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Author for correspondence:

Ricardo Martinez-Garcia

e-mail: ricardom@ictp-saifr.org

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Foraging behaviour and patch size distribution jointly determine population dynamics in fragmented landscapes

Johannes Nauta¹, Pieter Simoens¹, Yara Khaluf² and Ricardo Martinez-Garcia³

¹Department of Information Technology—IDLab, Ghent University—IMEC, Technologiepark Zwijnaarde 126, 9052 Ghent, Belgium

²Wageningen University and Research, Department of Social Sciences—Information Technology Group, Hollandseweg 1, 6706KN Wageningen, The Netherlands

³ICTP South American Institute for Fundamental Research and Instituto de Física Teórica, Universidade Estadual Paulista—UNESP, Rua Dr Bento Teobaldo Ferraz 271, Bloco 2 – Barra Funda, 01140-070 São Paulo, Brazil

id JN, 0000-0002-5859-2729; PS, 0000-0002-9569-9373; YK, 0000-0002-5590-9321; RM, 0000-0003-2765-8147

Increased fragmentation caused by habitat loss represents a major threat to the persistence of animal populations. How fragmentation affects populations depends on the rate at which individuals move between spatially separated patches. Whereas negative effects of habitat loss on biodiversity are well known, the effects of fragmentation *per se* on population dynamics and ecosystem stability remain less well understood. Here, we use a spatially explicit predator–prey model to investigate how the interplay between fragmentation and optimal foraging behaviour affects predator–prey interactions and, subsequently, ecosystem stability. We study systems wherein prey occupies isolated patches and are consumed by predators that disperse following Lévy random walks. Our results show that the Lévy exponent and the degree of fragmentation jointly determine coexistence probabilities. In highly fragmented landscapes, Brownian and ballistic predators go extinct and only scale-free predators can coexist with prey. Furthermore, our results confirm that predation causes irreversible habitat loss in fragmented landscapes owing to overexploitation of smaller patches of prey. Moreover, we show that predator dispersal can reduce, but not prevent or minimize, the amount of lost habitat. Our results suggest that integrating optimal foraging theory into population and landscape ecology is crucial to assessing the impact of fragmentation on biodiversity and ecosystem stability.

1. Introduction

Loss of habitat presents a major threat to global biodiversity [1] and typically leads to fragmented landscapes that contain smaller and more spatially isolated patches in which local extinctions are more likely to occur [2,3]. While ecologists agree that habitat destruction, and the subsequent increase in habitat fragmentation, affects biodiversity negatively [4], the potential effects of fragmentation *per se* on population densities and species' persistence are much less understood [5,6]. As it is known that fragmentation *per se* induces changes in demographic rates and drifts in population genetics [7], it is critical to assess its effects on population dynamics and ecosystem stability.

Fragmentation *per se* (hereafter, fragmentation) describes changes in the spatial habitat configuration without significant habitat loss [8]. Theoretical and experimental studies indicate that fragmentation can result in larger species' extinction probabilities, as small patches sustaining small populations are more sensitive to demographic fluctuations [8]. By contrast, fragmentation might also favour species' persistence by increasing immigration rates, patch connectivity and the diversity of habitat available within a smaller area (for a review, see [9]). Therefore, whether, and how, fragmentation impacts species' persistence strongly depends on the spatial configuration of the landscape

[10,11] and the dispersal behaviour (i.e. movement between fragments) of individual organisms [12,13]. Despite the interplay between landscape structure and individual movement being essential for understanding population dynamics, research on each of these fields has progressed mostly independent from one another [14,15]. As a result, a general framework to investigate how fragmentation, movement behaviour and demographic rates jointly determine species' persistence is lacking.

On the one hand, studies on individual movement are often grounded in optimal foraging theory [16]. These studies investigate foraging behaviour on short time scales and most often neglect demographic events and evolutionary processes (but see [17]). Instead, they examine how individual movement behaviour defines search times and study correlations between foraging efficiency and resource density [18]. Often, movement is modelled using scale-free random searches, known as *Lévy walks*, in which displacement lengths are sampled from power laws with varying exponents [19]. This particular choice for the distribution of displacement lengths is based on empirical observations reporting scale-free patterns in the movement of different species [20–24]. Although these patterns in displacement lengths might be recapitulated both by memoryless Lévy searchers and by area-restricted foragers, we consider here the former because they provide a simple mathematical framework to explore how individuals balance the exploration–exploitation trade-off underlying search processes [25]. In general, Lévy walks are a very efficient random foraging strategy in sparse resource landscapes [26–29], including fragmented landscapes [30,31].

