OIKOS

Research Article

The interplay between landscape change and plasticity in habitat selection determines dispersal movements and settlement in small non-flying vertebrates

Érika Garcez da Rocha[1], Luca Börger[2,3], Dmitri Finkelshtein[3,4], Eduardo Mariano[5], Marcus Vinícius Vieira[1]

[1]Programa de Pós-Graduação em Ecologia, Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brazil
[2]Department of Biosciences, Swansea University, Swansea, Wales, UK
[3]Centre for Biomathematics, Swansea University, Swansea, UK
[4]Department of Mathematics, Computational Foundry, Swansea University, Swansea, Wales, UK
[5]Programa de Pós-Graduação em Ecologia, Teoria, Aplicações e Valores, Universidade Federal da Bahia, Salvador, BA, Brazil

Correspondence: Érika Garcez da Rocha (erika.garcez.rocha@gmail.com)

Oikos
2026: e11898
doi: 10.1002/oik.11898

Subject Editor: Allan Edelsparre
Editor-in-Chief:
Paulo R. Guimaraes
Accepted 16 December 2025

The response of dispersers to landscape changes depends on both external environmental conditions and individual internal conditions, as well as movement and orientation abilities. Plasticity in habitat selection may also affect how individuals respond to landscape changes. We investigated the role of plasticity in habitat selection during the settlement stage of dispersal for three species of neotropical marsupials with varying perceptual ranges and movement abilities, as well as their interactions with the landscape context, including habitat amount and fragmentation. In addition, we considered the role of individual energetic conditions during dispersal and the trade-off between habitat quality and energetic conditions in settlement decisions. We developed an individual-based model (IBM), parameterised with empirical estimates of perceptual range and movements, to simulate dispersal, transfer and settlement stages in fragmented landscapes varying in habitat amount and clumpiness. Plasticity plays a crucial role in mitigating the impacts of fragmentation and habitat loss, but it may not always yield the optimal strategy. Fragmentation positively affects settlement rates, particularly in landscapes with intermediate habitat amounts, but it may also reduce habitat quality in settlement patches, impair individual energetic condition at settlement, and alter the ratio of total to Euclidean dispersal distance. Our results demonstrate that the impacts of landscape disturbance on dispersal depend on multiple interacting factors, including species-specific movement and orientation capacities. These factors should be incorporated into future studies to better understand and predict dispersal across heterogeneous landscapes.

Keywords: dispersal stages, fragmentation, habitat loss, small mammals

NORDIC SOCIETY OIKOS

www.oikosjournal.org

Introduction

Rapid human-induced landscape changes, such as habitat loss and fragmentation (Fardila et al. 2017, Pendrill et al. 2022), significantly impact a species' ability to disperse across these landscapes, thereby raising threats to biodiversity. The loss of appropriate available habitats for species occurrence affects their survival and reproduction (Lindenmayer and Fischer 2006). In addition, the effects of fragmentation, such as increasing isolation and decreasing fragment size, can reduce the ability of organisms to disperse, negatively impacting the dynamics of metapopulations, isolating populations in small fragments that may not be sufficient for their survival, causing the decline and possible extinction of species (Fahrig and Merriam 1985, Fahrig 2003). In fact, including the role of movement is crucial for understanding the effects of habitat fragmentation (Jacobs et al. 2025).

Dispersal is a complex, multicausal, three-stage process, beginning at the moment an individual decides to leave its current location (departure) and starts to move across the landscape (transfer) until it encounters a new suitable habitat to settle (settlement) (Clobert et al. 2004). The complexity of dispersal is due not only to the variety of factors involved in the process, but also to different drivers that may affect each stage differently, with each stage, in turn, affecting and impacting the other ones (Bowler and Benton 2005, Clobert et al. 2009). Despite the increasing number of studies on the three dispersal stages, the attention given to each stage is uneven, and an understanding of the main drivers is still lacking due to distinct factors and the link among these stages (Matthysen 2012). Many studies have focused on understanding which landscape context can encourage departure, and how landscape composition and configuration affect dispersers' movement ability and survival, whereas understanding is still lacking regarding the settlement stage (Baguette et al. 2012).

The choice of a new habitat to settle and establish depends on the criteria used by the organism to select the new habitat (Ronce 2007, Matthysen 2012). Importantly, settlement decisions are condition and phenotype-dependent, thus based on both external information, such as habitat quality, and individual internal state, such as behavioural state or body condition (Clobert et al. 2009). Ideally, organisms select high-quality habitats to optimise fitness, but individual habitat selection decisions depend on multiple criteria and might differ among species and individuals (Stamps 2001). Importantly, if habitat selection during settlement is constrained or limited, it may lead to frequent settlement into non-favourable habitats, a phenomenon more frequently observed in fragmented landscapes (Stamps 2001, Ronce 2007, van Langevelde 2015).

Habitat selection is also related to the energetic condition of the individual, which will expend energy to move and search for a new settlement area (Stamps 2006). According to the search hypothesis, dispersers in good conditions are more likely to settle in high-quality habitats than dispersers in poor conditions, with disperser conditions affecting their selectivity during dispersal movements (Stamps 2006, Matthysen 2012). Furthermore, Day et al. (2019) encountered temporal plasticity in the decrease of habitat selectivity during dispersal, indicating a tradeoff between habitat quality and risk of mortality. Therefore, individual settlement thresholds might change plastically with dispersal time and costs (Baker and Rao 2004, Bonte et al. 2012).

To decide whether to keep moving or settle in a new habitat, individuals must gather information during dispersal, a concept called informed dispersal (Clobert et al. 2009, Acker et al. 2017). Besides the internal state that influences the decision-making of dispersers, such as the energetic condition to start or end the dispersal, the use of external cues during the whole process is essential to acquire enough information to make decisions about what to do or where to go (Clobert et al. 2009). This ability to detect and use external cues might differ among species and individuals, being influenced directly by individual movement and navigational/perceptual abilities, including the perceptual range and the distance that the organism perceives environmental features (Lima and Zollner 1996) and therefore gathers information.

Understanding of the dispersal process is highly relevant for conservation to understand how to manage and conserve animals under the current intense anthropogenic disturbance on landscapes (Baguette et al. 2012, Travis et al. 2013, Atkins et al. 2019). In this regard, Arendt (2015) emphasised the plasticity of dispersal and that exploring the relationship among plasticity, dispersal distance, and other metrics and strategies to settle is essential to advance our understanding of the dispersal process. In this study, we developed an individual-based model (IBM) to analyse the complex interactions in a multicausal process such as dispersal (Baguette and Van Dyck 2007, Clobert et al. 2009, Benton and Bowler 2012). In particular, we focused on how variations in individual movement and condition-dependent decisions affect the complete dispersal process. IBMs are dynamic models that allow the simulation of individual variation and complex relationships of the organisms with the environment (DeAngelis and Mooij 2005), including the effects of feedback among interacting variables, as opposed to classical correlative models based on a priori relationships between response and explanatory variables (Potts and Börger 2022). We parameterised our IBM with empirical movement data from three species of small neotropical marsupials (*Didelphis aurita*, *Philander quica* and *Marmosa paraguayana*) with different movement patterns and perceptual ranges. The IBM simulates the transfer and settlement stage across heterogeneous landscapes, varying in composition and configuration. We aimed to investigate the effect of plasticity in habitat selection during the settlement stage of dispersal in heterogeneous landscapes, considering individuals' energetic conditions and orientation.

Material and methods

Overview

We developed a spatially explicit individual-based model in NetLogo ver. 6.2.2 (Tisue and Wilensky 2004) to simulate dispersal transfer and settlement stages on heterogeneous landscapes. In this study, we are considering different levels of plasticity in habitat selection during settlement based on the habitat quality threshold accepted by the individual to settle in the new habitat. Therefore, we investigated the effect of the interaction between plasticity in habitat selection and landscape composition and configuration on dispersal movement and settlement success. For detailed information about our IBM, see the complete ODD (overview, design concepts, and details) protocol (Supporting information), which was developed following (Grimm et al. 2010).

Landscape simulation

The landscape comprises a grid of 300 × 300 cells (−150, +150), each representing 10 m^2. We used 100 simulated landscapes varying in composition by the percentage of habitat amount, from 5 to 70%, and in the degree of clustering ('clumpiness') varying 5–99%, with smaller numbers representing a more fragmented landscape. Simulated landscapes were generated using QRULE with Hurst parameters regarding clumpiness degree (Gardner and Urban 2007). Landscapes were classified and exported in ASCII format to be imported into NetLogo. The landscape is characterised by cover type, which means habitat patches (cover = 1) or matrix of pasture or non-habitat (cover = 0), and each cell is also characterised by habitat quality (Q: 0~1), which is considered a proxy for the amount of resources available. The habitat quality surface was generated within the NetLogo model. The habitat quality of matrix cells is zero, and habitat cells vary from 0.5 to 1. These values are addressed by a random uniform deviation (U[0.5,1]) and then using a level of autocorrelation from 1 to 8 based on the level desired over each cell's eight neighbours (i.e. a more neighbourhood).

