising the possibility that our results reflect spatial placement (e.g., edge effects on the PCR
381 plate) rather than the effects of experimental treatments. However, supplementary analyses found no
382 evidence for location-specific effects (Appendix S4). Moreover, although the factorial design of our
383 experiment allowed us to isolate the effects of dispersal frequency and dispersal bias, these factors likely
384 covary in nature. For instance, pollinators may reduce visitation to regions dominated by bacteria, thereby
385 also lowering visitation to any yeast-dominated patches within those regions. Lastly, both our experiment
386 and model assumed conservative dispersal, whereas nectar consumption by pollinators implies that only a
387 fraction of microbes and nectar material are transferred among flowers. 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 has experimentally demonstrated that sink species can influence a resident metapopulation by modifying local conditions and altering metapopulation connectivity. More broadly, our results highlight that dispersing organisms carry with them the material conditions with which they have become associated, and that this flow of material can shape the resource landscape experienced by other species and, in turn, mediate their interactions. Our experiments also 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.

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Statement of Authorship

WJO and TF conceived the study with input from RMG. WJO conducted the experiments, developed the theoretical model, performed the analyses, and drafted the manuscript with input from RMG. RMG and

TF equally supervised the project, and all authors contributed to revising and approving the final manuscript.

TABLES

Table 1. ANOVA table for the effects of treatments on metapopulation size and variance

