Landscape configuration affects probability of apex predator presence and community structure in experimental metacommunities

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19 Abstract

20 Biodiversity is declining at an unprecedented rate, highlighting the urgent requirement for
21 well-designed protected areas. Design tactics previously proposed to promote biodiversity
22 include enhancing the number, connectivity, and heterogeneity of reserve patches. However,
23 how the importance of these features changes depending on what the conservation objective
24 is remains poorly understood. Here we use experimental landscapes containing ciliate
25 protozoa to investigate how the number and heterogeneity in size of habitat patches, rates
26 of dispersal between neighbouring patches, and mortality risk of dispersal across the non-
27 habitat 'matrix' interact to affect a number of diversity measures. We show that increasing
28 the number of patches significantly increases γ diversity and reduces the overall number of
29 extinctions, whilst landscapes with heterogeneous patch sizes have significantly higher γ
30 diversity than those with homogeneous patch sizes. Furthermore, the responses of predators
31 depended on their feeding specialism, with generalist predator presence being highest in a
32 single large patch, whilst specialist predator presence was highest in several-small patches
33 with matrix dispersal. Our evidence emphasises the importance of considering how top-down
34 effects can drive community responses to patch configuration.

35 **Keywords:** dispersal, diversity, heterogeneity, protected area, SLOSS.

36

37 Introduction

38 Efficient and effective protected areas are needed now more than ever due to the
39 widespread decline of global wildlife populations coupled with an increase in the pressures
40 driving these declines (Butchart et al., 2010). However, protected areas have been criticised
41 for insufficient coverage of biodiverse sites and not meeting the requirements of many taxa

(Butchart et al., 2015), prompting recent calls for 30% of land to be conserved by 2030 (CBD, 2020) and for nature reserves to be bigger and more connected (Lawton et al., 2010). However, despite being a popular topic for ecological research, the relative importance of the configuration (number of patches and size of patches) and connectivity (levels of dispersal and dispersal mortality) of landscapes on diversity remains contentious, with recent work demonstrating that the best configuration may depend on the trophic level of the species being conserved (Hammill & Clements, 2020).

The design of reserves is a key and long-running debate in ecology, formalised in the classic question of whether a single large or several small reserve patches (the SLOSS debate; Diamond, 1975) are better for biodiversity. Several small reserves are optimal when there is little overlap of species between different patches, meaning more species are supported overall (Bolgovics et al., 2019; McNeill & Fairweather, 1993; Peintinger et al., 2003). In addition, a several-small strategy may be best for biodiversity when several small patches support greater habitat diversity than a single large one (Honnay et al., 1999; MacDonald et al., 2018). Finally, when extinctions are asynchronous across several small patches, rescue effects can occur where dispersal between patches supports populations and enables recolonisation following local extinction (Brown and Kodric-Brown, 1977; Holyoak, 2000; Hattori and Shibuno, 2010). On the other hand, a single large reserve may support larger populations and have lower extinction rates (Burkey, 1997; Diamond, 1975; MacArthur & Wilson, 1967), can support more species when migration between patches is not possible (Liu et al., 2017), allows survival of species with large home ranges, such as large-bodied mammals (Mcnab, 1963) and often harbours more rare species than several small patches of the same total size (Berglund & Jonsson, 2003; Fukamachi et al., 1996; Godefroid & Koedam, 2003; Jain et al., 2017; Kendal et al., 2017). However, whilst much is

known about the relative importance of large and small patches, the effect of both large *and* small patches is rarely considered (Schippers et al., 2009), with previous experimental investigations of habitat configuration considering patches to be homogeneous in size (Burkey, 1997; Holyoak, 2000). Simulations have shown that landscapes containing varying patch sizes and shapes are more effective in increasing metapopulation survival probability than landscapes containing patches which are all one size (Schippers et al., 2009), but as yet we lack an understanding of the effects of variation in patch sizes in the metacommunity landscape scale. In landscapes with heterogeneous patch sizes, smaller patches can act as predator- or competitor-free refuges (Hattori & Shibuno, 2010), meanwhile larger patches support higher population densities (Mccarthy et al., 2011) and better support species with large home ranges (Mcnab, 1963). Therefore, we propose that different sized patches hold different communities and consequently heterogeneous landscapes may support higher diversity than homogeneous ones.