Species simulated

The model species simulated are three neotropical marsupials endemic to the Atlantic Forest of South America (*Didelphis aurita*, *Philander quica* and *Marmosa paraguayana*). Populations of these species have persisted despite intense habitat loss and fragmentation of the Atlantic forest, with only 15–25% of the original forest cover remaining (Ribeiro et al. 2009, Rezende et al. 2018, Rosa et al. 2021, Broggio et al. 2024). These species differ in body size and movement abilities: *D. aurita* is usually terrestrial and nocturnal (Cunha and Vieira 2002), it is the largest in body size among the studied species (850 g; Forero-Medina and Vieira 2009), and has the longest registered distances across the matrix (Crouzeilles et al. 2010); *P. quica* is semi-terrestrial, of medium body size and medium distances registered across matrices (395 g; Forero-Medina and Vieira 2009, Crouzeilles et al. 2010); *M. paraguayana* is the smallest (112 g; Forero-Medina and Vieira 2009), arboreal, moving shorter distances and frequently goes to the ground to move between fragments. The three species usually occupy forest fragments, moving occasionally across the anthropogenic matrix (Pires et al. 2002).

Movement characterisation and empirical calibration

Movement rules in the matrix were implemented similarly to Rocha et al. (2021) and based on Ríos-Uzeda et al. (2019) results. We implemented these rules as a discrete model consisting of a discrete series of steps and events of reorientation described by Lévy flights, with a Gaussian distribution for turning angles and a Pareto truncated distribution for step lengths. The movement parameters in the model include the minimum step length (ℓmin), maximum step length (ℓmax), exponent for the Pareto truncated distribution (μ), and the mean and standard deviation for the Gaussian distribution of turning angles. The estimation of parameters was species-specific and dependent on whether the individual was oriented to a landscape element. Habitat patches were detected if present within the perceptual range of each species. Parameter values for perceptual range were obtained from Forero-Medina and Vieira (2009), and movement parameters were calibrated using results from Ríos-Uzeda et al. (2019) (Table 1).

Movement rules in the forest habitat followed similar implementations for step length and turning angles. However, due to the lack of empirical data on movement within habitat fragments, and aiming to simulate a more tortuous and shorter movement in comparison with matrix movement (Van Dyck and Baguette 2005), parameter values for step length were those of non-oriented movement in the matrix, when steps are shorter. For turning, angles are a Gaussian distribution with a mean equal to 0 (zero) and a standard deviation equal to 90 (ninety). Figure 1 provides a sample of the distribution of movement parameters for the three species simulated in one landscape.

Energetic dynamics

Each individual starts the simulation with an energetic condition (En) equal to 1. At every step of the dispersal movement, the individual expends energy while moving proportionally to the distance moved during each step. The energy expenditure is calculated based on a discharge rate, which is double in the matrix than in the habitat, representing the possibility of

Table 1. Parameters of perceptual range and movement (step length and turning angle) implemented for oriented and non-oriented individuals of the three study species (based on Ríos-Uzeda et al. 2019).

Species	Perceptual range (m)	Individuals	Step length (m)			Turning angle (θ)	
			μ	ℓmin	ℓmax	Mean	Std
Didelphis aurita	200	Oriented	−1.17	0.25	26.0	0.34	50.45
		Non-oriented	−1.54	0.20	16.8	−0.74	55.81
Philander quica	100	Oriented	−1.47	0.25	48.0	3.11	58.19
		Non-oriented	−0.171	0.20	20.3	0.33	54.59
Marmosa paraguayana	100	Oriented	−1.46	0.10	11.5	−1.09	56.11
		Non-oriented	−1.98	0.20	19.4	−2.29	60.10

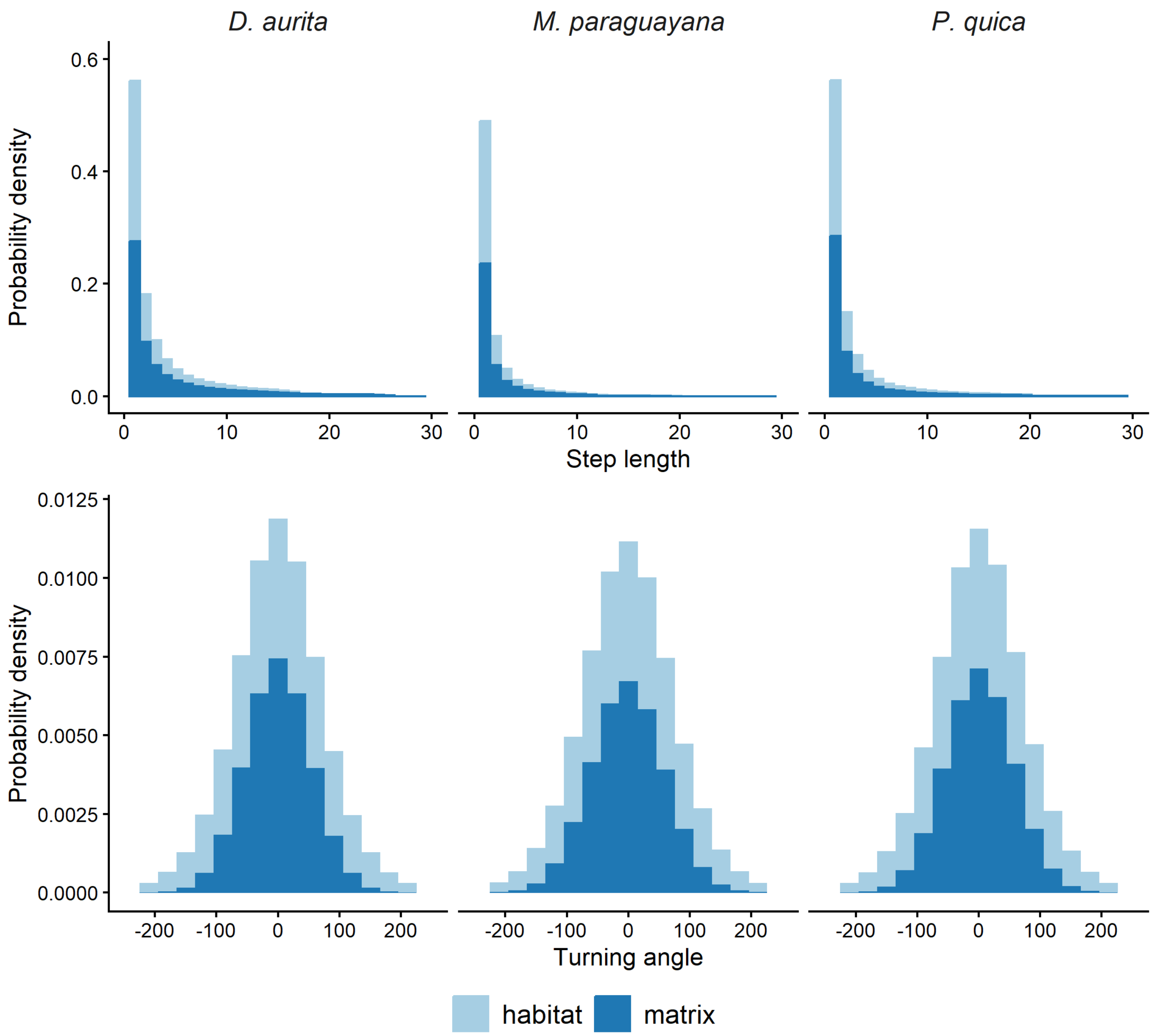

Figure 1. Histogram density of step length and turning angles for movements in the matrix and habitat cells in a sample simulation.

feeding and resting while dispersing within habitat fragments. At every movement step, the energy deducted from En is calculated by multiplying the discharge rate by the logarithm of the total distance moved. Calibrations were performed to define the optimum discharge rate to represent the cost of dispersal. Based on that, simulations were carried out with the discharge rate in the matrix as 0.0002 and, therefore, in the habitat as 0.0001. Each individual has a minimal energetic condition value (min_En) to keep dispersing, which is defined by a Gaussian distribution with parameters indicated in Table 2. When the individual reaches that energy level, it will settle in the following habitat patch regardless of its habitat quality.

