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European hare invasion in southeastern Brazil: identifying drivers of occupancy and abundance and analyzing the invader's impact on the Brazilian cottontail's spatial distribution

Nielson Aparecido Pasqualotto Salvador

Thesis presented to obtain the degree of Doctor in Science. Area: Applied Ecology

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Dedicatory

I dedicate my doctoral thesis to my family, especially to my sister Tatiana and my niece Betina,
who have been bravely fighting against cystic fibrosis since Betina's birth.
Count on me to help you with whatever you need.
You have already won this war,
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CONTENTS

RESUMO

Invasão da lebre europeia no sudeste do Brasil: identificação dos fatores determinantes da ocupação e abundância e análise do efeito do invasor na distribuição espacial do tapeti

A invasão de espécies não nativas é um grande impulsionador da perda de biodiversidade. Na América do Sul, a lebre europeia (*Lepus europaeus*) foi introduzida no final do século XIX na Argentina e Chile e expandiu rapidamente sua distribuição para o norte, chegando ao sudeste do Brasil na última década. Apesar dos danos ambientais significativos causados pela lebre europeia às comunidades por ela invadidas, pouca atenção tem sido dada para descobrir os principais impulsionadores da ocupação e abundância local da lebre europeia nos Neotrópicos, assim como sua influência na probabilidade do tapeti usar habitats neotropicais no sudeste do Brasil. Nesta tese de doutorado, utilizei dois conjuntos de dados, obtidos em paisagens dominadas por agricultura e localizadas no sudeste do Brasil, para investigar: i) os principais impulsionadores da ocupação da lebre europeia, avaliando o suporte para as hipóteses de distúrbio e resistência biótica (Capítulo I); ii) a importância relativa da heterogeneidade espacial (composicional e configuracional) e temporal em comparação com a quantidade de tipos de cobertura do solo como preditores da abundância local da lebre europeia (Capítulo II); e iii) a influência da presença de lebres europeias e da proximidade de residências rurais no habitat do tapeti do sudeste do Brasil (*Sylvilagus minensis*). Os dois conjuntos de dados foram projetados para fornecer: 1) esforço de amostragem semelhante entre áreas dominadas por habitats nativos (dentro de áreas protegidas) e áreas onde terras agrícolas e habitats nativos coexistem (fora de áreas protegidas) e um tamanho amostral relativamente grande (n = 205) em uma área geograficamente mais restrita (> 0,03 Mha; conjunto de dados 1); e 2) uma amostragem mais abrangente de sítios (n = 55) inseridos em paisagens dominadas pela agricultura e localizadas em uma área muito mais ampla (> 3 Mha; conjunto de dados 2). Utilizei modelagem de ocupação para investigar *a priori* minhas hipóteses, levando explicitamente em consideração erros de detecção. As principais descobertas indicaram que: i) a ocupação da lebre europeia é principalmente impulsionada pelas oportunidades de nicho criadas por habitats perturbados pelo homem; a resistência biótica desempenha um papel secundário e provavelmente apenas devido à floresta nativa, ii) a abundância local da lebre europeia foi alta em áreas com alta diversidade de tipos de cobertura de terra, incluindo a cana-de-açúcar, mas não savanas, e suas estimativas de abundância foram baixas e não variavam drasticamente entre os sítios de amostragem, sugerindo que a lebre europeia ainda não atingiu alta densidade local em nossa área de estudo; e iii) o tapeti tem maior probabilidade de usar locais predominantemente cobertos por floresta nativa e afastados de residências rurais, independentemente da presença da lebre europeia, sugerindo que essas duas espécies estão segregando espacialmente devido a suas diferentes preferências de habitats, em vez de a lebre europeia excluir competitivamente o tapeti. Em conjunto, essas descobertas melhoram nossa compreensão do sucesso da invasão da lebre europeia nos Neotrópicos e também fornecem informações valiosas sobre a interação da lebre europeia com o tapeti e o futuro desse processo de invasão na América do Sul.

Palavras-chave: *Lepus europaeus*, Biologia da invasão, Heterogeneidade de paisagem, Distúrbio antrópico, Espécies exóticas, Tapeti

ABSTRACT

European hare invasion in southeastern Brazil: Identifying drivers of occupancy and abundance and analyzing the invader's impact on the Brazilian cottontail's spatial distribution

Non-native species invasion is a major driver of biodiversity loss. In South America, European hare (*Lepus europaeus*) was introduced in the late 19th in central Argentina and Chile and rapidly expanded its distribution northwards, likely reaching southeastern Brazil during the last decade. Despite the significant environmental damage that European hare has caused to recipient communities worldwide, little attention has been given to uncover the main drivers of this non-native species occupancy and local abundance in the Neotropics, and the influence of this non-native hare on the Brazilian cottontail probability of using native Neotropical habitats in southeastern Brazil. In this doctoral thesis, I used two data sets obtained from agriculturally dominated landscapes of southeastern Brazil to investigate i) the main occupancy drivers of the European hare, assessing support for the disturbance and biotic resistance hypotheses (Chapter I); ii) the relative importance of spatial (compositional and configurational) and temporal heterogeneity compared to the amount of land cover types as predictors of the European hare local abundance (Chapter II); and iii) the influence of the presence of European hares and the proximity of farmhouses on the habitat of the Brazilian cottontail from southeastern Brazil (*Sylvilagus minensis*). The two datasets were designed to provide 1) similar sampling effort among areas dominated by native habitats (inside protected areas) and areas where agricultural lands and native habitats coexist (outside protected areas) and relative large sample size (n=205) in a more geographically restricted area (> 0.03 Mha; dataset 1); and 2) a more comprehensive sampling of sites (n=55) embedded in agricultural dominated landscapes located in a much wider area (> 3Mha; dataset 2). I used occupancy modeling to investigate *a priori* my defined hypotheses while explicitly accounting for detection errors. The main findings indicated that i) European hare occupancy is mainly driven by the niche opportunities created by human-disturbed habitats; biotic resistance plays a secondary role and likely only due to native forest, ii) local abundance of European hare was high in areas with high diversity of land cover types, including sugarcane but no savanna and species abundance estimates were low and did not vary dramatically among sites suggesting this non-native species have not yet attained high local density in our study area; and iii) the Brazilian cottontail is more likely to use sites predominantly covered by native forest and away from farmhouses, regardless of the European hare presence, suggesting that these two species are spatially segregating due to different habitat preferences rather than European hare competitively excluding the native cottontail. Collectively, these findings improve our understanding of the success of the European hare invasion in the Neotropics, and also provide valuable insights into the interaction of the European hare with a native cottontail and future of this invasion process in South America.

Keywords: *Lepus europaeus*, Invasive biology, Landscape heterogeneity, Anthropogenic disturbance, Alien species, Tapeti

1. INTRODUCTION

The emergency of highly globalized human societies has profoundly modified Earth's surface, challenging biodiversity conservation worldwide (Ricciardi 2007; Barnosky et al. 2011; Simberloff et al. 2013; Ramankutty et al. 2018). Humanity has gradually inhabited and shaped most of the terrestrial biosphere over the past 12,000 years; however, a global acceleration in human population growth and land use intensification – i.e., highly mechanized and chemically-based agricultural practices – started only recently in the history of our species (Ellis et al. 2021). Over the last centuries, intensive agriculture of highly globalized industrial societies has pervasively replaced the low-intensive subsistence practices of early farmers and hunter-gatherers, triggering the current biodiversity crisis (Ellis et al. 2021). Species extinction rates over the last 500 years have been comparable to or are even higher than the rates of the Big Five mass extinctions that occurred over millions or at least thousands of hundreds of years (Barnosky et al. 2011). Among vertebrates, extinction rates since 1900 AD are 8 to 100 times higher than the pre-human background rate, indicating that vertebrate extinctions that occurred over the last century would have taken 800 hundred years to several millennia to occur under the pre-human rate (Ceballos et al. 2015). Habitat loss (Wilcove et al. 1998) and overexploitation of biological resources (Bellard et al. 2016) have been widely accepted as the primary drivers of biodiversity loss. However, recent evidence has revealed that biological invasions by non-native species are the leading cause of recent plant and animal extinctions (Blackburn et al. 2019).

Biological invasions typically consist of non-native species – i.e., species that were translocated by humans into biogeographic realms where they have never occurred – achieving self-sustaining, abundant populations that spread widely and cause environmental damage to the recipient communities (Blackburn et al. 2011; Simberloff et al. 2013). However, the understanding that human-mediated invasions are a unique and unprecedented form of global change has been doubted (Sagoff 2005; Davis et al. 2011; Valéry et al. 2013). It has been argued that the threats posed by non-native invasive species are often overstated as the detrimental impacts of native invaders – i.e., spreading species that also attain high abundance within their natural range – do not substantially differ from those caused by non-native species (Sagoff 2005; Davis et al. 2011). Although native invaders are becoming increasingly common due to anthropogenic global changes (Nackley et al. 2017), multiple lines of evidence indicate that species origin is crucial in predicting their likelihood of becoming an invader and their environmental damage (Simberloff et al. 2012; Rejmánek and Simberloff 2017; Blackburn et al. 2019). Non-native species are 40 times more likely than natives to become invaders in a new place (Simberloff et al. 2012). Also, non-native species are directly implicated in 33.4% of recent animal extinctions, while native species were responsible for only 2.7% (Blackburn et al. 2019).

Although the biodiversity loss caused by non-native species invasion are undeniably worrisome, there have been claims to consider human-mediated and pre-historic invasions (i.e., before humans) as similar biological events. Specifically, it has been proposed that human-mediated invasions are only another mass invasion event, likely with no larger, lasting ecological damage than many other biological invasions that have already occurred on Earth without human assistance and produced only temporary consequences (Brown and Sax 2004). However, human-assisted invasions markedly differ from pre-historic invasions. Humans have introduced organisms beyond their natural range at unprecedented rate, impacting all continents simultaneously and giving rise to the ongoing massive wave of biological invasions that has threatened not only biodiversity but also human livelihood (Ricciardi 2007; Lambertini et al. 2011; Rejmánek and Simberloff 2017). The rate of mammal genera that humans have exchanged between South and North America over the past century (30,000 genera/million years), for example, is several orders of magnitude higher than the exchange rate that has taken place during the Great American Biotic Interchange (29.6 genera/million years) without human assistance (Webb 1991; Ricciardi 2007). Hence, this widespread and accelerated wave of human-mediated invasion may not implicate in only temporary consequences. Nevertheless, humans are already facing the harmful effects of invaders. Non-native invaders have caused tremendous economic impacts on human health, food security, and economy (Roy et al. 2023). Annual invasion cost amounted to US$140 billion in Europe in 2020 (Haubrock et al. 2021b), $21.08 billion in the USA in 2020 (Fantle-Lepczyk et al. 2022) and is estimated to exceed a global cost of $423 billion this year (Roy et al. 2023). Among the non-native invasive taxa, lagomorphs – i.e., mammal species of the Lagomorpha order – have been considered one of the most harmful and costliest invasive animals (Clout and Russell 2008; Haubrock et al. 2021a).

Lagomorpha is an order of small to medium-sized herbivore mammals that have been introduced by humans in several continents and successfully invaded almost all of them (Flux et al. 1990; Barbar and Lambertucci 2018). The Lagomorpha order currently has only two extant families: Ochotonidae (pikas) and Leporidae (rabbits and hare/jackrabbits, also known as leporids) (Caravaggi 2018; Wilson and Reeder 2023). Rabbits and hares/jackrabbits are leporids with striking morphological differences and constitute distinct phylogenetic lineages (Chapman and Flux 1990). All hares and jackrabbits belong to the genus Lepus and are all considered true hares; they are usually the larger living lagomorphs (2 - 5 Kg), with long hind feet and ears that make them easily distinguished from rabbits (Chapman and Flux 1990; Caravaggi 2018). Rabbits are usually small (0.5 - 2 Kg) and belong to ten non-*Lepus* genera – e.g., *Sylvilagus*, *Romerolagus*, *Oryctolagus*, *Pentalagus*, *Brachylagus*, *Bunolagus*, *Capolagus*, *Nesolagus*, *Poelagus*, and *Pronolagus* (Chapman and Flux 1990; Caravaggi 2018). The New World genus *Sylvilagus* (also known as cottontails) is the most diversified genera of extant rabbits, with 19 species currently recognized (Caravaggi 2018) – a number that may increase as new molecular lineages of South American cottontails have been recently recognized in Brazil (Silva et al. 2019). The Leporidae family originated in Asian, from where these mammals rapidly radiated and naturally colonized all continents, except Antarctica, Oceania, and southern South America (Ge et al. 2013; Barbar and Lambertucci 2018). Leporids became even more cosmopolitan after deliberated human translocations and introductions of rabbits and hares/jackrabbits in islands and mainland regions to serve as food source and game species (Flux et al. 1990; Barbar and Lambertucci 2018). Currently, 12 leporid species have been introduced beyond their natural range: the Eastern cottontail *Sylvilagus floridanus*, the European rabbit *Oryctolagus cuniculus*, and 10 *Lepus* species, including the European hare (Barbar and Lambertucci 2018).

The European hare (*Lepus Europaeus* Pallas, 1778) is the only *Lepus* species that was introduced beyond its native continent and became an invader in most of the species non-native range, threatening native animals and plants species (Caravaggi et al. 2016; Barbar and Lambertucci 2018; Dénes et al. 2018). European hare likely originated in the Asian-steppes of the Middle-East (Tapper and Yalden 2010). Forest cleanings caused by agriculture development in Europe may have favored the geographical expansion of the species in its native range, which currently spans from nearly all mainland Europe through parts of Asia (Chapman and Flux 1990; Thulin 2003). While European hare populations have severely declined over the past six decades in its native range, primarily due to intensification of agricultural practices and loss of landscape heterogeneity (Panek and Kamieniarz 1999; Smith et al. 2005; Pavliska et al. 2018), it has successfully invaded and flourished in several foreign continents (e.g., Oceania, North and South America) following human-assisted introductions (Grigera and Rapoport 1983; Stott 2003; Caravaggi et al. 2015). In South America, European hares were introduced in Argentina and Chile in the late 19th century. The first documented introduction consisted of 36 hares translocated from Germany and released at the Province of Santa Fe, Argentina in 1888 (Grigera and Rapoport 1983). European hares from France and Germany were also freed in Chile and other provinces from central Argentine about ten years later (Grigera and Rapoport 1983). Despite the low number of introduced individuals, this non-native hare became so abundant in central Argentine that was declared an agricultural pest in 1907 (Grigera and Rapoport 1983). European hare rapidly expanded its distribution northwards in the following decades, reaching southeastern

Brazil in the 1990s (Auricchio and Olmos 1999). Globally, European hare populations have hybridized and spatially replaced native lagomorphs in Northern Ireland and Sweden (Thulin 2003; Caravaggi et al. 2016), overlapped diets with native herbivores and livestock animals (Bonino et al. 1997; Puig et al. 2007) and acted as vector of disease in South America in southern South America (Kleiman et al. 2004; Novillo and Ojeda 2008). In addition, European hares have also caused significant damage to agricultural crops, especially citrus, vegetable and watermelon plantations in southern Brazil (de Oliveira et al. 2006; Wutke 2012). Despite the significant environmental damage European hare has caused to recipient communities around the world, the main drivers of this non-native species occupancy and local abundance in the Neotropics, and the influence of this non-native hare on native Neotropical leporids' spatial distribution, remained understudied until recently.

Here, I have crafted my thesis with the objective of addressing the previously identified gaps in scientific knowledge. Specifically, my primary aim was to understand the environmental drivers of European hare occupancy and local abundance in the Neotropics and the influence of this non-native species on the spatial distribution of the Brazilian cottontail (*Sylvilagus minensis*) that occurs in southeastern Brazil. I have organized my thesis in three chapters and the chapter's main objectives were:

- **Chapter I:** Identify the main driver of European hare occupancy in southeastern Brazil, assessing the empirical support to two major and concurrent hypotheses often investigated in invasion biology: i) niche opportunity provided by highly disturbed human-modified habitats (e.g., amount of agricultural lands, proximity to roads, and human settlements) and/or ii) biotic resistance imposed by species-rich Neotropical habitats (e.g., native forests, savannas, and riverine areas).

- **Chapter II:** Address the main question of why are European hare populations thriving in Brazilian agricultural landscapes with presumably low spatial (i.e., compositional or configurational) heterogeneity while landscape homogenization is the ultimate cause of population decline of this species in its native Europe? To address this question, I investigated the influence and relative importance of landscape (compositional, configurational, and temporal) heterogeneity and the proportion of land cover types as predictors of European hare local abundance in agricultural landscapes from southeastern Brazil.

- **Chapter III:** Understanding the influence of European hare presence and proximity to human habitations (mostly farmhouses) on the habitat use of Brazilian cottontail in southeastern Brazil. Uncovering the relative importance of these two drivers of biodiversity loss (i.e., human proximity and biological invasions) allowed us to discuss on the relative importance of competitive exclusion and spatial niche segregation as ecological processes driving Brazilian cottontail habitat use.

The findings of thesis improve our understanding of the main drivers of European hare invasion success in the Neotropics, and also shed light on the presumed detrimental impacts that European hare populations are imposing to native Neotropical animal species, particularly the native Brazilian cottontail. Identifying the ecological drivers of the European hare invasion is paramount to understand the current invasion stage of this non-native species in southeastern Brazil and also inform Brazilian Environmental Agencies and support potential management decisions.

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2. CHAPTER I: NICHE OPPORTUNITY CREATED BY LAND COVER CHANGE IS DRIVING THE EUROPEAN HARE INVASION IN THE NEOTROPICS

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Abstract

The European hare (*Lepus europaeus*) was introduced in the late 19th century in Argentina and has since rapidly expanded northwards, currently occupying the Brazilian south and southeast. Although European hare is known to be a farmland specialist in its native Europe, what habitat types or landscape features are facilitating its expansion in the Neotropics are not yet clear. Here we assessed support to the disturbance and biotic resistance hypotheses as general drivers of this invasion. We sampled with camera-traps and track surveys 205 sites in three landscapes in southeastern Brazil. We used occupancy models that corrected for both false positive and false negative errors. The disturbance hypothesis was the top-ranked ($w = 0.66$) with the amount of field, sugarcane, and managed forests all affecting strongly and positively hare occupancy. Support to the biotic resistance hypothesis was lower ($\Delta AICc = 2.14$; $w = 0.23$) and partial, since only native forests showed a negative effect on hare occupancy. Our findings indicate that in the expansion front occupancy of this invader is mainly dictated by niche opportunities created by native habitat transformation into agricultural lands. The biotic resistance imposed by remaining native habitats seems to play a secondary role and only due to native forests. We conclude that hare geographical expansion should increase given the prominent role of Brazil as a commodity producer and exporter. Nevertheless, fomenting forested protected areas and improving adherence of rural owners to the Brazilian Forest Act, which protects forests in private rural properties, might help lessen this spread.

Keywords: *Lepus europaeus*, misidentification model, invasion biology, occupancy, agricultural landscape, human-disturbed habitats.

2.1. Introduction

Biological invasions are among the top impacts to biodiversity worldwide (Clavero and García-Berthou 2005; Lambertini et al. 2011; Simberloff et al. 2013). In the invasion process, non-native species pass through a series of stages (i.e., transport, introduction, establishment, and spread) and must overcome several barriers (geography, captivity or cultivation, survival, reproduction, dispersal, and environment) to become an invader (Blackburn et al. 2011). Throughout these stages, human disturbances, such as fire, grazing, pollution, logging, seem to play a key role, facilitating the invasion of non-native species of plants (Jauni et al. 2015), marine invertebrates (Crooks et al. 2010), and small mammals (Loveridge et al. 2016). In fact, disturbances that rapidly disrupt the historical pattern of resources flux of a given locality, such as those caused by human activities, commonly promote invasions [the disturbance hypothesis, Hobbs and Huenneke (1992) and Sher and Hyatt 1999]. Native species might not have had enough time to evolve key adaptations for allowing them efficiently reduce resource availability in these novel environments, creating niche opportunities for invaders, especially for those with a long history of association with human-disturbed habitats in its native range (Shea and Chesson 2002). On the other hand, species-rich communities are expected to be more resistant to non-native species establishment and spread given the scarcity of vacant niche [the biotic resistance hypothesis, Elton (1958) and Levine and D'Antonio (1999)]. These species-rich communities may impose strong antagonistic interactions (e.g., interspecific competition and predation) to non-native species, making it difficult for them to become an invader (Thompson et al. 2019).

The European hare (*Lepus europaeus* Pallas, 1778; Mammalia, Lagomorpha) has been considered one of the most successful invader species among the leporids (Barbar and Lambertucci 2018), especially because of its high reproductive capacity (Tapper and Yalden 2010) and dispersal rate (Grigera and Rapoport 1983; de Faria et al. 2015). Native to mainland Europe (Chapman and Flux 1990), this leporid was introduced in many countries around the world, being currently found in all continents, except Antarctica and continental Africa (Barbar and Lambertucci 2018). In Sweden and Northern Ireland, its introduction has led to competition and hybridization with the mountain hare (*Lepus timidus*, Linnaeus 1758) and the endemic Irish hare (*Lepus timidus hibernicus*, Bell 1837), respectively, being considered the leading cause of the distribution contraction of the former (Thulin 2003) and of the long-term population decline of the later (Reid 2011; Caravaggi et al. 2015).

In South America, the European hare has high overlapping diets with native herbivores, such as mara (*Dolichotis patagonum*), mountain vizcacha (Bonino et al. 1997; Puig et al. 2007), and also with livestock (goats and horses; Puig et al. 2007), suggesting the European hare may compete for resources with native and domesticated species. This leporid also acts as a vector of diseases like fasciolosis since it might have a fundamental role in the life cycle of the parasite *Fasciola hepatica* in the Argentine Patagonia (Kleiman et al. 2004). In southern and southeastern Brazil, the European hare may impose detrimental effects on the regeneration of the Paraná pine (*Araucaria angustifolia*), a critically endangered tree species, by dramatically reducing seedling abundance through predation (Dénes et al. 2018).

In its native range, the European hare is an open-country species that has long benefited from the increase of farming in detriment of native forests, which started 9000 years ago in the Middle East, the geographical region that has been considered the natural range of this species at the end of the last glaciation period (Tapper and Yalden 2010). Currently, the European hare is a farmland specialist in Europe and occurs preferably and in higher density in human-modified landscapes composed by a mix of pastures, small fragments of native forest and different types of small field crops that may provide food all year round (Tapper and Barnes 1986; Lewandowski and Nowakowski 1993; Panek and Kamieniarz 1999; Petrovan et al. 2013; Pavliska et al. 2018). The European hare seems to often use farm tracks and unpaved footways since this species is more abundant when the density of this type of pathways is high (Roedenbeck and Voser 2008). Although the European hare occurrence is often negatively associated with native forests (Panek and Kamieniarz 1999), the species selects the edge of small woodland fragments as resting sites during its inactivity periods (Petrovan et al. 2013). In general, this leporid seems to be more common in arable (agricultural crops) than non-arable lands (pasture, grasslands, and woodlands; Tapper and Parsons 1984; Vaughan et al. 2003).

Given its preference for farmlands, some authors suggest that the conversion of native forests into croplands and pasture might have facilitated the European hare invasion in the Neotropics (Bonino et al. 2010; Costa and Fernandes 2010; da Rosa et al. 2017). In fact, since its introduction to Argentina and Chile during the late 19th century (Grigera and Rapoport 1983), the European hare has rapidly expanded its geographical distribution northwards, reaching the Brazilian south in the 1960s (de Faria et al. 2015) and southeast in the 1990s (Auricchio and Olmos 1999). Nowadays, this non-native species is the second most spread invasive mammal in Brazil (da Rosa et al. 2017), occurring in the Cerrado and Atlantic Forest transition zones in the Brazilian southeast, the current northern limit of its expansion front (de Faria et al. 2015) which, nevertheless, is still increasing (Costa and Fernandes 2010; de Faria et al. 2015).

The intense land cover change that has occurred in the Brazilian southeast (Kronka et al. 1993; Victor et al. 2005) may be the main cause of the ongoing geographical expansion of the European hare in Brazil. In the state of São Paulo, for example, native forest cover, predominantly composed by semi-deciduous forests (Atlantic Forest domain) but also including sclerophyllous woodland ("cerradão") of the Cerrado domain, was reduced from its original 81.8% to only 8.3% already in the early 1970s (Victor et al. 2005). This deforestation was mainly driven by the quick expansion of coffee plantations, started in the second half of the 19th century (Victor et al. 2005). On the other hand, a dramatic reduction of the Cerrado occurred much later, especially after the 1970s, following advances in agriculture technology that allowed crops to grow in the nutrient-poor Cerrado soils (Durigan and Ratter 2006). Typical Cerrado formations ("cerrado sensu stricto") lost 73% of the remaining coverage between the decades of 1970 and 1990, while more grassy formations ("campo cerrado", "campo sujo", and "campo limpo") lost between 96-99% of their cover in the same period (Kronka et al. 1993).

In fact, in human-modified landscapes of the Neotropics, the European hare seems to be found mostly in man-made habitats like pastures, managed forests and agricultural crops (Auricchio and Olmos 1999; Bonino et al. 2010). On the other hand, this non-native species has also been found in native habitats like grasslands and semideciduous forests, including well preserved protected areas (de Faria et al. 2015). What actually drives this non-native species occurrence in the Neotropics is, therefore, still unclear. Moreover, although the habitat use pattern of the European hare has been, albeit little, investigated in Patagonia, the results thus far seem to be mixed since one study supported human disturbances as a facilitator of this non-native species occurrence (Gantchoff and Belant 2015), while another suggests the European hare use similarly native vegetation and pine plantations (Lantschner et al. 2013).

Here, we addressed this information gap investigating the association of native and human-disturbed habitats with the European hare occurrence, near the northward expansion front of this Neotropical invader, in southeastern Brazil. We used camera-traps and track surveys to assess the species occurrence in native and human-disturbed habitats, sampling both inside and outside nature reserves. Since our sampling methods could fail to detect the species (camera traps) or might be prone to misidentification (track surveys), we undertook this investigation using occupancy models that account for both false negative and positive errors. Specifically, we evaluated support for two main hypotheses. In the first, based on the disturbance hypothesis (Hobbs and Huenneke 1992; Sher and Hyatt 1999), niche opportunities provided by human-disturbed habitats or features (sugarcane plantations, managed forests, fields, native forest edges and proximity to roads and edifications) are driving the European hare occupancy in the Neotropics. In the second, derived from the biotic resistance hypothesis (Elton 1958; Levine and D'Antonio 1999), the main driver is the biotic resistance *per se*, imposed by less disturbed and species-rich habitats or feature (native forest, savanna, and density of riverine areas). So, we interpret positive relationships between occupancy and human-disturbed habitats or features as indicative of support to the first hypothesis. Conversely, negative relationships between occupancy and native habitats indicate support to the second hypothesis. By assessing the relative support to these two concurrent hypotheses, we can have a better understanding of the key landscape features driving this invader and, consequently, better guide strategies for its control/mitigation and further spread.

