



Modeling the effect of habitat selection mechanisms on population responses to landscape structure



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ABSTRACT

Novel habitats can become ecological traps for mobile animals if individuals consistently select them over habitats with better fitness consequences. Due to challenges with the measurement of habitat selection and quality, ecological traps are difficult to study in the field. Previous modeling approaches have overlooked the importance of selection cues as a key component in the mechanisms giving rise to ecological traps. We created a spatially explicit, individual-based simulation model to evaluate the effects of landscape structure on population dynamics of a hypothetical species under two mechanisms of habitat selection. In *habitat-based* selection, individuals preferred high-quality patches (leading to adaptive outcomes), selected patches at random (equal-preference) or preferred lower-quality patches (severe ecological traps). In *cue-based* selection they chose based on a structural attribute that was not directly related to fitness (canopy cover). We applied the model to the case of resident birds in landscapes composed of remnant forests and shade coffee agriculture. We designed simulation experiments with scenarios varying in landscape composition, configuration, search area and criteria for habitat preference. While all factors affected population size and individual fitness, the most important variables were proportion of high-quality habitat in the landscape, criteria for habitat preference and their interaction. The specific arrangement of habitat patches and search area had weaker and sometimes unexpected effects, mainly through increasing outcome variance. There was more variation among scenarios when selection was *habitat-based* than *cue-based*, with outcomes of the latter being intermediate between those of adaptive and equal-preference choices. Because the effects of ecological traps could be buffered by increasing the amount of high-quality habitat in the landscape, our results suggest that to truly understand species adaptation to habitat transformation we must always include landscape context in our analyses, and make an effort to find the appropriate scales and cues that organisms use for habitat selection.

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1. Introduction

Habitat selection is one of the most important biological processes linking individual behavior with species distribution (Jones, 2001; Lima and Zollner, 1996). Early models of habitat selection made the simplifying assumption that organisms possessed perfect information about habitat quality (Fretwell and Lucas, 1969; Pulliam, 1988). However, mobile animals living in landscapes that have gone through widespread, rapid environmental change, may have less reliable information than those remaining in their original habitats (Battin, 2004; Schlaepfer et al., 2002). Ecological traps arise when individuals indirectly assess habitat quality through

cues that become uncoupled from the ultimate fitness consequences they experience after choosing that particular habitat (Remes, 2000; Stamps and Krishnan, 2005). The mismatch between cues and quality leads animals to consistently select unfavorable habitats (ecological traps), and/or to avoid favorable ones (undervalued resources or perceptual traps) (Gilroy and Sutherland, 2007; Patten and Kelly, 2010). The population consequences of these processes differ substantially from those of classic source and sink systems; where unfavorable habitats are only occupied when favorable habitat is either not available or not cost-efficient for a particular individual (Loehle, 2012; Pulliam, 1988; Robertson and Hutto, 2006). While there is general agreement on the potential evolutionary and conservation relevance of this phenomena, knowledge of what makes species vulnerable to traps is constrained by the difficulty in estimating true measures of habitat preference and quality at the appropriate spatial and temporal scales (Battin, 2004; Robertson and Hutto, 2006; Shustack and Rodewald, 2010).

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With ecological modeling, researchers are able to create scenarios where landscape structure is varied systematically while directly testing hypotheses about the interactions between habitat availability, selection, occupancy, and quality (Battin, 2004; Dunning et al., 1995; Pulliam and Danielson, 1991). Modeling has been increasingly used to evaluate the role that habitat selection plays in species adaptation to heterogeneous landscapes, and recently emphasis has been placed on: (1) modeling habitat attractiveness and quality separately to allow for the existence of ecological and perceptual traps (Delibes et al., 2001; Donovan and Thompson, 2001; Fletcher et al., 2012; Kokko and Sutherland, 2001; Kristan, 2003; Shustack and Rodewald, 2010), or (2) incorporating more realistic behavioral assumptions, movement rules and selection constraints to population models (Aarts et al., 2013; DeCesare et al., 2014; Loehle, 2012). Models of ecological traps have matured from comparing population responses to the proportion of sink habitat under different types of preference (Delibes et al., 2001), to incorporating details in their parameterization of habitat quality (Donovan and Thompson, 2001; Kristan, 2003), including life history characteristics and evolution (Kokko and Sutherland, 2001), taking into account differences in individual quality (Shustack and Rodewald, 2010), and differentiating ecological traps according to their origin (Fletcher et al., 2012). None of the models directly assessing ecological traps have been spatially explicit and, therefore, they do not incorporate movement rules or behaviors which may be important to generate realistic patterns (Matthiopoulos et al., 2005; Nakayama et al., 2011; Stephens et al., 2002).

Habitat selection functions in previous models vary according to their specific research aim, but habitat choice has predominately been modeled as individuals selecting among habitat categories. This overly simplistic mechanism may not be readily applicable to populations existing in mosaics or landscapes with habitat gradients (Kristan, 2003). For habitat selection to become maladaptive either selection cues have to make a lower quality habitat more attractive, habitat suitability has to decrease while cues stay the same, or both processes can happen simultaneously (Robertson and Hutto, 2006). By a combination of these mechanisms, novel, man-made habitats can become two different types of ecological traps for highly mobile habitat generalists: equal-preference traps arise when the animal is equally likely to settle in the higher and lower quality habitats whereas severe traps arise when animals favor the lower quality sites (Robertson and Hutto, 2006; Robertson et al., 2013). Given these mechanisms for the appearance of ecological and perceptual traps, we propose that model realism will improve by allowing individuals to use structural attributes that are distributed continuously throughout the landscape as selection cues. Further, we suggest that shifting the focus of model results from long-term effects on population persistence to trends in habitat-specific demography will better match known empirical cases of ecological traps (Battin, 2004; Fletcher et al., 2012).