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

FIGURES

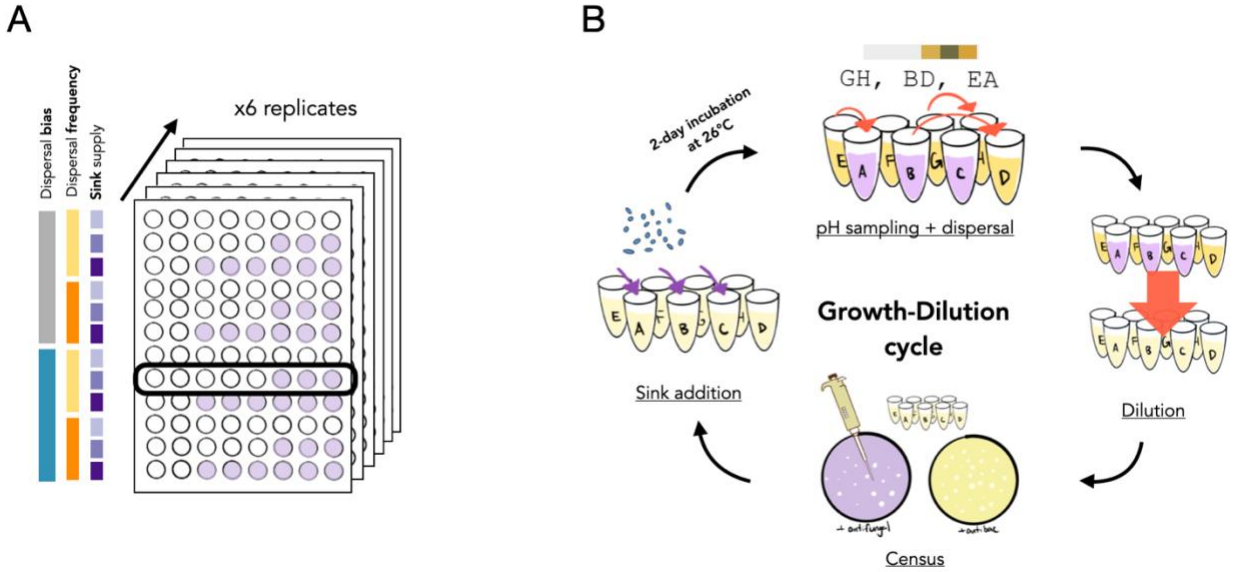

Figure 1. Overview of experimental setup. (A) The experiment followed a fully crossed dispersal bias (2) × dispersal frequency (2) × sink supply (3) design, each replicated six times. Each replicate metapopulation consisted of 8 patches (*i.e.*, wells on a PCR plate) connected by dispersal and underwent four 2-day growth-dilution cycles. **(B)** At the beginning of each cycle, patch-specific pH levels were sampled by transferring 5 µl of nectar onto pH strips. A sequence of donor-recipient pairs was then generated (see Methods) and used to conduct dispersal (red arrows) by pipetting 3 µl of nectar from the donor (arrow tail) to recipient (arrow head) patch. After dispersal, 5 µl of nectar was drawn from each patch and transferred to patches in the same location on a new PCR plate containing 95 µl of sterile nectar to emulate nectar production (*i.e.*, resource replenishment). Directly after the dilution, 5 µl of patch nectar was plated on agar plates (TSA for bacteria and YMA for yeast), on which colony forming units (CFUs) were later enumerated to estimate microbial density. Approximately 20,000 bacterial cells suspended in 1µl of sterile nectar were then inoculated into patches according to the Sink treatment (see Methods). Lastly, all plates were sealed with an air-permeable membrane and incubated at 26°C for two days.

