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Habitat selection in transformed landscapes and the role of novel ecosystems for native species persistence

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HABITAT SELECTION IN TRANSFORMED LANDSCAPES
AND THE ROLE OF NOVEL ECOSYSTEMS FOR NATIVE SPECIES PERSISTENCE

by

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ABSTRACT

To understand native species persistence in transformed landscapes we must evaluate how individual behaviors interact with landscape structure through ecological processes such as habitat selection. Rapid, widespread landscape transformation may lead to a mismatch between habitat preference and quality, a phenomenon known as ecological traps that can have negative outcomes for populations. I applied this framework to the study of birds inhabiting landscapes dominated by forest remnants and shade coffee plantations, a tropical agroforestry system that retains important portions of native biodiversity. I used two different approaches to answer the question: What is the role of habitat selection in the adaptation of native species to transformed landscapes? First, I present the results of a simulation model used to evaluate the effects of landscape structure on population dynamics of a hypothetical species under two mechanisms of habitat selection. Then I present the analyses of seven years of capture-mark-recapture and resight data collected to compare habitat preference and quality between shade coffee and forest for twelve resident bird species in the Sierra Nevada de Santa Marta (Colombia). I provide evidence for the importance of including the landscape context in the evaluation of ecological traps and for using long-term demographic data when evaluating the potential of novel ecosystems and intermediately-modified habitats for biodiversity conservation. Beyond suggestions to improve bird conservation in shade coffee, my findings contribute to theory about ecological traps and can be applied to understand population processes in a wide variety of heterogeneous landscapes.

A mi mamá y a mi hermano por su amor y apoyo incondicional,

A mi papá y mis abuelos por todas sus enseñanzas,

A mis grandes amigos por estar siempre conmigo,

¡Y a Matilda por ser mi más fiel compañera!

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LIST OF ACRONYMS USED FOR FOCAL SPECIES

BARU   *Basileuterus rufifrons*

EULA   *Euphonia laniirostris*

MIOLE   *Mionectes oleagineus*

MIOLI   *Mionectes olivaceus*

MYCO   *Myiothlypis conspicillata*

MYMI   *Myioborus miniatus*

RADI   *Ramphocelus dimidiatus*

SAMA   *Saltator maximus*

SAST   *Saltator striatipectus*

TAGY   *Tangara gyrola*

TUAL   *Turdus albicollis*

TUFL   *Turdus flavipes*

CHAPTER 1: INTRODUCTION

Theoretical foundations: populations in heterogeneous landscapes

Understanding species distributions in complex habitat mosaics requires an integration of three components (Dunning, Danielson & Pulliam 1992): 1) landscape structure, including both physiognomy and composition (Turner 1989); 2) habitat-specific responses of organisms living in those landscapes (Kareiva 1990); and 3) general ecological processes operating at the neighborhood (Addicott et al. 1987) and landscape scales (Dunning, Danielson & Pulliam 1992). All organisms live in a patchwork of habitats, and theories of increasing ecological complexity and detail have been developed to address the consequences of spatial heterogeneity on population dynamics. Spatially complex environments have generally been represented as island, stepping-stone, continuum or spatially explicit models (Kareiva 1990; Dunning et al. 1995; Kareiva & Wennergren 1995), and each approach carries advantages and disadvantages for the analysis of particular cases.

As an extension of the theory of island biogeography, metapopulation models conceptualize space as patches of suitable habitat embedded on a matrix of unsuitable habitat (Levins 1969; Levins 1970; Hanski 1991; Hanski 1994), and while they have provided an opportunity to link theoretical population ecology with landscape ecology (Hanski 1998; Hanski 1999), it is clear that not all subdivided populations exist in this arrangement (Harrison 1991; Harding & McNamara 2002; Baguette 2004; Ovaskainen & Hanski 2004). Additionally, most metapopulation models fail to address the effects of variation in habitat quality, which is key to modeling populations of mobile animals that use more than one type of habitat in a landscape (Moilanen & Hanski 1998; Vandermeer & Carvajal 2001; Schooley & Branch 2007).

The sources and sinks model formalized by H.R. Pulliam (Pulliam 1988) incorporates habitat quality into the dynamics of populations living in heterogeneous environments by distinguishing two types of subpopulations, based on growth and dispersal. These models are closely linked to the ecological process of habitat selection (Pulliam & Danielson 1991; Danielson 1992; Watkinson & Sutherland 1995), and provide an important framework for the study of mobile animals with high cognitive and navigation capacities. They are built on the assumption that individuals can have perfect information about habitat quality, but that either because of the costs of habitat search (preemptive habitat distribution - Pulliam 1988), the decrease of habitat suitability as density increases (ideal free distribution - Fretwell & Lucas 1969) or because of strong dominance hierarchies within species (ideal despotic distribution - Fretwell & Lucas 1969), not all individuals will establish themselves in good quality habitats. Under these assumptions, habitat selection defined as "the process whereby individuals preferentially use or occupy a non-random set of available habitats" (Morris 2003), is an evolutionary mechanism that allows adaptability to changing environments (Rausher 1984; Holt 1985).

Early tests of the ideal free distribution showed a consistent departure from the expected, which different authors attributed to differential perception abilities (Abrahams 1986), changing environmental conditions (Fagen 1988), the costs of searching for habitat (Rosenzweig 1981), the difference between generalist and specialist species (Wiens 1976; Rosenzweig 1981), the spatial and/or temporal scale of study (Johnson 1980), the costs that habitat choice has on individuals (Morris 1992), and problems with conceptual definitions and study design (Jones 2001), among others. Since the late 1970s, examples contradicting the prediction of these models

have emerged in studies about the effects of anthropogenic habitat transformation, and the term ecological trap was coined for cases in which individuals distinctly prefer habitats where their fitness is lower than in other available habitats (Gates & Gysel 1978; Schlaepfer, Runge & Sherman 2002; Battin 2004; Weldon & Haddad 2005; Robertson & Hutto 2006). The hypothesized mechanism underlying ecological traps is that rapid landscape change can decouple the correlation between experienced habitat quality and the cues that organisms use to select it (Remes 2000; Stamps & Krishnan 2005). Also described as "attractive sinks," the potential importance of ecological traps in population dynamics has been demonstrated in models based on real life populations (Delibes, Ferreras & Gaona 2001; Delibes, Gaona & Ferreras 2001), but other authors have also proposed three different mechanisms by which species may escape them: 1) changes in habitat preference brought about by natural selection, 2) phenotypic plasticity expressed as experience-based learning or 3) philopatric preference (i.e. preference to the site and conditions where the individual was born - Kokko & Sutherland 2001).

The evolutionary and ecological mechanisms to explain ecological traps have been generally accepted, but reviews of studies claiming their existence have identified weaknesses in the way the concept is used. Habitat quality is not a property of the habitats themselves, but rather an organism-specific result (Kawecki 1995), therefore it cannot be estimated by measuring the characteristics of a patch (no matter how many variables are measured). Additionally, compelling evidence exists that individual density is a misleading indicator of habitat quality (Van Horne 1983). Higher individual or nest density has also been interpreted as evidence that a habitat is preferred, ignoring predictions of habitat selection theories that contradict this assumption; and habitat quality has been measured only as reproductive output without

consideration of possible tradeoffs with survival (Donovan & Thompson 2001; Schlaepfer, Runge & Sherman 2002; Battin 2004; Robertson & Hutto 2006). In light of the important evolutionary, ecological and conservation implications of ecological traps, these authors have called for better empirical evidence of their existence, frequency and of the species and landscapes most prone to them. Others have modeled ecological traps in landscapes where habitat quality changes continuously and suggested evidence could come from a bottom-up approach, starting at the level of individual territories (Kristan 2003).

A further refinement of the framework for evaluating the adaptiveness of habitat selection leads to the consideration of undervalued resources, which are good quality habitats actively avoided by individuals who would benefit from occupying them (Gilroy & Sutherland 2007). The existence of avoided sources could also have important conservation implications, and have been described as perceptual traps by making an analogy with type I and II errors in statistics (Patten & Kelly 2010). Individual quality has also been incorporated into the decision model to differentiate between sinks and undervalued resources (Shustack & Rodewald 2010).

A framework including sources and sinks, and ecological and perceptual traps as two opposites in a continuum of possible correspondence between habitat selection and quality is ideal to study population processes at the landscape level (Kristan 2003). It allows the linkage of landscape structure (available habitat) with individual behavior (habitat selection) and population outcomes (habitat quality) (Lima & Zollner 1996). It is particularly well suited to cases in which species actively use both the original habitat they were adapted to and a novel habitat that shares some possible cues for habitat selection but that also probably differs in quality.

Practical applications: biodiversity conservation in transformed regions

Considering that more than three quarters of the planet's productive terrestrial surface have been altered by human residence and land use (Ellis & Ramankutty 2008), and that with continuing population growth the possibilities of preserving species and ecosystems as untouched samples in protected areas become unrealistic; it becomes critical to assess the true value of those human-modified landscapes that still include important portions of native biodiversity (Norris 2008; Chazdon et al. 2009; Child, Cumming & Amano 2009). Among these, tropical agroforestry systems stand out for retaining much higher richness and abundance of forest species than more structurally simple production systems (Perfecto et al. 1996; Moguel & Toledo 1999; Daily, Ehrlich & Sanchez-Azofeifa 2001; Hughes, Daily & Ehrlich 2002; Sodhi et al. 2005; Komar 2006; Philpott et al. 2007); therefore they have become a classical example of a situation in which balancing economic profit and biodiversity conservation may be possible (Perfecto et al. 2003; Perfecto et al. 2005; Gordon et al. 2007; Philpott et al. 2007; Philpott et al. 2008; Jha et al. 2014).

Even with considerable attention from the scientific community, a review of available literature on this topic reveals three trends that need to be addressed: (1) most studies have focused on comparing bird community composition, diversity and structure in different land-uses and along intervention gradients, considering species presence and abundance during sampling as the main response variables (Wunderle Jr & Latta 1996; Estrada, Coates-Estrada & Meritt Jr 1997; Greenberg et al. 1997; Greenberg, Bichier & Sterling 1997; Calvo & Blake 1998; Petit et al. 1999; Greenberg, Bichier & Angón 2000; Znajda 2000; Daily, Ehrlich & Sanchez-Azofeifa 2001; Reitsma, Parrish & McLarney 2001; Hughes, Daily & Ehrlich 2002; Jones et al. 2002;

Cárdenas et al. 2003; Perfecto et al. 2003; Petit & Petit 2003; Lindell, Chomentowski & Zook 2004; Tejeda-Cruz & Sutherland 2004; Cockle, Leonard & Bodrati 2005; Estrada & Coates-Estrada 2005; Faria et al. 2006); (2) habitat-specific measurements are taken and compared even when many species are highly mobile, and thus not limited to discrete patches or land use types; and (3) there is far more understanding about species distribution patterns than about the processes underlying them (Komar 2006; Sekercioglu et al. 2007; Sánchez-Clavijo, Arbeláez-Alvarado & Renjifo 2008), so there is urgency for more studies of resource use (Wunderle Jr & Latta 1998; Cohen & Lindell 2005; Peh et al. 2006), survival (Cohen & Lindell 2004), reproduction (Tewksbury, Hejl & Martin 1998; Willson et al. 2001; Lindell & Smith 2003), movement (Rappole, Ramos & Winker 1989; Graham 2001; Castellon & Sieving 2006; Githiru, Lens & Bennun 2007; Sekercioglu et al. 2007; Burgess et al. 2009), dispersal (Van Houtan et al. 2007) and inter-specific interactions (Greenberg et al. 2000; Roberts, Cooper & Petit 2000; Luck & Daily 2003; Smith-Ramirez & Armesto 2003; Perfecto et al. 2004; Philpott et al. 2004) in transformed landscapes.

The term novel ecosystems, understood as ecosystems that "contain new combinations of species that arise through human action, environmental change, and the impacts of the deliberate and inadvertent introduction of species from other regions" (Hobbs et al. 2006), has also been used to describe tropical agroforestry systems because they are halfway in the continuum between natural ecosystems and intensively managed agriculture (Ewel 1999; Hobbs et al. 2006). While later refinements of this framework have classified agroforestry closer to a "hybrid" (Hobbs, Higgs & Harris 2009) or a "designed" (Morse et al. 2014) system; I retain the term novel ecosystem in this work to emphasize the generality of this research for a variety of

intermediately-modified habitats in heterogeneous landscapes, and propose that tropical agroforestry systems represent both a good model system to study the adaptiveness of habitat selection, and an important conservation context to generate lessons applicable for a variety of systems.

<u>Bringing theory and practice together: habitat selection in transformed landscapes and the role of novel ecosystems for native species persistence</u>

Based on ecological trap theory, we would expect that in natural systems habitat selection and quality would be coupled, and in intensively-managed systems most species would simply disappear, making intermediately-modified landscapes an "ideal" setting for ecological traps (Hobbs, Higgs & Harris 2009; Fletcher, Orrock & Robertson 2012; Robertson, Rehage & Sih 2013). Tropical rural landscapes are very heterogeneous, so habitat and resource availability have high spatial and temporal variances, allowing for "natural experiments" on how associated biodiversity varies with habitat and landscape structure (Ewel 1999; Petit et al. 1999; Daily, Ehrlich & Sanchez-Azofeifa 2001; Perfecto et al. 2007). Forest generalist birds are common in both remaining forest fragments and in shaded crops (Hughes, Daily & Ehrlich 2002; Petit & Petit 2003; Komar 2006), which means these two types of habitats share environmental cues that make them attractive to less sensitive and highly mobile species. It is thought that some of these species have benefited from habitat conversion, and that because they persist after many years of landscape change, they are truly adapted to the heterogeneity in these regions. However, we can also expect that the obvious differences in habitat structure lead to differences in habitat quality, and under this context some species may be especially vulnerable to ecological and perceptual traps (Donovan & Thompson 2001; Battin 2004; Robertson & Hutto 2006).

In this project I use two different approaches to answer the question: What is the role of habitat selection in the adaptation of native species to transformed landscapes? I start by hypothesizing three possible roles for habitat selection:

1) Habitat selection acts as an adaptive process when a species' preferred habitat or landscape characteristics coincide with better outcomes in individual fitness, survival and reproduction at the population level.

2) Habitat selection acts as a neutral process when a species' preferred habitat or landscape characteristics vary randomly in response to outcomes in individual fitness, survival and reproduction at the population level.

3) Habitat selection acts as a maladaptive process when a species' preferred habitat or landscape characteristics are the opposite of those with better outcomes in individual fitness, survival and reproduction at the population level.

In chapter 2 I describe a spatially-explicit, individual-based simulation model that was created 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).

The model was applied to the case of resident birds in landscapes composed of remnant forests and shade coffee agriculture and to simulation experiments with scenarios designed to vary in landscape composition, configuration, search area and criteria for habitat preference. The advantages of this approach were that there were no limits in the number and types of landscapes that could be designed and tested, and that the virtual animals could be programmed to follow specific and known behaviors, giving the opportunity for exploration of emerging patterns at the population level. This meant conclusions (and the model itself) can be applied to a wide generality of mobile animals living in heterogeneous landscapes.

In chapter 3 I describe the field research carried out to compare indicators of habitat preference and quality between shade coffee plots and pre-montane forest remnants for twelve species of resident birds in the Sierra Nevada de Santa Marta (Colombia). This region is dominated by tropical mountain forests and commercial polyculture coffee crops (sensu Moguel & Toledo 1999 this system "involves complete removal of the original forest canopy trees and the introduction of a set of shade trees appropriate for coffee cultivation"). It is also a hotspot for endemicity, ecosystem, species and cultural diversity (Werger, van der Hammen & Ruiz 1989; Hernández-Camacho et al. 1992; Rangel 1995; Carbono & Lozano-Contreras 1997; Stattersfield et al. 2005). We worked in Hacienda La Victoria, an 800-hectare coffee growing company that has operated in the region since 1892 and currently has around 200 hectares of shade coffee with 60% average canopy cover. The farm also includes well conserved pre-montane forest, with some minor areas of scrub, bamboo groves, pastures and living and processing infrastructure. I collaborated with researchers from SELVA (Research for Neotropical Conservation) to gather seven years of capture-mark-recapture and resight data which I then analyzed using Bayesian

population models and generalized linear models. This approach allowed the calculation of demographic estimates to evaluate whether habitat selection was helping different types of species adapt to landscape changes that occurred over a century ago.

All models are simplifications, and therefore are meant to help us increase our general understanding of processes and to generate hypotheses to test in the field. Fieldwork on the other hand, allows us to estimate variables for specific species and landscapes, but also to characterize patterns that we can extrapolate to other settings. By using both methods in a complementary fashion, we aimed to help bridge the gap between theory and practice for biodiversity research and conservation in heterogeneous landscapes, increase knowledge about resident tropical birds, address an important conservation problem and methodological issues common in field ecology, and in general, contribute to the growth of a theoretical framework. Chapter 4 contains our general conclusions in regard to these objectives, as well as a discussion on where to go from here.

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CHAPTER 2: MODELING THE EFFECT OF HABITAT SELECTION MECHANISMS ON POPULATION RESPONSES TO LANDSCAPE STRUCTURE

<u>Chapter Summary</u>

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.

Keywords: ecological traps; habitat quality; habitat selection; individual-based model; landscape structure; spatially-explicit population model.

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).

With ecological modelling, 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). Modelling 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) modelling 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 modelled 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

Methods

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 modelling sequence consisted of three initialization procedures (landscape generator, initial population, and colonization) followed by a yearly cycle of breeding, survival, census, and dispersal (Figure 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 (Figure 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 (Figure 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 Figure 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, Figure 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.

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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-

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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 Figure 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.

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

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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.

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.

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, 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.

Local dispersal

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 (Figure B.1). Colonization patterns with cue-based selection resembled those of equal-preference (Figure 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 (Figure 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 (Figure 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.

<u>Population size</u>

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 (Figure 1). 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) (Figure 1).
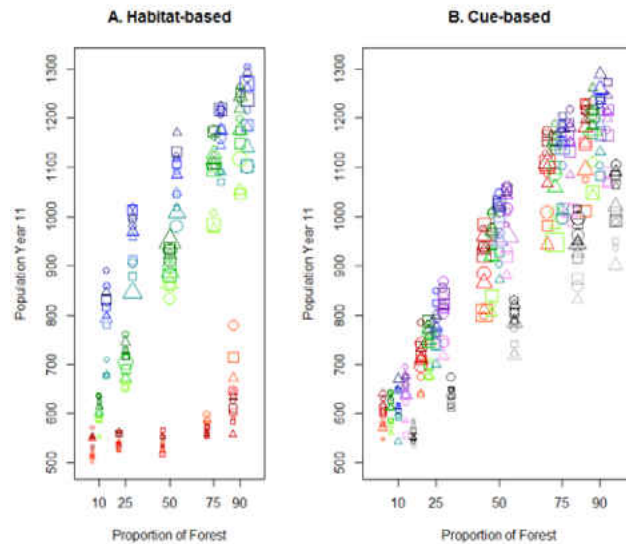
Figure 1. Effect of forest cover on population size at year 11 for scenarios with habitat-based and cue-based selection.

[A] *Habitat-based selection*: for each level of forest cover the three colors represent adaptiveness (red: severe traps, green: equal-preference traps, blue: 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] *Cue-based selection*: for each level of forest cover the five colors represent increasing canopy cover thresholds for preference (red: CC30%, green: CC45%, blue: CC60%, purple: CC75%, black: 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).

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).

Table 2. Structure of the most informative models for two fitness responses, with habitat-based and cue-based selection.

Factor or Interaction	N11 Habitat	N11 Cue	S11 Habitat	S11 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[a]	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

[a] Lowest AICc within set of 51 models
X, present
N11, population size at year 11
S11, mean individual size at year 11
L, landscape factors
B, behavioral factors

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 (Figure 2). 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 (Figure 2).
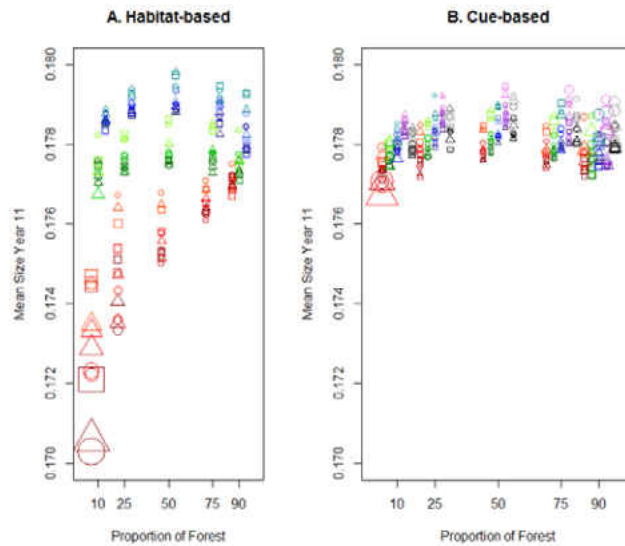
Figure 2. Effect of forest cover on mean individual size at year 11 for scenarios with habitat-based and cue-based selection.
[A] *Habitat-based selection*: for each level of forest cover the three colors represent the gradient of adaptiveness (red: severe traps, green: equal-preference traps, blue: 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] *Cue-based selection*: for each level of forest cover the five colors represent increasing canopy cover thresholds for preference (red: CC30%, green: CC45%, blue: CC60%, purple: CC75%, black: 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).

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 (Tables 2, B.3 and B.4).

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 (Figure 3 - top). 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% (Figure 3 - bottom).
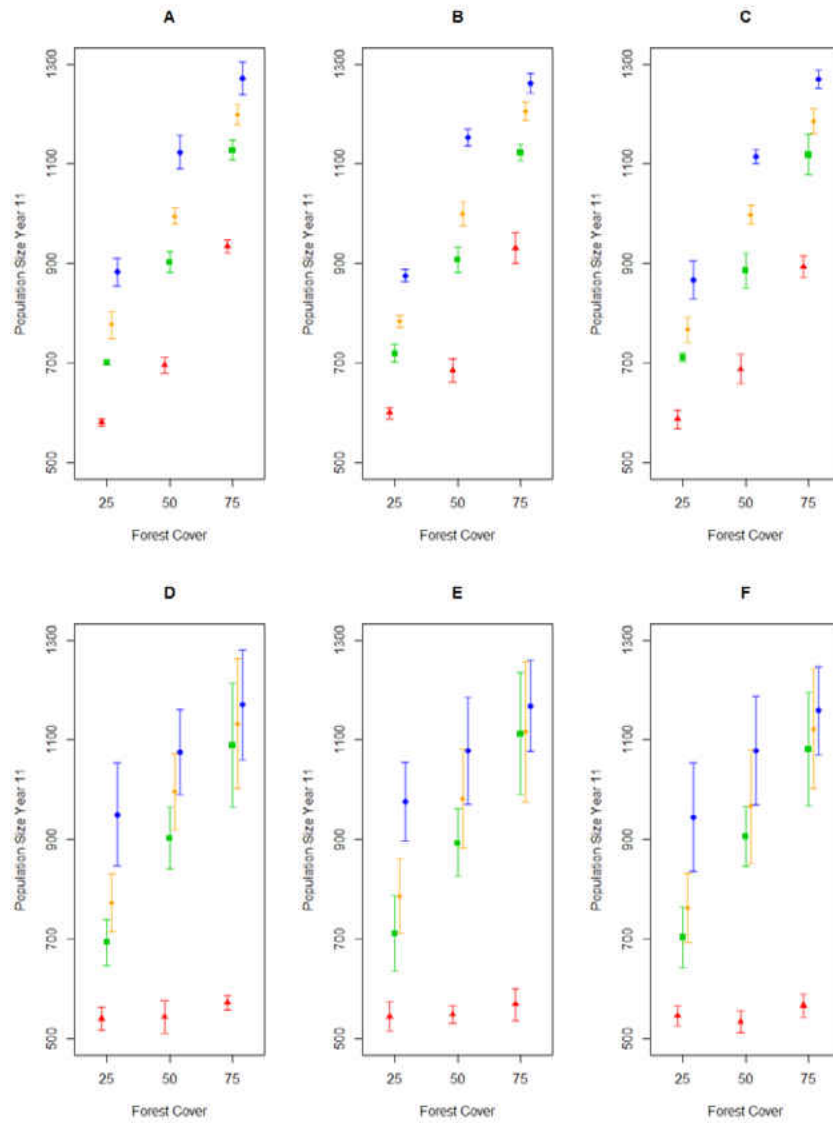
Figure 3. Effect of forest cover, type of habitat preference and landscape configuration on population size at year 11 for simulations with global (A, B and C) and local (D, E and F) dispersal.

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); colors represent types of selection (red: severe traps, green: equal-preference traps, orange: preference of sites with canopy cover ≥ 60%, blue: 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).

Discussion

Habitat selection has typically been modelled 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.

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.

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

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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 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.

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.

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).

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.

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.

Implications for tropical agroforestry systems

Our modelling 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 modelling 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.

Conclusions

Simulation modelling 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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**CHAPTER 3: HABITAT SELECTION IN TRANSFORMED LANDSCAPES
AND THE ROLE OF SHADE COFFEE
FOR THE CONSERVATION OF RESIDENT BIRD SPECIES**

Chapter summary

High species richness and abundance has been documented in agroforestry systems but long-term demographic data are required to assess their true value for biodiversity conservation, as intermediately-modified habitats could be functioning as ecological traps, making species persistence uncertain under further landscape change. We analyzed data from seven years of capture-mark-recapture and resight sampling to compare habitat preference and quality between shade coffee plots and pre-montane forest remnants for twelve species of resident birds in the Sierra Nevada de Santa Marta (Colombia). As indicators of preference we used estimates of occupancy, abundance, site fidelity, seasonal variance in abundance, segregation by age and sex, detectability and habitat switching to classify species as preferring forest, coffee, or representing equal-preference. As indicators of quality we used estimates for the effect of habitat on individual body condition, muscle and fat scores, incidence of body and primary plumage molts, breeding activity and proportion of juveniles to classify species as experiencing higher-quality in forest, in coffee, or representing equal-quality. Six species showed evidence of adaptive habitat selection (a match between their preferred and higher-quality habitats), four species showed neutral outcomes (evidence of preference but no differences in quality), and two species showed maladaptive outcomes (a mismatch between their preferred and higher quality habitats). We provide evidence that: 1) species considered as habitat generalists still commonly use, prefer and experience higher fitness in forest remnants, and therefore conservation strategies in rural landscapes should emphasize their conservation; 2) many species seem to be using shade coffee

plots in an adaptive or neutral way, reinforcing its role as a biodiversity-friendly matrix around forest fragments; 3) though rare, ecological traps can exist for common species, so when evaluating the contribution of novel habitats to biodiversity conservation it is important to understand that maintaining current conditions will not necessarily ensure species persistence.

Keywords: agroforestry systems; ecological traps; habitat preference; habitat quality; habitat selection; resident birds.

