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 [1–4]. The deposition of resources via feces, urine, seeds, placenta, and carcasses contribute to resource dispersal in the landscape [5–10]. Organismal activity will therefore impact spatial resource heterogeneity, which in turn facilitates the coexistence of species [11] and thus ecosystem functioning [12]. The distribution of resources in space is therefore an important landscape characteristic that shapes patterns of biodiversity and ecosystem functioning [13–16]. 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 [10,17,18]. For example, social aggregation creates spatial clustering of consumer-driven resource subsidies [19]. 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 [20]. Meanwhile, consumer body size influences resource dispersal through at least two pathways. First, energetic requirements scale nonlinearly with body size [21], and consequently so should resource consumption and excretion. Second, body size is associated with differences in movement ability and perceptual range [2,22], 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 [23], and specialist species more than generalists [24]. Moreover, as population sizes shift with global change [25], 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 [26], 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.* [27] 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 [28].

In this study, we present an 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-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 specialists would remove resources from lower-quality areas and 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 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

We used NetLogo v6.0.4 [29] 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 [30]): open, high-nutrient glades as clusters of pixels (each cluster forming a "Patch"), in a "Matrix" of bushy, lower-quality grassland [31]. 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 [32,33], while generalists, akin to impalas, can use both habitat types, but favor Patches [30,33]. Animals forage based on their metabolic needs and move within their perceptual range, both of which vary as a function of their body size [34,35]. Foraging behavior adheres to the marginal value theorem, with animals selecting pixels with better-than-average forage available [36]. 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.