Habitat selection requirements for settlement

Each individual has a habitat selection threshold (C), potentially varying from 0 (unselective) to 1 (only accepting the highest habitat quality), which means that the individual will settle when it finds a new habitat with equal or higher habitat quality than its threshold, or if it reaches the minimal energetic condition. Calibrations were performed to define the initial threshold (Ci) and variation to avoid extreme situations, such as all individuals dying or all succeeding. Based on that, everyone starts the simulations with a Ci chosen from a random value between 0.5 and 0.9. At every step, the individual updates the C values based on its energetic condition (En), which expresses the plasticity in habitat selection during settlement (e_C). Change in C as a function of Ci, En, and e_C was devised as a simple exponential decay (Fig. 2):

$$C(t) = Ci \times \mathrm{En} \wedge \mathrm{e\_C},$$

At every step during dispersal, the individual expends energy, and its energetic condition decreases; accordingly, the habitat

Table 2. Initial parameters of the simulation experiment

Parameter/variable	Value/range of values
Landscape	
Total landscape area	3000 × 3000 m (300 × 300 cells)
Representative area of each grid cell	10 × 10 m
Habitat quality (Q)	matrix: 0 / habitat patches: U[0.5,1]
Cover	matrix: 0 / habitat patches: 1
Habitat amount	5–70%
Habitat clumpiness (opposite of fragmentation)	5–99%
Individuals	
Species	*Didelphis aurita* (DA), *Philander quica* (PQ), *Marmosa paraguayana* (MP)
Perceptual range (PR)	DA – 200 m / PQ – 100 m / MP – 100 m
Step length parameters	as indicated in Table 1
Turning angles parameters	as indicated in Table 1
Start habitat quality threshold (Ci)	random value from 0.5 to 0.9.
Start energetic condition (En)	1
The minimum energy required (min_en)	Gaussian distribution: mean = 0.2, SD = 0.1
Plasticity level (exponent – e_C)	0, 0.5, 1, 1.5, 2 (zero means no plasticity)
Mortality rate dispersal	matrix: 0.002 / habitat: 0.001
Population size	1000 individuals
Minimal dispersal distance	1000 m

quality threshold for settlement also decreases. This relationship might change its intensity, which is based on the exponent of the function (e_C), representing different levels of plasticity (Fig. 2). The non-plastic behaviour is represented when e_C = 0, and then C does not decrease with the reduction of the energetic condition.

Model dynamics

The model simulates the transfer and settlement stages of dispersal in fragmented landscapes. Figure 3 provides a detailed flow diagram of the model simulation. The environment is created in the setup by importing the landscape files and generating the habitat quality surface. After that, the individuals are created and distributed randomly across the landscape in habitat patches. The simulation starts with all individuals moving to the matrix and starting the dispersal movement, corresponding to the transfer stage. At every step of the simulation, the individual checks his energy condition; when it reaches 0, the individual dies; otherwise, he updates his variables: the mean habitat quality within the perceptual range (H′) and habitat quality threshold (C). Then, the individual will disperse regardless of the cover of the cell he is in until he moves a distance (D') more than the minimal dispersal distance defined. The minimal dispersal distance is implemented in the model as a strategy to implement a 'dispersal mode' and avoid routine movement returning to the start location. In this study, we defined this parameter as 1 km (one kilometre) based on previous studies on marsupials

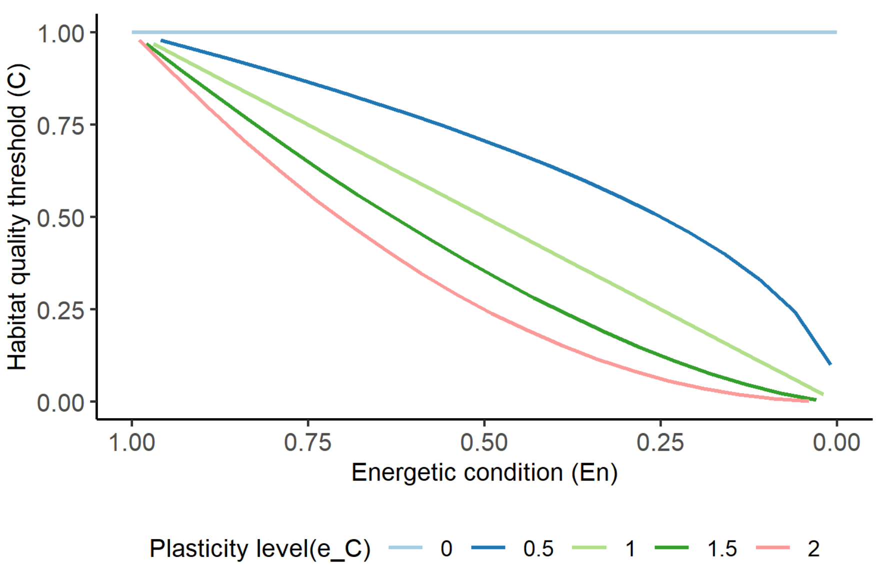

Figure 2. Relationship implemented in the model between the energetic condition (En) and habitat quality threshold (C) regarding plasticity levels (e_C).

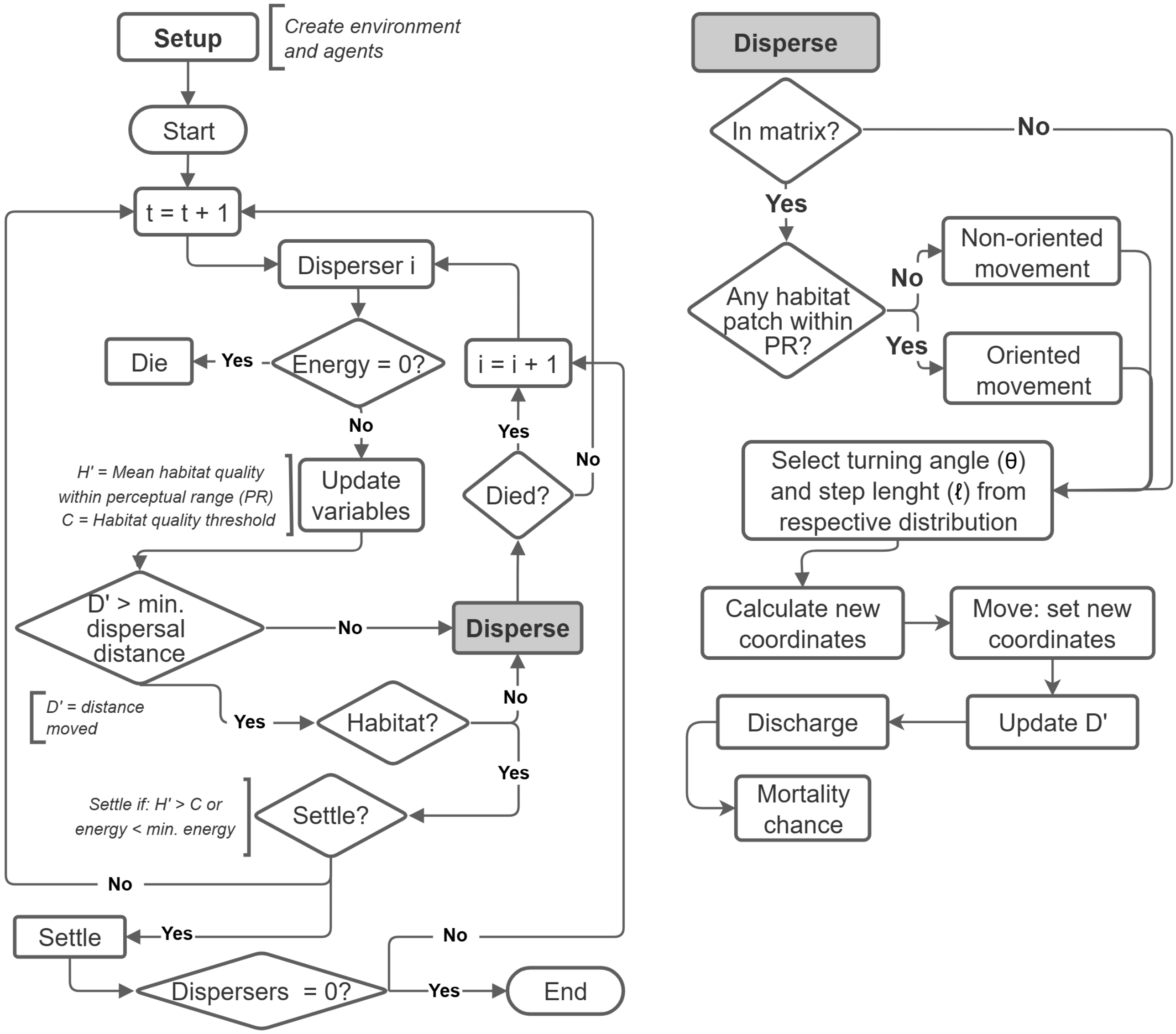

Figure 3. Flow diagram of the individual-based model describing decisions faced by individuals in the simulation.

crossing distances in the matrix (Crouzeilles et al. 2010). After that step, if the individuals are still in the matrix, it will keep dispersing; if it reaches a habitat cell, it decides whether to settle or not. The simulation stops if the individual decides to settle. Otherwise, it will keep dispersing. The decision to settle is based on the mean habitat quality within the perceptual range (H′), the energetic condition (En), and the habitat quality threshold (C). The settlement will occur if H′ is higher than C, which means that the habitat quality in the area is equal to or higher than the required for the individual, or if En is lower than the minimal energetic condition to disperse (min_En), which means that the individual has no energetic condition to keep dispersing.

The disperse submodel is detailed on the right of Fig. 3. Within this process, step length and turning angle are selected from the respective distributions according to the patch cover and orientation. If the individual is in a habitat patch and decides not to settle, parameters are pulled from the distribution of movement steps in the habitat, as explained before. If the individual is in the matrix and any habitat patch is within its perceptual range, then it will be oriented in the matrix toward the habitat patch, or if no habitat patch is encountered within its perceptual range, then it is non-oriented in the matrix. Afterwards, new coordinates are calculated and the individual moves to that location, and the total distance moved (D’) are updated. At that point, the individual expends energy proportional to the distance moved and faces the chance of mortality. The mortality chance is calculated at every movement step across the habitat and the matrix. Due to the lack of empirical data regarding mortality, the mortality rate values for habitat and matrix were calibrated to represent a dangerous matrix, a less dangerous habitat, and insufficient threats to kill all individuals. The simulation stops when all individuals are settled or dead.