2.2. Methods

2.2.1. Study areas

The study was carried out in three landscapes located in the northeast of São Paulo state, southeastern Brazil. This region is a transitional zone between the Cerrado (Brazilian savanna) and the Atlantic Forest domain. Each landscape is composed of at least one nature reserve – either state-owned protected areas (Protected Area, PA) or areas with native vegetation in private properties protected by the Brazilian Forest Act (Brancalion et al. 2016) such as Legal Reserve (LR) or Area of Permanent Protection (APP) – and a 5-km buffer surrounding its boundaries (Fig. 1). While LR is a land portion (in our study areas, from 20% to 35%) of a farm that must be set-aside for ensuring sustainable use of natural resources and biodiversity conservation (Brancalion et al. 2016), the APP, in turn, is mostly established as a strip alongside streams and rivers (but also on hilltops, water springs, steep slopes, etc.) and was conceived mainly to protect water resources and soil stability but also biodiversity (Brancalion et al. 2016). The first landscape (A) comprises two PAs: a Strict Nature Reserve [category Ia of IUCN category system (IUCN 2019)] – Jataí Ecological Station, with 9,010 ha; hereafter, JES – and a Habitat/Species Management Area [category IV of IUCN category system (IUCN 2019)] – Luiz Antônio Experimental Station, with 2,008 ha; hereafter LAES. The second landscape (B) is composed of APPs and LRs of a private farm ("Cara Preta" Forest, with 4,546 ha of native vegetation; hereafter, CPF). Lastly, the third landscape (C) is composed of a PA that also corresponds to a Habitat/Species Management Area – Cajuru State Forest, with 2,081 ha; hereafter CSF – and APPs and LRs of another private farm ("Dois Córregos" Forest, with 2,017 ha of native vegetation; hereafter DCF). Overall, all landscapes have a considerable percentage of native vegetation, mostly inside the PAs, but agricultural lands predominate in their 5-km buffers. However, the composition and arrangement of the main land cover classes vary among the three landscapes. In landscape A, sugarcane monocultures predominate, followed by native forests, mainly represented by a large block (~ 9,000 ha of the JES) that is essentially composed by the sclerophyllous woodland ("cerradão") of the Cerrado domain (Table 1). On the other hand, since CPF and DCF are private properties owned by a pulp and paper company (the International Paper Company), inside the landscapes B and C there are much more managed forests of *Eucalyptus* spp. plantations (Table 1). The native vegetations inside the landscapes B and C are more fragmented. Moreover, although native forest is the predominant native habitat in all three landscapes, notably in landscape A, savanna (mostly composed by flooded wetlands and "cerrado sensu stricto") and native forests cover less contrasting percentages in the other two landscapes (Table 1). According to the Köppen-Geiger climate classification, all landscapes have a climate defined as equatorial savanna with dry winter (Aw) since the precipitation of the driest month in these areas is < 60 mm (Kottek et al. 2006).

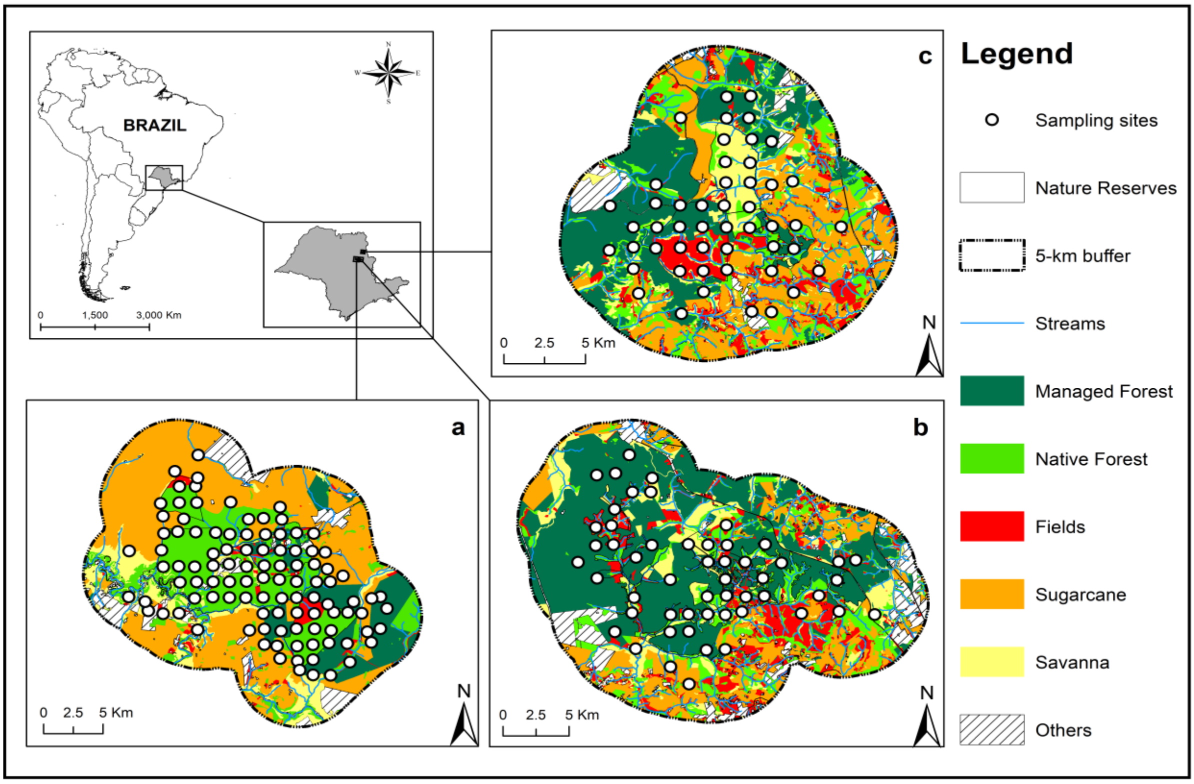

Fig. 1. Location of our three landscapes in the northeast of São Paulo state, southeastern Brazil and their main land cover classes. Camera trapping and track surveys were conducted inside the nature reserves of the landscape A (Jataí Ecological Station and Luiz Antônio Experimental Station; **a**), landscape B ("Cara Preta" Forest; **b**), landscape C (Cajuru State Forest and "Dois Córregos" Forest; **c**), and in their respective 5-km buffer.

Table 1. Percentage of the predominant land cover classes inside the three study landscapes located in the northeast of São Paulo state, southeastern Brazil.

Land cover class	**Landscape A**			**Landscape B**			**Landscape C**		
	Nature reserve	5-km buffer	**Total**	Nature reserve	5-km buffer	**Total**	Nature reserve	5-km buffer	**Total**
NatF	76.4	13.2	27.0	53.9	12.9	16.5	22.9	18.9	19.5
Sav	4.7	10.2	9.0	25.3	9.7	11.1	37.5	8.0	12.0
ManF	9.6	13.5	12.6	2.9	42.7	39.2	16.0	29.0	27.2
Sug	0.1	51.8	40.6	0.0	15.4	14.0	0.0	27.0	23.3
Fiel	8.4	1.5	3.0	17.8	10.4	11.1	23.4	10.2	12.0

NatF = Native Forest; Sav = Savanna; ManF = Managed Forest; Sug = Sugarcane; Fiel = Field.

2.2.2. Study design and data collection

The European hare occurrence was recorded with passive infrared camera-traps (Reconyx, model HC 500; Holmen, Wisconsin) and track surveys conducted only during the dry season (April-September) of 2013 (landscape A) and 2014 (landscapes B and C). We restricted the sampling to the dry seasons to have better access conditions to the sampling sites and also to reduce the interference of weather (e.g., humidity, heat, etc.) on camera-traps performance. Furthermore, by sampling in just one season, we minimized violations to the closure assumption of the single-season occupancy models framework [i.e., no extinction or colonization of the focal species at the sampling sites, during the sampling season (MacKenzie et al. 2002, 2006)].

Sampling sites consisted of a single camera-trap and a 200-meter transect. They were defined by overlaying a regular grid of square cells (200 ha or 1,414 m x 1,414 m wide each) over each of the three landscapes, considering the center of each square as a potential site for sampling. Since the 5-km buffers have a larger area than their respective reserves, all potential sites located inside these reserves were systematically sampled, whereas a corresponding number was randomly selected at the 5-km buffers. In this way, 102 sites were sampled at landscape A (52 inside the PAs and 50 inside the 5-km buffer), 53 at landscape B (25 inside the FCP and 28 inside the 5-km buffer) and 50 at landscape C (24 inside the reserves and 26 inside the 5-km buffer), totaling 205 sites (Fig. 1). Given logistical constraints and to avoid any camera-trap security issue, all selected sites situated further inside pasture or sugarcane plantations were relocated to the nearest contact between these land cover types and any arboreal structure, often a native forest. When this situation happened, camera-traps were positioned directed to the original land cover type that was randomly chosen. Thus, the average distance between two adjacent camera-traps was 1,265.70 m (*SD* = 275.83) for landscape A, 1,547.26 m (*SD* = 361.10) for landscape B and 1,460.22 m (*SD* = 335.79) for landscape C.

Camera-traps were programmed to operate uninterruptedly (24h/day) for 30 days. They were installed as close as possible to the square center of each selected site, fixing them on a tree trunk approximately 40-60 cm above the ground. Every month, about 18 camera-traps were installed in different sampling sites inside and outside (5-km buffer) the reserves. After 30 days, the camera-traps were removed, batteries and memory cards exchanged and then reinstalled into another 18 sites. This procedure was repeated over the two six-month periods (April-September of 2013 and 2014) until all 205 sites were sampled. Due to operating problems, some camera-traps worked more or less than 30 days, but the average was 31.01 camera days (*SD* = 2.31 camera days), totaling 6,357.37 camera days. In each sampling site, we also searched for European hare tracks and footprints on a 200-meter transect, sampling each transect in two different moments: one during the setup of the camera-traps (first track survey) and another 30 days later when the cameras were removed (second track survey). Track surveys were conducted on the nearest dirt road/farm track from the camera-trap locations, totaling a sampling effort of 82 km for this method. All tracks found were locally identified or photographed for further identification with the aid of track guides (Borges and Tomás 2008; Becker and Dalponte 2013; de Angelo et al. 2015).

2.2.3. Land cover map and covariates

Visual interpretation of high-resolution (0.42 m) aerial orthorectified images was conducted for mapping thirteen land cover classes in our three landscapes. The mapped classes were: water bodies, flooded wetlands, native forests, scrub forms of Cerrado (mostly "cerrado sensu stricto"), regenerating areas, mixed abandoned grasslands, sugarcane plantations, citrus orchards, eucalypt plantations, pines plantations, pastures, human buildings, and other (mostly annual crops that covered a very small area of our study landscapes). The orthophoto mosaics, dating from 2010, were gently provided by the Cartographic and Geographic Institute of São Paulo state, Brazil. The visual interpretation was performed using ArcGIS10.2 (ESRI 2019) and QuantumGIS 2.2 (QGIS Development Team 2019), generating maps at a scale of 1:20,000. Taken together, the three landscapes resulted in a mapped area of 132,885.54 ha. For assessing the mapping accuracy, we performed a kappa concordance analysis between our classified map and 200 points randomly selected from the three landscapes. These classification of the points were based on Google Earth high-resolution images (reference map). The concordance analysis showed that our map is highly accurate ($\kappa = 0.897$, $SD = 0.031$, $p = 0.001$), since its agreement with Google Earth images can be considered almost perfect (Cohen 1960). Kappa concordance analysis was performed in R environment 3.5.1 (R Core Team 2018), using the package 'epiDisplay' (Chongsuvivatwong 2018).

After mapping, seven composition-based landscape metrics were created. They were quantified in five concentric and circular spatial scales (circular polygons), with different sizes (12.5 ha, 25 ha, 50 ha, 100 ha, and 200 ha), created around each sampling site. The seven metrics are named as follows: 1) "Savanna"; 2) "Field"; 3) "Sugarcane"; 4) "Managed Forest"; 5) "Native Forest"; 6) "Hydrographic density" and 7) "Edge density". Besides these seven compositional-based landscape metrics, two distance-based landscape metrics were also quantified: 8) "Dirt Road distance" and 9) "Edification distance". Together, the seven compositional-based, the two distance-based landscape metrics and a categorical variable differentiating our three landscapes ("Study Area") were used as our native and human-disturbed covariates (see Table 2 for descriptions of these metrics and expected relationships with the estimated parameters).

Following a multi-scale approach, we empirically estimated the scale of effect – the spatial scale at which the predictors have the strongest effect on a given biological response (Martin and Fahrig 2012; Miguet et al. 2016) – of the seven composition-based landscape metrics on the European hare occurrence (for analysis details, see Appendix A). The selected scales were as follows: 25 ha for Savanna, Field, Sugarcane, Hydrographic density and Edge density, and 12.5 ha for Managed Forest and Native forest (Appendix A, Table S1). The scale of effect analysis was performed in R environment 3.5.1 (R Core Team 2018), using the packages 'rms' (Harrell Jr 2019) for logistic regressions and 'spatialEco' (Evans 2018) for randomly sampling with a minimum distance constraint. All landscape metrics were quantified in R environment 3.5.1 (R Core Team 2018), except for "Edge density" that was quantified in FRAGSTATS (McGarigal et al. 2012).

Table 2. Covariate (or effect) name, code, type, description and their expected a priori relationship with European hare occupancy probability (ψ), false positive detection probability (p_{10}), true positive detection probabilities estimated as different (p_{11}, r_{11}) and as the same ($p_{11} = r_{11}$) in the northeast of São Paulo state, southeastern Brazil.

Covariate/ Effect name	Code	Type	Description	Expected relationship with				
				ψ	p_{10}	p_{11}	r_{11}	$r_{11} = p_{11}$
Savanna	Sav	Native	Percentage of open native vegetation, mostly flooded wetlands and "cerrado sensu stricto", but also including "campo cerrado" and some regenerating areas.	-	NA	NA	NA	-
Field	Fiel	Human-disturbed	Percentage of pastures and mixed abandoned grasslands, often dominated by exotic species but also with some native.	+	NA	NA	NA	+
Sugarcane	Sug	Human-disturbed	Percentage of sugarcane plantations.	+	NA	NA	NA	+
Managed Forest	ManF	Human-disturbed	Percentage of *Eucalyptus* spp. and, to a lesser degree, *Pinus* spp. plantations.	+	NA	NA	NA	+
Native Forest	NatF	Native	Percentage of native forest, including "cerradão", semi-deciduous, deciduous, and riparian forests.	-	NA	NA	NA	-
Hydrographic density	Hyd_dens	Native	Total length, in meters, of the hydrographic network inside a given spatial scale, divided by that spatial scale area (m/ha).	-	NA	NA	NA	-
Edge density	Edg_dens	Human-disturbed	Total length, in meters, of all native forest patch edges inside a given spatial scale, divided by that spatial scale area (m/ha).	+	NA	NA	NA	+
Study Area	StudAr	Human-disturbed	Dummy covariate that assumes "00" for sites sampled at the landscape A (reference), "10" for sites sampled at the landscape B and "01" for sites sampled at the landscape C.	+	NA	NA	NA	+

Table 2 continued

Covariate/ Effect name	**Code**	**Type**	**Description**	**Expected relationship with**				
				ψ	p_{10}	p_{11}	r_{11}	$r_{11} = p_{11}$
Dirt Road distance	DR_dist	Human-disturbed	Linear distance (m) of the sampling sites to the nearest dirt road/farm track inside each landscape.	-	NA	NA	NA	NA
Edification distance	Edist	Human-disturbed	Mean linear distance (m) of random points, created around the sampling sites, to the nearest farmhouse or village inside each landscape.	-	NA	NA	NA	-
Time effect	t	Temporal	Time effect used to account for differences in detection probabilities over time (sampling season). Precisely, different detection probabilities were estimated for each sampling month (May-September) in relation to the first (April).	NA	NA	NA	NA	+
Trend effect	T	Temporal	Trend effect used to account for detection probabilities linearly increasing or decreasing over time (sampling season).	NA	NA	NA	NA	+
Year	Year	Temporal	Categorical covariate that assumes zero (0) for sites sampled in 2013 or one (1) for sites sampled in 2014.	NA	NA	NA	NA	-
Average Temperature	Aver_temp	Weather	Mean monthly temperature (°C) in each sampling point.	NA	NA	NA	NA	-
Accumulated Rainfall	Rainf	Weather	Accumulated rainfall (mm) in each sampling point.	NA	NA	NA	NA	-

Table 2 continued

Covariate/ Effect name	Code	Type	Description	Expected relationship with				
				ψ	p_{10}	p_{11}	r_{11}	$r_{11} = p_{11}$
Coldest months effect	Cold_mth	Weather	The effect of the coldest months (from May to August) on the true detection probabilities in relation to the other months (April and September). The coldest months were defined according to the climate historical data (1961-1990, (INMET 2019) of our sampling landscapes region, based on the mean minimum temperature of each month.	NA	NA	NA	NA	+
Track Survey effect	Surv	Method	Track survey effect used to account for differences in detection probabilities between our two track surveys. Precisely, we estimated the effect of the second survey (conducted during the removal of the camera-traps) in relation to the first (installation).	NA	+	+	NA	NA
Suitability for tracks	Suit_t	Method	Categorical covariate that assumes one (1) when the sampling conditions of tracks were inappropriate (e.g., rain during the sampling, very hard soil compaction hampering footprint impression, transects mostly covered by grasses or litter, etc.) or zero (0) when the track survey was done without any issue.	NA	+	-	NA	NA
Camera-trap position	CT_pos	Method	Categorical covariate that assumes one (1) for camera-traps positioned for locally sampling dirt roads/farm tracks or zero (0) otherwise.	NA	NA	NA	+	NA

Table 2 continued

Covariate/ Effect name	Code	Type	Description	Expected relationship with				
				ψ	p_{10}	p_{11}	r_{11}	$r_{11} = p_{11}$
Effort	Eff	Method	Camera-trap days of sampling (camera days) of the last camera-trap occasion for each one of the 205 sampled sites.	NA	NA	NA	+	NA

Weather data (rainfall and temperature) was gently provided by the National Institute of Meteorology (INMET 2019). NA: covariate (or effect) not evaluated for a given response variables (ψ, p_{10}, p_{11}, or r_{11}). The expected relationships among these response variables and predictors were based on previous studies and our own hypotheses. The seven compositional-based covariates were quantified in their estimated scale of effect.

2.2.4. Occupancy modeling

We used occupancy modeling as our statistical framework (MacKenzie et al. 2006) to investigate the effect of native and human-disturbed covariates on European hare occurrence, while accounting for imperfect detections (i.e., when species occur at a sampling site, but we fail to detect). Since a preliminary analysis provided strong evidence of false positive detection errors (i.e., when the species is detected at a site that is, in fact, unoccupied) on hare tracks identification (for the preliminary analysis details, see Appendix B), we decide to use the Miller model (Miller et al. 2011) instead of the standard Mackenzie model (MacKenzie et al. 2002). We selected the Multiple Detection Method Model (MDMM) parametrization as our Miller model because we have a site confirmation design (Chambert et al. 2015) and two different sampling methods. Detection histories were then constructed putting together camera trapping (certain method) and track surveys (uncertain method), coding with 0 (nondetection), 1 (track detections) and 2 (camera-trap detections). In our detection matrix, the first (1) and last (8) occasions correspond, respectively, to the track surveys conducted during the setup and the removal of the camera-traps, whereas the occasions 2-7 correspond to the 30-day period of camera trapping. Consequently, the size of all camera-trap occasions is the same (five days), except for the seventh occasion, since the total sampling effort varied between camera-traps. All occupancy analysis was performed using program Mark 9.0 (White and Burnham 1999).

Following the two-step approach (MacKenzie et al. 2006), with the MDMM parametrization, we carefully investigated in the first step which factors (covariates/effects, Table 2) better explained the European hare detection probabilities (i.e., the false (p_{10}) and true (p_{11}) positive detection probabilities of the track surveys; and the true positive detection probability of the camera trapping, r_{11}), retaining a general occupancy probability (ψ) structure (for details, see Appendix C). To avoid overparameterization issues, in the first modeling step, the response variables under investigation (detection probabilities) were always a function of only one covariate in each model. In the second step of our occupancy analysis, we fixed the detection structure with most empirical support for all models and constructed a priori hypotheses regarding niche opportunity and biotic resistance by estimating the occupancy probability (ψ), respectively, as a logit function of each human-disturbed and native habitat/feature covariate (Table 2). Although the native species richness has been the operational measure of resistance most often used to address the biotic resistance hypothesis, proxies of native species diversity have also been used (Jeschke et al. 2012, 2018). Since the Neotropical habitats are known to have a richer biota than agricultural ones (Macgregor-Fors and Schondube 2011), here we assume that amount of native habitats/features represent a proxy of native species diversity. Besides investigating the niche opportunity and the biotic resistance posed by each covariate individually, we also constructed additive models (multiple regressions) combining only native cover type covariates (native forest and savanna) or only human-disturbed cover type covariates (fields, sugarcane and managed forest). To avoid collinearity issues, only weakly correlated covariates ($r < 0.5$; Appendix B, Table S1) were used in our additive models. We also created a null model (occupancy [$\psi(.)$] estimated as constant) in this second step, allowing us to compare its empirical support with the biological hypotheses here investigated.

Model selection was based on the relative Kullback-Leibler information, using the Akaike Information Criterion, corrected for small samples, to rank our models (AICc; Anderson and Burnham 1999; Burnham and Anderson 2001). In each model set, for defining our well-supported hypotheses (models), we quantified the strength of evidence in favor of each model by calculating ΔAICc (the AICc of each model *i* minus the lowest AICc), the Akaike weights (w_i; the weight of evidence in favor of a model *i*) and evidence ratios (ER_i; w_i/w_j). We avoided the arbitrary cutoff $\Delta AICc < 2$, as argued by Burnham et al. (Burnham et al. 2011), and selected the hypotheses with most empirical support based on our own interpretation of the quantified evidence (Anderson and Burnham 2002; Burnham et al. 2011). Besides, the association direction of a given predictor in relation to our response variables was evaluated with the 95% confidence interval (CI) of its estimated parameter (β). If the 95% CI did not include zero (0), then we considered that the predictor has a real effect on the response variable under investigation. Average occupancy (ψ) and detection probabilities (p_{10}, p_{11}, and r_{11}) of the European hare were obtained by model averaging (Burnham and Anderson 2002) our hypotheses in each model set. This procedure was also performed using program Mark 9.0 (White and Burnham 1999).

2.3. Results

Over the 205 sampling sites, the European hare was detected in 52. In most of them (31 sites; 60%) the species was only detected by track surveys. Therefore, the species occurrence was confirmed (camera-trap detections) in 21 sites (40%), six of which having also a track detection.

In the first step of our occupancy modeling, we found strong evidence that the true positive detection probabilities of track surveys and camera trapping are different ($p_{11} \neq r_{11}$), since the European hare was, on average, much more truly detected by the track surveys than camera trapping (for detection result details, see Appendix C). Moreover, the true positive detection probability (p_{11}) in the first track survey was less than half of the second (Fig. 2a). Also, this leporid was much more truly detected by camera-traps (r_{11}) when they were locally sampling dirt roads/farm tracks (Fig. 2b). Although we did not find a covariate/effect associated with the false positive detection probability (p_{10}; Appendix C), the European hare occupancy probability (ψ) would have been overestimated if this error had not been accounted for (Appendix B).

In the second step, the first two best-ranked models were considered our hypotheses with most empirical support (Table 3). The top-ranked model is 2.9 times ($w_{top}/w_{2nd} = 0.66/0.23$) more likely than the second-ranked one and at least 13.5 times ($w_{top}/w_{3rd} = 0.66/0.05$) more likely than any other hypothesis here considered. Furthermore, the first two well-ranked models accumulated 89% of all Akaike weights of this model set (Table 3). Our top-ranked model for the European hare occupancy probability (ψ) included the additive effect of "Field", "Sugarcane", and "Managed Forest" covariates (Table 3). As predicted, these covariates had a positive and well-estimated association with the European hare occupancy ($\hat{\beta}_{Fiel} = 0.05$, $SE = 0.02$, CI = 0.02 to 0.08, Fig. 3a; $\hat{\beta}_{Sug} = 0.03$, $SE = 0.01$, CI = 0.01 to 0.06, Fig. 3b; and $\hat{\beta}_{ManF} = 0.02$, $SE = 0.008$, CI = 0.007 to 0.04, Fig. 3c, respectively). Moreover, according to the second-ranked model, the additive effects of "Native Forest" and "Savanna" covariates were also important for explaining the European hare occupancy probability (Table 3). As expected, the "Native Forest" covariate had a strong negative effect on this non-native species occupancy ($\hat{\beta}_{NatF} = -0.03$, $SE = 0.01$, CI = -0.05 to -0.01, Fig. 3d). However, while the "Savanna" effect was also negatively estimated, it was weak and inconclusive since its beta CI overlapped zero ($\hat{\beta}_{Sav} = -0.02$, $SE = 0.01$, CI = -0.05 to 0.0002). The model averaged European hare occupancy probability ($\hat{\psi}$) was 0.25 ($SE = 0.07$; CI = 0.13 to 0.41).

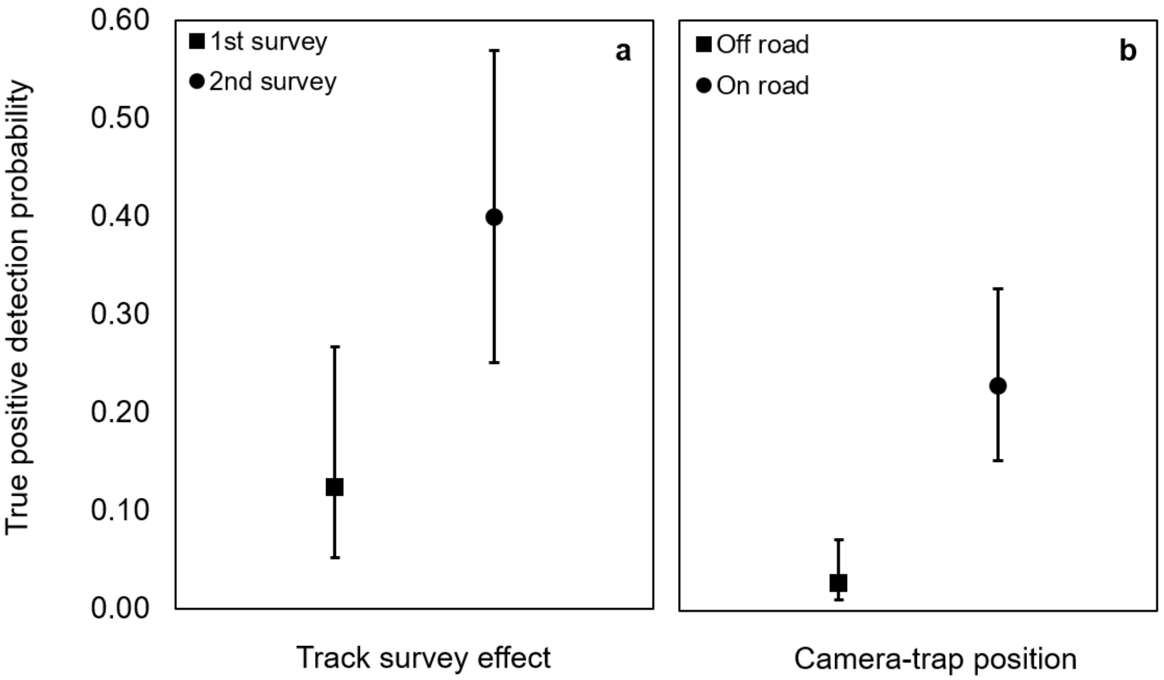

Fig. 2. Track survey (**a**) and camera-trap position (**b**) effect on the European hare true positive detection probabilities (p_{11} and r_{11}, respectively) in the northeast of São Paulo state, southeastern Brazil, as predicted by the top-ranked model of the detection (first) modeling step. The European hare was much more truly detected by track surveys (p_{11}) on the second survey (**a**) and much more truly detected by camera-traps (r_{11}) when they were locally sampling dirt roads/farm tracks (**b**) since the 95% confidence intervals (black whiskers) of these estimates are minimally overlapped.

Table 3. Model selection result for the European hare occupancy probability (ψ) in the northeast of São Paulo state, southeastern Brazil. Models with most empirical support (well-supported hypotheses) are highlighted in light gray.