Metacommunity theory states that communities in separate habitat patches can be linked by movement between patches which enables regional persistence of a species (Brown & Kodric-Brown, 1977; Levins, 1969). This suggests that understanding dispersal is of fundamental importance to understanding how diversity can be maintained in multi-patch landscapes. There are many ways in which dispersal enhances diversity – through rescue effects by preventing extinction (Brown & Kodric-Brown, 1977), by facilitating evolutionary rescue where movement enables the spread of beneficial mutations which confer adaptation to environmental stress (Bell & Gonzalez, 2009), and through spatial insurance whereby dispersal permits movement of species that are adapted to new conditions as a result of environmental change (Loreau et al., 2003).

The role dispersal plays in preventing extinction highlights why conservation practitioners may wish to promote dispersal in nature reserves. This may be achieved by adding corridors of habitat which directly connect two habitat patches (Dunning et al., 1995; Gillies et al., 2011; Haddad & Baum, 1999; Li et al., 2021), stepping stones, smaller patches of land in between two larger patches (Baum et al., 2004; Fischer & Lindenmayer, 2002), or decreasing resistance to movement in the non-habitat matrix surrounding the patches (Gascon et al., 1999). Furthermore, the quality of these connectivity elements can influence their efficacy through changes in dispersal rates and dispersal success. For example, recent work has shown that corridor quality increases not only the probability of individuals dispersing but changes the age-structure of the population in newly colonised patches (Li et al., 2021). Conversely, the potential for poor quality connectivity elements to have a detrimental effect was revealed by a high-resistance matrix increasing the effective isolation of habitat patches, reducing dispersal between them (Ricketts, 2001).

The impacts of habitat configuration and connectivity are typically quantified using measures of species richness (Bueno & Peres, 2019; MacDonald et al., 2018) or diversity (Bolgovics et al., 2019). However, as the impacts of connectivity and configuration are ultimately governed by species interactions, considering the responses of key species such as predators can further our understanding. For example, unexpected negative effects of corridors can occur when increased predator movement leads to overexploitation of prey (Burkey, 1997). Experimental evidence has revealed that corridors can even indirectly benefit predators, where corridors permitting dispersal of prey but not predators lead to increased predator abundance (Limberger & Wickham, 2011). In addition, competitive antagonism can drive patterns of patch occupancy. For example, because dominant competitors had high abundances in larger reef patches, inferior competitors occupied

smaller patches which they utilised as temporal refuges (Hattori & Shibuno, 2010). Furthermore, feeding specialism may also affect species' responses to habitat configuration and connectivity. Specialists by definition exploit a more limited range of resources than their more generalist counterparts, and consequently suffer more from fragmentation (Tscharntke et al., 2002) and therefore benefit from corridors more (Gillies et al., 2011; Haddad & Baum, 1999).

A useful system for investigating the effects of dispersal on diversity within multi-patch landscapes is protist microcosm experiments. Protists' short generation times enable observation of population change over a short period of time, something which would take years in the field (Altermatt et al., 2015). Direct manipulation of dispersal between patches enables consideration of the impact of dispersal rate (Cadotte, 2006; Laan & Fox, 2019) whilst manipulation of corridors enables consideration of the effects of corridor length (Laurent et al., 2020), matrix harshness (Jacob et al., 2020) and whether patches are connected for predators or prey (Limberger & Wickham, 2011). Landscape configuration can be investigated by custom designing multiple landscapes to represent different reserve design scenarios (Hammill & Clements, 2020) and populations can be closely monitored throughout the study duration, enabling many metrics to be recorded and compared.

