Spatial fingerprint of consumer body size and habitat preference on resource distribution

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Abstract

Consumers shape spatial patterns on landscapes by amplifying or dampening environmental heterogeneity through feeding, excretion, and movement of resources. The degree to which the environment is modified by consumers depends on species' traits, including body mass, movement behavior, sociality, and habitat specialization. Global change is altering the size and traits of consumer populations, but our understanding of how this may impact resource heterogeneity is limited. Here, we developed an individual-based model of habitat specialists' and generalists' movement and activity in a patchy landscape and investigated the impact of changes in population and mean body sizes on landscape-scale resource heterogeneity. We found

that consumers specializing on low-resource habitats (a common risk avoidance strategy) increased spatial resource heterogeneity regardless of their population and body size. By contrast, generalists eroded differences among habitats, and we further found that resource heterogeneity decreased with the average body size of generalist consumers, even while controlling for total consumer biomass. These nuanced spatial outcomes of consumer-resource interactions emerge from the unique metabolic demands of specialists vs. generalists, which scale nonlinearly with body size. Since global change disproportionately impacts larger species and specialists, indirect consequences on ecosystems may arise via biotic processes, affecting spatial heterogeneity of future landscapes.

Introduction

Resource landscapes are often thought of as an environmental template that organisms respond to, but this neglects the role that organisms play in shaping spatial distributions of resources. Animal consumers serve as important resource vectors in landscapes (Earl and Zollner 2017, McInturf et al. 2019, Little et al. 2022, Pringle et al. 2023). The deposition of resources via feces, urine, seeds, placenta, and carcasses contribute to resource dispersal in the landscape (McIntyre et al. 2008, Bump et al. 2009, Sitters et al. 2017, Schmitz et al. 2018, le Roux et al. 2020, Ferraro et al. 2023). Organismal activity will therefore impact spatial resource heterogeneity, which in turn facilitates the coexistence of species (Amarasekare 2003) and thus ecosystem functioning (Loreau et al. 2003b). The distribution of resources in space is therefore an important landscape characteristic that shapes patterns of biodiversity and ecosystem functioning (Tylianakis et al. 2008, Seiferling et al. 2014, Gonzalez et al. 2020, Rizzuto et al. 2024). With global change altering abiotic conditions and consumer populations, it is imperative to gain a better understanding of the processes shaping spatial resource heterogeneity.

The traits of species making up consumer communities may provide a key to understanding organismal effects on resource landscapes. A handful of studies have established that species' traits, such as behavior and body size, determine the amount, stoichiometry, and scale of consumer-driven resource cycling (Sitters et al. 2017, Veldhuis et al. 2018, Subalusky and Post 2019). For example, social aggregation creates spatial clustering of consumer-driven resource subsidies (Bampoh et al. 2021). Other traits such as diet preferences and risk avoidance strategies may concentrate consumer activity into specific habitat types, leading to divergent rates of resource cycling across the landscape (Peller et al. 2022). Meanwhile, consumer body size influences resource dispersal through at least two pathways. First, energetic requirements

scale nonlinearly with body size (Brown et al. 2004), and consequently so should resource consumption and excretion. Second, body size is associated with differences in movement ability and perceptual range (Little et al. 2022, Albaladejo-Robles et al. 2023, Straus et al. 2024), and thus the spatial dispersion of foraging and resource deposition.

Predicted shifts in consumer populations and communities due to global change may rewire resource distributions, yet understanding how they do so is made more challenging because species' responses to global change vary, in part due to their traits. Larger animals are more impacted by climate change and land use change (Albaladejo-Robles et al. 2023), and specialist species more than generalists (Clavel et al. 2011). Moreover, as population sizes shift with global change (Spooner et al. 2018), we can anticipate shifts in patterns of resource consumption and deposition across landscapes; however, our understanding of the net effect of these shifts on spatial resource distribution is limited. Because body size and population size often trade off (Gjoni and Glazier 2020), changes in body size might offset the effects of changes in population size and lead to unique spatial patterns of resource distributions that could not be predicted from body size alone. In one of the few examples of research addressing this topic, Ferraro *et al.* (2022) used an individual-based model of foraging caribou and showed that higher densities of caribou increased nutrient spatial heterogeneity through carcass depositions (resource hotspots) and over-grazed dead zones (resource coldspots). At even larger spatial scales, higher densities of bison increase the amount and change the timing of nutrients available in different regions of grassland landscapes (Geremia et al. 2019).

In this study, we present an empirically-calibrated, individual-based model of consumer movement and activity where we factorially manipulated i) population sizes, ii) mean body size, iii) risk-based habitat preferences, and iv) sociality, and investigated effects on spatial resource

heterogeneity in a patchy landscape. Our model was parameterized to capture key biological features of two consumer species—a generalist, and a specialist that avoids high-nutrient resource patches (a common predator avoidance strategy)—with scaled movement distances, metabolic requirements, and perceptual ranges associated with body size.

