

Habitat quality does not predict animal population abundance on frequently disturbed landscapes

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ABSTRACT

Increases in frequency of anthropogenic and natural disturbances exacerbated by climate change are disrupting animal movement patterns and, in turn, species distribution and abundance. Habitat models are a valuable approach for predicting how a species or population is distributed across habitats. However, in these models, the environmental characteristics describing habitat are typically constant over time which is inaccurate for a frequently disturbed landscape. The goal of this study is to assess the degree to which frequent disturbances can alter abundance and distribution, to the point of which inferences from static habitat maps are no longer relevant. We simulated individual animal movement in a dynamically disturbed landscape and compared the observed spatial relative abundance to the one predicted from a static habitat model fit to the simulated trajectories. We found that the prediction error is higher when the landscape is disturbed than where there are no disturbances. This result holds even with the addition of life-history and demographic processes to the model which would facilitate the discovery of novel habitat by increasing density-dependent movement, thereby bringing the spatial distribution of individuals closer to a proportion of habitat quality arising from the population at equilibrium assumption underlying most habitat models. In the context of species at risk recovery planning, using habitat models with constant environmental covariates to forecast animal locations in areas with more frequent disturbances as a result of climate change will likely produce inaccurate predictions.

1. Introduction

Large and unprecedented anthropogenic changes to the terrestrial systems are altering the distribution and abundance of global biodiversity (Raffa et al., 2008; Allen et al., 2010; Pereira et al., 2012; Boucher et al., 2018; Cadieux et al., 2020). Natural and anthropogenic disturbances are increasingly putting forest ecosystem and value at risk. The combined effect of multiple stressors exacerbated by climate change makes it difficult to understand and predict species responses to changes in the availability of essential resources (Mahon and Pelech, 2021). In boreal forest ecosystems for example, wildfires, insect outbreaks, drought, storms, and landslides are predicted to increase in frequency, intensity, and/or duration in the near future (Dale et al., 2001; Price et al., 2013). Our study focuses on these disturbances, whether natural or anthropogenic and their interactions, that present irregular spatio-temporal patterns so that animals are not able to anticipate them. As environmental conditions shift due to human activity and climate change, the modification of the size and location of natural habitats creates novel habitat conditions such as new land cover types,

where species responses include rapid population decline or proliferation and changes in phenology or distribution (Barnosky et al., 2011; Bellard et al., 2012; Pereira et al., 2012). Effective management of species-at-risk requires forecasting the quality and distribution of future habitats and the resulting viability of species populations (Unglaub et al., 2015; Heinrichs et al., 2017; Masood et al., 2017). Whereas relating populations to habitats is a central goal in ecology, predicting population abundance and demography in novel conditions remains challenging (He and Gaston, 2007; Weber et al., 2017). Model predictions of habitat quality in novel areas may be misleading due to unmeasured conditions (Johnson et al., 2020), leading to population sinks or ecological traps (Fretwell, 1969). However, a more fundamental concern for predicting population abundance across wide ranging and potentially disconnected novel habitats is the need to estimate whether, and over what time-span, a species population will discover and use habitat that emerges in currently unused areas. Indeed, whereas some species have strong negative responses to disturbances, others react positively to new opportunities created by some disturbance types (Fisher and Burton, 2018). For example, wolverines

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(*Gulo gulo luscus*) are attracted to foraging opportunities in areas of active logging (Scrafford et al., 2017). In this study, we focus on these positive relationships between a species and a disturbance type.

The probability that a species will discover and use novel habitat integrates the interacting effects of animal movement and demography, and the rate and predictability at which novel conditions, *i.e.* habitats of varying quality, emerge thereby determining the spatial and temporal landscape heterogeneity. For example, the effect of a wildfire on a caribou population (*Rangifer tarandus*) can be extremely complex over time, going from attraction to avoidance and back to attraction as different processes, such as windfallen trees, arise (Schaefer and Pruitt, 1991). When foraging, animal movement balances the need to leave recently depleted locations, return to known high quality patches (Charnov, 1976; van Moorter et al., 2009), and find new high quality habitat (Fahrig, 2007). When disturbances are frequent and memory of high quality habitat locations is less reliable, some species prioritize exploration leading to increased discovery and use of novel habitat (Travis and Dytham, 1999; Mueller and Fagan, 2008; Riotte-Lambert and Matthiopoulos, 2020). For example, Mongolian gazelle populations (*Procapra gutturosa*) experiencing unpredictable resource variations due to stochastic rainfalls display nomadic behaviour (*i.e.* low level of movement coordination; Mueller et al., 2011). Similarly, for red kangaroo populations (*Macropus rufus*), resource unpredictability leads to occasional and irregular excursions outside of the home range (Norbury et al., 1994). In contrast, barren-ground caribou populations experiencing predictable seasonal variations of their resources, display regular seasonal migration patterns (Mueller et al., 2011). However, other species display stronger site fidelity in unpredictable environments. For example, the Gunnison sage-grouse (*Centrocercus minimus*) chooses to always stay at the same nesting location when site quality is unpredictable (Gerber et al., 2019). Similarly, the green turtle (*Chelonia mydas*) have a high foraging site fidelity when their habitat is unpredictably disturbed (Dalleau et al., 2019).

Statistical models, such as species distribution models and habitat association models, characterize habitat from which abundance can be predicted (Weber et al., 2017). Increasing access to geographic information systems, remotely sensed data, computing power, and radio/GPS telemetry providing precise animal positional data (Northrup et al., 2013; Avgar et al., 2016) supported the expansion of many environmental-statistical modelling approaches, including logistic regressions and non-parametric equivalents, to become valuable approaches for predicting how a species or population is distributed across habitats (Boyce et al., 2016). Typically, in these methods, the environmental characteristics describing habitat are constant over time (Nielsen et al., 2010) and habitat use reflects the quality and abundance of resources (Fretwell and Lucas, 1969; Boyce and McDonald, 1999). These assumptions mean that the target population has reached an equilibrium (Boyce and McDonald, 1999), *i.e.* individuals distribute themselves in the landscape proportionally to the resources. When resource distribution or spatial availability and population demography vary over time, habitat models would fail to accurately predict population spatial distribution and abundance. Researchers have developed models that consider the unequal access to all locations of a domain (*e.g.* Forester et al., 2009; Avgar et al., 2013; Latombe et al., 2014). Furthermore, models can be modified to include temporal changes in the habitat characteristics (*e.g.* Keith et al., 2008; Nielsen et al., 2010; Zeller et al., 2020). But implementing temporal dynamics requires regular measures of the habitat characteristics, which is considerably more data than for a static landscapes, or at least an understanding of the mechanisms underlying landscape changes in order to simulate these variations.