On the other hand, studies on population dynamics consider longer time scales and often assume simplified individual movement [32–35]. Few studies have integrated optimal foraging behaviour in population-based models [14,36] and, to the best of our knowledge, only Dannemann *et al.* [37] have studied population dynamics in a system of optimal foragers while considering fragmented prey habitats. The study, however, mostly controlled for habitat availability and did not systematically investigate how the complex spatial distributions of habitat as observed in natural landscapes impact population dynamics. Here, we extend the framework proposed in [37] and scrutinize these effects using techniques from landscape ecology that allow us to generate lattices with precise levels of fragmentation [38,39].

To study the interplay between optimal forager movement, fragmentation and demographic rates, we develop a stochastic, spatially explicit predator–prey model in fragmented landscapes. Fragmentation restricts prey individuals to inhabit spatially separated fragments, whereas predators are assumed to display natural (optimized) foraging behaviour and disperse following a Lévy walk. By varying habitat fragmentation and predator movement, we quantitatively examine the effects of dispersal on ecosystem stability in fragmented landscapes.

2. Stochastic predator–prey model in fragmented landscapes

We develop a stochastic predator–prey model in a two-dimensional landscape with a fragmented prey habitat. The landscape is represented by a periodic square lattice in

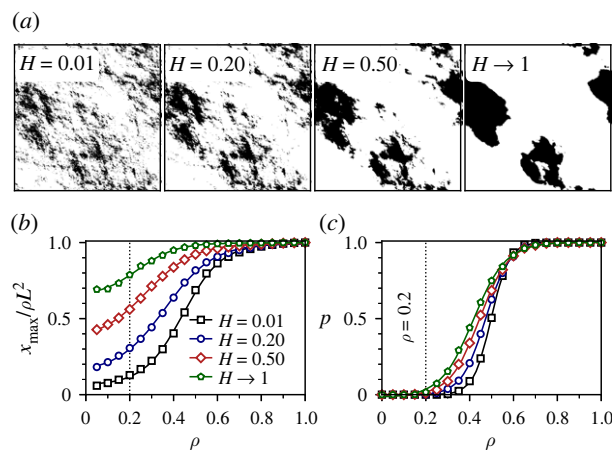


Figure 1. (a) Fragmented landscapes of prey habitat used in our model implementation with $L = 512$ and $\rho = 0.2$. The degree of fragmentation increases with the Hurst exponent H . Black and white regions depict prey habitat and matrix, respectively. (b) Normalized maximum patch size x_{\max} for different H versus habitat density ρ (electronic supplementary material). (c) Percolation probability p as a function of ρ (electronic supplementary material). The dotted vertical line indicates the habitat density $\rho = 0.2$ below the percolation threshold ($p \approx 0$) used in our experiments.

which a fraction $\rho \in [0, 1]$ of the sites provide prey habitat. To investigate how predator movement and the spatial distribution of prey habitat jointly determine predator–prey population dynamics, we fix the fraction of prey habitat ρ and vary only the statistical properties of the patch sizes. In other words, we focus on the spatial configuration of habitat (fragmentation *per se*) and do not consider the potential effects of habitat loss. The degree of fragmentation is determined by the spatial correlations in the distribution of prey habitat. In our model, these are controlled by the Hurst exponent $H \in (0, 1)$. In general, the limit $H \rightarrow 1$ defines low habitat fragmentation, whereas $H \rightarrow 0$ defines highly fragmented landscapes (figure 1; see the electronic supplementary material for more details).