Introduction

Regional species distributions are emergent properties of demographic and ecological processes happening at both the individual and habitat scales (Wiens *et al.* 1993; Kareiva & Wennergren 1995; Fletcher Jr & Sieving 2010). As a consequence of this complexity, there have been numerous theoretical frameworks used to study populations at the landscape level (Wiens 1976; Addicott *et al.* 1987; Dunning, Danielson & Pulliam 1992; Johnson *et al.* 1992). Metapopulation theory emphasizes the role of dispersal in determining local species colonization and extinction, and teaches us that species absence is not synonymous with bad-quality habitat (Hanski 1998; Moilanen & Hanski 1998; Quintana-Ascencio, Dolan & Menges 1998). Source: sink dynamics emphasize heterogeneity in demographic outcomes of geographically or ecologically distinct populations, and point towards habitat selection as the process linking landscape structure with the individual behavior of mobile animals (Pulliam 1988; Pulliam & Danielson 1991; Dias 1996). While both of these frameworks, as well as many early conceptualizations of habitat selection, accounted for individuals ending up in a habitat different than the one they preferred through mechanisms like density dependence and competitive

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displacement (Fretwell & Lucas 1969; Rosenzweig 1981; Morris 2003), neither raised the possibility of habitat selection acting as a maladaptive process (Remes 2000; Delibes, Ferreras & Gaona 2001; Kristan 2003; Stamps & Krishnan 2005). As empirical evidence accumulated of widespread, rapid landscape change leading to such outcomes, the term ecological trap was coined to describe those cases in which individuals consistently make mistakes by choosing lower-quality patches over available better-quality ones (Schlaepfer, Runge & Sherman 2002; Battin 2004; Robertson & Hutto 2006; Gilroy & Sutherland 2007). Theory on ecological traps has been refined to propose mechanisms for their emergence (Fletcher, Orrock & Robertson 2012; Robertson, Rehage & Sih 2013) and ecological and evolutionary consequences of their existence (Kokko & Sutherland 2001; Patten & Kelly 2010); and ultimately emphasizes that species presence by itself is not synonymous with a habitat contributing to its persistence.

Despite these arguments, species lists and habitat suitability models based exclusively on detection/non-detection data are among the most commonly used tools to evaluate the value of habitats and landscape structure for biodiversity conservation (Daily, Ehrlich & Sanchez-Azofeifa 2001; Hughes, Daily & Ehrlich 2002; Loiselle *et al.* 2003; Petit & Petit 2003; Rondinini *et al.* 2006; Hirzel & Le Lay 2008). This trend is of particular concern when addressing novel ecosystems resulting from intermediate habitat transformations, as they could very likely become ecological traps for animals that evolved their habitat selection cues before human modification took place (Battin 2004; Shustack & Rodewald 2010; Fletcher, Orrock & Robertson 2012). As an example, tropical agroforestry systems like shade coffee stand out for retaining important portions of native forest biodiversity (Perfecto *et al.* 1996; Moguel & Toledo 1999; Philpott *et al.* 2008), and while they have become a classic example of balancing

economic profit and conservation, and spurred a variety of incentives aimed to achieve their sustainability (Perfecto *et al.* 2003; Perfecto *et al.* 2005; Philpott *et al.* 2007; Jha *et al.* 2014); there is still a lot of information missing about the long-term demographic trends that will determine whether species truly adapt to living in these transformed landscapes (Komar 2006; Sekercioglu *et al.* 2007; Sánchez-Clavijo, Arbeláez-Alvarado & Renjifo 2008).

We designed a capture-mark-recapture and resight study to compare indicators of habitat preference and quality between shade coffee plots and pre-montane forest remnants for twelve species of resident Neotropical birds in the Sierra Nevada de Santa Marta (Colombia). As indicators of habitat preference we used estimates of occupancy, abundance, site fidelity, seasonal variance in abundance, segregation by age and sex, detectability and habitat switching to classify species as preferring forest, preferring coffee or representing equal-preference (Table 3). As indicators of quality we used estimates for the effect of habitat on individual body condition, muscle condition, fat scores, incidence of body and primary plumage molts, breeding activity and proportion of juveniles to classify species as experiencing better quality in forest, better quality in coffee or representing equal-quality (Table 3). Finally, by contrasting each species' classifications in terms of preference and quality we came up with hypotheses about the role that both habitats may be playing for their populations at the landscape level, and for the effect that the process of habitat selection may be having in their adaptation to landscape transformation.

Using previous information on frequency by habitat for our focal species (Hilty & Brown 1986; del Hoyo *et al.* 1992-2011; Stotz *et al.* 1996; Restall, Rodner & Lentino 2006), we assigned them as forest specialists (species rarely recorded in habitats other than forest), forest

generalists (species frequently recorded in both forest and more open vegetation), and treed-area

dwellers (species most frequently recorded in open areas with sparse tree cover). We expected

that forest specialists would exhibit higher preference and experience higher fitness in forest, and

that treed-area dwellers would exhibit higher preference and experience higher fitness in shade

coffee, thus displaying adaptive habitat selection behaviors. On the other hand, we expected that

any evidence of maladaptive habitat selection would probably come from the forest generalist

species, as they were more likely than forest specialists to use selection cues present in shade

coffee, but also more likely than treed-area dwellers to experience lower fitness in their novel

habitat.

Table 3. Variables used as indicators of higher habitat preference and quality in this project.

Characteristic	Variable	Prediction for preferred/ best habitat
Habitat preference	Occupancy	Higher
	Abundance	Higher
	Site fidelity	Higher
	Seasonal variance in abundance	Lower
	Segregation by age	Adults > immatures
	Segregation by sex	Females > males (during breeding)
	Detectability during observations	Higher (especially with playback)
	Resight habitat	Same as banding habitat
Habitat quality	Body condition index	Higher
	Muscle condition scores	Higher
	Fat stores	More likely
	Body plumage molt	More likely
	Primary plumage molt	More likely
	Breeding activity	More likely
	Juvenile captures	More likely

Based partly on the work and suggestions of (Ralph *et al.* 1993; Robertson & Hutto 2006; Gilroy & Sutherland 2007; Peig & Green 2010; Shustack & Rodewald 2010).

Methods

Field sampling

Sampling site - Field sampling took place in Hacienda La Victoria (11°7'20"N, 74°5'34"W, 850 to 1800 m), an 800-hectare agricultural estate devoted to coffee production and forest conservation in the Sierra Nevada de Santa Marta in northern Colombia (Figure 4), a region which is considered a global hotspot for biodiversity (Cracraft 1985; Myers et al. 2000; Kattan et al. 2004). Historically, the Gaira-Manzanares-Piedras watershed between 600 and 1,700 meters, where La Victoria is located, was dominated by pre-montane tropical humid forests, and as of 2012, close to 47% of this cover remained (Bayly et al. 2012). Coffee cultivation in La Victoria started in 1892 and because of the region's highly pronounced unimodal rainfall pattern, has always taken place under a canopy of trees. Currently, all coffee is grown in moderate to steep slopes, underneath cultivated shade dominated by *Inga codonantha* and *Albizia carbonaria*, with occasional interspersed trees of other edible and ornamental species, and is classified as a commercial polyculture (sensu Moguel & Toledo 1999). Canopy height is generally between 10 and 15m, and canopy percent cover varies greatly around a mean of 60%. Coffee shrub density and height varies according to when plots were last renewed (cut down) or replanted, and groundcover depends on the time of year (high after the dry season, cleared out when the rainy season intensifies). Coffee production is still the main economic activity of the farm, but most plots are not managed intensively, and have experienced cycles of temporal local abandonment followed by increases in intensification, and cycles of coffee leaf rust propagation followed by renewal of the coffee plants. Plant diversity in remnant forest patches is much higher, with a dominance of species from Lauraceae, Melastomataceae,

Araliaceae, Euphorbiaceae, Rubiaceae and Leguminosae. Canopy heights range from 15 to 30 m and canopy cover has a low variation around a mean of 80%. Most forest sites had a dense understory of palms, ferns, Heliconiaceae and other herbaceous shrubs, including occasional coffee plants either left over from previous plantings or that dispersed naturally from nearby crops. Currently forests are only used for biological research, low-intensity tourism and occasionally for wood extraction.
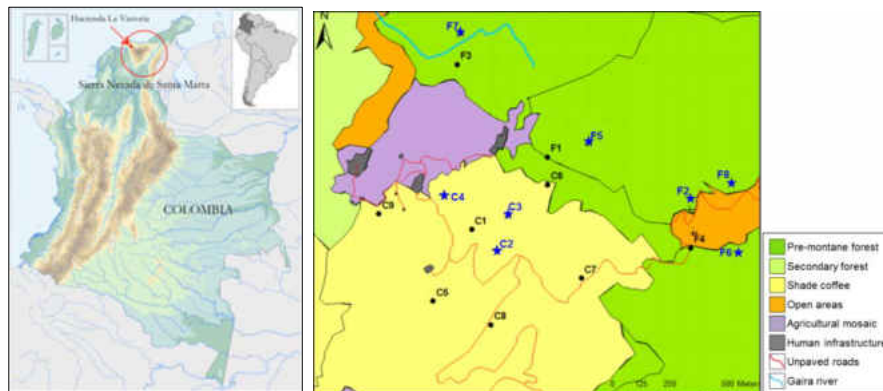
Figure 4. Location of Hacienda La Victoria in northern Colombia and schematic map of study site showing the approximate location of banding stations and vegetation cover.
F - forest banding stations
C - coffee banding stations
Black circles - original sites designated for this project
Blue stars - additional sites used by SELVA

Sampling scheme - We chose nine 4-hectare sampling stations that were located either within an extensive pre-montane forest patch (three sites at elevations ranging from 900 to 1,300 meters), or within a shade coffee plot (six sites with two each located near, mid-distance and far from forest) (Figure 4). During 2013-2014 we made a total of four visits to the site (from mid-March to mid-May which corresponds to the transition between the dry and rainy seasons or "dry-wet"; and from mid-June to mid-August which corresponds to the middle of the rainy season or "mid-wet"). We complemented our dataset with capture-recapture information from

pilot sampling and from an ongoing banding project at La Victoria (http://selva.org.co/research-programs/migratory-species/crossing-the-caribbean/), adding eight more sampling occasions from 2009 to 2015 (some taking place mid-September to mid-November which corresponds to the peak of the rainy season or "peak-wet"), taking place in three additional coffee and five additional forest sites (Figure 4). No sampling was ever carried out during the wet-dry transition or the core of the dry season (mid-November to mid-March). Sampling effort varied among sites and seasons depending on resources and logistical constraints (Table C.1).

Focal species - We chose twelve species of resident passerine birds that represented a gradient of habitat associations according to the literature (from primary forest to open areas with trees), were relatively common in the study region, had been reported for both habitats of interest, could be safely captured, marked and recaptured, and represented a variety of families, life histories and ecological functions (Table 4).

Table 4. Focal species of resident birds used for this study.

Family[1]	English Common Name	Scientific Name	Code[2]	Habitat Classification[3]
TYRANNIDAE	Olive-striped Flycatcher	*Mionectes olivaceus*	MIOLI	Forest specialist
	Ochre-bellied Flycatcher	*Mionectes oleagineus*	MIOLE	Forest specialist
TURDIDAE	Yellow-legged Thrush	*Turdus flavipes*	TUFL	Forest generalist
	White-necked Thrush	*Turdus albicollis*	TUAL	Forest specialist
THRAUPIDAE	Crimson-backed Tanager	*Ramphocelus dimidiatus*	RADI	Treed-area dweller
	Bay-headed Tanager	*Tangara gyrola*	TAGY	Forest generalist
	Buff-throated Saltator	*Saltator maximus*	SAMA	Forest generalist
	Streaked Saltator	*Saltator striatipectus*	SAST	Treed-area dweller
PARULIDAE	White-lored Warbler	*Myiothlypis conspicillata*	MYCO	Forest specialist
	Rufous-capped Warbler	*Basileuterus rufifrons*	BARU	Treed-area dweller
	Slate-throated Redstart	*Myioborus miniatus*	MYMI	Treed-area dweller
FRINGILLIDAE	Thick-billed Euphonia	*Euphonia laniirostris*	EULA	Forest generalist

[1] Taxonomic classification from South American Classification Committee (Remsen *et al.* Version 08/31/2016)
[2] Code corresponds to the first letters of both parts of the scientific name of the species
[3] From (Hilty & Brown 1986; del Hoyo *et al.* 1992-2011; Stotz *et al.* 1996; Restall, Rodner & Lentino 2006)

Capture-mark-recapture - Mist nets were setup in each of the 17 banding sites according to SELVA's standardized protocols and depending on the characteristics of the site, bird activity and experience of the bander(s) present (usually between 4 to 10 mist nets were deployed, for 5 to 6 hours, starting at sunrise). Nets were checked every 20-30 minutes according to standards of safety and ethical treatment of animals (under permits 10-17W/13-05W from IACUC and 0819 from ANLA). Individuals were transported in a holding bag to a banding station for processing; which included banding all individuals with one uniquely-coded metal band, and up to 50 individuals of each focal species per habitat were banded with a unique combination of color bands. We also recorded the following information for each individual: age (following Pyle *et al.* 1987 and SELVA's unpublished ageing guide), sex (based on plumage coloration, structural dimorphism and reproductive condition), fat score and muscle condition (scored from 0 to 3 following Ralph *et al.* 1993), state of cloacal protuberance and/or incubation patch (scored from 0 to 3, and 0 to 5 respectively - Ralph *et al.* 1993), primary plumage and body molt (the former according to Pyle *et al.* 1987 and the later scored qualitatively from 0 to 3). Additionally we measured wing chord (to the nearest mm) and body mass (to the nearest tenth of a gram). All individuals were liberated on site immediately after processing.

Observations and resights - Visual sampling of the focal species was concentrated in the 9 sites originally chosen for this study. Activities took place from 2 to 4 hours after sunrise or before sunset and were always carried out by a single observer. Although the initial aim of these sessions was to accumulate resightings of color banded birds, observers recorded all detected individuals of the focal species. During some of these sessions, playback was used to increase

bird detectability (we looped over a playlist that featured calls and songs from all focal species, plus a Neotropical owl mix - courtesy of the Cornell Lab of Ornithology).

Data analysis

Our final banding database consisted of 5,003 records of captures and our final count database contained 2,655 records of sightings for the twelve focal species, both of which were carefully checked for consistency, outliers and suspicious information. It is important to note that sample sizes vary according to species, habitat, variables of choice and type of analysis.

Occupancy - Results from species inventories (regardless of the method), are often assumed to be species presence/absence data, when in reality they represent species detection/non-detection information (Kéry & Schaub 2012). In order to use species site-occupancy (psi) to assess our species preferred habitat, we needed to account for factors that may have affected detection probability (p), as well as the effects of altitude on occupancy (Kattan & Franco 2004; Gómez et al. 2015). To avoid problems with differing sampling intensities, and because occupancy estimations need a lot less data than abundance estimation (Kéry & Schaub 2012), we used only data with comparable banding and sighting efforts from our main sampling occasions (a total of 20 bird banding and 16 bird sighting events at each of the nine sites - Table C.2). Following the JAGS code available at http://www.vogelwarte.ch/de/projekte/publikationen/bpa/code-for-running-bpa-using-jags.html for the Bayesian implementation of occupancy models (Kéry & Schaub 2012), we created a model with the following covariates: 1) effect of sampling method (sighting or banding) on p, 2) effect of habitat on p (forest or coffee), 3) effect of altitude on psi (scaled meters above sea level

measured at each banding station using a GPS), and 4) effect of habitat on psi. Analyses were run using R (R Core Team 2016), JAGS (Plummer 2016) and the "jagsui" package (Kellner 2016). After checking model outputs for convergence, we considered factors to be important in the estimation of detection and occupancy probability for the species when parameter estimates for their effect size did not include 0 in their 95% credibility intervals. We also plotted occupancy probability as a function of altitude and habitat, and interpreted evidence of higher occupancy as higher use by the species.

Abundance and site fidelity - To improve precision in habitat-specific demographic estimates we used the whole capture database, pooled together data from all sites into two habitat classes, and data from each mist-net day into twelve primary sampling occasions. We modified the JAGS code available at http://www.vogelwarte.ch/de/projekte/publikationen/bpa/code-for-running-bpa-using-jags.html for the Bayesian implementation of the Jolly-Seber population model parameterized as a multistate model (Royle & Dorazio 2008; Kéry & Schaub 2012), by introducing a quadratic effect of sampling effort (the scaled number of standardized mist net hours per habitat, per occasion) on detection probabilities (p). Apparent survival (phi) was allowed to vary randomly by occasion, estimates of the number of individuals alive per occasion (N) and over the whole sampling time (Nsuper) were calculated as derived population parameters, and analyses were carried out separately for each species and habitat. Analyses were run using R (R Core Team 2016), JAGS (Plummer 2016) and the "jagsui" package (Kellner 2016). Jolly-Seber models were chosen to allow for the simultaneous estimation of apparent survival and population size, however for some species: habitat combinations, recapture rates were too low to get reasonable estimates with this model. For those species, we used a separate

closed population model to calculate abundance over the whole sampling time, and a Cormack-Jolly-Seber model to calculate phi per occasion (Royle & Dorazio 2008; Kéry & Schaub 2012); in both cases including the same modification to make capture rate dependent on sampling effort. While parameters were not estimated with the same method for all species, we made sure to always keep the model we used, the number of augmented individuals and the simulation conditions constant for both habitats within species.

After checking model outputs for convergence, we considered species estimations of overall abundance as different between habitats when there was no overlap in their 50% credibility intervals, and plotted their posterior distributions together to visually asses overlap (using package "ggplot2" (Wickham 2016)). We also calculated the coefficient of variance between abundance per occasion for each iteration, and then derived the mean and standard deviation for all iterations to get an estimate of seasonal variance in abundance. We considered them as significantly different when there was no overlap of the mean +/- the standard deviation. Apparent survival is a compound measurement of site fidelity (which should be greater in preferred than non-preferred habitats – Robertson & Hutto 2006) and true survival (which would determine a better quality habitat – Battin 2004). Because of previously recorded longevities of tropical bird species (Ruiz-Gutiérrez et al. 2012), we can expect that when calculated over short periods of time, this parameter is more indicative of the former than the latter. We used model output to calculate mean phi between occasions for each iteration, and then derived the mean and standard deviation for all iterations to assess differences in overall site fidelity, and again plotted posterior distributions for both habitats together to asses overlap visually. Evidence of higher

abundance, lower seasonal variations in abundance and higher site fidelity were interpreted as evidence of habitat preference by each species.

Other indicators of habitat preference - Our other four indicators of habitat preference were analyzed using generalized linear models with binomial errors and logit links, followed by AICc model averaging, using R (R Core Team 2016) and package "AICcmodavg" (Mazerolle 2016). In all cases, we considered differences significant when the 95% confidence intervals for the model-averaged coefficient of the effect of habitat did not overlap zero. To test for segregation according to age (and therefore a possible despotic distribution of individuals *sensu* Fretwell & Lucas 1960), we excluded from the data all records for *M. olivaceus* and *M. oleagineus* (because age determination criteria for these species was not well defined throughout the study period), all individuals classified as juveniles and all individuals whose age could not be determined in the field or given their capture history. We considered a capture as a success when the individual was an adult (presumably dominant) and as a failure when it was an immature (presumably submissive). To test for segregation according to sex, we excluded all records for *M. oleagineus* and *T. albicollis* (because we did not have enough captures of both sexes in both habitats), and all individuals whose sex could not be determined in the field or given their capture history. We considered a capture as a success when the individual was a male and as a failure when it was a female (although we were more interested in females during breeding periods). In both cases the model set included a null model, a time model where the only predictor was the quadratic effect of day of the year (non-linear response), a habitat model with only habitat category as predictor (coffee or forest), and an additive model of time and habitat.

Individuals in their territory are expected to respond to playback more than transient individuals, therefore we hypothesized that using playback would increase our chances of detecting a species more when performed in their preferred habitat. To test this hypothesis, we used duration of bird observation sessions, habitat (coffee or forest), method (playback or no playback), and the interaction between habitat and method as predictor variables, and detection of at least one individual of each species as the response, giving us a total of seven models in the set for detectability (Table C.3 shows variation in sampling between sites and occasions). Our rate of resight of color-banded individuals was much lower than expected, but for six of our species, we compared the probability of resight habitat being different than the banding habitat, as a function of the habitat where individuals were banded, the number of days elapsed between banding and resight, and the interaction of habitat and time (five models in the set for resight). We expected this probability to be higher in the less-preferred habitat.

Species classification according to habitat preference - Because our seven indicators of habitat preference were very different in nature and mode of analysis, we had to qualitatively summarize the evidence they provided. We classified a species as preferring one habitat if the number of times evidence suggested higher preference in that habitat was greater than the number of times evidence suggested higher preference in the other, regardless of the number of times when we found no evidence of difference. If evidence for both habitats was the same, or we did not find any evidence of difference at all, the species was classified as having equal-preference. We added a qualification of each species' classification, by considering the evidence weak when less than a third of the tests ran supported the category it was assigned to,

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intermediate if between one and two thirds supported it, and strong if more than two thirds did (the total number of tests varied by species).

Body condition index - To compare physical individual condition between habitats we calculated a scaled index that corrects body mass with a size indicator (in our case wing chord) for each individual, and which uses standard major axis regression (performed with R package "smart" (Warton et al. 2012)) to account for error in the measurement of both variables (Peig & Green 2009; Peig & Green 2010). We ran generalized linear models with normal errors and identity link to create a set of four models akin to the ones we used for age and sex (null, quadratic effect of day of year (because of nonlinear responses), habitat, and the additive model of time and habitat), to get a model-averaged coefficient for the effect of habitat (which we considered significant when 95% confidence intervals did not overlap zero).

Other indicators of habitat quality - Our other six variables of individual condition reflecting habitat quality were analyzed as generalized linear models with binomial errors and logit link, using the same predictors and method described above to determine if there was a significant effect of habitat. For each analysis, we only considered individuals where the variable of interest was properly evaluated, so for some tests we had to eliminate species because of issues with sample size. In terms of muscle, we considered a capture a success if individuals had a muscle score of 3, and a failure if their muscle score was 2 (we eliminated individuals with scores of 0 and 1 because there were too few of them to analyze). For fat, we considered a capture a success if individuals had a fat score of 1 or higher. For both body and primary plumage molting, a success was defined by an individual having active molt, regardless of stage. A breeding success was defined by capturing either a female with active brood patch (categories

2-4) or a male with active cloacal protuberance (categories 2-3). To analyze the probability of capturing juveniles, we used age again, but this time defined individuals classified as juveniles as a success, and those classified as adults or immatures as a failure.

Species classification according to habitat quality - Because all analyses of fitness used the same predictors, the coefficients of the effect of habitat are directly interpretable and comparable (with larger, positive values indicating higher outcome probability in forest, larger, negative values indicating higher outcome probability in coffee, and values close to zero indicating no evidence of habitat differences). To get a quantitative estimate of the overall differences between habitats, we calculated the mean of effects sizes weighted by their standard deviation, in a manner akin to a meta-analysis using package "metaphor" (Viechtbauer 2010). If this estimate minus the standard error was larger than zero, a species was classified as having higher quality in forest. If the estimates plus the standard error was smaller than zero, the species was classified as having higher quality in coffee. If the interval of the estimate +/- the standard error included zero, the species was classified as having equal-quality outcomes in both habitats.

Contrasting habitat preference and quality - We compared each species' classifications to come up with hypotheses about the role that forest and coffee play for their populations at the landscape level, as well as for the role that habitat selection is playing for their adaptation to habitat transformation (Figure 5). Additionally, we ran a principal component analysis in R (R Core Team 2016) for the habitat effect sizes of body condition, body molt and breeding activity of the twelve species and plotted the results according to their habitat preference categories.
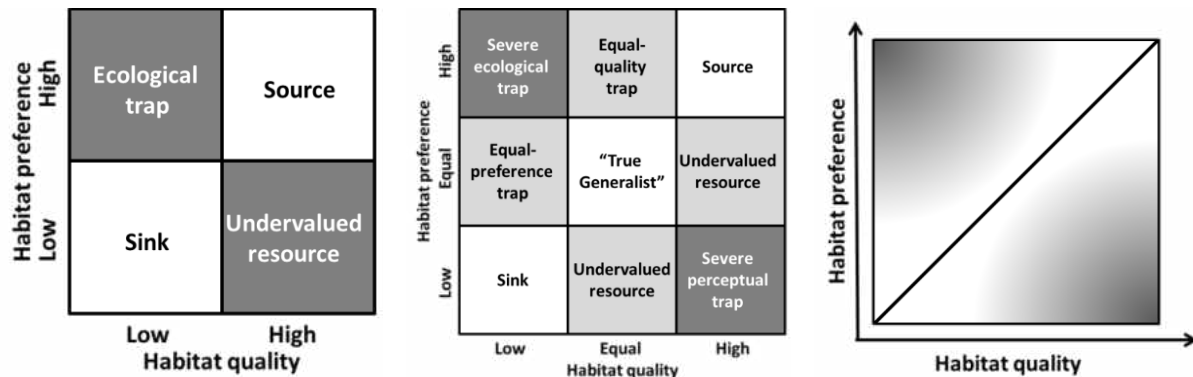
Figure 5. Progression of a general framework for evaluating the role of habitat selection in species adaptation to transformed landscapes.
Left: initial proposal by (Gilroy & Sutherland 2007)
Middle: augmented framework partially based on work by (Robertson & Hutto 2006; Patten & Kelly 2010; Fletcher, Orrock & Robertson 2012)
Right: evaluation of preference and quality as continuous variables (suggested for future work)

Results

After data processing our bird banding database consisted of 4,108 captures (894 of which were recaptures) from 3,214 individuals. Our bird observation database had 1,958 records of the focal species, plus 256 resights for 871 color-banded birds. There was a lot of heterogeneity in sample size according to species, habitat and method (Tables C.4 and C.5).

Habitat preference

Occupancy - Estimates of occupancy for nine species were always above 0.97, and showed no statistically significant effects of elevation or habitat. The remaining three species showed a significant effect of altitude (negative for MIOLE and EULA, positive for MYMI), with MIOLE also showing higher occupancy in forest and MYMI showing higher occupancy in coffee (Figure C.2; see Figure C.1 for effects of habitat and method on p).

Abundance - We found evidence for five species being more abundant in forest: MIOLE, MYCO (using the Jolly-Seber model), TUFL, EULA (using the closed population model) and TUAL (no recaptures in coffee). Three species were more abundant in coffee: RADI, BARU (Jolly-Seber) and SAST (only one recapture in forest). Conversely, we did not find evidence for differences in abundance between habitats for TAGY, MYMI (Jolly-Seber), MIOLI and SAMA (closed population) (Figure C.3; see table C.6 for effects of effort on p).

Site fidelity - Mean apparent survival was significantly higher in forest for TAGY, RADI (Jolly-Seber), MIOLI and TUAL (Cormack- Jolly-Seber); and significantly higher in coffee for SAST and EULA (Cormack- Jolly-Seber). We did not find evidence for differences in site fidelity between habitats for the three warblers (MYCO, BARU and MYMI studied with Jolly-Seber models), MIOLE, TUFL or SAMA (studied with Cormack-Jolly-Seber models) (Figure C.4).