Simulation experiments

The simulations were performed using 100 landscapes, varying in habitat amount and clumpiness, for the three species of marsupials (*D. aurita*, *P. quica* and *M. paraguayana*). Each run simulated 1000 individuals independently, summing to 100 000 individuals simulated per species. The initial parameters of the simulation are presented in Table 2, and the variables calculated during the simulation are presented in Table 3.

Model output

At the end of the simulations, two output files are created: the 'sim_parameters.txt' and the 'output.txt'. In the first file, all fixed variables are registered with the number of simulations. The second file registered individual initial and final variables for all successful settlers, such as identification, initial patch and its identification, minimal energetic condition to disperse, initial and final habitat quality threshold, level of plasticity, coordinates, the energetic condition of the individual when settled, the habitat quality of the settlement area, the decision to settle, the total distance moved, and the Euclidian distance from the start patch and the final patch in the settlement area.

Statistical analysis

Six response variables were calculated for all successful dispersal in each run of the simulation: 1) settlement rate, how many individuals were able to settle divided by the total number of individuals simulated; 2) mean habitat quality in the settlement area; 3) mean energetic condition when the disperser decided to settle; 4) mean total distance moved during dispersal; and 5) mean Euclidean distance moved; 6) mean ratio distance, which is the ratio between the total distance and the Euclidean distance. Then, two steps were performed. First, generalised linear models (GLMs) were applied to evaluate the influence of plasticity on the response variables and compare these results among the three species of marsupials. Secondly, generalised additive models (GAMs) were used to evaluate the effect of landscape composition (habitat amount) and configuration (clumpiness) on the same six response variables for the three species simulated. Even though we performed these statistical analyses to best comprehend the effects and patterns of our results, we also evaluated the effect size, which is the magnitude of the differences between all results, to avoid basing inferences solely on p-values, given the limitations of the latter in simulation studies (White et al. 2014). Data analysis was conducted using R ver. 4.1.2 (www.r-project.org), and details of the analysis are presented in the Supporting information.

Results

Effects of habitat selection plasticity on dispersal, transfer and settlement

The settlement rate increased with the level of plasticity for all three species by approximately 30% (Fig. 4A, $p < 0.001$) with no effect of the interaction between plasticity and species (DA-PQ: $p = 0.78$; DA-MP: $p = 0.39$), suggesting that the pattern of impact of plasticity for the three species is similar. Settlement success was 15% lower for *M. paraguayana* compared to *D. aurita* (Fig. 4A, $p < 0.001$), whereas the difference between *P. quica* and *D. aurita* was small and not significant ($p = 0.62$).

Regarding the mean habitat quality of settlement sites, no significant effect of plasticity ($p=0.25$) or interaction between it and species (DA-PQ: $p = 0.17$; DA-MP: $p = 0.43$) was found. However, the mean habitat quality at settlement differed among species, with *D. aurita* showing lower values than *P. quica* and *M. paraguayana* (Fig. 4B, $p < 0.001$). The energetic condition in the settlement area was positively related to plasticity for all species, increasing approximately two times more in individuals with a higher level of plasticity (Fig. 4C, $p < 0.001$). The strength of these patterns is directly related to perceptual range and movement abilities and is significantly stronger for *D. aurita*, which has the highest perceptual range and movement abilities (DA-PQ: $p < 0.001$; DA-MP: $p < 0.001$).

The total distance and Euclidean distance moved showed a strong negative correlation with plasticity ($p < 0.001$, $p < 0.001$, respectively), with a clear difference among species ($p < 0.001$, $p < 0.001$, respectively). *Marmosa paraguayana* had shorter dispersal distances than the other species (Fig. 4D–E) and a weaker influence of plasticity. *D. aurita*, which has the higher perceptual range and movement abilities, had greater total and Euclidean distances and a stronger effect on plasticity levels. Meanwhile, by looking at the ratio distance, *M. paraguayana* had the lower ratio and minor differences due to plasticity ($p < 0.001$), in comparison with *D. aurita* and *P. quica*, which showed a stronger effect of plasticity ($p < 0.001$) and with no significant difference among the two species ($p = 0.067$) (Fig. 4F).

Table 3. Variables calculated during the simulation experiment

Variables	Description
Individuals	
Energetic condition (En)	energetic condition of the individual at every step of the simulation
State	disperser (dis) or settler (set)
Habitat quality within perceptual range (H′)	the mean of habitat quality (Q) of the cells within the individual`s perceptual range
Decision	if the decision to settle was based on habitat quality (H) or energy (En)
Total Euclidean distance (linear_dist)	total linear distance in metres by an individual during dispersal
Total distance moved (total_dist)	total distance in metres moved by an individual during dispersal

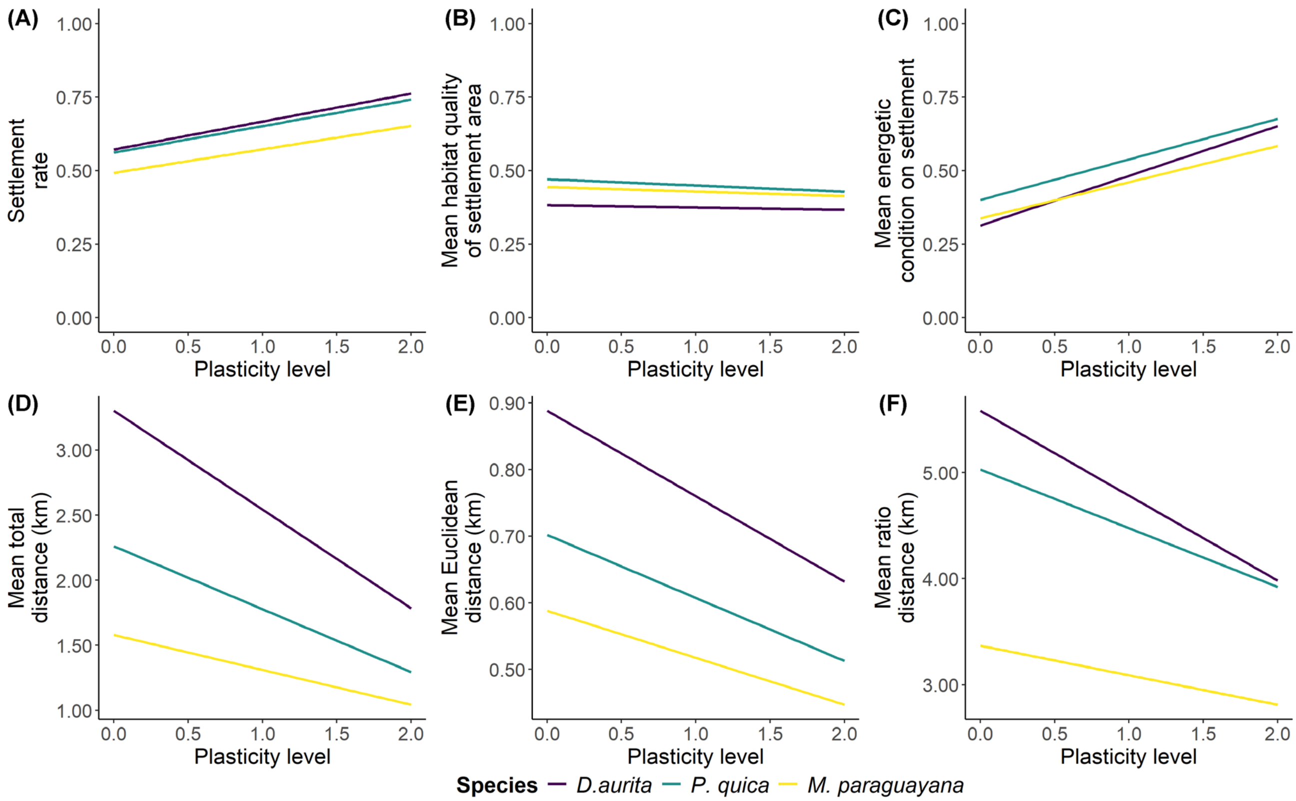

Figure 4. Effect of plasticity level on settlement rate (A), mean habitat quality in the settlement area calculated within the perceptual range (B), mean energetic condition of the individual when settled (C), mean total distance moved in km (D) mean Euclidean distance moved in km (E), and mean ratio distance (total distance / Euclidean distance) (F) for individuals of the three species (*Didelphis aurita*, *Philander quica* and *Marmosa paraguayana*).

Effects of the landscape and habitat selection plasticity on dispersal

In this section, most figures do not present a comparison among species due to the high quantity of variables, to avoid confusion and provide a better comprehension of the results. Figures comparing the three species are presented in the Supporting information, which are mentioned when needed. In addition, for a more straightforward visual interpretation, considering clumpiness, the opposite metric of fragmentation, all figures presented from now on have the clumpiness axis inverted.

