Landscape connectivity alters the evolution of density-dependent dispersal during pushed range expansions

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Abstract

As human influence reshapes communities worldwide, many species expand or shift their ranges as a result, with extensive consequences across levels of biological organization. Range expansions can be ranked on a continuum going from pulled dynamics, in which low-density edge populations provide the "fuel" for the advance, to pushed dynamics in which high-density rear populations "push" the expansion forward. While theory suggests that evolution by spatial sorting, a common feature of range expansions, could lead pushed expansions to become pulled with time, empirical comparisons of phenotypic divergence in pushed vs. pulled contexts are lacking. In a previous experiment using *Trichogramma brassicae* wasps as a model, we showed that expansions were more pushed when connectivity was lower. Here we used descendants from these experimental landscapes to look at how the range expansion process and connectivity interact to shape phenotypic evolution. Interestingly, we found no clear and consistent phenotypic shifts, whether along expansion gradients or between treatments, when we focused on low-density trait expression. However, we found evidence of changes in density-dependence, in particular regarding dispersal: populations went from positive to negative density-dependent dispersal at the expansion edge, but only when connectivity was high. As positive density-dependent dispersal leads to pushed expansions, our results confirm predictions that evolution during range expansions may lead pushed expansions to become pulled, but add nuance by showing environmental context may slow down or cancel this process. This shows we need to jointly consider evolution and ecological context to accurately predict range expansion dynamics and their consequences.

Keywords: biological invasions; context-dependent dispersal; experimental evolution; habitat fragmentation; spatial sorting; *Trichogramma*

Introduction

Many species distribution ranges are currently shrinking, shifting or expanding as a direct or indirect result of human influence. Climate-tracking species and invasive species, in particular, are the focus of research efforts aiming to describe and understand their dynamics (Chuang & Peterson, 2016; Lenoir et al., 2020; Renault et al., 2018). Within-species trait variability has reverberating impacts across organisation levels, from populations to ecosystem functioning (Des Roches et al., 2018; Jacob et al., 2019; Little et al., 2019; Raffard et al., 2019; Violle et al., 2012). Thus, knowing how phenotypes are redistributed in space during range expansions and range shifts is likely key to understand the ecological and evolutionary dynamics at play in the resulting communities (Cote et al., 2017; Renault et al., 2018).

The speed at which a species' range expands in space is, ultimately, a function of both population growth and dispersal (Lewis et al., 2016). As populations/species differ qualitatively in their growth and dispersal functions (Fronhofer et al., 2018; Gregory et al., 2010; Harman et al., 2020; Sibly & Hone, 2002), due to intrinsic and/or environmental drivers, we can expect them to differ in the way they advance during range expansions too. Building on the framework of reaction-diffusion equations, one can discriminate between "pushed" and "pulled" expansions (Lewis et al., 2016; Stokes, 1976), although it may be more accurate to think of it as a continuum of "pushiness" (Birzu et al., 2018). Pulled expansions are the type often implied "by default" in many ecological studies (Deforet et al., 2019; see e.g. Weiss-Lehman et al., 2017). Pulled expansions assume dispersal and growth are either constant or maximal at the lowest densities. This leads to expansions being "pulled" forward by the few individuals at the low-density, recently populated edge (Lewis et al., 2016; Stokes, 1976). However, in many species, dispersal is actually more likely at high densities, as a way to escape increased competition (Harman et al., 2020; Matthysen, 2005). Additionally, populations can exhibit Allee effects (Allee & Bowen, 1932; Courchamp et al., 2008), i.e. have their growth rate decrease at lower densities. In both cases, this leads to the product of per capita growth and dispersal being highest at intermediate or high densities; these expansions are thus "pushed" by older populations that have reached these densities, instead of being primarily driven by low-density edge populations.

Individuals founding new populations at the leading edge of an expansion are likely a non-random sample of available phenotypes, because individuals with traits facilitating spread are more likely to reach these new habitats in the first place. If these individual differences are heritable, this can lead to evolution by spatial sorting, where phenotypes facilitating spread accumulate at the expansion edge with time (Cwynar & MacDonald, 1987; Phillips & Perkins, 2019; Shine et al., 2011). Evolution of increased dispersal ability in leading-edge populations is now well documented, both in experimental and natural contexts (Chuang & Peterson, 2016; Deforet et al., 2019; Fronhofer et al., 2017; Weiss-Lehman et al., 2017). In addition, relaxed density-dependence at the lower-density edge can select for faster life-history, e.g. higher fecundity (Burton et al., 2010; Van Petegem et al., 2018). Both models and reshuffling experiments (where individuals' locations are regularly randomized to stop spatial evolution) have demonstrated how these evolutionary changes can accelerate expansions (Perkins et al., 2013; Schreiber & Beckman, 2020; J. M. Travis & Dytham, 2002; Van Petegem et al., 2018; Weiss-Lehman et al., 2017). However, summarizing empirical studies also shows that these directional shifts in population growth, dispersal or associated traits do not always happen during range expansions (Chuang & Peterson, 2016; Merwin, 2019; Van Petegem et al., 2018; Wolz et al., 2020). We need a better understanding of what determines whether or not this spatial selection will occur, and whether it will affect growth traits or dispersal traits, if we want to successfully predict (and potentially manage) the ecological and evolutionary dynamics of range expansions or shifts.

Where an expansion sits on the pushed-pulled continuum can have consequences on its evolutionary dynamics: for instance, (more) pushed expansions should conserve more genetic diversity (Birzu et al., 2018, 2019; Roques et al., 2012). While this effect of expansion type on neutral evolution has been confirmed experimentally (e.g. Gandhi et al., 2019), the possibility that pushed and pulled expansions may also differ in their adaptive evolutionary dynamics has remained almost completely unstudied (Birzu et al., 2019). This is surprising, given the distinction between pushed and pulled expansions rests, at its core, on traits (dispersal and fecundity) we now know can be under selection during range expansions, as mentioned above. Moreover, there is evidence that evolution during spatial sorting can lead to changes in not only average dispersal between core and edge populations, but also in the density dependence of dispersal, i.e. precisely one of the characteristics that determine whether an expansion is pushed or not. While studies (theoretical and empirical) are few, evolution during range expansions appears to move edge populations away from positive density-dependent growth and dispersal (Erm & Phillips, 2020; Fronhofer et al.,

2017; Travis et al., 2009; Weiss-Lehman et al., 2017; but see Mishra et al., 2020), which could lead pushed expansions to become more pulled with time (Erm & Phillips, 2020). A question remains, however, unexplored: do initial differences in ecological context lead to differences in (spatial) selection pressures? And if so, do these differences influence the stability of an expansion type (pushed or pulled) through time (Birzu et al., 2019; Erm & Phillips, 2020)?

In this context, we revisit a previous study of experimental range expansions using *Trichogramma* parasitic wasps as a model (Dahirel et al., 2020), in which we showed that reducing landscape connectivity led to increased "pushiness". We this time examine the phenotypic changes that have occurred in space and time depending on the type of expansion. We first ask whether body size, a trait that is linked to fitness in *Trichogramma* (Durocher-Granger et al., 2011), differs between core and edge populations and across connectivity treatments. We then conduct a common-garden experiment, using the descendants of the expansion experiments, to study whether different range expansion contexts led to contrasted evolutionary changes in traits directly linked to spread, namely dispersal, activity and reproductive success, with special attention to changes in density-dependence in part of the experiments.

Methods

Study species and range expansion experiment

This experimental protocol for the expansions is described in detail in a previous article (Dahirel et al., 2020); we here summarise its most relevant aspects.

Trichogramma wasps are small (body length ≈ 0.5 mm when adult) egg parasitoids that are relatively easy to maintain on standardised resources in the lab. We used three laboratory strains of *Trichogramma brassicae* Bezdenko, 1968 (Hymenoptera: Trichogrammatidae) for our experiment (**Fig. 1**). Each strain was obtained by mixing three pre-existing isoline populations using Fellous et al. (2014)'s protocol to ensure similar genetic representation of the isolines in the final mixes. Isolines were themselves derived from individuals collected in different sites across western Europe in 2013. The three resulting mixed strains had broadly similar levels of genetic diversity at the start of the experiment, with expected heterozygosity based on 19 microsatellite loci in the 0.3-0.4 range (Dahirel et al., 2020).