Without inclusion of an estimate of the relative effects and the associated uncertainty of animal movement, demography, and landscape heterogeneity on the probability of use of novel habitat, model predictions of species population or distribution across dynamic environmental conditions will be biased in time or space (*e.g.* Vallecillo

et al., 2009). The objective of this study is to use a simulation model that includes dynamic and unpredictable habitat disturbances, exploration, heterogeneous resource access, dispersal, and demography in the study species to evaluate how these variables impact the accuracy of relative abundance predictions based on a static representation of recent habitat. The results could help understand the consequences of violating a key assumption of commonly used habitat models: a population at equilibrium in a static landscape or rapid arrival at equilibrium in a dynamic landscape such that landscape dynamics can be ignored.

2. Material and methods

We used the R software (R Core Team, 2020) for all simulations and calculations.

We created a spatially explicit landscape *in silico* that was subject to dynamic and unpredictable disturbances. After disturbances, habitats gradually returned to their previous states prior to disturbance, but disturbances provided windows of opportunities for any intraspecific aspect such as foraging, nesting, territory, thereafter called “resources”. In this idealized system, we simulated movement of our target animals using a modular individual-based simulation model that included demography, dispersal, exploration, and movement. Target animals were of a theoretical species with the following characteristics. Individuals notice habitat changes and respond to them via movement. An increase in population density decreases habitat quality. For this purpose, we used (Hall et al., 1997)’s definition of habitat quality, *i.e.* “the ability of the environment to provide conditions appropriate for individual and population persistence”. Disturbances create resources, thereby increasing habitat quality which prompts a positive response from the individuals. We chose these characteristics with species of large primary consumers in a forested habitat in mind. However, any species following these characteristics would fit in the context of this study. Note that we did not include temporal changes in habitat preference. Therefore, migration patterns or population adaptation, which could either encourage or prevent new habitat discovery depending on the context, are not represented in this study.

In order to investigate the effects of local variations in the ecosystem dynamics and life-history of our target animal, we simulated scenarios of individual movement on a theoretical but spatially-explicit domain (described in Section 2.1) using the movement model developed by Avgar et al. (2013) described in Section 2.3. Then, we used the individual trajectories obtained by the simulations and the habitat characteristics of our domain to estimate a resource selection function (RSF) and predict the spatial relative abundance of the population (Section 2.4). Finally, we compared the predicted spatial relative abundance to the one observed at the end of the simulations (Section 2.4). A conceptual diagram summarizes these processes (Fig. 1).

We defined five different scenarios such that each scenario addressed a source of local variation. In the control scenario, a single individual moved in a dynamic landscape (resource depletion and regeneration) without disturbances. In the other four scenarios, the domain was subjected to the habitat dynamics with disturbances described in Section 2.2. In the “disturbance only” scenario, a single individual moved in a dynamic landscape (Section 2.6). In the “barriers” scenario, a single individual moved in a dynamic landscape featuring geographical barriers to movement (Section 2.7). In the “scramble competition” scenario, several individuals shared the same dynamic landscape and depleted resources resulting in negative density-dependence (Section 2.8). In the “demography” scenario, several individuals shared the same dynamic landscape and were subjected to demographic processes (Section 2.9).

We chose these scenarios to assess how habitat disturbances can break the population equilibrium assumption on their own and in combination with other common local spatio-temporal variations (barriers to movement, population density, and demographic processes).

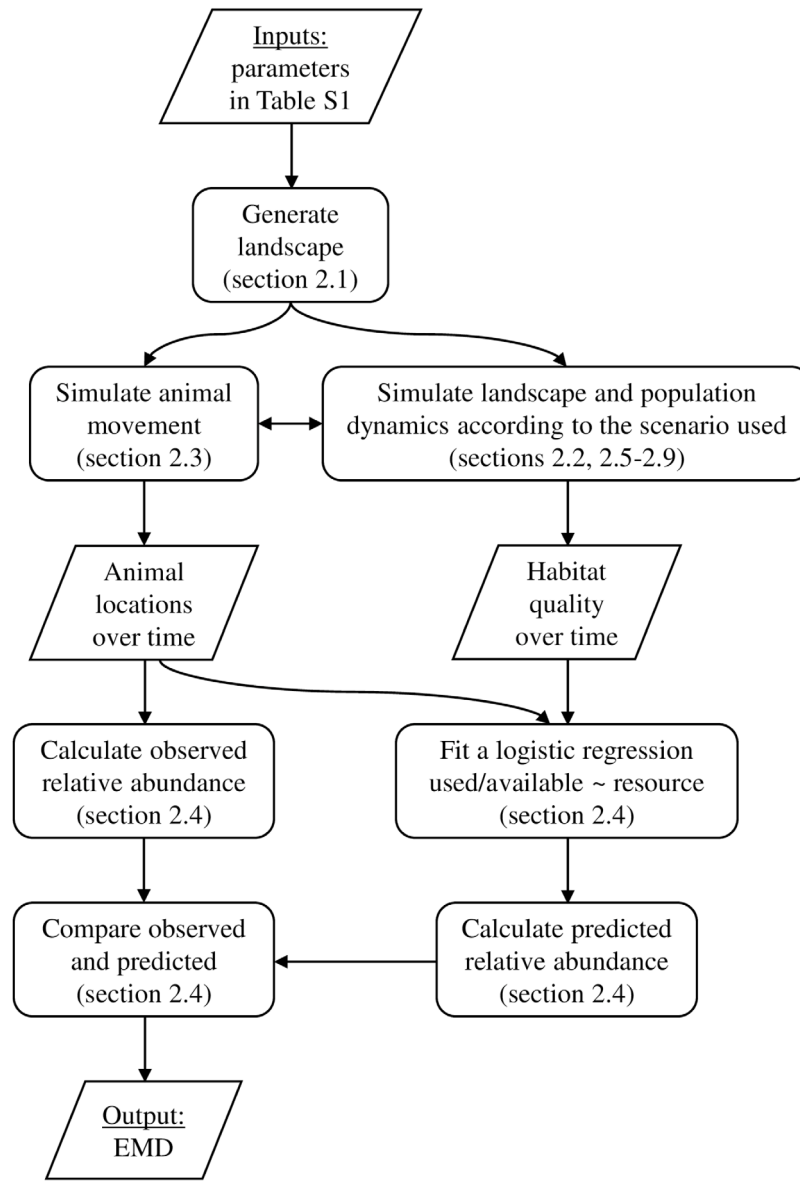


Fig. 1. Conceptual diagram of the processes implemented in this study to obtain the spatial relative abundance prediction error: landscape dynamics generation, individual-based movement model, resource selection function, Earth mover's distance computation.