Model	AICc	ΔAICc	w	K	-2log(L)
ψ(Fiel+Sug+ManF), p_{10}(.), p_{11}(Surv), r_{11}(CT_pos)	520.81	0.00	0.66	9	501.89
ψ(Sav+NatF), p_{10}(.), p_{11}(Surv), r_{11}(CT_pos)	522.95	2.14	0.23	8	506.22
ψ(NatF), p_{10}(.), p_{11}(Surv), r_{11}(CT_pos)	525.80	4.99	0.05	7	511.23
ψ(Hyd_dens), p_{10}(.), p_{11}(Surv), r_{11}(CT_pos)	527.12	6.31	0.03	7	512.55
ψ(Fiel+ManF), p_{10}(.), p_{11}(Surv), r_{11}(CT_pos)	529.27	8.46	0.01	8	512.54
ψ(Fiel+Sug), p_{10}(.), p_{11}(Surv), r_{11}(CT_pos)	529.70	8.89	0.01	8	512.96
ψ(ManF+Sug), p_{10}(.), p_{11}(Surv), r_{11}(CT_pos)	531.15	10.34	0.00	8	514.42
ψ(Fiel), p_{10}(.), p_{11}(Surv), r_{11}(CT_pos)	531.25	10.44	0.00	7	516.68
ψ(Edg_dens), p_{10}(.), p_{11}(Surv), r_{11}(CT_pos)	534.32	13.51	0.00	7	519.75
ψ(Sug), p_{10}(.), p_{11}(Surv), r_{11}(CT_pos)	537.30	16.49	0.00	7	522.73
ψ(.), p_{10}(.), p_{11}(Surv), r_{11}(CT_pos)	538.17	17.36	0.00	6	525.74
ψ(ManF), p_{10}(.), p_{11}(Surv), r_{11}(CT_pos)	538.35	17.54	0.00	7	523.78

Table 3 continued

Model	AICc	ΔAICc	w	K	-2log(L)
ψ(Sav), p_{10}(.), p_{11}(Surv), r_{11}(CT_pos)	538.56	17.75	0.00	7	523.99
ψ(Edist), p_{10}(.), p_{11}(Surv), r_{11}(CT_pos)	539.23	18.42	0.00	7	524.66
ψ(DR_dist), p_{10}(.), p_{11}(Surv), r_{11}(CT_pos)	540.06	19.25	0.00	7	525.49
ψ(StudAr), p_{10}(.), p_{11}(Surv), r_{11}(CT_pos)	542.06	21.25	0.00	8	525.32

AICc = Akaike Information Criterion corrected for small samples; ΔAICc = AICc of each model *i* minus the lowest AICc; w = Akaike weights; K = number of parameters; -2log(L) = twice the negative log-likelihood. Surv = track survey effect; CT_pos = camera-trap position; NatF = % of native forest in 12.5 ha; Hyd_dens = hydrographic density (m/ha) in 25 ha; Fiel = % of field in 25 ha; Edg_dens = edge density (m/ha) in 25 ha; Sug = % of sugarcane plantation in 25 ha; ManF = % of managed forest in 12.5 ha; Sav = % of savanna in 25 ha; Edist = mean random points distance (m) to the nearest edification; DR_dist = sampling points distance (m) to the nearest dirt road/farm track; StudAr = categorical covariate for the three landscapes sampled.

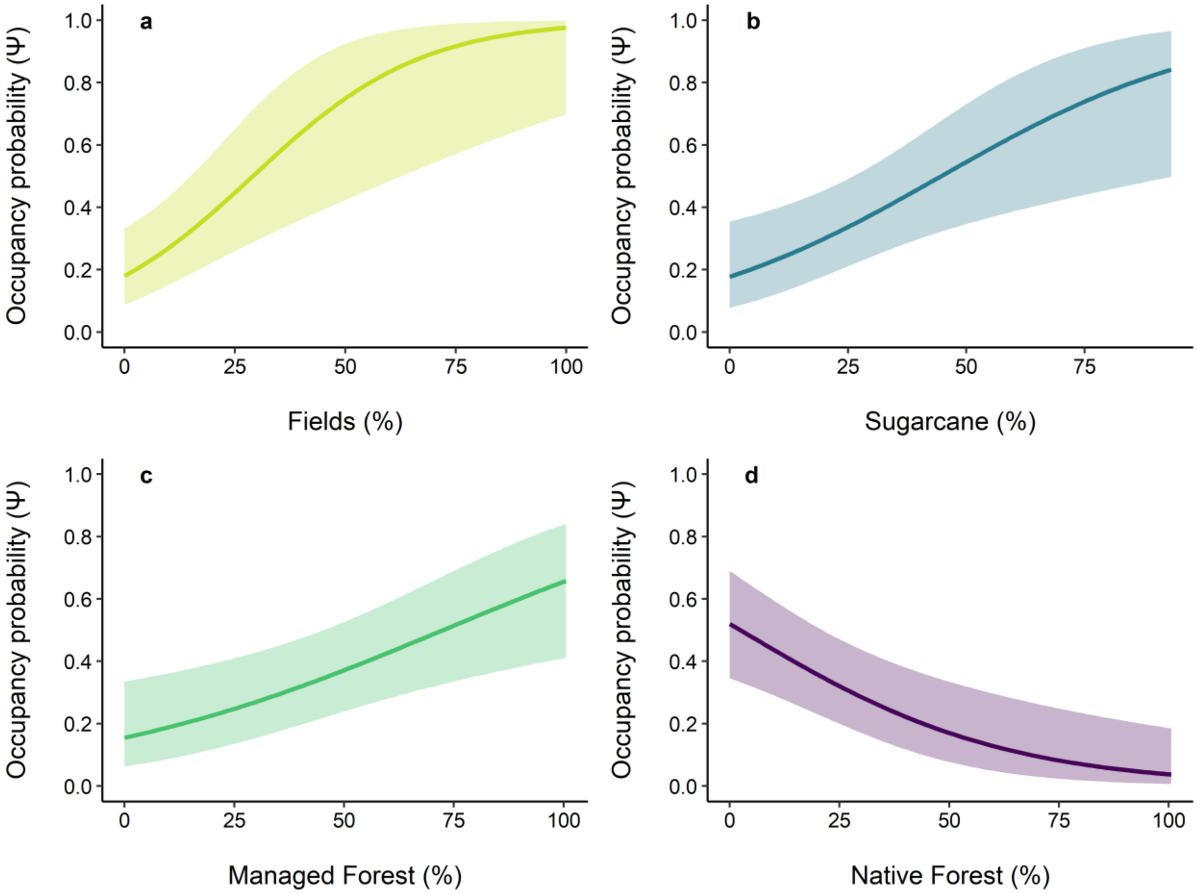

Fig. 3. The positive effect of fields (**a**), sugarcane (**b**), managed forest (**c**), and the negative effect of native forest (**d**) covariate on occupancy probability (ψ) of the European hare in the northeast of São Paulo state, southeastern Brazil, as predicted by the two well-ranked models of the occupancy (second) modeling step. The continuous lines indicate the predicted occupancy probabilities (ψ) while shaded areas represent their 95% confidence interval.

2.4. Discussion

To our knowledge, this is the first study dedicated to identifying occupancy drivers of the European hare in the Neotropics. Our results indicate strong support for the disturbance hypothesis. Although they also suggest some support for the biotic resistance hypothesis, the empirical evidence in favor of this hypothesis was weaker. Our results also show evidence for false positive sampling errors which, if not accounted for, would have led to a substantial overestimation of the occupancy probabilities (Appendix B). This reinforces previous findings that even small false positive detection errors can lead to considerable bias in occupancy estimates (Royle and Link 2006; McClintock et al. 2010; Miller et al. 2011).

Our occupancy results show evidence that fields, sugarcane plantations, and managed forests positively affect the European hare occurrence (Fig. 3a, b, and c, respectively). These findings lend support to the disturbance hypothesis, suggesting that niche opportunities created by agricultural lands, highly human-disturbed habitats, are the main driver of the European hare invasion in the Neotropics. Niche opportunities may arise in our agricultural lands mostly as resource and predator scape opportunities for the European hare. As this leporid species feeds preferably inside short crops (Tapper and Barnes 1986; Smith et al. 2004) and pastures (Tapper and Barnes 1986) in Europe, herbaceous plants from our fields and sugarcane itself, but most likely seedlings, might be consumed by this species. In *Eucalyptus* spp. plantations from southeastern Brazil, this non-native leporid was more frequently detected inside the early stages (0–1 year) of these managed forests, possibly because African grasses and other ruderals are commoner or more abundant in the early stages (Timo et al. 2015). Herbaceous plants, especially grasses, are indeed the preferred food of the European hare in its native (Chapuis 1990) and non-native range (Puig et al. 2007; Lush et al. 2017). Furthermore, invasive African grasses (e.g., species from *Melinis* and *Urochloa* genera) are widely distributed in Brazil and are known to thrive in highly disturbed environments (Zenni and Ziller 2011). In fact, inside the agricultural lands of our study landscapes, we found these ruderal plants growing abundantly in association with non-crop areas (e.g., dirt roads verges, fallow lands, field margins, fencerows, hedgerows, etc.). These non-crop areas are known to provide permanent cover for the European hare in Europe, being considered a key habitat for this farmland species, especially after crop harvesting (Tapper and Barnes 1986; Vaughan et al. 2003). As the European hare avoid resting sites that do not provide cover, habitats with permanent vegetation may be particularly important against predation (Tapper and Barnes 1986; Neumann et al. 2011). Thus, besides food, ruderal herbaceous plants that grow in non-crop areas might also provide shelter for the European hare.

On the other hand, although our second best-ranked model suggests some support for the alternative biotic resistance hypothesis, this evidence was weak since this model was almost three times less likely than the top-ranked one. Moreover, the second best-ranked model only partially supported the biotic resistance hypothesis. This is because while our occupancy results showed strong evidence for a negative effect of native closed-canopy forests (Fig. 3d), only weak evidence was found for the negative effects of savannas. These results suggest, therefore, that native closed-canopy forests may impose biotic resistance to the European hare invasion in the Neotropics. However, as our results did not provide enough evidence to assert that the savanna effect on hare occupancy is indeed negative, despite suggesting it, they prevented us from extending this invasion resistance to all best-preserved and species-rich native habitats. Although these findings indicate that Neotropical forests may impose biotic resistance to the European hare occurrence, our data do not allow us to determine the exact mechanism creating this resistance. We tentatively advance, therefore, two main explanations.

Firstly, Neotropical forests might impose resistance to the European hare occurrence given the low resource opportunity represented by these forests. The European hare is an herbivore that essentially feeds on herbaceous plants, such as grasses and forbs (Puig et al. 2007; Lush et al. 2017). As the ground of the sclerophyllous woodland ('cerradão") has often little or no herbaceous layer (Goodland 1971; Durigan and Ratter 2006), the interior of these woodlands may offer no or few foods for hares. Resource opportunities might be further diminished by competition with native grazers and browsers inhabiting these forests, including the Brazilian cottontail (*Sylvilagus brasiliensis* sensu lato; Silva et al. 2019) and the brocket deer (*Mazama* spp). Hence, forested protected areas might represent a "barrier" to the expansion of the European hare. Outside protected areas, this barrier effect might be exerted by native forests existing in private properties in the form of APPs and LRs (Brancalion et al. 2016).

Secondly, predation pressure might also be into play. In its native continent, the European hare seems to avoid woodlands as a response to predation risk. Although the European hare may use woodlands as shelter, especially when agricultural crops provide little or no vegetation cover (Tapper and Barnes 1986), the dens of this species are often located in places that provide wide-open view of the surroundings, indicating a strategy to avoid approaching predators (Angelici et al. 1999; Petrovan et al. 2013). Even under relatively low predator (red fox; *Vulpes vulpes*) abundance, this leporid only selects the edge (< 20 m from the boundary) of small patches of woodland, avoiding areas further inside during its active periods (Petrovan et al. 2013). On the other hand, when woodlands are commoner (> 20%), increasing the predation risk by red foxes, the amount of woodland negatively affects the European hare density in Polish agricultural lands (Panek and Kamieniarz 1999).

Likewise, outside its native range, the European hare occurrence is also negatively affected by the temperate forests of *Nothofagus dombeyi* in northern Patagonia, occurring more often in sites with low canopy and mid-storey cover (Lantschner et al. 2013) and high horizontal visibility (Gantchoff and Belant 2015). In different regions of the Patagonian province, many species of native predators have already learned to hunt the European hare, since this exotic leporid is one of their main prey (Novaro et al. 2000; Zanón Martínez et al. 2012; Barbar et al. 2016). In the Atlantic Forest domain, the species richness of native carnivores increases with the amount of native forest cover (Regolin et al. 2017). Also, recent studies carried out in the same region of the present study found the ocelot (*Leopardus pardalis*), a native feline very dependent upon tropical forest cover, occurring preferably (Paolino et al. 2018) and more frequently (Lyra-Jorge et al. 2010) in the native forests, suggesting that predation pressure might be higher inside the Neotropical forests than elsewhere. Besides the richer native carnivore community and unlike woodlands, Neotropical forests are often more closed structurally. Even the sclerophyllous woodland ("cerradão") of the Brazilian savanna domain (Cerrado), the predominant forest-like vegetation type present in our study areas, have much higher tree density (3215 trees ha^{-1}; Goodland 1971) than woodlands in Europe (693 trees ha^{-1}; Brzeziecki et al. 2018). Thus, these structurally closed forests might further facilitate predation by ambush, especially regarding an open-country species with a cursorial lifestyle as the European hare.

Even though the Neotropical forests may exert a resistance effect to the European hare occurrence by either lack of resources, predation, or something else, our results did not provide evidence that native open-canopy habitats (savanna) could similarly prevent or inhibit this non-native species invasion. Despite being more frequently recorded in open disturbed habitats (firebreaks) than in native forest-steppe mosaic – an open vegetation dominated by bunchgrasses – in northwest Patagonia (Lantschner et al. 2013), the European hare has also invaded some nature reserves of the Cerrado and Pampas domain in Brazil (de Faria et al. 2015). In fact, the European hare occupies 7% (48 km^2) of the Serra da Canastra National Park, a pristine native grassland reserve of the Cerrado (de Faria et al. 2015). On private properties of the Brazilian Pampas grasslands, this non-native species is also present, but its density was very high (31.9 ind./ km^2, $SE = 4.81$) only inside less intensive livestock ranches, located in a relatively well-preserved region (Kasper et al. 2012). Given the high availability of potential food (grasses), we reason that natural enemies (e.g., predators) might be the only significant detrimental effect to hares in these more grassy native habitats. This, however, lacks empirical evidence and awaits further investigation. Uncovering the relationship with the Brazilian savannas is of utmost importance since the European hare has only recently reached the southern limits of the Cerrado, the second largest biome in Brazil and which is already severely impacted by agriculture expansion.

In fact, knowing this, we will shed light on the important question of the impact of the European hare as native habitats of the Neotropics are transformed into agricultural lands. Recently, some ecologists (e.g., Davis 2011; Schlaepfer et al. 2011) have recognized many desirable effects of non-native species since they can provide shelter (Severns and Warren 2008; Sogge et al. 2008) and food (Carlsson et al. 2009) for native species, facilitate native plant recolonization (Rodriguez 2006), and even improve ecosystem services (Dick 2001). Would that be the case of the European hare?

On one hand, this exotic leporid may be (or become in the near future) a key prey to some South American predators (Buenavista and Palomares 2018), particularly when native prey abundance severely declines (Novaro et al. 2000). A recent study showed that in southeastern Brazil, especially in landscapes with low native vegetation cover, most of the puma prey may come from agricultural crops (Magioli et al. 2014), the current primary habitat of the European hare in its native range (Tapper and Yalden 2010). Thus, it seems reasonable to consider that the European hare may have some conservation value in severely modified landscapes, such as those extensively used for commodity production (e.g., ethanol, soybean), as found in many locations of our study region and further north in the Cerrado. On the other hand, as argued by Buenavista and Palomares (2018), we do not know yet how native prey populations will be impacted by the new trophic interactions among the native carnivores and the European hare. A recent study, however, suggested the European hare has a great potential to create apparent competition with native herbivores (Barbar and Lambertucci 2019). Besides, based on our findings, the European hare may not spatially co-occur with the Brazilian cottontail (*Sylvilagus brasiliensis* sensu lato; Silva et al. 2019), a forest dweller species according to our recent results (Pasqualotto et al., unpublished data, see Chapter III). However, although our data suggest that the European hare may not be a threat to the Brazilian cottontail, until now, there is no study specifically dedicated to assessing this gap of knowledge. Considering this and the fact that the European hare is a threat to other leporids (Thulin 2003; Reid 2011; Caravaggi et al. 2015; Dénes et al. 2018), it is recommended to consider the European hare a threat until future studies indicate otherwise.

Concluding, our main findings, particularly the strong support to the disturbance hypothesis, is in agreement with studies on other ecosystems, which also found that man-made habitats create opportunities for invaders (Dumont et al. 2011; Soares et al. 2020). The disturbance hypothesis has, indeed, often been supported by empirical studies worldwide (Jeschke and Heger 2018; Jeschke et al. 2018). On the other hand, empirical support in favor of the biotic resistance hypothesis seems to be equivocal, despite being the most tested among the major invasion biology hypotheses (Jeschke et al. 2012, 2018; Jeschke and Heger 2018).

Based on our main findings, we predict the European hare will continue to expand its geographical distribution further north in the Cerrado. This domain has already lost almost half of its original coverage due to the expansion of pasture and agricultural lands (Strassburg et al. 2017). Furthermore, given the increasing demand for food and biofuels worldwide, sectors in which Brazil is a key player (Gauder et al. 2011; Bordonal et al. 2018), agricultural expansion may continue to convert the Cerrado native vegetation (Strassburg et al. 2017). On the other hand, as our findings also indicate, protecting and restoring native habitats, particularly native closed-canopy forests, may pose constraints to this invasion. But considering that less than 10% of this domain is under public protected areas and that 40% of the remaining native vegetation is available to be legally converted into further agricultural lands (Klink and Machado 2005; Strassburg et al. 2017), the future of this invasion process may lie mostly in the hands of farmers and cattle ranchers. The protection of native vegetation occurring inside these properties is mandated by the Brazilian Forest Act (Brancalion et al. 2016). However, adherence to this law by rural owners is still relatively low and almost half of the Brazilian APPs are deforested (44 of 103 Mha; Sparovek et al. 2010). To increase adherence of rural owners to this code and to promote reforestation of degraded areas legally protected by the Forest Act are, therefore, recommended to lessen the European hare spread, further benefiting wildlife in general (Lees and Peres 2008; Metzger et al. 2019; Pereira et al. 2019).

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3. CHAPTER II: DETERMINING ABUNDANCE PREDICTORS OF A GLOBAL INVADER IN SOUTHEASTERN BRAZIL

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Abstract

European hare (*Lepus europaeus*), like many invasive species, have declined in much of their native range but flourished in non-native regions (e.g., South America). Previous studies suggest the loss of farmland heterogeneity due to agricultural intensification is the main driver of the species decline in its native range in Europe. Yet, little is known about the role of spatial and temporal heterogeneity and land cover types as predictors of European hare local abundance in Neotropical agricultural landscapes. We hypothesized that spatial and temporal heterogeneity, rather than land cover types, would be the most influential predictors of hare local abundance in intensively managed Neotropical agricultural landscapes. We sampled 55 sites embedded within agricultural dominated landscapes from southeastern Brazil with camera-traps and transect surveys. Sites were selected along an uncorrelated gradient of native vegetation cover and compositional heterogeneity. We estimated the relative abundance of European hare using an occupancy model that accounts for species imperfect detection induced primarily by variation in local abundance. We found that land cover diversity, sugarcane and savanna cover were the best predictors of European hare relative abundance. Hare relative abundance estimates were low and did not vary dramatically among sites, suggesting that this invader has not yet attained high local density in our study region. European hare attained the highest relative abundance in agricultural landscapes that locally combine higher compositional heterogeneity, including sugarcane crops, and little to no native savanna. Areas with these combined features may represent the most important nascent foci, fostering the ongoing northward spread of this invasive species in the Neotropics.

Keywords: biological invasion, *Lepus europaeus*, European hare, N-mixture model, Neotropics, agricultural landscape, field margins, abundant-center hypothesis, occupancy modeling.

3.1. Introduction

Human activities have dramatically changed land cover worldwide (Ramankutty et al. 2018; Ellis et al. 2021), with a third of the Earth's ice-free land surface already converted into agricultural lands (Ramankutty et al. 2018). Currently, large wild areas cover only 26% of the global land surface (Locke et al. 2019). Despite expanding at a slower rate, human population continues to grow globally (FAO 2017), increasing the demand for biofuels, human food, and livestock/fish feed (Tilman et al. 2011; Fróna et al. 2019). Land clearing is expected to occur over about 1 billion ha until 2050 if the trends of last decades continue, especially in the poorer nations (Tilman et al. 2011). This rapid conversion of natural environments into human habitats (agricultural lands, urban areas, infrastructure works, etc.) has created opportunities for several non-native species to invade (Umetsu and Pardini 2007; Soares et al. 2020; Pasqualotto et al. 2021).

The European hare (*Lepus europaeus* Pallas, 1778; Mammalia, Lagomorpha) is an open-country specialist that likely evolved in the Asian-steppes (Thulin 2003). The species' native range spans nearly all of mainland Europe through parts of Asia (Chapman and Flux 1990). European hare has been introduced in many countries around the world and is now found on all continents except Antarctica and continental Africa (Barbar and Lambertucci 2018). This species is widely distributed in South America (Rosa et al. 2020) and is the second most widespread invasive mammal in Brazil (da Rosa et al. 2017). Non-native European hares can negatively affect native species via hybridization and competition with endemic leporids (Reid 2011; Caravaggi et al. 2015) and their diets overlap with native rodents (Bonino et al. 1997; Puig et al. 2007) and livestock (Puig et al. 2007). Moreover, European hare presence has been related to reduced seedling abundance of a critically endangered plant species (Dénes et al. 2018).

Farmland became the primary habitat of European hare in its native range given the long-term association of the species with human activities (Tapper and Yalden 2010). However, the loss of farmland heterogeneity due to agricultural intensification – i.e., farmland management aimed at maximizing yield per unit area – is supported as the main driver of declines in European hare abundance throughout Europe, especially since the 1960´s (Tapper and Parsons 1984; Lewandowski and Nowakowski 1993; Panek and Kamieniarz 1999; Edwards et al. 2000; Smith et al. 2004, 2005). Agricultural intensification creates spatially homogeneous landscapes (Benton et al. 2003) both in terms of composition (number and proportion of different land cover types) and configuration (size and spatial arrangement of land cover patches, Fahrig et al. 2011). In its native range, landscapes with a low diversity of crop types (low compositional heterogeneity) are often negatively associated with hare abundance (Lewandowski and Nowakowski 1993; Smith et al. 2005). Additionally, landscapes with large crop fields (low configurational heterogeneity) also contain smaller European hare populations (Lewandowski and Nowakowski 1993; Panek and Kamieniarz 1999; Smith et al. 2005; Pavliska et al. 2018).

In contrast, existing studies in South America suggest European hare populations are thriving in agricultural landscapes with presumably low spatial (i.e., compositional or configurational) heterogeneity (Novaro et al. 2000; Kasper et al. 2012; Pasqualotto et al. 2021). European hare reach high densities of 47.5 individuals/km^2 in northwestern Patagonia (Novaro et al. 2000) and 31.9 individuals/km^2 in southern Brazil (Kasper et al. 2012) on private cattle ranches, a human-modified habitat with presumably low diversity of land cover types. In addition, hare occupancy is higher in landscapes from southeastern Brazil predominantly covered by intensive monocultures such as sugarcane, managed forests, and pastures (Pasqualotto et al. 2021). Niche opportunities provided by these intensively-managed monocultures has been suggested as the main driver of European hare invasion in the Neotropics (Pasqualotto et al. 2021). These findings are surprising considering that the long-term decline in hare populations in Europe is primarily caused by landscape homogenization (Tapper and Barnes 1986; Lewandowski and Nowakowski 1993; Pavliska et al. 2018). Still, no study has quantified the relative importance of compositional and configurational heterogeneity and land cover types as predictors of local abundance of this exotic species in Neotropical agricultural landscapes.

A further element, temporal heterogeneity in croplands – i.e., resource variation due to crop life cycle and management (Santos et al. 2021) – may also play a role in determining local European hare abundance in Neotropical landscapes. Sugarcane crop management in southeastern Brazil, with summer and winter planting (Nihei et al. 2015; Kavats et al. 2020), allows the spatial coexistence of different phenology stages. Locally, this creates habitat heterogeneity, despite being the same cover type, which may benefit hares by providing complementary resources. For example, sugarcane seedlings might be an important source of food for the European hare, an herbivorous species that feeds mostly on grasses (Chapuis 1990;

Puig et al. 2007; Lush et al. 2017), while mature sugarcane fields may provide critical shelter since hares select resting sites that provide vegetation cover (Neumann et al. 2011; Petrovan et al. 2013). Thus, high temporal heterogeneity of sugarcane crops may lead to high local hare abundance. The relative importance of temporal heterogeneity, induced by crop life cycle and management, as a predictor of European hare local abundance has never been explored. Since the abundance of an invader is strongly linked to its impact on native species' population sizes and diversity (Bradley et al. 2019), identifying factors influencing local hare abundance will provide better understanding of the invasion process and guide future management actions aimed at mitigating the spread of this invader in the Neotropics.

This study investigated the influence and relative importance of spatial and temporal heterogeneity and the proportion of land cover types as predictors of local abundance of the invasive European hare in agricultural dominated landscapes in southeastern Brazil. We randomly selected sites embedded within landscapes to represent an uncorrelated gradient of native vegetation cover and compositional heterogeneity along the northward expansion front of this invader. Landscape homogenization is generally accepted as the main reason for the European hare population decline in the species native range (Tapper and Parsons 1984; Lewandowski and Nowakowski 1993; Panek and Kamieniarz 1999; Edwards et al. 2000; Smith et al. 2004, 2005). Thus, we hypothesized that spatial heterogeneity, either composition or configuration, and temporal heterogeneity would be the most influential predictors of local abundance in this intensively managed agricultural region, rather than proportion of different land cover types. Specifically, we expect i) a strong positive relationship between European hare local abundance and compositional, configurational, and temporal heterogeneity. Secondarily, we also expect that land cover types may affect hare local abundance, ii) increasing with the amount of agricultural land cover types and iii) decreasing with the amount of native forest and savanna cover.

3.2. Methods

3.2.1. Study area

Our study was conducted in landscapes distributed throughout the northeast region of São Paulo state, southeastern Brazil (total study area = 34,069.26 km^2, Fig. 1). Historically, this region is a transition zone between the Cerrado (Brazilian Savanna) and the Atlantic Forest. Semi-deciduous Atlantic forests originally covered most of the region (Victor et al. 2005) with sclerophyllous woodlands ("cerradão"), dry grasslands ("campo limpo"), and the ecotonal savannic intermediate formations of the Cerrado ("cerrado sensu stricto", "campo cerrado", "campo sujo"; sensu (Coutinho 1978) also naturally occurring (Durigan and Ratter 2006). Due to intense land cover change over the last two centuries (Victor et al. 2005), the study region is currently dominated by agricultural lands (Souza et al. 2020). Sugarcane is the predominant crop, covering 44.2% of the area (EMBRAPA, 2015), followed by pasture (13.4%), other annual crops (6.8%), citrus orchards (5.8%), and managed forests (i.e., *Eucalyptus* spp. and rubber tree plantations; 3.2%; EMBRAPA, 2015). Remaining native vegetation covers 19.3% of this region (EMBRAPA, 2015), of which 61.2% are native forests (including sclerophyllous woodlands) and 38.8% are savannas. However, most remaining native fragments are severely degraded and dispersed in small and isolated patches (Durigan et al. 2007; Ribeiro et al. 2009).