Seasonal variation in abundance - For the six species in which we had independent abundance estimates for each occasion (Jolly-Seber models), the coefficients of variation among seasons were always lower in forest than coffee, and showed significant differences for TAGY and BARU (Figure C.5).

Segregation according to age and sex - Out of ten species analyzed for age, we found evidence of segregation for the two thrushes, with a higher probability of capturing adults over immatures in forest for TUAL and in coffee for TUFL (Figure C.6). For the ten species analyzed for sex, we found evidence of lower probability of capturing males over females for RADI in coffee and for TAGY in forest (Figure C.7).

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Observations and resights - MYCO, MYMI and EULA showed positive and significant responses to playback; while MIOLE showed higher probabilities of detection in forest, and BARU and MYMI higher probabilities in coffee. We found no evidence of significant interactions between method and habitat for any species. There were too few observations of TUAL in coffee for analysis, once again pointing to higher incidence in forest for this species (Figure C.8). Resight analysis was performed for five species, from which only MYMI showed a significant trend (higher probability of being spotted later in coffee when individuals were originally banded in forest) (Figure C.9).

Table 5. Summary of evidence for habitat preference according to eight chosen variables.

Species	OCC	TAB	PHI	SVA	AGE	SEX	OBS	RST	Evidence Strength	Preference Classification
MIOLI	NE	NE	F	-	-	NE	NE	-	Weak	FOREST
MIOLE	F	F	NE	NE	-	-	F	-	Intermediate	FOREST
TUFL	NE	F	NE	-	C	NE	NE	-	Contradictory	EQUAL
TUAL	NE	F	F	-	F	-	-	-	Strong	FOREST
RADI	NE	C	F	NE	NE	C	NE	NE	Weak	COFFEE
TAGY	NE	NE	F	F	NE	F	NE	NE	Intermediate	FOREST
SAMA	NE	NE	NE	-	NE	NE	NE	NE	None	EQUAL
SAST	NE	C	C	-	NE	NE	NE	-	Intermediate	COFFEE
MYCO	NE	F	NE	NE	NE	NE	NE	-	Weak	FOREST
BARU	NE	C	NE	F	NE	NE	C	NE	Weak	COFFEE
MYMI	C	NE	NE	NE	NE	NE	C	C	Intermediate	COFFEE
EULA	NE	F	C	-	NE	NE	NE	-	Contradictory	EQUAL

Variables: OCC – higher occupancy, TAB – higher total abundance, PHI – higher site fidelity, SVA – lower seasonal variation in abundance, AGE – more likely to capture an adult than an immature, SEX – less likely to capture a male than a female, OBS – more likely to be observed during bird counts, RST – less likely to change habitat after banding.
F - higher preference of forest
C - higher preference of coffee
NE - no evidence of differences in preference
Blank - test not performed for the species

Summary for habitat preference - based on the previous evidence we classified five species as preferring forest over coffee (in decreasing strength of signal): TUAL, MIOLE,

TAGY, MIOLI and MYCO; four species as preferring coffee over forest: MYMI, SAST, RADI and BARU; and for lacking evidence of preference or contradictory results, three species as having equal-preference for both habitats: SAMA, TUFL and EULA. This classification gave us a gradient of preference to compare against measures of habitat quality (Table 5).

Habitat quality

Body condition - We found evidence of higher BCI scores in forest for MIOLI and MYCO and of higher scores in coffee for RADI and EULA. There was also support for higher muscle scores in forest for MYMI and RADI and higher in coffee for TAGY. Finally, there was evidence for higher chances of fat storage in forest for MIOLE, TUFL, RADI and TAGY. Most species showed strong temporal variation in muscle score and fat storage, but not in their index of body condition (Figures C.10-C.12).

Plumage molting **-** We found evidence of differences in the incidence of body molt for one species: higher probability of capturing an individual with active body molt for TAGY in forest than in coffee. Similarly, we found no evidence of habitat having an effect on the incidence of individuals undergoing primary plumage molt for any of the species. Most species showed strong temporal variation for both variables (C.13-C.14).

Breeding **-** We found evidence of higher probabilities of capturing individuals actively breeding in forest for EULA, and in coffee for TUFL, TAGY, SAST and BARU; and no evidence of difference between habitats for the probability of capturing juveniles in any of the eight species analyzed. Once again, temporal effects were strong for most species, especially for breeding (Figures C.15-C.16).

Summary for habitat quality **-** based on the previous seven sources of evidence we have strong (MYMI, MYCO, SAMA and MIOLI) to medium (MIOLE) support to classify five species as birds that experience better habitat quality in forest than coffee. We only found medium support for better quality in coffee for one species (SAST), and for the remainder six birds (TAGY, BARU, TUFL, RADI, EULA and TUAL) we did not find evidence of differences in their overall habitat quality score (Figure 6).

Contrasting results of habitat preference and quality

When we contrast the habitat preference and quality classifications done for each species according to the framework summarized in Figure 5, we find: 1) four species that showed evidence of preferring the habitat where evidence showed quality was higher (MIOLI, MIOLE and MYCO for forest and SAST for coffee); 2) four species that showed evidence of preferring one habitat (TUAL and TAGY for forest, RADI and BARU for coffee), but no consistent evidence of differences in quality; 3) two species that showed no consistent evidence of differences in either preference or quality (TUFL and EULA); 4) evidence that SAMA may be caught in an equal-preference trap (preferring neither habitat, but with evidence of better quality in forest); and 5) evidence that MYMI may be caught in a severe ecological trap (higher preference in coffee combined with higher quality in forest) (Table 6).
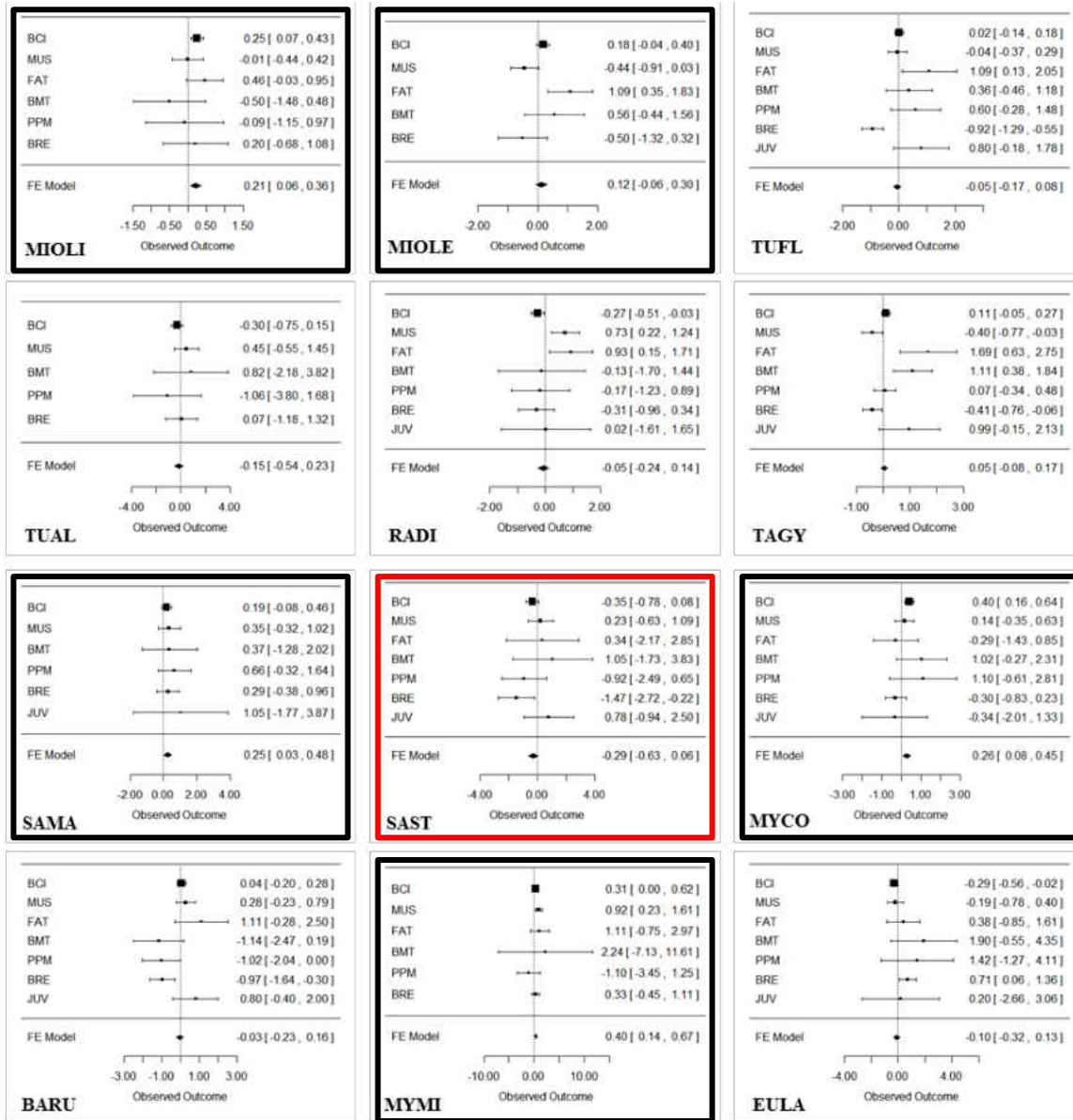
Figure 6. Summary of evidence for habitat quality according to seven chosen variables
Black frame: quality significantly higher in forest, red frame: quality significantly higher in coffee, no frame: no significant differences.
Variables: BCI – body condition index, MUS – muscle score, FAT – fat storage, BMT – body plumage molt, PPM – primary plumage molt, BRE – breeding activity, JUV – incidence of juveniles.
Squares: mid-point represents the mean effect estimate for each study, area represents weight given to it in the model, and lines represent 95% confidence intervals (negative values indicate higher quality in coffee, positive values higher quality in forest).
Diamond: overall effect of habitat on individual fitness with 95% confidence intervals (fixed effects model of the means weighted by the inverse of the variance).

Table 6. Contrasting habitat preference (HP) and habitat quality (HQ) classifications for twelve species of resident birds, as well as hypotheses on the role that shade coffee and pre-montane forest may play for their populations at the landscape level.

Species	HP Class	HQ Class	Role of Coffee	Role of Forest	Habitat Selection
MIOLI	FOREST	FOREST	Sink	Source	Adaptive
MIOLE	FOREST	FOREST	Sink	Source	Adaptive
TUFL	EQUAL	EQUAL	Generalist habitat	Generalist habitat	Adaptive
TUAL	FOREST	EQUAL	Undervalued	Equal-quality trap	Neutral
RADI	COFFEE	EQUAL	Equal-quality trap	Undervalued	Neutral
TAGY	FOREST	EQUAL	Undervalued	Equal-quality trap	Neutral
SAMA	EQUAL	FOREST	*Equal-preference trap*	*Undervalued*	*Maladaptive*
SAST	COFFEE	COFFEE	Source	Sink	Adaptive
MYCO	FOREST	FOREST	Sink	Source	Adaptive
BARU	COFFEE	EQUAL	Equal-quality trap	Undervalued	Neutral
MYMI	COFFEE	FOREST	*Ecological trap*	*Perceptual trap*	*Maladaptive*
EULA	EQUAL	EQUAL	Generalist	Generalist	Adaptive

The results of the principal component analysis carried out for the habitat effect sizes of body condition, body molt and breeding activity of the twelve species show an interesting ordination pattern; with species classified as preferring forest showing more consistency in their responses (especially along PC1), and species classified as preferring coffee showing a wide heterogeneity in their responses in relation to both PC1 (which contains positive loadings of breeding and molting) and PC2 (which contains positive loadings of body condition). Species classified as having equal-preference cover an intermediate area between the other two groups (Figure 7/Table C.7).
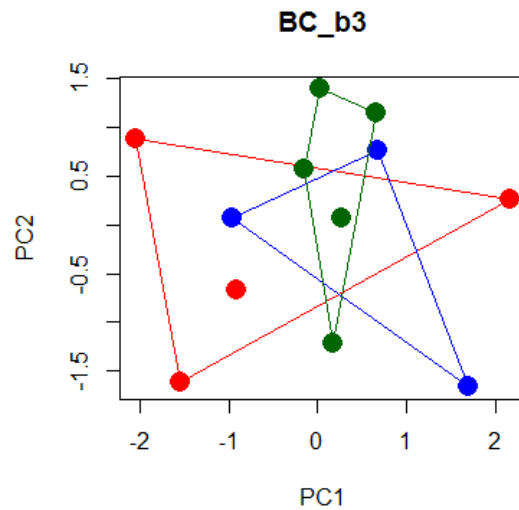
Figure 7. Plot of the first vs. the second principal components for the correlations between the habitat effect sizes for body condition index, body molt and breeding activity.
Each dot represents one of our focal species, colored by their category of habitat preference as follows: red – prefers coffee, green – prefers forest, blue – shows no consistent pattern of preference.
PC1 contains positive loadings of breeding and molting primarily, and explains 47% of the variance, while PC2 contains positive loadings of body condition primarily, and explains 34% of the variance.

Discussion

A great majority of the studies evaluating biodiversity associated with agricultural landscapes have focused on patterns of species richness at the habitat (mainly focusing in forest remnants) or between habitat scales (comparing species richness and composition between different land uses). This project aimed to complement that knowledge by understanding that patterns of species distributions emerge from the accumulation of habitat-specific responses of individuals, mediated by the constraints imposed by landscape level structure and dynamics (Wiens 1976; Levin 1992). By comparing indicators of habitat preference and quality between pre-montane forest remnants and shade coffee plantations for twelve species of resident birds, we found evidence suggesting that the adaptiveness of habitat selection may decrease as species switch from preferring the original to the novel habitat in the landscape. Since this hypothesis

may have important implications for research and conservation, it is important to assess how our findings compare with those of previous studies, caveats in the way we measured and interpreted the variables, and future lines of research needed to corroborate these patterns beyond our specific study site, years and species.

Patterns of habitat preference

Our focal species presented a range of preferences that coincided with their habitat descriptions in the literature (Hilty & Brown 1986; del Hoyo et al. 1992-2011; Stotz et al. 1996; Restall, Rodner & Lentino 2006). While in general, bird assemblages in tropical agroforestry ecosystems are comprised of disproportionately more frugivorous than insectivorous species when compared with forest (Tscharntke et al. 2008), we found two of our insectivorous species (BARU and MYMI) preferring shade coffee and our highly frugivorous Tyrannidae (MIOLI and MIOLE) preferring forest, showing that patterns of habitat preference in our species do not seem to be strictly associated with either trophic guild or body size (Thornton & Fletcher 2014).

Occupancy was not a very precise indicator of preference in our birds, as it is better used when studying rare species (Ruiz-Gutiérrez, Zipkin & Dhondt 2010). For eight of the species we found either very little evidence of preference or relatively consistent patterns. In the other four species estimated abundance was not always correlated with the other measures of preference (Battin 2004; Robertson & Hutto 2006). RADI showed higher abundance in coffee but higher site fidelity to forest, which could be explained by seasonality, since site fidelity in temporally correlated environments has been shown to enhance population persistence (Schmidt 2004), and forests are less affected by changes in precipitation (Dietsch 2003). However, EULA showed the

opposite pattern, leaving us with questions about this species' habitat preference. TUFL showed higher abundance in forest, but the higher proportion of adults in coffee, raises doubts about how to classify it. BARU was more abundant and more frequently detected in coffee, but abundance in forest was less variable, which could be linked to the seasonal shifts in foraging niche that have been documented previously for this species (Jedlicka et al. 2006).

Habitat selection results from a variety of individual and social, behavioral and environmental cues interacting with each other at different scales (Gavin & Bollinger 1988; Haas 1998; Jones 2001; DeCesare et al. 2014), which makes habitat preference a dynamic phenomenon which is very challenging to measure. We tried to overcome uncertainty in our assessments by combining different measures; however a critical next step for our research will be to determine which habitat and social characteristics are being used as selection cues by our species (Schlaepfer, Runge & Sherman 2002; Battin 2004; Robertson & Hutto 2006; Gilroy & Sutherland 2007), as well as how these are affected by interspecific interactions. Previous studies in shade coffee point to the importance of keystone plant species such as those in the genus *Inga* (which dominate shade in our site), for providing resources when plant diversity is low (Johnson 2000), and to the importance of epiphytes for foraging and breeding of certain resident species (Cruz-Angón, Sillett & Greenberg 2008). Telemetry studies have shown that residents of tropical agroecosystems may maintain similar home range sizes regardless of the amount of preferred habitat in them (Githiru, Lens & Bennun 2007), and that habitat-sensitive species associate frequently with remaining trees in the landscape (Sekercioglu et al. 2007). Characteristics like whether a species joins mixed flocks or not, may also result in seasonal shifts in habitat use (Colorado 2011), so it becomes important to link the patterns we have discovered so far with the

social information dimension (Fletcher Jr & Sieving 2010; Schmidt, Dall & Van Gils 2010), especially when studying species with complex social behaviors such as EULA and TAGY.

Patterns of habitat quality

In general, individual quality indicators were equal to or better in forest than coffee, which coincides with previous evidence accumulated for Neotropical migrants using shade coffee (Bakermans et al. 2009) and forest as their wintering habitats (Chandler & King 2011). We need more information to understand if the apparent dependence of our species on forest is related to issues of habitat supplementation and complementation (Dunning, Danielson & Pulliam 1992), to the seasonality in resources and predation offered by both habitats (Wunderle Jr & Latta 1998; Dietsch 2003; Shochat et al. 2005), to changes in community composition brought about by the presence of migrants (Greenberg, Reitsma & Angon 1996; Jedlicka et al. 2006), or to varying levels of landscape heterogeneity (Tscharntke et al. 2012); among other possible mechanisms.

Our habitat quality assessments were based solely on evaluations of captured individuals, so possible tradeoffs may exist with other components of quality such as survival and reproduction (Vickery, Hunter & Wells 1992; Donovan & Thompson 2001; Burel & Baudry 2005; Johnson et al. 2006). We would have needed more data accumulated over a longer period of time to properly estimate survival (Ruiz-Gutiérrez et al. 2012), and unfortunately, our nest search and monitoring efforts did not yield enough data to build informative models. Species associated with forest edge, open canopy or scrubby habitats, belonging to Turdidae, Tyrannidae, Cardinalidae and Thraupidae have been found commonly nesting in sun coffee plantations close

to forest before, and although nest mortality rates were not unusually high (Lindell & Smith 2003); there is evidence of forest being a better quality habitat in the post-fledging period for *Turdus assimilis* in a Costa Rican agricultural landscape (Cohen & Lindell 2004). Unlike our study (where individuals of most species were captured in both habitats during the same sampling occasion – Table C8), other studies have found that resident birds do not commute regularly to forest (Sekercioglu et al. 2007). Even within the same habitat patch, wanderer and sedentary birds can experience different mortality rates (Rappole, Ramos & Winker 1989), so further differences in quality may be masked when we do not distinguish between these types of individuals. Finally, density-dependence could also be changing the experienced habitat quality for the species seasonally or among different years (Pulliam & Danielson 1991), but our data was not suited to address this issue directly.

Evidence of ecological traps

Going back to our initial hypotheses, three of the forest specialists displayed evidence for adaptive selection; with the fourth possibly undervaluing the resources shade coffee could provide. Of the forest generalists, two species showed no differences in preference or quality, which can be interpreted as an adaptive response to the heterogeneity in this landscape, another could be undervaluing shade coffee and *Saltator maximus* could be caught in an equal-preference trap (as defined by Fletcher, Orrock & Robertson 2012). Of the treed-area dwellers, only one species showed evidence for adaptive preference; two of them might be underutilizing forest remnants and *Myioborus miniatus* may be caught in a severe ecological trap (as defined by Fletcher, Orrock & Robertson 2012).

Under the assumption that no significant differences in preference and/or quality actually means that the species show no preference or individual fitness outcome differences between forest remnants and shade coffee; ten of the study species showed either adaptive or neutral selection behavior. Based on our results, the three species that showed adaptive selection towards forest, *Mionectes olivaceus*, *Mionectes oleagineus* and *Myiothlypis conspicillata*, will probably only occupy shade coffee plantations in farms that are close enough to forest for them to use both habitats, but it is noticeable that despite the extension and relatively good condition of the forest they are still commonly captured and/or observed in coffee, meaning the latter may be providing important resources to certain individuals and/or during certain seasons or life stages. The opposite is true for *Saltator striatipectus*, that overall showed adaptive preference for shade coffee. The two species for which we found no differences in preference or quality, *Turdus flavipes* and *Euphonia laniirostris*, will probably be common in different types of heterogeneous, agricultural landscapes, while we would expect *Turdus albicollis* and *Tangara gyrola* to be more abundant in landscapes with remaining forest cover and *Ramphocelus dimidiatus* and *Basileuterus rufifrons* in landscapes with more intermediately-modified habitats. If the preference that *M. miniatus*, and in a lesser extent *S. maximus*, show for novel ecosystems is truly maladaptive, then we would expect both of these species to be less common in landscapes without forest than in those with forest, even if they are more commonly captured and/or detected in shade coffee.

Because most of our focal species have wide distribution ranges within the Neotropics, the next step will be to corroborate the patterns we found with capture and/or observation information from other projects and regions. Chandler and collaborators (2013) compared

abundance between primary forests, secondary forest, Integrated Open Canopy coffee farms (IOC farms have equal areas of sun coffee and regenerating forests) and shade coffee farms (which were also commercial polycultures) in Costa Rica from 2006-2008. Of the six species available for comparison, they classified *M. olivaceus*, *M. oleagineus*, *T. gyrola*, *M. miniatus* and *B. rufifrons* as having intermediate dependence from forest (3/5) and *S. maximus* as having low forest dependence (5/5). The number of captures per 100 net-hours for both *Mionectes* species was higher in forest remnants but *M. olivaceus* was higher in IOC than shade coffee, whereas *M. oleagineus* was rare in both. *T. gyrola* was only captured in secondary forest and *M. miniatus* was more abundant in IOC coffee and primary forest than in secondary forest and shade coffee. Both *B. rufifrons* and *S. maximus* were captured more frequently in shade coffee and secondary forest than in IOC coffee. In general these patterns match our data, but if we interpret these capture rates as preference *S. maximus* shows even higher preference for coffee than in our site, and *M. miniatus* more affinity for forests. However, without any information on habitat quality, we cannot corroborate if this reinforces or contradicts the apparent traps we found for the two species at our site.

In previous studies, the lower diversity of forest-dependent birds in agricultural landscapes has been linked to their sensitivity to the introduction of high-intensity farming uses (Dietsch 2003; Tejeda-Cruz & Sutherland 2004; Komar 2006). None of the species we studied are considered forest-dependent birds, yet the trend we found contradicts literature stating that habitat generalists benefit from processes such as forest loss (Carrara et al. 2015). High forest use by birds classified as non-forest species warrants caution when selecting such groups as indicators to evaluate the benefits of agriculture for conservation (Cohen & Lindell 2005; Ruiz-

Gutiérrez, Zipkin & Dhondt 2010; Fahrig et al. 2011), helps highlight the importance that natural remnants have for native species persistence in intermediately-modified landscapes, and points to agroforestry systems such as shade coffee being more valuable as matrices, corridors or buffers between natural vegetation remnants, than as a replacement habitat by themselves (Perfecto & Vandermeer 2002; Perfecto et al. 2007). In this study, species preferring coffee, and to a lesser degree those with equal-preference, showed stronger responses in quality (both positive and negative), suggesting that one of the mechanisms underlying the patterns described above may be that settling in shade coffee is a higher-risk strategy (offering the possibility of high rewards, but also more variability and chances of failure).

Avenues for further research

While carrying out this project, we used a simulation model to demonstrate that ecological traps that arise when selection cues are distributed continuously throughout the landscape may be very difficult to detect when comparing fitness measures between habitat categories (Sánchez-Clavijo, Hearns & Quintana-Ascencio 2016). Resident birds in tropical agroforestry systems have been shown to respond to different scales and variables than migrants (Colorado 2011), so variables like the amount of habitat edges in a landscape (Weldon & Haddad 2005), and the proximity to riparian forests (Petit et al. 1999) could have effects beyond those of internal habitat characteristics. Therefore, future studies of the interplay between habitat selection and quality should aim to compare more than two types of habitat, and to relate organism variables to continuous characteristics at the patch, neighborhood and landscape scales (Bennett, Radford & Haslem 2006; Tscharntke et al. 2012). Our sampling was designed so that

shade coffee sites were located at different distances from forest, with the idea of comparing the landscape and vegetation characteristics of each site to bird responses. In the end we had to pool by habitat because of very low recapture rates and a lot of individuals being commonly captured in more than one site even within the same sampling occasion. Both these characteristics are indicative of larger than expected home ranges, so it is important to take into consideration that the coffee and forest birds are not separate populations. Unfortunately movements between sites were not common enough to perform a spatially-explicit capture-recapture analysis.

A lot of the information we used is regularly collected in banding projects, but is seldom used to produce a general perspective about the role that different habitats have for species persistence. The latter has been identified as a priority in assessing whether coffee agroecosystems represent viable habitats for forest biodiversity, transitory habitats providing short-term resources, or corridors facilitating dispersal between remnants patches (Dietsch 2003; Perfecto et al. 2007). The value of our approach lies in going beyond species presence, and the assumption that common species thrive in all the habitats they are found. We based our results on several years of data and used a variety of indicators of preference and quality. For now our results represent working hypotheses, but with more and longer-term data, more species analyzed and more preference and quality variables measured in greater detail, we could start incorporating this type of information into tools and strategies for biodiversity management and conservation in heterogeneous landscapes.

Conclusions

Long-term demographic studies of native species occupying novel habitats should be considered a main objective of biodiversity monitoring, understanding that the assumptions of how we collect and analyze data can have important impacts on the design of conservation strategies. The analysis of seven years of capture-mark-recapture and resight data for twelve species of resident birds living in shade coffee plots and pre-montane forest remnants of the Sierra Nevada de Santa Marta allowed us to: 1) provide evidence that even species considered as habitat generalists still commonly use, prefer and experience higher fitness in available forest remnants, and that therefore conservation strategies in rural landscapes should emphasize the conservation of native vegetation; 2) establish that after a century of landscape transformation many species seem to be using shade coffee plots in an adaptive or at least neutral way, reinforcing the idea that this agroforestry system can be a biodiversity-friendly matrix around forest fragments; and 3) discuss possible evidence of ecological traps persisting for common species, and therefore showing that when evaluating the contribution of novel habitats to biodiversity conservation it is important to understand that species persistence is not necessarily ensured by maintaining current conditions.

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CHAPTER 4: CONCLUSIONS

Lessons learned from the theoretical model of ecological traps

Building the simulation model allowed us to change landscape structure and habitat selection criteria to study their interaction, which is impossible to do in real life. While all the factors we tested 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 suggested 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.