We assume that individual prey are sessile, can only occupy habitat patches and cannot survive in the matrix. At each time step, they reproduce with probability σ and can potentially die by encountering a predator. We assume that predators are, by contrast, highly motile and perform Lévy walks in which the dispersal length ℓ follows a discrete power-law distribution $p(\ell) \propto \ell^{-\alpha}$ with exponent $1 < \alpha \leq 3$. For $\alpha \geq 3$, predator movement converges to Brownian motion whereas the limit $\alpha \rightarrow 1$ recovers ballistic motion. In contrast to Lévy flights (which were discussed in [37]), in which relocations are instantaneous, Lévy walks represent movement at constant velocity. Hence, in our model, individual predators move a fixed distance every time step (the unit lattice spacing) and the duration of each relocation event is proportional to the length of the displacement [19]. Predator relocations can be interrupted by predator death or by an encounter with prey or other predators. When a relocation is interrupted, a new direction and dispersal length are sampled and the predator resumes its movement in the next time step.

For predator–prey encounters, we consider that, when predators cross a site occupied by prey, the probability that they interact $\hat{\Lambda}$ decays with the current dispersal length, i.e. $\hat{\Lambda} = \ell^{-1}$. This assumption models intermittent search

behaviour [25], which combines phases of non-reactive long, straight displacements with reactive phases featuring shorter displacements and more frequent turns [40–42]. In each predator–prey encounter event, prey is consumed and replaced with a new predator with probability λ (predator reproduction probability) and with the focal predator otherwise (no predator reproduction); see the electronic supplementary material for further details on the parameters and the model implementation.

3. Results

We simulate the predator–prey model on a square lattice of lateral length $L = 512$, with prey habitat density $\rho = 0.2$ and different levels of fragmentation $0 < H < 1$. We choose ρ considering that fragmentation impacts landscape properties more strongly when the habitat is not abundant (e.g. [1,43,44]; see the electronic supplementary material for more details) and that Lévy foraging maximizes prey intake only for low prey habitat density (e.g. [26]). We define the spatially averaged predator and prey densities, N and M , respectively, and initialize our simulations with $M_0 = N_0 = \rho$. Predators are distributed randomly on the matrix and prey individuals fully occupy the habitat patches. Measurements of species densities were taken when the system converged to a quasi-stationary stable state after $T = 10^4$ Monte Carlo time steps (electronic supplementary material, figure SI.4). Results in this quasi-stationary stable state did not depend on the specific initial condition chosen for the simulations.

We are interested in investigating the impact of fragmentation in *fragile* ecosystems (see [37]). That is, systems that are already close to an extinction threshold when habitat patches are large ($H \rightarrow 1$). Hence, we parameterize demographic rates such that they bring the predator–prey dynamics close to an extinction transition ([37]; see the electronic supplementary material) and consider fragmentation, defined by the Hurst exponent H , and predator dispersal, defined by the Lévy exponent α , as the only free model parameters. Using this simulation set-up, we study the impact of habitat structure and predator dispersal on population dynamics, ecosystem stability and patterns of irreversible habitat loss.

3.1. Population densities and species richness

We measure population sizes in the quasi-stationary stable state for different degrees of habitat fragmentation and foraging strategies. Since the prey reproduction rate is fixed in our simulations, equilibrium population sizes are determined by predator–prey encounter rates and predator reproduction rates. The long-time prey population density, M , decreases monotonically as predator movement goes from ballistic to Brownian (figure 2*b*). Predator density N , however, is maximal for an intermediate value of the Lévy exponent and its optimal value depends on the degree of fragmentation (figure 2*a*). For each degree of fragmentation H , we distinguish three different regimes in population dynamics that result in different outcomes for the predator–prey interaction (electronic supplementary material, figure SI.4).

First, owing to our choice for the predator–prey interaction probability $\hat{\lambda} = \ell^{-1}$, ballistic predators ($\alpha \rightarrow 1$) rarely consume prey and thus go extinct. Upon predator extinction, prey proliferate until they reach their maximum population