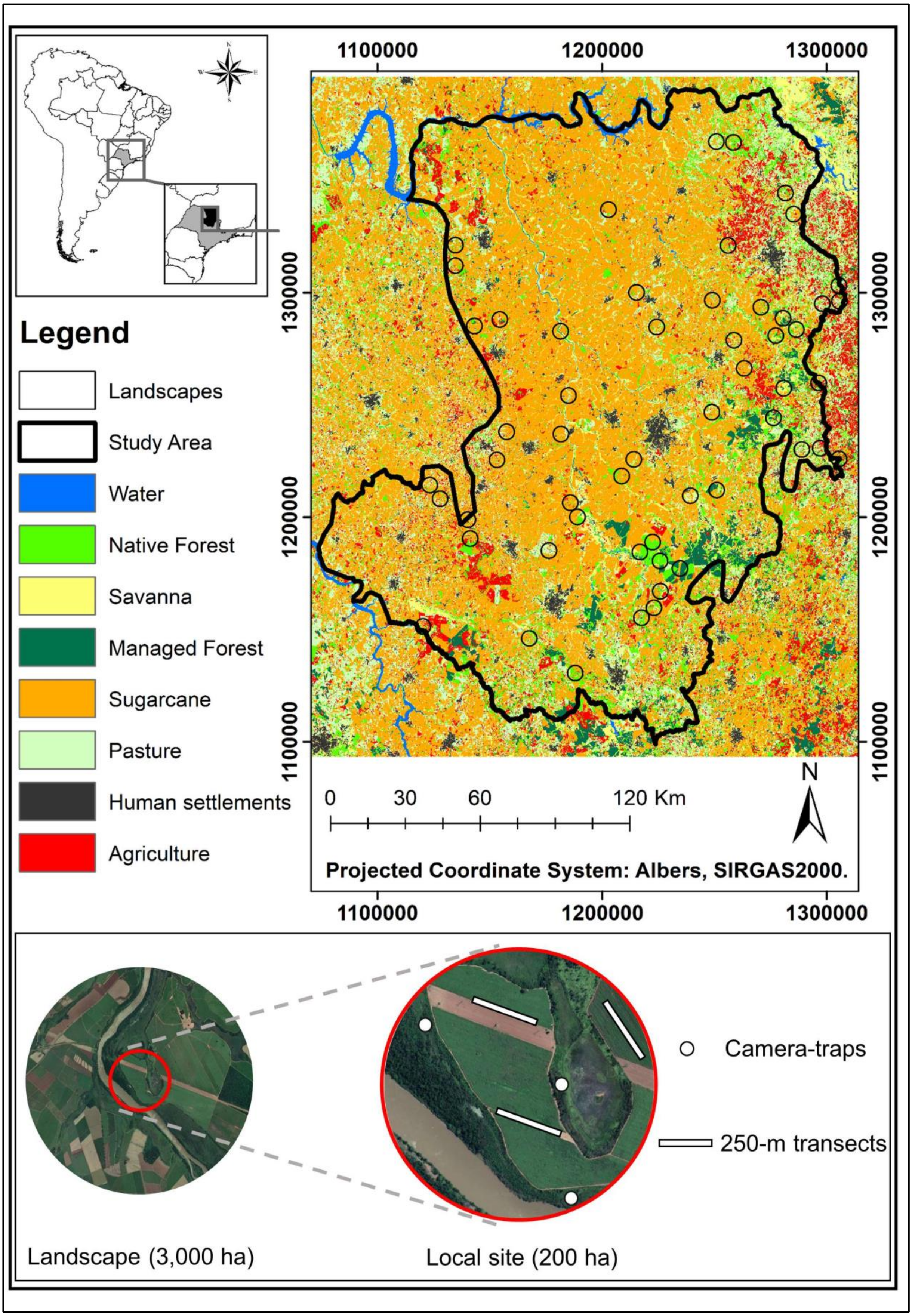

Fig. 1. Location of the study area, sampled sites, and respective surrounding landscapes, and mapped land cover classes in the northeast of São Paulo state, southeastern Brazil.

3.2.2. Study design

We used a two-step approach to select sampling units for our study. First, we wanted to avoid selecting units that contained only small native vegetation patches embedded within landscapes dominated by a few large patches of native vegetation. Large patches of native vegetation have higher abundances of many different taxa (Chase et al. 2020), including predators (Chiarello 1999) that prey upon invasive European hares (Cruz et al. 2022). Ensuring the same native vegetation patch dominance for each landscape and embedded sampling unit may prevent selecting a unit where high predation pressure in the surrounding landscape result in an unexpected low European hare local abundance in the unit. Accordingly, we used the Largest Patch Index (LPI) – the percentage area occupied by the largest patch of native vegetation – to develop a sample frame of units with similar native vegetation patch dominance in the unit and the respective surrounding landscape (Pasher et al. 2013). Specifically, we defined each sampling unit as a 200 ha local site (≅ 800 m radius) and the surrounding landscape as a wider concentric circle of 3,000 ha (≅ 3,090 m radius, see Fig. 1). The size of the local site is large enough to harbor multiple European hares, whose average home range is ≅ 30 ha (Jones et al. 2009). The landscape size was chosen to maximize the number of potential sites while limiting spatial overlap. We considered each pixel (30 m) of our study area as the center of a potential local site. We calculated the LPI for each pixel using moving windows of 200 ha (local site) and 3,000 ha (landscape). We only retained pixels that had the same LPI value for the local and landscape windows. Then, we randomly selected the largest possible number of the retained pixels using a minimum distance constraint of 6,180 m (diameter of a 3,000 ha landscape) to avoid selecting local sites with overlapping landscapes. This spacing allowed us to quantify predictors up to 3,000 ha around each local site without overlapping adjacent landscapes. This first step resulted in a sample frame of 523 local sites (hereafter, sites for brevity).

Next, we selected 55 sites (Fig. 1) from the sample frame that maximized uncorrelated variation of two hypothesized predictors of European hare local abundance: the diversity of land cover types (compositional heterogeneity) and the percentage of native vegetation cover (native forests and savannas, PNV). We used the Shannon's Diversity Index (SHDI), calculated based on the proportional land cover types in each site, as a measure of compositional heterogeneity. The final sample of 55 sites represented a wide, uncorrelated ($|r| = 0.13$) gradient of compositional heterogeneity (SHDI range: 0.15 – 1.47) and percentage of native vegetation (PNV range: 5.66 – 80.25%). See Appendix D for the geoprocessing details used to quantify LPI, PNV, and SHDI.

3.2.3. Field sampling

Fieldwork was conducted mostly during the dry seasons (April–September) of 2017 and 2018. Five sites were sampled in each month; 25 sites were sampled between June and October 2017 and the remaining 30 sites were sampled from April to September 2018. We restricted our sampling to the dry seasons to better access the sites. Sampling over a short time period (30 days) also minimized the chance of violating the population closure assumption required by our analysis methods (see Data analysis section).

European hare detections within each site were obtained with passive infrared camera-traps (Reconyx, model HC 500; Holmen, Wisconsin) and transect surveys. Each site was sampled with three camera-traps and three track-pellet transects (≅ 250-m each) for a total of 6 sampling entities per site (Fig. 1). Camera-traps were placed near the edge, but inside native forest patches (average distance = 27 m, *SD* = 23 m). The three transects were sampled on dirt roads/farm tracks located between crop fields or in transition zones between the crop fields and native vegetation (native forest or savanna). Camera-traps and transects were at least 50 m apart from each other. Cameras were fixed on tree trunks about 40-60 cm above the ground. We did not bait or lure our camera-traps because attractants might be ineffective or even decrease detection of lagomorphs (Fidino et al. 2020). Cameras were programmed to operate uninterrupted (24h/day) for approximately 30 days. Due to operating problems, some cameras were active more or less than 30 days, with an average effort in each site of 92.29 camera days (*SD* = 17.89 camera days). We surveyed transects once for fresh European hare feces and footprints, usually the same day the cameras were deployed. Transect length varied slightly, but the average effort in each site was 806.38 m (*SD* = 72.10 m). We also opportunistically searched for feces and footprints while moving between transects and camera locations within each site. Footprints were immediately identified or photographed for further identification using track guides (Borges and Tomás 2008). However, identifying European hare using fecal morphology is prone to identification errors (Zahratka and Buskirk 2007; Rodrigues et al. 2020); therefore, fecal samples were collected and identified using the molecular approach proposed by Rodrigues et al. (2020).

3.2.4. Mapping land cover and quantifying associated predictors

We used the best existing land cover maps (IBAMA, CAR, and MapBiomas) to select our sites (see Appendix D); however, maps from MapBiomas do not completely discriminate between agriculture and pasture (Souza et al. 2020). We developed a new map of the study area after field sampling to accurately quantify the heterogeneity and land cover metrics used as predictors in our analysis below (see Appendix E for mapping details). To test our hypotheses regarding relationships between estimated European hare local abundance and spatial and temporal heterogeneity and proportion of land cover types, we quantified 11 metrics (Table 1) for each site at three spatial scales: 800 m radius (200 ha local site), 2,000 m radius (1256 ha, intermediate scale), and 3,090 m radius (3000 ha, landscape scale). Six metrics described the percentage of area for the main land cover classes (hereafter, land cover predictors) found in our study area (Table 1). The remaining five are heterogeneity metrics – two compositional, two configurational and one temporal metric (hereafter, heterogeneity predictors; Table 1). All land cover and spatial heterogeneity predictors were quantified in R 3.6.2 (R Core Team 2019), using the 'landscapemetrics' package (Hesselbarth et al. 2019). See Appendix F for details about the quantification of the temporal heterogeneity metric.

We quantified our 11 predictors in three spatial scales to empirically estimate their scale of effect (Martin and Fahrig 2012; Miguet et al. 2016). We performed the scale of effect analysis using the Royle and Nichols model (Royle and Nichols 2003) detailed in the next section. Specifically, we created three simple models for each predictor (one model for each spatial scale) and used Akaike's Information Criterion for small samples (AICc, Burnham and Anderson 2002) to determine the best-supported scale. Each model contained constant individual detection probability and the abundance parameter λ was a function of a predictor at one of the three spatial scales. We found that models with the same predictor at different spatial scales usually had similar AIC values (ΔAICc < 2). In addition, the three spatial scales were highly correlated ($|r| \geq 0.7$, Dormann et al. 2013) for most predictors (See Appendix G, Table S1), suggesting any of the scales will represent predictors' relationship with hare local abundance (Martin and Fahrig 2012). Therefore, we decided to use the same scale for all predictors, namely the scale associated with the collected field data (i.e., 800 m radius), to investigate European hare local abundance. We performed correlation analyses among the 11 predictors quantified at the 800 m radius scale. We found Edge Density (ED) and Simpson's Diversity Index (SIDI) strongly correlated ($|r| \geq 0.7$, (Dormann et al. 2013) with other predictors (see Appendix G, Table S2). To avoid collinearity issues, we did not include these predictors (i.e., ED and SIDI) in hare abundance and detection modeling described in the next section.

Table 1. Predictor name (notation), variable type and description, and the expected *a priori* effect on European hare relative abundance (λ) and individual detection probability (r). All predictors were quantified at the same scale field data were collected (800 m radius).

Predictor	**Variable type**	**Range**	**Expected effect**		**Description**	**Rationale**
			λ	**r**		
Native Forest (NatF)	Land cover	0.00 – 82.77	-	NA[a]	Percentage of "cerradão", semi-deciduous, deciduous, and riverine forests.	European woodlands negatively affect European hare abundance in its native range (Panek and Kamieniarz 1999). Neotropical forests exert a strong negative effect on this species occurrence (Pasqualotto et al. 2021) and may also negatively affect its local abundance.
Savanna (Sav)	Land cover	0.00 – 54.90	-	NA	Percentage of open-canopy native vegetation, mostly "cerrado sensu stricto" and flooded wetlands.	Flooded wetlands and vegetation dominated by small trees and shrubs (e.g., "cerrado sensu stricto") may be a suboptimal habitat for European hare, an open country species (Tapper and Yalden 2010), hindering its ability to achieve locally large populations.

Table 1 continued

Predictor	Variable type	Range	Expected effect		Description	Rationale
			λ	r		
Managed Forest (ManF)	Land cover	0.00 – 37.85	+	NA	Percentage of *Eucalyptus* sp., *Pinus* sp., and rubber tree plantations.	European hare is open-country species (Tapper and Yalden 2010) and agricultural lands is currently its primary habitat (Tapper and Barnes 1986; Tapper and Yalden 2010; Schai-Braun et al., 2013). However, landscape homogenization due to agricultural intensification is the main driver of European hare declines in Europe (Lewandowski and Nowakowski, 1993; Edwards et al., 2000; Smith et al., 2004; Smith et al., 2005). Therefore, we do not expect to find European hare populations with high local abundance in landscapes dominated by these agricultural land covers because they are monocultures intensively managed in our study area.
Sugarcane (Sug)	Land cover	0.00 – 94.77	+	NA	Percentage of sugarcane plantations.	
Pasture (Past)	Land cover	0.00 – 74.76	+	NA	Percentage of grasslands dominated by exotic grasses used for cattle ranching.	
Other agriculture (Agr)	Land cover	0.00 – 45.50	+	NA	Percentage of other annual crops, coffee, citrus orchards, and and other fruit crops.	

Table 1 continued

Predictor	Variable type	Range	Expected effect		Description	Rationale
			λ	r		
Shannon's Diversity Index (SHDI)	Compositional Heterogeneity	0.22 – 1.57	+	NA	$-\sum_{i=1}^{m}(P_i * lnP_i)$, where P_i is the proportion of land cover class i and m is the number of classes.	Higher land cover type richness and evenness (i.e., high compositional heterogeneity) may provide, in a relatively small area, more shelter and food resources (Lewandowski and Nowakowski 1993; Tapper and Barnes 1986).
Simpson's Diversity Index (SIDI)	Compositional Heterogeneity	0.10 – 0.78	+	NA	$1-\sum_{i=1}^{m}P_i^2$, where P_i is the proportion of land cover class i and m is the number of classes.	
Sugarcane NDVI standard deviation (SugNDVI_sd)	Temporal Heterogeneity	0.01 – 0.22	+	NA	Standard deviation (sd) of the Normalized Difference Vegetation Index (NDVI) quantified only for pixels belonging to the sugarcane class.	Coexistence (sd) of different sugarcane phenology stages obtained with NDVI – i.e., high temporal heterogeneity – may provide food (seedlings) and shelter (mature stage) for European hare.

Table 1 continued

Predictor	Variable type	Range	Expected effect		Description	Rationale
			λ	r		
Edge Density (ED)	Configurational Heterogeneity	15.51 – 106.19	+	NA	Total edge length (contact between the boundaries of different land cover classes) (m/ha).	Landscapes with a higher amount of edge habitat and smaller patches on average (high configurational heterogeneity) may facilitate hare movement in search of food and shelter regardless of the land cover types (Schai-Braun and Hackländer 2014; Tapper and Barnes 1986).
Mean Patch Size (MPSz)	Configurational Heterogeneity	4.47 – 40.23	-	NA	The average size of the patches for all land cover classes (ha).	
Effort (Eff)	Sampling Effort	250.00 – 2321.70	NA	+	Distance traveled (m) in each transect or opportunistic survey multiplied by the number of observers.	Longer transects or those sampled by more observers are expected to have a higher probability of detecting hare pellets.
Opportunistic Survey (OS)	Survey types	0, 1	NA	+	Categorical variable differentiating an opportunistic survey (1) from a transect survey.	Individual detection probability is expected to be higher on opportunistic survey as more than 250 m and higher diversity of local habitats may have been surveyed moving between transects and camera locations.

[a]NA: predictor not evaluated for a given response variable (λ or r).

3.3. Data analysis

We modeled local European hare abundance using the Royle and Nichols model (hereafter, RN model; Royle and Nichols 2003; Kéry and Royle 2016). The RN model is a hierarchical model that estimates a distribution of species' abundance from replicated surveys (i.e., detection-nondetection data) at sampled sites. The model contains two different response variables (parameters) – the local mean population size of individuals exposed to sampling (λ) and the per-individual detection probability (r) (Royle and Nichols 2003; Kéry and Royle 2016). The RN model assumes that heterogeneity in species detection probability is primarily induced by variation in local abundance (Royle and Nichols 2003). Previous studies suggest that the European hare preferably occurs inside human-disturbed habitats in the Neotropics, avoiding native habitats, particularly native forests (Pasqualotto et al. 2021). Therefore, it seems reasonable to expect the abundance of this non-native species to vary among our sampled sites, creating heterogeneity in the species detection probability. The RN model estimates the species' abundance distribution (λ) without marking individuals (Royle and Nichols 2003); however, abundance estimates from the RN model are sensitive to animals' home range size (Nakashima 2020) and we do not know the effective sampling area of our detection methods (Gilbert et al. 2020). Accordingly, the λ parameter should not be interpreted as a true hare density. Instead, we interpret λ as the mean relative local abundance (hereafter, "relative abundance" for brevity) of our focal species among our sampled sites (Paolino et al. 2018; Gilbert et al. 2020). For more details about the RN model, see Appendix H.

European hare detection via camera-traps was extremely low (see Results) and species identification via footprint detections is prone to misidentification (Pasqualotto et al. 2021). Accordingly, we used only confirmed molecular identification via collected feces to construct detection histories using the three transects surveys (spatial replicates), where "0" denote nondetection and "1" denote detection of hare sign (feces) on each transect survey. In addition, we included a fourth 'opportunistic' survey, that denoted whether hare feces were detected or not during the researcher's movement between transects and camera locations within each site. Although we used spatial replicates surveys without replacement – i.e., we did not perform multiple visits – we believe our relative abundance estimates are unbiased. The use of spatial replicates surveys without replacement can cause biased occupancy estimates when the number of locations inside sampling sites where the focal species is expected to be found is limited across all sites (Kendall and White 2009). European hares are highly mobile organisms, so it is reasonable to assume that if hares occupy a site, they deposit their pellets widely within the areas we sampled for fresh pellets; namely, dirt roads/farm tracks and areas that observers walked between the transects and the camera-traps.

We investigated the relative importance and influence of spatial and temporal heterogeneity and land cover predictors on European hare relative abundance (λ). Specifically, we used detection histories from our 55 sampled sites to fit RN models with different individual detection probability (r) and relative abundance (λ) structures. See Table 1 for our expected a priori relationships for each predictor and RN model parameter (λ and r). We used a two-step modeling approach, where we first investigated predictors influencing per-individual detection probability (r) while using a general structure for the relative abundance (λ). To avoid overparameterization issues, our general λ structure included additive effects of three uncorrelated heterogeneity predictors and the two land cover predictors least correlated with the heterogeneity predictors (Appendix G, Table S2). Specifically, our general λ structure included the compositional (SHDI), configurational (MPSz), and temporal (SugNDVI_sd) heterogeneity predictors and savanna (Sav) and managed forest (ManF) land cover predictors (Table 1). Using this general λ structure, we fit models where individual detection probability, r: 1) varied among transects according to sampling effort or length of the transect (r(Eff)), 2) was different between transect and opportunistic surveys (r(OS)), or 3) was constant among all four surveys (r(.)). Next, using the best-supported individual detection probability structure, we modeled relative hare abundance (λ) as a function of heterogeneity and land cover predictors. We considered all possible λ structures containing additive combinations of up to four of our nine uncorrelated predictors (Appendix G, Table S2). All predictors were standardized ((value – mean value)/standard deviation) and models were fit in R 3.6.2 (R Core Team 2019), using the package 'unmarked' (Fiske and Chandler 2011).

Model selection was based on the AICc (Burnham and Anderson 2002). Our modeling approach resulted in a balanced model set in the final (second) step (Doherty et al. 2012) – i.e., each predictor was included in the same number of models. Accordingly, we use cumulative AICc (w_+) weights to determine the most important predictors ($w_+ > 0.50$; Barbieri and Berger 2004) of the European hare relative abundance (λ). We performed a goodness-of-fit test and estimated the overdispersion parameter (c) using the parametric bootstrap approach (MacKenzie and Bailey 2004) with the global model of the second step (10,000 simulations). The goodness-of-fit test was performed in R 3.6.2 (R Core Team 2019), using the package 'AICcmodavg' (Mazerolle 2020). An estimate of mean European hare occupancy (ψ) by model averaging (Burnham and Anderson 2002) the relative abundance ($\hat{\bar{\lambda}}$) and using Eq. 4 (see Appendix H).

3.4. Results

European hare occurrence was predominately detected via molecular identification of fecal samples obtained during transect surveys (40 sites). As this detection data contains no false positive errors, we used this data to model hare relative abundance (naïve occupancy = 0.73). European hare footprints were detected at 26 sites, but footprint identification is subject to species misidentification (Pasqualotto et al. 2021) and these data would have added hare detections at only four sites where the species was not detected through molecular identification. Consequently, we did not include footprint detections in our subsequent analysis as aforementioned. Similarly, camera-traps detected the European hare at only one site where the species was also detected via molecular data.

We found no evidence of lack of fit or overdispersion in our data ($\chi^2 = 16.01$, p = 0.28, $\hat{c} = 1.18$). We found little evidence that individual detection probability varied with sampling effort or between transect and opportunistic surveys (Appendix I). The null model with constant individual detection probability ($w_+ = 0.60$, Appendix I) was over twice as well-supported as the second-ranked model ($w_{r(.)}/w_{r(OS)} = 0.60/0.25 \cong 2.4$). Model averaged estimate of individual detection probability ($\hat{\bar{r}} = 0.13$; unconditional *SE* = 0.07, CI = 0.04 to 0.36) indicated that if a hare is present in a site, there is only a 13% chance of detecting fresh feces in a single 250-m transect. In occupied sites with low hare relative density, such as in our study area (see below the model averaged relative abundance, $\hat{\bar{\lambda}}$), multiple transects would need to be sampled to confirm the presence of this invasive species.

While European hares appear to be widespread across the study area ($\hat{\bar{\psi}} = 0.96$, *SE* = 0.08), the estimated relative abundance is low ($\hat{\bar{\lambda}} = 3.15$ individuals/site; unconditional *SE* = 1.95; CI 95% = 0.98 to 9.97) and did not vary dramatically among sites. Compositional heterogeneity (SHDI; $w_+ = 0.63$) was the most important predictor of European hare relative abundance (Fig. 2). As expected, sites with higher richness and evenness of land cover types (i.e., high SHDI values) had higher relative abundance of hares ($\hat{\beta}_{SHDI} = 0.65$, *SE* = 0.23, Fig. 3). Sugarcane (Sug; $w_+ = 0.58$) and native savanna cover (Sav; $w_+ = 0.52$) were also important predictors of European hare relative abundance (Fig. 2). We found a positive relationship between the dominant agricultural cover type, sugarcane, and relative hare abundance ($\hat{\beta}_{Sug} = 0.51$, *SE* = 0.20, Fig. 4). We also found lower relative hare abundance in sites with high remaining native savanna cover ($\hat{\beta}_{Sav} = -0.35$, *SE* = 0.19, Fig. 5). It is worth noting though that evidence for the effect of compositional heterogeneity as well as sugarcane and savanna was only found in additive models (see Table 2 and Appendix J). All estimates mentioned above were based on the top-ranked model (Table 2 and Appendix J). Rather surprisingly, configurational heterogeneity, as measured by the mean patch size (MPSz), and temporal heterogeneity of sugarcane crops (SugNDVI_sd) had little to no influence on hare relative abundance (Fig. 2, Appendix J). None of the other land cover types influenced European hare relative abundance.

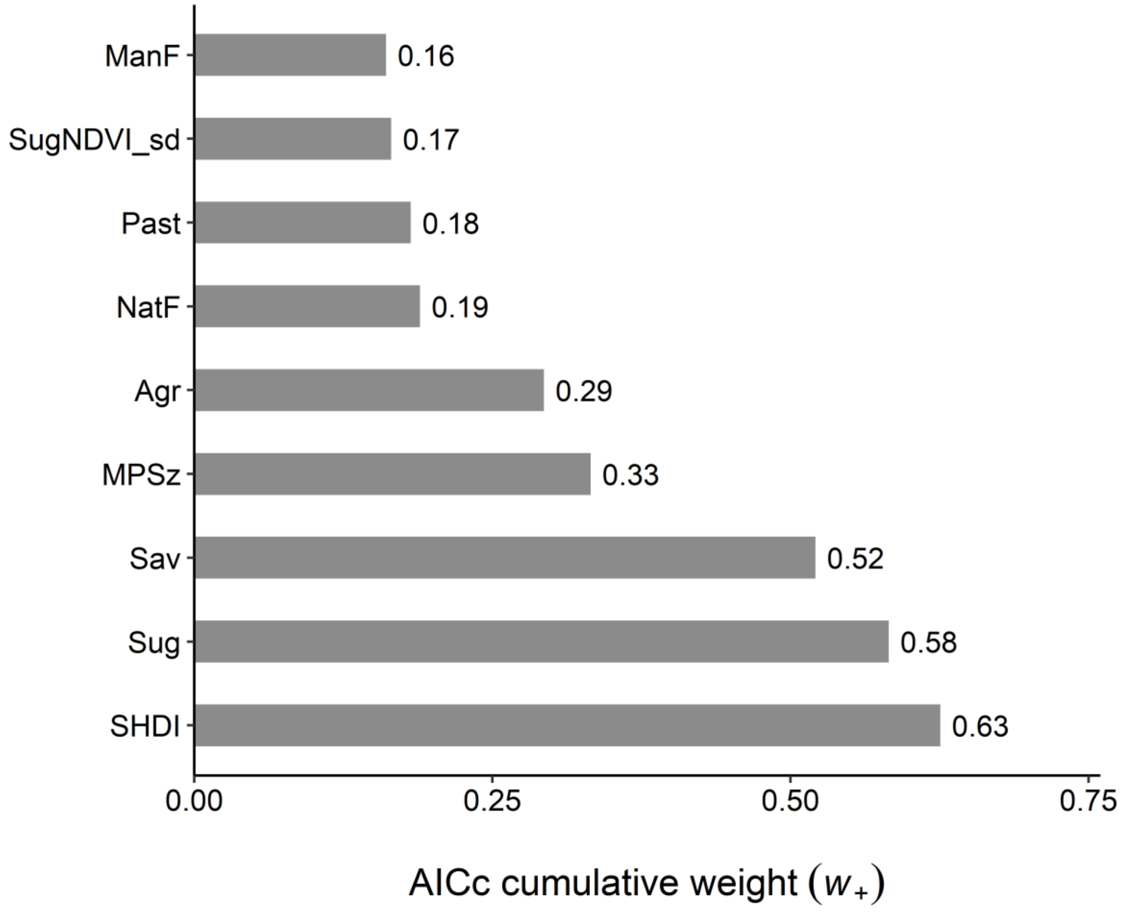

Fig. 2. Cumulative AICc weight of evidence (w_+) for each predictor of the relative abundance (λ) of European hare in the northeast of São Paulo state, southeastern Brazil. NatF = % of Native Forest; Sav = % of Savanna; ManF = % of Managed Forests; Past = % of Pastures; Agr = % of other Agriculture; SHDI = Shannon's Diversity Index; MPSz = Mean Patch Size; SugNDVI_sd = Sugarcane NDVI standard deviation. All predictors were quantified at the 800 m radius scale.

Fig. 3. The positive effect of Shannon's Diversity Index (compositional heterogeneity) on the relative abundance (λ) of the European hare in the northeast of São Paulo state, southeastern Brazil, based on the top-ranked λ structure. The continuous line indicates the estimated relative abundance (λ) and the shaded area represents 95% confidence intervals.

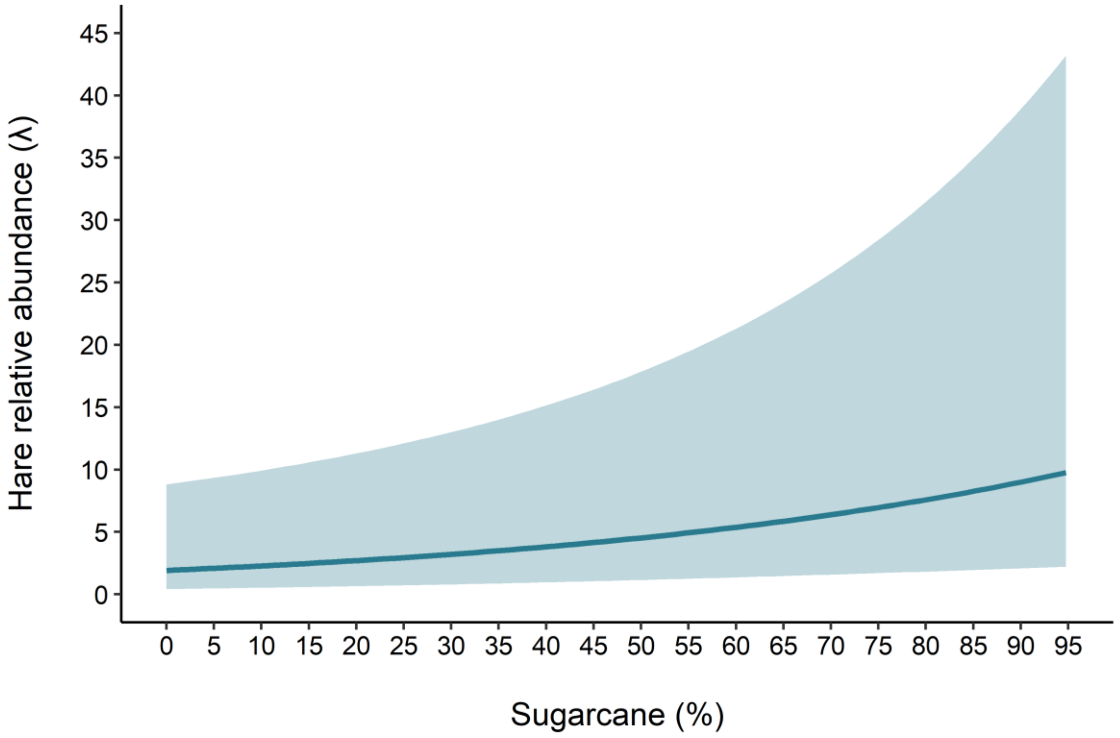

Fig. 4. The positive effect of Sugarcane on the relative abundance (λ) of the European hare in the northeast of São Paulo state, southeastern Brazil, based on the top-ranked λ structure. The continuous line indicates the estimated relative abundance (λ) and shaded area represents 95% confidence intervals.