Lessons learned from the field assessment of ecological traps

From the analysis of data collected in the field we found that while the majority of the species showed adaptive (six species) or neutral (four species) roles for habitat selection, two species showed maladaptive outcomes (*Saltator maximus*, a forest generalist, may be caught in an equal-preference trap, while *Myioborus miniatus*, a treed-area dweller, may be caught in a severe ecological trap). Therefore, we provided evidence that ecological traps may arise for common species even after a century of landscape transformation, and that this phenomenon may

be more widespread and common than previously thought; that species considered as habitat generalists still commonly use, prefer and experience higher fitness in available forest remnants, and therefore conservation strategies in rural landscapes should take into account landscape characteristics and not only the characteristics of a particular habitat; and finally argued that when evaluating the contribution of novel habitats for biodiversity conservation it is important to understand that species persistence is not necessarily ensured by maintaining current conditions.

<u>Bringing together the theoretical model and the field assessment of ecological traps</u>

Based on the characteristics of the field study, as well as on some of the lessons learned from the theoretical model, there are several reasons why the power to detect maladaptive habitat selection in this study was low: 1) We chose species that were relatively common in both habitats, and resident generalists, which have been predicted in the literature to be less likely to "get caught" in an ecological trap; 2) Our site had gone through strong landscape transformation over a century ago, so species had a long time to adapt or completely fail to do so and disappear from the region; 3) From the model we learned that when comparing habitat-specific individual fitness, the effect of habitat could be masked when territorial and vagrant individuals are given the same weights in the analyses and in our fieldwork we did not distinguish between these two types of individuals; 4) We also learned from the model that when selection is based on habitat cues that are shared by different components in the landscape, but outcomes are compared between land-cover types, the effects of ecological traps are fuzzier and harder to detect; 5) Our initial plan was to compare measures of individual fitness, but also survival and reproductive

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output as indicators of habitat quality. Since there may be tradeoffs between the different aspects of fitness, a true ecological trap can only be proved if all are assessed simultaneously.

However we did detect evidence of ecological traps, and if we look at the model results for habitat-based selection in a landscape of characteristics similar to our study site (50:50 forest: coffee cover, resulting from radial transformation), and specifically at those scenarios where species had large search areas (the very low recapture rates by site gives us an indication that most of our species probably have large home ranges), we would expect: 1) larger populations of species carrying out adaptive habitat selection than of those carrying out maladaptive habitat selection, with those showing equal-preference being much closer to the former than the latter; 2) strong differences in individual condition between species carrying out adaptive, neutral and maladaptive selection. We cannot compare mean body condition between species because they all have different sizes, however we can compare overall abundance of each species on our study site (adding the estimates for coffee and forest) as long as we only compare within a method of estimation (closed population models will always yield larger estimates than those that allow openness between sampling occasions). The two species for which we hypothesized maladaptive habitat selection had significantly smaller population sizes than those for which we hypothesized neutral or adaptive selection, and there was a lot of overlap between the former two categories. This pattern is held even when comparing species within the same family (see Parulidae where *Myiothlypis conspicillata* is hypothesized to have adaptive selection and has the largest overall population, followed by *Basileuterus rufifrons* which is hypothesized to have neutral selection, and where *Myioborus miniatus,* which may be caught in an ecological trap, shows the smaller population size (Table 7).

Table 7. Contrasting hypothesized roles for habitat selection with the overall abundance estimated at the site level according to species and method of estimation.

Species	Habitat Selection	Overall abundance*
JS models		
TAGY	Neutral	1,149 [1038-1245]
RADI	Neutral	942 [767-1097]
MIOLE	Adaptive	927 [822-1012]
MYCO	Adaptive	921 [783-1026]
BARU	Neutral	800 [647-916]
MYMI	Maladaptive	504 [328-585]
CP models		
MIOLI	Adaptive	2,430 [1972-2713]
TUFL	Adaptive	2,005 [1797-2171]
EULA	Adaptive	855 [651-1003]
SAMA	Maladaptive	373 [318-414]
Other species		
TUAL	Neutral	NA
SAST	Adaptive	NA

*Overall abundance shows the mean of the posterior distribution and the 50% credibility intervals between parenthesis obtained by adding independent estimates for coffee and forest populations.
JS: Jolly-Seber population model
CP: closed-population model
NA: not available because we could not get estimates for both habitats.

In the future, we will use the model to apply findings from the field, specifically by designing new simulation experiments that: 1) Use the data from capture and observation probabilities by habitat to account for habitat-specific detection rates and the effect that this sampling bias could introduce to analyses when trying to detect ecological traps, 2) Compare emergent patterns when species have varying degrees of differences in quality between habitats, and therefore evaluate how strong signals have to be before they can be detected under realistic sampling conditions; 3) Incorporate more variation in the selection cue and relate its distribution to quality outcomes in a continuous framework, which will also require using larger landscapes and longer simulations times.

<u>How can these lessons be applied for research and conservation?</u>

We used a novel methodological approach to carry out a field test of the theoretical predictions of an important ecological framework for the study of populations in heterogeneous landscapes, and integrated theory with practice by using tropical agro-ecosystems, a study system with high potential to prompt generally applicable lessons for management and conservation. What makes shade coffee and other tropical agroforestry systems so interesting from a conservation perspective is that while they are set up and managed for the production of goods and services for humans, with small changes they can strongly contribute to the conservation of associated biodiversity as well. So although they may not be able to replace forest as habitat for many species, it is important to recognize that they are a preferred alternative over more intensively managed land uses such as open monocultures and cattle pastures, and that latter conversion is precisely what biodiversity-friendly labels and other economic and social incentives have been trying to avoid. Recognizing the trade-offs between the positive and negative aspects of novel ecosystems "will allow managers the pragmatic flexibility needed to make informed and sensible decisions concerning resource use and ecosystem maintenance" (Morse et al. 2014). Based on the evidence we accumulated throughout this project, four concepts have been reinforced:

First, that the focus for research and conservation should not be solely on the intrinsic characteristics of a particular habitat (in this case of the shade coffee plantations), but it should also include the contextual characteristics where the patch is found (Hobbs et al. 2006; Lindenmayer et al. 2008). Having large patches of well conserved forest or even connected networks of riparian and secondary vegetation in a landscape may help compensate for

characteristics such as low canopy tree diversity, more open canopy cover (which may be necessary in places with very high cloud cover throughout the year), and more seasonal changes in vegetation structure, just to name a few. As long as we keep studies at the patch level, or keep doing them in the same type of landscapes, we will never find out how to balance characteristics at both scales – as in the land sparing vs. land sharing debate (Holzkämper, Lausch & Seppelt 2006; Chandler et al. 2013; Hobbs et al. 2014). To go beyond discrete habitat descriptors (i.e. forest vs. coffee), we need to make sure that when studying mobile animals we design our sampling at appropriate scales for the processes of interest (Orians & Wittenberger 1991; Morris 1992; Parody & Milne 2005).

Second, with an increase in the spatial scale of our research and conservation efforts comes an increase in their temporal scale as well, especially if we want to understand how species, goods and services respond to landscape transformation through time (Burel & Baudry 2005; Lindenmayer et al. 2008; Hobbs et al. 2014). We found a considerable diversity in responses using only twelve species over seven years, but as mentioned before, a lot more time is needed to accurately estimate parameters such as survival. Even on the shorter temporal scale, seasonal changes were so important when we analyzed our preference and quality variables, that usually differences between coffee and forest could only be detected after accounting for time of year. Management practices such as clearing undergrowth between coffee rows, cutting large branches from shade trees or removing epiphytes may be necessary for the productivity of shade coffee plantations, but further attention into when these practices take place could improve habitat quality for species living there. For example, in our field site vegetation is allowed to grow freely between coffee rows after the harvest takes place (October-December) and through

the dry season to conserve water and prevent the soil from drying up. This creates a dense layer of vegetation where we have found bird species nest frequently, but since this vegetation is removed as soon as it starts raining, most of these nests fail and use of coffee by understory birds decreases in general. By knowing local species' breeding peaks, we could recommend farm managers the best time to do this, especially in plots where diversity is high.

Third, we need to expand from using species richness (which is the summation of species presences) as the one and only indicator variable of biodiversity health (Fleishman, Noss & Noon 2006). Since species richness emerges from population processes at the landscape level, if phenomena like ecological traps are pervasive, then that richness could be decreasing without notice. Even when using species groups as indicators of functional diversity, we must make sure to test out assumptions about them beforehand. We were surprised to find that the species that seemed to be more prone to maladaptive habitat selection in our study were precisely those that have been stated by previous literature to have benefited from landscape conversion. We chose to work with birds because previous experience in coffee-growing regions of Colombia had taught us their responses were intermediate between those of completely managed diversity (such as plants) and very sensitive groups whose communities get quickly oversimplified (such as ants) (Sánchez-Clavijo et al. 2008). However, other studies comparing bird responses to other broad taxonomic groups have found both similarities and inconsistencies in their responses to management intensity and landscape structure (Perfecto et al. 2003; Lindenmayer et al. 2008; Philpott et al. 2008), so it is definitely necessary to expand efforts taxonomically as well.

Finally, the most common responses used in studies evaluating the contribution of agroforestry systems to biodiversity conservation are species richness, diversity and some

measure of how many forest species occupy them. These measures are not always corrected for differences in detectability and/or effort between habitat types, but even when they are, they are still aggregated measures of species presence and abundance and cannot provide a complete picture of processes such as habitat selection and its interplay with habitat quality. The most direct way to address habitat quality would be to measure survival and reproduction directly, but this takes a lot of time, effort and resources to do for even one species, let alone a suit of them. Since many ongoing banding projects are already collecting information on the physical and demographic condition of individuals, we propose that using individual fitness as an indicator of habitat quality can be a good compromise between the two approaches outlined above. My work has highlighted the importance of being careful about the assumptions we make during the design, sampling and analysis of data such as:

1)   Higher species abundance or density in a habitat does not necessarily imply higher habitat preference and/or better habitat quality, and these two variables are not always matched after landscapes transformation.

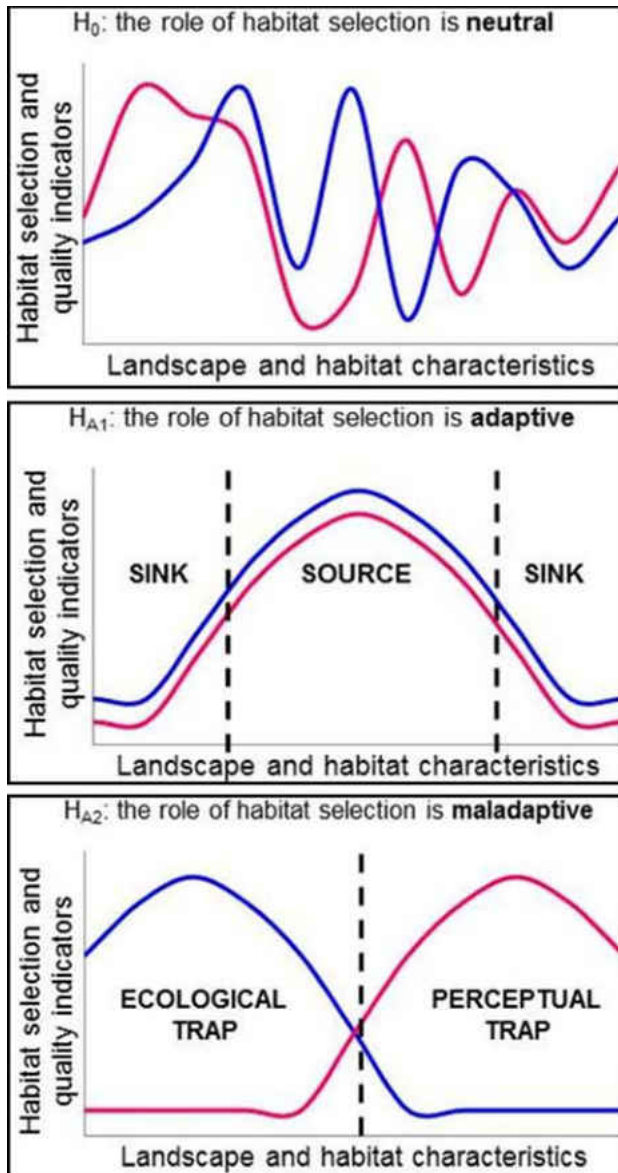2)   The role that a particular land-use plays for biodiversity conservation will vary with time, and according to species and landscape characteristics, so it may not be detectable when grouping species into functional groups.

3)   Species classified as habitat generalists based on patterns of habitat use throughout their whole distribution range, will not necessarily benefit from further landscape transformation.

4)   Community structure (and therefore species richness) is dynamic, and will change in temporal scales ranging from seasons to years, therefore species presence is not an indicator of species persistence.

<center>Future challenges</center>

Following the points above, I maintain that studying the role that habitat selection plays in the adaptation of native species to transformed landscapes is a useful framework to simultaneously increase our knowledge of population processes at the landscape level, and help us generate conservation recommendations for biodiversity in intermediately-modified landscapes. The next step for research in this field is to identify the cues species are using for habitat selection, and to complete the evaluation of quality by including direct measures of survival and reproduction. Because we suggest comparing different landscapes while also collecting demographic data, and since the needs for spatial and temporal replication usually represent a tradeoff for research resources, a compromise might be to combine easy-quick sampling at large scales (for example detection/non-detection surveys scattered randomly throughout multiple environmental gradients) with a few sites where long-term demographic data is collected (for example setting permanent bird banding stations in systems of interest such as shade coffee). Through such studies, which will inevitably require collaboration between researchers and institutions, we may characterize the adaptiveness of habitat selection in more detail (Figure 8), and further advance our understanding of the mechanisms that allow species persistence in disturbed landscapes.

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Figure 8. Future research hypotheses for regressions of habitat preference and quality indicators against continuous landscape and habitat characteristics.
Habitat preference is shown in blue, habitat quality in pink.

The next step in this research will be to disseminate the findings from this project to a wider community, including but not limited to, farm owners and workers in La Victoria and neighboring coffee plantations, Cenicafé (Colombia's National Center for Coffee Research) and the extension personnel from the Colombian Coffee Growers Federation, people and institutions

working with certifying labels for biodiversity-friendly coffee, as well as other regional and national environmental authorities. Working with such institutions will help us combine ecological information with the human dimensions of coffee growing, which must be taken into account when working on a productive system of such economic, social and cultural importance.

There are three scales at which shade coffee, and other agroforestry systems can be researched and manipulated to be more biodiversity-friendly: 1) at the landscape scale, what types of land-uses surround or are intermingled with shade coffee will inevitably change the type of species it harbors, and the use that these species can make of it; 2) at the farm and/or plot scale, vegetation structure and diversity of the actual agroforestry system will influence which species are attracted to each site (preference) and the experienced fitness of those individuals that use them (quality); 3) management of the agricultural system will affect the variation that species have to adapt to, from the timing, frequency and methods of habitat structure manipulation (e.g. undergrowth clearance, shade coping, epiphyte removal), to the presence of domestic species and the influence of human settlement, movement and labor. Factors at these three levels interact to determine not only species persistence, but also community structure and ecosystem functioning. Each biodiversity-friendly label assigns weights differently to aspects in each level, but a lot of research has focused primarily on habitat structure of the agroforestry plots (land sharing approach), and to a lesser degree on forest protection and regeneration (land sparing approach).

Based on the results of my studies I suggest that conservation of native vegetation cover within coffee-growing regions should be one of the top priorities for farmers, certifying labels and local environmental authorities. Actions to ensure this range from protection of forest remnants to allowing regeneration of secondary vegetation in areas that are not being used

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productively, between coffee plots and especially surrounding water sources and streams. The benefits of these actions will go well beyond improving habitat quality and connectivity for forest species, and other studies have shown they lead to enhanced provision of goods and services as well as of human welfare.

Species richness or high abundance of species belonging to certain groups should not be the only indicator and/or measurable goal for biodiversity conservation in agricultural regions. Knowledge of habitat-specific demography, but even of habitat use and movement between habitats can help align farming practices with improvements for associated biodiversity. For example, knowing when the most energy-demanding periods are for wildlife (e.g. breeding) and how this relates to rainfall seasonality in a site like ours may mean that by adjusting the timing of vegetation clearance in coffee plots by only a few weeks, species nesting in the undergrowth may actually have a chance of success. Minimizing the traffic and access of people and domestic animals to plots closer to forest and secondary vegetation remnants will probably enhance quality for species that use both types of habitats, as will creating some sort of buffer around human infrastructure such as buildings and roads. Many such small measures may help enhance biodiversity conservation at the local level and the accumulation of many sites carrying out these practices will carry these effects over to the regional level, but a better integration of research and practice is imperative to make sure we can monitor whether our actions are having the desired effect.

We also hope that the lessons learned in this project are generally applicable to any region that retains native biodiversity in a combination of remnant and managed ecosystems. Species conservation in heterogeneous landscapes is one of many disciplines in which theory and

practice have not grown together, and only by basing conservation tools and strategies on information that reflects important ecological processes, will we be able to maximize species persistence in those scenarios that are currently labeled as sustainable.

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APPENDIX A.
MODEL DESCRIPTION FOLLOWING ODD (OVERVIEW, DESIGN AND DETAILS)
PROTOCOL FOR AGENT-BASED SIMULATION MODELLING
(GRIMM ET AL., 2006; GRIMM ET AL., 2010).

The code for this model consists of a sequence of loops and decision algorithms that determine and are affected by two main interacting matrices: a habitat matrix and an animal matrix. It was written and executed in MATLAB version R2013b (The MathWorks, Inc. 1984-2013) and it is publicly available at http://pascencio.cos.ucf.edu/Research.htm.

1. Purpose

The purpose of this model is to explore the effects of landscape structure on population fitness under habitat-based and cue-based mechanisms of habitat selection. Specifically, we evaluate the case of mobile species that are 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. This will allow for a better understanding of population phenomena such as ecological traps, which arise from interactions ranging from the individual to the landscape scale (Wiens et al., 1993).

2. Entities, state variables and scales

2.1. Animals

The main agents in this model are individuals that can move between, choose from, breed and survive in two different habitats. Their state variables include a unique identity (used to generate outputs), life stage (juveniles or adults), territorial status (settled or floaters), size (size-corrected body mass) and spatial location (for settled individuals the cell and habitat type they occupy, for

floaters the type of habitat in which they are detected). Except for identity, all state variables change throughout the simulations, as explained in further sections.

2.2. Habitats

Each cell in the model represents an individual breeding territory with two state variables: habitat type (source or sink) and a value for a particular habitat cue. The model space is a bounded square grid that generates a closed system where immigration and emigration are ignored. Landscape size is determined by the total number of cells chosen by the user.

2.3. Scales

The spatial extent that the model reflects will depend on the characteristics of the animals being studied, the key being that only one individual can settle in each cell but that the total number of individuals in the landscape can exceed the total number of cells (non-settled animals continue existing in the landscape as floaters). After initialization, the model runs with a 1-year time step for as many years as indicated in the simulation parameters.

3. Process overview and scheduling

The modelling sequence consists of three initialization procedures followed by a yearly cycle of four processes that occur for the remaining simulation time (Figure A.1).
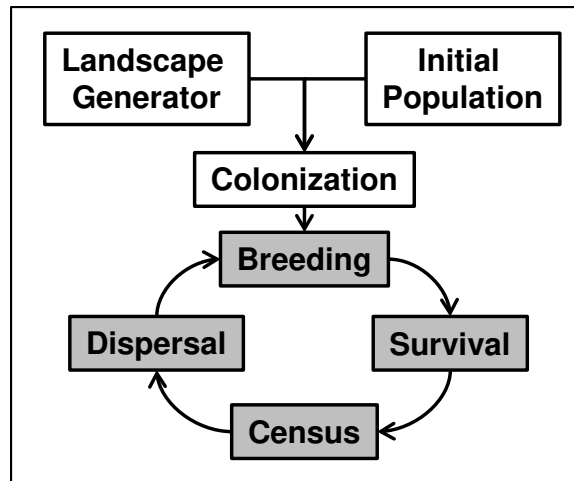
Figure A.1. Modelling sequence showing initialization procedures (white) and yearly processes (grey).

3.1. Landscape generator

Different landscape compositions are achieved by choosing a proportion of the cells to be converted from source to sink habitat. Different landscape configurations are achieved by simulating four types of landscape conversion: random, lateral, radial and percolation. Once each cell has been assigned a habitat type, it also receives a value for the habitat cue that remains unaltered throughout the simulations. Therefore, a unique landscape structure is generated and stored in the habitat matrix for each simulation run.

3.2. Initial population

In order to populate the landscape, an initial number of adults must be chosen and assigned a size. All individuals share the same habitat selection criteria which may be habitat-based (equal-preference, prefer sources or prefer sinks), or cue-based (prefer cells with a habitat cue value equal to or above a predefined threshold). These individuals become the first entries in the animal matrix.

3.3. Colonization

The initial individuals go through the process of colonizing the empty landscape one by one, in order of decreasing size. In a manner analogous to pre-emptive habitat selection models (Pulliam and Danielson, 1991), they randomly search a maximum number of empty cells and either settle on the first cell that matches their habitat selection criteria, or settle in the last cell they examine. After this stage, the animal matrix is updated to show the cell and habitat occupied by each individual during this initial year.

3.4. Breeding

Settled adults produce offspring based on habitat-specific distributions that incorporate demographic stochasticity but ensure that, on average, individuals breeding in sources produce more offspring than individuals breeding in sinks. New individuals are designated as juveniles.

3.5. Survival

Survival probabilities are applied independently to each individual according to their life stage and territorial status, but independent of their habitat. Juvenile survival is much lower than adult survival. Floaters (individuals without a breeding territory) have a density-dependent survival function that approaches zero as the landscape reaches its carrying capacity. After this stage, the animal matrix is updated when surviving juveniles become adults, and when all of the sizes are modified according to habitat and territorial status (individuals settled in sources are on average larger than those in sinks, but floaters are intermediate between them).

3.6. Census and sampling

In order for floaters to be counted they are assigned a temporary habitat according to landscape proportion. Census functions assume perfect knowledge of individual location and history, and allow for the separation of breeders and floaters in both habitats. Sampling functions count individuals according to habitat-specific detection probabilities.

3.7. Dispersal

Once a year individuals are allowed to move within the landscape to try to improve their breeding territory. The outcome of this process (which cell they occupy for the next year) depends on the interactions between their size, location, and allowed search area.

4. Design concepts

4.1. Basic principles

The main hypotheses underlying the model's design describe the ecological process of habitat selection. The simplest way to model habitat choice is to assume that individuals do not have a particular habitat preference, and that their distribution is therefore a direct result of habitat availability (in our model we call this *equal-preference traps* (Robertson and Hutto, 2006)). Early habitat selection models assumed that individuals always had an accurate way of assessing habitat quality, in other words, that given the chance they would always choose sources over sinks (*adaptive selection* in our model (Pulliam, 1988)). After evidence appeared of ecological

and perceptual traps (Battin, 2004; Robertson and Hutto, 2006), models decoupled selection and quality so that individuals could make mistakes and systematically choose sinks over sources (*severe traps* in our model, but also called maladaptive selection (Delibes et al., 2001). Theoretically, ecological traps are caused by the decoupling of previously adaptive selection cues and experienced habitat quality (Gilroy and Sutherland, 2007). Our model adds further realism to the process of habitat selection by comparing *habitat-based* choices (as described above) to *cue-based* selection, where a particular habitat characteristic is used by the individuals to assess whether to settle on a patch or not, regardless of habitat type (source or sink). Because habitat-based and cue-based mechanisms could potentially alter population outcomes, it is important to assess how varying the mode of habitat selection can interact with landscape characteristics and individual behavior to determine species distribution and persistence in heterogeneous regions.

4.2. Emergence

The yearly spatial distribution of individuals in the landscape and all population consequences thereafter emerge from the dynamical interactions among landscape structure, behavior rules, random and stochastic processes in the model.

4.3. Adaptation

Since the model explicitly prohibits individuals from modifying their habitat selection behavior in response to changes in themselves or their environment, selection criteria is only an adaptive trait when they are preset to prefer source habitat. By fixing habitat decisions on all individuals

during a simulation run our model assumes that these traits are innate, and cannot evolve during the selected time horizon. For an exploration of the consequences of adaptation in a similar setting see (Kokko and Sutherland, 2001).

4.4. Objectives

Although individuals want to occupy the habitat that maximizes their fitness (quantified in the model as the number of surviving juveniles and individual size), they cannot evaluate this directly and therefore have to rely on their innate choice criteria.

4.5. Learning and 4.6. Prediction

Individuals do not learn from past experiences nor can they directly predict the consequences of habitat choice, however when they choose the correct patch they acquire a larger body size, which allows them to disperse first and thus leads to a positive feedback mechanism reinforcing the probability of correct choice (and vice versa).

4.7. Sensing

When dispersing, individuals know the habitat type or the habitat cue of their own patch and of other patches in their ecological neighborhood. However, the size of the neighborhood is limited by the search area and the number of patches they are allowed to sample before having to settle in a cell. They are also allowed to know whether cells are empty or occupied, and in the latter case whether the individual occupying a cell is smaller than themselves. These particular settings

ensure that large birds settle in preferred patches (and smaller birds are forced to settle in less preferred patches) more often, but not always.

4.8. Interaction

Individuals interact indirectly by competing for breeding territories, with larger individuals having the capacity of displacing smaller individuals during dispersal. Habitat cells only interact at the landscape generator, where the probability of a cell being converted from source to sink is larger for cells neighboring cells that are already transformed.

4.9. Stochasticity

The model has three mechanisms for inserting stochasticity which were included to reflect variation and uncertainty in natural systems: 1) During landscape generation, colonization and dispersal, the combination of deterministic rules and random decisions ensure that even under the same initial conditions, the end results will display variability; 2) By sampling values from a real data set to assign the habitat cue to each cell, and from probability distributions to assign the size and number of juveniles born to each individual, we incorporated environmental and demographic stochasticity; 3) During survival and sampling, survival and detection probabilities are applied independently to each individual and not as a deterministic proportion to the whole population, again incorporating realism to the processes. As a consequence of this design, several runs of each simulation scenario are needed to make sure we get an accurate representation of the central tendency and dispersion of outcomes.

4.10. Collectives

There are no collectives in this model.

4.11. Observation

The model was designed to collect both a census output where all individuals can be traced throughout their lifetimes, and a sampling output where some individuals are not detected, and where information on their identities and histories is lost. The former allows us to follow the behavior of the model in detail, while the later adds realism about what we would encounter in an empirical study. Each year, both functions tally the number of individuals, number of surviving juveniles per adult breeder, and the average size of individuals for each habitat.

5. Initialization

While the overview and the design concepts of the model were explained in its general conception of following mobile animals in a landscape with source and sink habitats; to truly explain model details and our simulation experiments we refer to a specific study system: forest birds that inhabit landscapes where some of the forest has been converted to shade coffee. We chose forest as the source and coffee as the sink because forest is the original habitat where this hypothetical bird species would have evolved its habitat selection cues in. However, in real life there can be species that have equal or higher fitness in the shade coffee plots as in the remnant forests, which is currently being researched by L.M.S.C. in a coffee-growing region of

Colombia. As described below, we used four types of information to define the parameters

needed to initialize each model run (Table A.1).

Table A.1. Initialization parameters used in the simulation experiments, organized by process sequence (submodels). Sources of information to define parameters include: P - values modified from model parameters in (Pulliam and Danielson, 1991); F - values based on field data; S - values selected after experimentation with the model's sensibility; E - predictor factors varied to create scenarios for simulation experiments.