We would expect that increased step length or the addition of juvenile dispersal should decrease differences between the utilization distribution proportional to resources and the simulated population abundance because individuals are able to reach better resources more easily. Introducing barriers to movement would have the opposite effect by preventing individuals from reaching better resources. Increasing population density would push individuals away due to local decreases in resource forcing them to distribute themselves proportionally to the resources.

2.1. Spatial domain

We defined a 32×32 squared landscape composed of 1166 hexagonal cells where each cell had a resource value between 0 (low) and 1 (high). We chose a hexagonal grid as it is more appropriate than a rectangular grid to model landscape connectivity and movement paths (Birch et al., 2007). In all scenarios but the barriers scenario, the resource values were spatially distributed according to a midpoint displacement neutral landscape model (*i.e.* fractal) using the function `mpd` of the `NLMpy` python package with a level of autocorrelation

set to 0.7 (Etherington et al., 2015). Therefore, cells with high level of resources were spatially arranged in patches (see Fig. 2A for the example of the disturbances only scenario). We defined the domain as a torus which meant that individuals disappearing on one side would reappear on the opposite side.

In the barriers scenario, the domain consisted of two layers: a resource layer and a barrier to movement layer (Fig. 2B). We manually organized cells with medium to high resource level to be surrounded by cells with low resource level (Fig. 2B right panel) in order to reproduce an example of a realistic landscape. Furthermore, the low resource cells could act as partial or complete barriers to movement (value of 1: complete barrier) or facilitated movement (value of 0: no barrier; Fig. 2B left panel). The medium to high resource cells neither restrained nor facilitated movement (value of 0.5). Values were smoothed in-between these features by spline interpolation using the `interp` function of the R package `akima` (Akima and Gebhardt, 2020). In this scenario, the domain boundaries were reflective, as a torus would defeat the purpose of the barriers. In the context of an ungulate, this landscape could be interpreted as valleys (medium to high resources, no impact on movement) surrounded by mountains (low resources,

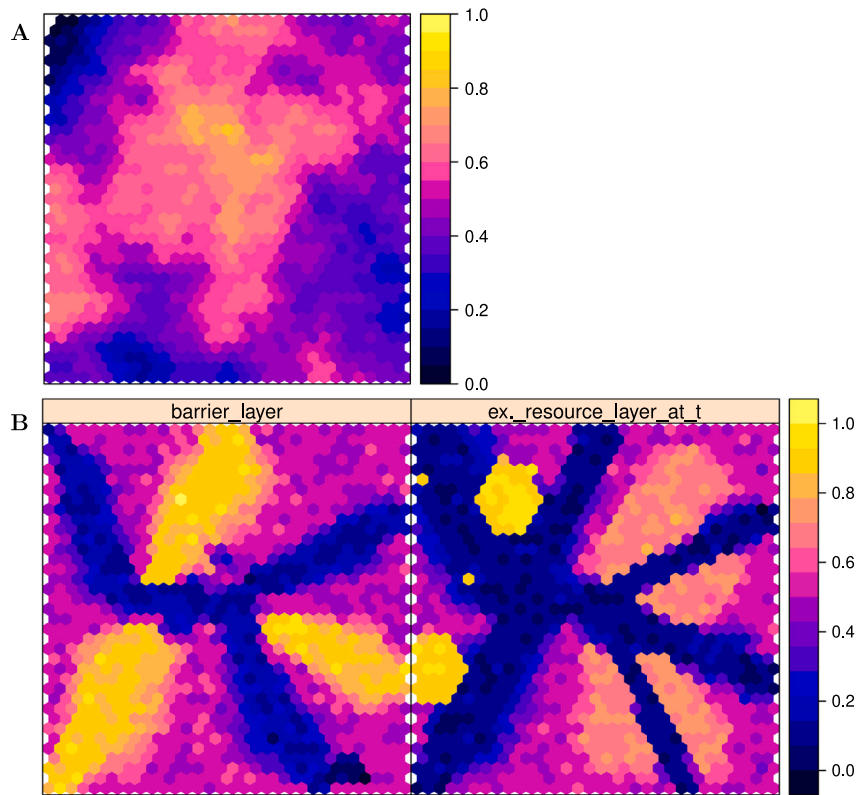


Fig. 2. Spatial domain with one layer used in the disturbances only scenario where resources are generated using a midpoint displacement neutral landscape model (panel A) and spatial domain with two layers used in the barriers scenario (panel B): barriers to movement (left) and example of resources during the simulation where successive disturbances created patches of excellent habitat on the left of the domain (orange–yellow) (right). Regarding resources, the colours represent the resource value: low/0 (black) to high/1 (yellow). Regarding barriers to movement, the colours represent the cost of crossing over a cell: low/0 (black) to high/1 (yellow).

barriers to movement) and connected by roads (low resources, facilitate movement). In the context of a small mammal or reptile, this landscape could be interpreted as foraging or nesting areas surrounded by barriers such as roads and other human infrastructures and connected by blue and/or green corridors.

2.2. Disturbance regime

We disturbed the domain described in Section 2.1, *i.e.* created novel habitat, by changing the resource values in affected cells. At each time step, affected cells were located within a circle with its centre randomly selected within the entire domain (except for the barrier scenario, see Section 2.7) and radius drawn from a power law distribution. Therefore, at the scale of a cell, the disturbance frequency depended on the power law scaling parameter k . The disturbance magnitude was constant: we set the average resource value of the affected cells just after disturbance to 0.95 which means that disturbances created resources, thus generating new habitats. This represents, for example, a fire creating an open area in a forest where shrubs can grow and provide resources for ungulates.

To investigate the changes in population spatial relative abundance due to the disturbance rate, we explored the values 2.0 to 3.0 by increments of 0.1 for the power law scaling parameter k representing the disturbance rate. This range of values covers landscapes subjected to few disturbances to highly disturbed landscapes (Supplementary Information Fig. S.1). A value of 3.0 would lead to fewer disturbances than a value of 2.0. After the simulations, we recorded the cumulative number of cells affected by a disturbance over time and space. For a same combination of parameters in each scenario, we kept the disturbance locations and sizes the same over the simulations to be able to combine the simulation results for the rest of the analysis. Therefore, different scenarios or parameter combinations had different realized values of disturbance locations and sizes.

2.3. Movement model

We used the movement model from Avgar et al. (2013) in which an individual chooses its next location in the domain depending on the attractiveness of each cell calculated from the habitat quality as perceived by the individual. We chose this model because it captures the processes by which we hypothesize an individual animal discovers and uses new habitat, namely habitat quality, experience, and memory, which lead to the use and loss of information. Eq. (1), (2), and (3) are reproduced from Avgar et al. (2013) for a single habitat component. See Supplementary Information Table S.1 for parameter values.