We created a spatially explicit and individual-based model to explore the effect of habitat and cue-based selection mechanisms on population responses to landscape structure. To explore the consequences that proposed mechanisms for the appearance of ecological traps have in a wide range of ecological contexts, it was necessary to assess the importance of interactions between variables occurring at two very distinct scales: the individual and the landscape level (Lima and Zollner, 1996). Therefore, our model system is one where a mobile animal is present in two habitat types of which one is better quality (source) than the other (sink), but where individuals have innate habitat choice behaviors that cannot be modified after landscape change. We designed two types of choice algorithms: (1) selection based on the habitat type of the cell, from now on called *habitat-based selection*, allowed individuals to either prefer sources over sinks (adaptive selection), show no habitat preference (equal-preference traps), or constantly prefer

sinks over sources (severe ecological and perceptual traps); and (2) selection based on an internal characteristic of the cell, from now on called *cue-based selection*, allowed individuals to prefer sites having values for a structural attribute that were equal to or larger than a predetermined threshold, assuming that higher threshold values would result in better differentiation of the habitat types and therefore on more adaptive outcomes.

We chose resident forest birds using shade coffee as the system to parameterize the model because despite the fact that these tropical agroforestry systems stand out for retaining important elements of native biodiversity (Moguel and Toledo, 1999; Perfecto et al., 1996; Philpott et al., 2007), the possibility remains that they function as ecological traps for species with broad habitat requirements (Komar, 2006; Sekercioglu et al., 2007). Whether traps exist or not in the system, and what consequences they could have for the apparent balance between agricultural profit and biodiversity conservation, remains unanswered because with a few exceptions (Cohen and Lindell, 2004; Graham, 2001; Lindell and Smith, 2003; Sekercioglu et al., 2007), studies have either focused on migrants and/or species presence and detection rates as indicators of habitat suitability (Komar, 2006; Sánchez-Clavijo et al., 2008). While this model complements, and is partly based on, ongoing field research trying to address some of these issues (Sierra Nevada de Santa Marta, Colombia); it is still a highly simplified representation of a bird population in our study system, so parameter values were a mix of field and theoretical data. The structure was designed so that it can also be easily adapted to further explore this and other systems.

We designed simulation experiments where we varied landscape structure (composition and configuration) and behavioral rules (habitat preference and search area) to: (1) address which of these four factors (and their interactions) had a larger effect on fitness (measured as population and mean individual size); (2) compare the patterns produced by different levels of *habitat-based* and *cue-based* selection; and (3) compare emerging patterns of population size between simulations with local and global dispersal. We anticipated that all else being equal, more high-quality habitat, less complex landscapes with larger habitat patches, greater search areas, and adaptive or strict *cue-based* selection criteria would lead to faster occupancy of forest, larger individuals, and larger population sizes.

2. Methods

2.1. Model description

We describe here only the general behavior of the model (for a detailed description following the ODD protocol for agent-based models (Grimm et al., 2006; Grimm et al., 2010) see Appendix A). The modeling sequence consisted of three initialization procedures (landscape generator, initial population, and colonization) followed by a yearly cycle of breeding, survival, census, and dispersal (Fig. A.1). Habitat preference criteria were fixed throughout each simulation and for all individuals, while the outcomes from occupying a particular patch changed yearly through habitat-dependent functions. We assumed that forest, being the original habitat, would represent the source for our hypothetical species, while shade coffee, being the novel one, would represent the sink. Percent canopy cover was the shared structural characteristic that individuals used for cue-based selection. All code was written and executed in MATLAB version R2013b (The MathWorks, Inc. 1984–2013).

Landscape generator – the simulation environment was a bounded square grid, made of cells of equal area that represented individual breeding territories. Landscape size was specified as 400 cells, all of which started out as forest. At the beginning of each

simulation, a proportion of cells were converted to coffee to determine landscape composition, and landscape configurations were created by choosing from lateral, radial, and percolation transformation processes, which reflect common ways in which tropical forests are converted to agriculture (Fig. A.3). Each cell was randomly allocated a value for percent canopy cover from a pool of data sampled in the field for both forest remnants and shade coffee. While mean canopy cover in forest was higher (forest: 82.36, coffee: 58.99), standard deviation in coffee was wider (forest: 6.11, coffee: 20.42) allowing for overlap between habitats (Fig. A.2). A different landscape grid was generated for each simulation run, even under the same initial conditions.

Initial population – the initial number of adults to populate the landscape was chosen to ensure population persistence, and allow a few years between initialization and landscape saturation. Each bird was assigned a wing length from a normal distribution common for all birds, and a weight from a forest-specific normal distribution (Table A.1). Size-corrected body mass (hereafter referred to as size) was calculated by dividing weight by wing length and was chosen as the measure of individual condition to combine individual and habitat-dependent effects. We used wing length and body mass data of Ochre-bellied Flycatcher (*Mionectes oleagineus* M. H. K. Lichtenstein, 1823) in our field site to build these distributions.

Colonization – birds were sorted by size so that the largest/most competitive individuals had better chances of acquiring their preferred habitat. One by one they searched a predetermined number of patches at random, in a way analogous to pre-emptive habitat selection models (Pulliam and Danielson, 1991). They were either assigned to the first patch that matched their habitat selection criteria, or forced to settle in the last one they examined. Because cells could only hold one breeding adult, the process ended when all birds had either settled on a patch or remained in the landscape as floaters (see flowchart of this process in Fig. A.4).