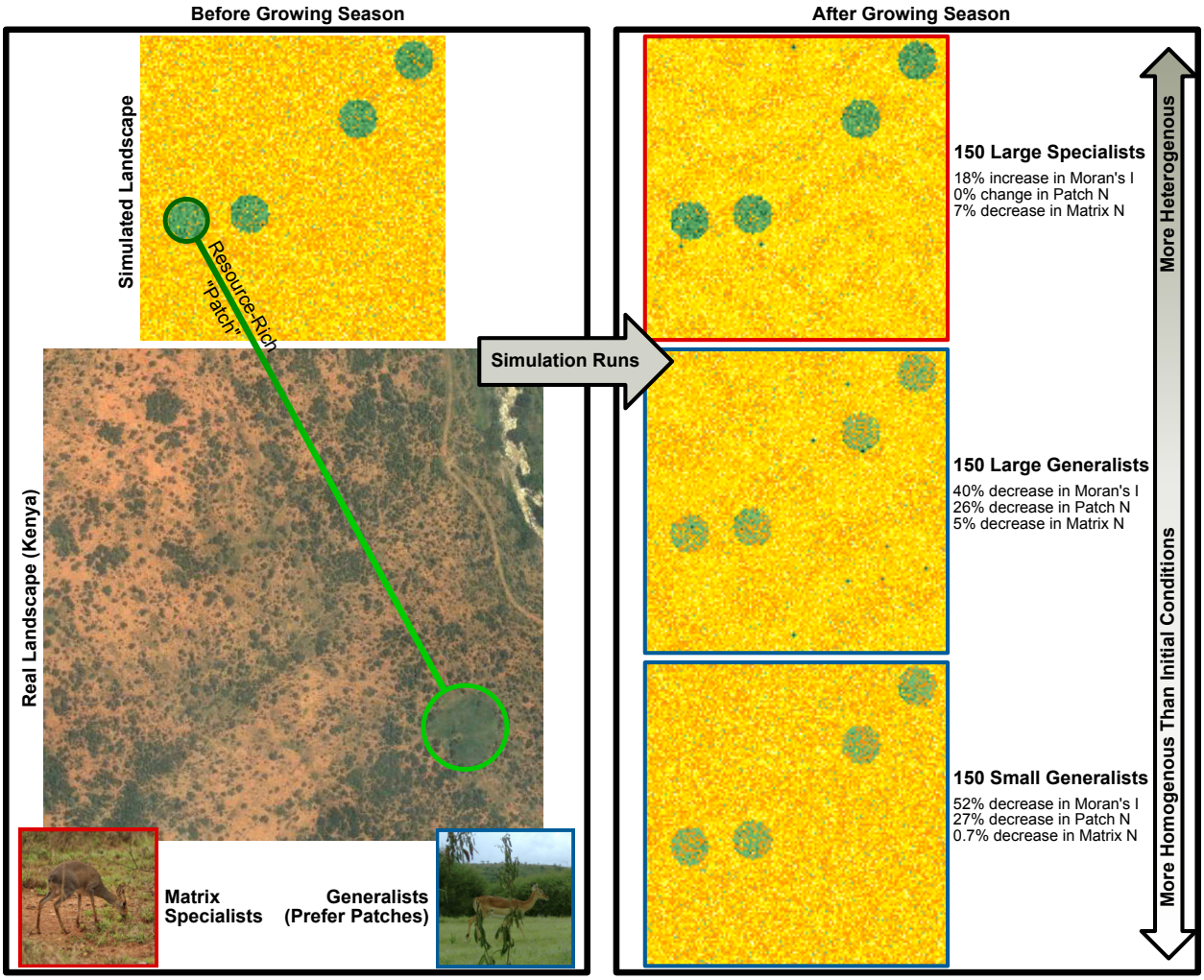

Figure 1. N distributions within Patches and Matrix at the beginning (top left) and end (right) of the growing season in simulated landscapes, which are based on a Kenyan savanna (bottom left) with habitat specialists that forage only in Matrix, and generalists that forage across the whole landscape 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 [37], 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.

We designed scenarios to look at the impact of changes in population size (500 - 6000 kg total biomass) and mean body size (10, 25, and 40 kg) on nitrogen (N) heterogeneity when

individual consumers choose foraging locations independently, as well as for consumers that forage in social groups (see Appendices II and III; Table S1). While consumers were inspired by dik-diks (small and solitary) and impala (larger and herd-living), we varied all traits factorially, and thus implemented sociality independently of specialists/generalist status or body size. For each scenario, we performed 25 replicate simulations using the R package 'nlrx' [38], which interfaces with Netlogo.

For each simulation, we then analyzed non-spatial changes in N before and after the growing season by calculating the four statistical moments (i.e. mean, variance, skewness, and kurtosis across all pixels). We also analyzed variables providing insight into animal behavior, such as the net change in N (N deposited minus N eaten) in Patches and in Matrix. To analyze spatial changes in N distribution, we calculated Global Moran's I ("Moran's I"), a statistical test measuring spatial autocorrelation (Moran 1950), using the package 'spdep' [39]. Here, Moran's I quantifies the clustering of nutrients, with higher values indicating stronger spatial autocorrelation. For each scenario, we present the mean and standard deviation of 25 replicates for all statistics. We performed all statistical analysis using R version 4.2.2. Full analysis details can be found in Appendix II.

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	[31]
Mean forage per Matrix pixel (g)	3300	[31]
Mean N per Patch pixel (g)	300 (6% of forage)	[31]

Mean N per matrix patch (g)	132 (4% of forage)	[31]
N in consumers' body (g)	2% * bodymass	[40]
Daily metabolic needs of consumers (g)	(7.94 * (bodymass) ^ 0.646 / 11.5)	[35]
Yearly % chance of death for animals	10%	[41,42]
N deposited on landscape per defecation event (g)	50% of N absorbed since last defecation event	[43]
N deposited on landscape per death event (g)	All body N + 100% N absorbed since last defecation event	

Results

Spatial distribution of N varied across simulated landscapes at the end of the growing season. As predicted, solitary habitat specialists foraging only in the Matrix accentuated differences between habitat types (note increase in Moran's I in **Fig. 2a,** top panel); 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. 2a,** bottom panel). Although larger body sizes and larger population sizes lead to greater N depletion in the total landscape for both specialists and generalists (**Fig. S1**), changes in the spatial heterogeneity of N resulted from the interplay between N depletion in Patches and Matrix. 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.