Here, we conducted protist microcosm experiments to investigate the effects of patch-size heterogeneity and dispersal on the SLOSS debate. We utilised custom-designed, 3D-printed landscapes to assess the effects of two features of habitat configuration: the number of patches and patch-size heterogeneity. In addition, we manually manipulated dispersal between patches within a landscape to investigate the effects of local and matrix dispersal, acting as proxies for dispersal through corridors and dispersal across the non-habitat matrix, respectively. In order to provide a comprehensive overview of the effects of

the dispersal events and habitat configuration, we measured population abundances of each species in the system to record a variety of diversity measures: γ diversity, overall number of extinctions, and probability of specialist or generalist predators being present.

Materials and methods

Experimental design

To investigate the effects of patch number, patch-size heterogeneity, and dispersal, we manipulated dispersal of protists within microcosms designed to mimic five different habitat patch configurations (Fig. 1). The experimental landscapes were custom-designed using FreeCAD 3D-design software (Riegel et al., 2020) then 3D-printed using a LulzBot TAZ 6 printer in black PLA filament. To ensure the landscapes were watertight they were then coated in clear epoxy resin. Experimental landscapes consisted of either a single, four, or six circular wells arranged in a ring (Fig. 1). Additionally, wells in landscapes with more than one patch (i.e., four or six patches) were either all the same size (homogeneous) or two different sizes (heterogeneous). This led to five reserve configurations (Fig. 1), each with a total volume of 48ml and made up of wells with a constant depth of 13mm to standardise light penetration. Controlling for total volume enabled us to disentangle the effects of heterogeneity and patch number from the effects of landscape area by comparing landscapes with different patch-size distributions. Additionally, we chose patch sizes to ensure that the average patch size remained constant between homogeneous and heterogeneous landscapes with the same number of patches. Dispersal between wells was conducted manually rather than via printed corridors as this allowed us to investigate the effects of ‘quality’ of dispersal events by manipulating both dispersal frequency and dispersal-based mortality. There were nine possible dispersal regimes (see ‘dispersal’ below)

which were applied to every landscape type (Fig. 1), resulting in 45 possible treatment combinations (nine dispersal treatments across five landscape types), which were replicated four times for a total of 180 landscapes. Due to the time required for sampling, we blocked the replicates by time so that each was sampled on a different day of the week from Monday to Thursday. The experimental landscapes were kept in incubators at a constant temperature of 20 °C for the duration of the experiment.

Each landscape was filled with experimental media containing bacteria for the bacterivorous protozoa to feed on, and a carbon source for the bacteria to consume. Experimental media was created by dissolving crushed protozoa pellets (Blades Biological LTD, UK) in spring water (Tesco Ashbeck English natural mineral water) at a concentration of 0.5g/L and then autoclaving this mixture. On day -5 each bottle of media was inoculated with three bacteria species (*Bacillus subtilis*, *Micrococcus luteus*, and *Pseudomonas fluorescens*). This provided sufficient time for the bacteria to increase to levels which would sustain the protist communities which were added on day 0.

The protist community consisted of eight protist species, including three apex predators (*Didinium nasutum*, *Dileptus anser*, and *Stentor coeruleus*) and five potential prey species (Fig. 2) (all obtained from Sciento, Manchester, UK). *Didinium* and *Dileptus* were considered to be specialists because they fed on two prey species each (Worsfold et al., 2009), whilst *Stentor* was considered as a generalist because it fed on four of the five available prey species (Jiang and Morin, 2005; Cadotte, Fortner and Fukami, 2006; Fig. 2). We created the experimental community by mixing the eight species in a sterilised jar at densities determined by preliminary experiments (apex predators 1 ind./ml, all prey apart from *Colpidium striatum* 10 ind./ml, *Colpidium striatum* 100 ind./ml). This mixture plus the

experimental media were then distributed to fill every patch in each landscape so that each landscape contained a total of 48ml protist-containing media.