Submodel	Variable	Type	Values	Source
Landscape generator	Landscape length (size)	Integer	20 cells (400 cells)	S
	Landscape composition	Proportion	0.10, 0.25, 0.50, 0.75, 0.90 (F->C)	E
	Landscape configuration	Categorical	1: lateral, 2: radial, 3: percolation	E
	Number of openings for percolation	Integer	2	S
	Transformation probability (0 edges)	Probability	0	S
	Transformation probability (1 edge)	Probability	0.2	S
	Transformation probability (2 edges)	Probability	0.4	S
	Transformation probability (3 edges)	Probability	0.6	S
	Transformation probability (4 edges)	Probability	0.8	S
	Canopy percent cover in forest	Integer	Picked randomly from 52 values	F
	Canopy percent cover in coffee	Integer	Picked randomly from 156 values	F
Initial population	Initial number of birds	Integer	15	S
	Wing length (mm)	Continuous	Picked from Normal (59.4,2.21)	F
Colonization and dispersal	Number of searched patches	Integer	9(SA1), 25(SA2), 49(SA3), 81(SA4)	E
	Search area (SA)	Categorical	SA1, SA2, SA3, SA4	E
	Type of habitat selection	Categorical	0: habitat-based, 1:cue-based	E
	Habitat-based selection	Categorical	0: equal-pref., 1: adaptive, 2: severe	E
	Cue-based selection	Threshold	$CC\% \geq 0.30, 0.45, 0.60, 0.75, 0.90$	E
Breeding	Juveniles produced in forest (F)	Discrete	Picked from Binomial (6,0.80)	P
	Juveniles produced in coffee (C)	Discrete	Picked from Binomial (3,0.65)	P
Survival	Juvenile survival	Probability	0.1	P
	Adult survival	Probability	0.6	P
	Floater carrying capacity	Integer	1 individual per cell	S
	Floater maximum number	Integer	3 individuals per cell	S
	Weight in forest (grams)	Continuous	Picked from Normal (11.5,0.51)	F
	Weight in coffee (grams)	Continuous	Picked from Normal (9.5,0.51)	F
	Weight for floaters (grams)	Continuous	Picked from Normal (10.5,0.51)	F
Census and sampling	Detectability in forest	Probability	1 (no sampling)	S
	Detectability in coffee	Probability	1 (no sampling)	S
Simulation parameters	Simulation time	Integer	15 years	S
	Number of simulations	Integer	30	S

1) Originally we based model construction on (Pulliam and Danielson, 1991) sources and sinks model, so we relied upon their methods and parameters for creating differences in reproductive output between habitats and survival between life stages, as well as to represent the initial landscape colonization. We changed from a normal to a binomial distribution to determine the number of offspring to better represent the discrete nature of the variable. In the future we hope to acquire habitat-specific demographic data for real birds in order to use the model to make more realistic predictions (parameters derived from this source have a [P] to distinguish them in table A.1).

2) To ensure that the two variables needed to calculate bird size had realistic distributions, we used field data of wing chord length and body mass collected for 145 individuals of Mionectes oleagineus (Ochre-bellied Flycatcher) to calculate the parameters needed to generate the associated probability distributions. One distribution for wing length was generated to assign the value for all adult birds, and once a bird had its value assigned, it remained constant through its lifetime. In contrast, we used three different distributions for weight, one for individuals settled in forests, a second one for those settled in coffee and a third one for floaters. The weight differentiation between forest and coffee was created through k-means clustering of the body mass data, but the two clusters did not correspond to different habitat types in real life. The mean for floaters was the mean for the two groups (parameters derived from this source have an [F] to distinguish them in table A.1). Field data was also used to determine canopy cover percent (see section 6 on this appendix).

3) To determine the initial values for those variables that were not the focus of our simulation experiments, we relied on early sensitivity analyses of the model, and chose values that consistently lead to stable populations but that nonetheless allowed for variations in the responses to our variables of interest (parameters derived from this source have an [S] to distinguish them in table A.1).

4) To determine the range of variation in the parameters for our simulation experiment, we had to find a balance between exploring the full response ranges and keeping the number of scenarios manageable. Landscape composition: Even though we were mainly interested in intermediately-modified landscapes (scenarios with 75%, 50% and 25% of remnant forest cover) where ecological traps may be most important (Fletcher et al., 2012) , we also included the extremes (90% and 10%) to account for any non-linear effects that may occur as heterogeneity decreases. Landscape configuration: we removed random transformation, as it produces configurations that are not realistic in the case of forests being turned to shade coffee. All other three types (lateral, radial and percolation are commonly seen in the tropical countryside). Search area: even though the model allows for the selection of a search area and the number of patches sampled by each bird separately (simulating travel distance and time spent searching) we decided to focus on the former for our simulations and therefore allowed birds to sample their complete ecological neighborhoods. The four areas chosen (SA1 to SA4) allow birds to sample 2.25%, 6.25%, 12.25% and 20.25% of the 400-cell landscape, and simulate birds with different dispersal strategies. Habitat-based selection: we used all three possible mechanisms as this was the main focus of our simulation design. Cue-based selection: we chose CC60% as our middle value of

canopy cover threshold because it is both the value that has been promoted as the minimum to ensure biodiversity conservation in shade coffee (Jha et al., 2014), and also happens to be the mean found for shade coffee in vegetation structure plots in our field site. We added values 30% higher (CC90%) to simulate birds that have a very strong preference for forest, and 30% lower (CC30%) to simulate those that are more associated with open habitats with trees; and additionally two intermediate values (CC45%, CC75%) to explore the range of responses better (parameters derived from this source have an [E] to distinguish them in table A.1).

6. Input data

Because of the difficulty in finding a function to build an idealized distribution for percent canopy cover of both forest and coffee, the model pools values from a file containing field data. The sample for forest contained 52 values with a mean of 82.36 and a standard deviation of 6.11 (range: 70.62 to 95.84). The sample for coffee contained 156 values with a mean of 58.99 and a standard deviation of 20.42 (range: 0 to 96.88) (Figure A2). It is important to note that while this achieves a realistic distribution of values from a statistical perspective, we did not include spatial autocorrelations to generate distributions that are spatially realistic. For example, coffee plots next to forest may be managed differently from those that are far and so high canopy cover values could be aggregated and not evenly spread throughout our coffee habitat.
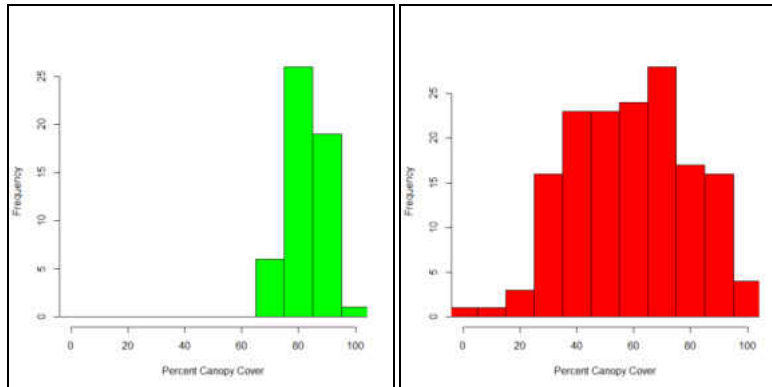
Figure A.2. Histograms of percent canopy cover for forest (green-left) and coffee (red-right) vegetation plots sampled in Santa Marta, Colombia (forest: n = 52, coffee: n = 156).

7. Submodels

7.1. Landscape generator

Landscape structure is determined by composition (the amount of each type of habitat) and configuration (the placement of landscape elements relative to each other), and despite a focus of research on the effects of composition, both are important to understand population processes at the landscape level (Dunning et al., 1992; Turner, 1989). This model is spatially-explicit so that individuals can be affected by configuration during dispersal (see section 7.7). Instead of inputting complex landscapes, but to still create a diversity of structures for simulation scenarios, we created four processes of landscape transformation (all the cells are created as sources at first): 1) Random – transformation starts at a random point in the grid and from then on, all cells can be chosen for transformation with equal probabilities; 2) Lateral – transformation starts and spreads at one edge of the grid and from then on, it is more likely for a cell sharing an edge with a transformed cell to change into coffee; 3) Radial – transformation starts and spreads at one corner of the grid and from then on, the more edges a cell shares with a transformed cell, the higher the probability that it changes; 4) Percolation – a predetermined number of cells is

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changed at random, and gaps continue to grow in all directions until the desired composition is achieved (Figure A.3).
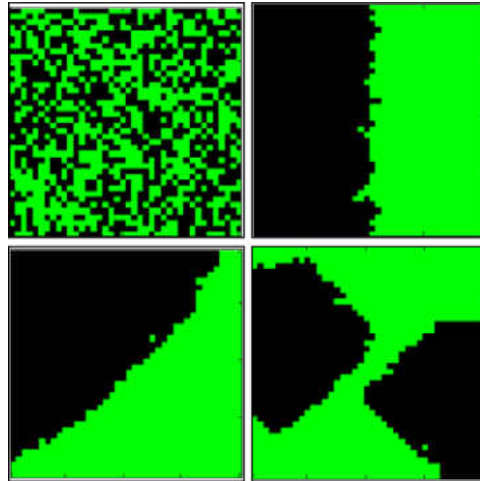

Figure A.3. Landscape representations for a 50% source (green): 50% sink (black) composition with random (upper left), lateral (upper right), radial (lower left) and percolation (lower right) configurations.

7.2. Initial population

Early sensitivity analyses showed that the initial number of birds affected the time until landscape saturation, but did not alter population size or fitness outcomes once the overall number of birds stabilized. We chose size-corrected body mass (weight divided by wing chord length) as our measure of size because it is a commonly used metric to evaluate individual condition in the field and also because it allowed us to create a measure simulating a compound of genetic (represented by wing length) and environmental (represented by body mass) stochasticity. Therefore, wing length for all birds was derived from the same normal distribution and stayed fixed for their whole life. The weight for all the initial birds came from the forest-specific distribution.

7.3. Colonization

The process of colonization is a mix between the ideal despotic (Fretwell and Lucas, 1969) and the preemptive habitat (Pulliam, 1988) distributions; with the added change that habitat selection is not necessarily configured to lead to adaptive outcomes at the population level. We incorporated a dominance hierarchy among the birds to simulate intraspecific competition for breeding sites, by means of size sorting before colonization and dispersal. Although an individual's competitive ability is conditioned by many factors, size has been widely used as a measure of individual condition in the field (Bakermans et al., 2009) and as a proxy for dominance in modelling (Shustack and Rodewald, 2010). The largest bird from the initial population selects up to m patches from the landscape at random. It is then either assigned to the first patch that matches its habitat selection criteria, or forced to settle in the last patch it examines. Once the patch is assigned, the program selects the second largest bird and repeats this process until either all birds have a patch (if the initial population is less than the total number of cells) or until all patches are full (if the initial population is greater than the total number of cells). In the latter case, patch-less birds become floaters (non-settled individuals) (Figure A.4).
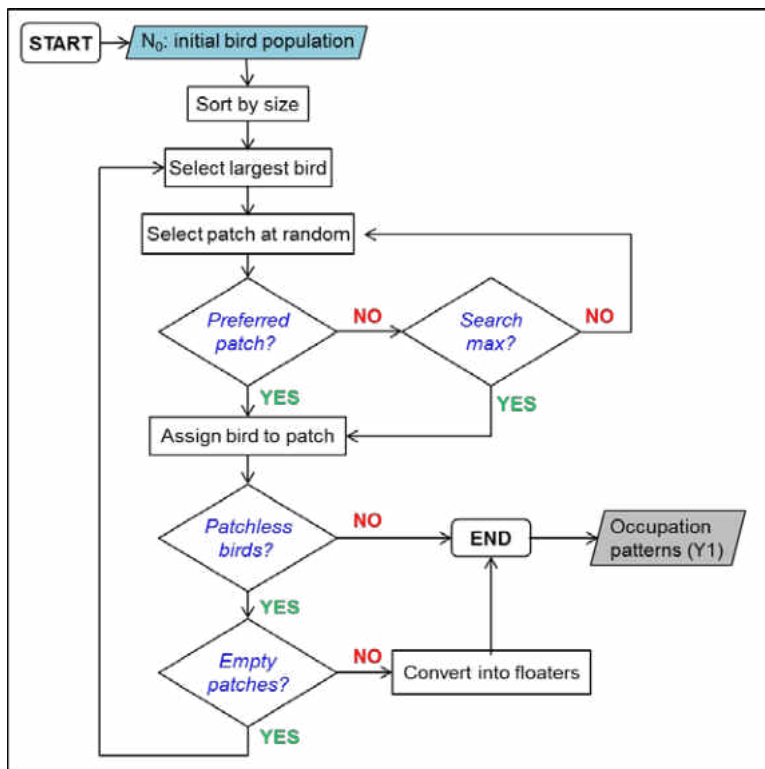
Figure A.4. Flowchart depicting landscape colonization by the initial bird population.

7.4. Breeding

Only those birds that have settled on a patch are allowed to produce offspring, meaning none of the birds existing as floaters get to breed. Because we do not have a wealth of information on habitat-dependent demographic indices of the species on our study site, we kept the parameters for juvenile production as in Pulliam & Danielson's 1991 model, but replaced their normal distribution with a binomial one that lead to mean expected values of five juveniles produced in forest and two in coffee (Figure A.5). New birds are designated as juveniles and assumed to stay in their natal patch until they become adults and then disperse (see next sections). Technically all the animals in the model can breed, although once the landscape is saturated a lot of them wont. However we decided to ignore sex because adding yet another state variable to our agents would complicate processes even further.

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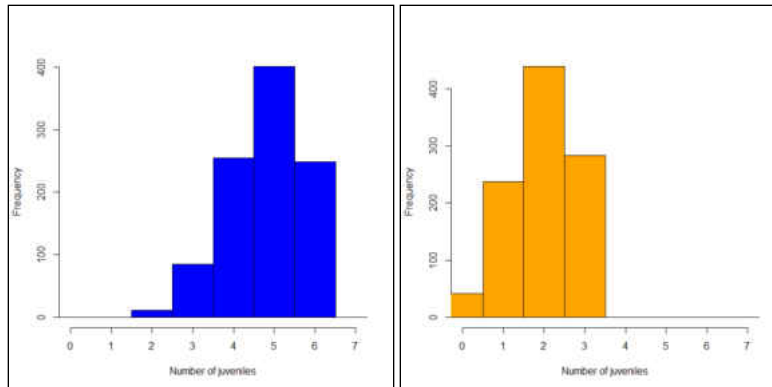
Figure A.5. Histograms for 1,000 iterations of the function to determine the number of juveniles in source (blue-left) and sink (orange-right) during breeding.

7.5. Survival

Two important events happen to birds during this stage: death and resizing. Tropical forest birds suffer a lot more predation during the nesting-fledgling stage than when they become reproductive adults (Karr et al., 1990). Therefore, we made survival dependent on life stage rather than on habitat. Having different survival probabilities per habitat would have incorporated further differences in quality, but due to lack of information on whether this is true or not, we opted for a more conservative approach (although the model could be modified to accommodate a species with habitat-dependent survival). To ensure stochasticity, survival probabilities (0.6 for adults and 0.1 for juveniles) were applied to each individual as opposed to us just removing a deterministic proportion of individuals per year.

In earlier versions of the model, floater mortality was equal to adult mortality but this left the simulated populations with no mechanism to regulate population growth. We modified floater survival probability to be a density-dependent function that approaches zero as the landscape reaches its carrying capacity, which does indeed limit growth, but also adds the assumption that when density is high, fitness is going to be lower for non-breeding than breeding individuals.

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While this would not be true for species with tradeoffs between reproduction and survival, it might be that because floaters have larger home ranges they may incur in higher levels of predation and stress, and have to compete more for food resources.

After mortality is applied to all individuals, surviving juveniles are counted and assigned to the adult and patch that produced them. They become adults, are added to the animal matrix as new individuals and are assigned a size. Their wing length is sampled from the same distribution as the initial birds, but their body mass is taken from the habitat-dependent distributions according to the patch where they were born. This gives individuals born in the source an advantage over those born in sinks. Pre-existing adults are also assigned a new weight each year depending on their habitat and/or their status as floaters. We assumed that floaters had larger home ranges spanning both types of habitat, and therefore their weight after winter is derived from a distribution intermediate between that of forest and coffee.

7.6. Census and sampling

During this stage the model takes stock of the number of birds present, their size, location and the number of surviving juveniles they produced, and stores this yearly information in three new columns in the animal matrix. During this stage floaters are assigned a temporary habitat according to landscape proportion (e.g. if 75% of the landscape was coffee, we expected to detect approximately 75% of the floaters in coffee and the remaining 25% in forest). The full census option assumes perfect knowledge of individual location and history, and allows for the separation of breeders and floaters according to habitat type. The partial sampling function

counts the birds according to habitat-specific detection probabilities and recreates field sampling conditions by losing their identity, and more importantly, their territorial status (Zurell et al., 2010). Currently we focus only on census results, but future analyses will make use of the sampling function.

7.7. 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 which is affected by their current location, individual size, and allowed search area. As in colonization, size sorting ensures a dominance hierarchy, further reinforced by the process no longer being preemptive i.e. individuals can search occupied patches. All birds start by evaluating their current patch (floaters start at a random patch), and then randomly search all the patches in their ecological neighborhood (local dispersal) or the whole landscape (global dispersal). The decision to stay or leave a patch depends on whether it is preferred or not, empty or occupied, and if the latter is true, whether the occupant is smaller than the individual searching for a patch. As progressively smaller birds go through the process, the possibility increases for them to be left without a patch and become floaters. The process ends when the smallest bird has either been assigned a patch or turned to a floater, and the animal matrix is updated with the new location and status for each individual (Figure A.6).
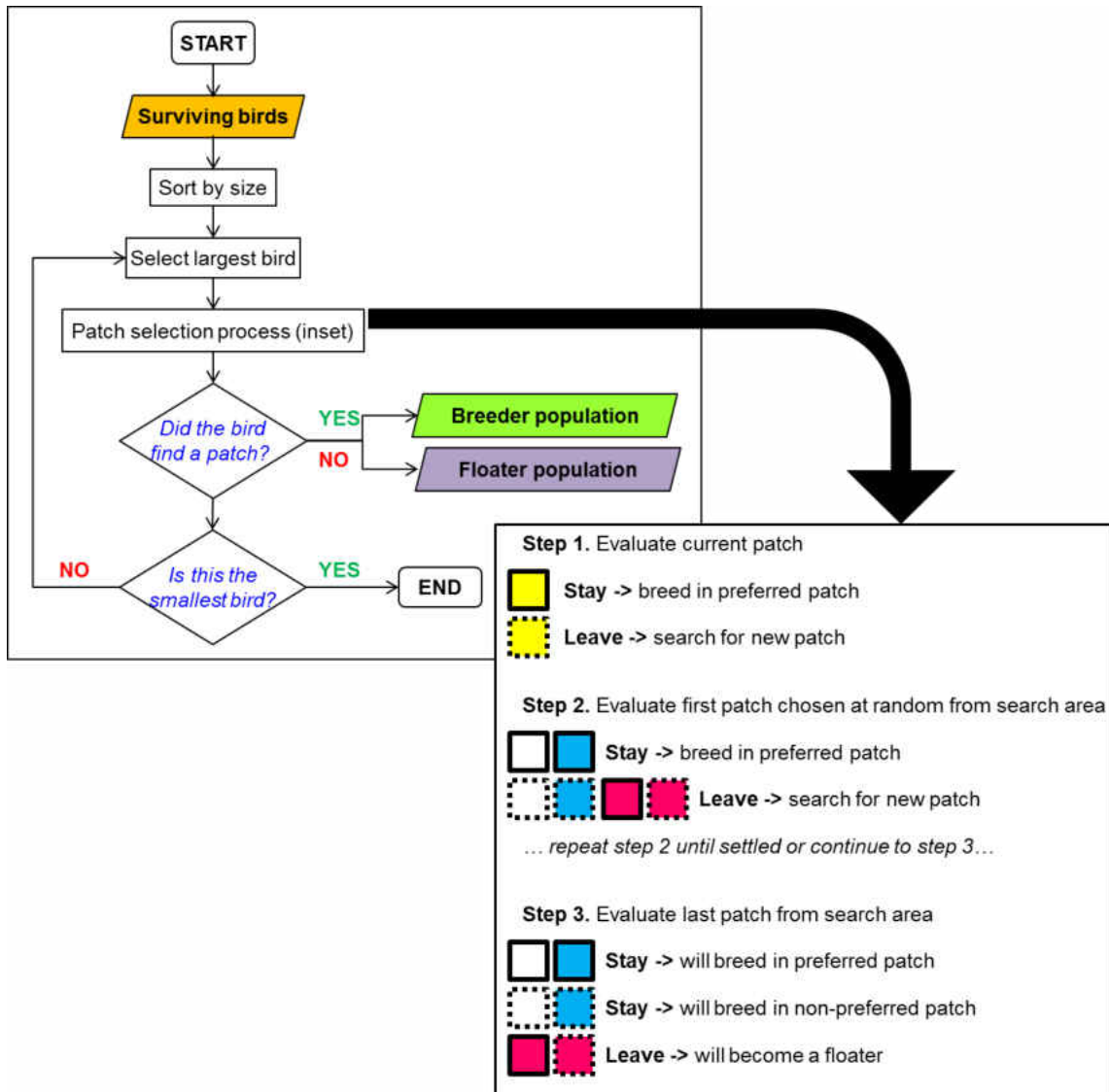
Figure A.6. Flowchart depicting yearly dispersion by the adult bird population (Inset legend: preferred patches are have a solid outline, while non-preferred patches have a dotted outline; current patches are shaded yellow, empty patches white, patches occupied by a smaller bird are blue, and patches occupied by an equal or larger bird are pink).