We hypothesized that larger populations (compared to smaller populations) of generalists would preferentially graze high-quality areas until they resemble lower-quality areas, reducing spatial heterogeneity. By contrast, we predicted that by removing resources from lower-quality areas, specialists would accentuate the differences between nutrient-rich and nutrient-poor parts of the landscape, and thus larger populations (compared to smaller populations) of specialists would increase spatial heterogeneity. We also expected that, while keeping the total consumer biomass constant, body size would have contrasting effects on resource redistribution by generalists and specialists: decreasing the mean body size of generalists would reduce resource heterogeneity, while reducing the mean body size of specialists would amplify resource heterogeneity. This is because the metabolic load of smaller individuals is higher, and thus more resources should be consumed by a population of many small individuals than an equivalent biomass of fewer large consumers. Therefore, we predicted that for a given population biomass, the largest differences in the impacts of consumers on resource heterogeneity would occur between small-bodied specialists (which would amplify heterogeneity) and small-bodied generalists (which would dampen heterogeneity). Finally, we predicted that spatial aggregation of consumers would increase clustering of consumers' impacts on the landscape, thus increasing spatial resource heterogeneity.

Methods

Modeling approach

We used NetLogo v6.0.4 (Wilensky 1999) to model generalists and specialists moving in a landscape, where consumers withdraw resources by foraging and deposit resources through feces and carcasses. Key parameters are indicated in Table 1, and a detailed explanation is found in Appendix I. This landscape is divided into a 141 x 141 grid of equal-sized pixels, each pixel representing 10 m^2. The landscape has two discrete habitat types (**Fig. 1**), approximating a Kenyan savanna (see Ford et al. [2014]): open, high-nutrient glades as clusters of pixels (each cluster forming a "Patch"), in a "Matrix" of bushy, lower-quality grassland (Augustine 2004). Each pixel is classified as Patch or Matrix and is assigned a forage amount drawn from a normal distribution centered on 50 g/m^2 for Patches and 33 g/m^2 for Matrix, with forage containing 6% nitrogen (N) in Patches and 4% in Matrix. Landscapes contained an average of four Patches, making up ~5% of the landscape area (**Fig. 1**).

Individuals in the model are either generalists or specialists. Specialist consumers, resembling Guenther's dik-diks, stay in the Matrix to avoid predators (Kingswood and Kumamoto 1996, Otieno et al. 2019), while generalists, akin to impalas, can use both habitat types, but favor Patches (Ford et al. 2014, Otieno et al. 2019). Animals forage based on their metabolic needs and move within their perceptual range, both of which vary as a function of their body size (Nagy 2001, Mech and Zollner 2002). Foraging behavior adheres to the marginal value theorem, with animals selecting pixels with better-than-average forage available (Charnov 1976). Patch pixels are not considered by specialists, while generalists can choose any pixel (Patch or Matrix) and preferentially graze Patches at the start of each simulation because of the higher forage and N concentration. Model timesteps represent 3 hours of movement/activity (see Appendix I for details

on movement, foraging, excretion, and death), and simulations were run for three months, or the length of one growing season.