Breeding – settled adults produced offspring based on habitat-specific binomial distributions that generated higher average reproductive output in forest than coffee (Table A.1, Fig. A.5). New birds were designated as juveniles and assumed to stay in their natal patch until dispersal occurred. Birds existing as floaters did not breed.

Survival – survival probabilities were dependent on age and territorial status, and were applied at the individual level to introduce stochasticity. Adult survival was much higher than juvenile survival and floater survival probability was a density-dependent function that approached zero as the landscape reached its carrying capacity. After dead individuals were removed from the system, all surviving juveniles became adults. Their wing length was sampled from the same distribution as the initial birds, and their body mass from habitat-dependent normal distributions with a higher mean for forest than coffee. Adults retained the same wing length throughout their lifetime, but were assigned a new weight each year depending on their habitat. We assumed floaters had larger home ranges spanning both habitats; therefore their weight after survival was derived from a distribution intermediate between those of forest and coffee (Table A.1).

Census and sampling – during this stage the program updated the data for each individual's location, size, and the number of surviving fledglings it produced. In order to count floaters they were assigned a temporary habitat according to landscape proportion. At the end of each year of simulation, the program collected aggregate measures for all the individuals, separated by habitat (sources or sinks) and territorial status (breeders and surviving juveniles or floaters).

Dispersal – our individuals represent resident birds that do not vacate the landscape each year to repeat the colonization process, instead they go through a spatially explicit dispersal

process affected by their individual size, current location and allowed search area. For scenarios with *habitat-based* selection, individuals were either given a type of breeding site that was preferred over the other (forest or coffee), or let to choose breeding sites randomly. With *cue-based* selection they were given a preferred threshold value for percent canopy cover; all the cells that had canopy cover equal to or larger than their threshold were considered preferred sites, while those below were avoided. Birds selected habitat in descending order of size, using a decision algorithm that first evaluated whether a chosen patch complied with their selection criteria, and if so, continued by assessing if it was either empty or if it contained an individual which they could displace (smaller bird). Birds who failed to settle became floaters (see flowchart of this process in Fig. A.6). Local dispersal occurred when the birds were given a search area around their current patch which was smaller than the total landscape. Global dispersal occurred when they could search the whole landscape for a new patch.

2.2. Simulation experiments

Our main focus is on a set of simulations with local dispersal, where we combined different levels of our four factors of interest to create 480 scenarios. For *landscape composition* we chose scenarios with 90%, 75%, 50%, 25% and 10% of remnant forest cover to get a representation of increasing transformation. For *landscape configuration* we used lateral transformation to represent cases in which forest clearing starts from a linear feature, radial to represent transformation following topographical contours, and percolation to simulate small scale farming that expands outwards from several points. We selected four *search areas* to represent dispersal capabilities ranging from birds sampling less than 3% to around 20% of the whole landscape. For *habitat-based* selection we used all three possible behaviors (adaptive, equal-preference and severe traps). For *cue-based* selection we chose five canopy cover thresholds: 30%, 45%, 60%, 75% and 90%. It has been proposed that 60% canopy cover is the minimum to ensure biodiversity conservation in shade coffee (Sánchez-Clavijo et al., 2007), and was the mean for measured coffee plots in our field site (Table 1). For this set of simulations, we ran 30 repetitions per scenario. In a second set of simulations we replaced local with global dispersal by allowing the individuals to search three patches at random from all the landscape. We used the same three levels for landscape configuration and *habitat-based* preference, but varied the levels for landscape composition and *cue-based* preference differently (Table 1). This design resulted in 36 scenarios common to both sets of simulations, allowing us to compare broad patterns between local and global dispersal.

2.3. Data analysis

The output for each simulation consisted of matrices showing the number of adult birds, mean number of juveniles produced per adult that bred successfully, and the mean size of birds per habitat, territorial status, year, and run. The model always reached stable population sizes after both landscape saturation and maximum floater density were reached, therefore we inspected population growth curves and chose a year before saturation to compare population responses during transient conditions. We calculated emergent properties at the population-level for each scenario, and focused on population size and mean size of individuals. Because each year the census happened after the birds born on that year had become adults, the output did not separate the breeders of one year from the offspring they produced. Therefore, population sizes are a combined measure of reproductive output (which is habitat-dependent) and survival (which is age-dependent). The mean size of individuals in the landscape is used as a surrogate of average individual fitness. We analyzed means and variances between runs,

Table 1
Variable levels changed to create 480 simulation scenarios with local dispersal (30 repetitions) and 54 with global dispersal (50 repetitions).

Variable	Level 1	Level 2	Level 3	Level 4	Level 5
Landscape composition	10% forest – 90% coffee ^b	25% forest – 75% coffee ^c	50% forest – 50% coffee ^c	75% forest – 25% coffee ^c	90% forest – 10% coffee ^b
Landscape configuration	Lateral ^c	Radial ^c	Percolation ^c		
Search area	1 (9 cells) ^b	2 (25 cells) ^b	3 (49 cells) ^b	4 (81 cells) ^b	ALL (3 cells) ^a
Habitat-based selection	Prefer forest (adaptive) ^c	Equal-preference ^c	Prefer coffee (severe trap) ^c		
Cue-based selection	CC \geq 30% ^b CC \geq 40% ^a	CC \geq 45% ^b	CC \geq 60% ^c	CC \geq 75% ^b	CC \geq 90% ^b CC \geq 80% ^a

CC, canopy cover.

^a Used only with global dispersal.

^b Used only with local dispersal.