Note: The data generated by the simulation experiments is also available at

http://pascencio.cos.ucf.edu/Research.htm

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APPENDIX B.
SUPPLEMENTARY TABLES AND FIGURES FOR CHAPTER 2.
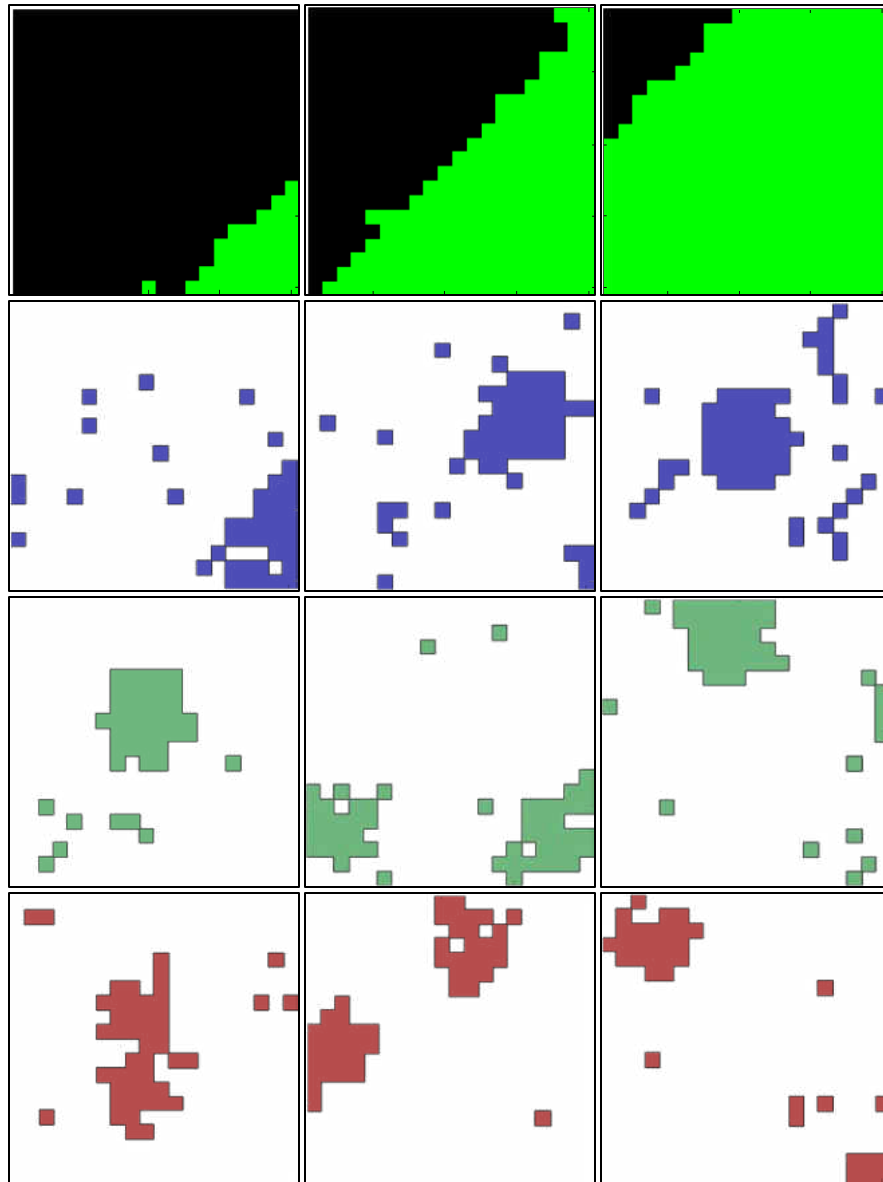
Figure B.1. Early occupation patterns of birds under different strategies of habitat selection in scenarios with *habitat-based* preference (keeping search area constant at 9 cells). The upper row shows habitat distribution in radial landscapes with 25%, 50% and 75% forest cover, respectively (green: forest, black: coffee). Remaining panels show sites occupied by birds after five years of simulation. Columns correspond to the landscape compositions on row 1, and lower rows represent adaptive (second row - blue), neutral (third row - green) and maladaptive (bottom row - red) habitat selection.
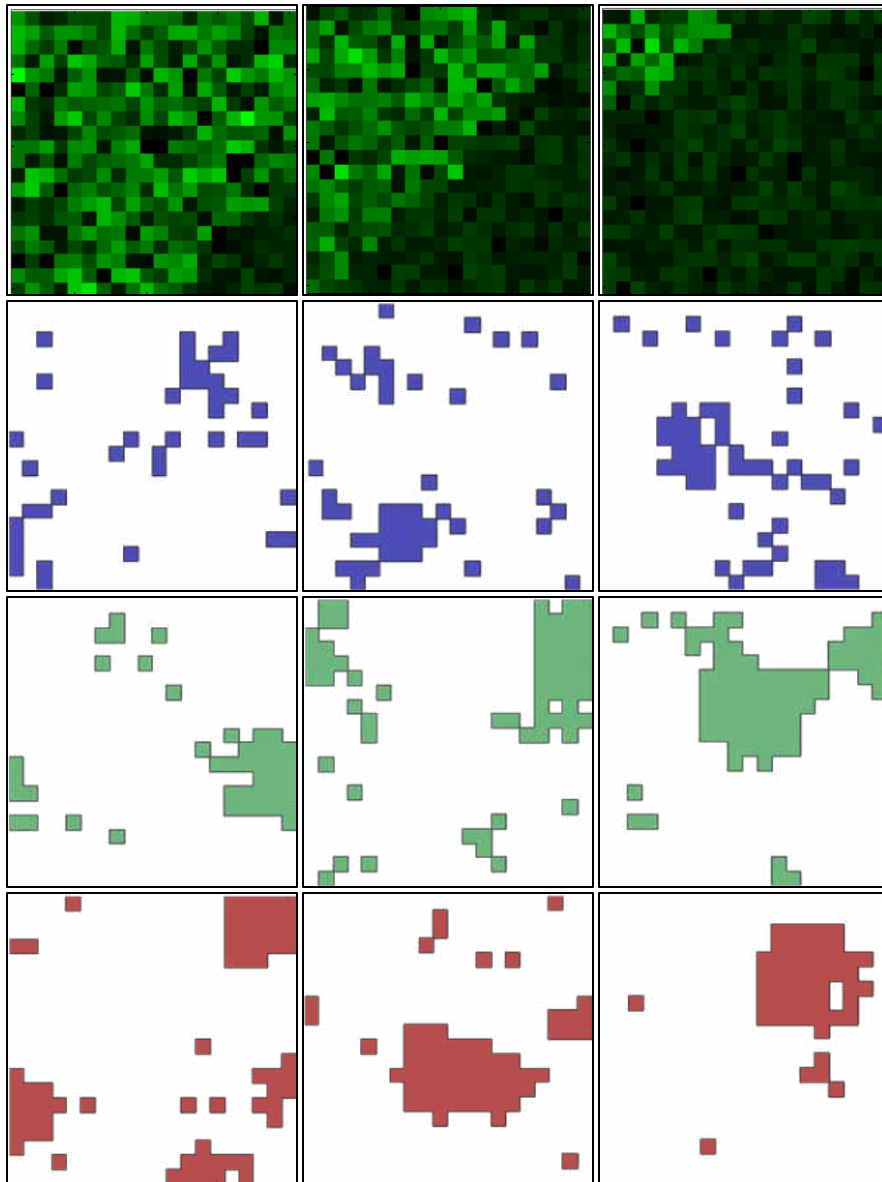
Figure B.2. Early occupation patterns of birds under different strategies of habitat selection in scenarios with *cue-based* preference (keeping search area constant at 9 cells). The upper row shows habitat distribution in radial landscapes with 25%, 50% and 75% forest cover, respectively (darker tone means higher canopy cover). Remaining panels show sites occupied by birds after five years of simulation. Columns correspond to the landscape compositions on row 1, and lower rows represent CC90% (second row - blue), CC60% (third row - green) and CC30% (bottom row - red) thresholds for canopy cover preference.
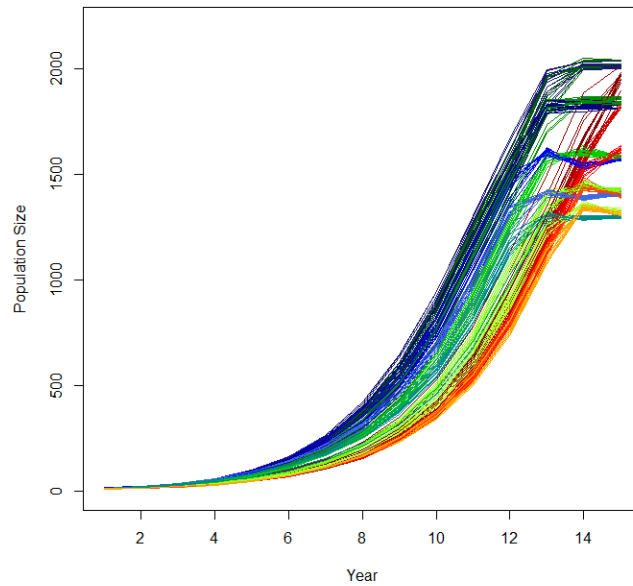
Figure B.3. Population growth for all scenarios with *habitat-based* selection; blue lines represent adaptive selection, green represents equal-preference traps and red represents severe traps; the darker the shade, the higher the forest cover in the landscape.
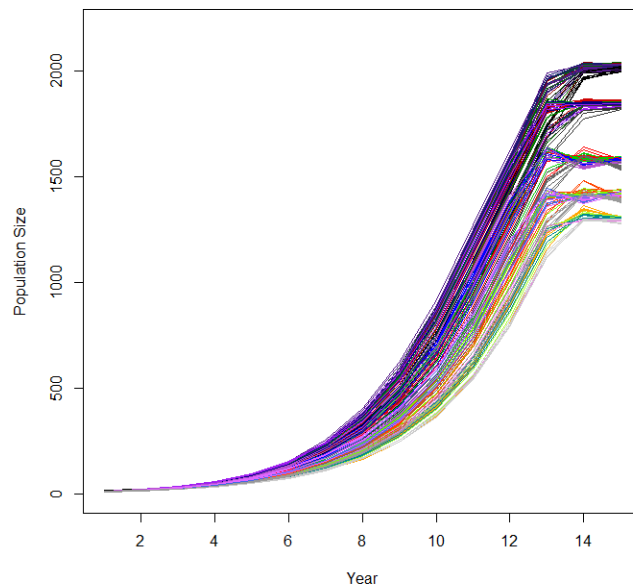
Figure B.4. Population growth for all scenarios with *cue-based* selection; grey -> CC90%, purple -> CC75%, blue -> CC60%, green -> CC45% and red -> CC30%; the darker the shade, the higher the forest cover in the landscape.

Tables B.1 to B.4.

Model selection results including the number of parameters (k), absolute and change in AICc, and cumulative weight comparing relative support for different models of fitness responses at year 11. The analysis was based on a set of 51 models that include forest cover, habitat preference and up to four of their two-way interactions. PROP = proportion of forest, PREF = habitat preference, CONF = landscape configuration, SEAR= search area. For simplicity in each table we only include those models with AICc weight above 0.001, the null and the full interactive models.

Table B.1. Population sizes at year 11 in scenarios with habitat-based selection.

Model structure	k	AICc	ΔAICc	Cum.Wt.
N11 ~ PROP+PREF+CONF+SEAR +PROP:PREF+PREF:SEAR	**12**	**1837.331**	**0.000**	**0.504**
N11 ~ PROP+PREF+SEAR +PROP:PREF+PREF:SEAR	10	1839.216	1.886	0.700
N11 ~ PROP+PREF+CONF+SEAR +PROP:PREF+PROP:SEAR+PREF:SEAR	13	1839.633	2.303	0.859
N11 ~ PROP+PREF+SEAR +PROP:PREF+PROP:SEAR+PREF:SEAR	11	1841.465	4.135	0.923
N11 ~ PROP+PREF+CONF+SEAR +PROP:PREF+PROP:CONF+PREF:SEAR	14	1841.865	4.534	0.975
N11 ~ PROP+PREF+CONF+SEAR +PROP:PREF+PROP:CONF+PROP:SEAR+PREF:SEAR	15	1844.224	6.894	0.991
N11 ~ PROP+PREF+CONF+SEAR +PROP:PREF+PREF:CONF+PREF:SEAR	16	1846.080	8.749	0.998
N11 ~ PROP+PREF+CONF+SEAR +PROP:PREF+PROP:SEAR+PREF:CONF+PREF:SEAR	17	1848.498	11.168	0.999
N11 ~ PROP+PREF+CONF+SEAR +PROP:PREF+PROP:CONF+PREF:CONF+PREF:SEAR	18	1850.847	13.517	1.000
N11 ~ PROP*PREF*CONF*SEAR	37	1870.203	32.872	1.000
N11 ~ 1	2	2512.627	675.297	1.000

Table B.2. Population sizes at year 11 in scenarios with *cue-based* selection.

Model structure	k	AICc	ΔAICc	Cum.Wt.
N11 ~ PROP+PREF+CONF+SEAR +PROP:PREF+PROP:SEAR+PREF:SEAR	**19**	**3020.827**	**0.000**	**0.599**
N11 ~ PROP+PREF+CONF+SEAR +PROP:PREF+PROP:SEAR	15	3022.744	1.917	0.828
N11 ~ PROP+PREF+CONF+SEAR +PROP:PREF+PROP:CONF+PROP:SEAR+PREF:SEAR	21	3025.285	4.458	0.892
N11 ~ PROP+PREF+SEAR +PROP:PREF+PROP:SEAR+PREF:SEAR	17	3025.530	4.703	0.949
N11 ~ PROP+PREF+CONF+SEAR +PROP:PREF+PROP:CONF+PROP:SEAR	17	3027.077	6.251	0.976
N11 ~ PROP+PREF+SEAR +PROP:PREF+PROP:SEAR	13	3027.247	6.420	1.000
N11 ~ PROP*PREF*CONF*SEAR	61	3116.103	95.277	1.000
N11 ~ 1	2	4088.168	1067.341	1.000

Table B.3. Mean individual size at year 11 in scenarios with *habitat-based* selection.

Model structure	k	AICc	ΔAICc	Cum.Wt.
S11 ~ PROP*PREF*CONF*SEAR	**37**	**-2212.88**	**0.000**	**1.000**
S11 ~ 1	2	-1771.41	441.476	1.000

Table B.4. Mean individual size at year 11 in scenarios with *cue-based* selection.

Model structure	k	AICc	ΔAICc	Cum.Wt.
S11 ~ PROP+PREF+CONF+SEAR +PROP:PREF+PROP:CONF+PROP:SEAR	**17**	**-4049.37**	**0.000**	**0.728**
S11 ~ PROP+PREF+CONF+SEAR +PROP:PREF+PROP:CONF	16	-4047.06	2.310	0.958
S11 ~ PROP+PREF+CONF+SEAR +PROP:PREF+PROP:CONF+PROP:SEAR+PREF:SEAR	21	-4041.75	7.616	0.974
S11 ~ PROP+PREF+CONF+SEAR +PROP:PREF+PROP:SEAR	15	-4041.10	8.268	0.986
S11 ~ PROP+PREF+CONF+SEAR +PROP:PREF+PROP:CONF+PREF:SEAR	20	-4039.49	9.884	0.991
S11 ~ PROP+PREF+CONF+SEAR +PROP:PREF	14	-4038.95	10.422	0.995
S11 ~ PROP+PREF+CONF+SEAR +PROP:CONF+PROP:SEAR	13	-4038.26	11.110	0.998
S11 ~ PROP+PREF+CONF+SEAR +PROP:CONF	12	-4036.18	13.191	0.999
S11 ~ PROP+PREF+CONF+SEAR +PROP:PREF+PROP:CONF+PROP:SEAR+PREF:CONF	25	-4035.27	14.099	0.999
S11 ~ PROP+PREF+CONF+SEAR +PROP:PREF+PROP:SEAR+PREF:SEAR	19	-4033.55	15.818	1.000
S11 ~ PROP*PREF*CONF*SEAR	61	-3955.92	93.454	1.000
S11 ~ 1	2	-3702.21	347.162	1.000

APPENDIX C.
SUPPLEMENTARY TABLES AND FIGURES FOR CHAPTER 3.

Table C.1. Capture effort in standardized mist-net hours, per site and sampling season.

	PW09	DW10	PW10	DW11	MW11	PW11	DW12	DW13	MW13	DW14	MW14	DW15
C1	152	1,245	415	1,062	277	-	663	832	174	126	168	109
C2	-	-	-	755	-	-	484	-	-	-	-	-
C3	-	-	-	-	248	-	-	-	-	-	-	-
C4	-	-	-	-	-	-	156	-	-	-	-	-
C5	-	-	-	-	-	-	-	599	141	133	179	-
C6	-	-	-	-	-	-	-	113	143	126	164	-
C7	-	-	-	-	-	-	-	142	164	135	179	-
C8	-	-	-	-	-	-	-	129	172	126	175	-
C9	-	-	-	-	-	-	-	137	148	117	210	-
F1	1,144	2,072	928	2,846	256	1,008	2,448	1,266	147	548	167	1,007
F2	-	-	-	1,183	-	-	878	245	-	82	-	-
F3	-	-	-	-	262	657	775	625	147	373	178	619
F4	-	-	-	-	-	-	1,001	591	170	392	168	-
F5	-	-	-	-	-	-	-	434	-	372	-	448
F6	-	-	-	-	-	-	-	610	-	570	-	834
F7	-	-	-	-	-	-	-	342	-	366	-	479
F8	-	-	-	-	-	-	-	-	-	-	-	443

C - banding stations in shade coffee
F - banding stations in pre-montane forest
DW - "dry-wet" (March-May)
MW - "mid-wet" (June-August)
PW - "peak-wet" (September-November)
[1] Differences in effort stem from different lengths of each sampling occasion, different numbers of mist nets set up per site, and different duration of sampling per day
[2] Numbers after the season correspond to the year sampling took place

Table C.2. Site description and number of banding and sighting events carried out in each site during our four main sampling occasions.

Site Description			DW13		MW13		DW14		MW14	
Station	**Habitat**	**Altitude**	**Band**	**Sight**	**Band**	**Sight**	**Band**	**Sight**	**Band**	**Sight**
C1	Coffee	1,180	5	2	5	4	5	7	5	7
C5	Coffee	1,207	5	2	5	4	5	7	5	7
C6	Coffee	1,122	5	2	5	4	5	7	5	7
C7	Coffee	1,292	5	2	5	4	5	7	5	7
C8	Coffee	1,343	5	2	5	4	5	7	5	7
C9	Coffee	1,014	5	2	5	4	5	7	5	7
F1	Forest	1,100	5	2	5	4	5	7	5	7
F3	Forest	920	5	2	5	4	5	7	5	7
F4	Forest	1,325	5	2	5	4	5	7	5	7

DW - "dry-wet" (March-May)
MW - "mid-wet" (June-August)
[1] Numbers after the season correspond to the year sampling took place

Table C.3. Observation effort (in hours) for each site, occasion, method and habitat.

Site/Method	MW13 BW	MW13 PB	DW14 BW	DW14 PB	MW14 BW	MW14 PB	Total BW	Total PB
C1	4.00	5.50	2.00	6.67	10.00	9.17	16.00	21.33
C5	4.00	4.00	2.00	6.67	10.00	9.17	16.00	19.83
C6	4.00	4.17	2.00	6.00	10.17	8.00	16.17	18.17
C7	4.00	3.17	2.00	6.25	10.17	8.17	16.17	17.58
C8	4.00	6.00	2.00	6.42	10.83	8.50	16.83	20.92
C9	4.00	4.33	2.00	6.42	10.17	8.83	16.17	19.58
COFFEE	24.00	27.17	12.00	38.42	61.33	51.83	97.33	117.42
F1	4.00	4.67	2.00	6.17	10.17	8.00	16.17	18.83
F3	4.00	4.92	2.00	6.50	10.25	9.17	16.25	20.58
F4	4.00	4.33	2.00	6.25	10.00	8.50	16.00	19.08
FOREST	12.00	13.92	6.00	18.92	30.42	25.67	48.42	58.50
TOTAL	**36.00**	**41.08**	**18.00**	**57.33**	**91.75**	**77.50**	**145.75**	**175.92**

DW - "dry-wet" (March-May)
MW - "mid-wet" (June-August)
BW - regular bird watching sessions
PB -bird watching sessions where playback was used
C - sites in shade coffee
F - sites in pre-montane forest
[1] Numbers after the season correspond to the year sampling took place

NEXT PAGES:

- Species always appear in taxonomic order
- For figures with 12 panels species always appear in the same position
- When a variable was not tested for a species the space is left blank
- Plots with **black outline**: response significantly higher in forest
- Plots with **red outline**: response significantly higher in coffee
- We use the following species acronyms:

MIOLI – *Mionectes olivaceus*
MIOLE – *Mionectes oleagineus*
TUFL – *Turdus flavipes*
TUAL – *Turdus albicollis*
RADI – *Ramphocelus dimidiatus*
TAGY – *Tangara gyrola*
SAMA – *Saltator maximus*
SAST – *Saltator striatipectus*
MYCO – *Myiothlypis conspicillata*
BARU – *Basileuterus rufifrons*
**MYMI –** *Myioborus miniatus*
EULA – *Euphonia laniirostris*

Table C.4. Summary of banding data available for capture-mark-recapture analyses for the twelve focal species in shade coffee plots and pre-montane forest remnants.

| Species	Habitat	Captures	Individuals(I)	Recaptures(R)	Ratio R/I
MIOLI	Coffee	124	117	7	0.06
	Forest	577	462	115	0.25
MIOLE	Coffee	95	66	29	0.44
	Forest	318	235	83	0.35
TUFL	Coffee	223	195	28	0.14
	Forest	392	339	53	0.16
TUAL	Coffee	19	19	0	0.00
	Forest	330	244	86	0.35
RADI	Coffee	126	101	25	0.25
	Forest	119	88	31	0.35
TAGY	Coffee	182	138	44	0.32
	Forest	398	267	131	0.49
SAMA	Coffee	91	74	17	0.23
	Forest	92	71	21	0.30
SAST	Coffee	70	60	10	0.17
	Forest	34	33	1	0.03
MYCO	Coffee	86	64	22	0.34
	Forest	247	188	59	0.31
BARU	Coffee	174	131	43	0.33
	Forest	83	61	22	0.36
MYMI	Coffee	90	62	28	0.45
	Forest	46	30	16	0.53
EULA	Coffee	95	80	15	0.19
	Forest	97	89	8	0.09

Table C.5. Summary of count and color-banding data available for capture-mark-resight analyses for the twelve focal species in shade coffee plots and pre-montane forest remnants.

Species	Habitat	Counts	Color-banded(C)	Resights(R)	Ratio R/C
MIOLI	Coffee	17	50	3	0.06
	Forest	13	52	0	0.00
MIOLE	Coffee	15	15	2	0.13
	Forest	23	50	2	0.04
TUFL	Coffee	138	50	5	0.10
	Forest	39	50	0	0.00
TUAL	Coffee	2	10	0	0.00
	Forest	9	51	0	0.00
RADI	Coffee	176	50	14	0.28
	Forest	80	29	7	0.24
TAGY	Coffee	319	50	42	0.84
	Forest	159	51	34	0.67
SAMA	Coffee	114	47	15	0.32
	Forest	32	17	7	0.41
SAST	Coffee	86	35	12	0.34
	Forest	34	7	0	0.00
MYCO	Coffee	66	39	5	0.13
	Forest	35	50	7	0.14
BARU	Coffee	275	53	44	0.83
	Forest	77	21	11	0.52
MYMI	Coffee	168	38	30	0.79
	Forest	27	8	6	0.75
EULA	Coffee	56	33	10	0.30
	Forest	25	15	0	0.00
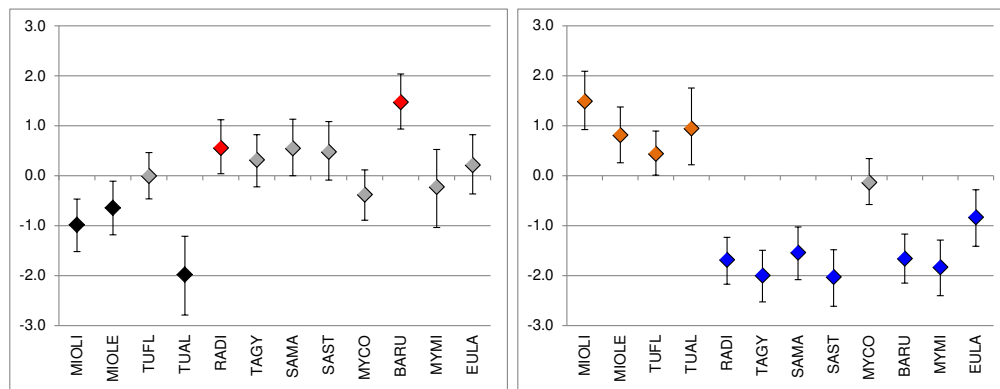
Figure C.1. Coefficient estimates and 95% credibility intervals for linear models of species detection probability in occupancy models. LEFT: effect of habitat (black - negative values indicate higher detectability in forest, red - positive values indicate higher detectability in coffee, grey – values overlapping zero indicate no effect of habitat). RIGHT: effect of sampling method (blue - negative values indicate higher detectability during observations, orange - positive values indicate higher detectability during mist-netting, grey – values overlapping zero indicate no effect of sampling method).
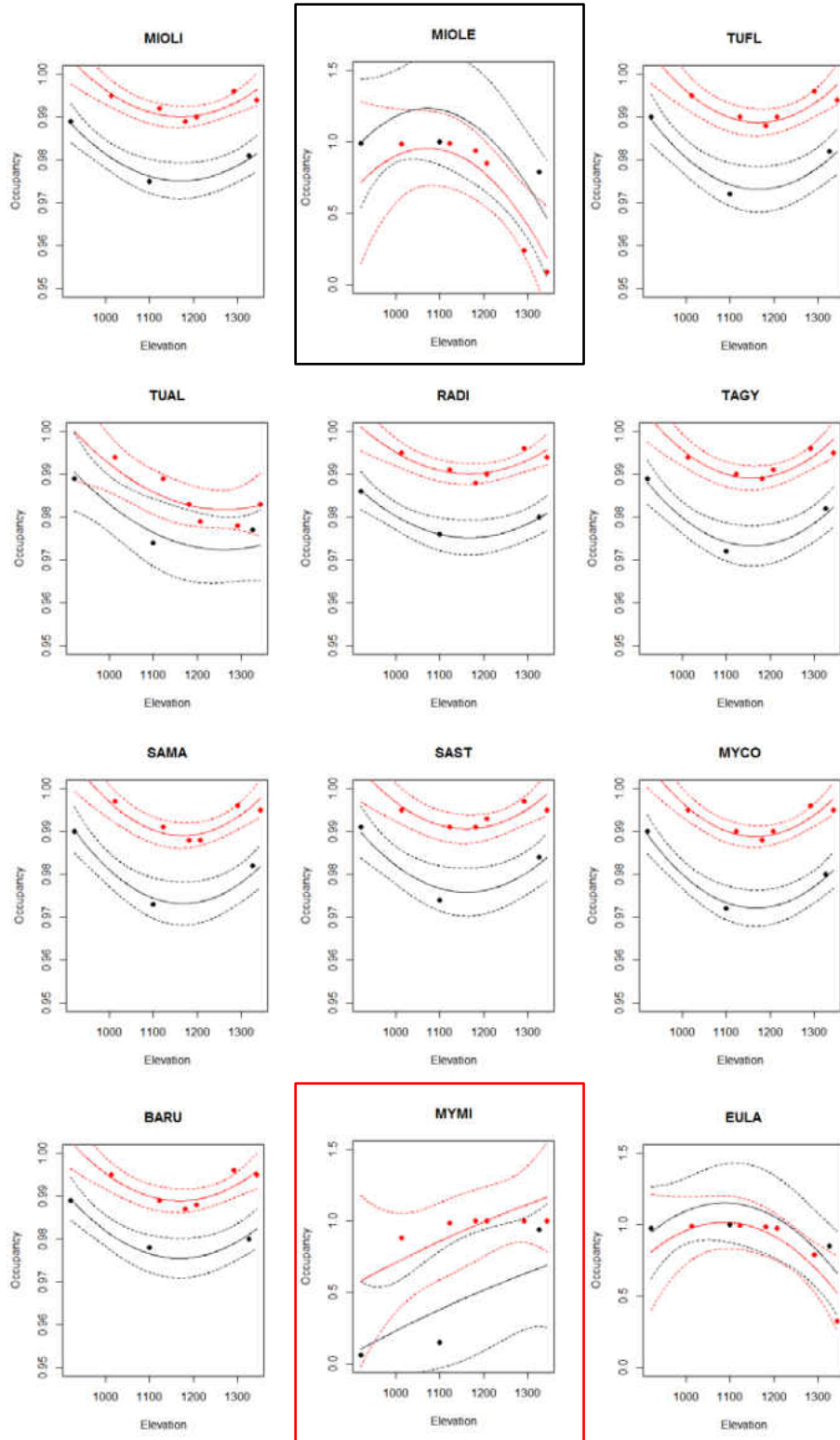
Figure C.2. Occupancy estimates for each species according to elevation (masl) and habitat (coffee in red and forest in black). Points show mean values from 3,000 samples of the posterior distribution; lines are included for heuristic purposes and show a fitted regression model of quadratic effects of elevation + habitat (solid lines) together with their 95% confidence intervals (dotted lines).