They were raised using irradiated eggs of the Mediterranean flour moth *Ephestia kuehniella* Zeller 1879 (Lepidoptera: Pyralidae) as a substitution host (St-Onge et al., 2014).

We monitored *T. brassicae* spread in 24 experimental linear landscapes (8 per genetic strain) for 14 non-overlapping generations (Generations 0-13, with initially released adults counted as Generation 0, and the experiment stopped at the emergence of Generation 13 adults). Landscapes were made of plastic vials (10 cm height, 5 cm diameter) connected to their nearest neighbours by flexible tubes (internal diameter 5 mm). In half of the replicate landscapes, patches were connected by three 20 cm long tubes ("reference" connectivity). In the other half, connectivity was reduced and patches were only connected by one longer (40 cm) tube (**Fig. 1**). Patches contained approximately 450 *Ephestia* eggs, on paper strips to facilitate handling, renewed every generation at adult emergence. We started landscapes by placing ≈ 300 unsexed adult wasps in one extremity patch (expansion was only possible in one direction), a number close to the expected equilibrium population size in such a system (Morel-Journel et al., 2016). Each generation, adult individuals were allowed to disperse, mate and lay eggs for 48 hours before they were removed. The landscapes with reduced connectivity had on average more pushed dynamics than the "reference" ones, drawing on both genetic (direct) and expansion velocity (indirect) arguments (Dahirel et al., 2020). Experimental landscapes, as well as subsequent experiments described below, were kept under controlled conditions (23°C, 70% relative humidity, 16:8 L:D).

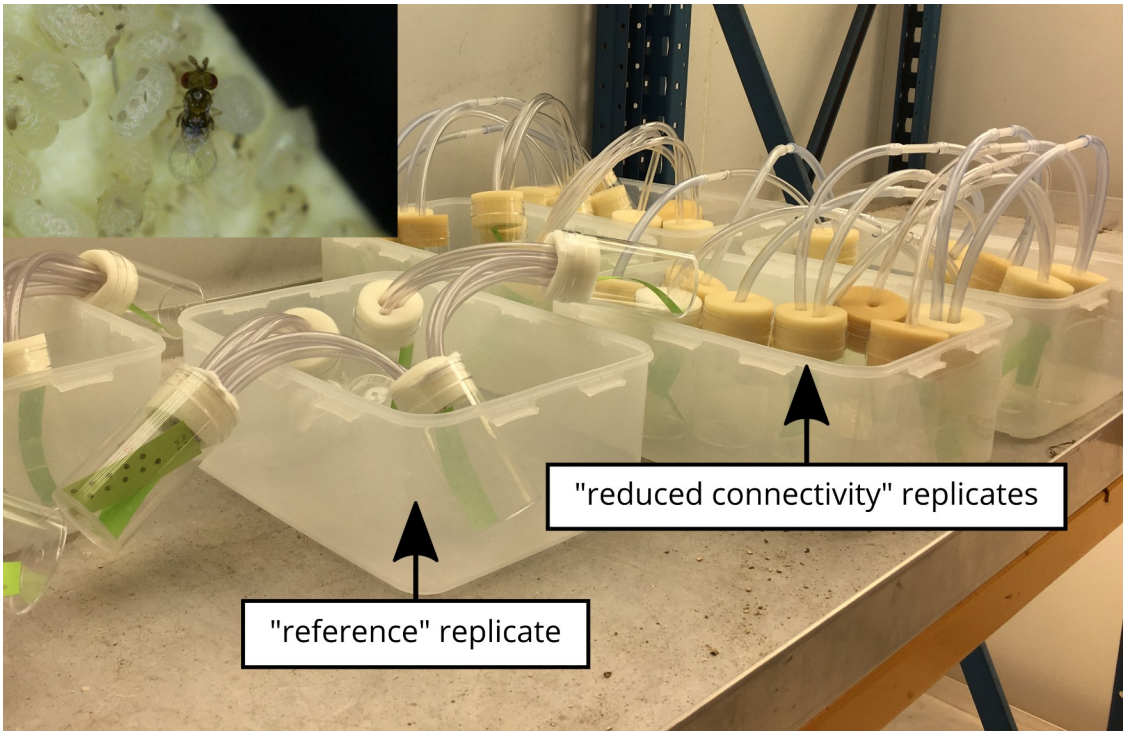


Figure 1 Replicate landscapes used in the range expansion experiment. Picture (credit: Aline Bertin) shows both reference landscapes (patches connected by three 20 cm tubes) and "reduced connectivity" landscapes (patches connected by one 40 cm tube). Clusters of host eggs on paper strips can be seen in each patch. Inset: *Trichogramma brassicae* on *Ephestia kuehniella* eggs (credit: Géraldine Groussier).

Phenotypic measurements

For our analysis of trait change, we focused on descendants of individuals born towards the end of the experiment in "core" patches (here, the release patches or their immediate neighbours, x = 0 or 1) or in the corresponding "edge" patches (i.e. the farthest populated patch in a landscape at the time of sampling, or the farthest two if there were not enough individuals in the farthest one). We compared them to wasps from the "stock" populations initially used to start the experimental expanding landscapes. Note that mentions of "X^{th} generation" wasps below indicate the number of generations of experimental landscape expansion before sampling/ transfer to common garden conditions. For some traits (short-term movement, and fecundity and dispersal during the density-independent tests), data was also collected on one or two intermediate generations. For consistency and simplicity,

we only analysed (and described below) the latest tested generation for each trait, but made available all data, including intermediate samples (**Data availability**).

Wasp size

To determine whether the expansion context had an effect on body size, we selected female wasps from the stock populations, and compared them to 12th generation females from the experimental landscapes. Due to logistical constraints, the latter were selected in 8 edge-core pairs of populations drawn at random among the 24 available. Adding the three stock populations, and accounting for the fact one edge-core pair was only sampled in the core due to limited numbers in the edge population, we measured 316 (91 to 116 per strain) wasps in 18 populations (mean ± SD: 17.6 ± 4.0 wasps per population).

Wasps were kept in 70% ethanol before phenotypic measurements. We used hind tibia length (in µm) as a body size proxy (e.g. Durocher-Granger et al., 2011). We used a Zeiss AxioImager Z1 microscope equipped with a 40x/0.75 objective to photograph tibias after dissection. Images were managed and measurements done using the OMERO platform (Allan et al., 2012). Wasps were measured by two independent observers; inter-observer agreement was good but not perfect (r = 0.93). We thus decided to use a hierarchical approach to explicitly include measurement error in-model (see **Statistical analysis** below) rather than averaging observations before fitting.

Short-term movement

To study differences in short-term movement between treatments and between core and edge patches, we analysed F1 offspring of 10th generation wasps, and compared them to each other and to wasps from the stock populations. To control for population density (and other) variations among landscapes, we used a common-garden protocol: wasps removed from their natal landscapes after the egg-laying phase were allowed to lay eggs on new host egg strips for 48h (with ≈ 20 females per ≈ 450 host eggs, i.e. low density conditions). Emerging offspring (unsorted by sex) were placed in an empty and lit 15×19 cm rectangular arena, 2 cm high, sealed above and below with a glass sheet. Groups of 15.8 individuals on average (SD: 3.3) were introduced per replicate trial, and their movements filmed for five minutes. To reduce behavioural changes at the edge of the arenas, and their effect on our metrics, we only tracked individuals within a central 7×11 cm area, and the outer parts of the arena were kept in the dark to discourage individuals from approaching the edges. A total of 119 replicate groups were tested, coming from 27 populations (core and edge from

12 of the 24 experimental landscapes + the three stock populations). Video files were analysed using Ctrax (Branson et al., 2009) for tracking and the `trajr` R package (McLean & Volponi, 2018) for computation of movement statistics from trajectories. Most individuals were not tracked continuously for the entire five minutes due to either leaving the filmed area or the loss of individual identity information. We therefore first computed metrics at the tracklet level (consecutive bout of movement longer than 2 seconds), and then averaged them, weighted by tracklet duration, to generate replicate-level metrics. We used the proportion of total tracked time individuals were active, the average speed and the average sinuosity (Benhamou, 2004). All three movement metrics responded similarly to the experimental protocol; for simplicity, we only present and discuss results from the "proportion of time active" metric here, and models for the other metrics are included in the associated analysis code (see **Data availability**).