^c Used in all simulations.

because the latter gives a measure of the stability for the outcomes of any given scenario.

We used model selection with AICc (Burnham and Anderson, 2002) to identify the most plausible model structure for scenarios with habitat and cue-based selection separately. Preliminary analyses suggested that proportion of forest and habitat preference were the most important factors so our model sets included all possible models that could be built without removing those two factors, and including only up to four of their two-way interactions. We also included a null model and the completely saturated model in the set, for a total of 51 alternative structures.

3. Results

3.1. Local dispersal

3.1.1. Early occupation patterns and population growth

Adaptive choices in scenarios with *habitat-based* selection led most birds to occupy forest sites, but as forest cover decreased, spill-over of individuals to coffee became more common. Equal-preference selection led to random occupation patterns and maladaptive selection to faster occupancy of coffee sites (Fig. B.1). Colonization patterns with *cue-based* selection resembled those of equal-preference (Fig. B.2). Starting with 15 individuals, all populations with *habitat-based* selection grew fast for the first 12 years, and then leveled off as they hit carrying capacity. Populations in scenarios with adaptive selection and equal-preference grew faster than those with severe traps, and therefore stabilized earlier. By the end of the simulations (year 15) all populations had similar sizes for each level of forest cover (Fig. B.3). With *cue-based* selection, growth was slower for CC90% preference and, up to year thirteen when populations stabilized, was very similar for all other values. At the end of the simulations the only clear differences in population size were brought about by forest cover (Fig. B.4). Saturation ranges were equivalent between the two types of selection, and because we were more interested in transient patterns after disturbance than in stable environments, we chose to carry out all subsequent analyses for year 11.

3.1.2. Population size

As the proportion of forest in the landscape increased, so did the mean and the variance for population size at year 11 in all 480 scenarios. With *habitat-based* selection, the general trend was for adaptive selection to lead to larger populations than equal-preference when forest cover was low, but very similar values when forest cover was high. Severe traps led to smaller populations consistently, but the difference with equal-preference was significantly larger with high values of forest cover. All else being equal, there were occasional differences between configurations but the patterns were not consistent. Larger search areas lead to larger populations for adaptive selection and equal-preference but

to smaller populations with severe traps, especially when forest cover was high (Fig. 1A). With *cue-based* selection, larger canopy percent thresholds lead to larger populations except for CC90%, which consistently lead to much smaller populations than any other value. There were no consistent patterns related to landscape configuration. Larger search areas lead to larger populations, but there was a lot of overlap between the top three categories (areas of 25, 49 and 81 cells) (Fig. 1B).

The most plausible model explaining population size at year 11 in scenarios with *habitat-based* selection included all four additive factors, an interaction between the two behavioral variables and a landscape-behavior interaction between forest cover and habitat preference (Table 2). The most plausible model in scenarios with *cue-based* selection additionally included the interaction between forest cover and search area, which was very hard to detect from visual examination of the results (Table 2). Both population size models have AICc weights lower than 0.6 suggesting that other interactions may be worth investigating further (Tables B.1 and B.2).

3.1.3. Individual size

The mean size of all individuals alive by year 11 increased with forest cover when there were severe ecological traps (as variance rapidly decreased). With adaptive selection and equal-preference the pattern was more subtle and showed slightly higher values at landscapes with similar areas of forest and coffee. For equal-preference and severe traps, scenarios with radial configurations lead to larger individual sizes, especially when forest cover was high. For adaptive selection, radial landscapes produced larger individuals when forest cover was low. Larger search areas lead to smaller individuals within the habitat-preference categories (Fig. 2A). With *cue-based* selection the patterns were different; size was higher at middle values of forest cover but increased with canopy cover percent threshold (except for CC90%). Variance was also greater at landscape compositions in the extremes. Landscapes with lateral and percolation configurations lead to larger individuals when forest cover was low, but those with radial configurations lead to the same outcome when forest cover was high. As with *habitat-based* selection, smaller search areas lead to on average, larger individuals (Fig. 2B).

The most plausible models explaining the variation in mean individual size between scenarios were more complex than those for population size. For *habitat-based* selection the highest ranked model was the full interactive model between the four factors of interest, with an AICc weight of 1.000 within the model set, which suggests that all other models we tested were missing important interactions (Table 2). For *cue-based* selection, the most informative model included the interactions between the two landscape factors, as well as the landscape: behavior interactions between forest cover, preference and search area (Table 2, Tables B.3 and B.4).