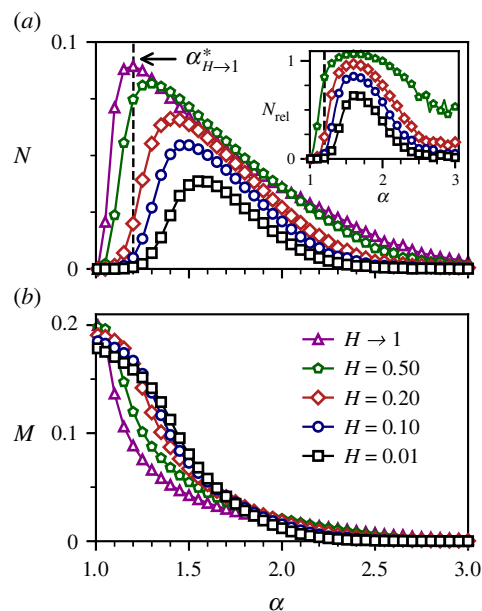


Figure 2. Effect of the Lévy exponent α on population densities for different Hurst exponents H . Other rate parameters are $\mu = 1/L$, $\sigma = 0.1$ and $\hat{\lambda} = 0.1$ (electronic supplementary material). (a) Predator density N . The dashed vertical line shows the optimal Lévy exponent $\alpha_{H \rightarrow 1}^* \approx 1.2$ for $H \rightarrow 1$ and indicates predator extinction if predators cannot rapidly adapt to significant increases in fragmentation (see text). (inset) Relative predator densities $N_{rel} = N_H/N_{H \rightarrow 1}$ displays decreases in N when predators forage with the same α in landscapes with higher fragmentation. Note that for some ranges of α there exists a preferred intermediate spatial correlation H (see text). (b) Prey density M declines as predators are less dispersive (higher α) regardless of the degree of fragmentation.

size. Note, however, that this population size does not correspond with the prey habitat density ρ in fragmented landscapes because small habitat patches become irreversibly uninhabited (see below).

Second, in the Brownian limit, $\alpha \rightarrow 3$, predation is intense and prey are overexploited regardless of the level of landscape fragmentation. Interestingly, Brownian-like dispersal effectively induces area-restricted (or area-concentrated) search patterns [45,46], as only those foragers that initially spawn near a fragment have the opportunity to reproduce (see the electronic supplementary material for more details). This cross-generational patch fidelity results in prey extinction followed by predator extinction because of a lack of prey. Note that predator extinctions are asymptotic as a result of our choice of the predator death rate and we still observe a few individuals in our simulations when they are stopped (electronic supplementary material).

Third, for intermediate values of the Lévy exponent, our model predicts stable species coexistence at different population sizes that are jointly determined by predator movement, α , and habitat fragmentation, H . For landscapes that display little fragmentation ($H \rightarrow 1$), habitat patches are large and predator relocations intersect with prey often. As a result, predation still occurs during the non-reactive phases—represented by long displacements—and predators maximize population densities with near-ballistic foraging for $\alpha \approx 1.2$. In contrast, for highly fragmented landscapes ($H = 0.01$), the model trade-off between displacement length and prey detection probability becomes more important because predator–prey encounters are more rare. It is thus more critical that predators adopt strategies that increase

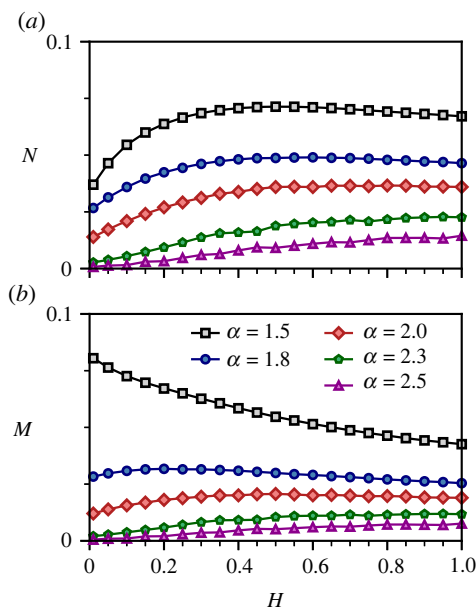


Figure 3. Effect of the Hurst exponent H on population densities for different Lévy exponents α . Note that, for $\alpha \rightarrow 1$, we have $N \rightarrow 0$ as prey encounter rates fall since $\hat{\Lambda} \rightarrow 0$. Additionally, for approximately $\alpha \geq 3$, we have $M \rightarrow 0$ owing to prey overconsumption. As a result, these values for α are not shown. (a) Predator density N . For sufficiently high dispersal rates, we observe maximized predator densities for intermediate fragmentation. (b) Prey density M . Note that for sufficiently high dispersal rates (low α) prey densities are highest in highly fragmented landscapes with $H \rightarrow 0$ (see text).

predation rates while ensuring sufficient encounters with prey. This balance is attained when short displacements are more frequently interspersed with long-range relocations, leading to maximum predator population sizes for $\alpha \approx 1.6$.