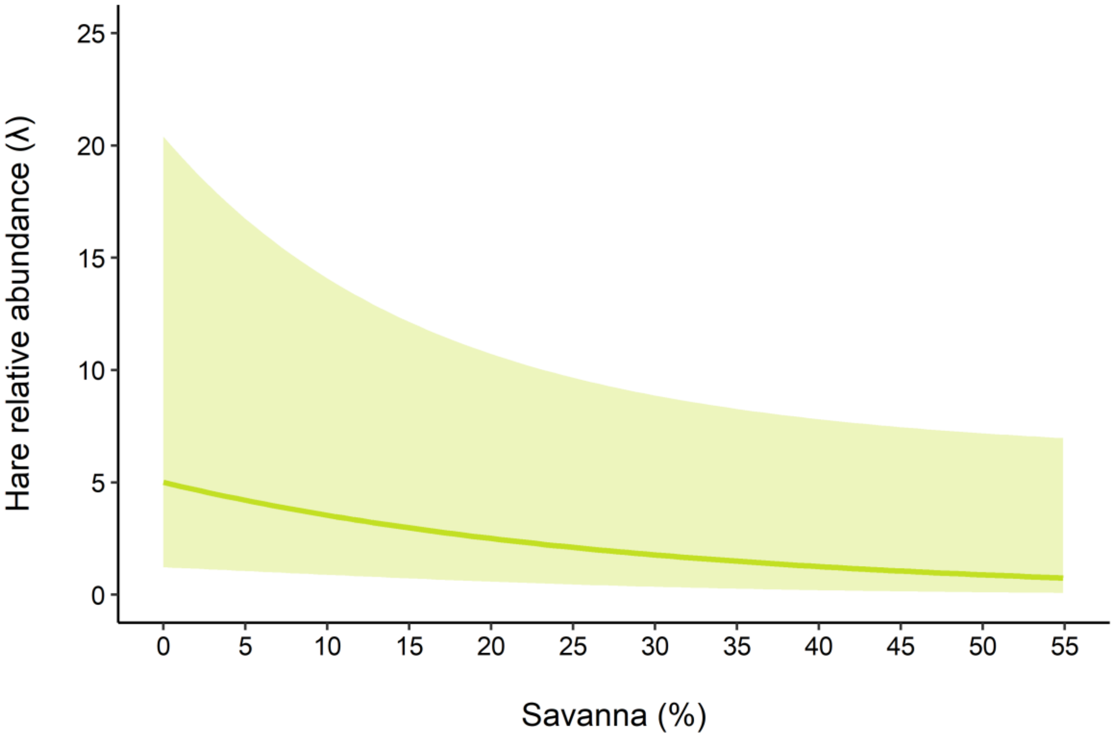

Fig. 5. The negative effect of the Savanna on the relative abundance (λ) of the European hare in the northeast of São Paulo state, southeastern Brazil, based on the top-ranked λ structure. The continuous line indicates the estimated relative abundance (λ) and shaded area represents 95% confidence intervals.

Table 2. Model selection results for the 20 best-supported models of the relative abundance (λ) of the European hare in the northeast of São Paulo state, southeastern Brazil. All models included the best-supported, constant individual detection probability structure (i.e., r(.)). For the full model selection table, see Appendix J.

Model	**AICc**	**ΔAICc**	**w**	**K**	**-2log(L)**
λ(SHDI + Sug + Sav + MPSz)	277.56	0.00	0.08	6	263.81
λ(SHDI + Sug + MPSz)	278.94	1.39	0.04	5	267.72
λ(SHDI + Sav + Agr)	279.31	1.75	0.04	5	268.08
λ(SHDI + Sug)	279.38	1.83	0.03	4	270.58
λ(SHDI + Sug + Sav)	279.40	1.84	0.03	5	268.17
λ(SHDI + Sav + Agr + MPSz)	279.95	2.39	0.03	6	266.20
λ(SHDI + Sug + Sav + Agr)	279.98	2.42	0.03	6	266.22
λ(Sug)	280.47	2.91	0.02	3	274.00
λ(SHDI + Sug + MPSz + Past)	280.60	3.04	0.02	6	266.85
λ(Sav)	280.68	3.12	0.02	3	274.21
λ(SHDI + Sug + MPSz + SugNDVI_sd)	280.98	3.42	0.02	6	267.23
λ(SHDI + Sav + Agr + NatF)	281.11	3.55	0.01	6	267.36
λ(Sug + Sav)	281.22	3.66	0.01	4	272.42

Table 2 continued

Model	**AICc**	**ΔAICc**	**w**	**K**	**-2log(L)**
λ(.)	281.25	3.69	0.01	2	277.02
λ(SHDI + Sug + SugNDVI_sd)	281.26	3.70	0.01	5	270.04
λ(SHDI + Sug + NatF)	281.31	3.75	0.01	5	270.08
λ(Sav + Agr)	281.31	3.76	0.01	4	272.51
λ(SHDI + Sav + Agr + Past)	281.33	3.78	0.01	6	267.58
λ(SHDI + Sug + MPSz + NatF)	281.34	3.78	0.01	6	267.59
λ(SHDI + Sug + Agr + MPSz)	281.45	3.90	0.01	6	267.70

AICc = Akaike Information Criterion for small samples; ΔAICc = AICc of each model *i* minus the lowest AICc; w = Akaike weights; K = number of parameters; -2log(L) = twice the negative log-likelihood. NatF = % of Native Forest; Sav = % of Savanna; ManF = % of Managed Forests; Sug = % of Sugarcane crops; Past = % of Pastures; Agr = % of other Agriculture; SHDI = Shannon's Diversity Index; MPSz = Mean Patch Size; SugNDVI_sd = Sugarcane NDVI standard deviation.

3.5. Discussion

We found that both compositional heterogeneity (quantified by the Shannon's Diversity Index) and land cover types (sugarcane cover and savanna) are key predictors of European hare relative abundance in agricultural landscapes of southeastern Brazil (Fig. 2). Our findings only partially support our hypothesis that spatial and temporal heterogeneity are important predictors of hare relative abundance in Neotropical agricultural landscapes intensively managed. We found that European hare is more likely to locally attain higher relative abundance in landscapes with diverse land cover types (i.e., high compositional heterogeneity), including sugarcane but no savanna. (Fig. 3-5). However, relative abundance estimates were low and did not vary dramatically among our sites (Fig. 3-5), suggesting that the European hare in our study area has not yet attained the dramatically high densities observed in South America regions invaded earlier by this non-native species (Novaro et al. 2000; Kasper et al. 2012; Barbar et al. 2018).

The low relative abundance estimates we found near the hares' northward expansion front in South America may reflect actual low densities. European hare invaded our study area rather recently, probably during the last decade. The first records of this invasive species north of the Tietê River, where our study area is located, are from mid-2000's (Auricchio and Olmos 1999; Rosa et al. 2020). Hence, European hare populations may not have had enough time to attain high local density in our study area. Furthermore, populations occurring near the geographical periphery of the species range tend to have lower density than populations located in the center of the species distribution (the abundant-center hypothesis; Brown 1984; Brown et al. 1995).

Previous studies reported impressive high densities of European hare near the species' release locations in South America (47.5 individuals/km^2, Novaro et al. 2000; 249 individuals/km^2, Barbar et al. 2018), which also roughly coincide with the center of the species distribution in this new, invasive range (Novillo and Ojeda 2008). Far from being a biogeographical rule, the abundant-center hypothesis has often received empirical support (39%, Sagarin and Gaines 2002) and might explain the low relative abundance estimates we found. Understanding the geographical pattern in invasive species abundance may provide valuable insights on limiting factors of invader spread and genetic diversity distribution among populations, which are useful to guide control and management actions (Guo 2014). No study has yet investigated the abundance distribution pattern of European hare populations throughout South America, but based on our findings future studies should consider increasing sampling effort or sampling more transects to increase individual detection probabilities and improve estimator precision, especially in areas near the invasion front where local abundances may be low.

Still, small but expanding local populations play a key role in the invasion process of terrestrial invaders (Moody and Mack 1988). Biological invasions usually do not occur through individuals radiating from a single large focal population but on the continued establishment of small nascent foci in outlying areas of the invasive species distribution (Moody and Mack 1988; With 2002; Forsyth et al. 2019). Among the nascent foci, those located in places that better fulfill the niche requirements of the invasive species can become invasion hubs, allowing invasive populations to persist under unfavorable conditions and continue to spread (Florance et al. 2011). Based on our findings, landscapes that locally combine high diversity of land cover types, sugarcane crops and no native savanna have relatively high hare abundance. Such landscapes may harbor satellite populations less susceptible to local extinction due to environmental and demographic stochasticity and serve as key source of dispersing hares fostering the ongoing northward range expansion of this invader in South America (de Faria et al. 2015; Rosa et al. 2020). Theoretical and empirical studies provide evidence that eradicating part of these satellite populations is an effective strategy to curb the overall rate of spread of invasive plant and vertebrate species (Moody and Mack 1988; Cook et al. 1996; Florance et al. 2011).

Our results suggest that preservation of open canopy Cerrado savannas and flooded wetlands may hamper or prevent this invader from reaching locally large populations. Savannas in our study area may not completely satisfy the European hare niche requirements (Hutchinson 1957). "Cerrado sensu stricto" has a considerable amount of grasses due to a lower (19%, on average) canopy cover (Goodland 1971) but is typically dominated by small trees and shrubs (Goodland 1971; Durigan and Ratter 2006) that hinder horizontal visibility. Although grasses are a key food resource for European hare (Chapuis 1990; Lush et al. 2017), sites with high mid-story cover (Lantschner et al. 2013) and low horizontal visibility (Gantchoff and Belant 2015) are less likely to be used by this species. The strong active antipredatory behavior of European hare may help explain this species avoidance for vertically structured and flooded habitats. In general, hares are well adapted to escape from predators by running, reaching high speeds (up to 80 km/h) during full flight (Chapman and Flux 1990). However, under predation risk, European hare only achieve high speeds in open habitats with low vertical vegetation structure (Weterings et al. 2016). Furthermore, hare resting sites are open dens, often selected to allow wide views to anticipate stealth predators (Tapper and Barnes 1986; Angelici et al. 1999; Petrovan et al. 2013). Hence, native savannas of our study area may represent suboptimal habitats for the European hare, where this species does not achieve dense populations.

The present study also adds further evidence that compositional heterogeneity is a positive predictor of European hare abundance (Tapper and Barnes 1986; Lewandowski and Nowakowski 1993). This positive effect may be related to the dietary requirements of this species. European hares are selective feeders that preferably feed on field crop plants (e.g., beet, soybean) and also on a high diversity of non-crop weeds/grasses rich in crude fat and protein (Schai-Braun et al. 2015). The spatial coexistence of different crop types may provide suitable foraging conditions year-round. In contrast, hares inhabiting landscapes with low diversity of land covers may face food shortages. Indeed, adult hares living in agricultural landscapes with low crop diversity have low body weights (Frylestam 1980). Further, Tapper and Barnes (1986) found European hares increasing their home ranges to include more diverse types of land covers when living in low-crop diversity farmlands, a possible strategy to supply their nutritional needs.

Contrasting the long-term decline in hare populations in Europe following agriculture intensification (Tapper and Parsons, 1984; Panek and Kamieniarz, 1999; Smith et al. 2005), we found evidence that sugarcane proportion, a monoculture intensively managed, positively influences European hare relative abundance in our study area. Even though our data prevent us from asserting the mechanism behind this association, we tentatively advance an explanation. Agricultural field margin is a habitat selected by hares in Europe, possibly due to the diversity of high-quality food (Petrovan et al. 2013; Schai-Braun et al. 2013). We hypothesize that ruderal plants growing in sugarcane field margins may compensate for the absence of other crop plants inside sugarcane plantations, providing appropriate foraging conditions for European hares. Leon et al. (2017) found high weed (forbs and grasses) richness (120 species) growing in areas managed for sugarcane crops in the dry tropics of Costa Rica. Interestingly, weed richness in the field margins almost doubled that in the management areas (rows and furrows) located inside the sugarcane crop fields (Leon et al., 2017). Low use of herbicides, which is typically sprayed just after sugarcane planting (Nihei et al., 2015), combined with artificial soil fertilization and light availability provide appropriate conditions for weeds to thrive in sugarcane field margins (Leon et al., 2017). Moreover, our findings related to the sugarcane temporal heterogeneity may add support to the hypothesis that sugarcane field margins are key element accounting for the positive association between European hare relative abundance and sugarcane crops. The unexpected weak influence we found for sugarcane temporal heterogeneity on hare relative abundance suggests that sugarcane itself may not provide high-quality food and shelter for hares. Hence, high diversity of ruderal plants growing on sugarcane field margins might play a key food resource for European hares. Still, we lack studies investigating this invasive species food habits associated with sugarcane crops in the Neotropics.

Also contrary to our a priori expectations, we did not find configurational heterogeneity to be a key predictor of European hare relative abundance. We suspect this might be related to the breakdown level of our land cover maps, even though our mapping effort improved accuracy classification compared to MapBiomas (Souza et al., 2020). European hare abundance is often associated with configurational heterogeneity when this metric quantifies the size of individual crop fields (e.g., Vaughan et al. 2003; Pavliska et al. 2018). The relatively wide geographic range investigated in the present study and the limited spatial resolution of land cover data available prevented us from further delimiting crop fields in our mapping. A finer crop field delimitation would allow to quantify the density of sugarcane field margins and investigate its effect on hare relative abundance, shedding some light on the association of this invader with an intensively managed crop. We thus encourage further studies to investigate configurational heterogeneity using high-resolution land cover to clarify its importance in explaining European hare abundance in Neotropical agricultural landscapes.

Our results provided evidence that areas that combine high compositional heterogeneity, including sugarcane, and no cover by native savanna are more likely to locally sustain higher relative abundance of European hare. Considering the current trend of commodity row crops expansion replacing the Brazilian native Cerrado savannas (Zalles et al. 2019) and the Brazilian leadership in sugarcane production (FAOSTAT 2020), we expect that invasion of this non-native species will continue to expand northwards as previously suggested (Pasqualotto et al. 2021). Brazil is a key player in the international commodity market (Bordonal et al. 2018; Zu Ermgassen et al. 2020). From 2000 to 2014 croplands in the Brazilian north and northeast regions, notably soybean, replaced huge area of Cerrado (Zalles et al. 2019), a habitat that precludes high relative abundance of European hare as demonstrated here. Brazil is also the world's largest sugarcane producer (FAOSTAT 2020), a crop type associated with higher European hare relative abundance, according to our findings. These results suggest that retaining native vegetation in rural landscapes, either via public protected areas or permanent preservation areas and legal reserves protected by the Brazilian Forest Act within rural properties, is an important obstacle to the expansion of this invasive species. Our study therefore reinforces the need for rural owners to adhere to the Brazilian Forest Code, via implementation or restoration of these native areas in their properties. We further stress that monitoring these Cerrado landscapes with low or no savanna coverage in the transition of sugarcane crops with other land covers is highly advisable, since they might play a key role in the northward spread of this invader, with potential to become abundance hotspots in a near future (Brown 1995).

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4. CHAPTER III: NATIVE FOREST AND PROXIMITY TO HUMANS ARE STRONGER DRIVERS OF BRAZILIAN COTTONTAIL HABITAT USE THAN INVASIVE EUROPEAN HARE

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Abstract

Human activities and biological invasions have caused unprecedented biodiversity loss over the past 500 years. Proximity to humans drives the spatial distribution of species toward less disturbed habitats. Invasive species can competitively exclude native species, but species may coexist due to different habitat preferences. Here, we investigated how proximity to farms and the presence of the non-native European hare (*Lepus europaeus*) influence the habitat use by the Brazilian cottontail (*Sylvilagus minensis*) in southeastern Brazil. We found that the probability of cottontail site use increased with native forest cover and decreased with farmhouse proximity, ranging from 0.05 (SE = 0.02) at sites close to farmhouses (≅ 900 m) with no native forest to 0.70 (SE = 0.15) at sites far from farmhouses (≅ 2500 m) dominated by native forest. Higher risk of harassment and predation by free-roaming dogs and cats may explain the negative effect of farmhouse proximity on cottontail habitat use. We found little evidence for competitive exclusion by the European hare. Instead, our results suggest that the two species spatially segregate due to different habitat preferences. While the European hare more likely uses farmland in its native and non-native range, our results suggest that the Brazilian cottontail is a forest dweller. Although we found only weak evidence of competitive exclusion, we advise caution because invasive species may delay the onset of detrimental effects due to initial low population densities in newly invaded areas as is the case of the European hare in southeastern Brazil.

Keywords: occupancy modeling, lagomorph, human disturbance, spatial niche segregation, tapeti, competitive exclusion, interspecific competition, non-native species.

4.1. Introduction

Human activities have caused unprecedented biodiversity loss over the past 500 years (Barnosky et al. 2011; Dirzo et al. 2014), with vertebrate extinction rates more than 100 times higher than the pre-human background rate (Ceballos et al. 2015). The range and abundance of remaining vertebrate species are decreasing, especially in the tropics where most declining mammal species are found (Dirzo et al. 2014). Human activities (e.g., hunting, recreation, and aircraft) often disrupt animal movement patterns more strongly than habitat alterations from agricultural encroachment and logging (Doherty et al. 2021), forcing spatial distribution shifts towards less affected habitats (Anton et al. 2020; Lewis et al. 2021). While some species (domestic dogs, raccoons) often occur near areas of increased human activity (e.g., human habitations), other species occur less frequently in these human-disturbed areas (Ordeñana et al. 2010). Humans also induce stronger fear responses in wildlife than natural predators (Clinchy et al. 2016; Suraci et al. 2019), which can lead to altered activity patterns such as increased nocturnal behavior (Gaynor et al. 2018).

The detrimental effects of human activities (hereafter defined as anthropogenic disturbances that occur near human habitations) are not the only human-related threats to wildlife conservation. Human-facilitated invasion by non-native species is another major driver of biodiversity loss (Hoffmann et al. 2010; Blackburn et al. 2019). Invasive species are directly related to 33% of recent animal extinctions (261 spp.) and are currently recognized as the main extinction driver of plants and animal species (Blackburn et al. 2019; but see IPBES 2019). Invasion success of non-native species may result from the competitive exclusion of native species (MacDougall and Turkington 2005), especially when diets and activity patterns substantially overlap (e.g., Harris and Macdonald 2007). Alternatively, non-native and native species may naturally segregate in space due to their different evolutionary histories and habitat preferences, allowing them to coexist (Crowley et al. 2018, Goyal et al. 2019). Invaders may become abundant and dominant in invaded communities without strongly interacting with native species; for example, adaptations to the pervasive anthropogenic disturbances may allow non-native species to thrive in human-modified environments where some native species are rare (MacDougall and Turkington 2005; Crowley et al. 2018; Goyal et al. 2019). While the influence of human activities and biological invasions on spatial distribution and habitat use has been extensively investigated for many native animal taxa (Cayuela et al. 2013; Kass et al. 2020; Nickel et al. 2020), little is known about how these threats affect native South American cottontails.

The habitat use patterns of the South American cottontails are poorly known, especially for newly recognized species (Ruedas et al. 2017, 2019; Silva et al. 2019) occurring in human-dominated regions. Cottontails in Brazil are nocturnal animals (Gómez et al. 2005; Carvalho et al. 2019), usually found in tropical forests, savannas, and gallery forests (Fonseca and Redford 1984). Observational data suggest these cottontails are not forest interior species in the Amazon; instead, locations used are often forest edges and disturbed fragments (Júnior et al. 2005).

Anecdotal evidence also suggests cottontails use croplands in northern Brazil (Emmons and Feer 1997). In addition to little known habitat requirements, the taxonomy of Brazilian cottontails is also poorly understood. *Sylvilagus brasiliensis* Linnaeus, 1758 was considered a widely distributed cottontail species, ranging from northern Argentina to Mexico (Chapman and Flux 1990). However, recent evidence suggests this widespread taxon is a complex of species likely threatened by human activities (Ruedas et al. 2017; Silva et al. 2019). In southeastern Brazil, a newly recognized cottontail species (*Sylvilagus tapetillus* [Thomas, 1913]) is either restricted to a narrow coastal area or already extinct due to intense anthropogenic disturbances in this region (Ruedas et al. 2017; Silva et al. 2019). Other cottontails from southeastern Brazil have unclear taxonomic status – pro tempore *Sylvilagus minensis* [Thomas 1901] hereafter, Brazilian cottontail (Ruedas et al. 2017) and might also be negatively impacted by human activities or the widespread and abundant non-native European hare (*Lepus europaeus* Pallas, 1778).

Competition between European hare and Brazilian cottontail has long been suggested given these species' ecological similarities (Grigera and Rapoport 1983; Novillo and Ojeda 2008; de Faria et al. 2015). Equivalent to the Brazilian cottontail, European hares are mostly nocturnal (Schai-Braun et al. 2012). Farmlands are the primary habitat of the European hare in its native range (Tapper and Barnes 1986; Thulin 2003), but this species also uses forest edges, especially as resting sites when agricultural fields do not provide adequate vegetation cover (Petrovan et al. 2013). European hare was introduced throughout the world and has successfully invaded most continents (Barbar and Lambertucci 2018), given its high dispersal capacity (Grigera and Rapoport 1983; de Faria et al. 2015) and reproduction rate (Chapman and Flux 1990). Non-native European hares have spatially replaced native mountain hare populations in Northern Ireland (*Lepus timidus hibernicus*) and Sweden (*Lepus timidus*) likely through competition (Thulin 2003; Caravaggi et al. 2016). In southern South America, introduced hares rapidly expanded northwards, reaching southeastern Brazil during the last decades (Auricchio and Olmos 1999; Rosa et al. 2020). Despite ecological similarities of European hares and Brazilian cottontails, and negative effects of the hare in other areas, no study has been conducted to determine if competitive exclusion is occurring. Therefore, understanding how European hares influence Brazilian cottontails' spatial distribution and habitat use is paramount to inform conservation and management actions.

In this study, we use an occupancy modeling framework (MacKenzie et al. 2018) to investigate the effects of proximity to human habitation (mostly farmhouses in our study), presence of the European hares, and other habitat variables on the probability that Brazilian cottontails use areas in southeastern Brazil. Our study included areas covered predominantly by native vegetation (protected areas) and areas where native vegetation and agricultural land coexist (outside protected areas). We hypothesized that Brazilian cottontail habitat use was either: 1) not influenced by non-native hare presence, proximity of farmhouses, or the amount of various habitat covariates (null hypothesis), 2) only influenced by the human-modified habitats (i.e., the amount of sugarcane plantations, managed forests, pastures), 3) only influenced by the native habitats (i.e., the amount of native forests, savannas, riverine areas, and native forest edges), 4) only influenced by farmhouse distance; 5) only influenced by non-native hare presence; 6) influenced by the native habitats, but this relationship depended on farmhouse proximity (additive and interactive relationships), or 7) influenced by the native habitats, but this relationship depended on non-native hare presence (additive and interactive relationships). If spatial niche segregation is the main process driving the native cottontail habitat use, we would expect the species probability of use to be independent of hare presence and positively influenced by the amount of native habitat and distance from the nearest farmhouse. Alternatively, if hares competitively exclude native cottontails, we expect lower probability of habitat use by cottontails at sites occupied by the non-native hare.

4.2. Methods

4.2.1. Study areas

Our study was conducted in three areas from northeast São Paulo state, southeastern Brazil (Fig. 1). Historically, this region is a transition zone between the Cerrado and the Atlantic Forest. The climate is classified as an equatorial savanna with dry winter – from April to September (Kottek et al. 2006). Each study area comprises privately- or state-owned protected areas and a surrounding 5-km buffer. Study Area 1 includes two state-owned protected areas: Jataí Ecological Station (~ 9000 ha, JES) and Luiz Antônio Experimental Station (~ 2000 ha). These protected areas are mainly covered by sclerophyllous woodland of the Cerrado domain, with a large continuous block of native forest (~ 9000 ha) inside JES. Sugarcane crops dominate the 5-km buffer of Area 1 (Fig. 1a). Study Area 2 includes a privately owned protected area, the Cara Preta Forest (~ 4500 ha), that mainly consists of riparian forests protected by the Native Vegetation Protection Law (NVPL) of Brazil (Brancalion et al., 2016). *Eucalyptus* spp. plantations dominate the 5-km buffer of Area 2 (Fig. 1b). Study Area 3 includes a state-owned protected area and a private area also protected by the NVPL: Cajuru State Forest (~ 2100 ha) and Dois Córregos Forest (~ 2000 ha), respectively. Flooded wetlands and open Cerrado formations –

mostly "cerrado sensu stricto" and grasslands dominated by invasive grasses – cover the protected areas of Area 3. The 5-km buffer of Area 3 is comprised of similar percentages of *Eucalyptus* spp. plantations and sugarcane crops (Fig. 1c).

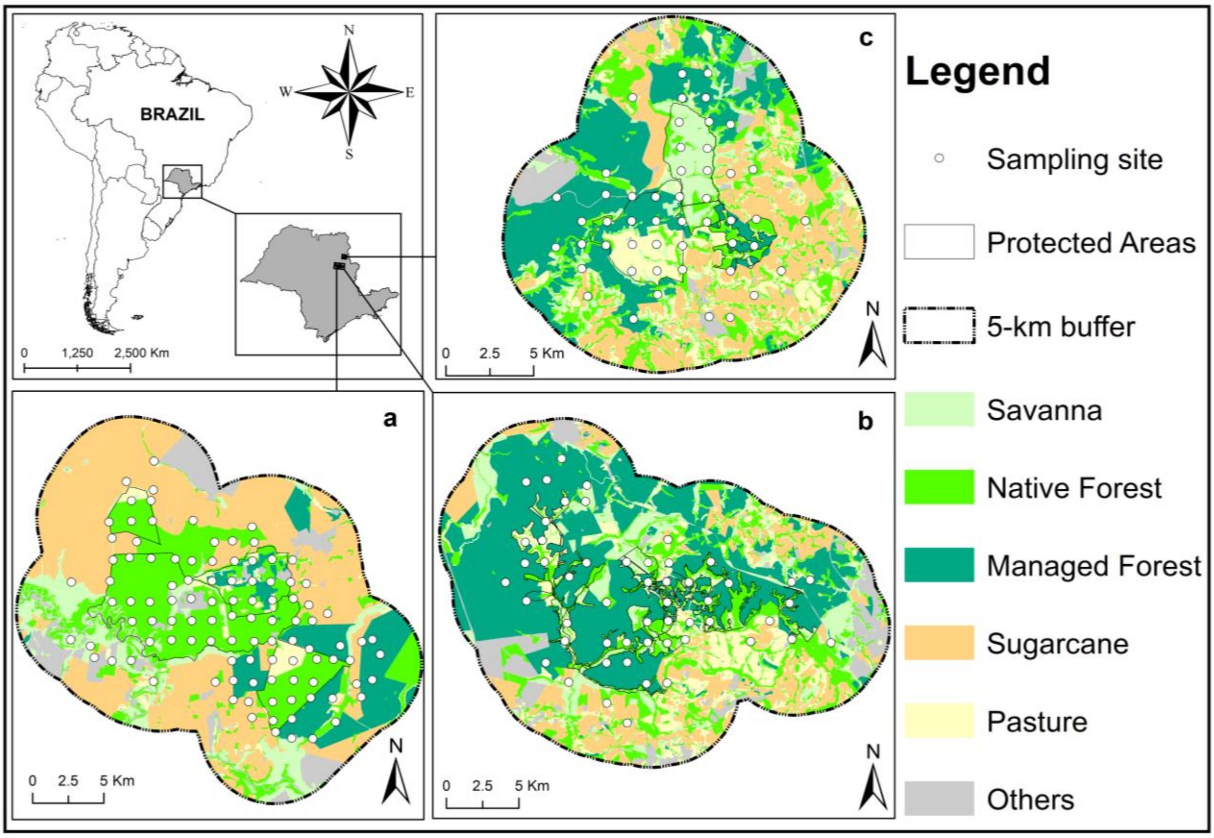

Fig. 1. Location of sampled sites inside our three study areas from southeastern Brazil: **a** = Jataí Ecological Station and Luiz Antônio Experimental Station; **b** = Cara Preta Forest; **c** = Cajuru State Forest and Dois Córregos Forest.