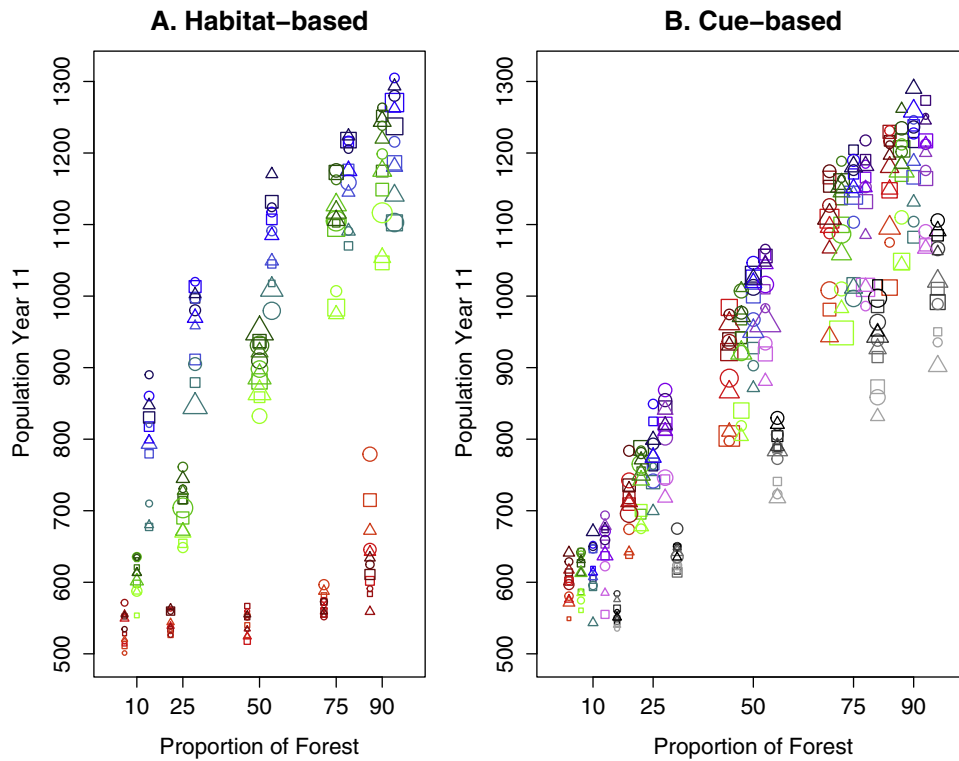


Fig. 1. (A) Effect of forest cover on population size at year 11 for scenarios with *habitat-based* selection; for each level of forest cover the three columns represent adaptiveness from left to right (severe traps, equal-preference traps, adaptive selection); shapes represent landscape configuration (squares: lateral, circles: radial, triangles: percolation); shades represent search area (the darker the shade the larger the area); and the size of the dots represents the variance divided by a factor of 10,000 (+0.2). (B) Effect of forest cover on population size at year 11 for scenarios with *cue-based* selection: for each level of forest cover the five columns represent increasing canopy cover thresholds for preference from left to right (CC30%, CC45%, CC60%, CC75%, CC90%); shapes represent landscape configuration (squares: lateral, circles: radial, triangles: percolation); shades represent search area (the darker the shade the larger the area); and the size of the dots represents the variance divided by a factor of 10,000 (+0.2).

Table 2
Structure of the most informative models (lowest AICc within set of 51 models) for two fitness responses, with *habitat-based* and *cue-based* selection (X-present, N11-population size at year 11, S11-mean individual size at year 11, L-landscape factors, B-behavioral factors).

Factor or interaction	N11		S11	
	Habitat	Cue	Habitat	Cue
Composition (L)	X	X	X	X
Configuration (L)	X	X	X	X
Composition × configuration (LL)	-	-	X	X
Habitat preference (B)	X	X	X	X
Search area (B)	X	X	X	X
Habitat preference × search area (BB)	X	X	X	-
Composition × habitat preference (LB)	X	X	X	X
Composition × search area (LB)	-	X	X	X
Configuration × habitat preference (LB)	-	-	X	-
Full interactive model	-	-	X	-
AICc weight within model set	0.504	0.599	1.000	0.728
Figure no. (results)	Fig. 1A	Fig. 1B	Fig. 2A	Fig. 2B
Table no. (Appendix B)	B.1	B.2	B.3	B.4

3.2. Local vs. global dispersal

Simulations with landscape-wide dispersal showed faster saturation times than those where it was restricted to the local neighborhood. By year 11, population sizes of scenarios with maladaptive habitat selection were already closer to the values of the other types of selection and were positively and strongly affected by the amount of forest in the landscape (Fig. 3A–C). Restricting

dispersal to the local neighborhood and varying search area greatly increased the variance in population sizes at scenarios where all other factors were kept the same. This increase in variance made the differences in population sizes overlap to a greater extent than when search was a constant parameter, but significant differences could still be seen in maladaptive selection vs. other types of selection at all times, and between adaptive selection vs. equal-preference and CC60% scenarios, only when forest cover was 25% (Fig. 3D–F).

4. Discussion

Habitat selection has typically been modeled as a choice between habitat categories – where individuals either prefer or avoid each type of habitat (Battin, 2004). However, this approach may obscure the mechanism responsible for ecological traps: the mismatch between selection cues and habitat quality (Schlaepfer et al., 2002) and the fact that these cues overlap in remnant and novel habitats. Our simulation experiment showed that habitat selection based on a continuously distributed structural attribute can lead to more subtle and sometimes different patterns than those found for selection based on patch type, which in turn will make ecological traps harder to detect if we characterize the later but ignore the former. Although our model could be adapted further by changing the distributions of the preference cue, the thresholds used for selection, including additional structural attributes, or even social responses and species interactions, our findings point to interesting hypotheses about species adaptation to transformed landscapes.