The perceived habitat quality $q_{j,t}$ in spatial cell j at time t was calculated following:

$$q_{j,t} = e^{-\alpha d_{j,t}/\Delta t} Q_{j,t} + (1 - e^{-\alpha d_{j,t}/\Delta t}) \times (e^{-\beta \Delta t} q_{j,t-\Delta t} + (1 - e^{-\beta \Delta t}) q^*) \quad (1)$$

where $d_{j,t}$ was the Euclidean distance (or cost distance in Section 2.7) between the current location and cell j , $Q_{j,t}$ was the actual habitat quality, α was the sensory attenuation coefficient, Δt was the time step, β was the memory decay coefficient, and q^* was the default expectation of habitat quality. Therefore, the individual's perception of a cell's quality changed from perfect knowledge to default expectation as distance to the individual and time to last visit increased.

The attractiveness $A_{j,t}$ of a cell j at time t was calculated following the equation:

$$A_{j,t} = e^{-\gamma d_{j,t}/\Delta t} q_{j,t}^\omega \quad (2)$$

where γ was the friction coefficient and ω was the attraction toward the habitat (a negative value represents repulsion). Therefore, cell attractiveness depended on perceived habitat quality and was higher for the cells that were within the animal's reach.

The probability $p_{j,t}$ of the individual relocating at location j at time t was:

$$p_{j,t} = \left(\frac{I(d_{j,t} \leq d_{\max})A_{j,t}}{\sum_j I(d_{j,t} \leq d_{\max})A_{j,t}} \right)^\theta \quad (3)$$

where $I(\cdot)$ was an indicator function with value 1 if the argument was true and 0 otherwise, and $d_{\max} = -\Delta t \ln(0.01)/\gamma$ (i.e. the redistribution kernel was truncated where the travelling propensity was below 1%). This process helped reduce the computing power required by dropping very low probabilities to zero. We added to the (Avgar et al., 2013) model the exponent θ , which controls the level of determinism of the cell selection process: $\theta = 0$ represented a random choice whereas $\theta \rightarrow \infty$ represented a deterministic choice (i.e. the location with the highest probability was always selected). The animal's next step was then randomly selected in the domain according to the probability distribution $p_{j,t}$.

The individual started in a random location in the domain, except for the barrier scenario where the individual started in the centre of the landscape (Section 2.7), and moved for 300 time steps.

To have a better understanding of how the scale of movement (step length) impacts spatial abundance, we explored the values 4.5, 0.915, 0.46, 0.307, 0.23, 0.184, 0.1535, 0.1151, 0.0921, 0.0614, and 0.04605 for the movement friction coefficient γ which corresponded to the values 1, 5, 10, 15, 20, 25, 30, 40, 50, 75, and 100 for the maximum distance covered in one time step d_{\max} (values between 75 and 100 allow an individual to cover the entire domain in one time step whereas values between 1 and 10 restrain individuals to the nearest locations). After the simulations, we recorded the average of the realized animal step length over time, number of individuals, and number of simulations. In preliminary simulations, values of $d_{\max} > 100$ did not correspond to higher values of realized step length (see Supplementary Information Fig. S.2).

2.4. Resource selection function and spatial relative abundance

We compared the predicted relative abundance of animal locations modelled from an RSF and the observed relative abundance obtained at the end of the simulations. For each parameter combination and scenario, we randomly selected a subset of 30 individual trajectories from the last 50 time steps of the movement model output (all simulations pooled). We then randomly generated 1166 alternative locations in the entire domain (i.e. on average one alternative location per cell). Finally, we fitted a logistic regression modelling the response variable "used step" (which takes the value "used" for the 30 individual trajectories and "available" for the 1166 alternative locations) as a function of the simulated landscape habitat values to this newly created used/available dataset. See Supplementary Information A for details on the choice of RSF over step selection function.

We calculated the predicted relative abundance over space by taking the probability density $U_{\text{pred}}(j)$ for each cell j using the following equation:

$$U_{\text{pred}}(j) = \frac{w(j) \times 1}{\sum_j w(j) \times 1} \quad (4)$$

where each cell had an area of 1 and the logistic discriminant $w(j) = \exp(\beta x(j))$ was obtained using the coefficient β from the logistic regression and a new dataset $x(j)$ consisting of the average of the resource during the last 50 time steps for each cell j . We used the average of the last 50 time steps in order to reproduce what could be predicted of a future landscape under disturbances. In additional simulations, using the average of the last 50 time steps lead to less prediction error than using the last two time steps (Supplementary Information B).

We calculated the observed relative abundance over space by taking the probability density $U_{\text{obsv}}(j)$ for each cell j using the final location

of all individuals (all simulations pooled) as described by the following equation:

$$U_{\text{obsv}}(j) = \frac{\text{number of individuals in cell } j}{\sum_j \text{number of individuals in cell } j}. \quad (5)$$

We compared the observed and predicted relative abundances using the Earth mover's distance (EMD; Rubner et al., 2000) using the function `emd` of the R package `emd` (Urbanek and Rubner, 2012). The EMD, also called the Wasserstein metric, is a measure of the difference between two distributions by calculating the cost of transforming one distribution into the other. This metric allowed us to obtain a single number representing the difference between two 2-dimensional distributions.

2.5. Control

A single individual moved on a landscape where resources could be depleted and regenerated over time. We performed 5000 simulations with a very large step length ($\gamma = 0.001$ corresponding to $d_{\max} = 4605$) and no disturbances, and repeated this process 100 times. At each time step, we

1. selected the animal's new location $L(t)$ according to $p_{j,t}$,
2. depleted the resource at location $L(t)$ by an amount $\sim \mathcal{N}(\text{depl}, 0.01)$,
3. updated the habitat quality perceived value at location $L(t)$ to be the real habitat quality after resource depletion,
4. regenerated the habitat quality of each cell of the entire domain toward the initial values $Q_{j,1}$ (decrease or increase) by an amount $\sim \mathcal{N}(\text{reg}, 0.01)$ which allows habitat recovery after depletion up to time t and after disturbances (absent in the control scenario) up to time $t - 1$.

2.6. Disturbances only

In the disturbances only scenario, a single individual moved in a dynamic landscape where resources could be depleted, regenerated, or exposed to disturbances. We repeated simulations 5000 times for each combination of γ and k (121 combinations) so we obtained 5000 individual trajectories per combination. In addition to the steps described in Section 2.5, we

5. introduced one disturbance of radius $\sim \mathcal{P}\ell(\min = 0.2, k)$ randomly located in the domain where $\mathcal{P}\ell(\cdot)$ is the power law distribution, and
6. modified the resource value of the cells affected by the disturbance to an amount $\sim \mathcal{N}(\text{dis}, 0.02)$.