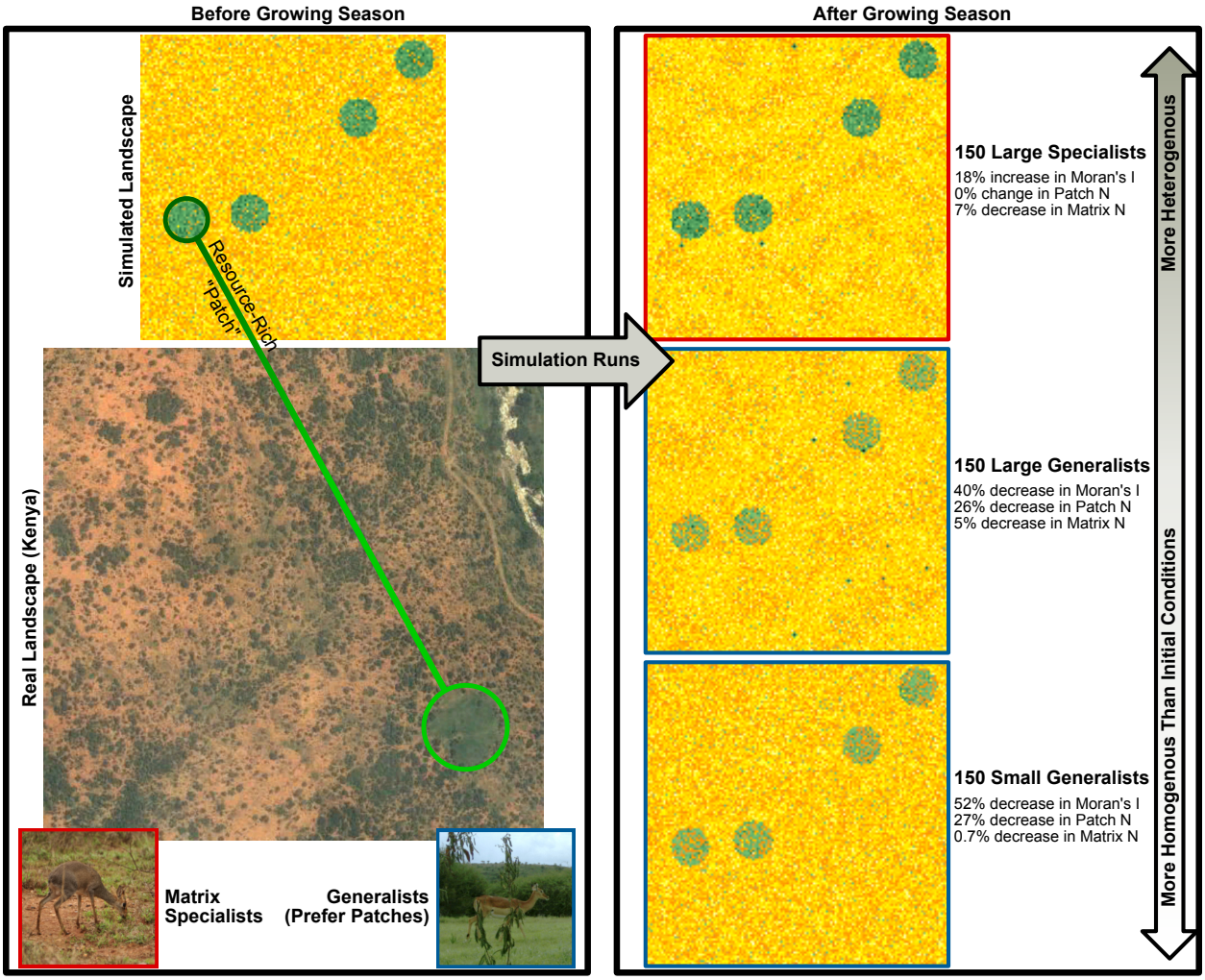

Figure 1. N distributions within Patches and Matrix at the beginning (top left) and end (right) of the growing season in simulated landscapes, which are based on a Kenyan savanna (bottom left) with habitat specialists that forage only in Matrix, and generalists that forage across the whole landscape but prefer Patches. In our model, consumers realistically increase perceptual range, movement ability, and metabolic needs with body size. N ranges from low (yellow) to intermediate (orange) and high (green). On right, N distributions after grazing, movement, and nutrient deposition for three example scenarios out of the study's total 64 (see Table S1): here, by equal numbers of large (40kg) specialists, large generalists, or small (10kg) generalists in example simulations. Percent changes in Moran's I, a measure of spatial autocorrelation (Moran 1950), and in the nitrogen content of each pixel in Patches and Matrix are indicated for each simulation. In the upper right panel, note the waves of N distribution in the Matrix created by foraging specialists compared to the initial landscape. Small dark green spots at the end of the growing season represent nutrient deposition by carcasses of consumers that died during the simulation, which is most evident for larger consumers. Real landscape image © 2024 Maxar Technologies.

Simulation Scenarios

We designed our scenarios (Table S1) to look at the impact of 4 different factors on landscape heterogeneity: species role (habitat generalists or specialists), aggregation type (solitary or herd), body size, and total biomass on the landscape where the total biomass on the landscape is determined by the mean body size multiplied by the number of individuals. We tested combinations of aggregation type (solitary or herd), body size (10kg, 25kg or 40kg), and total biomass on the landscape (varying between 500kg and 6000kg) for each of the species. We varied the total biomass to allow for comparisons where the total number of individuals is the same (50, 100, or 150 individuals) and where the total biomass is the same (1000kg, 2000kg, or 4000kg). We varied those factors to test all combinations possible. This resulted in 64 scenarios as described in Table S1. All scenarios were replicated 25 times. The Netlogo simulations were processed through R version 4.2.2 using the package 'nlrx' (Salecker *et al.* 2019). They were performed on the high-performance computer Cedar from Digital Research Alliance of Canada.

The outputs from the simulation experiments focus on changes that happen in the distribution of nutrients on the landscape and are recorded at the pixel level. They include the initial and final forage amount, the initial and final N amount, the N eaten through foraging, the N deposited through defecation or animal death, the coordinates and whether the pixel is Patch or Matrix. We also recorded the number of times a pixel was grazed, defecated on, and the number of deaths that occurred on a given pixel to help with results interpretation.

Table 1: Key parameters influencing the initial distribution of N on the landscape and the withdrawals and deposits of N by animals.

Parameter (units)	**Value**	**Reference**
Mean forage per Patch pixel (g)	5000	(Augustine 2004)
Mean forage per Matrix pixel (g)	3300	(Augustine 2004)
Mean N per Patch pixel (g)	300 (6% of forage)	(Augustine 2004)
Mean N per matrix patch (g)	132 (4% of forage)	(Augustine 2004)
N in consumers' body (g)	2% * bodymass	(Pace and Rathbun 1945)
Daily metabolic needs of consumers (g)	(7.94 * (bodymass) ^ 0.646 / 11.5)	(Nagy 2001)
Yearly % chance of death for animals	10%	(Ogutu et al. 2012, Owen-Smith and Goodall 2014)
N deposited on landscape per defecation event (g)	50% of N absorbed since last defecation event	(Singer and Schoenecker 2003)
N deposited on landscape per death event (g)	All body N + 100% N absorbed since last defecation event	

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Model Analysis

We analyzed changes in the spatial and non-spatial nutrient distribution across the landscape to determine the effect of species role, aggregation type, body size, and total biomass on landscape heterogeneity. The key variables of interest were the initial and final N amount of each pixel. For each individual simulation, we calculated the four statistical moments (i.e. mean, variance, skewness and kurtosis) for the initial and final N amount across all pixels. Comparing the value of those statistics for the initial N and final N amount indicates the change in the non-spatial N distribution across the landscape resulting from the simulation. For each scenario, we then calculated the mean and standard deviation of the 25 replicates for all statistics calculated at the individual simulation level. For a given statistic, we then plotted the mean with a standard deviation error bar of the specific scenarios that we wanted to compare, such as different body sizes or different number of individuals on the landscape. All statistical analyses were performed using R version 4.2.2 and the skewness and kurtosis were calculated using the package 'geodiv' (Smith et al. 2021).