We also find that the range of foraging strategies, i.e. values of α , that ensure predator survival becomes more narrow as habitat fragmentation increases (figure 2a, inset). This result suggests a stronger selective pressure on the foraging strategy in highly fragmented landscapes. Moreover, our results further indicate that foraging strategies that maximize predator population sizes in slightly fragmented landscapes ($\alpha_{H \rightarrow 1}^*$) lead to predator extinction as fragmentation increases (figure 2a), suggesting a large impact of fragmentation on foraging strategies that result in stable coexistence in weakly fragmented landscapes.

In the intermediate α regime, our model suggests that habitat fragmentation does not necessarily affect population densities negatively. Predator populations with $\alpha < 2$ display maximal densities for intermediate values of H (figure 3a), although densities do not decrease significantly when fragmentation decreases (H increases). Prey populations can benefit from high levels of fragmentation when predator movement approaches the ballistic regime, approximately for $\alpha \leq 2$ (figure 3b). This benefit results from ballistic predators rarely interacting with prey, which allows prey to avoid predation by taking advantage of fragmentation and spreading thinly. This aligns with established results obtained for predators performing area-restricted searches [45,47–49]. Such predators exert pressure on prey species to live well spaced out, and our results indicate that this is also true when predators are Lévy searchers. In our model, however, because prey are sessile and cannot space out during the predator–prey dynamics, they need to adopt such a spatial configuration in the initial condition. Moreover, these spatial

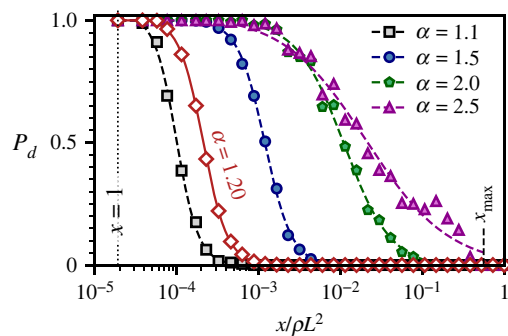


Figure 4. Influence of the Lévy exponent α on the probability of patch depletion, P_d , as a function of patch size x for an intermediate degree of fragmentation with $H = 0.5$. Dotted vertical lines indicate minimum patch sizes at $x = 1$ (single site). The dashed vertical line indicates the maximum patch size for this particular level of fragmentation and patches with $x > x_{\max}$ do not exist; hence, $P_d(x > x_{\max}) = 0$. All other parameters are as in figure 2. Lines are a guide to the eye, and the red curve displays P_d for the Lévy exponent that maximizes species richness ($\alpha = 1.2$; see figure 6, inset). Note that less diffusive foraging strategies (small α) result in less depletion as ρ_{eff} remains high.

distributions of prey are more prone to localized extinctions owing to stronger demographic fluctuations in small prey patches and to overpredation. This further inhibits the effectiveness of area-restricted search under our model assumptions, as both predator and prey tend to go extinct (figures 2 and 3; electronic supplementary material).

Next, we determine ecosystem health using a weighted species richness \mathcal{R} that captures how numerous predator and prey are relative to each other as well as the total population size within the environment (electronic supplementary material). We define the species richness as

$$\mathcal{R} = ({}^1D - 1)(N + M), \quad (3.1)$$

where $1 \leq {}^1D \leq S$ is the entropy-based diversity index and $S = 2$ is the total number of species in the system (see electronic supplementary material and, for example [50]). This metric for species richness predominantly follows predator density (electronic supplementary material, figure SI.5). However, because of the effect of prey density, the predator foraging strategy that maximizes species richness is consistently more ballistic than that maximizing predator density $\alpha_{\mathcal{R}}^* < \alpha_N^*$ (electronic supplementary material, figure SI.5). This shift results from the decrease in predator–prey interaction rates $\hat{\Lambda}$ when α decreases, which consequently increases prey population size.