2.7. Barriers to movement scenario

This scenario implemented the habitat dynamics described in Section 2.6 with disturbances only located in the top left corner of the domain (see below). We implemented barriers to movement (described in Section 2.1) by adjusting the cost of movement across the landscape using graph theory and the least cost path method. Specifically, we created a landscape of resistance (Fig. 2B left panel) where a value of 1 characterize a location where movement was impeded whereas a value of 0 represented a location where movement was facilitated. Using these resistance values as weight, we calculated the length of all the shortest paths from or to the locations in the domain using the function `distances` of the R package `igraph` (Csardi and Nepusz, 2006). We then used the resulting matrix of cost distance (as opposed to Euclidean distance) in Eqs. (1), (2), and (3) for the parameter $d_{j,t}$.

The main barriers to movement isolated the top left corner of the domain, which was only accessible by a small opening (Fig. 2B). Another barrier in the bottom right corner helped define other resource areas but did not isolate part of the landscape. The individual started in the middle of the domain. On this side, there were resource patches

of medium quality. In the top left corner area, however, disturbances created several new patches of high quality over time (see second row of Supplementary Information Fig. S.1). This scenario can be interpreted as a disturbance creating a high amount of resources in an area previously unused by a population. However, the access was limited which means that individuals did not have free and equal access to the entire domain.

2.8. Scramble competition scenario

This scenario implemented the habitat dynamics described in Section 2.6 with one exception: multiple animals interacted with the same landscape at the same time. As resources were locally depleted by individuals, they became unavailable for others, such that individuals moved away to more abundant locations and, thereby, this process introduced negative density-dependence in their movements. We simulated animal densities ranging from 1 to 700 individuals. The number of simulations for each combination of γ , k , and density (1452 combinations) was 5000 divided by the density and rounded up. This calculation allowed us to get approximately 5000 individual trajectories per combination, matching the other scenarios. At each time step, we selected the new locations $L(t)$ of all animals according to the corresponding perceived habitat quality $p_{j,t}$ of each individual. Then, we simulated the habitat dynamics described in Section 2.6 with the following modification: resource depletion happened at all locations $L(t)$ and if several animals shared the same location, depletion was accumulated.

2.9. Demography scenario

This scenario implemented the habitat dynamics described in Section 2.6 and the scramble competition described in Section 2.8 with an initial density of 50 individuals over the entire landscape. Additionally, we implemented four demographic processes: adult survival, fecundity, juvenile dispersal and recruitment. We tested three subscenarios: increasing, stable, and decreasing population size over time. We specified this change in population size using the values of the demographic processes described below (Supplementary Information Table S.1). We performed 50 simulations for each combination of γ , k , and population size change (363 combinations), which allowed us to obtain on average 3341 individual trajectories per combination. In this case, the computing power available (i.e. 20 CPU cores Intel Xeon E5-2689 v4 3.1 GHz with 512 GB RAM) limited the number of simulations.

2.9.1. Adult survival

To account for survival over time as a function of the habitat recently encountered by individuals, we calculated the probability of survival of an individual at each time step according to:

$$S_{t,\text{ind}}^a = 1 - m_a(1 - Q_{\text{past}}) - \lambda, \quad 0 \leq Q_{\text{past}} \leq 1 \quad (6)$$

where λ was the hazard constant over the landscape and time period ($0 \leq \lambda \leq 1$), m_a was the added mortality if the individual's two previous locations were of quality 0 ($0 \leq m_a \leq 1 - \lambda$), and Q_{past} was the actual past habitat quality of the habitat the two previous time steps at the location of the individual. The past quality of a location at the last two time steps was calculated according to:

$$Q_{\text{past}} = \begin{cases} \frac{1}{2} \sum_{j,t-i}^2 Q_{j,t-i} & \text{if } \omega \geq 0, \\ \frac{1}{2} \sum_{j,t-i}^2 (1 - Q_{j,t-i}) & \text{otherwise.} \end{cases} \quad (7)$$

This allowed us to take into account how the individual relied on the habitat type (repulsion or attraction represented by ω). Therefore, the survival probability of an individual up to time declined over time and survival was more likely when the individual was located in locations of good quality the previous two time steps. We drew the survival event at t from a Bernoulli distribution with probability of survival $S_{t,\text{ind}}^a$.

2.9.2. Fecundity

To account for fecundity as a function of the habitat recently encountered by individuals, we calculated the probability for each individual to produce a youngling at each time step according to:

$$F_{t,\text{ind}} = \begin{cases} f Q_{\text{past}} & \text{if population size} < K, \\ 0 & \text{otherwise,} \end{cases} \quad (8)$$

where f was the birth rate of new individuals in an habitat of past quality 1 ($0 \leq f \leq 1$) and K was the carrying capacity of the domain. Therefore, individuals who had access to high quality resources were more likely to reproduce. We drew the birth event at t from a Bernoulli distribution with probability $F_{t,\text{ind}}$.

2.9.3. Juvenile dispersal and recruitment

Juveniles did not have the adult's memory of the environment so their perceived habitat quality was set to the default expected quality q^* . Juveniles immediately dispersed from the parent location randomly in any direction by a distance $\sim \mathcal{N}(d_y, 5)$ where d_y was the average juvenile dispersal distance. We set this value to half of the domain size, i.e. 16. We assumed that juveniles dispersed on a straight line.

We assumed juveniles recruited to adults and joined the population if they survived dispersal, which was a function of habitat encountered during its dispersal journey described by:

$$S_{t,\text{ind}}^y = 1 - m_y(1 - Q_{\text{journey}}^y) \quad (9)$$

where Q_{journey}^y was the average quality of the locations on the juvenile's dispersal journey and m_y was the probability of the juvenile dying if the locations on its dispersal journey were of average quality 0 ($0 \leq m_y \leq 1$).

The average quality of the locations on the juvenile's dispersal journey was calculated according to:

$$Q_{\text{journey}}^y = \begin{cases} \frac{1}{\text{path length}} \sum_{j \in \text{path}} Q_{j,t} & \text{if } \omega \geq 0, \\ \frac{1}{\text{path length}} \sum_{j \in \text{path}} (1 - Q_{j,t}) & \text{otherwise.} \end{cases} \quad (10)$$

Therefore, juvenile recruitment after dispersal increased with the average habitat quality along the dispersal path. We drew the juvenile survival event at t from a Bernoulli distribution with probability of survival $S_{t,\text{ind}}^y$. If the juvenile survived, it became adult and followed the regular movement rules on the following time step.

2.10. Statistical analysis

The response variable EMD represented the error between the RSF predictions and the observations of relative abundance measured at the end of each scenario. We performed pairwise Mann-Whitney rank sum tests with Bonferroni correction on the EMD values among scenarios (pairwise.wilcox.test function of the R package stats). We used a non-parametric test since the EMD does not follow a normal distribution. Furthermore, to reveal non-linear patterns in the relationships between the covariates step length or disturbance rate, and the response variable EMD, we used a generalized additive model (GAM) approach using the gam function of the R package mgcv (Wood et al., 2016). Additionally, we added to the model the covariate animal density for the scramble competition scenario and the factor change in population size for the demography scenario. Each covariate was passed into a smoothing function with parameters selected by a restricted maximum likelihood approach (REML; Wood, 2011; Wood et al., 2016) before being passed into a linear model.