We also explored the spatial changes in N distribution by calculating the Global Moran's I ("Moran's I") on initial and final N for each individual simulation. The Moran's I is a statistical test that measures spatial autocorrelation, indicating how similar are the pixels from their neighbors (Moran 1950). The Moran's I sums covariances between pixels and, in its standard form using Queen connectivity (pixels are neighbors if they share a border or a point), gives equal weight to the 8 closest neighbors (first order neighbors) of a given pixel in the calculations. An increase in Moran's I means that the pixels are more autocorrelated, indicating spatial clustering of resources and increased spatial heterogeneity. A decrease in Moran's I means that the pixels are less autocorrelated and the distribution of N is less clustered on the landscape.

To determine if the relative impact of body size on spatial autocorrelation varies depending on the size of the neighborhood considered, we also calculated Moran's I using 4th order neighbors (80 neighbors), 10th order neighbors (440 neighbors) and 17th order neighbors (1224 neighbors) with an inverse distance spatial weight (i.e. the correlation between the closest neighbors weighs more than the correlation between neighbors further away). The 4th, 10th, and 17th order neighbors were selected to approximate the perceptual range of individuals with a body size of 10kg, 25kg, and 40kg respectively. Individuals with larger body sizes can access pixels that are located further away than individuals with smaller body sizes, but are more likely to select nearby pixels to minimize energy costs. We found no qualitative differences in the results between the "queen" configuration Moran's I and Moran's I with 4th, 10th, and 17th order neighbors, and hence present results with the standard Moran's I only. The Moran's I analysis was conducted using the package 'spdep' (Bivand and Wong 2018) in R version 4.2.2.

To better understand the drivers of the changes in the spatial and non-spatial N distribution at the landscape level, we analyzed the variables making up the final amount of N amount (for a given pixel, Final N = Initial N + N Deposited – N Eaten) at the landscape level and separately for Patches and Matrix. We calculated the mean and variance for N deposited, N eaten, and net N (difference between N Deposited and N Eaten) for the landscape as a whole and for Patches and Matrix separately for each individual simulation. As potential explanatory variables for N dynamics, we calculated the mean and variance in the number of times a pixel was grazed and defecated on, and the total number of death events at the landscape level for each individual simulation.

Results

Spatial distribution of N varied across simulated landscapes at the end of the growing season. Although larger body sizes and larger population sizes led to more forage consumed (**Fig. 2**) and greater N depletion (**Fig. S1**) in the total landscape for both specialists and generalists, changes in the spatial heterogeneity of N resulted from the interplay between N depletion in Patches and Matrix.

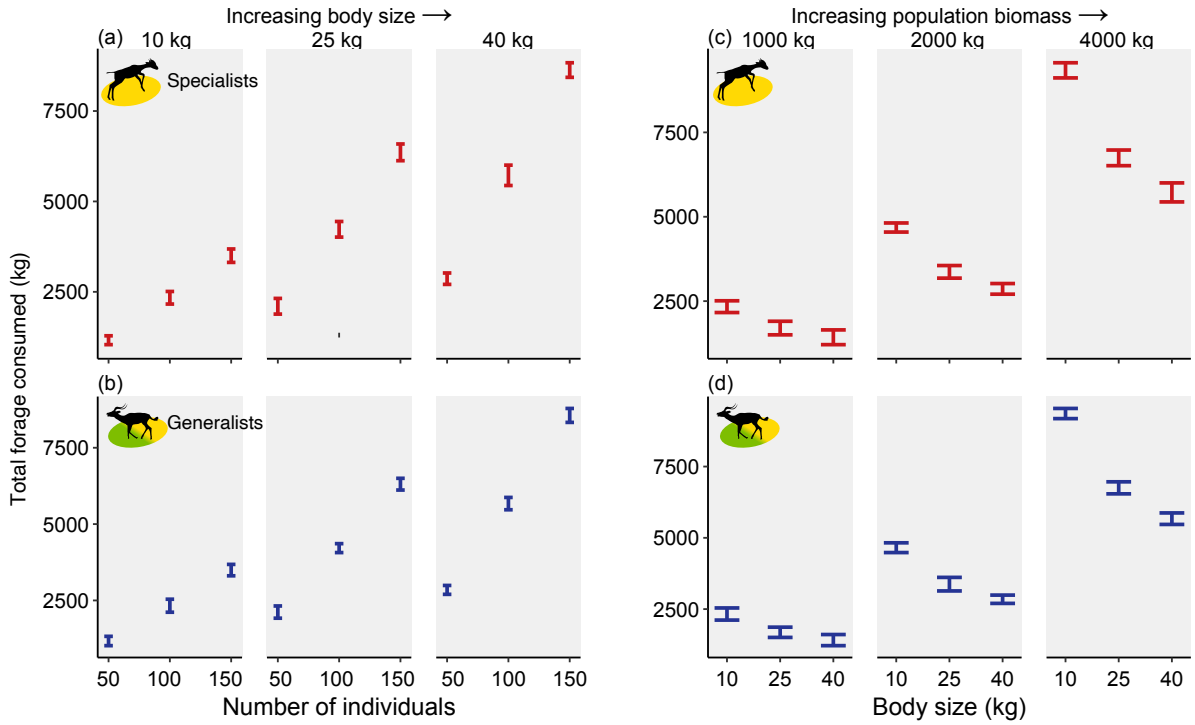

Figure 2. Total forage consumed during simulations with different combinations of parameters. (a) and (b) show the effect of increasing population size (on the x-axis) at small, medium, or large mean individual body size (left, center, and right panels), when the landscape is populated either with specialists that forage only in Matrix (a) or generalists that forage in both habitats (b). (c) and (d) show the effect of increasing mean body size (on the x-axis) when the total population biomass on the landscape is 1000 kg (left column), 2000 kg (middle column), or 4000 kg (right column) of specialists (c) or generalists (d). Bars show mean ± one standard deviation of 25 simulations for each scenario.