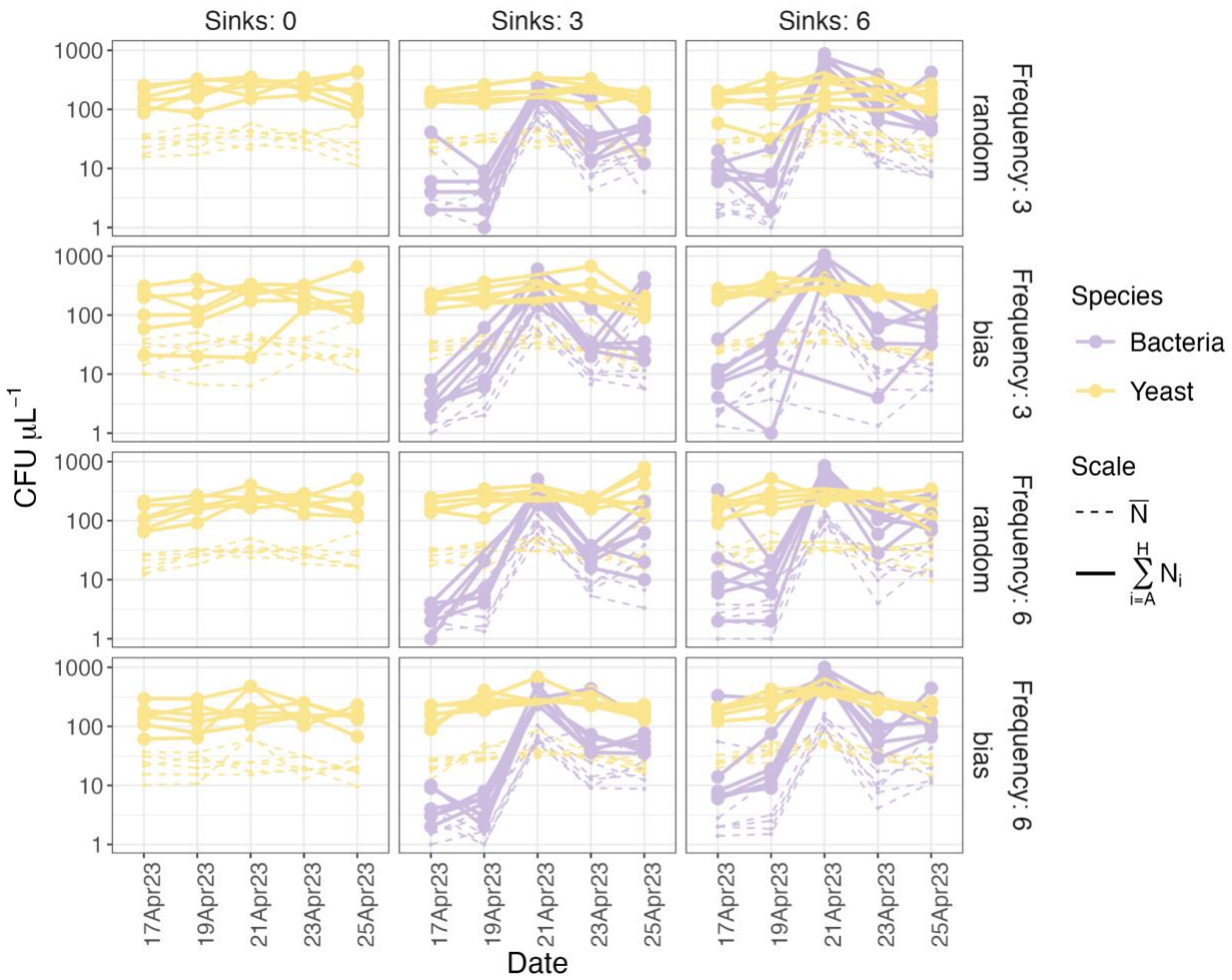

Figure 2. Time-series data of bacteria and yeast densities at local and regional scales. Lines show the time-series of the microbial densities of a single replicate metapopulation. The densities of bacteria (strain: FNA17) and yeast (strain: MR1) are colored in purple and yellow, respectively. Solid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