Habitat amounts positively affected the settlement rate (Fig. 5A) with no apparent difference among the three species. Settlements were affected negatively by habitat clumpiness, i.e. higher settlement rates occurred in highly fragmented landscapes (note the inverted x-axis scale in Fig. 5). Both the effects of habitat amount and habitat clumpiness were nonlinear across species, with higher settlement rates at intermediate levels of habitat clumpiness/fragmentation and more nonlinear patterns at intermediate habitat amount levels.

Mean habitat quality in settlement areas increased with habitat amount and clumpiness (Fig. 5B–6), similarly among species. Landscapes with low habitat amount (0–40%) showed markedly more variation in settlement habitat quality across the range of clumpiness, with a more intense effect at lower values of clumpiness (Fig. 5B). In other words, regarding habitat quality in settlement areas, fragmentation had more impact on landscapes with lower habitat amounts. Interestingly, individuals with more habitat selection plasticity consistently achieved lower values of habitat quality in the settlement area, except for individuals with no plasticity. The latter achieved higher settlement habitat quality in non-fragmented landscapes (i.e. high habitat clumpiness values, but lower habitat quality in more fragmented landscapes, especially at low habitat amounts.

Interactions between plasticity and landscape composition and configuration are further presented in Fig. 6, which, for better comprehension, contains only three levels of plasticity (0, 1 and 2). The non-plastic individuals (purple) were more affected by changes in habitat amount and clumpiness than the ones with plasticity for the three species, as we can see by the more substantial shift from low-quality to high-quality settlement habitats with increasing habitat amount in the landscape by non-plastic individuals (Fig. 6 upper), i.e. settlement habitat quality varied markedly less substantially depending on landscape habitat amount and configuration than for plastic individuals (Fig. 6). For all species, plasticity seems to be more advantageous, particularly in landscapes with habitat amounts lower than 30%, when the peak of non-plasticity is higher at low-quality habitats, and the peak

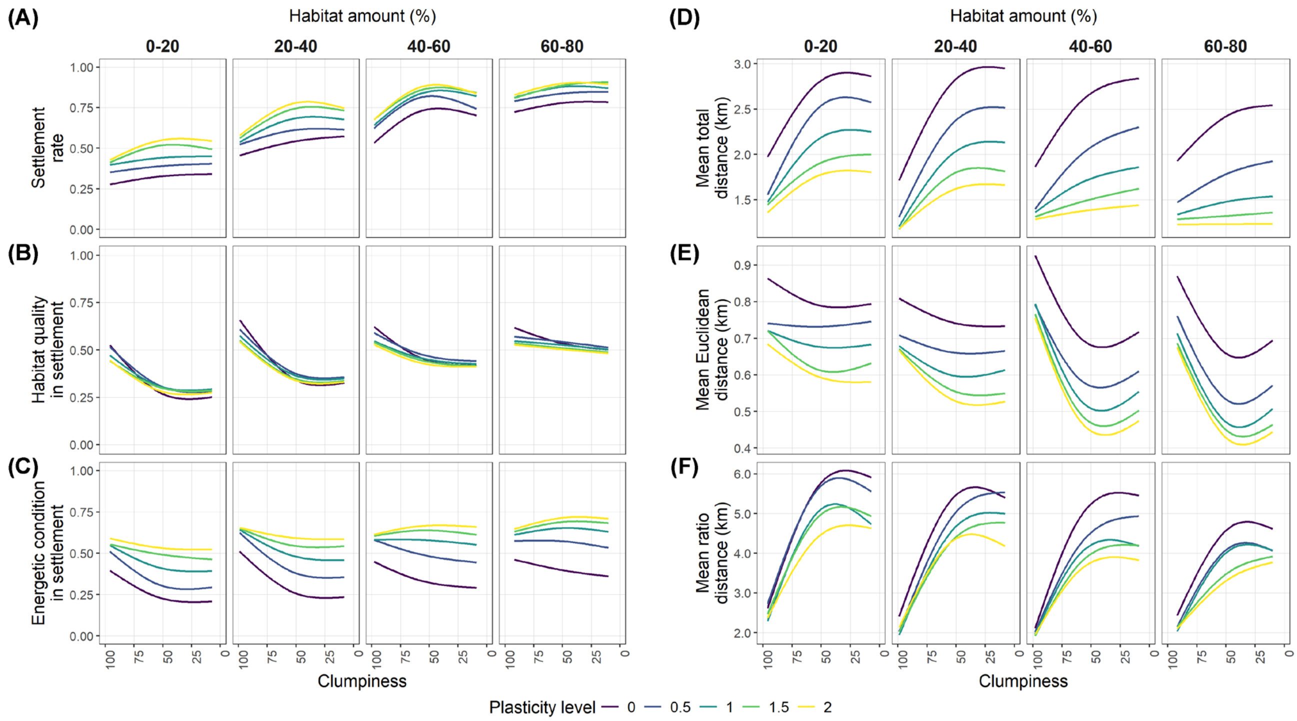

Figure 5. Effects of landscape (habitat amount and clumpiness) and plasticity on settlement rate (A), mean habitat quality at settlement (B) and energetic condition at settlement (C).

of plasticity levels is higher in intermediate-quality habitats. Over 30% of the habitat amount, the non-plastic individuals started to reach higher-quality habitats, resulting in the shift from low to high-quality habitats with increasing habitat amounts. Except for *D. aurita*, individuals with intermediate plasticity (green lines in Fig. 6) seemed to be favoured, which means settling in habitats with higher quality than the ones with higher plasticity (yellow lines).

The effect of clumpiness was also stronger for individuals with no plasticity level (purple lines), which indicates that fragmentation has a negative impact on settlement habitat quality. *Didelphis aurita* showed a more intense effect, with the shift to high values of habitat quality happening more strongly at 80–100% of clumpiness.

Crucially, the energetic condition of individuals at settlement was consistently and strongly higher for individuals with higher plasticity levels across all landscape-level habitat amount conditions across species (Fig. 5C). Energetic conditions at settlement also consistently increased for all individuals, with an increase in landscape-level habitats. In contrast, it decreased with decreasing levels of clumpiness, except for high plasticity individuals in landscapes with over 40% of the habitat amount available.

Effects of habitat amount were similar when evaluating total and Euclidean distance moved before settlement, with shorter distances moved in landscapes with more habitat amount (Fig. 5D–E). However, the clumpiness effect was different between the distance metrics. Increasing clumpiness (i.e. reducing fragmentation) decreased total distance, and the intensity of this effect was inversely related to plasticity (Fig. 5D–F). In contrast, the Euclidean distance increased with clumpiness, and the intensity was directly related to plasticity (markedly lower for more plastic individuals).

More fragmentation results in longer total distance and shorter Euclidean distance moved, which means a higher ratio of distance, and plasticity reduces the negative effect of fragmentation on total distance dispersed but intensifies the positive impact on Euclidean distance, in other words, a lower ratio of distance (Fig. 5F). The three species differed regarding distance metrics in the level of variation, which was higher for *D. aurita*, followed by *P. quica* and *M. paraguayana*, consistent with the species decreasing values of movement abilities and perceptual range.

Discussion

Deepening our understanding of the complexity of dispersal stages, their interdependence and interactions with internal and external factors is a key research theme (Stamps 2001, Ronce 2007, Clobert et al. 2009, Baguette et al. 2012, Travis et al. 2012, Maag et al. 2018, Morales-González et al. 2022). We used a simulation model built using empirical movement parameters to advance the comprehension of how the dispersal transfer and settlement stages are affected by landscape changes, considering the complex interactions with a key individual and behavioural aspects related to the dispersal movement and settlement decisions – perceptual range, energetic condition, and plasticity in habitat selection – together with differences in landscape structure and