As predicted, solitary habitat specialists foraging only in the Matrix accentuated differences between habitat types (note increase in Moran's I in **Fig. 3,** top panels); for these

specialists, larger population sizes and larger body sizes were associated with greater increases in spatial heterogeneity. Also as predicted, solitary generalists, who preferentially forage in Patches, homogenized the landscape, reducing differences between Patches and Matrix (note decrease in Moran's I in **Fig. 3,** bottom panels). Here, we have presented results only from scenarios where consumers are solitary. Results from herd simulations were qualitatively similar, but produced slightly higher levels of spatial resource heterogeneity (**Fig. S2**), in line with our predictions.

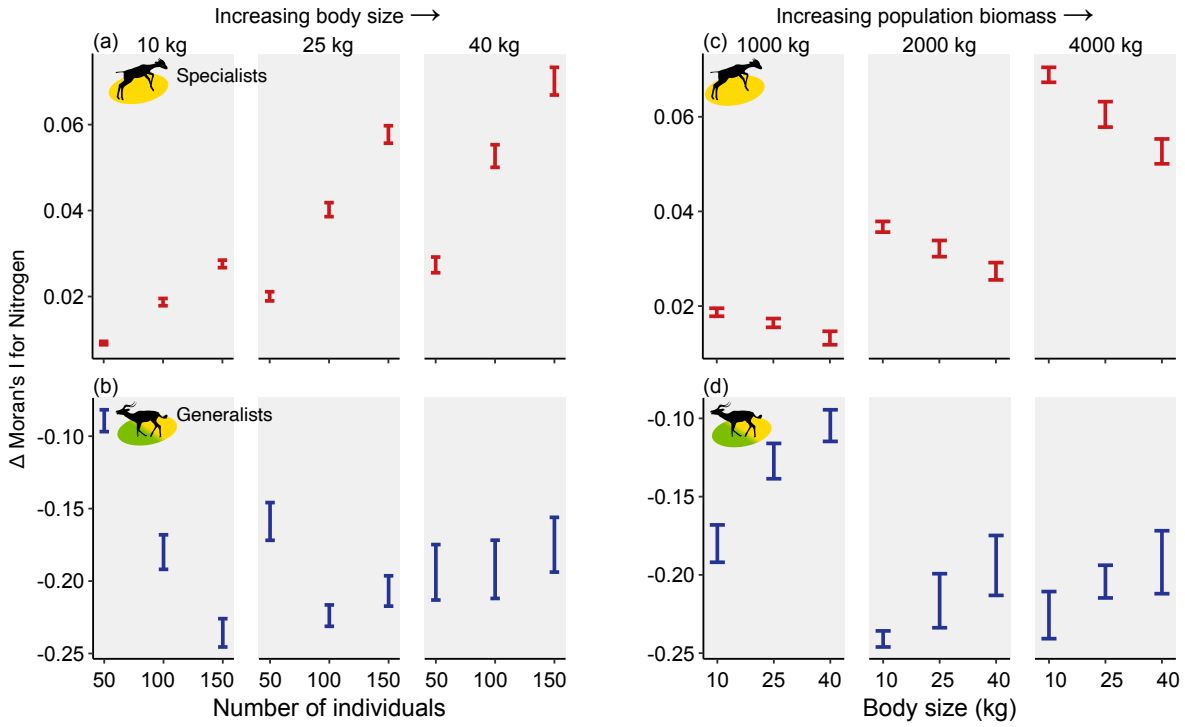

Figure 3. Change in Moran's I for the distribution of nitrogen between beginning and end of simulations. (a) and (b) show the effect of increasing population size (on the x-axis) at small, medium, or large mean individual body size (left, center, and right panels), when the landscape is populated either with specialists that forage only in Matrix (a) or generalists that forage in both habitats (b). (c) and (d) show the effect of increasing mean body size (on the x-axis) when the total population biomass on the landscape is 1000 kg (left column), 2000 kg (middle column), or 4000 kg (right column) of specialists (c) or generalists (d). Bars show mean ± one standard deviation of 25 simulations for each scenario. Note different y-axes in top and bottom panels.

For small generalists, larger population sizes led to greater homogenization of N distribution over the course of the simulations than that caused by smaller population sizes. Since small generalists, even at larger population sizes, did not remove enough forage from the Patches to make them of comparable quality as the Matrix, N removal from the Matrix was negligible (i.e., the first panel of **Fig. 4c**) and larger population sizes were nearly linearly associated with reductions in Moran's I (i.e., the first panel in **Fig. 4b**). However, for large generalists, the reduction in Moran's I was consistent across population sizes. Larger generalists depleted Patches faster than smaller generalists, subsequently removing N from the Matrix (**Fig. 4a**). However, the increased N depletion of Patches by the largest population sizes of large generalists (x-axis in rightmost panel of **Fig. 4b**) was of a similar magnitude to their increased removal of N from the Matrix (x-axis in rightmost panel of **Fig. 4c**), and as a result the difference between Patch and Matrix quality (and thus Moran's I) was fairly stable across population sizes of large generalists (**Fig. 3a**).