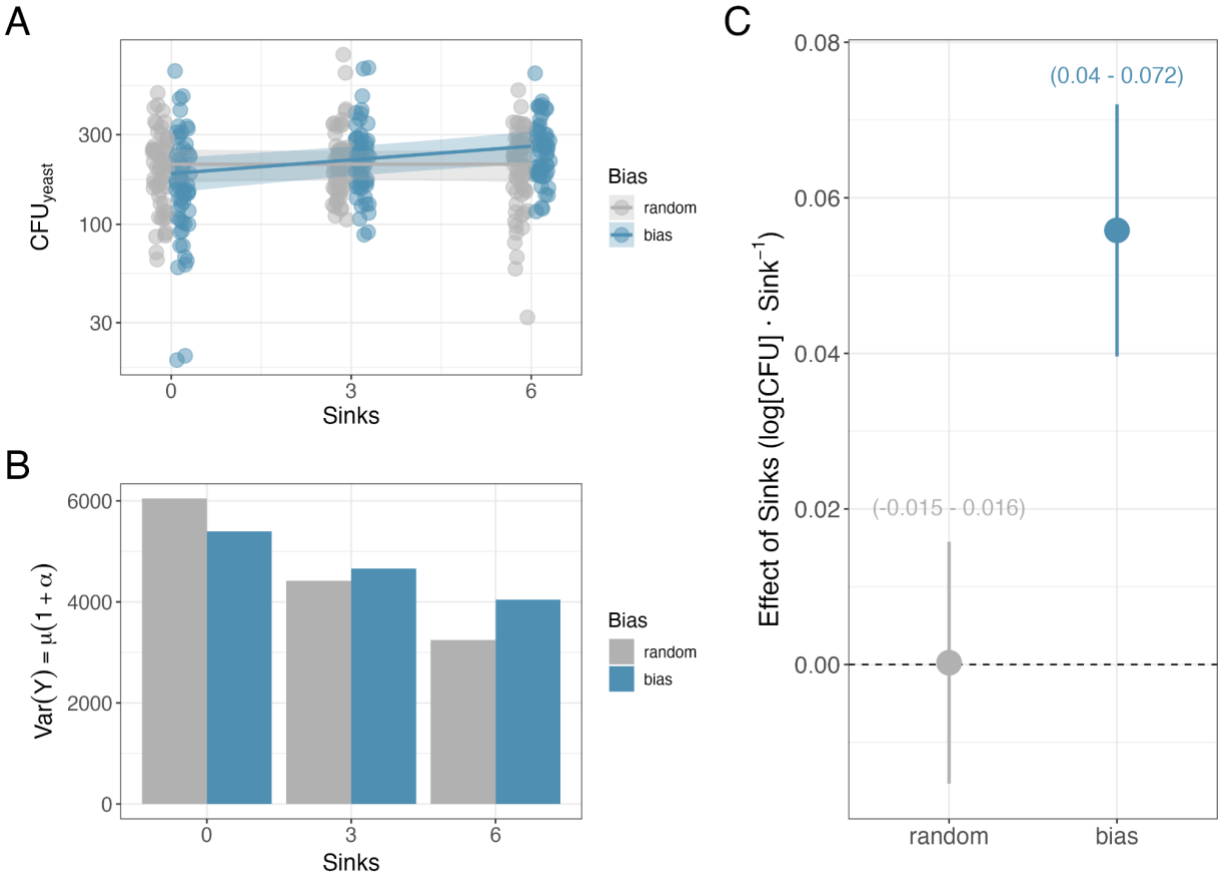

Figure 3. Effects of bacterial sinks and dispersal bias on yeast metapopulation size and variance. (**A**) Estimated treatment effects on the metapopulation-level colony forming units of yeast per µl, while fitted lines and 95% confidence intervals are from GLMM estimates. Bar plots in (**B**) show the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