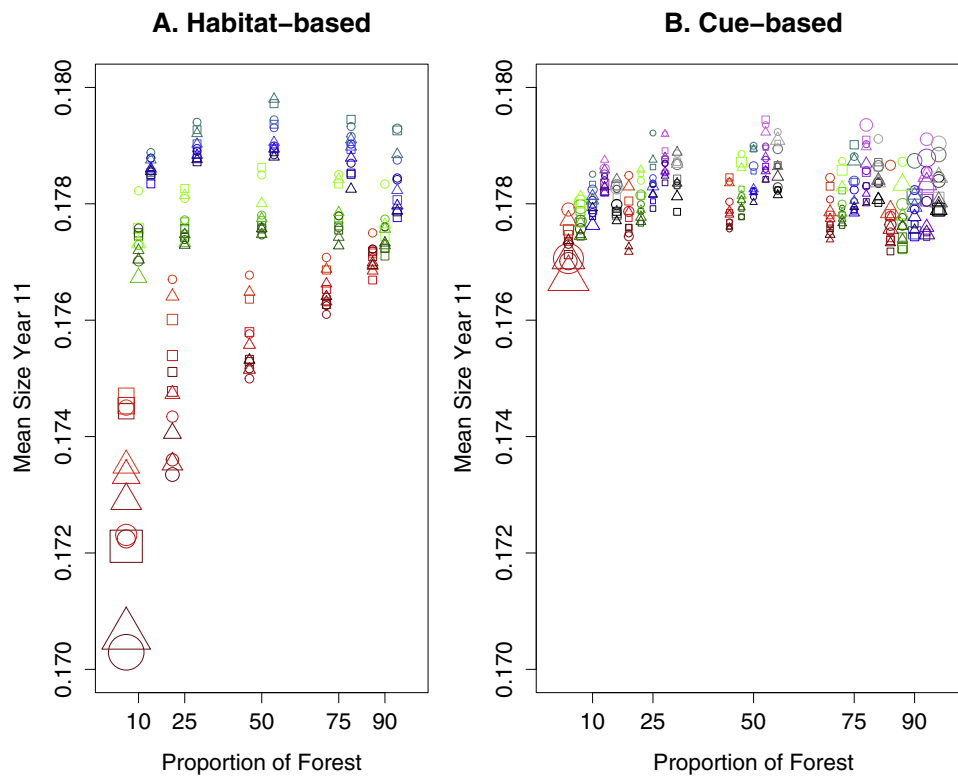


Fig. 2. (A) Effect of forest cover on mean individual size at year 11 for scenarios with *habitat-based* selection: for each level of forest cover the three columns represent adaptiveness from left to right (severe traps, equal-preference traps, adaptive selection); shapes represent landscape configuration (squares: lateral, circles: radial, triangles: percolation); shade represents search area (the darker the shade the larger the area); and the size of the dots represents the variance divided by a factor of 0.00001 (+1). (B) Effect of forest cover on mean individual size at year 11 for scenarios with *cue-based* selection: for each level of forest cover the five columns represent increasing canopy cover thresholds for preference from left to right (CC30%, CC45%, CC60%, CC75%, CC90%); shapes represent landscape configuration (squares: lateral, circles: radial, triangles: percolation); shades represent search area (the darker the shade the larger the area); and the size of the dots represents the variance divided by a factor of 0.000001 (+0.5).

4.1. Landscape factors

Our results are consistent with previous models of habitat selection where the relative amount of high vs. low quality habitat was the most critical factor in determining population outcomes (Delibes et al., 2001; Pulliam and Danielson, 1991). However, the importance of remnant habitat to generalist species depends on the spatial and temporal variation of habitat quality (Donovan and Thompson, 2001; Kristan, 2003; Robertson et al., 2013), which in our model was kept relatively constant despite evidence that this might not be the case for certain species in shade coffee (Cohen and Lindell, 2004; Lindell and Smith, 2003). Responses to decreases in forest were not linear, and displayed different shapes for population and individual size, as these variables were affected by several interactions with the other predictor factors. Both responses were affected by the number of breeders and juveniles produced in each habitat, and by the number of floaters in the system, which depended on the speed of population growth. Not being able to differentiate between transients and permanent residents in field sampling may be one of the reasons why it is difficult to find landscape-level differences in demography between habitats, and our simulations showed that, especially for body size, including floaters could greatly dilute the effects caused by maladaptive selection. Given the landscape compositions and search areas we used in our simulations, differences in configuration did not prevent birds from reaching their preferred habitat; however this should not be interpreted as evidence that landscape configuration will not be important to determine

ecological traps in more complex regions with a higher habitat diversity.

4.2. Behavioral factors

Populations preferring high-quality habitat grew faster than those selecting randomly or preferring low-quality patches. In our model, the differences between each level changed according to the simulation year, suggesting that the effect of ecological traps may change in strength depending on the time since landscape perturbation. Even though we expected increases in the cue criteria to effectively increase the accuracy of habitat choices, the responses from this type of selection were always close to those of equal-preference. These outcomes, while not entirely maladaptive, are still different from what adaptive selection would bring about. It was especially noticeable that if selection was very strict (as in CC90%), individuals encountered their preferred habitat so sparsely that it no longer allowed for any discrimination of quality. This could indicate that the attractiveness provided by habitat selection cues to a specific site will change with the spatial distribution of the attribute at the landscape level, reinforcing that to advance our knowledge of ecological traps, it is necessary to understand which cues species use to select habitat, and how the distribution of these cues relative to habitat quality ultimately determines species persistence in transformed regions (Battin, 2004; Robertson and Hutto, 2006).