4.2.2. Data collection and covariates

Species detection-nondetection data were obtained from 200-ha sites (n = 205) sampled during the dry seasons (April-September) of 2013 and 2014. Sites were randomly selected from a regular grid of square cells (1.4 km x 1.4 km wide) overlaid onto each study area. Each site was large enough to harbor multiple European hares and Brazilian cottontails; the home range sizes of European hare and *Sylvilagus* spp. are ≅ 30 ha and ≤ 3 ha, respectively, but the home range size for the Brazilian cottontail is unknown (Jones et al. 2009). We employed two detection methods at each site: a camera-trap (Reconyx, model HC 500) and a 200-m transect survey for footprints conducted on a dirt road/farm track. Camera-traps were fixed on tree trunks about 40-60 cm above the ground and set to record continuously (24 h.day^{-1}) for approximately 30 days. Due to logistic and operating problems, some cameras were active for more or less than 30 days, with an average effort of 31.01 camera days (*SD* = 2.31 camera days). We surveyed each transect twice for footprints of the two focal species – first when the camera-trap was deployed and about 30 days later when cameras were removed. We identified lagomorph footprints with the aid of track guides (Borges and Tomás 2008; Becker and Dalponte 2013; Angelo 2017) and a pachymeter for footprint measurements. Our sampling design provided a similar number of sites in areas predominantly covered by native habitats (protected areas) and areas where native and human-modified habitats coexist (5-km buffers). Specifically, we sampled 101 sites inside protected areas (Area 1 = 52, Area 2 = 25, and Area 3 = 24) and 104 inside the 5-km buffers (Area 1 = 50, Area 2 = 28, Area 3 = 26).

To test our hypotheses regarding the habitat use of the Brazilian cottontail, we quantified covariates after mapping the main land cover classes in our study areas. Our map is highly accurate (≅ 90 %, see section 2.2.3 in Chapter I) and provides finer land cover data (1:20,000 scale, 10 m pixel resolution) than other available maps – e.g., MapBiomas, 30 m pixel resolution (Souza et al. 2020). Using our map, we quantified the amount of human-modified habitats as the percentage of each 200-ha site covered by: Sugarcane (Sug), Managed Forests (ManF), and Pastures (Past). The amount of native habitat was quantified as the percentage of area covered by Native Forest (NatF) or Savanna (Sav), and the density of Streams (StrD) and native Forest Edges (FED). We also quantified the conditional occupancy probability of the invasive European hare (H) at each site (see Appendix K for details) and the proximity to the nearest farmhouse (FDist). We performed correlation analyses among these covariates. Stream density (StrD) was strongly correlated ($|r| > 0.7$, Dormann et al., 2013) with native Forest Edge Density (FED) (Appendix L, Table S1). To avoid collinearity issues, we did not include these two covariates together in any occupancy model described in the next section. All covariates were quantified in R 3.6.2 (R Core Team 2019) using the 'landscapemetrics' package (Hesselbarth et al. 2019).

We also quantified covariates that may influence native cottontail detection. These covariates are directly related to each survey method (method specific) or vary over time (e.g., temperature, rainfall, sample season). We considered the method specific covariates, including the number of days a camera was operating within each 5-day period (Camera-trap Effort, CT_eff) and Camera Position (on/off dirt road/farm track; CT_pos), and a transect-specific covariate that differentiate among early and late season surveys (TS). Regardless of the survey method, we also allowed detection probability to vary with local weather conditions (Rainfall (Rainf) and Daily Minimum Temperature (MinTemp)), among the primary and 'shoulder' months of the dry seasons (S), or among months (Time-varying (t) or Trend (T, Sq_T), and years (Year, Y). For more details about covariates, see Table 1.

Table 1. Covariate name, type, description, and parameters modeled as a function of each covariate. Parameters include probability of use (ψ) by the Brazilian cottontail, detection probability with the certain (r_{11}, camera trap) and uncertain (p_{11}, transect) methods, and a misidentification parameter representing probability of false detection (p_{10}, transect only). Covariates were determined for 200-ha sites (n = 205) in the northeast of São Paulo state, southeastern Brazil.

Covariate	Type	Description	Parameter	Range
Site-specific covariates				
Sugarcane (Sug)	Human-modified habitat	Percentage of sugarcane crops.	ψ, $p_{11} = r_{11}$	0.00 – 95.06
Managed Forest (ManF)	Human-modified habitat	Percentage of planted forests, mostly *Eucalyptus* spp. but also *Pinus* spp. plantations.	ψ, $p_{11} = r_{11}$	0.00 – 100.00
Pasture (Past)	Human-modified habitat	Percentage of pasturelands predominantly represented by exotic grasses.	ψ, $p_{11} = r_{11}$	0.00 – 90.28
Native Forest (NatF)	Native habitat	Percentage of native forest, including “cerradão”, semi-deciduous, deciduous, and riparian forests.	ψ, $p_{11} = r_{11}$	0.00 – 100.00
Savanna (Sav)	Native habitat	Percentage of open native vegetation dominated by flooded wetlands and “cerrado sensu stricto”, but also including “campo cerrado” and regenerating areas.	ψ, $p_{11} = r_{11}$	0.00 – 90.69
Stream Density (StrD)	Native habitat	Total length (m) of streams inside each sampled site, divided by the site area.	ψ, $p_{11} = r_{11}$	0.00 – 26.31
Forest Edge Density (FED)	Native habitat	Total length (m) of native forest edges inside a sampled site, divided by the site area. The higher the edge density, the higher the native forest fragmentation in each site.	ψ, $p_{11} = r_{11}$	0.00 – 95.52

Table 1 continued

Covariate	Type	Description	Parameter	Range
Farmhouse Distance (FDist)	Human proximity	Mean linear distance (m) from random points (≅ 46 points, *SD* = 14) inside each sampled sites to the nearest farmhouse.	ψ, $p_{11} = r_{11}$	252.5 – 4482.5
Hare (H)	Hare presence	Conditional occupancy probability of the European hare (Pasqualotto et al. 2021).	ψ, $p_{11} = r_{11}$	0.01 – 1.00
		Time-varying covariates		
Time (t)	Monthly	Categorical covariate to account for variation in the true positive detection probability over time (months).	$p_{11} = r_{11}$	0, 1
Trend (T, Sq_T)	Monthly	Covariate to model the true positive detection probability linearly increases over time (sampling months). We also considered a squared trend (Sq_T) structure to account for a non-linear effect.	$p_{11} = r_{11}$	1, 6; 1, 36
Seasonality (S)	Monthly	Categorical covariate differentiating primary months during the dry season (May - August, ”1”) from “shoulder months” (April and September, “0”).	$p_{11} = r_{11}$	0, 1
Year (Y)	Years	Categorical covariate differentiating sites sampled in 2014 (1) or 2013 (0).	$p_{11} = r_{11}$	0, 1
Daily Minimum Temperature (MinTemp)	Weather	The average daily minimum temperature (°C) in each site during the month each site was sampled.	$p_{11} = r_{11}$	9.60 – 16.53
Rainfall (Rainf)	Weather	Accumulated rainfall (mm) in each sampled site.	$p_{11} = r_{11}$	0.70 – 117.70

Table 1 continued

Covariate	**Type**	**Description**	**Parameter**	**Range**
		Survey method covariates		
Camera-trap Position (CT_pos)	Method-specific	Categorical covariate differentiating camera-traps that locally sampled dirt roads/farm tracks (1) from cameras that sampled other local environments (0).	r_{11}	0, 1
Camera-trap Effort (CT_eff)	Method-specific	The number of sampling days of each camera-trap occasion.	r_{11}	0.21 – 13.69
Transect Surveys (TS)	Method-specific	Categorical covariate differentiating transect surveys conducted during camera-trap deployment (0) and camera-trap removal ≅ 30-days later (1).	p_{10}, p_{11}	0, 1

Temperature data were provided by the Agronomic Institute of Campinas (IAC). Rainfall data were provided by the National Institute of Meteorology (INMET).

4.2.3. Analysis

We tested our hypotheses regarding how the presence of European hare and the proximity of farmhouses affect the habitat use of the Brazilian cottontail using occupancy modeling (MacKenzie et al. 2018). We confidently identified European hare and Brazilian cottontail with camera-trap photos because the species have striking morphological differences – European hare has longer ears with black tips, longer legs and hind feet, and larger body size (3-5 kg) than the cottontail (< 1 kg, Chapman and Flux 1990; Ruedas et al. 2017). However, cottontail footprints are only partially imprinted – typically four nails and no toes (Borges and Tomás 2008; Becker and Dalponte 2013) – and prone to misidentification. Species misidentification can lead to false positive detections – i.e., sites that are incorrectly assigned as occupied by the target species (Miller et al. 2011), an observational error that introduces serious biases in occupancy analyses (McClintock et al. 2010). A preliminary analysis suggested that cottontail footprint identifications likely contained false positive detections (Appendix M, Table S1). Accordingly, we used the misidentification model (Miller et al. 2011) to investigate our hypotheses assuming that footprints observed during the transect surveys are prone to misidentifications (uncertain method) and camera-trap photos allowed species identification with certainty (certain method; Appendix M). Specifically, we used cottontail detection-nondetections from camera trapping and transect surveys to create detection histories with eight occasions. The first (1) and last (8) occasions represent the transect surveys conducted during the camera-trap deployment and removal, respectively. Occasions 2-7 represent 5-day camera-trap surveys (30 days total). We investigated our competitive exclusion hypotheses by using the estimated conditional occupancy probability of the European hare (H) as a covariate in modeling cottontail occupancy, as has been done by other studies (Amburgey et al. 2014; Steen et al. 2014; Paschoal et al. 2018).

We used the cottontail detection histories from 205 sites to fit models with different structures for the occupancy (ψ) and two types of detection parameters – false positive detection (p_{10}) for the uncertain method (transect) and true positive detection for certain (r_{11}, camera trapping) and uncertain (p_{11}, transect) methods. See Table 1 for details about the covariates used to model each parameter (p_{10}, p_{11}, r_{11}, and ψ). We interpreted the occupancy parameter (ψ) as the probability that a 200-ha site was used at least once by the Brazilian cottontail during the 30-day sampling period (Lele et al. 2013; MacKenzie et al. 2018) – hereafter, probability of use for simplicity. False positive detection is the probability of detecting a cottontail during a transect survey, given the site was not used by the cottontails. True positive detection is the probability of detecting a cottontail during a transect (p_{11}) or 5-day camera-trap survey (r_{11}), given the site was used by the cottontails.

We used a sequential-by-sub-model strategy with a p-first modeling approach, which works well for static occupancy models (Morin et al. 2020), such as the misidentification model. We first investigated covariates influencing the native cottontail detection probability parameters (p_{10}, p_{11}, r_{11}) while using a general structure for the probability of use (ψ). We used the general ψ structure to avoid forcing any ψ variation onto the detection parameters (MacKenzie et al. 2018, page 210). To avoid using an arbitrary structure, we defined our general ψ structure as the most parsimonious structure among all additive combinations of up to three ψ covariates using constant detection parameters: ψ(ManF + FDist + H). We fit 46 models with different detection parameter structures in the first modeling step (Appendix N, Table S1). Specifically, we considered structures where true positive detection probability parameters were equal for the two survey methods but varied as a function of habitat types, farmhouse proximity, hare presence, time-varying, sampling season, and weather covariates ($p_{11} = r_{11}$; Appendix N, Table S1 models 1-34). We also considered structures where the true detection probability differed between transect and camera surveys and was a function of method-specific covariates, such as camera position and effort, or between early and late transect surveys ($p_{11} \neq r_{11}$; Appendix N, Table S1 models 35-46). Regardless of whether or not the two survey methods differed in true positive detection probability of native cottontails, we considered structures where the probability of falsely detecting cottontail tracks on transect surveys was constant among surveys (p_{10}(.); Appendix N, Table S1 models 1-17, 35-40,) or differed between the first and last survey conducted at each site (i.e., transect surveys, p_{10}(TS); Appendix N, Table S1 models 18-34, 41-46).

Next, using the best-supported structure for each detection parameter, we modeled cottontail probability of use (ψ) as a function of habitat covariates, farmhouse proximity, and conditional hare occupancy (Table 2). To test our a priori hypotheses regarding the influence of human-modified and native habitats, farmhouse proximity and non-native hare presence on Brazilian cottontail habitat use, we considered a null ψ(.) structure, nine univariate structures containing each covariate alone (Table 2: models 2-4, 6-9, 11-12), one additive ψ structure containing all human-modified habitat covariates (Table 2: model 5), and another additive ψ structure containing the two native land cover covariates (Table 2: model 10). We also considered eight ψ structures containing the additive and interactive combinations involving farmhouse proximity (FDist) and each of the four native habitat covariates (Table 2: models 13-20) and eight ψ structures containing the additive and interactive combinations involving the conditional hare occupancy covariate (H) and each native habitat covariates (Table 2: models 21-28). These models examined whether farmhouse proximity and non-native hare presence modified the relationship between the probability of cottontail use and native habitats. We performed the occupancy analyses in program Mark 9.0 (White and Burnham 1999) and the correlation analyses in R 3.6.2 (R Core Team 2019).

We selected the best-supported models based on the Akaike Information Criterion, corrected for small sample – AICc (Burnham and Anderson 2002). We used the Akaike weights (wi, weight of evidence of model i) and evidence ratios (wi/wj) to interpret results of each modeling step. We reported all models but dismissed those that included uninformative (pretending) variables – i.e., variables that do not improve the model fit (Arnold 2010).

Table 2. List of models used to investigate our hypotheses regarding Brazilian cottontail habitat use. All models included the best supported detection structure p_{10}(.) $p_{11}=r_{11}$(S), but different structures for probability of use (ψ).

	Model	**Hypotheses**
1	ψ(.)	1) Null hypothesis
2	ψ(Past)	2) Only influenced by the human-modified habitats
3	ψ(Sug)	
4	ψ(ManF)	
5	ψ(Past + Sug + ManF)	
6	ψ(Sav)	3) Only influenced by the native habitats
7	ψ(NatF	
8	ψ(StrD)	
9	ψ(FED)	
10	ψ(Sav + NatF)	
11	ψ(FDist)	4) Only influenced by farmhouse proximity
12	ψ(H)	5) Only influenced by non-native hare presence
13	ψ(FDist + Sav)	6) Influenced by native habitats, but dependent on farmhouse proximity
14	ψ(FDist + NatF)	
15	ψ(FDist + StrD)	
16	ψ(FDist + FED)	
17	ψ(FDist * Sav)	
18	ψ(FDist * NatF)	
19	ψ(FDist * StrD)	
20	ψ(FDist * FED)	

Table 2 continued

	Model	Hypotheses
21	ψ(H + Sav)	7) Influenced by native habitats, but dependent on non-native hare presence
22	ψ(H + Nat)	
23	ψ(H + StrD)	
24	ψ(H + FED)	
25	ψ(H * Sav)	
26	ψ(H * Nat)	
27	ψ(H * StrD)	
28	ψ(H * FED)	

4.3. Results

We found evidence that the native cottontail's true positive detection probability varied seasonally (Appendix N, Table S2; top-ranked model $w = 0.31$). Specifically, the probability of detecting a cottontail at a used site was higher during the primary months of the dry season (May to August: $\hat{p}_{11} = \hat{r}_{11} = 0.18$, $SE = 0.03$) compared to the shoulder months (April or September: $\hat{p}_{11} = \hat{r}_{11} = 0.05$, $SE = 0.02$). We also found some evidence that the cottontail's true positive detection probability varied with two survey methods and camera-trap position (Appendix N, Table S2; second model $w = 0.17$), where detection probability was highest for cameras facing off-road ($\hat{r}_{11}$ off_road = 0.23; $SE = 0.06$) relative to cameras oriented on-road ($\hat{r}_{11}$ on_road = 0.07; $SE = 0.03$) or transect surveys ($\hat{p}_{11} = 0.11$; $SE = 0.04$). The false positive detection probability (p_{10}) of transect surveys was low (top-ranked model: $\hat{p}_{10} = 0.011$, $SE = 0.009$) and did not vary between the first and last survey (Appendix N, Table S2). Notice, the inclusion of the 'transect survey' covariate (TS) did not improve model fit (-2Log(L)) and is thus a pretending variable (Appendix N, Table S2).

We found evidence that the farmhouse proximity influenced the probability of the cottontail using native forests (Table 3). Cottontail probability of use (ψ) increased with native forest coverage (Table 3, top-ranked model $w = 0.49$), ranging from 0.05 ($SE = 0.02$, low forest cover) to 0.42 ($SE = 0.18$, high forest cover) at sites nearby farmhouses (892.75 m, Fig. 2). However, cottontail probability of use (ψ) was much higher at sites far from farmhouses (2435.80 m), ranging from 0.13 ($SE = 0.06$) for sites with low or no native forest cover to 0.70 ($SE = 0.15$) at sites dominated by native forests (Fig. 2). We found no evidence of an interactive relationship between farmhouse proximity and native forest coverage as the interaction between these covariates was an uninformative parameter (Table 3; second-ranked model). We found some evidence of a negative effect between European hare occupancy and cottontail probability of use ($\hat{\beta}$ = -2.66, *SE* = 1.29), but the precision of this estimate is poor and the strength of evidence in favor of this hypothesis (*w* = 0.10; third-ranked model) is more than four times lower than that for an additive relationship between farmhouse proximity and native forest (Table 3). We also found little evidence that the native cottontail is a forest edge species. Models that included native forest edge density (FED) as a covariate received little (e.g., fourth-ranked model, *w* = 0.08, Table 3) or no empirical support (last-ranked model, Table 3). No human-modified habitats (i.e., sugarcane plantations, managed forests, pastures) influenced the native cottontail habitat use.

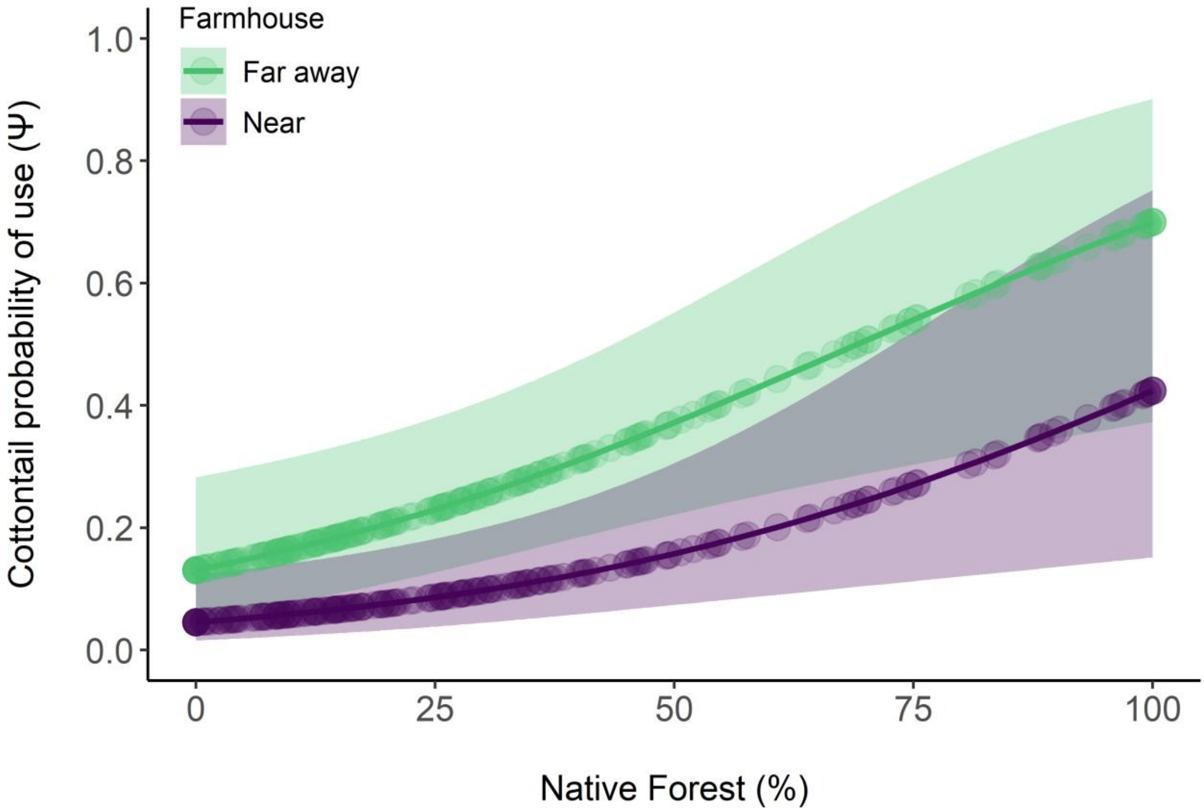

Fig. 2. Estimated probability of use (ψ) of the Brazilian cottontail in southeastern Brazil, based on the top-ranked ψ structure: ψ(FDist + NatF). Cottontail probability of use increases with the percentage of native forest cover and is higher at sites further from farmhouses. Distance values for sites near farmhouses (purple; 892.75 m) and sites away from farmhouses (green; 2435.80 m) correspond to the 1st and 3rd quartile for the Farmhouse Distance covariate. The shaded areas represent 95% confidence intervals.

Table 3. Model selection results for 28 structures for the probability of use (ψ) of the Brazilian cottontail in southeastern Brazil. All models included the best-supported detection structure – i.e., $p_{10}(.)$ $p_{11}=r_{11}(S)$.

Model	AICc	ΔAICc	w	K	-2log(L)
ψ(FDist + NatF)	433.58	0.00	0.49	6	421.16
ψ(FDist * NatF)	435.65	2.07	0.17	7	421.08
ψ(H + NatF)	436.83	3.25	0.10	6	424.40
ψ(FDist * FED)	437.11	3.53	0.08	7	422.55
ψ(FDist + FED)	438.48	4.90	0.04	6	426.06
ψ(H * NatF)	438.97	5.39	0.03	7	424.40
ψ(FDist * StrD)	440.41	6.83	0.02	7	425.84
ψ(FDist * Sav)	440.84	7.26	0.01	7	426.27
ψ(NatF)	441.34	7.76	0.01	5	431.04
ψ(FDist)	441.87	8.29	0.01	5	431.57
ψ(H)	441.87	8.29	0.01	5	431.57
ψ(FDist + StrD)	442.34	8.76	0.01	6	429.91
ψ(Sav + NatF)	442.78	9.20	0.00	6	430.36
ψ(Past + Sug + ManF)	443.17	9.59	0.00	7	428.60
ψ(H + Sav)	443.38	9.80	0.00	6	430.95
ψ(FDist + Sav)	443.85	10.27	0.00	6	431.42
ψ(H + StrD)	443.96	10.38	0.00	6	431.53
ψ(H + FED)	443.98	10.41	0.00	6	431.56
ψ(ManF)	445.14	11.56	0.00	5	434.84
ψ(H * Sav)	445.51	11.93	0.00	7	430.95
ψ(H * StrD)	445.87	12.29	0.00	7	431.31
ψ(H * FED)	446.07	12.49	0.00	7	431.50
ψ(Past)	452.97	19.39	0.00	5	442.67
ψ(.)	454.16	20.58	0.00	4	445.96
ψ(Sav)	456.24	22.66	0.00	5	445.94
ψ(Sug)	456.24	22.67	0.00	5	445.94
ψ(StrD)	456.26	22.68	0.00	5	445.95
ψ(FED)	456.26	22.68	0.00	5	445.96

AICc = Akaike Information Criterion corrected for small samples; ΔAICc = AICc of each model *i* minus the lowest AICc; w = Akaike weights; K = number of parameters; -2log(L) = twice the negative log-likelihood; Sug = % of Sugarcane; ManF = % of Managed Forest; Past = % of Pastures; NatF = % of Native Forest; Sav = % of Savanna; StrD = Stream Density; FED = native Forest Edge Density; FDist = Farmhouse Distance; H = European hare conditional occupancy probability.

4.4. Discussion

To our knowledge, this is the first study to investigate the habitat use of the Brazilian cottontail. Our findings indicate that this tropical cottontail uses sites with high native forest cover away from farmhouses in southeastern Brazil (Fig. 2). We also found little evidence that the Brazilian cottontail is more likely to use human-modified habitats (i.e., sugarcane fields, managed forests, and pastures) and native forest edges than native forests. Instead, our results suggest that the Brazilian cottontail is a forest-dweller rather than an open-country or edge species, as suggested for Amazon forest cottontails (Júnior et al. 2005). Amazon forest cottontails and the cottontails found in our study areas represent distinct molecular lineages, suggesting these putative taxa (Silva et al. 2019) may have different fundamental niches and habitat requirements. Despite long-standing calls (Grigera and Rapoport 1983; Novillo and Ojeda 2008; de Faria et al. 2015), our study found little evidence of a negative influence of the non-native European hares on the native cottontail habitat use, as predicted by the competitive exclusion hypothesis. In contrast to the native cottontail habitat use pattern we found, European hares are less likely to use sites predominantly covered by native forest and more likely to use human-modified habitats (e.g., sugarcane fields, managed forests, pastures) in southeastern Brazil (Pasqualotto et al. 2021). Therefore, our findings are more consistent with the spatial niche segregation hypothesis, suggesting that the Brazilian cottontail and the non-native European hare are naturally spatially segregated due to their different habitat preferences (Kamieniarz et al. 2013; Petrovan et al. 2013; Pasqualotto et al. 2021).

Although we found only weak support for the predictions of the competitive exclusion hypothesis, we highlight a potential caveat associated with this finding. We conducted our study near the European hare northern expansion front in Brazil (Rosa et al. 2020) where hares are only recently established. Our study areas are north of the Tietê river where the first records of European hares date from mid-2000's (Auricchio and Olmos 1999; Rosa et al. 2020), indicating hares invaded this area during the last decade. Hare populations are currently widespread, but at relatively low densities (Pasqualotto et al. in press) compared to other regions of Brazil and South America (Novaro et al. 2000; Kasper et al. 2012; Barbar et al. 2018). Even if the species' realized niches overlap substantially, low hare densities would naturally lead to a weak competitive interaction with the Brazilian cottontails, as supported by our findings. However, occupancy–environmental relationships obtained at the edge of an expanding invasive species' range may poorly predict the invader–environmental relationship in the future because invader spatial distribution is unlikely to be at equilibrium (Yackulic et al. 2015). Empirical evidence from other systems suggests that non-native species may become the ultimate cause of native species' decline after decades (Dugger et al. 2016) or even centuries (Gilbert and Levine 2013) of coexistence with no evidence of strong antagonistic interactions. Hence, the current spatial distribution and occupancy–environmental relationships of the European hare may change in the following decades and could later drive the Brazilian cottontail populations to decline. Monitoring European hare invasion dynamics would appropriately address the invasive hare occupancy changes over time (Yackulic et al. 2015). It would also provide stronger inferences about these species interaction by determining local extinction drivers of the Brazilian cottontail (Bailey et al. 2009; MacKenzie et al. 2018).

Direct interactions (e.g., competition) are not the only way that coexisting species can affect each other, as indirect interactions also occur and are key to predicting extinction dynamics (Pires et al. 2020). In our study system, European hares may provide additional food for native predators, increasing predator density and predation pressure on native prey species, an indirect interaction known as apparent competition (Holt 1977). The Brazilian cottontail may be susceptible to increased predation pressure caused by the presence of non-native hares, which may ultimately lead to local extinction of the cottontail. Native predators (e.g., maned-wolves, pumas) prey on European hares (Cruz et al. 2022) and select them as a primary food source (Novaro et al. 2000) in the Neotropics. In addition, European hare has a high potential to create apparent competition in invaded communities from Argentine Patagonia (Barbar and Lambertucci 2019) and may outcompete the Brazilian cottontail through this mechanism. Considering the role of indirect interactions in future studies may better predict the vulnerability of the cottontail to extinction in our study system.