3.2. Fragmentation induces irreversible habitat loss

As mentioned above, predators may induce irreversible prey habitat loss in fragmented landscapes because they overexploit small patches that cannot be recolonized because prey individuals are sessile. As a result, following predator extinction, prey population density does not converge to habitat density ρ (figure 2a). To investigate this further, we measure the patch depletion probability, P_d , as a function of patch size and predator foraging strategy (see the electronic supplementary material). Our results indicate that small patches have a higher depletion probability regardless of the predator foraging strategy α (figure 4), because they host smaller prey populations that are more likely to be exhausted and subjected to stronger demographic fluctuations. The effect of α

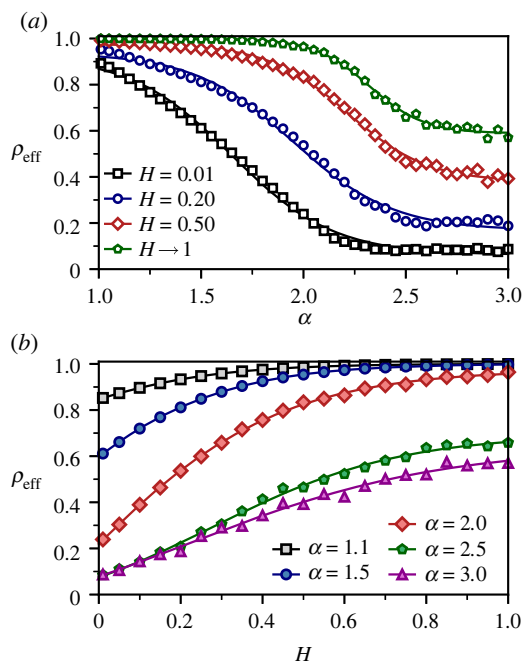


Figure 5. Influence of the Lévy exponent α and the Hurst exponent H on the effective habitat density ρ_{eff} in the quasi-stationary stable state. All other parameters are as in figure 2. Solid lines are a guide to the eye. See also electronic supplementary material, figure SI.7 for typical spatial configurations. (a) ρ_{eff} as a function of α for different H and (b) as a function of H for different α .

on the depletion probability is stronger for intermediate patch sizes as higher values of α lead to more local predation and, as a consequence, higher patch depletion probability (figure 4). Importantly, significant patch depletion occurs even when predators adopt foraging strategies that maximize species richness (electronic supplementary material, figures SI.6 and SI.7).

To further evaluate the impact of the patch depletion probability P_d on habitat loss, we define the effective habitat density ρ_{eff} as the fraction of initial habitat ρ that remains available to prey in the quasi-stationary stable state (figure 5). Ballistic foraging results in low levels of habitat loss, because predators rapidly go extinct and only a few small patches are depleted (figure 4). When α increases and short predator displacements become more frequent, the depletion probability is higher for a broader range of patch sizes (compare, for example, the curves for $\alpha = 1.1$ and $\alpha = 1.5$ in figure 4). As a result, effective habitat density is a monotonically decreasing function of the Lévy exponent and Brownian foragers minimize the effective habitat density regardless of the level of fragmentation (figure 5). However, how much habitat is lost in already fragmented landscapes will depend on the level of fragmentation. For example, Brownian foragers in slightly fragmented landscapes ($H \rightarrow 1$) eliminate approximately 40% of the initial habitat. In highly fragmented habitats, this percentage is approximately 90% and most of the prey–predator dynamics occurs in the few (relatively) large patches that remain available for prey.

Finally, we measure how habitat fragmentation affects effective habitat loss for different foraging strategies, α . As expected, ballistic predators minimize the effective habitat loss because they minimize predation rates (figure 5). In contrast, Brownian predators maximize effective habitat loss because they overexploit prey patches locally. Intermediate