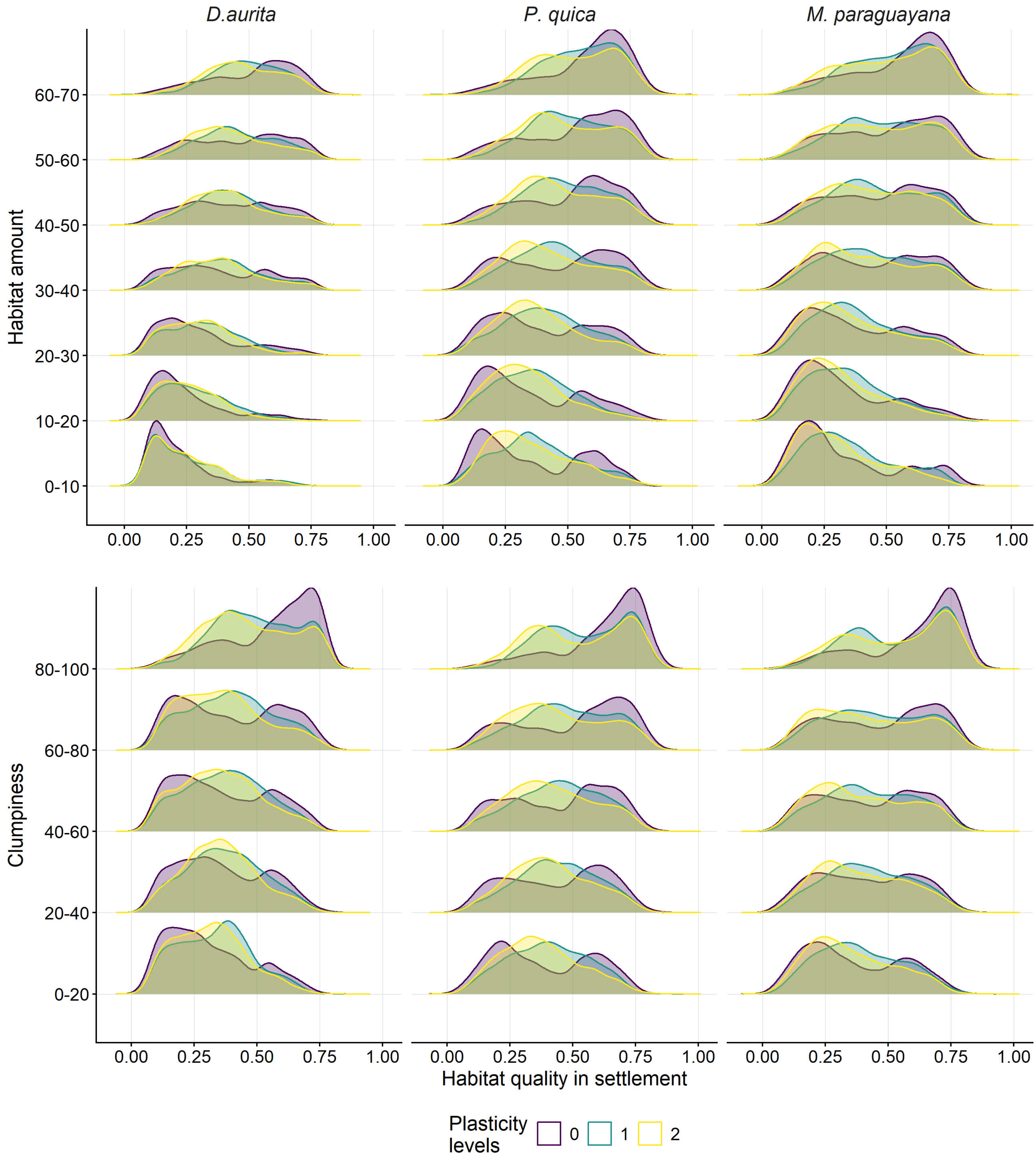

Figure 6. Density plots of the distribution of habitat amount and habitat clumpiness versus habitat quality in the settlement patches for the three species, separated by plasticity level (0, 1 and 2).

fragmentation (habitat amount and clumpiness). Our results provide interesting and relevant insights into how multiple factors interact to determine dispersal, transfer and settlement stages. In the following sections, we will thoroughly debate our main results and discuss their conservation implications.

Role of settlement habitat selection flexibility during dispersal

Plasticity of behaviour during dispersal may be key to dealing with environmental changes (Raynor et al. 2017), with studies discussing the role of plasticity in the behaviours of dispersers and how it might affect the dispersal process (Hollander et al.

2014, Arendt 2015, Day et al. 2019, Campana et al. 2022). Accordingly, our results suggest that plasticity in habitat preferences during settlement plays an essential role in dispersal success. Increased plasticity increases settlement rate, resulting in settlers moving shorter distances to find new habitats and ending dispersal with better energetic conditions. In addition, increasing the plasticity level reduces the ratio between the total and Euclidean distance to settlement, which means that to reach the same linear distance, a plastic individual needs to move less in total. The flexible behaviour of habitat selection allows an increasing sampling of available habitats to settle over time, compared to individuals who search for a specific habitat quality threshold without plasticity. This strategy relies strongly on the particular type of habitats available (Edelaar et al. 2017). Besides increasing the chance of finding a suitable habitat to settle and reducing mortality during dispersal, plastic individuals can settle in good individual (energetic) conditions, which is crucial for reproduction and survival in the new habitat (Rémy et al. 2011).

The degree of selectivity of the settlement habitat is directly related to the dispersal condition, in accordance with the silver spoon effect (Stamps 2006) and dispersal time (Stamps et al. 2005). Our model considers this effect by implementing the idea that the individual spends energy during movement and then reduces its threshold of settlement habitat quality over time accordingly. This tradeoff between energetic conditions and habitat quality during dispersal is probably the reason why plasticity did not affect the mean habitat quality selected by settlers. Conversely, non-plastic individuals unable to reach a high-quality habitat will keep moving until all their energy is spent. They then have to settle in the first available habitat encountered, probably at low-quality sites. That result is similar to Rémy et al. (2011), in which individuals with smaller body sizes, related to a low condition, settled more in low-quality habitats.

On the other hand, plastic individuals can settle before their energy is used up, but they accept low-quality habitats, resulting in no considerable difference in mean settlement habitat quality among plasticity levels. Conversely, the tradeoff implemented in our plasticity strategy resulted in a direct tradeoff between settlement rate and habitat quality, whereby plasticity increased the settling rate at the expense of habitat quality. The significant advantages of plasticity are thus manifested in improved energetic conditions and a greater overall settlement rate. Notably, different plasticity strategies with a less flexible or more iterative reduction of the settlement threshold would likely lead to an increase in mean habitat quality, though probably at the cost of lower settlement rates.

These findings also indicate some differences among species with different mobility abilities. *Marmosa paraguayana*, the species with the lowest perceptual range and mobility, had a lower settlement rate and was less impacted by plasticity, despite showing the same pattern compared to the other species. *Marmosa paraguayana* is known to be more sensitive to fragmentation and habitat quality (Honorato et al. 2015) and has lower dispersal ability (Crouzeilles et al. 2010). Therefore, they are more dependent on connectivity and less influenced by plasticity due to the shorter distances moved. On the other hand, despite the higher settlement rates, *D. aurita* showed low values of habitat quality in the settlement area and a higher ratio between total and Euclidean distance. *Didelphis aurita* is a generalist species that moves long distances compared to other species (Crouzeilles et al. 2010). They can explore more of the landscape and find a new habitat faster, but also are more affected by plasticity due to the intensity of movement, considering plasticity related to the energetic condition. In our model, the habitat quality of the settlement area is based on the perceptual range of the individual because it represents the information gathered by the individual. Therefore, *D. aurita*'s higher perceptual range (200 m) allows for a larger area to calculate average habitat quality, which explains the lower habitat quality primarily in landscapes with lower habitat amount and higher edge density (Supporting information). As expected, *P. quica*, a species with intermediate characteristics, showed intermediate responses between the other two studied species.

Effects of habitat loss and fragmentation on dispersal

A high amount of available habitat in the landscape allowed individuals to easily find new suitable habitats, which increased the settlement rate and high-quality settlement habitats due to the high availability of proper sites. Therefore, settlers had to move shorter distances in total and settle closer to the original habitat and with good energetic conditions at settlement. Our results agree with most of the literature on habitat loss impacts on dispersal rate (Travis and Dytham 1999, Wiegand et al. 2005, Niebuhr et al. 2015). For instance, Delciellos et al. (2018) indicated a negative association between habitat loss and condition by encountering individuals with lower body conditions on forest fragments compared to contiguous forests. However, they highlighted that, in fragmented landscapes, this impact is different among species, which indicates a combination of factors affecting dispersal.

The settlement rate was negatively influenced by clumpiness, indicating a positive effect of fragmentation per se on movement, with more habitat fragments spread in the landscapes, which increases connectivity and facilitates individual orientation and movement within the matrix (Niebuhr et al. 2015, Fahrig 2017). For highly plastic individuals, fragmentation had a non-linear effect on settlement rate, wherein the highest values emerged in landscapes with intermediate fragmentation. This pattern was stronger in landscapes with intermediate habitat amount. This pattern fits the positive effect of fragmentation per se, considering that the increase in connectivity matters at intermediate habitat amounts (Villard and Metzger 2014, Rocha et al. 2021). Too low habitat availability and high fragmentation result in more isolation and lower habitat quality due to increasing quantity of edge, and on the other extreme, too much habitat reduces isolation to the point that there is no need for fragmentation to enhance individual orientation, and the only effect is lowering habitat quality.

This phenomenon can also justify the negative effect of fragmentation on settlement habitat quality, which means that highly fragmented landscapes, with an increasing quantity of edges, might have low availability of high-quality areas, which results in average low-quality areas for the ones that were able to settle (Ye et al. 2013, Atkins et al. 2019). This effect was stronger in low habitat amount landscapes and for non-plastic individuals, showing an advantage of plasticity in landscapes with less than 20% of habitat amount, which are the ones that have been shown to have a more negative impact on biodiversity (Andrén 1994, Swift and Hannon 2010, Hanski 2015, Fletcher et al. 2018, Rocha et al. 2021). Increasing habitat amount smoothed fragmentation impacts, but curiously, the plasticity effect reversed, and highly plastic individuals showed lower values of habitat quality. This pattern highlights the tradeoff inherent to plasticity, where higher settlement rates are achieved at the cost of settling in lower-quality habitats, particularly in landscapes with little habitat and high fragmentation. Such findings might indicate that plasticity in habitat selection during settlement may benefit dispersal and reduce fragmentation and habitat loss impacts; however, it may not always be the best strategy. The spatial pattern of habitat quality within patches can significantly affect species persistence in fragmented landscapes (Ye et al. 2013). Because in this study, we only simulated the habitat quality with intermediate autocorrelation, the patterns encountered here for fragmented landscapes might change with heterogeneous spatial patterns of habitat quality.