Fecundity

F1 offspring of 12th generation wasps (reared in a common-garden setting as described above) were used to evaluate fecundity differences between treatments. We placed newly emerged and mated females individually in vials containing 90 host eggs, and let them lay eggs for 24h. We then counted the number of darkened host eggs after 7 days (an indication of successful parasitoid development) as our measure of reproductive success. Because superparasitism (more than one egg per host) frequently happens in *Trichogramma* wasps (Corrigan et al., 1995), this is not a measure of eggs produced *stricto sensu*, but rather a metric of reproductive success [in most cases, a single adult emerges per host, even when superparasitism occurs; Corrigan et al. (1995)]. A total of 492 F1 females coming from 50 populations were used, (from all 24 experimental landscapes _excluding one population_ + the three stock populations) with 9.8 individuals per population on average (SD: 3.3).

Effective dispersal

We placed groups of 50 unsexed newly emerged wasps (obtained at the same time and in the same way as the ones used to measure fecundity) in a *departure* vial connected to an *arrival* vial by one 40 cm flexible tube (i.e. reduced connectivity conditions). Both vials contained 90 host eggs. We tested 99 groups coming from 47 populations (from all 24 experimental landscapes, excluding four populations, plus the three stock populations). We let wasps in vials for 24h, removed them, then waited 7 days and counted parasitised (darkened) host eggs. We used the proportion of parasitised eggs found in the *arrival*

patches, relative to the total parasitised eggs in a replicate (*departure* and *arrival* patches), as our measure of dispersal rate. As such, it is important to note it is not a measure of the percentage of individuals that dispersed (as dispersers and residents may differ in sex-ratio, fecundity, competitive ability and survival, Ronce & Clobert, 2012), but rather a context-specific measure of effective dispersal or gene flow.

Density-dependent fecundity and dispersal

F2 descendants of the last (12th) generation to emerge from experimental landscapes (and from a new set of stock population wasps) were subjected to the same dispersal and reproduction experiments as F1 wasps, with the difference that developmental density conditions before the experiments were this time manipulated. For these experiments, due to logistic constraints, we studied wasps coming from each of the three stock populations and one randomly selected landscape per connectivity × genetic strain combination. High-density wasps were obtained by placing ≈ 90 F1 parasitised eggs close to maturity with ≈ 90 fresh host eggs; this in effect mimics the conditions in core patches during the expansions, with populations at carrying capacity and a 1 to 1 replacement of host eggs from one generation to the next. Low-density wasps were obtained by placing ≈ 90 parasitised eggs with ≈ 450 fresh hosts; these conditions are closer to the conditions experienced at the range edge. Higher densities likely led to higher superparasitism and higher within-host competition during early development (Corrigan et al., 1995; Durocher-Granger et al., 2011). 341 F2 females were tested in total for the reproductive success experiment (N = 19 or 20 per density level for each of the three stock populations, while 9.3 females were tested on average for the other populations × density combinations (SD: 1.7)). For the dispersal experiment, we used 72 groups of 50 wasps, with 2 groups per population × density combination, except for stock populations where we used 4 groups per mix × density.

Statistical analyses

Analyses were done using R, version 4.0.4 (R Core Team, 2021). We analysed data in a Bayesian framework using the `brms` R package (Bürkner, 2017) as a frontend for the Stan language (Carpenter et al., 2017). We mostly relied on the `tidybayes` (Kay, 2019), `bayesplot` (Gabry et al., 2019), `patchwork` (Pedersen, 2019) packages, and on the `tidyverse` suite of packages (Wickham et al., 2019), for data preparation, model diagnostics and plotting. We ran four Markov chains per model; the number of iterations per chain was model-dependent (but always ≥ 2000 after excluding warmup iterations),

and set to be large enough to ensure convergence ($\hat{R} \leq 1.01$) and satisfactory effective sample sizes (both bulk- and tail-effective sample sizes sensu Vehtari et al., 2020 > 1000). When posteriors are summarised, all credible/compatibility intervals given are highest posterior density intervals. Priors were chosen to be weakly informative and mostly follow suggestions by McElreath (2020); they are described in detail in **Supplementary Material S1**, along with a formal description of each model.

We used (generalized) linear mixed models to analyse how phenotypic traits (size, short-term movement, reproductive success and effective dispersal) varied between treatment × location combinations (hereafter "context," 5 possible combinations including "stock"). We used nested random effects (random intercepts) of genetic strain, experimental landscape and source location (stock, edge or core patch) to account for phylogenetic relatedness/ shared ancestry among populations (Clutton-Brock & Harvey, 1977; Hadfield & Nakagawa, 2010).

- We used a Gaussian model for size, with tibia length (centred and scaled to unit 1 SD) as the response. In addition to the fixed effect of context and the "phylogenetic" random effects described above, and because individuals were measured twice, this model included a random effect of individual identity, allowing us to split (within-population) individual variation from (residual) observation error.

- We analysed the percentage of time active per test group as a function of context and phylogeny using a Beta model.

- We analysed reproduction data (number of eggs successfully parasitized) using zero-inflated negative binomial models, as initial analyses revealed zero-inflation. The submodels for the probability of excess zeroes p (i.e. reproductive failure) and for the number of eggs otherwise (λ) both included effects of phylogeny and context. For simplicity, we do not discuss in the Results section the two submodels separately, but only the overall posterior average fecundities $(1-p) \times \lambda$. The density-dependent experiment was analysed using a very similar model, with added fixed effects of density and density × context interactions.

- Finally, we analysed effective dispersal rates using binomial models. As for fecundity, models included effects of phylogeny and context (+ density and density × context effects for the density-dependent experiment). Initial models presented some evidence of overdispersion. This was accounted for by adding the total

number of eggs laid (centred and scaled to unit 1 SD) as a covariate: while it may indicate a dispersal-fecundity syndrome, a positive link between effective dispersal and total fecundity is also very likely to arise "artificially" in our setup simply because once the departure patch is saturated, individuals can only successfully reproduce if they disperse. Note that in *Trichogramma*, we expect *a priori* such saturation to appear well below the nominal limit based on host number, due to competition (Dahirel et al., 2020; Morel-Journel et al., 2016). The main conclusions we derive from the model do not change if we do not control for the total number of eggs laid.

Results

Average tibia length did not differ clearly between contexts (**Fig. 2**), although there were indications that wasps from "reference connectivity" edge populations may be smaller than stock individuals on average (see **Supplementary Material S2** for pairwise comparisons).

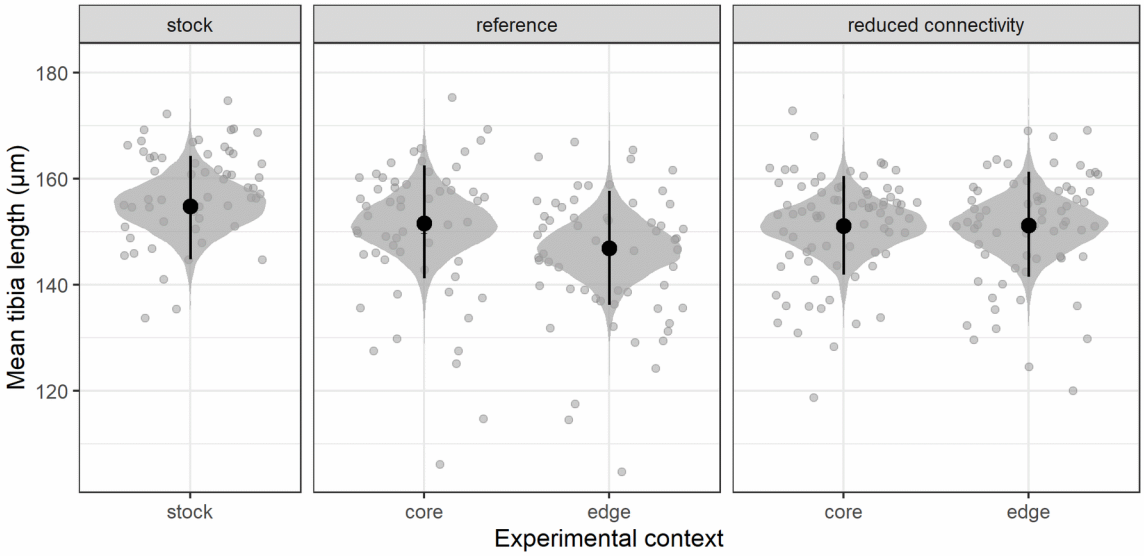


Figure 2. Posterior distribution of mean tibia length (proxy of body size); black dots and segments: posterior means and 95% credible intervals. Grey dots: individual observed values (average of the two observers' measures).