Search area was introduced to simulate species having different search capabilities (Danielson, 1991), and to restrict dispersal

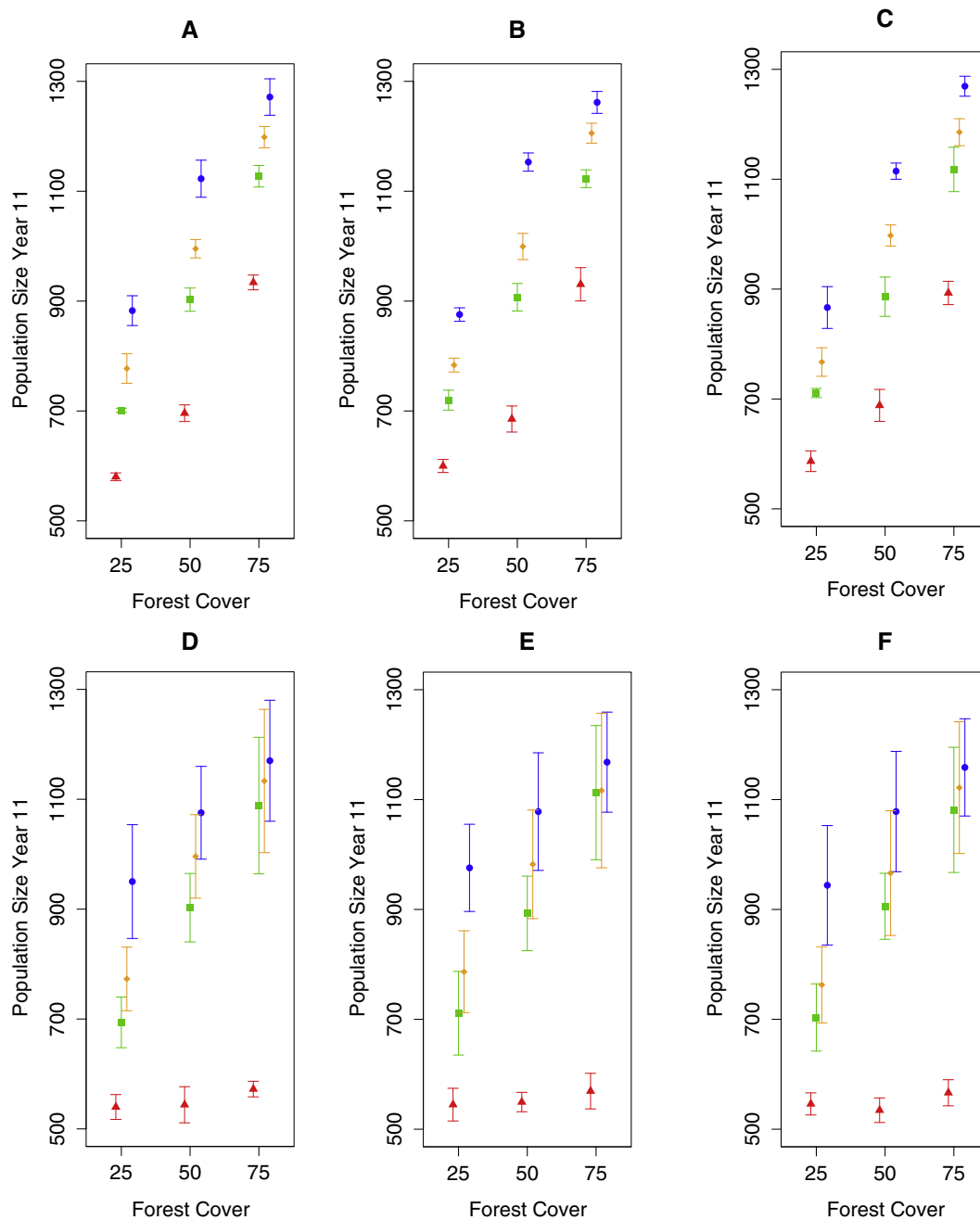


Fig. 3. Effect of forest cover, type of habitat preference and landscape configuration on population size at year 11 for simulations with global (A, B and C) and local (D, E and F) dispersal. Panels on the left (A and D) show landscapes with lateral configurations, middle show radial (B and E), and right show percolation (C and F); shapes represent types of selection (triangles: severe traps, squares: equal-preference traps, rhombus: preference of sites with canopy cover $\geq 60\%$, circles: adaptive selection); error bars represent the 95% confidence intervals from a sample of four scenarios under each combination of factors (after averaging all the simulation runs for each one).

to the local neighborhood. It was important in all the models and had the effect of increasing population size; as individuals sampled more patches, there was a higher probability that they found the preferred kind. Surprisingly, the effect on average individual size was the opposite; larger search areas lead to smaller mean individual sizes and larger variances, particularly in extreme landscapes (forest covers of 10% and 90%). Intermediately modified landscapes had more edges between habitats so there were higher chances of individuals being forced to become floaters, and this increased with search area. In landscapes representing those regions where forest has recently been converted or almost totally converted, birds will move less between habitats if they are not located near the edge, but greater search areas may prevent this

from happening. More floaters in the system mean more dilution of the size difference between habitats.

4.3. Interactions between landscape and behavioral factors

Interactions between composition and configuration were important for individual size variation, but not to explain population size. Interactions between preference and search were important in all scenarios except the *cue-based* models for individual size, although generally species that search smaller areas are also expected to have stricter habitat selection criteria (Rabinowitz et al., 1986). All analyses showed interactions between factors at individual and landscape levels, indicating the relevance of both

ecological context and behavior for studies of habitat selection (Lima and Zollner, 1996). Landscape change that leads to severe, or even equal-preference ecological traps will reduce fitness for species that cannot adapt their selection criteria (Robertson and Hutto, 2006) and our model shows that this situation becomes worse when the remnant good-quality habitat in the landscape is further decreased.

4.4. Habitat vs. cue-based selection

We chose percent canopy cover as the selection cue for our birds because it has been shown to be positively related to species richness and the proportion of forest species inhabiting shade coffee (Moguel and Toledo, 1999; Philpott et al., 2008). We expected birds to make more selection mistakes with lower threshold values of preference, and to behave more adaptively when their thresholds were strict; and while this was true, population and individual sizes were intermediate between those of equal-preference and adaptive selection. Increases in landscape heterogeneity may result in preferred patches no longer being next to each other, so that configuration and search distances become obstacles for the best competitors to get to their preferred condition. Mobile animals probably use a collection of environmental gradients as selection cues (Aarts et al., 2013; Robertson et al., 2013), so resulting patterns are probably even harder to characterize in nature (Battin, 2004; Kristan, 2003).