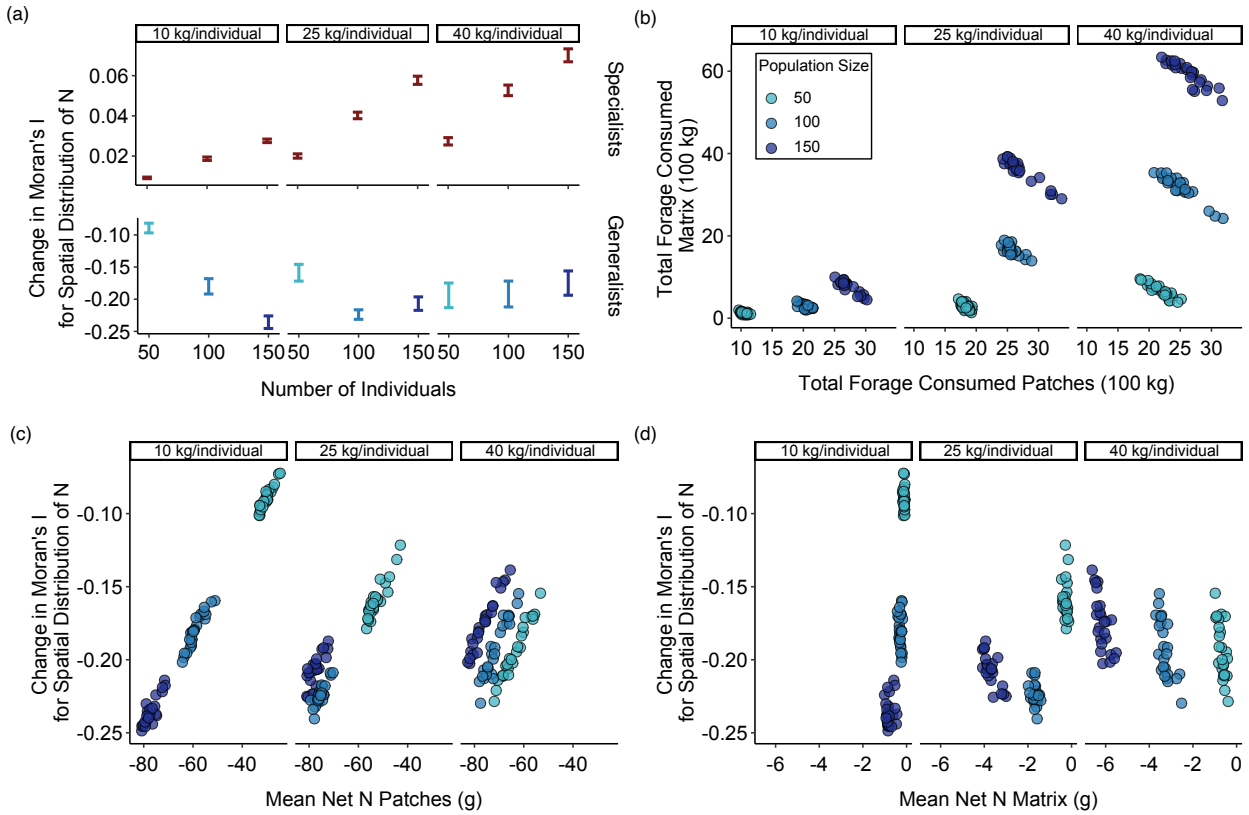

Figure 2: Changes in the spatial distribution of nitrogen (N) from beginning to end of simulations with population mean body mass of 10 kg, 25 kg, and 40 kg. In (a), bars show mean change in Moran's I and standard deviation of 25 simulations for each scenario. Note different y-axis scales for generalists and specialists. Panels (b) through (d) include only generalists, and colors differentiate simulations with 50, 100, and 150 individuals; each point is one replicate simulation. (b) Relationship between total forage consumed in Patches and total forage consumed in Matrix. (c) and (d) Relationship between mean Net N in Patches (c) and Matrix (d), respectively, with the change in Moran's I.

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. 2d**) and larger population sizes were nearly linearly associated with reductions in Moran's I (i.e., the first panel in **Fig. 2c**). 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. 2b**). However, the increased N depletion of Patches by the largest population sizes of large generalists (x-axis in rightmost panel of **Fig. 2c**) was of a similar magnitude to their increased removal of N from the Matrix (x-axis in rightmost panel of **Fig. 2d**), 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. 2a**, top panel).