Effects of fragmentation were also apparent regarding dispersal distances. In highly fragmented landscapes, individuals move longer distances to find suitable habitats and settle in a habitat closer to the departure site. That impact is reduced by increasing habitat amount and plasticity, reinforcing our findings of how advantageous plasticity can be at the low-habitat amount in highly fragmented landscapes. In our model, increasing dispersal distances are related to individual energetic condition, which, when constrained, might lead individuals to low-quality habitats and low rates of settlement (Delciellos et al. 2018, Atkins et al. 2019), which might be intensified with increasing fragmentation (van Langevelde 2015). Accordingly, our results showed that in low habitat amount landscapes, a high degree of fragmentation resulted in settlers with low energy. That pattern was similar for all plasticity levels but stronger for non-plastic individuals. In this case, the isolation of fragments and overall reduced availability of high-quality habitats resulted in longer distances moved to reach a new habitat and much more frequent movement across the matrix, hence more energy expenditure during movement. However, beyond these adverse effects, our findings also indicate possible positive effects of fragmentation on the individual's energetic condition when settled in the new habitat. In high habitat-amount landscapes, the energetic condition of the plastic individuals increased with fragmentation, showing a tendency for a non-linear pattern with high plasticity values at intermediate levels of fragmentation. That inverse result did not occur for non-plastic individuals, but the negative effect of fragmentation was reduced in high habitat amount percentage. In the context of high habitat amounts, intermediate fragmentation enhances orientation and provides more connectivity (Rocha et al. 2021), which explains the high energetic condition. Non-plastic individuals, instead, are an exception, as the reduced high-quality habitat availability impacts them more due to fragmentation.

Conclusion

Some authors have pointed out the relevance of plasticity on dispersal to allow organisms to better deal with changing environments (Travis et al. 2013, van Baaren and Candolin 2018, Snell-Rood and Steck 2019, Shaw 2020). Our study reinforces that statement and goes further by showing how plasticity in habitat selection during settlement might attenuate fragmentation and habitat loss impacts on dispersal. However, we also highlighted that plasticity might be advantageous regarding settlement habitat quality only in some specific contexts, for instance, landscapes with less than 20% habitat amount and highly fragmented. Conversely, plasticity allows individuals to settle in better energetic conditions, which tends to increase survival and fitness rates post-settlement. Furthermore, our study provided insights into how the trade-off between habitat quality and energetic conditions affects settlement decisions and the interaction with landscape composition and configuration. Habitat loss and fragmentation might lead individuals to move longer distances, expend more energy and settle more in low-quality habitats. These immediate impacts are probably affecting the survival and persistence of these species on heterogeneous landscapes in the long run. Therefore, further studies must further enhance our understanding of how factors affecting dispersal interact among them and their effects on each dispersal stage to comprehend the immediate and future impacts on biodiversity.

Acknowledgements – I am grateful to my advisory committee, Renato Crouzeilles and Érica Pellegrini Caramaschi, for their continuous guidance throughout this work. I also thank the members of my thesis defence committee – Dr Márcio Zikan, Dr Nina Attias, Dr Elaine Cristina Cambuí Barbosa and Dr Leonardo de Carvalho Oliveira – for their valuable contributions and feedback. The Article Processing Charge for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614).

Funding – The research project was fully sponsored by CNPq (National Council for Scientific and Technological Development), providing my PhD full scholarship, and by CAPES (Brazilian Federal Agency for Support and Evaluation of Graduate Education) with the awarded PRINT scholarship.

Conflict of interest – The authors declare no conflict of interest.

Author contributions

Érika Garcez da Rocha: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Software (lead); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead). **Luca Börger**: Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting); Resources (supporting); Supervision (supporting); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Dmitri Finkelshtein**: Formal analysis (supporting); Methodology (supporting); Software (supporting). **Eduardo Mariano**: Formal analysis (supporting); Methodology (supporting); Software (supporting); Supervision (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Marcus Vinícius Vieira**: Conceptualization (supporting); Formal analysis (supporting); Funding acquisition (supporting); Methodology (supporting); Project administration (supporting); Resources (supporting); Supervision (lead); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (supporting).

Data availability statement

Data are available from Zenodo: https://doi.org/10.5281/zenodo.16543549 (da Rocha et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Acker, P., Besnard, A., Monnat, J.-Y. and Cam, E. 2017. Breeding habitat selection across spatial scales: is grass always greener on the other side? – Ecology 98: 2684–2697.

Andrén, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. – Oikos 71: 355–366.

Arendt, J. D. 2015. Effects of dispersal plasticity on population divergence and speciation. – Heredity 115: 306–311.

Atkins, J. L., Perry, G. L. W. W. and Dennis, T. E. 2019. Effects of mis-alignment between dispersal traits and landscape structure on dispersal success in fragmented landscapes. – R. Soc. Open Sci. 6: 181702.

Baguette, M. and Van Dyck, H. 2007. Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. – Landsc. Ecol. 22: 1117–1129.

Baguette, M., Legrand, D., Fréville, H., Van Dyck, H. and Ducatez, S. 2012. Evolutionary ecology of dispersal in fragmented landscape. – In: Clobert, J. et al. (eds), Dispersal ecology and evolution, vol. 2. Oxford Univ. Press, pp. 381–391.

Baker, M. B. and Rao, S. 2004. Incremental costs and benefits shape natal dispersal: theory and example with *Hemilepistus reaumuri*. – Ecology 85: 1039–1051.

Benton, T. G. and Bowler, D. E. 2012. Linking dispersal to spatial dynamics. – In: Clobert, J. (ed.), Dispersal, ecology and evolution. Oxford Univ. Press, pp. 251–265.

Bonte, D. et al. 2012. Costs of dispersal. – Biol. Rev. 87: 290–312.

Bowler, D. E. and Benton, T. G. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. – Biol. Rev. 80: 205–225.

Broggio, I. S., Silva-Junior, C. H. L., Nascimento, M. T., Villela, D. M. and Aragão, L. E. O. C. 2024. Quantifying landscape fragmentation and forest carbon dynamics over 35 years in the Brazilian Atlantic forest. – Environ. Res. Lett. 19: 034047.

Campana, J. L. M., Raffard, A., Chaine, A. S., Huet, M., Legrand, D. and Jacob, S. 2022. Dispersal plasticity driven by variation in fitness across species and environmental gradients. – Ecol. Lett. 25: 2410–2421.

Clobert, J., Ims, R. A. and Rousset, F. 2004. Causes, mechanisms and consequences of dispersal. – In: Hanski, I. and Gaggiotti, O. E. (eds), Ecology, genetics and evolution of metapopulation. Elsevier Academic Press, pp. 307–335.

Clobert, J., Le Galliard, J. F., Cote, J., Meylan, S. and Massot, M. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. – Ecol. Lett. 12: 197–209.

Crouzeilles, R., Lorini, M. L. and Grelle, C. E. V. 2010. Deslocamento na matriz para espécies da mata atlântica e a dificuldade da construção de perfis ecológicos. – Oecol. Australis 14: 875–903.

Cunha, A. A. and Vieira, M. V. 2002. Support diameter, incline, and vertical movements of four didelphid marsupials in the Atlantic forest of Brazil. – J. Zool. Lond. 258: 419–426.

da Rocha, É. G., Börger, L., Finkelshtein, D., Mariano, E. and Vieira, M. V. 2025. Data from: The interplay between landscape change and plasticity in habitat selection determines dispersal movements and settlement in small non-flying vertebrates. – Zenodo, https://doi.org/10.5281/zenodo.16543549.

Day, C. C., McCann, N. P., Zollner, P. A., Gilbert, J. H. and MacFarland, D. M. 2019. Temporal plasticity in habitat selection criteria explains patterns of animal dispersal. – Behav. Ecol. 30: 528–540.

DeAngelis, D. L. and Mooij, W. M. 2005. Individual-based modeling of ecological and evolutionary processes. – Annu. Rev. Ecol. Evol. Syst. 36: 147–168.

Delciellos, A. C., De Barros, C. S., Prevedello, J. A., Ferreira, M. S., Cerqueira, R. and Vieira, M. V. 2018. Habitat fragmentation affects individual condition: evidence from small mammals of the Brazilian Atlantic forest. – J. Mammal. 99: 936–945.

Edelaar, P., Jovani, R. and Gomez-Mestre, I. 2017. Should I change or should I go? Phenotypic plasticity and matching habitat choice in the adaptation to environmental heterogeneity. – Am. Nat. 190: 506–520.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. – Annu. Rev. Ecol. Evol. Syst. 34: 487–515.

Fahrig, L. 2017. Ecological responses to habitat fragmentation per se. – Annu. Rev. Ecol. Evol. Syst. 48: 1–45.