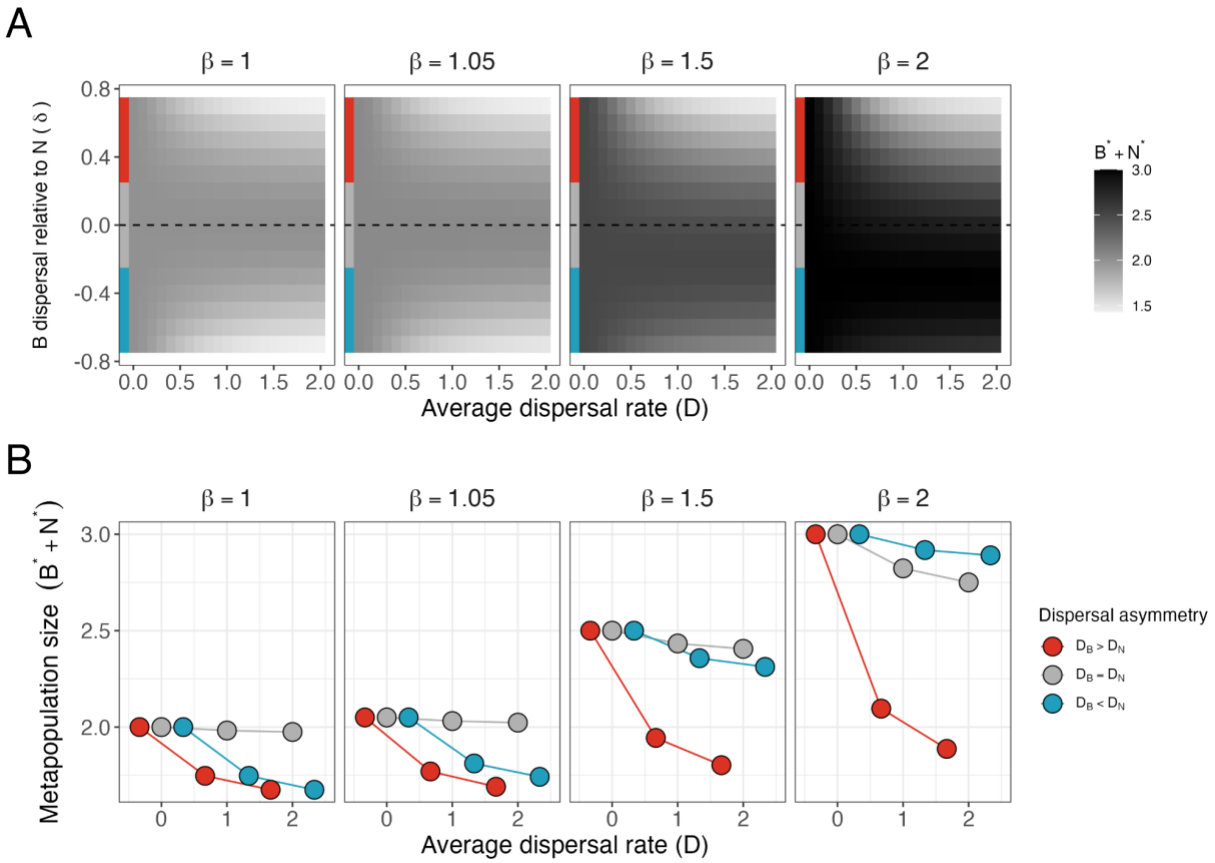

Figure 4. Metapopulation equilibrium in a two-patch model with asymmetric dispersal and patch-specific carrying capacities. Parameter D is the average dispersal rate, while δ and β determine the asymmetry in dispersal rate and the carrying capacity between patches, respectively. Specifically, when $\delta > 0$, the per-capita dispersal rate is higher from patch B to N than from patch A to B. When $\beta > 1$, patch B has a carrying capacity that is a factor β larger than patch N. Metapopulation equilibrium is defined as the sum of equilibrium densities of each patch. Panel (**A**) shows equilibrium values across the parameter space. Because we do not know the quantitative value of δ that corresponds to our dispersal bias treatment (qualitatively, $\delta < 0$), we averaged the metapopulation equilibria across a range of δ values, grouped into three classes based on dispersal asymmetry (indicated by color bars along the y-axis in A). Panel (**B**) shows these averages, where red, grey, and teal indicate cases where patch B disperses more than, equal to, or less than patch N on average, respectively.

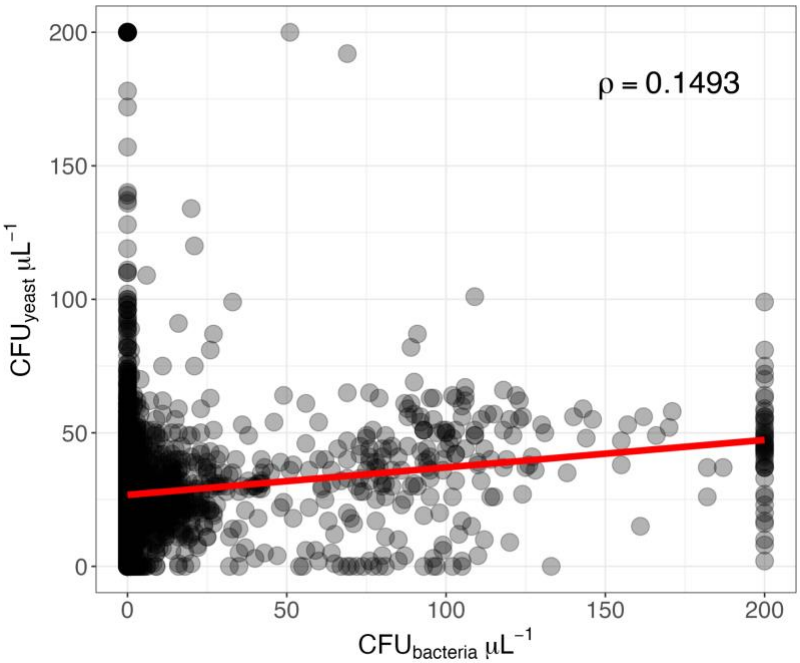

Figure 5. Association between patch-level yeast and bacteria densities. Points indicate the number of colony forming units (CFU) of bacteria and yeast per μl in a single patch of a metapopulation. Line of best fit was drawn to aid visualization and ρ is the Pearson correlation coefficient ($p < 0.01$).

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