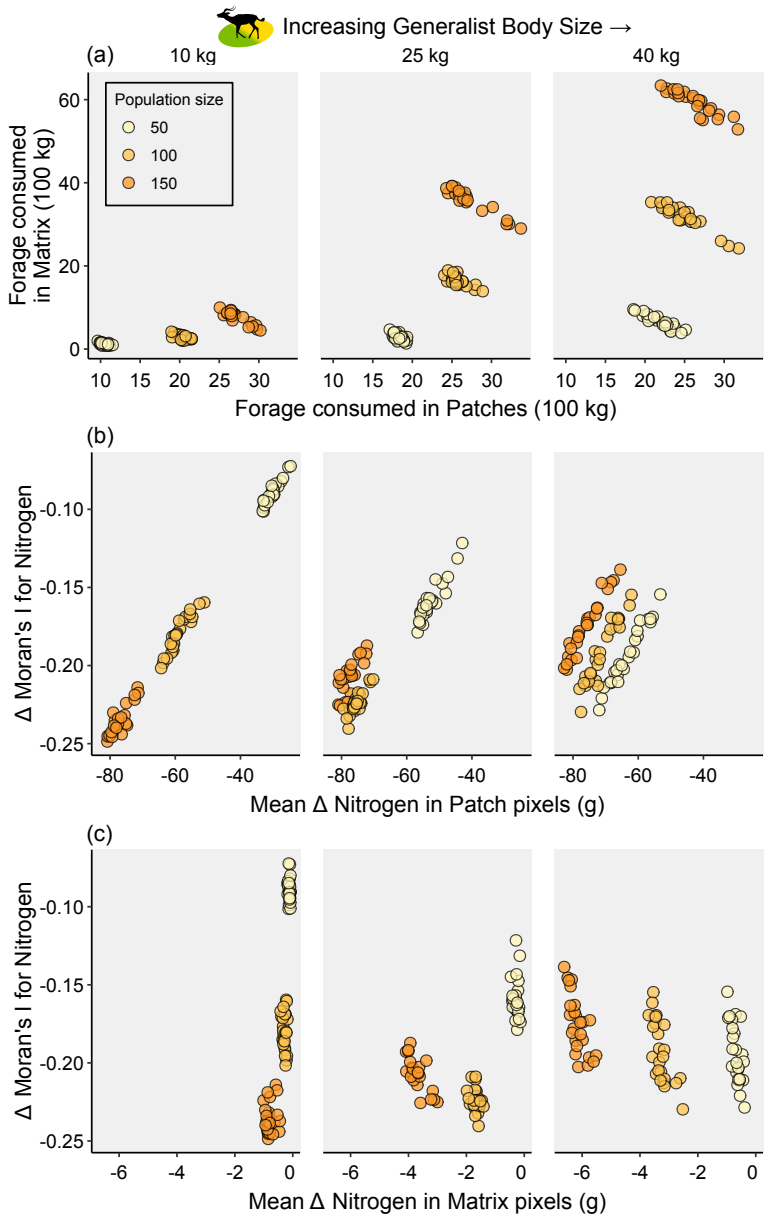

Figure 4. Changes in forage consumed in Patches and Matrix and in the spatial distribution of nitrogen in simulations with varying generalist body size and population size. Each dot represents one simulation, with the color of the dots indicating the number of individuals in the simulation. Within a panel, the leftmost graph shows results from simulations with 10 kg as the generalists' mean body size, 25 kg for middle graph, and 40 kg for right graph. (a) Relationship between the total forage consumed in Patches and the total forage consumed in the Matrix. (b) Change in Moran's I varies nearly linearly with net nitrogen loss from Patches when generalists are small, but less so when generalists are large. (c) When generalists are small, net nitrogen loss varies only minimally with population size, yet the spatial distribution of that nitrogen substantially changes at larger population sizes; when generalists are large, there is much greater variation in net nitrogen loss in the Matrix depending on population size, but less impact of population size on the spatial clustering of nitrogen distribution.

Comparing scenarios with equal total population biomass but with many small versus fewer large consumers revealed the effects of nonlinear scaling of metabolic requirements on spatial distribution of N (**Fig. 5**). Total forage consumption was higher with many small consumers compared to few large ones (**Fig. 2**). At lower total biomass, generalists of all body sizes spent most of their time in Patches (**Fig. 5b)**, but small generalists consumed more forage there (**Fig. 5b**), leading to a stronger homogenizing effect than their larger counterparts (**Fig. 3c**) as hypothesized. However, at larger total biomass, smaller generalists depleted and left Patches and spent upwards of 60% of their time in the Matrix (**Fig. 5c**), consuming markedly more forage in the Matrix than populations of large generalists did despite similar forage consumption in Patches (**Fig. 5a**), and thus changes in Moran's I were less differentiated.