Fahrig, L. and Merriam, G. 1985. Habitat patch connectivity and population survival. – Ecology 66: 1762–1768.

Fardila, D., Kelly, L. T., Moore, J. L. and McCarthy, M. A. 2017. A systematic review reveals changes in where and how we have studied habitat loss and fragmentation over 20 years. – Biol. Conserv. 212: 130–138.

Fletcher, R. J., Reichert, B. E. and Holmes, K. 2018. The negative effects of habitat fragmentation operate at the scale of dispersal. – Ecology 99: 2176–2186.

Forero-Medina, G. A. and Vieira, M. V. 2009. Perception of a fragmented landscape by Neotropical marsupials: effects of body mass and environmental variables. – J. Trop. Ecol. 25: 53–62.

Gardner, R. H. and Urban, D. L. 2007. Neutral models for testing landscape hypotheses. – Landsc. Ecol. 22: 15–29.

Grimm, V., Berger, U., DeAngelis, D. L., Polhill, J. G., Giske, J. and Railsback, S. F. 2010. The ODD protocol: a review and first update. – Ecol. Modell. 221: 2760–2768.

Hanski, I. 2015. Habitat fragmentation and species richness. – J. Biogeogr. 42: 989–993.

Hollander, J., Verzijden, M., Svensson, E. and Brönmark, C. 2014. Dispersal and phenotypic plasticity. – In: Hansson, L.-Å. and Åkesson, S. (eds), Animal movement across scales. Oxford Univ. Press, pp. 110–125.

Honorato, R., Crouzeilles, R., Ferreira, M. S. and Grelle, C. E. V. 2015. The effects of habitat availability and quality on small mammals abundance in the Brazilian Atlantic forest. – Nat. Conserv. 13: 133–138.

Jacobs, J., Salmaniw, Y., Lam, K. Y., Zhai, L., Wang, H. and Zhang, B. 2025. Fundamental principles of the effect of habitat fragmentation on species with different movement rates. – Conserv. Biol. 39: e14424.

Lima, S. L. and Zollner, P. A. 1996. Towards a behavioral ecology of ecological landscapes. – Trends Ecol. Evol. 11: 131–135.

Lindenmayer, D. B. and Fischer, J. 2006. Habitat fragmentation and landscape change. – Island Press.

Maag, N., Cozzi, G., Clutton-Brock, T. and Ozgul, A. 2018. Density-dependent dispersal strategies in a cooperative breeder. – Ecology 99: 1932–1941.

Matthysen, E. 2012. Multicausality of dispersal: a review. – In: Clobert, J. (ed.), Dispersal, ecology and evolution. Oxford Univ. Press, pp. 3–13.

Morales-González, A., Fernández-Gil, A., Quevedo, M. and Revilla, E. 2022. Patterns and determinants of dispersal in grey wolves (*Canis lupus*). – Biol. Rev. 97: 466–480.

Niebuhr, B. B. S., Wosniack, M. E., Santos, M. C., Raposo, E. P., Viswanathan, G. M., da Luz, M. G. E. and Pie, M. R. 2015. Survival in patchy landscapes: the interplay between dispersal, habitat loss and fragmentation. – Sci. Rep. 5: 11898.

Pendrill, F. et al. 2022. Disentangling the numbers behind agriculture-driven tropical deforestation. – Science 377: eabm9267.

Pires, A. S., Lira, P. K., Fernandez, F. A. S., Schittini, G. M. and Oliveira, L. C. 2002. Frequency of movements of small mammals among Atlantic Coastal forest fragments in Brazil. – Biol. Conserv. 108: 229–237.

Potts, J. R. and Börger, L. 2022. How to scale up from animal movement decisions to spatiotemporal patterns: an approach via step selection. – J. Anim. Ecol. 92: 16–29.

Raynor, E. J., Beyer, H. L., Briggs, J. M. and Joern, A. 2017. Complex variation in habitat selection strategies among individuals driven by extrinsic factors. – Ecol. Evol. 7: 1802–1822.

Rémy, A., Le Galliard, J. F., Gundersen, G., Steen, H. and Andreassen, H. P. 2011. Effects of individual condition and habitat quality on natal dispersal behaviour in a small rodent. – J. Anim. Ecol. 80: 929–937.

Rezende, C. L., Scarano, F. R., Assad, E. D., Joly, C. A., Metzger, J. P., Strassburg, B. B. N., Tabarelli, M., Fonseca, G. A. and Mittermeier, R. A. 2018. From hotspot to hopespot: an opportunity for the Brazilian Atlantic forest. – Perspect. Ecol. Conserv. 16: 208–214.

Ribeiro, M. C., Metzger, J. P., Martensen, A. C., Ponzoni, F. J. and Hirota, M. M. 2009. The Brazilian Atlantic forest: how much is left, and how is the remaining forest distributed? Implications for conservation. – Biol. Conserv. 142: 1141–1153.

Ríos-Uzeda, B., Brigatti, E., Vieira, M. V., Uzeda, B. R., Brigatti, E. and Vieira, M. V. 2019. Lévy patterns in the small-scale movements of marsupials in an unfamiliar and risky environment. – Sci. Rep. 9: 2737.

Rocha, É. G. da, Brigatti, E., Niebuhr, B. B., Ribeiro, M. C. and Vieira, M. V. 2021. Dispersal movement through fragmented landscapes: the role of stepping stones and perceptual range. – Landsc. Ecol. 36: 3249–3267.

Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. – Annu. Rev. Ecol. Evol. Syst. 38: 231–253.

Rosa, M. R., Brancalion, P. H. S., Crouzeilles, R., Tambosi, L. R., Piffer, P. R., Lenti, F. E. B., Hirota, M., Santiami, E. and Metzger, J. P. 2021. Hidden destruction of older forests threatens Brazil's Atlantic forest and challenges restoration programs. – Sci. Adv. 7: eabc4547.

Shaw, A. K. 2020. Causes and consequences of individual variation in animal movement. – Movm. Ecol. 8: 12.

Snell-Rood, E. C. and Steck, M. K. 2019. Behaviour shapes environmental variation and selection on learning and plasticity: review of mechanisms and implications. – Anim. Behav. 147: 147–156.

Stamps, J. 2001. Habitat selection by dispersers: integrating proximate and ultimate approaches. – In: Clobert, J. (ed.), Dispersal. Oxford Univ. Press, pp. 230–242.

Stamps, J. A. 2006. The silver spoon effect and habitat selection by natal dispersers. – Ecol. Lett. 9: 1179–1185.

Stamps, J. A., Krishnan, V. V. and Reid, M. L. 2005. Search costs and habitat selection by dispersers. – Ecology 86: 510–518.

Swift, T. L. and Hannon, S. J. 2010. Critical thresholds associated with habitat loss: a review of the concepts, evidence and applications. – Biol. Rev. 85: 35–53.

Tisue, S. and Wilensky, U. 2004. A simple environment for modeling complexity. – In: International conference of complex systems, pp. 1–10. https://www.researchgate.net/publication/230818221_NetLogo_A_simple_environment_for_modeling_complexity.

Travis, J. M. J. and Dytham, C. 1999. Habitat persistence, habitat availability and the evolution of dispersal. – Proc. R. Soc. B 266: 723–728.

Travis, J. M. J., Mustin, K., Bartón, K. A., Benton, T. G., Clobert, J., Delgado, M. M., Dytham, C., Hovestadt, T., Palmer, S. C. F., Van Dyck, H. and Bonte, D. 2012. Modelling dispersal: an eco-evolutionary framework incorporating emigration, movement, settlement behaviour and the multiple costs involved. – Methods Ecol. Evol. 3: 628–641.

Travis, J. M. J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., Boulangeat, I., Hodgson, J. A., Kubisch, A., Penteriani, V., Saastamoinen, M., Stevens, V. M. and Bullock, J. M. 2013. Dispersal and species' responses to climate change. – Oikos 122: 1532–1540.

van Baaren, J. and Candolin, U. 2018. Plasticity in a changing world: behavioural responses to human perturbations. – Curr. Opin. Insect Sci. 27: 21–25.

Van Dyck, H. and Baguette, M. 2005. Dispersal behaviour in fragmented landscapes: routine or special movements? – Basic Appl. Ecol. 6: 535–545.

van Langevelde, F. 2015. Modelling the negative effects of landscape fragmentation on habitat selection. – Ecol. Inform. 30: 271–276.

Villard, M. A. and Metzger, J. P. 2014. Beyond the fragmentation debate: a conceptual model to predict when habitat configuration really matters. – J. Appl. Ecol. 51: 309–318.

White, J. W., Rassweiler, A., Samhouri, J. F., Stier, A. C. and White, C. 2014. Ecologists should not use statistical significance tests to interpret simulation model results. – Oikos 123: 385–388.

Wiegand, T., Revilla, E. and Moloney, K. A. 2005. Effects of habitat loss and fragmentation on population dynamics. – Conserv. Biol. 19: 108–121.

Ye, X., Skidmore, A. K. and Wang, T. 2013. Within-patch habitat quality determines the resilience of specialist species in fragmented landscapes. – Landsc. Ecol. 28: 135–147.