We found no evidence that short-term activity had evolved depending on experimental context (**Fig. 3**, **Supplementary Material S2**). Individuals were on average active 53% of the time, regardless of experimental context (grand mean across contexts; 95% CI: [41%; 64%]).

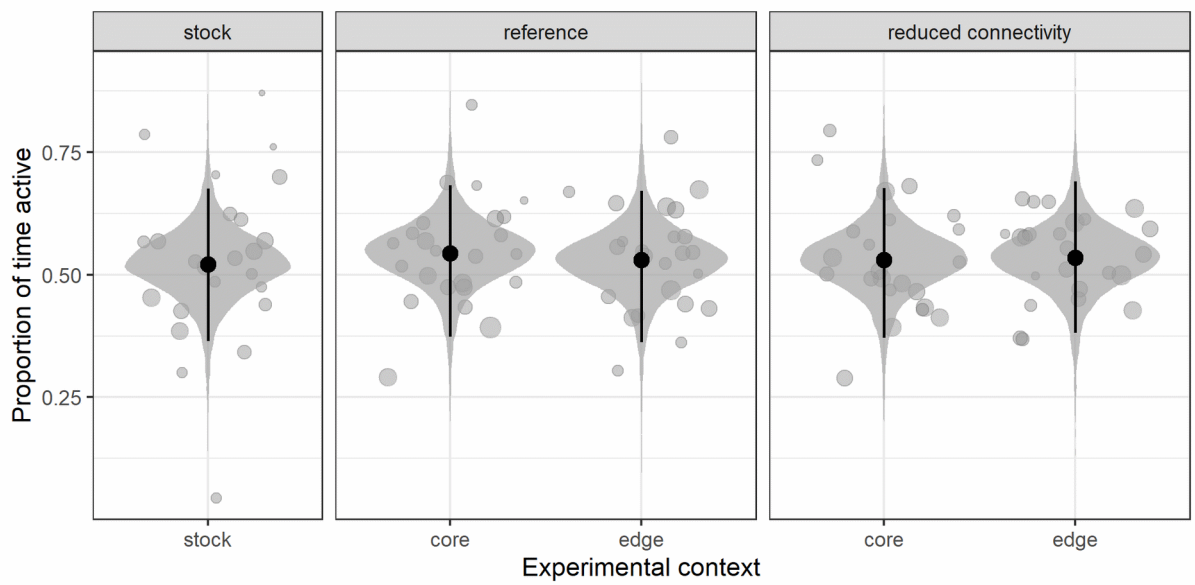
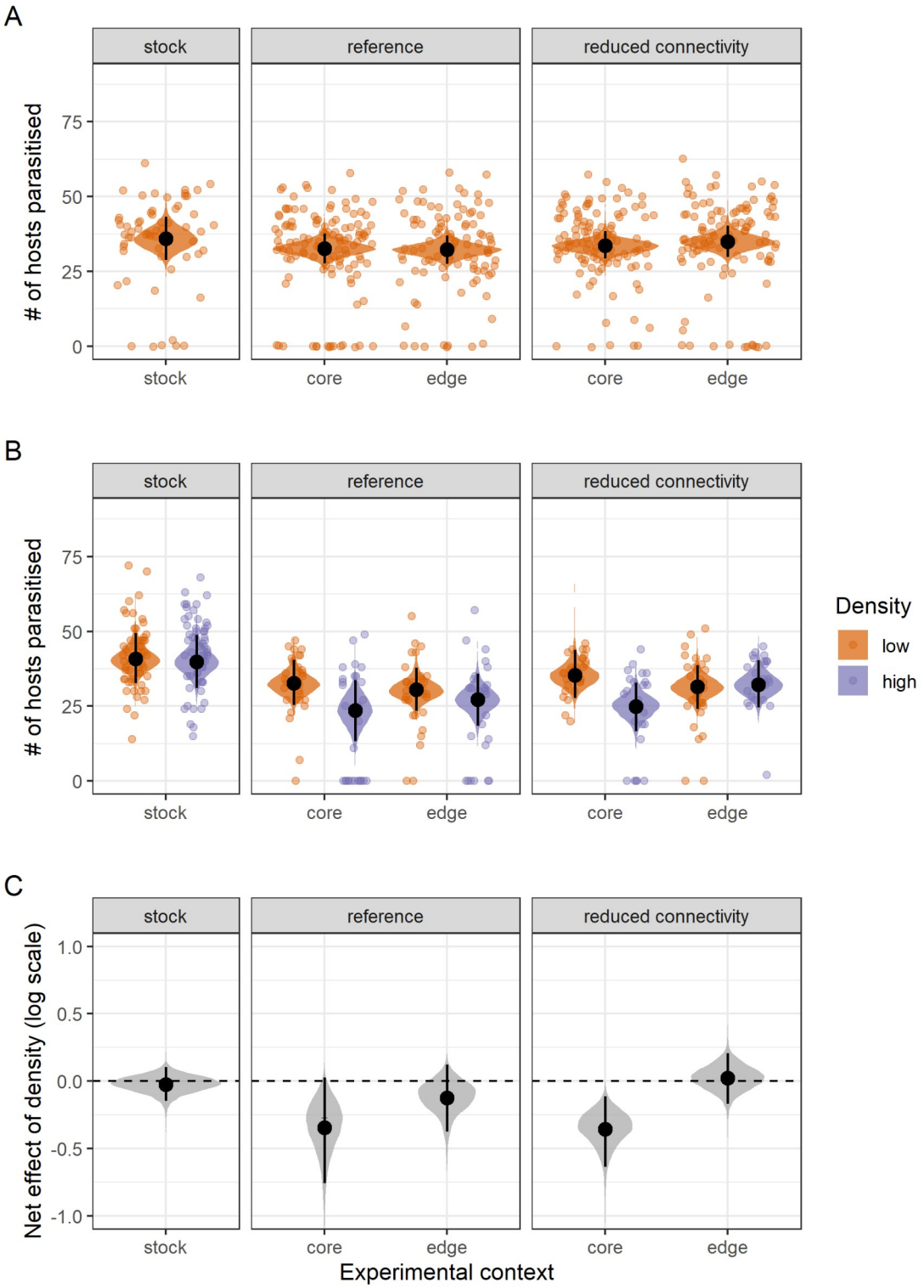


Figure 3. Posterior distributions of mean short-term activity, based on filmed movement tracks; black dots and segments: posterior means and 95% credible intervals. Grey dots: replicate-level observed values; point size is proportional to the total valid observation time for a replicate (sum of all movement bouts).