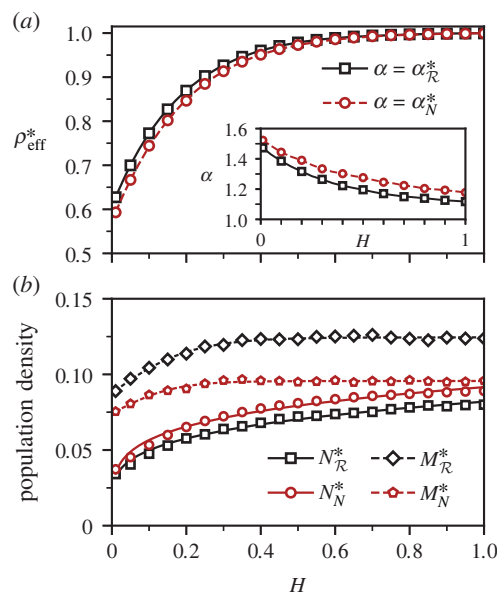


Figure 6. Effect of the optimal predator response α^* to a particular level of fragmentation defined by the Hurst exponent H . Optimal responses are considered to optimize either predator population N or species richness \mathcal{R} , denoted by their respective subscripts. All other parameters are as in figure 2. Solid lines are a guide to the eye. (a) Effective habitat density ρ_{eff} (main panel) and optimal response α^* (inset). (b) Predator and prey densities N and M .

values of α maximize the difference between effective habitat loss at low and high fragmentation (figure 5b). For foraging strategies that maximize species richness and predator densities (figure 6), increased fragmentation may result in an effective habitat loss of 40%. Importantly effective habitat loss is a nonlinear function of the fragmentation level with much faster decay when landscapes transition from slightly to highly fragmented (figure 6a). Population sizes, however, decay much more slowly in response to increased fragmentation (figure 6b), illustrating the importance of foraging strategies in maintaining the stability of ecological communities in response to increased fragmentation and habitat loss.

4. Discussion

Our stochastic predator–prey model reveals that the interplay between predator foraging behaviour and fragmentation strongly influences species persistence, ecosystem stability and prey habitat conservation (figure 7). Predator and prey populations, and the resulting species richness, are maximal for a specific predator foraging strategy α that depends nonlinearly on the spatial correlation of habitat H . Moreover, increased fragmentation reduces the range of possible α values that result in stable species coexistence (figures 2 and 7), which suggests a stronger evolutionary pressure on foraging strategies in highly fragmented environments. We considered here power-law dispersal kernels to model predator foraging; however, similar results have been found for predators exhibiting exponential dispersal kernels [51], which further supports that dispersal is a critical component of long-term ecosystem stability [13,52]. Moreover, as habitat fragmentation increases, prey habitat consists of more and smaller patches. Extinctions within these smaller patches are more likely to be due to overpredation and stronger demographic fluctuations, ultimately resulting in irreversible

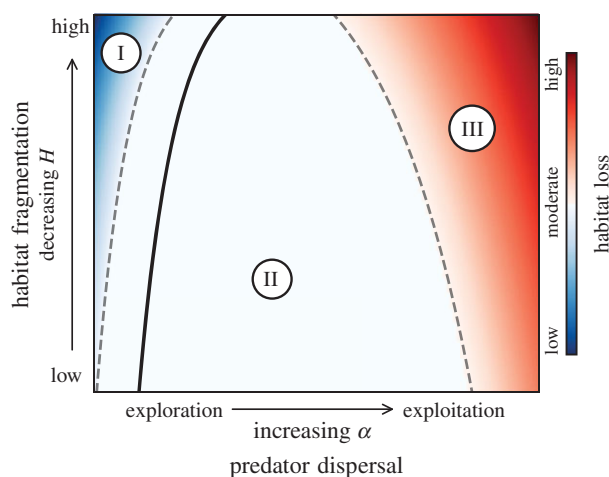


Figure 7. Schematic phase diagram that illustrates model outcomes for population dynamics and irreversible habitat loss as a function of habitat fragmentation and predator dispersal. Our model identifies three qualitatively distinct phases: (I) low habitat loss with predator extinction caused by lack of predation (blue), (II) predator–prey coexistence with moderate habitat loss (white), and (III) high habitat loss due to overexploitation of prey species, leading to full species extinction (red). The black solid line indicates the qualitative behaviour of optimal dispersal as a function of habitat fragmentation (see also figure 6, inset). The dashed lines indicate transitions between predator–prey coexistence (II) and predator extinction (I) or full extinction (III). Both the optimal dispersal value (solid line) and the transitions (dashed lines) are gathered and interpolated from simulation data (figure 2).

prey habitat loss. Our results suggest that optimal predator responses can decrease, but not prevent or minimize, the amount of lost habitat, and that this reduction is more pronounced when habitat is highly fragmented. The possible outcomes of our model for different predator foraging strategies and habitat fragmentation are summarized in figure 7.