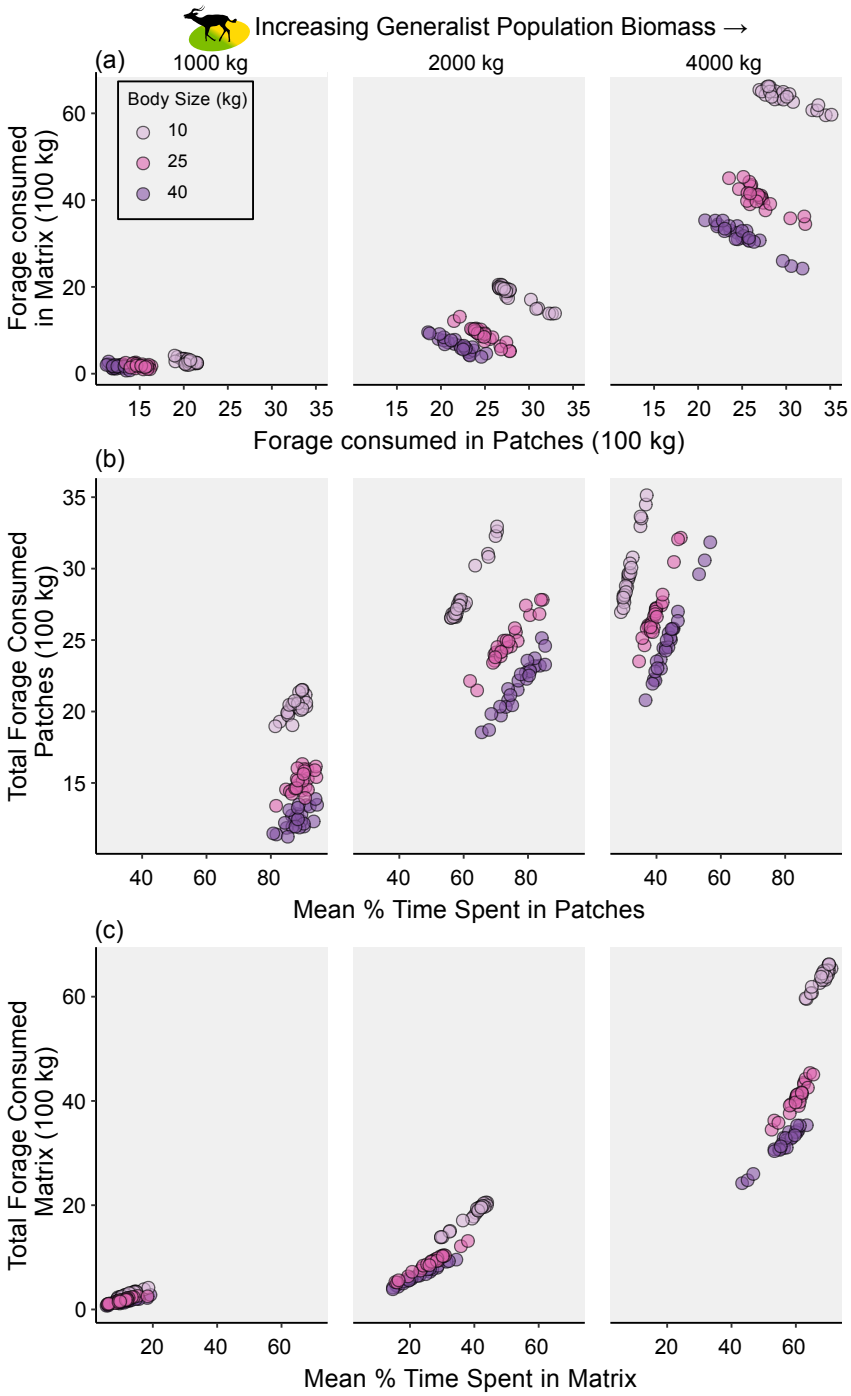

Figure 5. Changes in forage consumed in Patches and Matrix with different amounts of total generalist biomass on the landscape (shown in left, center, and right panels), and when that biomass is made up of different average body sizes (indicated by color of points). (a) Relationship between the total forage consumed in Patches and total forage consumed in the Matrix. (b) Relationship between the mean percentage of time individuals spent in Patches and the total forage consumed in Patches. (c) Relationship between the mean percentage of time individuals spent in the Matrix and total forage consumed in the Matrix.

Discussion

The role of animals in structuring resource patterns is poorly understood. Here, using a spatially-explicit, individual-based model, we show that organismal traits can make the difference in whether consumers amplify or erode spatial resource heterogeneity. We found that a key trait determining whether consumers amplify or erode resource patchiness is species' activity in the different habitats, modeled here to represent different risk avoidance strategies. Patchy landscapes have driven the development of ecological theory (Macarthur and Wilson 1967, Hanski 1999, Loreau et al. 2003a), yet to date, models assessing the effects of animal movement, foraging, and resource deposition have primarily focused on landscapes without spatial structure in resource availability (Earl and Zollner 2014, Bampoh et al. 2019, 2021, Ferraro et al. 2022). When spatial structure is included, over seasonal time scales, we showed that specialists on lower-quality (Matrix) habitat amplified existing resource heterogeneity between the resource hotspots (which they avoided) and the low-quality habitat. Conversely, generalists who could take advantage of high-resource Patches eroded the landscape's spatial structure. This is a particularly important insight in an era of global change because generalists often thrive where specialist species are more vulnerable to habitat loss and fragmentation (Clavel et al. 2011, Keinath et al. 2017), and because of the proliferation of non-native species and the association between generalism and invasion success (Romanuk et al. 2009, Ord and Hundt 2020).