Regarding individual fecundity, we found no evidence that landscape context or patch location had any effect in the first fecundity experiment (**Fig. 4A**). Similarly, in the second (density-dependent) experiment, we mostly found no differences in low-density fecundity between post-experimental contexts (**Fig. 4B**, **Supplementary Material S2**). The only potential effect was that low-density edge populations were less fecund than the corresponding stock (**Fig. 4B**, **Supplementary Material S2**). There was no effect of juvenile density on fecundity in stock populations (**Fig. 4C**); after experimental evolution, individuals from core populations were less fecund if they came from high-density than if they came from a low-density background, independently of connectivity treatment (**Fig. 4C**). There was no such density effect for individuals from edge populations (**Fig. 4C**, **Supplementary Material S2**). As a consequence of the effects described above, when reared at high densities, wasps coming from the experimental landscapes are in almost all cases less fecund than the corresponding stock wasps (the exception being wasps from the expansion edge of "reduced connectivity" landscapes; **Fig. 4B**, **Supplementary Material S2**).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Net effect of density (log scale)
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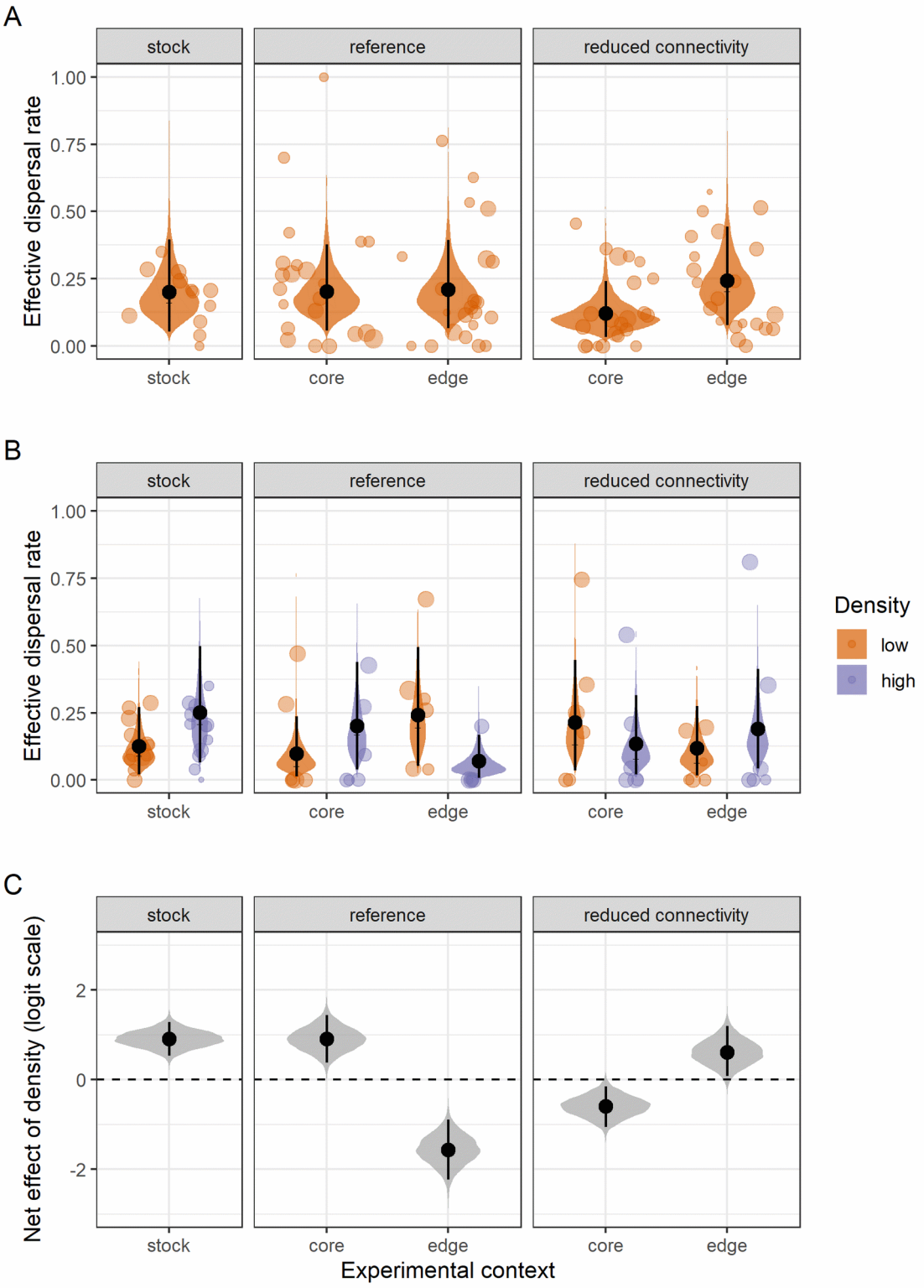
Experimental context

Figure 4. (A; B) Posterior distributions of mean per-capita fecundity, based on either the first experiment (A) or the second experiment (B; one generation later, with some wasps tested at high density). Black dots and segments: posterior means and 95% credible intervals; coloured dots: observed values. (C) Net effect of juvenile density on fecundity (difference between posterior mean fecundity at high and low densities, expressed on the log scale).

We found no consistent deviations from stock population dispersal in the first dispersal experiment, as posteriors were wide (**Fig. 5A**). Dispersal rates were nonetheless higher in edge than core populations, but only in landscapes with reduced connectivity (**Fig. 5A**, **Supplementary Material S2**). In the low-density part of the second experiment, there is similarly no consistent evolution of dispersal away from stock population rates (**Fig. 5B**), although edge populations in reference landscapes tended to disperse more (**Fig. 5B**, **Supplementary Material S2**). Similarly to the first experiment, dispersal from edge populations was higher than in core populations, but this time only in "reference" landscapes (**Fig. 5B**, **Supplementary Material S2**).

Stock populations exhibited positive density-dependent dispersal (**Fig. 5C**). After experimental evolution, this pattern was reversed, leading to negative density-dependent dispersal, in wasps coming from edge populations of "reference" landscapes or from core populations of landscapes with reduced connectivity (**Fig. 5C**, **Supplementary Material S2**).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Effective dispersal rate
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Net effect of density (logit scale)
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core
edge
Experimental context

Figure 5. (A; B) Posterior distributions of mean effective dispersal rate, based on either the first experiment (A) or the second experiment (B; one generation later, with some wasps tested at high density). The effect of total fecundity (see Methods) on posterior means is averaged out. Black dots and segments: posterior means and 95% credible intervals; the effect of total fecundity (see Methods) on posterior predictions has been averaged out. Coloured dots are observed values, dot size is proportional to total fecundity in each replicate (departure + arrival patches combined). (C) Net effect of juvenile density on dispersal (difference between posterior mean dispersal at high and low densities, expressed on the logit scale).

Discussion

We showed before that variation in landscape connectivity shapes the position of an experimental range expansion on the pushed/pulled expansion axis in *Trichogramma* wasps (Dahirel et al., 2020). We here find that these previously documented changes in expansion and neutral diversity dynamics due to connectivity were not consistently accompanied by clear phenotypic shifts at the range edge. This is despite targeting traits influencing the differences between pushed and pulled expansions, or proxies of these traits (e.g. size, Durocher-Granger et al., 2011). However, and importantly, we found that the density-dependence of dispersal, one of the two key parameters determining the pushed vs. pulled nature of expansions (Birzu et al., 2019), changed during the range expansion process, and these changes depended on the connectivity level.

We did not find any clear evidence for evolutionary changes in short-term activity, nor in fecundity or effective dispersal when density-dependence was ignored (**Figs 2, 3, 4**). Hints that edge individuals tended to be smaller in some contexts may be worth deeper explorations in future studies (**Fig. 2**, **Supplementary Material S2**), especially in the context of dispersal-competition trade-offs (Burton et al., 2010). Reproductive success did vary between contexts, but only in the density-dependent experiment, and the only consistent shift was that post-experimental evolution wasps were less fecund than wasps from stock populations, when looking at individuals born from high density environments (**Fig. 4**). We found evidence of higher low-density dispersal in edge compared to core populations, as expected from spatial sorting theory (Chuang & Peterson, 2016; Shine et al., 2011; Travis et al., 2009). However, this effect was inconsistent: it was only seen in one connectivity treatment in one dispersal experiment, but in the other in the second (**Fig. 5**,

Supplementary Material S2). It was also not associated with clear divergence from the starting stock populations themselves (**Fig. 5**, **Supplementary Material S2**). While clear increases in average dispersal or per capita growth rates are often expected at the edge of range expansions (Chuang & Peterson, 2016; Fronhofer et al., 2017; Phillips & Perkins, 2019; Van Petegem et al., 2018; Weiss-Lehman et al., 2017), there are enough exceptions to the "rule" (Chuang & Peterson, 2016; Van Petegem et al., 2018; Wolz et al., 2020) for these null/uncertain results not to be entirely surprising by themselves.

However, focusing on trait expression at only one density is limiting, as the density-dependence of dispersal or growth actually plays a key role in shaping the dynamics of range expansions (Birzu et al., 2019). We previously found that, in our *Trichogramma* experimental system, expansions were more pushed when connectivity was reduced, which means that connectivity influenced the density-dependence of growth and/or dispersal, through plastic and/or evolved responses (Dahirel et al., 2020). We here find evidence for density-dependent effective dispersal and reproductive success, and more importantly for variation in this density-dependence across contexts. Because we tested wasps using a common garden protocol, the differences we observed are likely the result of evolutionary divergence during expansions [although parental and grandparental effects on density-dependent dispersal cannot be ruled out entirely; Bitume et al. (2014)].