The lower probability of the Brazilian cottontail use of native forest patches near farmhouses might be related to higher harassment and predation risk imposed by free-ranging dogs and cats. Domestic dogs (*Canis familiaris*) and cats (*Felis catus*) usually range freely through tropical and subtropical landscapes and invade native forests (Paschoal et al. 2016; Maeda et al. 2019). However, native forest invasion by free-ranging dogs and cats typically depends on human subsidies. Unlike feral animals, free-ranging dogs and cats do not establish self-sustained populations inside native forests and strongly rely on human feeding (Morters et al. 2014; Maeda et al. 2019). Consequently, the probability of dogs using and persisting in tropical forests increases with the density and the proximity to rural human housing (Paschoal et al. 2016, 2018). Free-ranging dogs and cats concentrate their activities near their owner's homes (Dürr and Ward 2014; Sepúlveda et al. 2015; Maeda et al. 2019) but are able to travel hundreds of meters inside native forest patches (Paschoal et al. 2012; Maeda et al. 2019), increasing the likelihood of interacting with native wildlife. Indeed, free-ranging cats kill endemic species, such as the endangered forest dwelling Amami rabbit (*Pentalagus furnessi*) in Japan (Maeda et al. 2019). Likewise, the diet of free-ranging dogs in Mexico includes the native cottontails *Sylvilagus floridanus* and *Sylvilagus cunicularius* (Carrasco-Román et al. 2021). Scientific evidence on free-ranging dogs and cats killing or preying upon native animal species is scarce in Brazil. Yet, a study found that the Brazilian cottontail was the animal species most killed by dogs in an urban reserve in southeastern Brazil (Galetti and Sazima 2006). Hence, Brazilian cottontails inhabiting forest patches near the farmhouse may face antagonistic interactions with free-ranging dogs and cats.

Our study is also the first to report detection probabilities for Brazilian cottontails for two methods commonly used to sample lagomorphs in Brazil/South America. We found that time of survey and camera placement are likely to influence the species detection probability. Specifically, sampling during the primary months of the dry season in southeastern Brazil (May to August) and using camera-traps to sample non-road/tracks environments inside tropical forests increases Brazilian cottontail detection. The period from May to August in our study areas roughly corresponds to the part of the year with the lowest precipitation rates (tropical dry season) and temperatures. In the northern hemisphere, American cottontails and European rabbits (*Oryctolagus cuniculus*) increase their feeding activity throughout the winter, possibly due to food scarcity and higher energy needs (Rödel 2005; O'Connor and Rittenhouse 2017). Similarly, home ranges of the Eastern cottontails (*Sylvilagus floridanus*) increase during months of low food availability (Trent and Rongstad 1974). Hence, we speculate that the combined weather conditions from May to August in our study areas may cause Brazilian cottontails to increase foraging activity and detection. The lower probability of detecting the Brazilian cottontails at camera-traps sampling dirt roads/farm tracks may reflect cottontails attempt to avoid encounters with predators, including free-ranging dogs and native terrestrial carnivores, which preferably use these linear structures to move efficiently (Andersen et al. 2017). Brazilian cottontails are small ($<$ 1 kg, Ruedas et al. 2017) and likely have limited dispersal capabilities similar to most *Sylvilagus* species (home ranges $\leq$ 3 ha; Jones et al. 2009). These characteristics may contribute to the species low true detection probability (≤ 0.23). We recommend future studies sample native forest interiors with camera-traps during the primary months of the tropical dry season to increase cottontail detection probability and estimator precision. Transect surveys may be used to supplement camera traps surveys, but these surveys are subject to misidentification so should not be used as the only sampling method.

Based on our findings, increased human proximity to tropical forests and tropical deforestation are currently more relevant threats to the conservation of the Brazilian cottontail in southeastern Brazil than the European hare invasion. The current trend in urban growth will increase the proximity of human development to tropical protected areas (The Nature Conservancy 2018) and may intensify human impacts on wild animals such as the Brazilian cottontails. Additionally, tropical forest clearing continues globally at high rates (Vancutsem et al. 2021). In Brazil, 85% of the original Atlantic Forest has been lost and most of the remaining fragments are small (< 50 ha) and isolated (Ribeiro et al. 2009). Over 45% (88 Mha) of the Cerrado has been converted (Strassburg et al. 2017) and a further 40 Mha of the remaining Cerrado areas can be legally converted into croplands (Soares-Filho et al. 2014), which may drive local extinctions of the Brazilian cottontail. While public protected areas comprise less than 7.5% of the Atlantic Forest and Cerrado (Ribeiro et al. 2009; Strassburg et al. 2017), the Brazilian Forest Act requires that 20% of each private rural property must be set aside as native vegetation (Brancalion et al. 2016). Our study demonstrates the importance of these native habitats for the current distribution of Brazilian cottontail populations and other native species and emphasizes the importance of compliance with the Brazilian Forest Act.

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5. CONCLUDING REMARKS

All findings that I have provided in my doctoral thesis are essential to better understand European hare invasion success in the Neotropics, offering valuable insights regarding potential interaction between non-native European hares and the Brazilian cottontail. Recalling briefly, in Chapter I (Pasqualotto et al. 2021) I found out that the replacement of native Neotropical habitats with agricultural lands is the main driver of European hare occupancy near the expansion front of this invader in southeastern Brazil. Biotic resistance imposed by native Neotropical habitats plays a secondary role and only due to native forest as this land cover class was negatively associated with European hare occupancy. We hypothesized that low resource opportunities and high risk of ambush predation by Neotropical carnivores might be the main mechanism behind the negative association between European hare occupancy and closed-canopy Neotropical forests. We discuss that while European hare expansion may continue northwards due to the ongoing Cerrado conversion into agricultural lands, restoring native forest may constrain the European hare invasion in Brazil.

In Chapter II (Pasqualotto et al. 2023, in press), I tried to understand why European hare is thriving in highly homogenous agricultural landscapes from southern and southeastern Brazil while the loss of landscape heterogeneity is the ultimate cause of European hare population declines in its native range. I identified that areas with high diversity of land cover types, including sugarcane but no savanna are more likely to attain high European hare local abundance. Surprisingly, the amount of sugarcane, an intensively managed monoculture in our study areas, was a better predictor of European hare local abundance than temporal and configurational heterogeneity. We hypothesized that field margins of the sugarcane crops might provide high quality food and shelter for hares, playing a key role in this species invasion. In addition, European hare abundance estimates we obtained were low and did not vary dramatically among our sites, suggesting this non-native species has not yet attained the dramatically high densities reported in southern South American.

In Chapter III (Pasqualotto et al. 2023, under review), I found out only little evidence to support that the European hare is competitively excluding the Brazilian cottontail. As I have shown in Chapter I, the European hare occupancy has been driven by niche opportunities provided by agricultural lands. Contrastingly, the Brazilian cottontail is more likely to use site predominantly covered by native forest away from farmhouses, regardless of the European hare presence. Hence, these findings are more consistent with spatial niche segregation hypothesis, suggesting European hare and the Brazilian cottontail naturally segregate due to different habitat preferences. Consequently, we argue that European hare invasion is currently a less significant threat to the Brazilian cottontail than tropical deforestation and increased human proximity to tropical forest patches.

Taken together, these findings indicate that the European hare has not yet become a harmful invader in southeastern Brazil, as I expected based on the reported environmental damage caused by the species in other parts of its invaded range. MacDougall and Turkington (2005) have argued that most invaders have taken advantage of the pervasive environmental change caused by humans to invade new areas they have never occurred, suggesting invasive species are merely passengers than drivers of environmental chance. Would that be the cause of European hare in agricultural dominated landscapes from southeastern Brazil? All evidence I have presented in my thesis showed that European hare i) invasion success is mainly due to niche opportunity provided by highly human-disturbed habitats, ii) have probably not attained high local density as reported in southern South America, and ii) are likely not competitively excluding the Brazilian cottontail, suggesting this non-native species is more likely a passenger following the current environmental change (Didham et al. 2005). In addition, many native predators are consuming European hares in South America (Novaro et al. 2000; Cruz et al. 2022), further suggesting European hare may currently have some conservation value in our study areas. Nevertheless, we have learned from past invasion studies that human introduced species remain harmless for long periods before spreading and invading native communities (Simberloff et al. 2013). Native species extinctions may occur only after centuries of coexistence (Gilbert and Levine 2013). Therefore, monitoring European hare demographic parameters (e.g., abundance, occupancy) over time is highly advisable as to inform environmental agencies and guide management actions in the case European hare substantially increase its density in the future.

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APPENDICES

Appendix A – Chapter I: Scale of effect

In order to determine the spatial scale in which the seven composition-based landscape metrics (predictors) have the strongest effect on European hare occurrence (response), we created one set of models for each landscape metric with five models, one model for each spatial scale (Table S1). Then, we modeled the European hare occurrence as a function of these metrics using logistic regressions. Following (Boscolo and Metzger 2009), we used the bootstrap procedure (Manly 2007) on the logistic regressions to determine the best spatial scale on average for each landscape metric. To avoid problems with spatial autocorrelation, the selected sites were always apart from each other by at least 3 km. Because of this spatial constraint, the bootstrap procedure was done by randomly selecting 40 of the 205 sampling sites, performing each model 1,000 times. For each set of models, the model with the highest average explained variance (mean R^2) was considered the scale of effect for that predictor (Martin and Fahrig 2012; Miguet et al. 2016).

Table S1. The scale of effect analysis for the seven compositional-based landscape metrics. For each metric, the spatial scale (12.5 ha, 25 ha, 50 ha, 100 ha, or 200 ha) with the highest explained variance on average (mean R^2; highlighted in light gray) was considered the scale of effect for that metric.

Model number	Spatial Scale	Mean Explained Variance (mean R^2)
mod_01	Sav_12_5ha	0.0712
mod_02	Sav_25ha	0.0759
mod_03	Sav_50ha	0.0668
mod_04	Sav_100ha	0.0579
mod_05	Sav_200ha	0.0469
mod_06	Fiel_12_5ha	0.0837
mod_07	Fiel_25ha	0.0846
mod_08	Fiel_50ha	0.0783
mod_09	Fiel_100ha	0.0657
mod_10	Fiel_200ha	0.0567
mod_11	Sug_12_5ha	0.0366
mod_12	Sug_25ha	0.0372
mod_13	Sug_50ha	0.0342
mod_14	Sug_100ha	0.0321
mod_15	Sug_200ha	0.0301

Table S1 continued

Model number	**Spatial Scale**	**Mean Explained Variance (mean R^2)**
mod_16	ManF_12_5ha	0.0598
mod_17	ManF_25ha	0.0573
mod_18	ManF_50ha	0.0528
mod_19	ManF_100ha	0.0517
mod_20	ManF_200ha	0.0546
mod_21	NatF_12_5ha	0.1073
mod_22	NatF_25ha	0.1057
mod_23	NatF_50ha	0.0924
mod_24	NatF_100ha	0.0808
mod_25	NatF_200ha	0.0795
mod_26	Hyd_dens12_5	0.1086
mod_27	Hyd_dens25	0.1224
mod_28	Hyd_dens50	0.0893
mod_29	Hyd_dens100	0.0643
mod_30	Hyd_dens200	0.0662
mod_31	Edg_dens12_5	0.0798
mod_32	Edg_dens25	0.0849
mod_33	Edg_dens50	0.0768
mod_34	Edg_dens100	0.0616
mod_35	Edg_dens200	0.0448

Landscape metrics code: Sav = % of savanna in each spatial scale; Fiel = % of field in each spatial scale; Sug = % of sugarcane plantations in each spatial scale; ManF = % of managed forest in each spatial scale; NatF = % of native forest in each spatial scale; Hyd_dens = hydrographic density (m/ha) in each spatial scale; Edg_dens = edge density (m/ha) in each spatial scale.

Appendix B – Chapter I: False positive detections and covariates correlations

Although the standard single-season/single-species occupancy model parametrization (the "Mackenzie model"; MacKenzie et al. 2002) deals appropriately with imperfect detections, it has a key assumption that a species is never falsely detected at a site when it is absent (MacKenzie et al. 2002). However, indirect observations of species, like tracks, scats, interviews, and vocalization, may often result in misidentifications (McClintock et al. 2010; Miller et al. 2011; Molinari-Jobin et al. 2012; Mohanty et al. 2018), even when collected by expert observers (McClintock et al. 2010). Misidentifications can create false positive detection, which occurs when species is detected at a site that is actually unoccupied. If not accounted for, even very low false positive detection errors lead to a substantial overestimation of occupancy probability (Royle and Link 2006). To overcome this limitation, Royle and Link (2006) developed the misidentification model, further modified by (Miller et al. 2011; the "Miller model") given some numerical issues, that explicitly accounts for false positive detections. Miller model relaxes the assumption of never falsely detecting species by estimating three different detection parameters in the Multiple Detection Method Model parametrization (MDMM): 1) p_{10}, the probability of incorrectly detecting a species at a site when it is unoccupied, using an uncertain method (the false positive detection probability); 2) p_{11}, the probability of a true positive detection of the species, also using an uncertain method and 3) r_{11}, the probability of a true positive detection of the species, using a certain method (Miller et al. 2011).

Under this theoretical background, the preliminary analysis was performed by fitting two occupancy models with no covariates for the detection probabilities: 1) the full Miller model and 2) a model where the false positive detection probability was fixed to zero ($p_{10} = 0$), thus reproducing the Mackenzie model. In this preliminary analysis, we defined a general structure for occupancy probability (ψ). As stated by (Nagy-Reis et al. 2017), defining a general structure for one response variable that is not being investigated within a given model set (ψ) is desirable to perform our statistical analysis on other response variables (here, the detection ones) with the most variation coming from what was not explained by the former, thus producing more reliable results. Here, only covariates that represented a reasonable biological hypothesis for European hare ψ were considered for this general structure and only those ones that provided a substantial fit to the models were kept. Besides the fit, only weakly correlated covariates ($r < 0.5$; Table S1) were used in this general ψ structure.

Table S1. Pearson correlations between our nine quantitative predictor covariates, the seven composition-based quantified on their respective estimated scale of effect. Sav = % of savanna in 25 ha; Fiel = % of field in 25 ha; Sug = % of sugarcane plantations in 25 ha; ManF = % of managed forest in 12.5 ha; NatF = % of native forest in 12.5 ha; Hyd_dens = hydrographic density (m/ha) in 25 ha; Edg_dens = edge density (m/ha) in 25 ha; DR_dist = sampling points distance (m) to the nearest dirt road/farm track; Edist = mean random points distance (m) to the nearest edification.

	Sav	Fiel	Sug	ManF	NatF	Hyd_dens	Edg_dens	DR_dist	Edist
Sav	1								
Fiel	-0.05	1							
Sug	-0.16	-0.14	1						
ManF	-0.24	-0.13	-0.31	1					
NatF	-0.29	-0.26	-0.14	-0.52	1				
Hyd_dens	0.14	0.06	-0.04	-0.12	0.004	1			
Edg_dens	0.12	0.01	0.06	-0.13	-0.03	0.41	1		
DR_dist	0.07	0.03	-0.20	-0.31	0.38	-0.15	-0.2	1	
Edist	-0.14	-0.06	-0.05	0.05	0.09	-0.08	-0.36	0.02	1

In this preliminary analysis we found strong evidence of false positive detections errors on hare tracks' identification since the Mackenzie model (i.e., ψ(General), p(.)) had essentially no empirical support (ΔAICc > 10, Table S2; Burnham et al. 2011). Although the false positive detection probability estimated was very small ($\hat{p}_{10}$ = 0.09; *SE* = 0.02, CI = 0.06 to 0.12), the Mackenzie model overestimated the European hare occupancy probability ($\hat{\psi}$ = 0.35, *SE* = 0.06, CI = 0.23 to 0.48) with respect to the Miller model ($\hat{\psi}$ = 0.07, *SE* = 0.03, CI = 0.03 to 0.15).

Table S2. Preliminary occupancy analysis performed with the misidentification model (Miller model, ψ(General), p_{10}(.), p_{11}=r_{11}(.)) and the single-season/single-species occupancy model (Makenzie model, (ψ(General), p(.)), both used to evaluate the presence of false positive detections errors on hare tracks. Model selection showed strong evidence in favor of the Miller model (highlighted in light gray).

Model	AICc	ΔAICc	w	K	-2log(L)
ψ(General), p_{10}(.), p_{11} = r_{11}(.)	536.86	0	1	6	524.44
ψ(General), p(.)	596.86	59.99	0	5	586.55

AICc = Akaike Information Criterion corrected for small samples; ΔAICc = AICc of each model *i* minus the lowest AICc; w = Akaike weights; K = number of parameters; -2log(L) = twice the negative log-likelihood. ψ(General) = % of native forest in 12.5 ha + hydrographic density (m/ha) in 25 ha + % of sugarcane in 25 ha.

Appendix C – Chapter I: Detection modeling approach and detection results

In the first occupancy modeling step, we investigated which factors (covariates/effects) better explained the European hare detection probabilities (p_{10}, p_{11}, and r_{11}), defining a general structure for occupancy probability (ψ), as we did in the preliminary analysis (Appendix B). Specifically, since we used two different sampling methods, it seemed reasonable to investigate if the true positive detections probabilities (p_{11} and r_{11}) could be different between them. Therefore, we first built a model set with two main groups of a priori hypotheses. In the first group (no method effect; Table S1), the true positive detection probabilities were estimated as the same ($p_{11} = r_{11}$), allowing them to be constant ($p_{11} = r_{11}(.)$; null model) or vary as a logit function of our habitat, temporal, and weather covariates/effects (Table 2). On the other hand, in the second group (method effect; Table S1), the true positive detection probabilities were allowed to vary between the two methods ($p_{11} \neq r_{11}$) and they were also allowed to be constant ($p_{11}(.)$, $r_{11}(.)$; null model) or to vary only as a logit function of their method-specific covariates (Table 2). Regardless of these two groups of hypotheses and following the same reasoning, the false positive detection probability p_{10}, that is restricted to the uncertain method (track surveys) in the MDMM, was estimated as constant ($p_{10}(.)$) or only as a logit function of its method-specific covariates/effects (Table S1 and Table 2).

Table S1. List of the models (hypotheses) used for investigating the detection probabilities (p_{10}, p_{11}, and r_{11}) of the European hare in the northeast of São Paulo state, southeastern Brazil.

Model	Method effect	Hypothesis type
ψ(General), $p_{10}(.)$, $p_{11} = r_{11}(.)$	No	Null
ψ(General), $p_{10}(.)$, $p_{11} = r_{11}$(Sav)	No	Habitat
ψ(General), $p_{10}(.)$, $p_{11} = r_{11}$(Fiel)	No	Habitat
ψ(General), $p_{10}(.)$, $p_{11} = r_{11}$(Sug)	No	Habitat
ψ(General), $p_{10}(.)$, $p_{11} = r_{11}$(ManF)	No	Habitat
ψ(General), $p_{10}(.)$, $p_{11} = r_{11}$(NatF)	No	Habitat
ψ(General), $p_{10}(.)$, $p_{11} = r_{11}$(Hyd_dens)	No	Habitat
ψ(General), $p_{10}(.)$, $p_{11} = r_{11}$(Edg_dens)	No	Habitat
ψ(General), $p_{10}(.)$, $p_{11} = r_{11}$(StudAr)	No	Habitat
ψ(General), $p_{10}(.)$, $p_{11} = r_{11}$(Edist)	No	Habitat
ψ(General), $p_{10}(.)$, $p_{11} = r_{11}$(t)	No	Temporal
ψ(General), $p_{10}(.)$, $p_{11} = r_{11}$(T)	No	Temporal

Table S1 continued

Model	Method effect	Hypothesis type
ψ(General), p_{10}(.), $p_{11} = r_{11}$(Quad_T)	No	Temporal
ψ(General), p_{10}(.), $p_{11} = r_{11}$(Year)	No	Temporal
ψ(General), p_{10}(.), $p_{11} = r_{11}$(QuadAver_temp)	No	Weather
ψ(General), p_{10}(.), $p_{11} = r_{11}$(Rainf)	No	Weather
ψ(General), p_{10}(.), $p_{11} = r_{11}$(Cold_mth)	No	Weather
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(.)	No	Null
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(Sav)	No	Habitat
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(Fiel)	No	Habitat
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(Sug)	No	Habitat
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(ManF)	No	Habitat
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(NatF)	No	Habitat
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(Hyd_dens)	No	Habitat
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(Edg_dens)	No	Habitat
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(StudAr)	No	Habitat
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(Edist)	No	Habitat
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(t)	No	Temporal
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(T)	No	Temporal
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(Quad_T)	No	Temporal
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(Year)	No	Temporal
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(QuadAver_temp)	No	Weather
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(Rainf)	No	Weather
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(Cold_mth)	No	Weather
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(.)	No	Null
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(Sav)	No	Habitat
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(Fiel)	No	Habitat
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(Sug)	No	Habitat
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(ManF)	No	Habitat
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(NatF)	No	Habitat
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(Hyd_dens)	No	Habitat
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(Edg_dens)	No	Habitat
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(StudAr)	No	Habitat
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(Edist)	No	Habitat
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(t)	No	Temporal
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(T)	No	Temporal
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(Quad_T)	No	Temporal
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(Year)	No	Temporal
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(QuadAver_temp)	No	Weather
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(Rainf)	No	Weather
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(Cold_mth)	No	Weather

Table S1 continued

Model	**Method effect**	**Hypothesis type**
ψ(General), p_{10}(.), p_{11}(.), r_{11}(.)	Yes	Null
ψ(General), p_{10}(.), p_{11}(.), r_{11}(CT_pos)	Yes	Camera trapping
ψ(General), p_{10}(.), p_{11}(.), r_{11}(Eff)	Yes	Camera trapping
ψ(General), p_{10}(.), p_{11}(Surv), r_{11}(.)	Yes	Track surveys
ψ(General), p_{10}(.), p_{11}(Surv), r_{11}(CT_pos)	Yes	Both
ψ(General), p_{10}(.), p_{11}(Surv), r_{11}(Eff)	Yes	Both
ψ(General), p_{10}(Surv), p_{11}(Surv), r_{11}(.)	Yes	Track surveys
ψ(General), p_{10}(Surv), p_{11}(Surv), r_{11}(CT_pos)	Yes	Both
ψ(General), p_{10}(Surv), p_{11}(Surv), r_{11}(Eff)	Yes	Both
ψ(General), p_{10}(Suit_t), p_{11}(Suit_t), r_{11}(.)	Yes	Track surveys
ψ(General), p_{10}(Suit_t), p_{11}(Suit_t), r_{11}(CT_pos)	Yes	Both
ψ(General), p_{10}(Suit_t), p_{11}(Suit_t), r_{11}(Eff)	Yes	Both

Covariates/effects code: Sav = % of savanna in 25 ha; Fiel = % of field in 25 ha; Sug = % of sugarcane plantations in 25 ha; ManF = % of managed forest in 12.5 ha; NatF = % of native forest in 12.5 ha; Hyd_dens = hydrographic density (m/ha) in 25 ha; Edg_dens = edge density (m/ha) in 25 ha; StudAr = categorical covariate for the three landscapes sampled, Edist = mean random points distance (m) to the nearest edification; t = time effect; T = linear trend effect; Quad_T = quadratic trend effect; Year = sampling years (2013 and 2014); QuadAver_temp = quadratic effect of average temperature (°C), Rainf = accumulated rainfall (mm), Cold_mth = coldest months effect, Surv = track survey effect; Suit_t = suitability for tracks; CT_pos = camera-trap position, Eff = camera-trap sampling effort. ψ(General) = % of native forest in 12.5 ha + hydrographic density (m/ha) in 25 ha + % of sugarcane in 25 ha.

Regarding the results of the first occupancy modeling step, the first two well-ranked models were considered our well-supported hypotheses (Table S2). Based on the evidence ratios, the top-ranked model is only 1.5 times (w_{top}/w_{2nd} = 0.52/0.35) more likely than the second-ranked one and at least 7.4 times (w_{top}/w_{3rd} = 0.52/0.07) more likely than any other hypothesis here considered. Besides, the first two well-ranked models accumulated 87% of all Akaike weights of this model set (Table S2). Based on our two well-supported hypotheses, we found strong evidence that the true positive detection probabilities of the two methods are different ($p_{11} \neq r_{11}$, method effect). We also found that the true positive detection probabilities of track surveys (p_{11}) and camera trapping (r_{11}) were, respectively, best explained by the "Track Survey effect" and "Camera-trap position" covariate, since these effect/covariates were explicitly estimated in the two models with the most empirical support (Table S2). Furthermore, as predicted (Table 2), the "Track Survey effect" and "Camera-trap position" covariate had a positive and well-estimated association with p_{11} ($\hat{\beta}_{Surv}$ = 1.54, *SE* = 0.57; CI = 0.43 to 2.66) and r_{11} ($\hat{\beta}_{CT\_pos}$ = 2.33, *SE* = 0.54; CI = 1.29 to 3.38), respectively. We did not find a covariate/effect associated with the false positive detection probability (p_{10}). Although p_{10} has been best explained by the "Track Survey effect" in the second well-ranked model, its estimate was imprecise ($\hat{\beta}_{Surv}$ = 0.83, *SE* = 0.72; CI = -0.57 to 2.23) and then we did not consider it as real effect. Therefore, although the first two well-ranked models were considered equally well-supported, in the second step, we only fixed the detection structure of the top-ranked model (p_{10}(.), p_{11}(Surv), r_{11}(CT_pos) for modeling our a priori biological hypotheses regarding niche opportunity and biotic resistance. On average, the estimated true positive detection probability of the first track survey ($\hat{p}_{11} = 0.15$, $SE = 0.07$; CI = 0.05 to 0.35) was less than half of the second ($\hat{p}_{11} = 0.37$, $SE = 0.10$; CI = 0.21 to 0.57). Both of them were much higher than the true positive detection probability estimated by camera trapping ($\hat{r}_{11} = 0.08$, $SE = 0.05$; CI = 0.02 to 0.27) and the false positive detection probability was the lowest detection probability estimated ($\hat{p}_{10} = 0.04$, $SE = 0.02$; CI = 0.02 to 0.11).

Table S2. Model selection result for the European hare detection probabilities (p_{10}, p_{11}, and r_{11}) in the northeast of São Paulo state, southeastern Brazil. Models with most empirical support (well-supported hypotheses) are highlighted in light gray.