Sampling and dispersal

We conducted sampling once a week for each treatment block. Sampling involved searching a well with a microscope for a maximum of five minutes and recording presence or absence of each species. A species was marked as present when at least one individual of the species was spotted. On day 21, the final sampling day, we calculated the abundance of each species by counting individuals in a 0.5ml subsample taken from each well and multiplying this value according to the well's total volume. We pipetted up and down within a well to ensure a roughly homogenous distribution of individuals, thus minimising potential bias caused by aggregation of individuals, then pipetted the 0.5ml subsample onto a sterile petri dish for counting (as in Clements et al., 2013). If a species which was not known to be extinct appeared absent from the subsample, we then checked the whole well and counted all individuals of that species within the well. Although 0.5ml is a small volume relative to the total volume of the larger wells, this was the maximum amount we could sample in the available time, in particular due to high densities of certain species (>100 individuals in a single subsample).

Following weekly sampling, we conducted nutrient replenishment by mixing each well, removing 10% of each well's total volume and replacing this with fresh sterile nutrient medium to fill the well to its original volume. This prevented build-up of waste materials and compensated for any evaporation which may have occurred.

We conducted two types of dispersal which each had two treatment levels plus a no-dispersal control. "Local dispersal" occurred between adjacent habitat patches and acted as a proxy for dispersal through corridors connecting neighbouring patches. Local dispersal was

208 either low or high frequency, representing the fact that corridor quality can influence
209 dispersal frequency (Haddad, 1999). “Matrix dispersal” occurred from each patch to any
210 patch in the landscape, acting as a proxy for dispersal across the non-habitat matrix to any
211 patch in the landscape. Matrix dispersal was either low or high mortality risk, representing
212 the role an inhospitable matrix can play in causing dispersal mortality (Nowicki et al., 2014).
213 We chose to manipulate mortality risk of matrix, but not local, dispersal because, although
214 dispersal through corridors is not risk-free, corridors are often created to provide a
215 relatively safer route for passing wildlife, for example when over- and under-passes are
216 added to roads (Simpson et al., 2016). The two local dispersal manipulations plus control,
217 and two matrix dispersal manipulations plus control were factorially crossed, leading to nine
218 possible dispersal regimes. The dispersal manipulations and their treatment levels were
219 designed to demonstrate how general variations in dispersal regime affect diversity
220 outcomes, rather than representing dispersal frequencies or dispersal mortality risk for any
221 one taxon.

222 We conducted dispersal manipulations following nutrient replenishment. Dispersal
223 occurred weekly for all regimes apart from high frequency local dispersal treatments (see
224 below). Matrix dispersal was conducted by gently mixing a patch through pipetting then
225 removing 0.6ml from each patch onto a sterile petri dish. This mixture was then gently
226 mixed and either 0.48ml (equivalent to 20% mortality, the “low mortality” treatment) or
227 0.12ml (equivalent to 80% mortality, the “high mortality” treatment) was pipetted back into
228 every patch (Fig. 1). The remaining solution was discarded, representing the mortality risk
229 associated with dispersing across the matrix. Every patch was topped up with 0.12ml (low
230 mortality) or 0.48ml (high mortality) of sterile nutrient medium to account for the volume

discarded. This dispersal mode meant that a protist may move into any patch including returning to their initial patch (Fig. 1).

We conducted local dispersal by gently mixing and then pipetting 1.2ml from every patch onto a sterile petri dish labelled with the initial patch location. 0.6ml from the 1.2ml droplet was pipetted into both patches adjacent to the original, transferring protists to their neighbouring patches (Fig. 1). This occurred weekly for the low frequency local dispersal, and twice weekly for high frequency local dispersal, on the sampling day and then again three days later. When a dispersal regime consisted of both local and matrix dispersal, all the media to be dispersed was removed from the landscape prior to pipetting any back, ensuring that no protists were dispersed more than once.

Statistical analyses

The following parameters were used as descriptive variables in our analyses: number of patches (one, four, or six), patch-size heterogeneity (homogeneous or heterogeneous), matrix dispersal (none, low mortality, or high mortality), and local dispersal (none, low frequency, or high frequency). Using data from presence / absence sampling, we calculated the overall number of extinctions in a landscape and probability of specialist (*Didinium nasutum* and *Dileptus anser*) and generalist (*Stentor coeruleus*) apex predator presence. Using the final population count data, we calculated γ diversity. This was calculated using the 'entropart' package in R (Marcon & Hérault, 2015).