The specialists in our simulations provided an example of how risk avoidance strategies can reinforce spatial structure and patchiness of landscapes by strengthening existing resource gradients (for an empirical example, see [Germain et al. 2013]). In addition to accentuating the difference between Patch and Matrix habitat, these same specialists also created finer-scale

spatial resource heterogeneity where it was previously lacking: our landscapes featured no initial spatial clustering of resources *within* a habitat type, but over the course of our simulated growing season, spatial heterogeneity in the Matrix increased. This was because the removal of nutrients by foraging followed individuals' movement patterns, which were spatially autocorrelated at the scale of the individual's perceptual range. This increase in fine-scale heterogeneity was not captured by Moran's I, which better reflected the larger differences in nutrient concentrations between Matrix and Patches, but is visible as waves of resource concentrations in landscape depictions (**Fig. 1**, "150 Large Specialists"). Thus, the effect of organismal activity on nutrient spatial heterogeneity depends on both the existing structure of the landscape and the scale of observation.

Globally, many species of large-bodied vertebrates are experiencing range contractions, whereas smaller-bodied vertebrates are more likely to be experiencing range expansions (Pacifici et al. 2020), and the largest consumer species are also at higher risk of extinction than are their smaller counterparts (Enquist et al. 2020). Our results imply that in patchy landscapes, the impact of species turnover from large to small generalists depends on both initial community biomass and whether shifts in body size are accompanied by altered total biomass (i.e., the summed biomass of all individuals in the population). For the same total biomass, smaller consumers consume more forage due to higher mass-specific metabolic needs (Brown et al. 2004). In terms of spatial ramifications, at small body sizes and low total biomass, larger populations of generalists homogenized the landscape more than smaller populations by depleting resource hotspots. However, at larger body sizes and greater total biomass, foraging behavior whereby generalists left depleted Patches to forage in the Matrix meant that the further depletion of resource hotspots by a larger population was offset by the increased consumption of

resources in the lower quality habitat—that is, spatial homogenization plateaued. Thus, we suggest that where generalists are already dominant, a shift from large to small body size may have minimal effects on spatial structure if total biomass remains the same, however, such a shift would increase overall rates of consumption and recycling of resources. This is because smaller individuals have higher metabolic demands per unit mass compared to larger individuals (a universal feature of metabolic scaling).

Our model did not include population dynamics of either consumers (beyond mortality) or forage resources, and only considered the spatial dynamics of net resource availability. This increased computational feasibility and enabled us to isolate the impact of vertebrates on nutrient distributions. Despite simplifications, our finding that generalists (which we based on impalas) homogenize N distributions by reducing N in Patches aligns with empirical results in an intriguing way: impalas increase the relative density of a well-defended plant species (Ford et al. 2014) which has less foliar N than a poorly-defended congener (Coetsee et al. 2023) that is abundant where impala are rare, thus altering spatial heterogeneity of N in plants.

Another caveat is that in our model, not all N consumed in forage is returned to the landscape. Some N is incorporated into consumer bodies, and consumer death was not high enough in our model to offset this. This dynamic is not unrealistic over the course of a single wet season, based on mortality estimates from the literature (Ogutu et al. 2012, Owen-Smith and Goodall 2014). We also did not explicitly model processes such as predator and scavenger export of nutrients, leaching, or nutrient volatilization, instead incorporating assumptions about how much N was returned to the landscape by excretion, egestion, and carcass deposition (see Appendix I, and **Fig. S3** for a sensitivity test).

Here, we showed through simulations that animals have the ability to shape resource heterogeneity on the landscape over short periods of time such as a single season, thus shifting the environmental template for subsequent consumer-resource interactions. Landscape heterogeneity is important because it creates different niches that can serve to sustain biodiversity (Ryser et al. 2021). Our results suggest that species' traits and abundance are key mediators of their effect on resource distributions, which could lead to varying impacts of future biodiversity change. We propose two future directions for spatially-explicit, agent-based modeling to explore the impacts of these projected changes. The first is to explicitly model different chemical forms of nutrients, which are more or less bioavailable to organisms (Hempson et al. 2015). This approach would account for the fact that nutrients deposited through dung and urine are not immediately available to consumers, but must first be transformed into plant shoots. We expect that coupling these considerations with longer simulations that account for consumer population dynamics would lead to new spatial patterns of foraging movement by consumers, and thus new emergent dynamics of nutrient spatial distributions. Second, further work should also explore how competing consumers and trophic interactions modify the patterns found in this study. For example, we modeled species based on known risk-avoidance strategies rather than including predators in the models, but doing so may lead to behavioral shifts and emergent dynamics, additionally because trophic role influences resource deposition (Mackay et al. 2021). Furthermore, consumers exist in multi-species communities and trait-based differences among co-occurring species could lead to complementarity of resource use, altering the patterns that we found here. Incorporating additional ecological complexity into spatially-explicit models could enable a better understanding of how organisms will shape their own fates via resource dynamics in future landscapes.

Data / code availability

Data and code are available to peer reviewers at https://vault.sfu.ca/index.php/s/YT0XQKrzX0gZqlV. Data and code will be deposited in Dryad before publication of the manuscript.

Acknowledgments

This research was enabled in part by support from the BC DRI Group, Simon Fraser University's Supercomputer Cedar (www.sfu.ca/research/supercomputer-cedar), and the Digital Research Alliance of Canada (www.alliancecan.ca). We thank Matteo Rizzuto and members of the Little Ecology Group for valuable feedback on the manuscript.

Funding

This work was supported by a Killam Postdoctoral Research Fellowship from the Killam Trusts and a Discovery Grant from the Natural Science and Engineering Research Council of Canada.

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