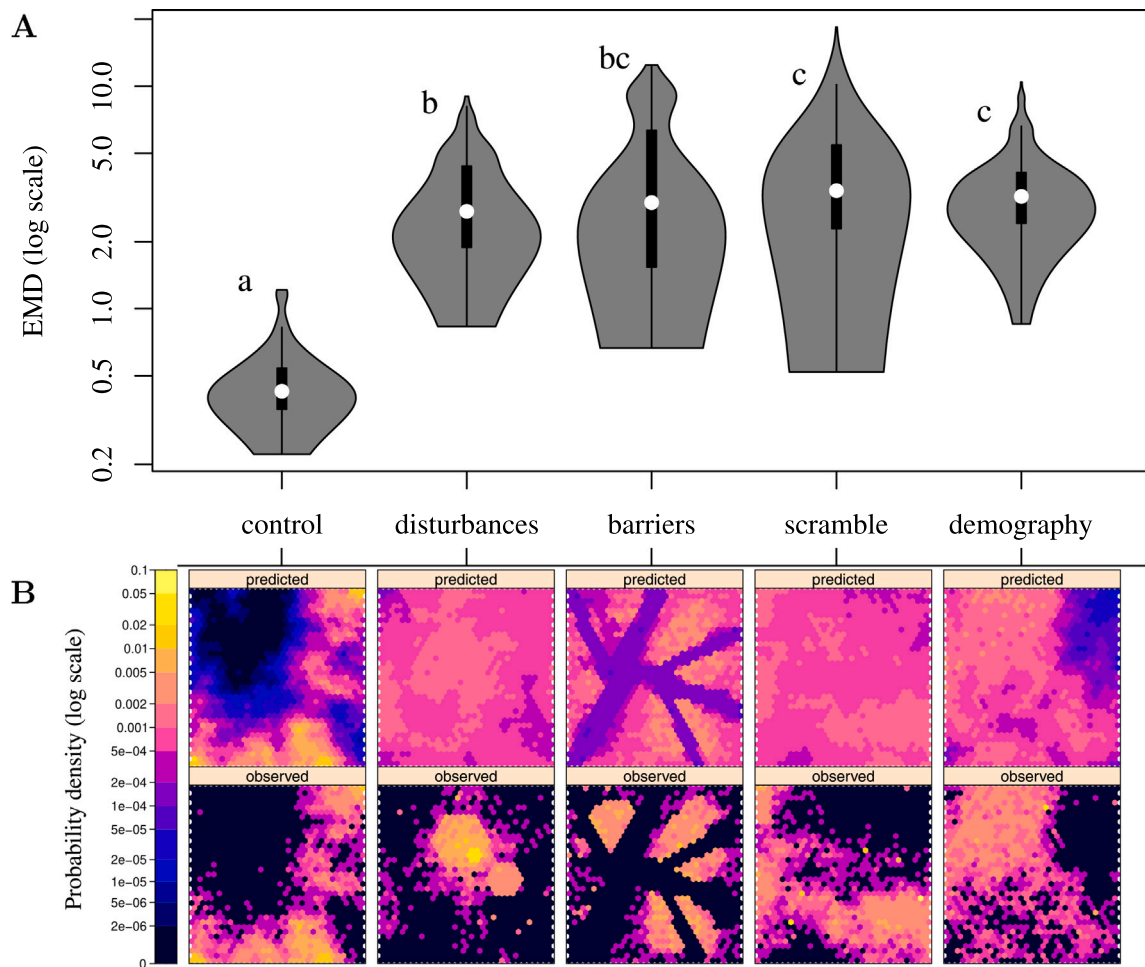


Fig. 3. Earth mover's distance (EMD; panel A) for each scenario and examples of corresponding population relative abundances (panel B; predicted from the resource selection function fit in the top row, and observed in simulations in the bottom row). Scenarios sharing the same letter in panel A) do not have significantly different EMD values (pairwise Mann–Whitney rank sum tests with Bonferroni correction and a significance threshold of 0.05). In panel B), the relative abundances examples showcased come from simulations with the following values for the EMD, average step length, and cumulative number of affected cells, respectively: 0.42, 15.97, 0 for the control, 7.52, 7.37, and 5,445 for the disturbances only scenario, 3.05, 7.33, and 2,031 for the barriers scenario, 4.65, 9.14, and 6,002 for the scramble competition scenario with 50 individuals, 4.08, 7.43, 5,636 for the demography scenario with increasing population size.

3. Results

The error of relative abundance predictions (*i.e.* EMD) calculated using the RSF in scenarios with disturbances, barriers to movement, density-dependence, demography, and dispersal were four to ten times larger than when they were no disturbances (pairwise Mann–Whitney rank sum tests with Bonferroni correction, p -values < 0.001 , $n = 2, 157$; Fig. 3A). Moreover, the prediction error from the disturbances only scenario was slightly lower in average than the prediction error from the scramble competition and demography scenarios (pairwise Mann–Whitney rank sum tests with Bonferroni correction, respectively p -value < 0.001 and p -value = 0.038, $n = 2, 157$; Fig. 3A). The population relative abundance predicted using the RSF function was always more spatially uniform than the one observed at the end of the simulations in all scenarios (examples in Fig. 3B).

Overall, the EMD showed highly non-linear relationships with the average step length and the cumulative number of cells affected by disturbances (Table 1, Fig. 4, Fig. 5). However, the GAMs were a poor fit to data (see “deviance explained” in Table 1, Fig. 4) except for the barriers scenario. In this scenario, the EMD decreased 5-fold for a small step length increase and then plateaued. Additionally, the EMD was 5 times higher when the domain was highly disturbed than when it was little disturbed (Fig. 4 second row).

4. Discussion

In this study, we show that population disequilibrium arising from realistic landscape dynamics, resources access, demography, and survival highly impact the spatial abundance of individuals through their movement. Therefore, our results confirm that predictive models that assume populations at equilibrium and a static landscape produce biased spatial relative abundance. Furthermore, the prediction error is higher on a landscape with disturbances than without whether life-history and demographic processes are present or not. This result suggests that population spatial abundance can be more sensitive to local variations in landscape dynamics, such as unpredictable disturbances, rather than variations arising from life-history and demographic processes at a small spatio-temporal scale. When a population is not at equilibrium, Boyce et al. (2016) suggests to include population density to model abundance. We show that, under frequent disturbances, this is not enough, even when there are no other factors influencing fitness.