To investigate the relationship between the predictor variables and the response variables, we conducted analyses using Generalised Linear Models (GLMs). The γ diversity GLM had a Gaussian error distribution, specialist and generalist predator presence probabilities had a binomial error distribution, and extinctions had a Quasi-Poisson error distribution due to underdispersion. The saturated model included all descriptive variables

and their two-way interactions. To select the best model for each response variable we used Akaike's Information Criterion corrected for small sample size (AICc, Burnham and Anderson, 2002) which ranks models with different parameter combinations by ΔAICc , selecting the 'best' model with the lowest AICc. Model simplification was conducted using the 'dredge' function from the MuMIn package in R (Bartón, 2020) which ranks models according to their AICc values. All models within $\Delta\text{AICc} \leq 2$ of the top model were considered equivalent in their descriptive ability. These top models were subsequently averaged using the 'model.avg' function in MuMIn, producing coefficients which were extracted and used for plotting and parameter reporting. In addition to reporting p-values and effect sizes, we used hierarchical partitioning (Chevan & Sutherland, 1991) to estimate the proportion of total variation in each response variable explained by each descriptive variable, thus demonstrating their importance. This analysis was conducted using the 'hier.part' package in R (Walsh & MacNally, 2020). Furthermore, to investigate the effect of probability of generalist predator presence on probability of specialist predator presence at the patch level we performed a logistic regression (GLM with binomial error distribution). All analyses were conducted in R (version 3.6.3, R Development Core Team, 2020)

Results

Landscape configuration

Increasing the number of patches in a landscape positively influenced all four diversity measures considered. Increasing the number of patches increased the probability a landscape contained specialist predators (65% variance explained) and increased γ diversity (43.63% variance explained) (Table 1; Fig. 4b; Fig. 5). Patch number was therefore the most important predictor of the probability of specialist predator presence, accounting for the

highest proportion of variance. In addition, increasing the number of patches increased the number of extinctions in a landscape (58.08% variance explained), reduced the probability a landscape contained generalist predators (94.13% variance explained), and was the most important predictor of these variables (Table 1; Fig. 3; Fig. 4a).

Heterogeneity did not significantly affect the overall number of extinctions, or the probability of specialist or generalist predator presence. Heterogeneous landscapes had significantly higher γ diversity than homogeneous landscapes (Table 1; Fig. 5), and hierarchical partitioning revealed that heterogeneity was the most important explanatory variable for γ diversity (47.87% variance explained).

Dispersal

The probability that a landscape contained specialist predators was significantly increased by matrix dispersal at both low and high mortality levels (Table 1; Fig. 4b), accounting for 25.29% of the variation in the data. However, whilst matrix dispersal had significant effects on the probability of specialist predator being present, it had no effect on the probability of generalist predator presence (Table 1; Fig. 4a).

Unlike matrix dispersal, local dispersal showed no significant main effects on the presence of predators, the number of extinctions, or γ diversity, although local dispersal was included in the top model and explained 6.57% of the variation in γ diversity (Table 1; Fig. 5).

Predator coexistence

Analysing data from the patch level revealed that the generalist predator had a significant negative effect on the presence of the specialist predator in our system ($P = <0.05$, Fig. 6).

303 Discussion

304 Understanding the potential trade-offs associated with designing nature reserves is vital if
305 we are to effectively conserve those species most at risk. Here we investigated
306 experimentally how two key elements of reserve configuration – number of patches and
307 patch-size heterogeneity – interact with two types of dispersal – local and across the matrix
308 – to alter species diversity. Our results reveal that increasing the number of habitat patches
309 can have significant positive effects not just in terms of increased diversity, but also reduced
310 extinctions and increased probability of specialist predator presence. Interestingly, this
311 pattern was reversed for the generalist predator, whose presence was highest in a single
312 large habitat patch. Differences between specialist and generalist predators were further
313 seen in their responses to dispersal, with generalists being unaffected by dispersal whilst
314 specialist predator presence was significantly increased by matrix dispersal, even at high
315 mortality levels. Our results reveal no significant effects of local dispersal on any of the
316 diversity measures considered. Finally, patch-size heterogeneity was the most important
317 predictor of, and significantly increased, γ diversity.