Table C.6. Coefficient estimates for the effect of sampling effort on capture probability for all species in both habitats (mean value of the posterior distribution). CP – estimation done with a closed population model, JS – estimation done with a Jolly-Seber population model, values in *italics* show that 95% credibility intervals did not overlap 0).

| Species	Model	Habitat	Effort	Effort^2
MIOLI	CP	Coffee	0.09	-0.12
		Forest	*0.89*	*-0.58*
MIOLE	JS	Coffee	*-0.54*	0.18
		Forest	*-0.53*	0.23
TUFL	CP	Coffee	*1.52*	*-0.73*
		Forest	*0.46*	*-0.25*
TUAL	CP	Coffee	-	-
		Forest	*0.60*	*-0.24*
RADI	JS	Coffee	*-0.74*	0.17
		Forest	*-0.58*	-0.05
TAGY	JS	Coffee	-0.32	0.22
		Forest	*-0.46*	0.09
SAMA	CP	Coffee	*1.38*	*-0.70*
		Forest	*0.65*	-0.16
SAST	CP	Coffee	*0.74*	-0.04
		Forest	-	-
MYCO	JS	Coffee	-0.41	-0.36
		Forest	*-0.59*	*0.54*
BARU	JS	Coffee	*-0.68*	0.27
		Forest	*-0.50*	0.39
MYMI	JS	Coffee	*-0.89*	0.19
		Forest	-0.22	0.25
EULA	CP	Coffee	*3.40*	*-1.45*
		Forest	*1.23*	*-0.71*
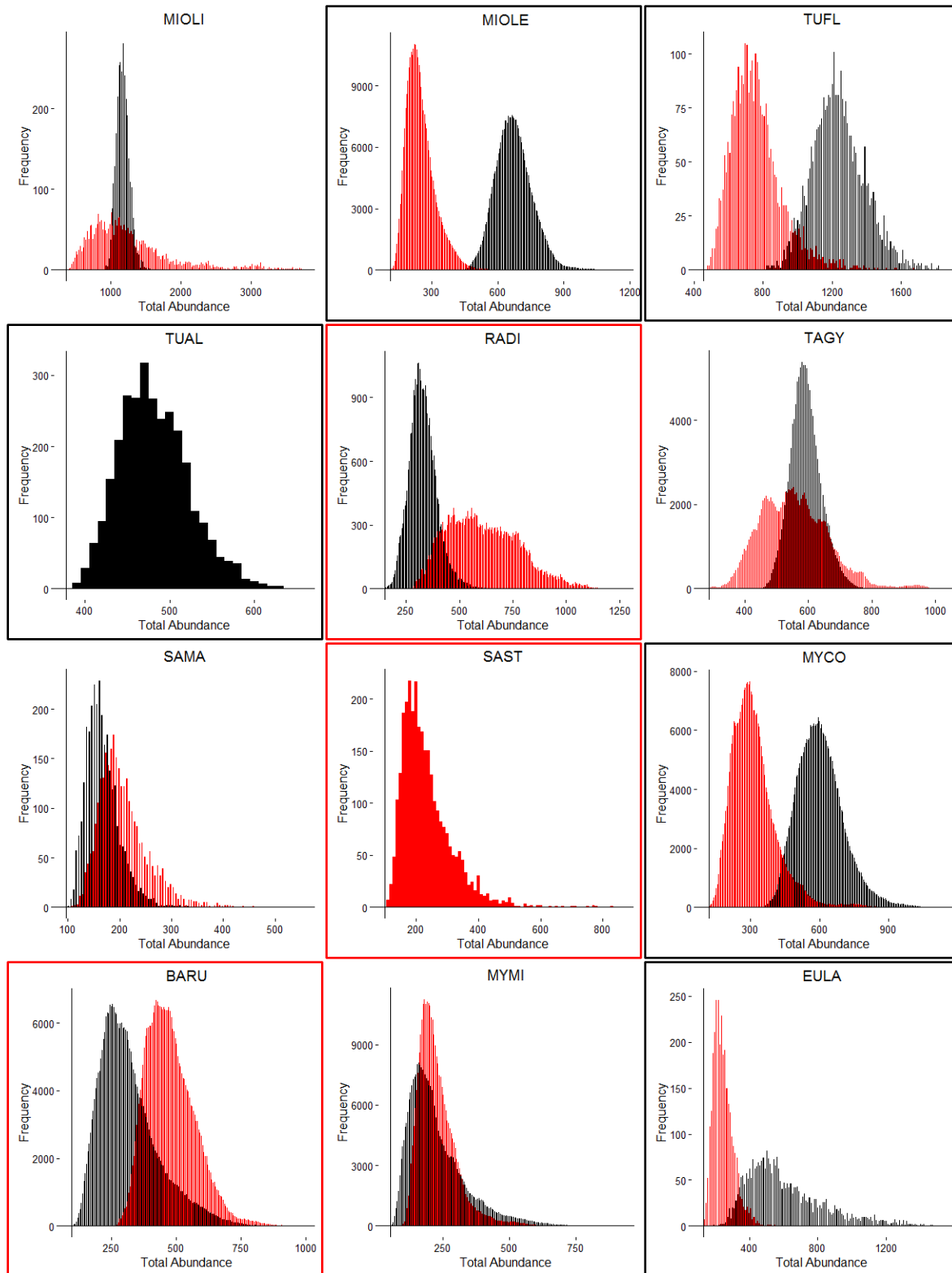
Figure C.3. Posterior distributions for the estimates of total abundance for the twelve focal species in coffee (red bars) and forest (black bars); less overlap means higher probability of differences between habitats. Estimation method and simulations conditions varied among species but not between habitats within a species.

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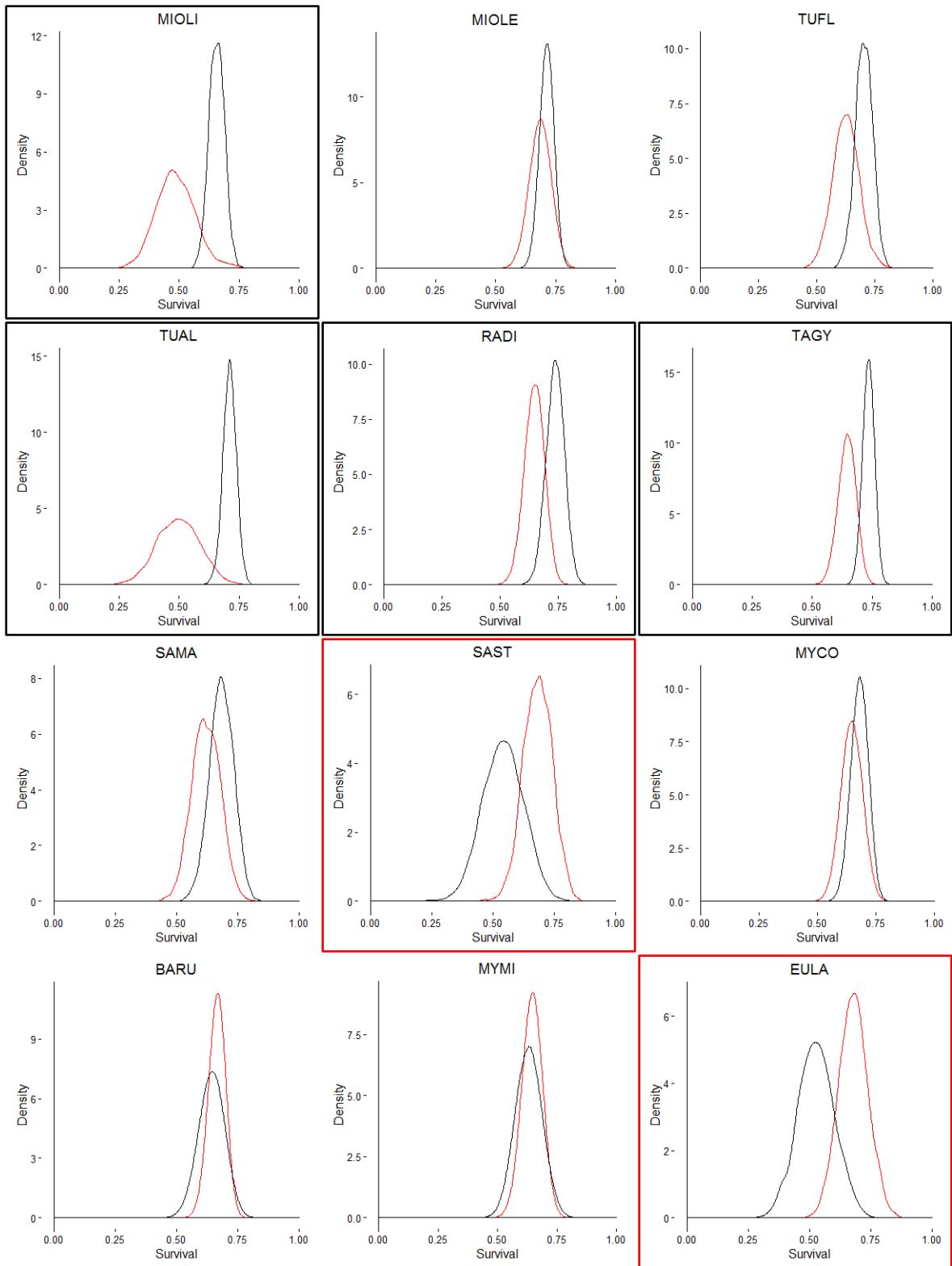
Figure C.4. Posterior distributions for the estimates of apparent survival for the twelve focal species in coffee (red lines) and forest (black lines); less overlap means higher probability of differences between habitats. Estimation method and simulations conditions varied among species but not between habitats within a species.

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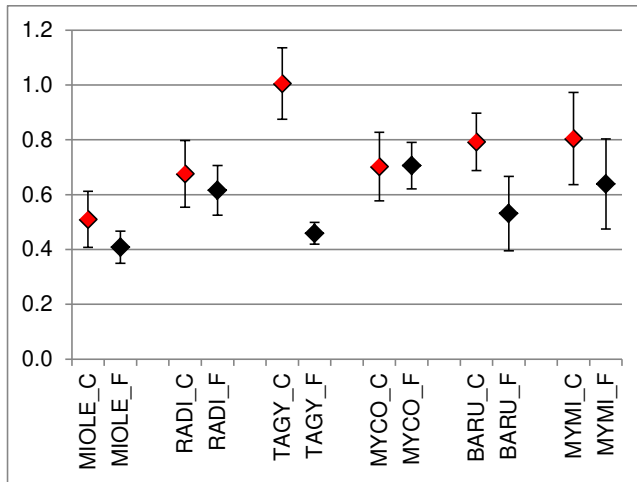
Figure C.5. Mean and standard deviation for the coefficient of variation among estimates of abundance per occasion (calculated from output of the Jolly-Serber model).
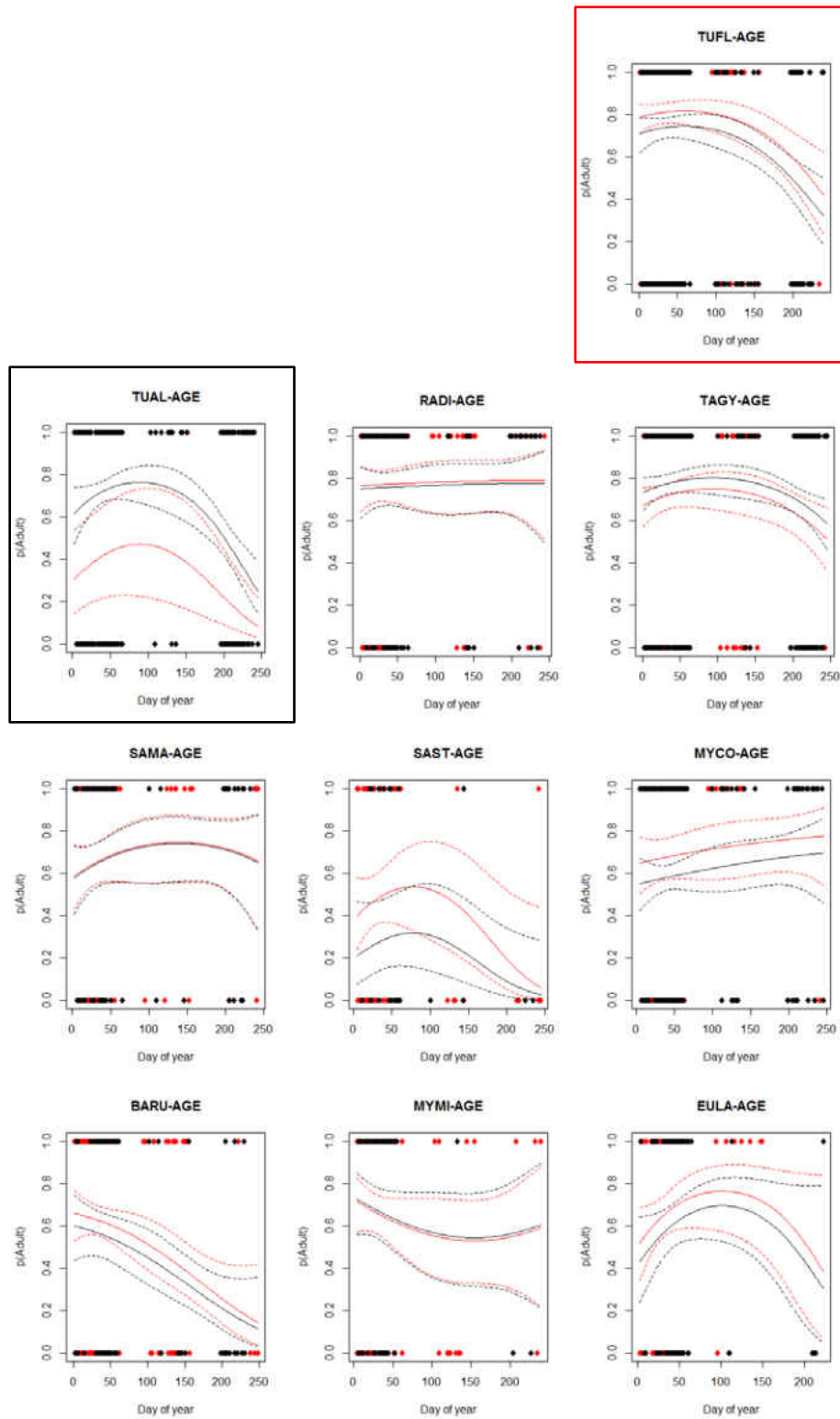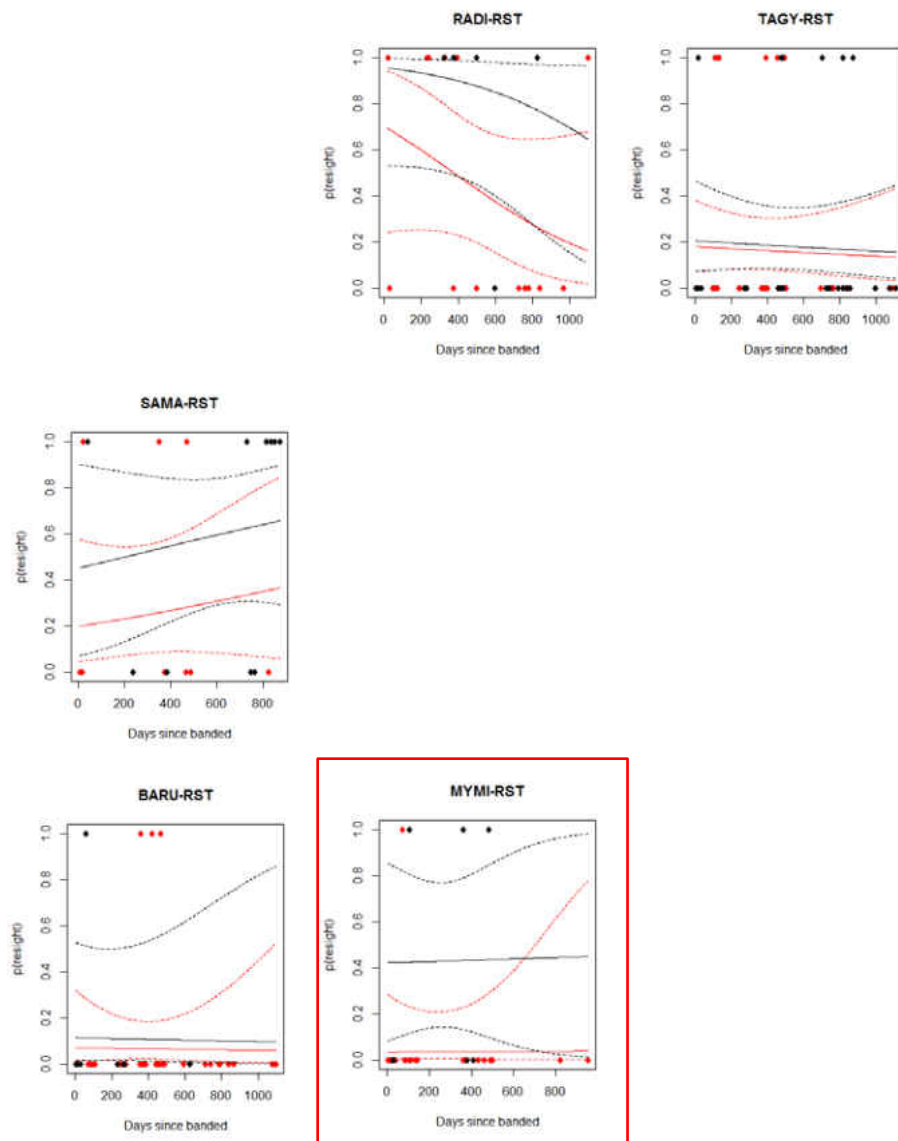
Figure C.6. Effect of day of year (day 0: earliest date of sampling) and habitat (coffee in red and forest in black) in estimates for the probability of capturing an adult individual (over an immature one). Predicted model (solid line) and 95% confidence intervals (dotted lines) for the generalized linear model of DAY + DAY^2 + HABITAT with binomial error family and logit link; points show observed data.
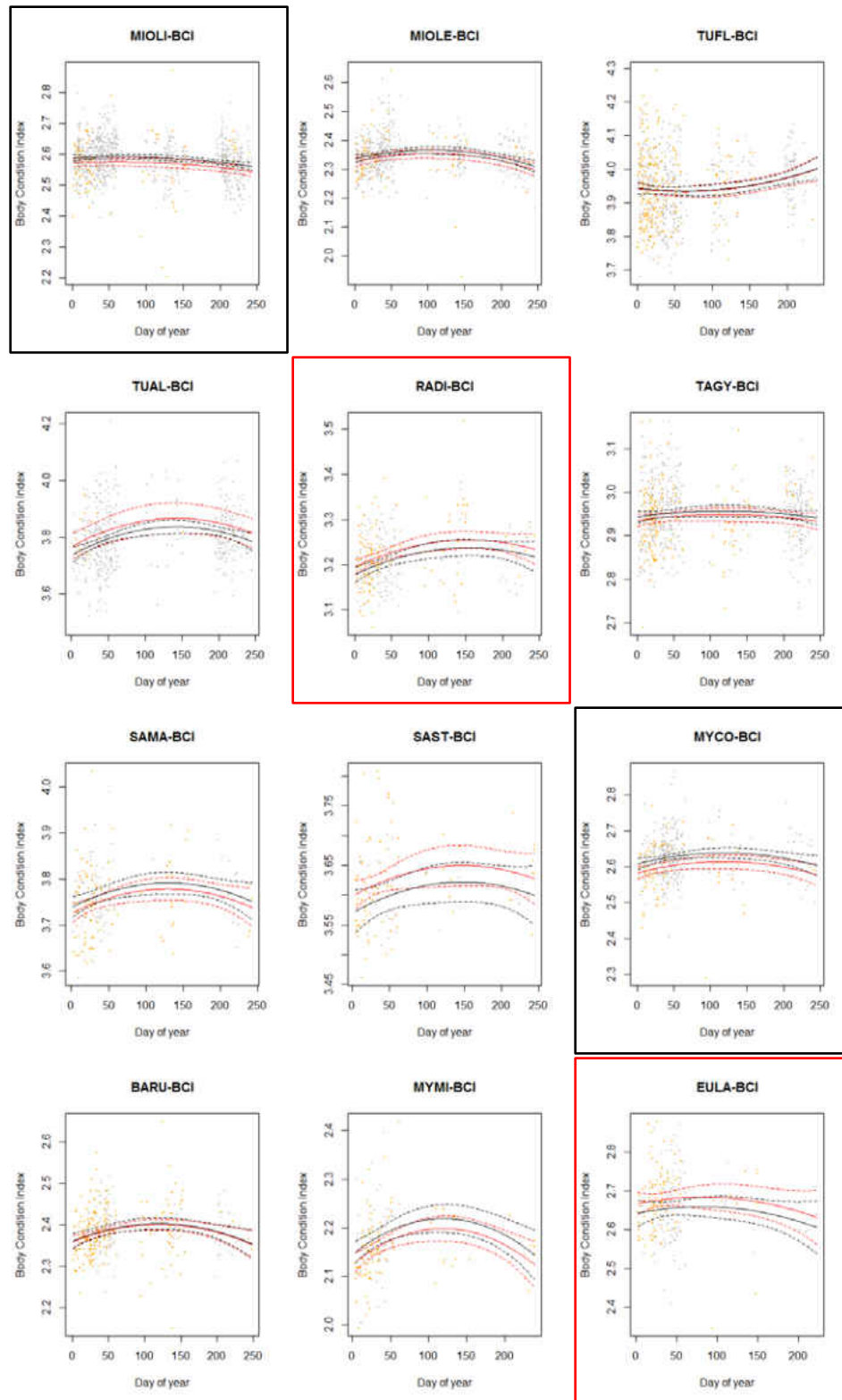
160
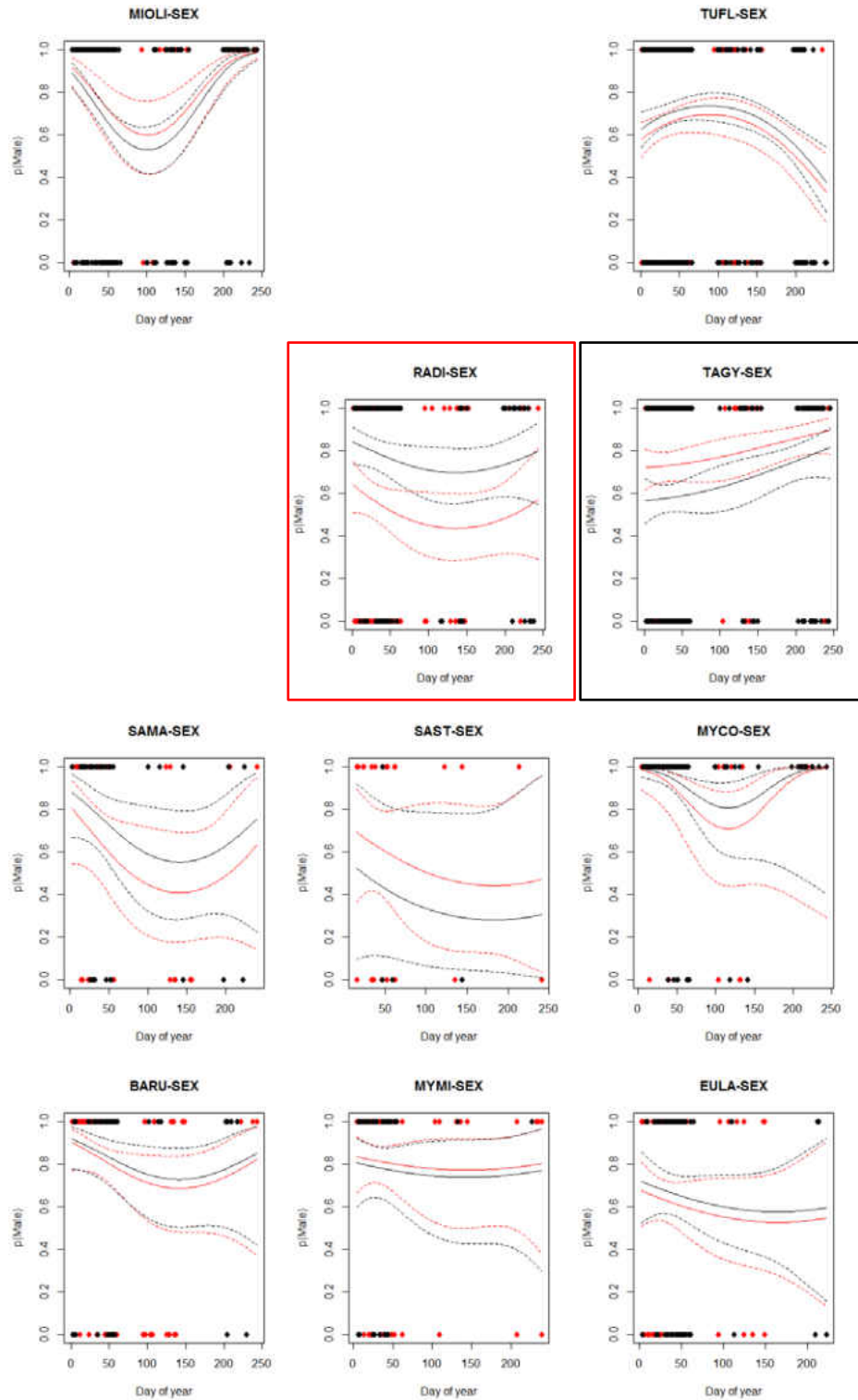
Figure C.7. Effect of day of year (day 0: earliest date of sampling) and habitat (coffee in red and forest in black) in estimates for the probability of capturing a male (over a female). Predicted model (solid line) and 95% confidence intervals (dotted lines) for the generalized linear model of DAY + DAY^2 + HABITAT with binomial error family and logit link; points show observed data.
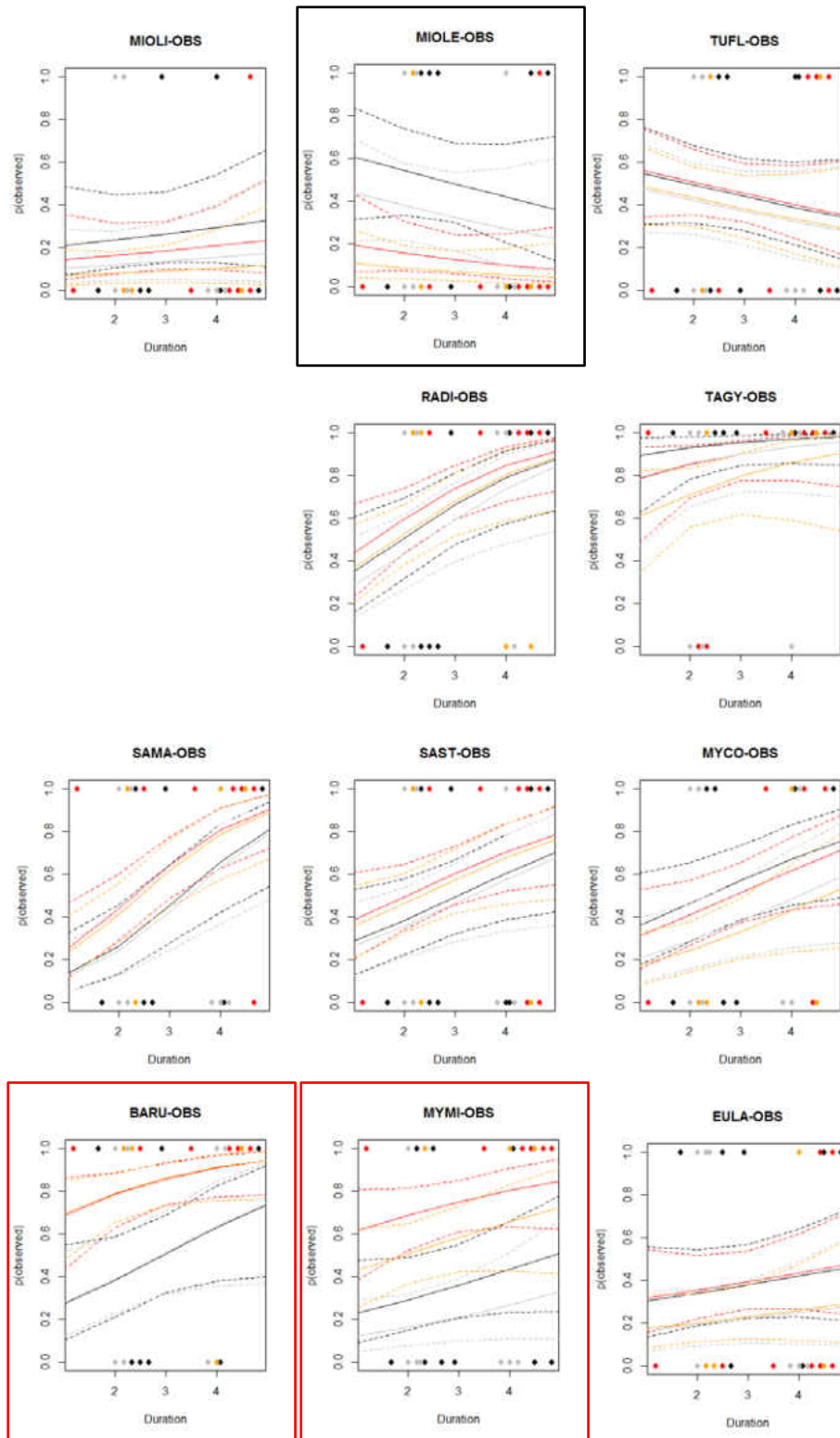
Figure C.8. Effect of sampling duration (in hours), habitat and method (red: coffee with playback, orange: coffee without playback, black: forest with playback, grey: forest without playback) in estimates for the probability of observing a species during visual counts. Predicted model (solid line) and 95% confidence intervals (dotted lines) for the generalized linear model of DURATION + HABITAT + METHOD with binomial error family and logit link; points show observed data.