Increases in the disturbance rate generally increases the prediction error and the animal step length has a varied impact on the prediction error depending on the scenario. However, the low deviance explained by the models (with the exception of the barrier scenario) highlights the high variability in prediction error which prevents us from drawing strong conclusions from these patterns. This high uncertainty in the

Table 1
Summary of the generalized additive model results.

Scenario	Variable	<i>p</i> -value	Deviance explained	Sample size
Disturbances only	Average step length	< 0.001	38.2%	121
	Cum. # of affected cells	< 0.001		
Barriers	Average step length	< 0.001	63.7%	121
	Cum. # of affected cells	< 0.001		
Scramble competition	Average step length	< 0.001	29.7%	1452
	Cum. # of affected cells	< 0.001		
	Individual density	< 0.001		
Demography	Average step length	0.226	11.7%	363
	Cum. # of affected cells	< 0.001		
	Increasing vs stable pop. size	0.291		
	Increasing vs decreasing pop. size	0.012		
	Stable vs decreasing pop. size	0.134		

result suggests that disturbances have a highly varying effect on population spatial relative abundance. Increases in exploratory behaviour often result from low environmental predictability (Mueller and Fagan, 2008; Riotte-Lambert and Matthiopoulos, 2020). When this movement pattern follows stochastic occurrences of novel habitat, the resulting population spatial distribution would indeed randomly deviate from the habitat model predictions.

We would expect that increased movement should decrease differences between the proportional distribution of individuals to the resources and the simulated population abundance because individuals are able to reach better resources more easily (Moorcroft and Barnett, 2008). We would also expect that adding juvenile dispersal (over distances larger than the average step length) would enable individuals to reach good habitat quickly. This should make simulated results proportional to resources, and the deviations of the habitat model predictions from simulations should decrease. However, increasing step length (*i.e.* increasing accessibility) in our model does not decrease the prediction error (except for the barrier scenario) and neither does the inclusion of juvenile dispersal (demography scenario). A possible explanation is that, in our simulations, the resource availability used by the model (*i.e.* the entire domain) is likely representative of what is actually available to the simulated individuals in the case where there are no movement impediments. Thus, habitat selection in our simulations is done at the scale of the home range or within the home range (second- and third-order selection; Johnson, 1980). In a larger simulated domain, *i.e.* in a domain with areas that are inaccessible to individuals with small step length, such decrease of the prediction error should become apparent similarly to what we observe in the barriers scenario.

Moreover, these results differ from Barnett and Moorcroft (2008) where step length dictates the population spatial abundance in a habitat constant in time without disturbances: at very large step length, the population spatial abundance steady-state is proportional to the RSF whereas it is proportional to its square at very small step lengths. Therefore, including disturbances changes this relationship due to their transient and stochastic nature. Similarly, transient population dynamics (allowed in the demography scenario) can affect local survival and therefore the final population spatial abundance (*e.g.* Courtois et al., 2007; Shriver et al., 2019). These local changes in population and habitat dynamics are expected. Yet, they are not taken into account when predicting population spatial abundance using habitat models.

While climate change is driving more variability in natural disturbances regime in boreal forests, it is essential to account for uncertainties arising from unpredictable ecosystem dynamics (Vallecillo et al., 2009; Schindler and Hilborn, 2015). Management plans built from deterministic projections of central tendencies of ecosystem dynamic drivers lose efficiency by failing to take into account uncertainty (Daniel et al., 2017). In our simulations, we show that the error amplitude that results from ignoring animal movement and demography in response to landscape dynamics when projecting relative abundance is significant. Dynamic habitat models, where the resource

quality is derived for each time step, are a possible methodological solution to unpredictable ecosystems (Nielsen et al., 2010). However, forecasting the resource variations under climate change needed for this method can be challenging or highly uncertain in itself (*e.g.* Braunsch et al., 2013). Our results suggest that models that account for local variations in ecosystem dynamics, animal distribution, behaviour and demography will provide improved estimates of uncertainty when enough simulations are run. Whereas the model we created in this study could be used for that purpose, it requires extensive parametrization and prior information concerning animal vital rates, movement, and cognition. When such information is missing, we recommend the inclusion of as much information of this kind as possible, even if only the species' current distribution, generation time, or movement speed. Nonetheless, researchers must account for landscape dynamics and the associated animal life history response in areas affected by disturbances in order to address the uncertainty around spatial abundance projections.

Our model does not account for the fact that disturbances can be a novel phenomenon for individuals. They might be reticent in using the resource created depending on their risk-taking level. Our analysis also omits the potential immediate negative effects of disturbances and focuses only on resource creation. Indeed, we used a positive magnitude for disturbances, creating novel habitat on the landscape whereas disturbances can have a variable impact on resource levels (*e.g.* Lafontaine et al., 2019; Johnson et al., 2020; Stewart et al., 2020). A more complex behaviour of recently disturbed areas could be implemented following, for example, the observations of caribou reactions to recent burns from Silva et al. (2020) or the temporal changes in bird species abundance in response to wildfires in Mediterranean ecosystems from Jacquet and Prodon (2009). Purely negative responses to disturbances could also change the conclusions given that this situation would push individuals out of their current habitat instead of providing other resource options.

5. Conclusion

Given increasing anthropogenic pressures and natural disturbances exacerbated by climate change, managing populations of invasive and/or species at risk requires flexible decision-making tools to adapt to the uncertainty and complexity of rapidly changing landscapes. In this study, we show that local variations in ecosystem dynamics, such as unpredictable disturbances, as well as animal location and movement impact emergent properties at a population level such as spatial abundance. We provide a quantitative assessment of the error associated with the assumption that population are at equilibrium in a static landscape in habitat models. The implications for species at risk recovery planning are twofold. First, given foraging and density-dependence assumptions, animal movement responds dramatically to the presence of disturbances. Second, in an area that is subject to more severe or frequent climate-derived disturbances, using habitat models to forecast animal location or abundance will likely produce inaccurate