Effective habitat loss mainly results from small patches becoming irreversibly depleted and only large patches remaining inhabitable (figure 4). As a result, the effective spatial correlation in the landscape increases, and prey fragmentation decreases, resulting in an effective H larger than the one used to generate the habitat landscape. Assuming that predators can rapidly respond to such a change in fragmentation, possible predator adaptations to this new habitat configuration should result in predators foraging more ballistically (lower α , figure 6, inset). Because habitat loss is less severe for lower values of α (figure 5), such a response can inhibit further habitat destruction. Hence, our results agree with previous work that indicated that predator dispersal can stabilize irreversible habitat loss and population declines [37,51,53–56].

Our model predicts that higher dispersal rates, represented by lower values of α , tend to increase ecosystem stability by allowing predators to exploit several prey patches. We neglect, however, all types of dispersal costs that could increase predator death rates when they travel between prey patches [57]. Including such costs might be especially relevant when studying the impact of fragmentation on species with low dispersal abilities, such as small mammals [58] and amphibians [59] (but see [60]). Additionally, we also make simplifying assumptions about the landscape. More specifically, we considered a binary lattice and globally fixed demographic rates. Instead, including matrix and edge effects on both predator dispersal and

prey reproduction—e.g. by studying a non-binary, heterogeneous habitat matrix [61], movement responses to habitat edges [62], etc.—might reveal potential (de)stabilizing effects that we did not find in our analysis. Furthermore, we did not consider interventions that increase landscape connectivity, e.g. designing corridors to connect spatially separated fragments allowing prey populations to repopulate previously exhausted patches [63,64]. Finally, we omitted habitat heterogeneity in predator reproduction rates, e.g. when a different habitat is needed for reproduction, such as aquatic breeding grounds for terrestrial amphibians [65,66]. Future work should incorporate these aspects and investigate their effects on ecosystem stability.

We also did not investigate the possible responses of the prey population to predation and habitat loss. In our model, prey is sessile and can only diffuse as a result of reproduction onto adjacent sites. Therefore, their only response to avoid local extinctions is to increase their reproduction rate σ . Hence, environments that contain static prey that cannot cross hard boundaries are subjected to an evolutionary pressure that might favour prey species with higher reproduction rates [67,68].

We also neglected several features that might affect predator foraging behaviour, such as satiation [69], interactions with conspecifics [70,71], spatial memory [72,73], long-range perception [74,75] and complex patterns of adaptive movement in response to prey encounters [22]. We further considered a trade-off between displacement length and predation efficiency that biases selection against ballistic movement. Although this choice is based on the existing literature on intermittent search [25], considering different shapes for this trade-off might alter our results. All these factors can change the optimal foraging strategy in landscapes with varying degrees of fragmentation and hence affect the impact of fragmentation on ecosystem stability.

Finally, higher order interactions are known to stabilize the population dynamics of multi-species systems [76–78] and extinctions in one trophic level may destabilize species' coexistence and cause extinctions higher up the trophic network [79,80]. Extending our framework to describe multi-species systems with more complex trophic interactions is needed to understand how foraging behaviour and fragmentation jointly determine ecosystem stability.

Our work displays the intricate interplay between foraging behaviour and habitat fragmentation, and highlights the role of dispersal on population persistence and ecosystem stability in fragmented landscapes. It furthermore shows how increased levels of fragmentation lead to higher irreversible habitat loss and how optimal foraging responses can reduce, but not prevent or minimize, the amount of lost habitat. Owing to their profound ecological consequences, our results suggest that future models of population dynamics should explicitly include optimal foraging arguments when discussing the potential effects of landscape fragmentation on ecosystem stability.

Data accessibility. Python code to reproduce the results of our model is freely available via Zenodo: <https://doi.org/10.5281/zenodo.6585088>.

The data are provided in the electronic supplementary material [81].

Authors' contributions. J.N.: conceptualization, formal analysis, investigation, methodology, project administration, resources, software, validation, visualization, writing—original draft, writing—review

and editing; P.S.: supervision, writing—review and editing; Y.K.: supervision, writing—review and editing; R.M.-G.: supervision, conceptualization, investigation, methodology, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed herein.

Conflict of interest declaration. We declare we have no conflict of interest.

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