Figure C.9. Effect of days since and habitat where an individual was color-banded (red: coffee, black: forest) in estimates for the probability of resighting it in a different habitat. Predicted model (solid line) and 95% confidence intervals (dotted lines) for the generalized linear model of DAYS + HABITAT with binomial error family and logit link; points show observed data.
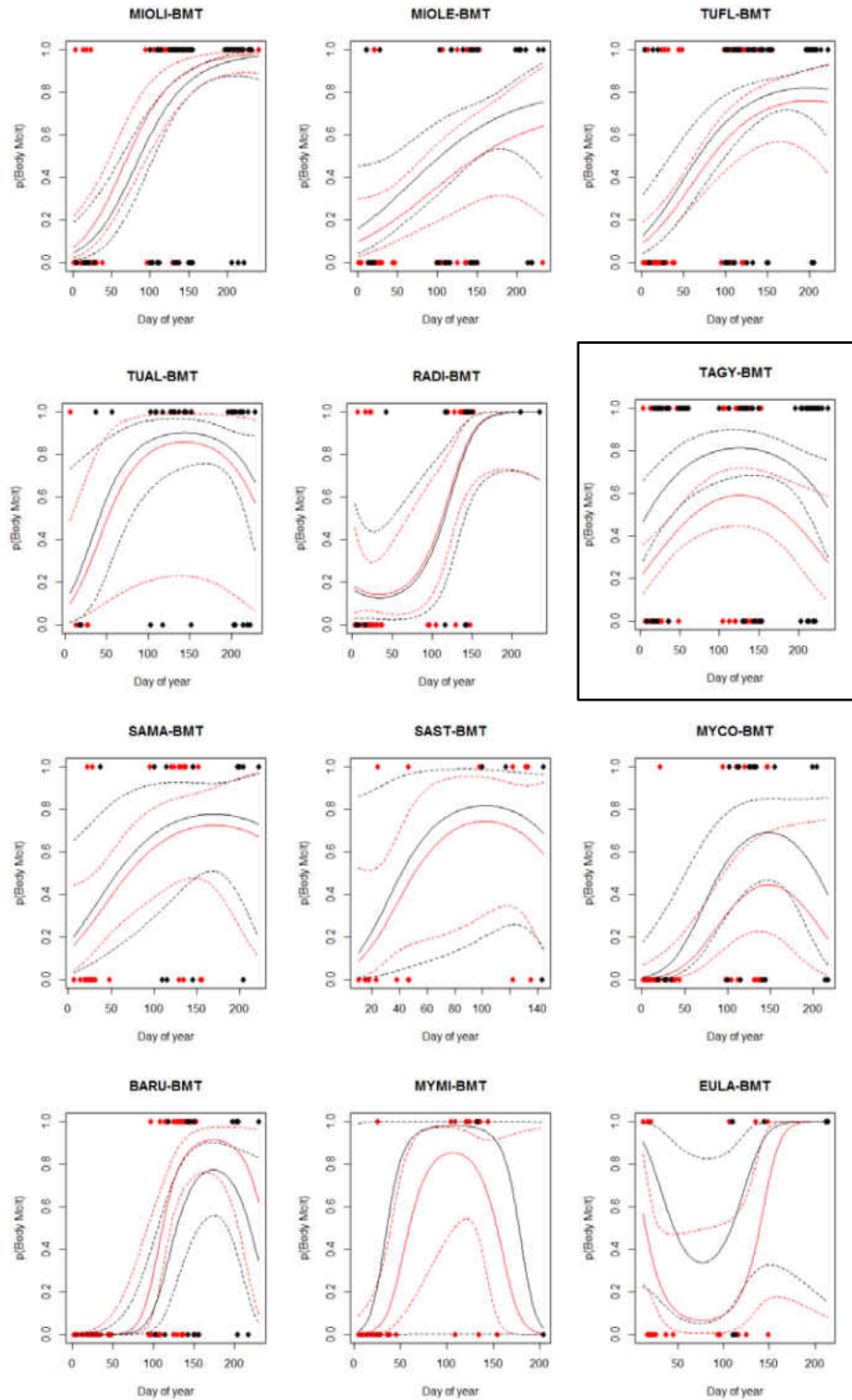
Figure C.10. Effect of day of year (day 0: earliest date of sampling) and habitat (coffee in red and forest in black) on body condition index. Predicted model (solid line) and 95% confidence intervals (dotted lines) for the generalized linear model of DAY + DAY^2 + HABITAT with normal error family and identity link; orange points show observed data for coffee and grey points observed data for forest.
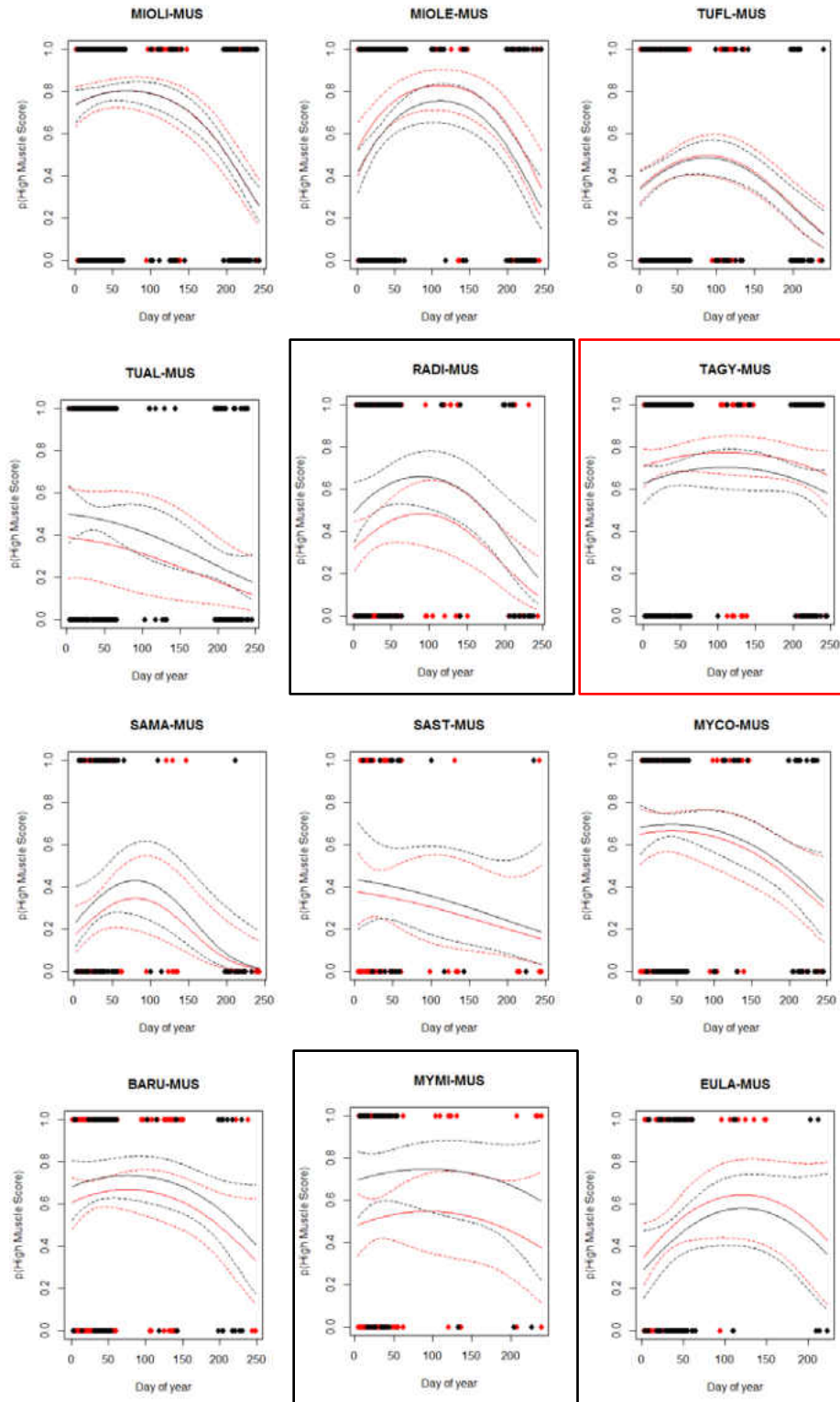
Figure C.11. Effect of day of year (day 0: earliest date of sampling) and habitat (coffee in red and forest in black) in estimates for the probability of capturing an individual with high muscle score (over one with medium). Predicted model (solid line) and 95% confidence intervals (dotted lines) for the generalized linear model of DAY + DAY^2 + HABITAT with binomial error family and logit link; points show observed data.
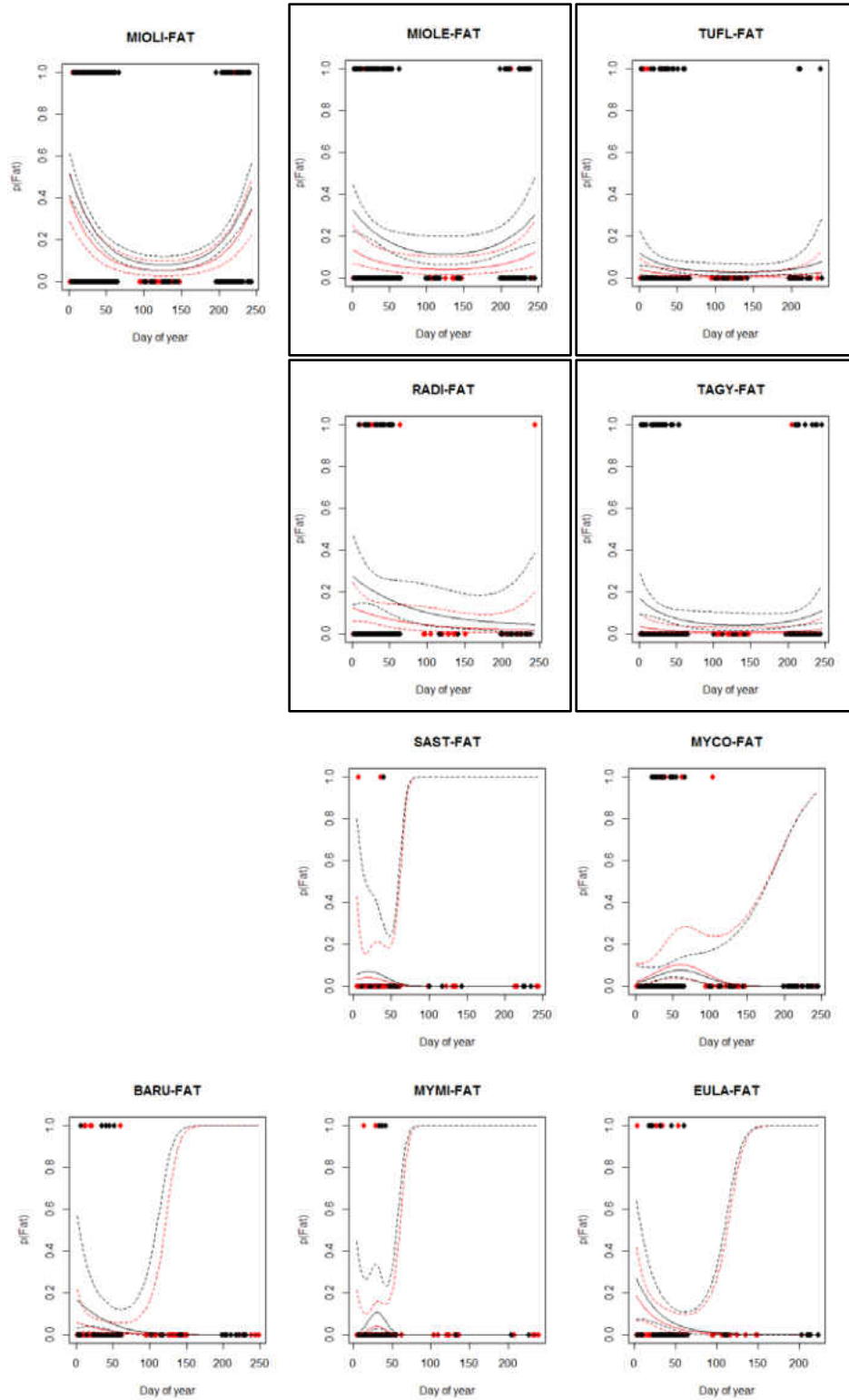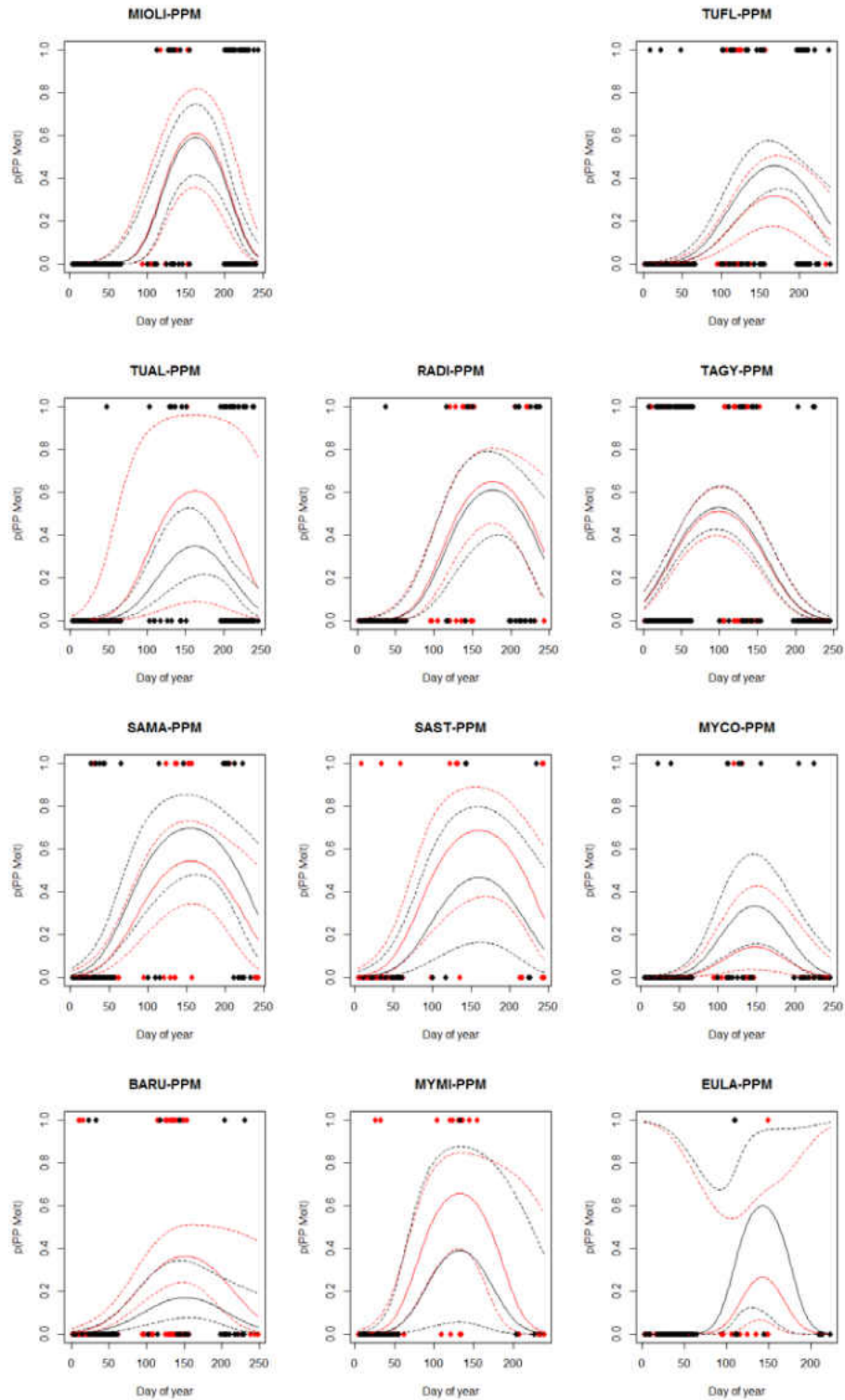
Figure C.12. Effect of day of year (day 0: earliest date of sampling) and habitat (coffee in red and forest in black) in estimates for the probability of capturing an individual with fat storage (over one without). Predicted model (solid line) and 95% confidence intervals (dotted lines) for the generalized linear model of DAY + DAY^2 + HABITAT with binomial error family and logit link; points show observed data.
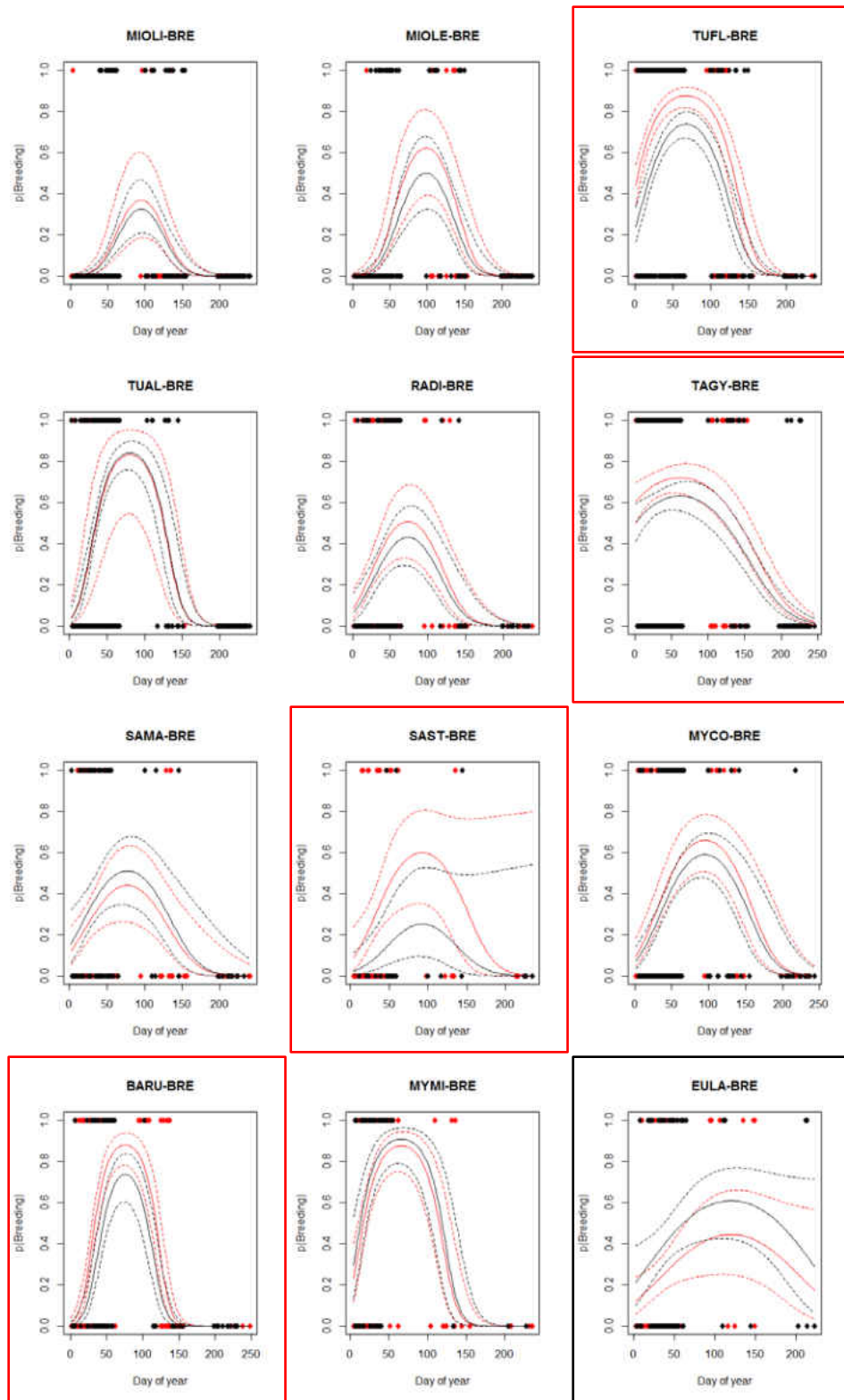
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Figure C.13. Effect of day of year (day 0: earliest date of sampling) and habitat (coffee in red and forest in black) in estimates for the probability of capturing an individual with active body plumage molt (over one without). Predicted model (solid line) and 95% confidence intervals (dotted lines) for the generalized linear model of $DAY + DAY^2 + HABITAT$ with binomial error family and logit link; points show observed data.

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Figure C.14. Effect of day of year (day 0: earliest date of sampling) and habitat (coffee in red and forest in black) in estimates for the probability of capturing an individual with active primary plumage molt (over one without). Predicted model (solid line) and 95% confidence intervals (dotted lines) for the generalized linear model of DAY + DAY^2 + HABITAT with binomial error family and logit link; points show observed data.
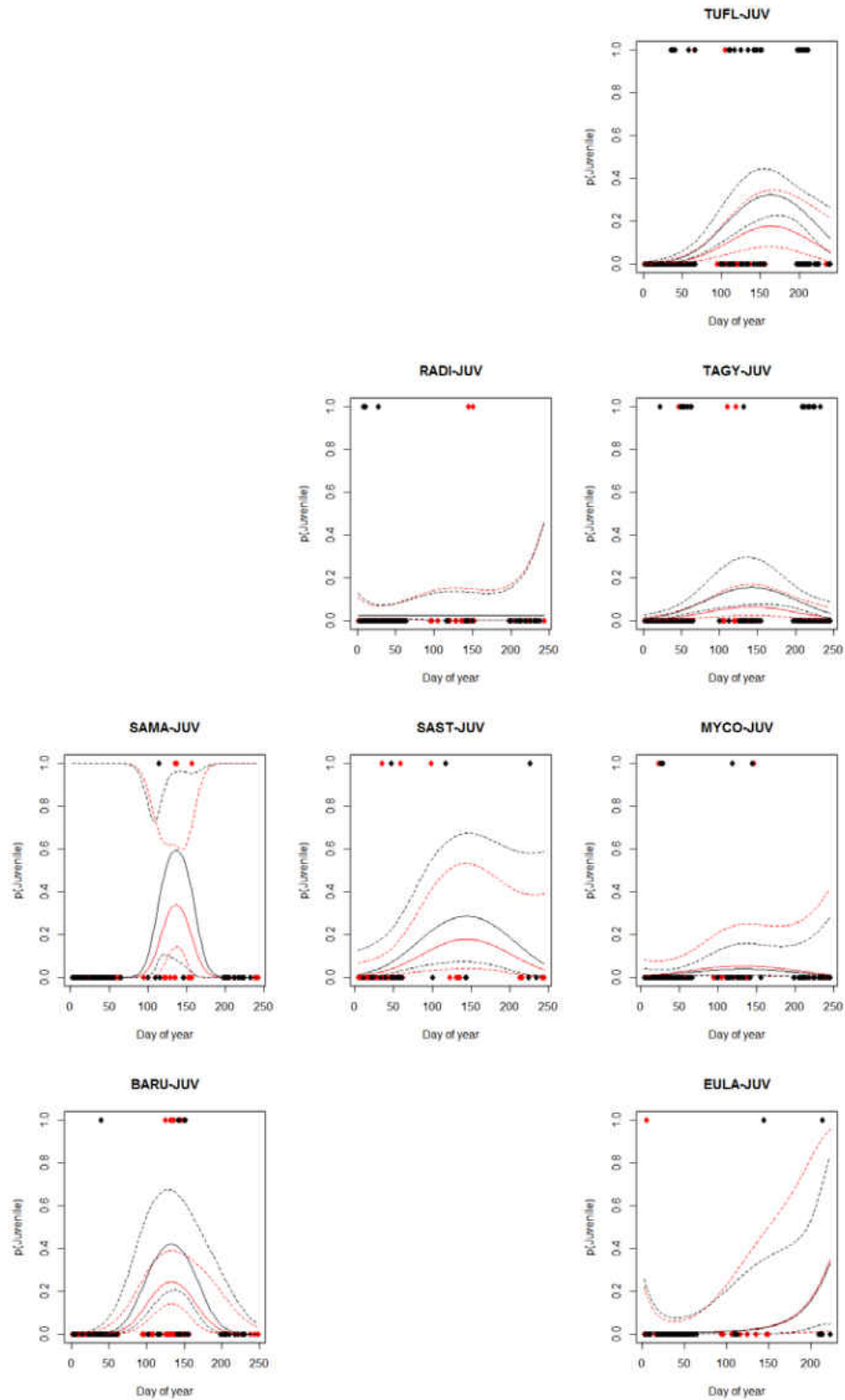
Figure C.15. Effect of day of year (day 0: earliest date of sampling) and habitat (coffee in red and forest in black) in estimates for the probability of capturing an individual in active breeding (over an inactive one). Predicted model (solid line) and 95% confidence intervals (dotted lines) for the generalized linear model of DAY + DAY^2 + HABITAT with binomial error family and logit link; points show observed data.

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Figure C.16. Effect of day of year (day 0: earliest date of sampling) and habitat (coffee in red and forest in black) in estimates for the probability of capturing a juvenile individual (over an adult or immature). Predicted model (solid line) and 95% confidence intervals (dotted lines) for the generalized linear model of DAY + DAY^2 + HABITAT with binomial error family and logit link; points show observed data.

Table C.7. Principal component analysis output for the ordination of habitat effect sizes for body condition index, body molt and breeding activity for the twelve focal species.

Summary	Comp.1	Comp.2	Comp.3
Standard deviation	1.187	1.012	0.754
Proportion of Variance	0.469	0.341	0.189
Cumulative Proportion	0.469	0.811	1.000

Scores	Comp.1	Comp.2	Comp.3
MYCO (1)	0.659	1.142	-0.812
BARU (2)	-2.052	0.881	0.404
EULA (3)	1.693	-1.663	0.693
MIOLE (4)	-0.147	0.574	-0.421
MIOLI (5)	0.018	1.393	1.019
MYMI (6)	2.158	0.268	-0.805
RADI (7)	-0.913	-0.667	0.893
SAMA (8)	0.666	0.759	0.605
SAST (9)	-1.550	-1.612	-1.145
TAGY (10)	0.265	0.063	-0.601
TUAL (11)	0.168	-1.213	0.716
TUFL (12)	-0.965	0.076	-0.546

Loadings	Comp.1	Comp.2	Comp.3
BCI.b3	0.284	0.894	-0.347
BMT.b3	0.637	-0.447	-0.628
BRE.b3	0.716	0.000	0.696

Table C.8. Frequency of individuals from our focal species captured in both habitats during the same sampling occasion.

Species	Number	Percentage of total
MIOLI	16	3%
MIOLE	23	8%
TUFL	22	5%
TUAL	4	2%
RADI	4	2%
TAGY	7	2%
SAMA	2	1%
SAST	1	1%
MYCO	1	0%
BARU	0	0%
MYMI	2	2%
EULA	14	10%