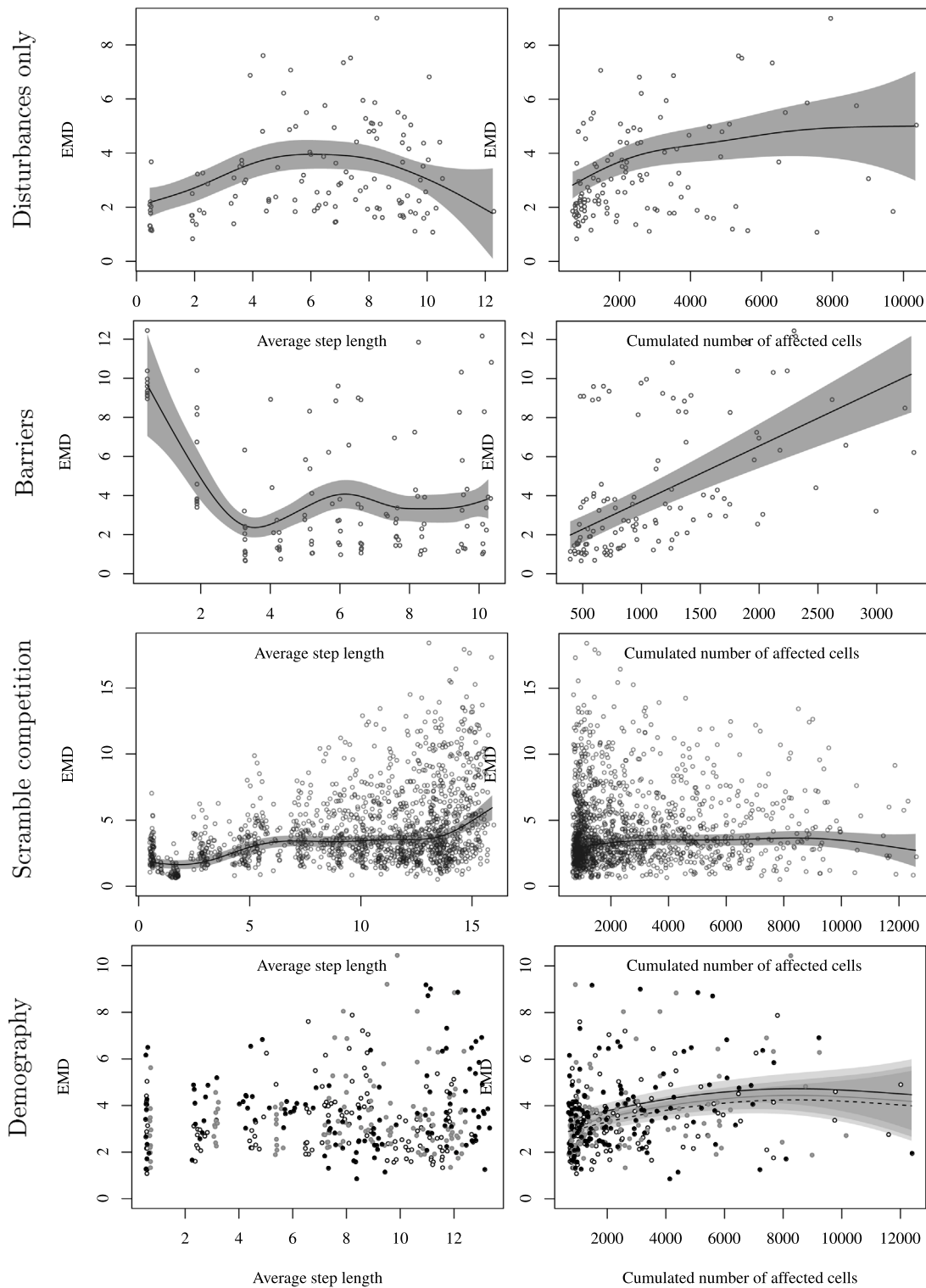


Fig. 4. Relationship between the Earth mover's distance (EMD) and the average step length (left) and cumulative number of cells affected by disturbances (right) as estimated using a generalized additive model for each scenario (see result values in Table 1). The curve for the average step length in the demography scenario is not included as that covariate was not significant. Approximate 95% confidence interval of the mean is represented in dark grey (solid line for the first three rows; dashed black: increasing population size, solid grey: stable population size, solid black: decreasing population size for the last row). The points represents the actual data (for the demography scenario in the last row, white: increasing population size, grey: stable population size, and black: decreasing population size).

projections. However, researchers should not discard static habitat components when they are the best information available. Instead, they should determine the potential for bias given the specifics of their study area. Population management and conservation plans require

habitat and population abundance forecasts. Without knowledge or understanding of the effect of landscape dynamics on animal space use, a population may be projected to do well or poorly in a domain with insufficient or mismatched resources (Heinrichs et al., 2017).

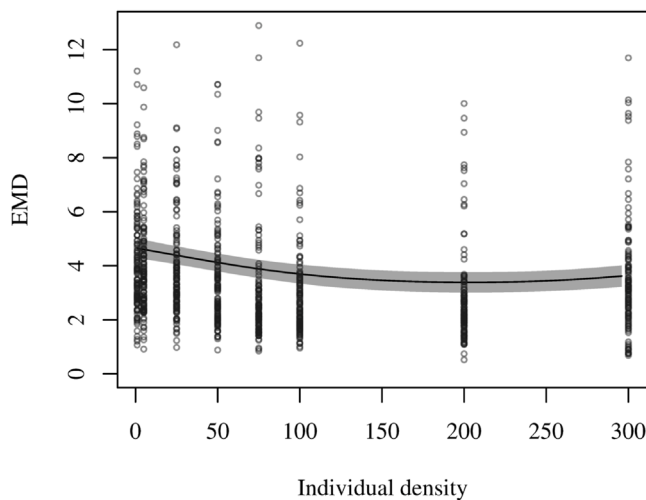


Fig. 5. Relationship between the Earth mover's distance (EMD) and the individual density on the landscape as estimated using the generalized additive model in the scramble competition scenario. Approximate 95% confidence interval is represented in dark grey around the mean (solid line). The points represent the actual data. For densities greater than 200–300 individuals, the simulations are unrealistic as the domain becomes barren but no animal death process was implemented in this scenario. Therefore the graph was cropped (see the full graph in Supplementary Information Fig. S.4).

Therefore, it is essential that land managers and researchers collaborate to produce models that improve decision-making (Bodner et al., 2021), i.e. models providing accurate predictions by including the relevant dynamical aspects of the study area and species.

CRedit authorship contribution statement

Mélodie Kunegel-Lion: Conceived the ideas, Designed the methodology, Performed the modelling work, Analysed output data, Wrote the first draft of the manuscript, Contributed substantially to revisions. **Eric W. Neilson:** Conceived the ideas, Designed the methodology, Contributed substantially to revisions. **Nicolas Mansuy:** Conceived the ideas, Designed the methodology, Contributed substantially to revisions. **Devin W. Goodman:** Conceived the ideas, Designed the methodology, Contributed substantially to revisions.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data and code availability

Data output from the simulations is available from Kunegel-Lion et al., 2022a, Dryad (<https://doi.org/10.5061/dryad.prr4xgxm0>) and the code used to generate the data from Kunegel-Lion et al., 2022b, Zenodo (<https://doi.org/10.5281/zenodo.4688764>).

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at <https://doi.org/10.1016/j.ecolmodel.2022.109943>.

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