318 As with previous work (Bolgovics et al., 2019; MacDonald et al., 2018), we find
319 evidence that several small habitat patches maintain higher diversity than a single large
320 habitat patch of the same total area. This reinforces the notion that increasing the number
321 of habitat patches may better promote biodiversity than increasing the area of a single
322 habitat patch (Hammill & Clements, 2020). Furthermore, we show that several small
323 patches have fewer extinctions than a single large patch, a finding which is supported by
324 recent evidence (Hammill & Clements, 2020), but runs contrary to the traditional belief that
325 larger patches have lower extinction rates (MacArthur & Wilson, 1967).

However, whilst increasing the number of patches increased the probability of specialist predator presence, it decreased the probability of generalist predator presence (Fig. 4a, b). This counters the perception that specialists are more sensitive to fragmentation than generalists (dos Anjos et al., 2019) and consequently occur more frequently in larger reserves (Bartonova et al., 2016). This reduced presence of the generalist predator *Stentor coeruleus* in the several-small landscapes may be explained by its resource requirements not being met. Apex predators often have large energy requirements and large home ranges (Mcnab, 1963), and *Stentor* likely reflects this pattern, requiring more resources due to its body size (~10 times larger than *Didinium nasutum* (Hewett, 1988; Jiang & Morin, 2005)).

Indeed, this loss of *Stentor* may be an explanatory factor in the patterns observed in the presence of specialist predators: *Stentor* is a voracious generalist predator, known to over-exploit prey and reduce local richness (Cadotte et al., 2006), and therefore may be competitively superior to the specialist predators, reducing their survival when present. We provide evidence that this occurred at the patch level, where there was a negative relationship between probability of generalist predator presence and probability of specialist predator presence (Fig. 6). However, *Stentor's* resource requirements are not met in the smaller patches, reducing its presence, lessening the competitive antagonism, and increasing the probability of the specialist predators being present in the several-small landscapes. Furthermore, *Stentor* is likely responsible for much of the patterns seen in the diversity responses to landscape design too, particularly that a single large patch had lower γ diversity and more extinctions than the several small patches, as *Stentor* survives best and thus reduces local richness in the single large landscapes (Cadotte et al., 2006). Increasing the number of patches therefore provides positive outcomes for a number of different diversity measures, however the differences between the responses of generalist and

specialist predators highlights the importance of remembering that species interactions ultimately govern community structure at the local scale.

By directly manipulating patch size we show heterogeneity to be the most important predictor of γ diversity, significantly increasing diversity at the landscape scale. This complements previous simulation modelling demonstrating that metapopulations have a higher survival probability in landscapes containing a mixture of small, large, and linear patches than those containing homogeneous patches (Schippers et al., 2009). Schippers *et al.* (2009) proposed that this was beneficial because large patches were able to support larger populations, reducing extinction risk, whilst small patches promoted overall landscape connectivity. In the experiments presented here we propose this pattern reflects differences in the specialist and generalist predators: larger patches better meet the range requirements of the larger generalist predator (Fig. 4a), whilst the smaller patches better support specialist predators (Fig. 4b) and reduce the predation pressures on the prey, providing a form of refuge. This is supported by research highlighting the role that small patches play in promoting coexistence when antagonists dominate in larger patches (Hattori & Shibuno, 2010). This effect of heterogeneity may be explained by a patch-size threshold effect where a heterogeneous landscape contains patches above and below the size threshold for generalist predator persistence. Patches below the threshold exclude the generalist predator, consequently promoting prey and releasing specialist predators from the negative effects imposed by the generalist predator (Fig. 6). Meanwhile, patches above the threshold support the generalist predator, ultimately increasing landscape-level diversity. Patch-size heterogeneity is potentially an important and overlooked driver of diversity and would benefit from future research on a larger scale.