First, in core populations, the experiments led to the apparition of a link between density and per capita fecundity that is absent from edge populations (as well as from stock populations). Specifically, wasps coming from these expansion core lineages had fewer offspring on average when raised in high-density conditions (**Fig. 4**). This lower fecundity is expected if there is an egg number-egg size trade-off, as higher competition in core patches would favour larger, more competitive larvae (Segoli & Wajnberg, 2020). For instance, in *Callosobruchus chinensis* beetles parasitising seeds, higher larval competition within seeds leads to adults producing both a reduced number of eggs (Vamosi, 2005) and larger eggs [after accounting for emerging female size; Yanagi et al. (2013)]. To definitely confirm our hypothesis however, further experiments would be needed to determine whether there actually is an egg number-egg size trade-off in our tested populations. Looking at differences in adult size (or the absence thereof, **Fig. 1**) is not sufficient here, as adult size depends strongly on the actual intensity of superparasitism and larval competition (Durocher-Granger et al., 2011).

Second, *Trichogramma* wasps from the stock populations dispersed more on average if they came from a high density background (**Fig. 5**). This finding fits with the classic view of density-dependent dispersal as a response to increased competition (Bowler & Benton, 2005; Harman et al., 2020), and is a logical extension of previous results showing *Trichogramma brassicae* wasps left host eggs patches earlier if more were already parasitised (Wajnberg et al., 2000). The direction of this density-dispersal relationship was reversed in "reference" edge populations after 12 generations of evolution and expansion (**Fig. 5**), with wasps dispersing more from low-density populations. Our results here broadly agree with theory, which tends to predict the loss of positive density-dependent dispersal at low-density expansion edges (cf e.g. Travis et al., 2009). There is one key nuance in that theoretical models often predict unconditional high dispersal over most of the range of densities as a result, where we found a shift to negative density-dependent dispersal. It is difficult to say whether the former is the "true" expected endpoint during range expansions, however, given many dispersal models are designed or parametrised in a way that excludes the possibility of negative density-dependent dispersal (Kun & Scheuring, 2006; e.g. Poethke & Hovestadt, 2002; Travis et al., 2009). By contrast, while studies are rare, empirical results show shifts to truly negative density-dependent dispersal are possible outcomes at the edge of range expansions (Fronhofer et al., 2017; Simmons & Thomas, 2004). In any case, the key result remains consistent with theory, in that evolution at the range edge removes the positive density-dependence of dispersal that existed initially.

By contrast, when connectivity was reduced, no clear evolutionary changes in dispersal reaction norm occurred at the range edge (**Fig. 5**): the slope remained positive, albeit slightly shallower (as in Weiss-Lehman et al., 2017). Strong enough increases in dispersal costs (such as those that may be caused by reduced connectivity) are predicted to favour more positive density-dependent dispersal (Govindan et al., 2015; Rodrigues & Johnstone, 2014; Travis et al., 1999): our results at the expanding edge are here consistent with existing theory. In core populations however, dispersal actually became negative density-dependent when connectivity was reduced (**Fig. 5**), seemingly contradicting the previous argument. As discussed above, the theory explaining negative density-dependent dispersal is much less developed in stable metapopulations, let alone in range expansions. Among the few existing models, Rodrigues and Johnstone (2014) predicted that, at least in a non-expanding context, reduced temporal variability should favour negative density-dependent dispersal. Reusing population size data in Dahirel et al. (2020), we find that reduced

connectivity did indeed lead to lower temporal variability in core patches (**Supplementary Material S3**). We can thus interpret our results as the interplay of three "forces." On one side, the expansion process itself drives the loss of positive density-dependent dispersal at the expansion edge. On the other side, connectivity has dual and contradictory effects: the direct effects of reduced connectivity on dispersal costs would favour positive density-dependent dispersal; while the indirect effects through demographic stochasticity would favour negative density-dependent dispersal.

Taken altogether, our results confirm the importance of context-dependence when studying dispersal (Bonte & Dahirel, 2017; Matthysen, 2012). This is especially true for range expansions, which are often associated with a core-to-edge density gradient. We argue that not considering this context-dependence may explain (some of the) previous failures to detect trait evolution during range expansions (see e.g. compilation in Chuang & Peterson, 2016), and we recommend testing for density-dependence whenever it is logistically possible (as in e.g. Weiss-Lehman et al., 2017). We acknowledge that these findings regarding dispersal come from the experiment with the lowest sample size within this study (see Methods) and may need further confirmation; they are nonetheless fully consistent with previous results and expectations regarding pushed vs. pulled expansions (Birzu et al., 2019; Dahirel et al., 2020), as detailed below.

Conclusion: implications for the evolution of pushed expansions

Although *Trichogramma brassicae* wasps start the experiments with positive density-dependent dispersal, edge populations end up evolving away from that rapidly if left to expand in relatively connected "reference" landscapes (**Fig. 5**). Our experimental results agree with Erm and Phillips (2020)'s model, in which evolution should lead initially pushed expansions to become pulled (in their case with Allee effect-induced pushed expansions, in ours with density-dependent dispersal). Taken alone, these results would imply pushed range expansions are rare in nature since evolution would tend to "erase" them, or at least not as common as would be expected from general frequencies of Allee effects (Gregory et al., 2010) and positive density-dependent dispersal (Harman et al., 2020) in non-expanding populations. On the other hand, we found that positive density-dependent dispersal is comparatively maintained in edge populations, even after >10 generations of expansion, in landscapes with reduced connectivity. Accordingly, these expansions were previously shown to have more "pushed" characteristics than controls (Dahirel et al., 2020). Thus, persistent pushed expansions may actually be favoured in the many landscapes

experiencing anthropogenic connectivity loss (e.g. Horváth et al., 2019). In any case, our results show that environmental conditions and constraints may be key to the maintenance of pushed expansion dynamics in the face of evolutionary dynamics, and that the context dependence of pushed expansions needs to be further explored. We note however that more work (experimental or modelling) is needed to confirm this, especially to understand the implications of our results on longer time scales (Birzu et al., 2019).

Pushed and pulled expansions can differ in (relative) speed, genetic diversity (Dahirel et al., 2020) and, as our results show here, phenotypic composition. Lineages/individuals with different dispersal strategies may also differ in traits influencing population stability (Jacob et al., 2019) or ecosystem functioning (Cote et al., 2017; Little et al., 2019). Understanding what environmental conditions favour or disfavour the evolutionary maintenance of "pushiness" during expansions may help more generally to understand the evolution of many traits during range expansions, and the possible functional effects of expanding species on ecosystems.

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Data availability

Data and R scripts to reproduce all analyses presented in this manuscript are available on Github (https://github.com/mdahirel/pushed-pulled-2020-phenotype) and archived in Zenodo (v1.1; https://doi.org/10.5281/zenodo.4570235).