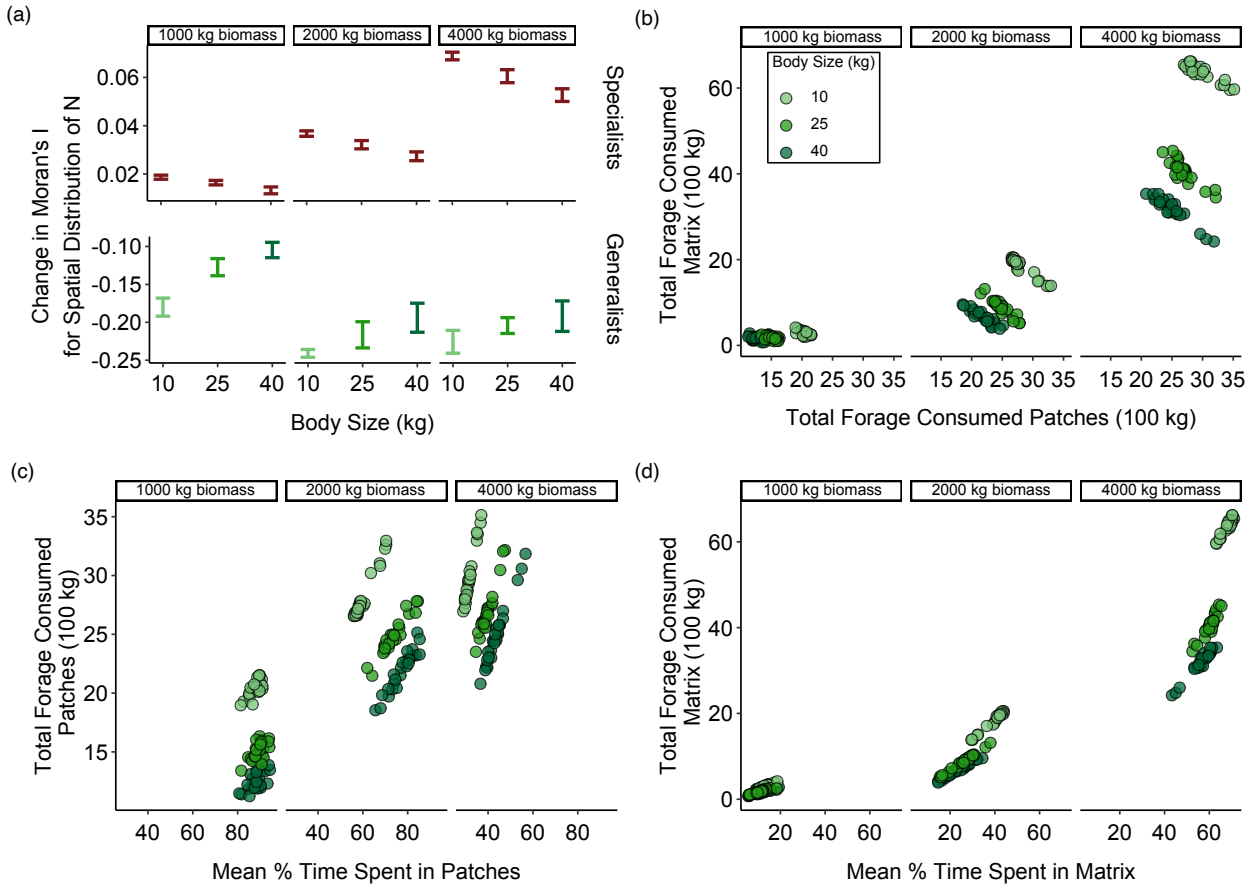

Figure 3: Changes in the spatial distribution of nitrogen (N) from beginning to end of simulations with total population biomass of 1000kg, 2000kg, and 4000kg of. Bars and y-axis in (a) are as for Fig. 2. (b-d) show only generalists. (b) is as for Fig. 2. (c) and (d) Relationship between mean time individuals spent in Patches (c) and Matrix (d) with the total forage consumed in the respective habitat type.

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. 3**). Total forage consumption was higher with many small consumers compared to few large ones (**Fig. S3**). At lower total biomass, generalists of all body sizes spent most of their time in Patches (**Fig. 3c)**, but small generalists consumed more forage there (**Fig. 3c**), leading to a stronger homogenizing effect than their larger counterparts (**Fig. 3a**) 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. 3d**), consuming markedly more forage in the Matrix than populations of large generalists did despite similar forage consumption in Patches (**Fig. 3b**), and thus changes in Moran's I were less differentiated.

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 [44–46], 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 [19,27,47,48]. 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

214 (which they avoided) and the low-quality habitat. Conversely, generalists who could take
215 advantage of high-resource Patches eroded the landscape's spatial structure. This is a particularly
216 important insight in an era of global change because generalists often thrive where specialist
217 species are more vulnerable to habitat loss and fragmentation [24,49], and because of the
218 proliferation of non-native species and the association between generalism and invasion success
219 [50,51].

220 The specialists in our simulations provided an example of how risk avoidance strategies
221 can reinforce spatial structure and patchiness of landscapes by strengthening existing resource
222 gradients (for an empirical example, see [52]). In addition to accentuating the difference between
223 Patch and Matrix habitat, these same specialists also created finer-scale spatial resource
224 heterogeneity where it was previously lacking: our landscapes featured no initial spatial
225 clustering of resources *within* a habitat type, but over the course of our simulated growing
226 season, spatial heterogeneity in the Matrix increased. This was because the removal of nutrients
227 by foraging followed individuals' movement patterns, which were spatially autocorrelated at the
228 scale of the individual's perceptual range. This increase in fine-scale heterogeneity was not
229 captured by Moran's I, which better reflected the larger differences in nutrient concentrations
230 between Matrix and Patches, but is visible as waves of resource concentrations in landscape
231 depictions (**Fig. 1**, "150 Large Specialists"). Thus, the effect of organismal activity on nutrient
232 spatial heterogeneity depends on both the existing structure of the landscape and the scale of
233 observation.

234 Globally, many species of large-bodied vertebrates are experiencing range contractions,
235 whereas smaller-bodied vertebrates are more likely to be experiencing range expansions [53],
236 and the largest consumer species are also at higher risk of extinction than are their smaller

counterparts [54]. 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 [21]. 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 [30] which has less foliar N than a poorly-defended congener [55] 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 [41,42]. 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. S4** 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 [57]. 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 [56]. 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 [58]. 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.

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