373 To obtain the benefits of both small and large patches in a heterogeneous system,
374 species within a metacommunity must be able to move between the patches. In our
375 experiments, local dispersal between adjacent patches surprisingly had no significant effects
376 on any of the diversity outcomes considered. There are two possible explanations for this:
377 dispersal into neighbouring patches had little effect at the local scale, or that the possible
378 advantages of increased dispersal were outweighed by the disadvantages. Previous research
379 has shown dispersal through corridors to have no effect when populations are not declining
380 and therefore will not benefit from increased dispersal (Rantalainen et al., 2004). This,
381 however, does not explain the lack of local dispersal effects in the present study because
382 extinctions did occur in patches, implying that immigration may permit rescue effects.
383 Therefore, it is possible that the positive and negative effects of local dispersal outweighed
384 each other. Dispersal can have a positive impact through rescue effects (Brown & Kodric-
385 Brown, 1977; Holyoak, 2000) and by enhancing local richness (Cadotte et al., 2006; Schuler
386 et al., 2017). However negative effects may arise, for example when dispersal through
387 corridors enables predators to spread across a system and exploit prey (Burkey, 1997;
388 Limberger & Wickham, 2011). Additionally, excessive dispersal through corridors can
389 homogenise communities within multi-patch landscapes, causing them to effectively
390 operate as one single large patch (Mouquet & Loreau, 2003). The combination of
391 advantages and disadvantages has been revealed in previous research where dispersal had
392 positive effects on local richness, but these were diminished by the negative effects of
393 predation on prey richness (Cadotte et al., 2006). In the present study it is therefore
394 possible that local dispersal had both positive and negative effects, enabling the spread of
395 prey to support populations via rescue effects, but also the spread of predators to
396 competitively exclude on another, or reduce abundance of prey.

Matrix dispersal had significant effects on one of the four diversity outcomes considered – probability of specialist predator presence (Table 1; Fig. 4b). This positive effect of matrix dispersal on specialist, but not generalist, predator presence may be explained by the predators' respective feeding specialisms. Generalist can exploit multiple different food sources so can transfer to another prey source without moving to a new area if one species becomes diminished. Specialists, on the other hand, have limited prey food options so if these become exploited, they have two options: disperse to a new patch in search of a new food source, or risk starvation. By dispersing across the matrix to enter any patch in the landscape, specialists have a chance of reaching a patch containing their prey food, thus increasing their survival probability (Fig. 4b). This highlights an important finding, that matrix dispersal which gives individuals the opportunity to disperse to one of several patches may be more beneficial than local dispersal only permitting dispersal between adjacent patches.

In conclusion, whilst the number of habitat patches (Bolgovics et al., 2019), heterogeneity of patch size (Schippers et al., 2009), corridor (Schuler et al., 2017), and matrix dispersal (Åström & Pärt, 2013) are all known to influence biodiversity, their interactive effects are rarely considered, especially in relation to more than one conservation goal (but see Pedruski and Arnott, 2011; Altermatt and Holyoak, 2012). Here, by simultaneously examining the effects of the number of patches, patch-size heterogeneity, local, and matrix dispersal, we are able to – for the first time – disentangle the relative importance of these factors on various measures of biodiversity. We show that matrix dispersal, multiple patches, and heterogeneity of patch size all positively affected one or more measures of diversity in our system, highlighting their potential use in promoting diversity on a larger scale. Our results also demonstrate the opposing responses

of specialist and generalist predators to patch number and matrix dispersal, implying that the role of predator feeding specialism may be an important consideration for designing reserves which cater for a broad range of species. Crucially, we highlight that the most important driver of diversity at the landscape scale in our experimental system was patch-size heterogeneity, suggesting that experiments considering habitat patches to be homogeneous in size may miss an important driver of biodiversity.