4.5. Scale of dispersal

Had our model not been spatially explicit, we would not have detected the effects of landscape configuration, search area and their interactions. Starting each simulation year with an empty landscape, as used in previous models for migratory birds (Donovan and Thompson, 2001; Pulliam and Danielson, 1991), will not be appropriate to simulate the behavior of resident species. As shown in our simulations, introducing constraints to dispersal scale allowed us to explore the variation brought about by differing movement ranges as has been done previously in other types of simulation models (Deutschman et al., 1997). Search and selection rules in our model are obviously simplistic, so real-life complex behaviors and movement patterns would determine the degree to which landscape configuration is important. The main difference between the simulation experiments with the two types of dispersal was seen in saturation times and variance, but unlike in Loehle (2012), final population sizes were not very different in our model after increasing behavioral rules.

4.6. Model assumptions, caveats and future improvements

Contrary to classic models (Fretwell and Lucas, 1969), we designed habitat selection as a process that was neither ideal (birds could make mistakes) nor free (search was limited). By making the model individual-based and spatially explicit, we created population patterns that emerged from the interactions between landscape structure and individual behavior (Dunning et al., 1992). However, our model ignored trade-offs between factors such as food availability and predation risk (Aarts et al., 2013; DeCesare et al., 2014) and assumed individuals had no way of directly assessing the factors that ultimately affected their fitness. We did not incorporate learning mechanisms, ways for the species to adapt, or social cues such as conspecific attraction, which may all be important in habitat selection (Gilroy and Sutherland, 2007; Kokko and Sutherland, 2001).

Density dependence also alters the interactions between habitat availability, selection behaviors and quality outcomes (Matthiopoulos et al., 2005). Instead of having density dependence

affect all individuals, we simplified our model by incorporating limits to population size only through floater mortality following landscape saturation. Floaters allowed us to recognize the effect of non-breeding individuals on population dynamics since it is logical to suppose that they will have higher mortalities and wider, more variable home ranges (Loehle, 2012; Pulliam and Danielson, 1991; Stephens et al., 2002). Although characteristics such as age, sex and other measures of individual quality may directly affect intraspecific competition, we addressed individual differences only through size sorting, which has been suggested as a reasonable proxy (Nakayama et al., 2011; Shustack and Rodewald, 2010).

Because novel habitat introduction may have milder effects on population persistence than habitat degradation (Fletcher et al., 2012), and because resident animals are predicted to be more resistant to ecological traps (Robertson et al., 2013), we chose to focus on responses beyond extinction or persistence. All our scenarios led to stable populations, and as suggested by several authors (Donovan and Thompson, 2001; Gilroy and Sutherland, 2007; Shustack and Rodewald, 2010), we evaluated the effects of habitat on simulated populations by examining more than one demographic variable (abundance and individual size). We explored the means and variation in early simulation years to incorporate transient dynamics that could potentially mirror population responses to short-term disturbance events.

4.7. Implications for tropical agroforestry systems

Our modeling assumption of higher quality in forest than coffee has not been proven, and for some species shade coffee could represent an undervalued resource (Gilroy and Sutherland, 2007) or simply a good quality habitat. Moreover, the opportunities to conserve native biodiversity in these systems vary greatly depending on the level of management, vegetation and structural complexity (Moguel and Toledo, 1999; Philpott et al., 2008). Our simulations point to the fact that landscape context could also be extremely important in determining the ability of shade coffee to become beneficial for forest species and ecosystem services, and this view has been supported by previous field and modeling research (Chandler et al., 2013; Railsback and Johnson, 2011). Using real habitat-specific demographic parameters (i.e. field measurements of survival and reproduction), this model could help researchers to form better hypothesis and sampling designs to evaluate alternative conservation strategies in agricultural landscapes. For example, criteria for biodiversity-friendly coffee suggests that canopy cover should be at least 60%, although this is rarely found in highly industrialized farms or regions with high cloud cover (Jha et al., 2014; Sánchez-Clavijo et al., 2007). Scenarios could be created to contrast the effects of changing internal characteristics of agroecosystems such as canopy cover, with the effects of conserving forest remnants at the regional level for a wide suite of native species.

5. Conclusions

Simulation modeling allowed us to build on previous habitat selection models by introducing two complex mechanisms related to individual behavior: selection based on habitat cues and spatially explicit dispersal. We showed that ecological traps, whether severe or of equal-preference, can reduce population fitness at the landscape level for a wide variety of species and ecological contexts. Cue-based selection mechanisms in natural conditions will make ecological traps harder to detect if measurements are not done appropriately e.g. if the cue and its distribution are unknown or if territorial and transient individuals are given the same weight in habitat-level measurements. Therefore, we advise that more attention to the assumptions and measurements with which we

describe habitat selection is necessary to truly understand ecological traps.

Whether populations adapt or not to the transformation of the region they inhabit will depend on processes at scales ranging from the individual to the landscape, and on interactions between them. The effects of ecological traps on a given species will not be the same in different landscapes and knowledge of this should be used to inform conservation decisions. A situation where a mobile species is found in two different types of habitat, but where habitat preference and quality are variable between them is widely applicable to many taxa and ecosystems. We hope that other researchers are motivated to use and improve on this model to advance knowledge about population processes in heterogeneous landscapes.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2016.03.004>.

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