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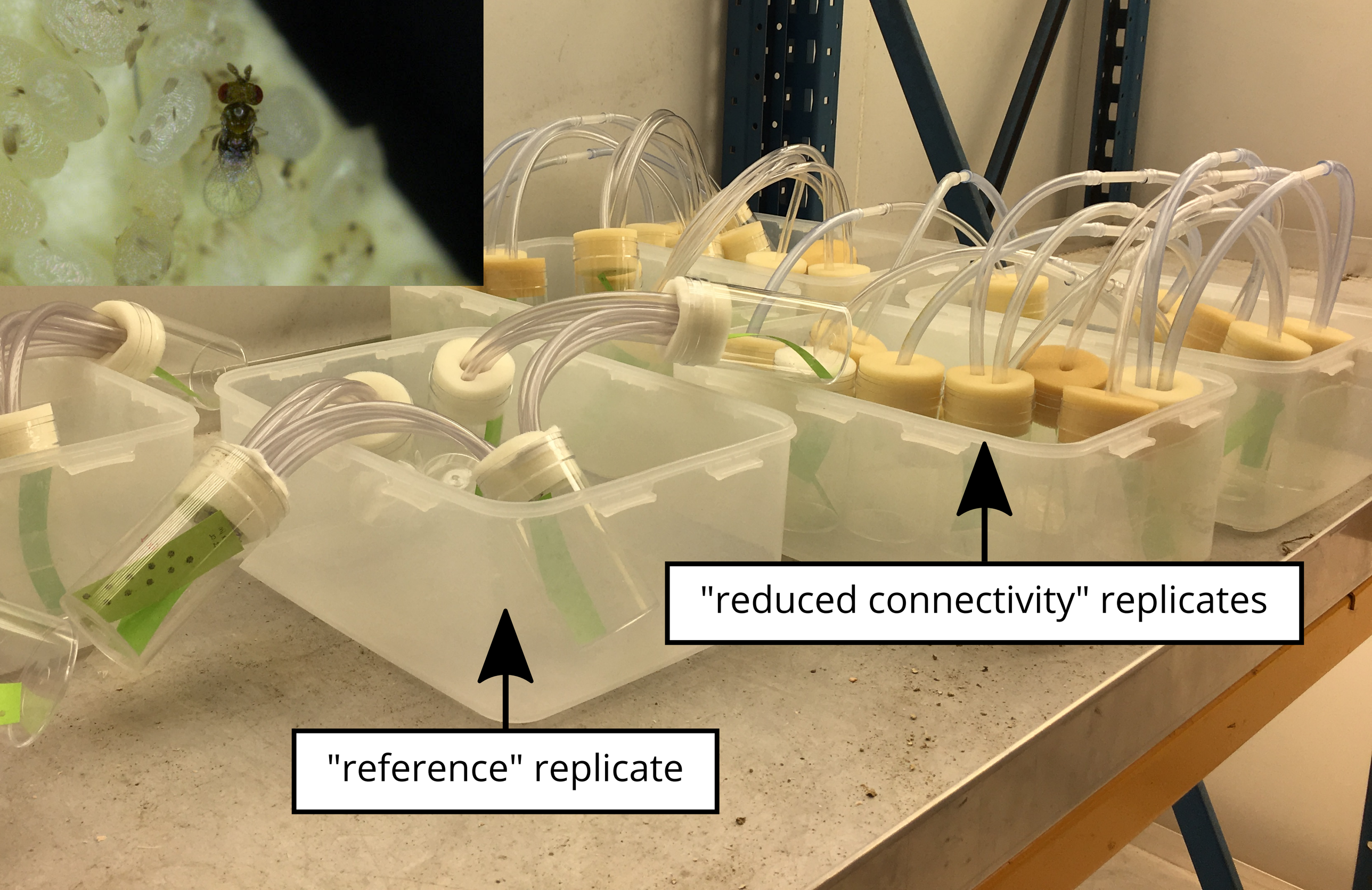
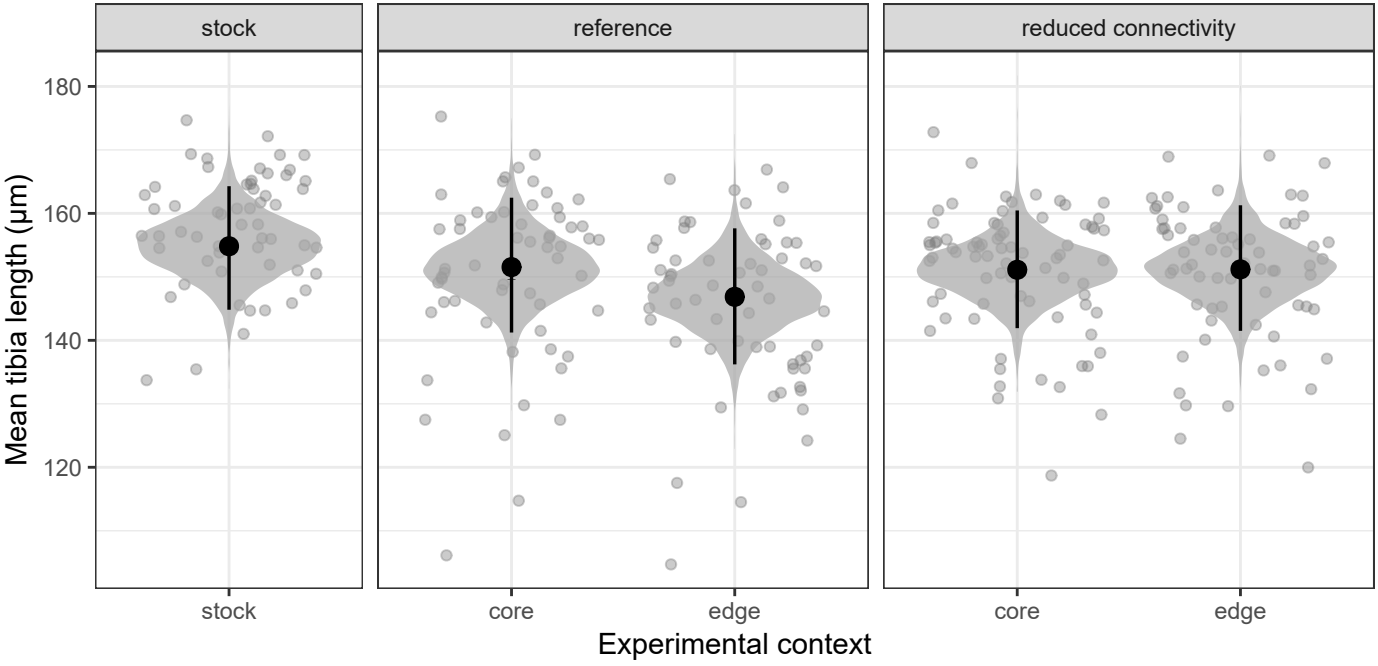
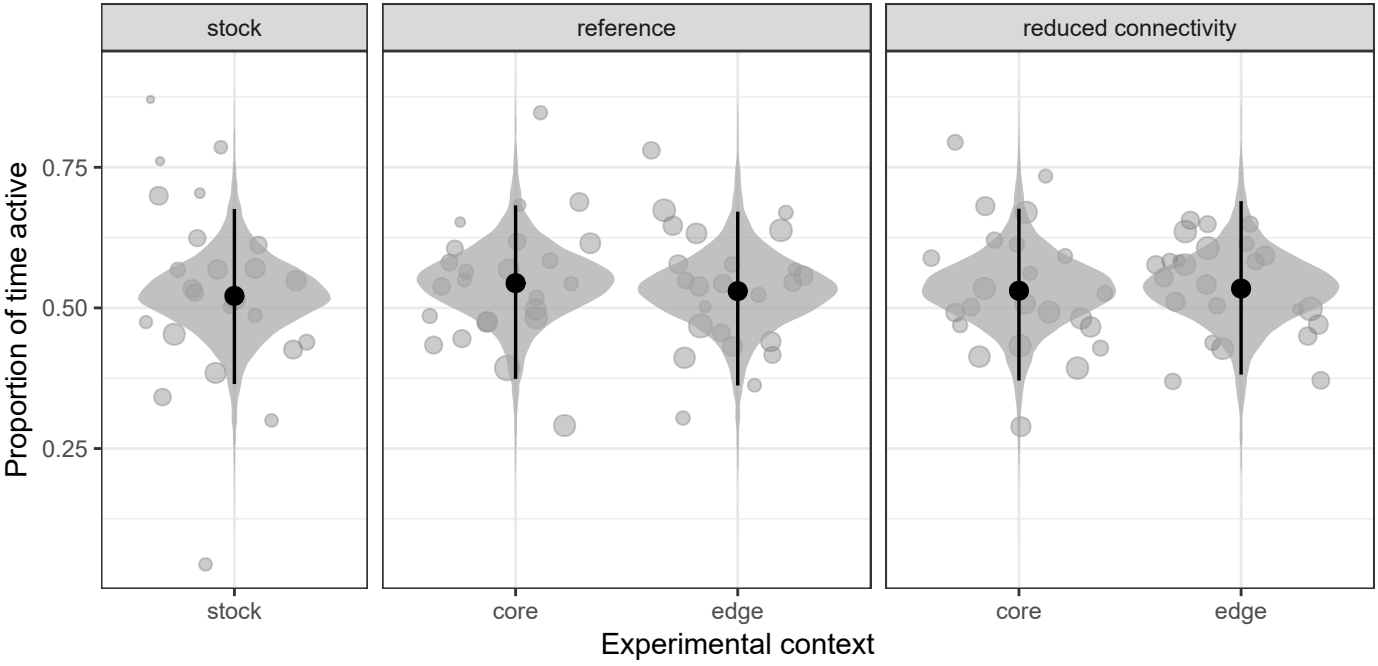
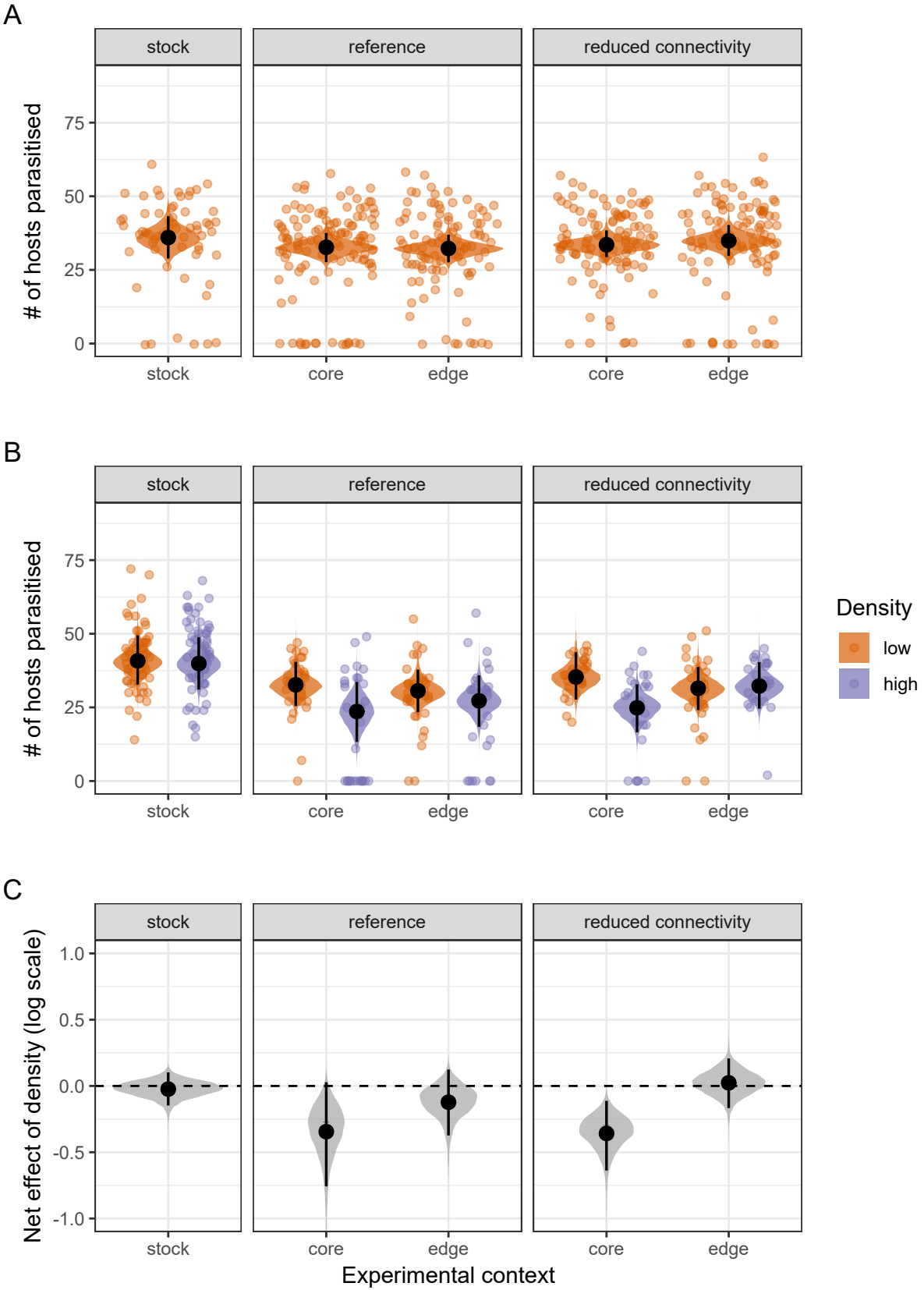
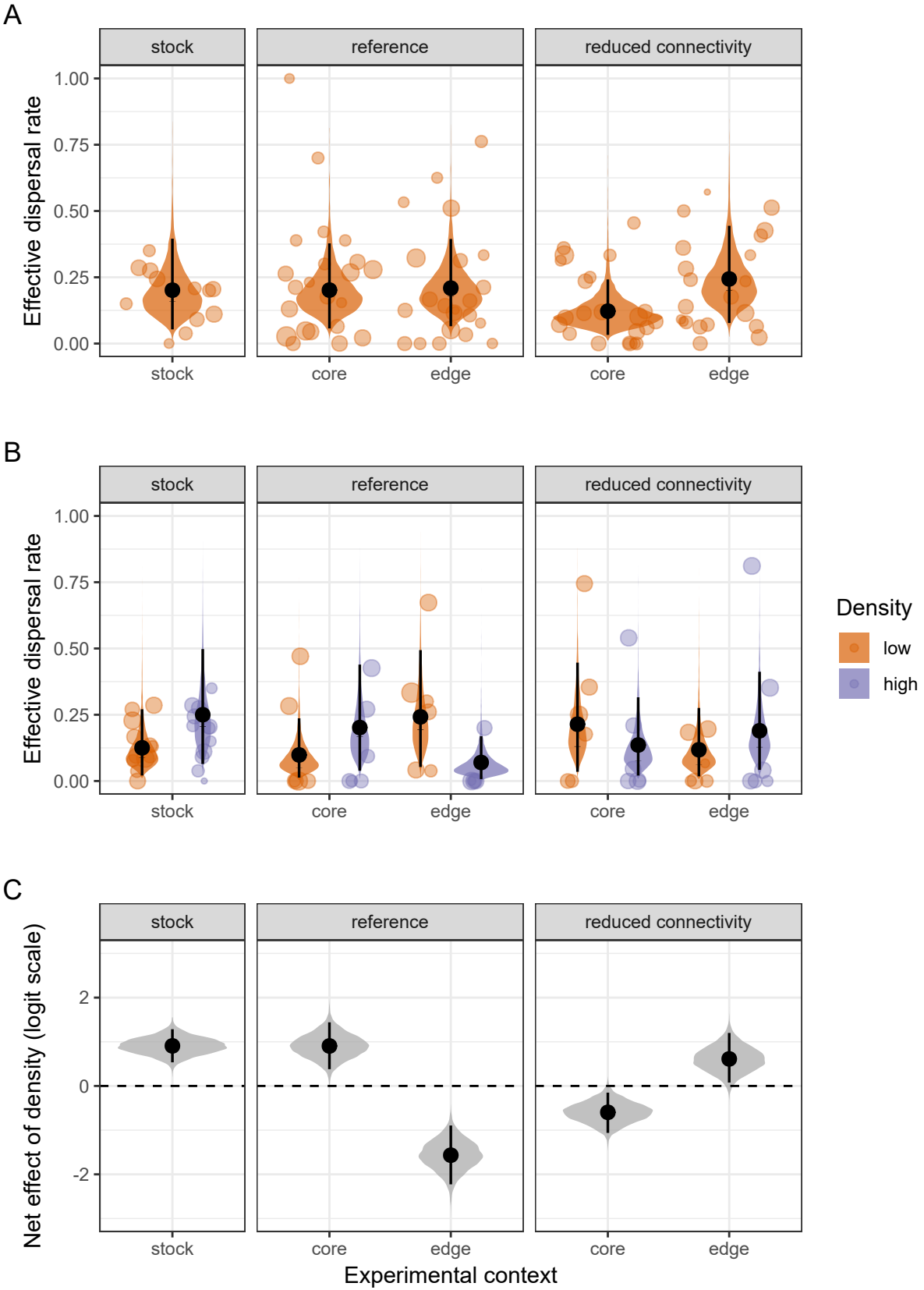

"reduced connectivity" replicates
"reference" replicate


stock
reference
reduced connectivity
Mean tibia length (µm)
180
160
140
120
stock
core
edge
core
edge
Experimental context


stock
reference
reduced connectivity
Proportion of time active
0.75
0.50
0.25
stock
core
edge
core
edge
Experimental context


A
stock
reference
reduced connectivity
# of hosts parasitised
75
50
25
0
stock
core
edge
core
edge
B
stock
reference
reduced connectivity
# of hosts parasitised
75
50
25
0
stock
core
edge
core
edge
Density
low
high
C
stock
reference
reduced connectivity
Net effect of density (log scale)
1.0
0.5
0.0
-0.5
-1.0
stock
core
edge
core
edge
Experimental context


A
stock
reference
reduced connectivity
Effective dispersal rate
1.00
0.75
0.50
0.25
0.00
stock
core
edge
core
edge
B
stock
reference
reduced connectivity
Effective dispersal rate
1.00
0.75
0.50
0.25
0.00
stock
core
edge
core
edge
Density
low
high
C
stock
reference
reduced connectivity
Net effect of density (logit scale)
2
0
-2
stock
core
edge
core
edge
Experimental context