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Code availability. The code is available in a GitHub repository (<https://github.com/chrit88/Experimental-data>)

Author contributions. EW, CFC, and EH conceived the ideas and designed the experiments. EW performed the experiments and wrote the first draft of the paper. All authors contributed to statistical analyses, contributed critically to the drafts, and gave final approval for the paper.

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649 Figures & Tables

650 **Fig. 1** Schematic representation of the five reserve configurations plus dispersal
 651 manipulations. Habitat patches (grey circles), their volume in mL (number within grey
 652 circles), plus potential local dispersal (dotted lines) and matrix dispersal (solid lines) are all
 653 shown
 654 **Fig. 2** Food web of the metacommunity used in the experiment, with feeding relationships
 655 including predation, intraguild predation, and cannibalism. Arrows represent feeding links,

obtained from: (Burkey, 1997; Cadotte et al., 2006; Holyoak, 2000; Kuhlmann & Heckmann, 1994; Warren et al., 2003; Worsfold et al., 2009)

Fig. 3 Effect of heterogeneity and number of patches in an ecosystem on overall number of extinctions in a landscape. Top models ($\Delta AICc < 2$) did not include matrix or local dispersal as explanatory variables so they are not presented here. Lines are model-averaged Quasi-Poisson GLM model outputs, shaded polygons are 95% confidence intervals, and points are observed data points

Fig. 4 Effects of heterogeneity and number of patches in an ecosystem for each matrix dispersal regime on the probability of a landscape containing (a) generalist predators and (b) specialist predators. Lines are model-averaged binomial GLM outputs, shaded bands are 95% confidence intervals, and points are observed data points

Fig. 5 The effects of heterogeneity and number of patches for each dispersal regime on γ diversity. Columns are local dispersal quality level and rows are matrix dispersal quality level. Lines are model-averaged Gaussian GLM coefficients from the top models ($\Delta AICc > 2$), shaded polygons are 95% confidence intervals, and points are the observed data points

Fig. 6 Probability of specialist predator presence as a function of probability of generalist predator presence. Fitted line is the logistic regression, shaded polygon shows 95% confidence intervals, and points are observed data points, jittered slightly for clarity.

Relationship was significant ($P = 0.0000023$)

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758 **Fig. 6**

Table 1. Model-averaged coefficients $\pm$ standard errors (SE) from models explaining specialist and generalist predator presence probabilities, overall number of extinctions, and γ diversity.
 (*) $p < 0.05$, (**) $p < 0.01$, (***) $p < 0.001$.

	Extinctions	Predator presence		γ diversity
		Generalist	Specialists	
Intercept	1.447 $\pm$ 0.052 ***	5.359 $\pm$ 1.229 ***	5.945 $\pm$ 1.269 ***	2.088 $\pm$ 0.254 ***
Patch number	-0.055 $\pm$ 0.013 ***	-1.024 $\pm$ 0.242 ***	0.674 $\pm$ 0.229 **	0.177 $\pm$ 0.059 **
Heterogeneity	- 0.017 $\pm$ 0.252	-1.195 $\pm$ 1.903	-1.130 $\pm$ 2.188	0.547 $\pm$ 0.109 ***
Matrix dispersal (low mortality)		- 0.018 $\pm$ 0.191	1.709 $\pm$ 0.592 *	0.153 $\pm$ 0.262
Matrix dispersal (high mortality)		-0.117 $\pm$ 0.325	1.244 $\pm$ 0.607 *	0.286 $\pm$ 0.364
Local dispersal (low frequency)				-0.218 $\pm$ 0.227
Local dispersal (high frequency)				0.013 $\pm$ 0.204
Patch number: Heterogeneity	-0.039 $\pm$ 0.052		0.276 $\pm$ 0.427	
Patch number: Matrix dispersal (low mortality)				-0.034 $\pm$ 0.058
Patch number: Matrix dispersal (high mortality)				-0.083 $\pm$ 0.098
Patch number: Local dispersal (low frequency)				0.008 $\pm$ 0.034
Patch number: Local dispersal (high frequency)				-0.017 $\pm$ 0.044