Model	**AICc**	**ΔAICc**	**w**	**K**	**-2log(L)**
ψ(General), p_{10}(.), p_{11}(Surv), r_{11}(CT_pos)	518.12	0.00	0.52	9	499.19
ψ(General), p_{10}(Surv), p_{11}(Surv), r_{11}(CT_pos)	518.95	0.83	0.35	10	497.81
ψ(General), p_{10}(Suit_t), p_{11}(Suit_t), r_{11}(CT_pos)	522.08	3.96	0.07	10	500.94
ψ(General), p_{10}(.), p_{11}(.), r_{11}(CT_pos)	524.41	6.29	0.02	8	507.67
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(T)	526.41	8.29	0.01	8	509.67
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(T)	526.46	8.34	0.01	8	509.73
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(t)	528.32	10.20	0.00	12	502.69
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(Quad_T)	528.60	10.48	0.00	9	509.67
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(t)	528.64	10.52	0.00	12	503.01
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(Quad_T)	528.64	10.53	0.00	9	509.72
ψ(General), p_{10}(.), $p_{11} = r_{11}$(T)	530.39	12.27	0.00	7	515.82
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(NatF)	531.06	12.94	0.00	8	514.32
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(NatF)	531.73	13.62	0.00	8	515.00
ψ(General), p_{10}(.), $p_{11} = r_{11}$(t)	532.14	14.02	0.00	11	508.77
ψ(General), p_{10}(Surv), p_{11}(Surv), r_{11}(Eff)	532.48	14.36	0.00	11	509.11
ψ(General), p_{10}(.), $p_{11} = r_{11}$(Quad_T)	532.55	14.44	0.00	8	515.82
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(.)	532.84	14.73	0.00	7	518.27
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(.)	533.29	15.17	0.00	7	518.72

Table S2 continued

Model	**AICc**	**ΔAICc**	**w**	**K**	**-2log(L)**
ψ(General), p_{10}(Surv), p_{11}(Surv), r_{11}(.)	533.31	15.19	0.00	9	514.38
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(ManF)	533.40	15.29	0.00	8	516.67
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(Sav)	533.61	15.49	0.00	8	516.88
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(ManF)	533.95	15.84	0.00	8	517.22
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(Fiel)	533.96	15.85	0.00	8	517.23
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(Rainf)	534.21	16.09	0.00	8	517.47
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(Sav)	534.26	16.14	0.00	8	517.53
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(Edg_dens)	534.28	16.16	0.00	8	517.54
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(QuadAver_temp)	534.29	16.18	0.00	9	515.37
ψ(General), p_{10}(Suit_t), p_{11}(Suit_t), r_{11}(Eff)	534.48	16.37	0.00	11	511.11
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(Fiel)	534.52	16.41	0.00	8	517.79
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(Sug)	534.55	16.43	0.00	8	517.81
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(Rainf)	534.64	16.53	0.00	8	517.91
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(Year)	534.80	16.69	0.00	8	518.07
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(Edg_dens)	534.85	16.73	0.00	8	518.12
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(Edist)	534.94	16.83	0.00	8	518.21
ψ(General), p_{10}(.), p_{11}(Surv), r_{11}(Eff)	534.94	16.83	0.00	10	513.81
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(Cold_mth)	534.97	16.85	0.00	8	518.23
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(Hyd_dens)	535.00	16.89	0.00	8	518.27
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(Sug)	535.01	16.89	0.00	8	518.27
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(QuadAver_temp)	535.12	17.01	0.00	9	516.20
ψ(General), p_{10}(.), $p_{11} = r_{11}$(NatF)	535.16	17.04	0.00	7	520.59
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(Year)	535.24	17.12	0.00	8	518.50
ψ(General), p_{10}(Suit_t), p_{11}(Suit_t), r_{11}(.)	535.31	17.19	0.00	9	516.38
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(Edist)	535.36	17.24	0.00	8	518.62
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(Cold_mth)	535.38	17.27	0.00	8	518.65
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(Hyd_dens)	535.43	17.31	0.00	8	518.70
ψ(General), p_{10}(.), p_{11}(Surv), r_{11}(.)	535.65	17.54	0.00	8	518.92
ψ(General), p_{10}(.), $p_{11} = r_{11}$(.)	536.86	18.75	0.00	6	524.44
ψ(General), p_{10}(Suit_t), $p_{11} = r_{11}$(StudAr)	536.99	18.88	0.00	9	518.07
ψ(General), p_{10}(Surv), $p_{11} = r_{11}$(StudAr)	537.43	19.31	0.00	9	518.50
ψ(General), p_{10}(.), $p_{11} = r_{11}$(ManF)	537.47	19.36	0.00	7	522.90

Table S2 continued

Model	**AICc**	**ΔAICc**	**w**	**K**	**-2log(L)**
ψ(General), p_{10}(.), p_{11} = r_{11}(Sav)	537.74	19.62	0.00	7	523.17
ψ(General), p_{10}(.), p_{11}(.), r_{11}(Eff)	537.82	19.70	0.00	9	518.90
ψ(General), p_{10}(.), p_{11} = r_{11}(Fiel)	537.83	19.72	0.00	7	523.26
ψ(General), p_{10}(.), p_{11} = r_{11}(Rainf)	538.24	20.12	0.00	7	523.67
ψ(General), p_{10}(.), p_{11} = r_{11}(Edg_dens)	538.37	20.26	0.00	7	523.80
ψ(General), p_{10}(.), p_{11} = r_{11}(QuadAver_temp)	538.49	20.37	0.00	8	521.75
ψ(General), p_{10}(.), p_{11} = r_{11}(Sug)	538.58	20.46	0.00	7	524.01
ψ(General), p_{10}(.), p_{11}(.), r_{11}(.)	538.72	20.61	0.00	7	524.15
ψ(General), p_{10}(.), p_{11} = r_{11}(Year)	538.79	20.67	0.00	7	524.22
ψ(General), p_{10}(.), p_{11} = r_{11}(Edist)	538.94	20.83	0.00	7	524.38
ψ(General), p_{10}(.), p_{11} = r_{11}(Cold_mth)	538.95	20.83	0.00	7	524.38
ψ(General), p_{10}(.), p_{11} = r_{11}(Hyd_dens)	538.99	20.87	0.00	7	524.42

AICc = Akaike Information Criterion corrected for small samples; ΔAICc = AICc of each model *i* minus the lowest AICc; w = Akaike weights; K = number of parameters; -2log(L) = twice the negative log-likelihood. Covariates/effects code: Sav = % of savanna in 25 ha; Fiel = % of field in 25 ha; Sug = % of sugarcane plantations in 25 ha; ManF = % of managed forest in 12.5 ha; NatF = % of native forest in 12.5 ha; Hyd_dens = hydrographic density (m/ha) in 25 ha; Edg_dens = edge density (m/ha) in 25 ha; StudAr = categorical covariate for the three landscapes sampled, Edist = mean random points distance (m) to the nearest edification; t = time effect; T = linear trend effect; Quad_T = quadratic trend effect; Year = sampling years (2013 and 2014); QuadAver_temp = quadratic effect of average temperature (°C), Rainf = accumulated rainfall (mm), Cold_mth = coldest months effect, Surv = track survey effect; Suit_t = suitability for tracks; CT_pos = camera-trap position, Eff = camera-trap sampling effort. ψ(General) = percentage of native forest in 12.5 ha + hydrographic density (m/ha) in 25 ha + percentage of sugarcane 25 ha.

Appendix D – Chapter II: Geoprocessing details for site selection

We quantified the Largest Patch Index (LPI) and percentage of native vegetation cover (PNV) using the best native vegetation maps available at the time of the study design. Specifically, we joined the maps of the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA; 1:50,000 scale) and the Rural Environmental Registry (CAR; 1:20,000 scale) into a single raster map (30 m spatial resolution). Native vegetation on both state- and privately owned nature reserves (i.e., Legal Reserves, [LR] and Areas of Permanent Protection [APP], (Brancalion et al. 2016) were appropriately included. Shannon's Diversity Index (SHDI) was quantified using the Brazilian Annual Coverage and Land Use Mapping Project (MapBiomas, collection 2, 2016, 30 m spatial resolution; (Souza et al. 2020) as the former maps only mapped native vegetations. We quantified LPI, PNV, and SHDI for each pixel of our entire study area using a moving window analysis in FRAGSTATS (McGarigal et al. 2012). All geoprocessing was undertaken in ArcGIS v. 10.2 and QGIS v. 2.8.6.

Appendix E – Chapter II: Land cover mapping of the study area

We created a land cover map for our study area (total area = 34,069.26 km^2) using cloud-free Landsat composites. These composites were created with Landsat-8 OLI images (bands 2–7; 30 m spatial resolution) atmospherically corrected, radiometrically calibrated, and orthorectified (Collection 1/Tier 1/Surface Reflectance). This is the highest data quality available for Landsat images. They were obtained from a ~ 3-year time interval that included most of our sampling period (i.e., from Jan/2015 to Mar/2018). This time interval was sufficient to create cloud-free composites and was considered short enough to prevent intense land cover changes. We created one composite for each season as we expected strong spectral differences between the dry and rainy seasons, especially for agricultural lands. First, we performed an automatic image segmentation in RSGISLib – Remote Sensing and GIS Software Library (Bunting et al. 2014), using the two cloud-free Landsat composites. Then, we trained a predictive machine learning model and performed an object-based supervised classification over our entire study area. We also used the Normalized Difference Vegetation Index (NDVI) and the Normalized Difference Water Index (NDWI) to improve the differentiation among land cover classes, especially for open-canopy vegetation types. These vegetation indexes were quantified as individual images based on the Landsat-8 bands. All cloud-free Landsat-8 composites were created with Google Earth Engine (Gorelick et al. 2017).

Specifically, we randomly allocated 1148 points (samples) inside our study area to create the predictive model. These points were classified into eight land cover classes (≅ 150 points for each class [mean = 143.5 points, *SD* = 9.5 points]) based on visual interpretation of Google Earth high-resolution images. The land cover classes were as follows: 1) water bodies – rivers, lakes, and reservoirs; 2) native forest – sclerophyllous woodlands ("cerradão"), semi-deciduous, deciduous, and riverine forests; 3) savanna – mostly "cerrado sensu stricto" and flooded wetlands, including the more grassy Cerrado formations despite being extremely rare in the study area (see Durigan et al. 2003; Durigan and Ratter 2006); 4) managed forest – *Eucalyptus* sp., *Pinus* sp., and rubber tree plantations., 5) sugarcane – sugarcane crops, 6) pasture – grasslands dominated by exotic grasses used for cattle ranching, 7) human settlements – cities, urban and rural villages, and rural buildings in general, and 8) agriculture – other annual crops, coffee, citrus orchards, as well as other fruit crops. The samples were then randomly divided into training (808; 70%) and test (340; 30%). The test samples were used to assess model accuracy while the training samples were used for model training and tuning. Our final model was created using the Random Forests machine learning algorithm. The training and tuning steps were performed in R 3.6.2 (R Core Team 2019), using the package 'caret' (Classification and Regression Training; Kuhn 2019).

The predicted overall accuracy of our final model was high (0.92). We then performed the classification in the RSGISLib (Bunting et al., 2014), using the Scikit-learn module (Buitinck et al. 2013) in the Python programming language.

Using the test sample (340 points; 340 samples/34,069.26 km^2 of study area ≅ 1 sample/100 km^2), the overall accuracy of our map was estimated as 1.00. Thus, we decided to provide an additional accuracy assessment with a higher sample density. We randomly created 400 samples (50 points by each class) allocated inside a smaller area (586.47 km^2) located inside our study area (400 samples/586.47 km^2 = 68 sample/100 km^2). We did not perform this additional accuracy assessment for the entire study area due to time constraints necessary to achieve the same sample density as this smaller area (over > 23,000 samples would have been required for the entire 34,069.26 km^2 study area). We used these new samples to estimate again the overall accuracy (i.e., agreement) and also the overall quantity and allocation disagreement of our map. We found the overall agreement was 84.50%. The estimated overall quantity disagreement was 10.75% and the estimated overall allocation disagreement was 4.75%. Thus, we concluded that our land cover map was accurate enough to be used for investigating our hypotheses. Overall accuracy assessment was performed in R 3.6.2 (R Core Team, 2019) using the package 'rsacc' (Silva and Ferreira-Ferreira, 2018), based on (Pontius and Millones 2011; Pontius and Santacruz 2014).

Appendix F – Chapter II: Temporal heterogeneity metric quantification

A temporal heterogeneity metric, Sugarcane NDVI standard deviation (SugNDVI_sd) – the standard deviation of the Normalized Difference Vegetation Index (NDVI) of all pixels belonging to the sugarcane class – was also quantified for the three spatial scales. NDVI has been widely used to identify different stages of sugarcane phenology (Wang et al. 2019; Kavats et al. 2020) since sugarcane growth positively correlates with this vegetation index. Our metric was designed to measure the temporal heterogeneity (standard deviation) of the sugarcane phenology stages (NDVI) coexisting inside a given spatial area for each of our sampled sites. We used Sentinel-2 Level-1C (i.e., orthorectified Top-Of-Atmosphere [TOA] Reflectance) cloud-free imagery provided by European Space Agency (ESA) to quantify our temporal heterogeneity metric. Sentinel-2 is an optical multispectral satellite that provides images with a high spatial resolution (10 m for visible [Blue, Green, and Red] and Near Infra-Red [NIR] bands) and high (5 days) revisiting frequency (ESA 2015). We used the Google Earth Engine (Gorelick et al. 2017) to: 1) obtain cloud-free Sentinel-2 images with the acquisition date closest to the date each site was sampled (mean = 6.38 days, *SD* = 7.79 days), 2) crop each image with its respective landscape boundary (3,000 ha), 3) mosaic all cropped images into a single image, and 4) calculate the NDVI for each pixel as a single band image, using Red and NIR bands (spatial resolution = 10 m). Then, we calculated the standard deviation of the NDVI values for each the three spatial scales (800 m radius, 2000 m radius, 3090 m radius) associated with each sampled site using only the pixels that overlapped sugarcane areas, according to our land cover map. The quantification of temporal heterogeneity metric was performed in R 3.6.2 (R Core Team 2019), using the 'exactextractr' package (Baston 2021).

Appendix G – Chapter II: Correlations among predictors

Table S1. Pearson correlations among the three spatial scales (800 m radius (800), 2000 m (2k) radius, and 3090 m (3k) radius) for each predictor.

	NatF_800	NatF_2k	NatF_3k
NatF_800	1		
NatF_2k	0.94	1	
NatF_3k	0.91	0.97	1
	Sav_800	Sav_2k	Sav_3k
Sav_800	1		
Sav_2k	0.87	1	
Sav_3k	0.86	0.97	1
	ManF_800	ManF_2k	ManF_3k
ManF_800	1		
ManF_2k	0.72	1.0	
ManF_3k	0.70	0.98	1.0
	Sug_800	Sug_2k	Sug_3k
Sug_800	1		
Sug_2k	0.94	1	
Sug_3k	0.90	0.98	1
	Past_800	Past_2k	Past_3k
Past_800	1.00		
Past_2k	0.91	1.00	
Past_3k	0.85	0.96	1.00
	Agr_800	Agr_2k	Agr_3k
Agr_800	1.00		
Agr_2k	0.89	1.00	
Agr_3k	0.85	0.95	1.00
	SHDI_800	SHDI_2k	SHDI_3k
SHDI_800	1		
SHDI_2k	0.85	1	
SHDI_3k	0.74	0.89	1
	SIDI_800	SIDI_2k	SIDI_3k
SIDI_800	1		
SIDI_2k	0.88	1	
SIDI_3k	0.80	0.90	1
	ED_800	ED_2k	ED_3k
ED_800	1		
ED_2k	0.85	1	
ED_3k	0.82	0.97	1

Table S1 continued

	MPSz_800	MPSz_2k	MPSz_3k
MPSz_800	1		
MPSz_2k	0.87	1	
MPSz_3k	0.74	0.94	1
	SugNDVI_sd_800	SugNDVI_sd_2k	SugNDVI_sd_3k
SugNDVI_sd_800	1		
SugNDVI_sd_2k	0.59	1	
SugNDVI_sd_3k	0.50	0.85	1

NatF = % of Native Forest; Sav = % of Savanna; ManF = % of Managed Forests; Sug = % of Sugarcane crops; Past = % of Pastures; Agr = % of other Agriculture; SHDI = Shannon's Diversity Index; SIDI = Simpson's Diversity Index; ED = Edge Density; MPSz = Mean Patch Size; SugNDVI_sd = Sugarcane NDVI standard deviation.

Table S2. Correlations (Pearson or Spearman, depending on the covariate pair under analysis) among our 11 predictors, quantified at the 800 m radius scale. Strong correlations ($|r|$ or $|\rho| \geq 0.7$) are highlighted in bold.

	NatF	**Sav**	**ManF**	**Sug**	**Past**	**Agr**	**SHDI**	**SIDI**	**ED**	**MPSz**	**SugNDVI_sd**
NatF	1										
Sav	0.04	1									
ManF	0.08	0.43	1								
Sug	-0.51	-0.28	-0.39	1							
Past	-0.29	-0.27	-0.24	-0.40	1						
Agr	0.00	-0.17	0.10	-0.56	0.35	1					
SHDI	0.42	0.23	0.31	-0.53	0.30	0.49	1				
SIDI	0.47	0.23	0.33	-0.58	0.30	0.50	**0.98**	1			
ED	0.17	0.05	0.09	-0.45	0.39	0.67	**0.75**	**0.72**	1		
MPSz	0.32	0.01	-0.15	0.14	-0.24	-0.40	-0.60	-0.54	**-0.73**	1	
SugNDVI_sd	-0.16	0.09	0.01	0.12	-0.09	0.03	0.08	0.06	-0.01	-0.09	1

NatF = % of Native Forest; Sav = % of Savanna; ManF = % of Managed Forests; Sug = % of Sugarcane crops; Past = % of Pastures; Agr = % of other Agriculture; SHDI = Shannon's Diversity Index; SIDI = Simpson's Diversity Index; ED = Edge Density; MPSz = Mean Patch Size; SugNDVI_sd = Sugarcane NDVI standard deviation.

Appendix H – Chapter II: Details of the Royle & Nichols (RN) model

As a hierarchical model, the RN model is composed of two submodels: an observational (or measurement error) process submodel and an ecological (or state) process submodel (Kéry and Royle 2016). According to the observational submodel, for a given sampling site *i*, the probability of detecting the focal species (pi) is conditional on its local abundance (Ni):

$$p_i = 1 - (1 - r)^{N_i} \qquad \text{Eq. (1)}$$

where, r is the probability to detect a single individual – hereafter, the per-individual detection probability. The per-individual detection probability can be modeled as a function of covariates using a logit link:

$$\mathrm{logit}(r_i) = \beta_0 + \beta_i \mathrm{cov}_i \qquad \text{Eq. (2)}$$

where β_0 is the intercept, β_i is the effect of a given covariate, and cov_i is the value of the covariate at site *i*. In the ecological submodel, the latent species abundance, N_i, is modeled as a Poisson distribution ($N_i \sim \mathrm{Poisson}(\lambda_i)$), where λ_i is the mean of the Poisson distribution (Royle and Nichols 2003; Kéry and Royle 2016). The λ_i parameter can be interpreted as the local abundance of individuals exposed to sampling (Paolino et al. 2018). However, the λ parameter should not be interpreted as a true hare density. Instead, we interpret λ as the mean relative local abundance ("relative abundance" for brevity) of our focal species among our sampled sites (Paolino et al. 2018; Gilbert et al. 2020). In the RN model, λ_i can be modeled as a function of covariates using a log link:

$$\log(\lambda_i) = \beta_0 + \beta_i \mathrm{cov}_i \qquad \text{Eq. (3)}$$

In the RN model, the species detection (p_i) and the species occupancy (ψ_i) at given site *i* are derived parameters (i.e., not directly estimated). While species detection (p_i) can be obtained with Eq. 1, based on r and λ estimates provided by Eq. 2 and 3, site-specific species occupancy (ψ_i) is derived from the estimated relative abundance (λi), as follows:

$$\psi_i = 1 - e^{-\widehat{\lambda_i}} \qquad \text{Eq. (4)}$$

Appendix I – Chapter II: European hare individual detection results

Table S1. Model selection results for three models investigating variation in individual detection probability (r) of the European hare using transects and opportunistic surveys for fresh feces at 55 sites in the northeast of São Paulo state, southeastern Brazil. All models included a general λ structure for the relative abundance of European hare: λ(SHDI + MPSz + SugNDVI_sd + Sav + ManF).

Model	**AICc**	**ΔAICc**	**w**	**K**	**-2log(L)**
r(.)	287.63	0.00	0.60	7	271.25
r(OS)	289.41	1.77	0.25	8	270.28
r(Eff)	290.36	2.72	0.15	8	271.23

AICc = Akaike Information Criterion for small samples; ΔAICc = AICc of each model *i* minus the lowest AICc; w = Akaike weights; K = number of parameters; -2log(L) = twice the negative log-likelihood. Eff = Effort; OS = Opportunistic Survey; SHDI = Shannon's Diversity Index; MPSz = Mean Patch Size; SugNDVI_sd = Sugarcane NDVI standard deviation; Sav = % of Savanna; ManF = % of Managed Forests.

Appendix J – Chapter II: European hare relative abundance results

Table S1. Complete model set (256 models) and model selection results for the relative abundance (λ) of European hare in the northeast of São Paulo state, southeastern Brazil. All models used the best-supported, constant individual detection structure (i.e., r(.)).

Model	AICc	ΔAICc	w	K	-2log(L)
λ(MPSz + Sav + SHDI + Sug)	277.56	0.00	0.08	6	263.81
λ(MPSz + SHDI + Sug)	278.94	1.39	0.04	5	267.72
λ(Agr + Sav + SHDI)	279.31	1.75	0.04	5	268.08
λ(SHDI + Sug)	279.38	1.83	0.03	4	270.58
λ(Sav + SHDI + Sug)	279.40	1.84	0.03	5	268.17
λ(Agr + MPSz + Sav + SHDI)	279.95	2.39	0.03	6	266.20
λ(Agr + Sav + SHDI + Sug)	279.98	2.42	0.03	6	266.22
λ(Sug)	280.47	2.91	0.02	3	274.00
λ(MPSz + Past + SHDI + Sug)	280.60	3.04	0.02	6	266.85
λ(Sav)	280.68	3.12	0.02	3	274.21
λ(MPSz + SHDI + Sug + SugNDVI_sd)	280.98	3.42	0.02	6	267.23
λ(Agr + NatF + Sav + SHDI)	281.11	3.55	0.01	6	267.36
λ(Sav + Sug)	281.22	3.66	0.01	4	272.42
λ(.)	281.25	3.69	0.01	2	277.02
λ(SHDI + Sug + SugNDVI_sd)	281.26	3.70	0.01	5	270.04
λ(NatF + SHDI + Sug)	281.31	3.75	0.01	5	270.08
λ(Agr + Sav)	281.31	3.76	0.01	4	272.51
λ(Agr + Past + Sav + SHDI)	281.33	3.78	0.01	6	267.58
λ(MPSz + NatF + SHDI + Sug)	281.34	3.78	0.01	6	267.59
λ(Agr + MPSz + SHDI + Sug)	281.45	3.90	0.01	6	267.70
λ(Sav + SHDI + Sug + SugNDVI_sd)	281.46	3.90	0.01	6	267.71
λ(MPSz + ManF + SHDI + Sug)	281.47	3.91	0.01	6	267.72
λ(Past + SHDI + Sug)	281.57	4.01	0.01	5	270.34
λ(NatF + Sav + SHDI + Sug)	281.60	4.05	0.01	6	267.85
λ(Agr + SHDI + Sug)	281.60	4.05	0.01	5	270.38
λ(Agr + ManF + Sav + SHDI)	281.70	4.14	0.01	6	267.95
λ(ManF + SHDI + Sug)	281.80	4.25	0.01	5	270.58

Table S1 continued

Model	**AICc**	**ΔAICc**	**w**	**K**	**-2log(L)**
λ(Agr + Sav + SHDI + SugNDVI_sd)	281.82	4.26	0.01	6	268.07
λ(ManF + Sav + SHDI + Sug)	281.84	4.28	0.01	6	268.09
λ(Past + Sav + SHDI + Sug)	281.92	4.36	0.01	6	268.17
λ(Sav + SHDI)	282.20	4.65	0.01	4	273.40
λ(NatF + Past + SHDI + Sug)	282.29	4.73	0.01	6	268.54
λ(Past + Sav)	282.29	4.73	0.01	4	273.49
λ(Agr)	282.57	5.01	0.01	3	276.10
λ(NatF + Sav)	282.57	5.01	0.01	4	273.77
λ(Sug + SugNDVI_sd)	282.59	5.03	0.01	4	273.79
λ(MPSz + Sav + SHDI)	282.70	5.15	0.01	5	271.48
λ(Past + Sug)	282.71	5.15	0.01	4	273.91
λ(NatF + Sug)	282.75	5.19	0.01	4	273.95
λ(MPSz + Sug)	282.77	5.21	0.01	4	273.97
λ(MPSz + Sav)	282.78	5.23	0.01	4	273.98
λ(ManF + Sug)	282.80	5.24	0.01	4	274.00
λ(Agr + Sug)	282.80	5.24	0.01	4	274.00
λ(MPSz + NatF + Sav + SHDI)	282.82	5.26	0.01	6	269.07
λ(NatF)	282.93	5.37	0.01	3	276.45
λ(Sav + SugNDVI_sd)	282.97	5.41	0.01	4	274.17
λ(ManF)	282.98	5.42	0.01	3	276.51
λ(ManF + Sav)	283.01	5.45	0.01	4	274.21
λ(SHDI)	283.26	5.71	0.01	3	276.79
λ(Agr + Sav + Sug)	283.31	5.75	0.01	5	272.08
λ(Past)	283.34	5.78	0.01	3	276.87
λ(MPSz)	283.36	5.81	0.01	3	276.89
λ(NatF + SHDI + Sug + SugNDVI_sd)	283.37	5.82	0.01	6	269.62
λ(ManF + Sav + Sug)	283.39	5.83	0.00	5	272.17
λ(SugNDVI_sd)	283.40	5.84	0.00	3	276.93
λ(Agr + NatF + Sav)	283.40	5.85	0.00	5	272.18
λ(Past + Sav + SHDI)	283.46	5.91	0.00	5	272.24
λ(Agr + Past + Sav)	283.49	5.93	0.00	5	272.26

Table S1 continued

Model	**AICc**	**ΔAICc**	**w**	**K**	**-2log(L)**
λ(Sav + Sug + SugNDVI_sd)	283.52	5.96	0.00	5	272.29
λ(Past + SHDI + Sug + SugNDVI_sd)	283.55	5.99	0.00	6	269.79
λ(MPSz + Sav + Sug)	283.57	6.01	0.00	5	272.35
λ(Past + Sav + Sug)	283.60	6.05	0.00	5	272.38
λ(Agr + SHDI + Sug + SugNDVI_sd)	283.63	6.07	0.00	6	269.88
λ(NatF + Sav + Sug)	283.64	6.08	0.00	5	272.41
λ(Agr + ManF + Sav)	283.65	6.09	0.00	5	272.43
λ(Agr + SHDI)	283.71	6.15	0.00	4	274.91
λ(Agr + Sav + SugNDVI_sd)	283.73	6.17	0.00	5	272.50
λ(Agr + MPSz + Sav)	283.74	6.18	0.00	5	272.51
λ(Agr + NatF + SHDI + Sug)	283.76	6.20	0.00	6	270.01
λ(ManF + SHDI + Sug + SugNDVI_sd)	283.78	6.23	0.00	6	270.03
λ(Agr + Past + SHDI + Sug)	283.83	6.27	0.00	6	270.08
λ(ManF + NatF + SHDI + Sug)	283.83	6.27	0.00	6	270.08
λ(NatF + Past + Sav)	283.84	6.29	0.00	5	272.62
λ(NatF + Sav + SHDI)	283.97	6.41	0.00	5	272.75
λ(ManF + Past + SHDI + Sug)	284.07	6.51	0.00	6	270.31
λ(Agr + ManF + SHDI + Sug)	284.09	6.53	0.00	6	270.34
λ(Agr + NatF)	284.39	6.83	0.00	4	275.58
λ(MPSz + Past + Sav + SHDI)	284.44	6.88	0.00	6	270.69
λ(NatF + Past + Sav + SHDI)	284.47	6.91	0.00	6	270.72
λ(Agr + ManF)	284.51	6.96	0.00	4	275.71
λ(MPSz + NatF + Sav)	284.53	6.97	0.00	5	273.30
λ(Sav + SHDI + SugNDVI_sd)	284.54	6.98	0.00	5	273.31
λ(ManF + Sav + SHDI)	284.55	6.99	0.00	5	273.32
λ(MPSz + Past + Sav)	284.64	7.09	0.00	5	273.42
λ(Past + Sav + SugNDVI_sd)	284.65	7.09	0.00	5	273.42
λ(ManF + Past + Sav)	284.71	7.15	0.00	5	273.48
λ(ManF + SHDI)	284.71	7.15	0.00	4	275.91
λ(Agr + SugNDVI_sd)	284.82	7.26	0.00	4	276.02
λ(MPSz + NatF)	284.83	7.27	0.00	4	276.03

Table S1 continued

Model	**AICc**	**ΔAICc**	**w**	**K**	**-2log(L)**
λ(ManF + NatF)	284.85	7.29	0.00	4	276.05
λ(NatF + Past)	284.85	7.29	0.00	4	276.05
λ(NatF + Past + Sug)	284.86	7.30	0.00	5	273.63
λ(Agr + Past)	284.89	7.33	0.00	4	276.09
λ(Agr + MPSz)	284.90	7.34	0.00	4	276.10
λ(NatF + Sav + SugNDVI_sd)	284.92	7.36	0.00	5	273.69
λ(Agr + ManF + SHDI)	284.92	7.36	0.00	5	273.69
λ(NatF + SHDI)	284.92	7.37	0.00	4	276.12
λ(Past + Sug + SugNDVI_sd)	284.92	7.37	0.00	5	273.70
λ(MPSz + SHDI)	284.94	7.39	0.00	4	276.14
λ(NatF + Sug + SugNDVI_sd)	284.98	7.42	0.00	5	273.75
λ(ManF + NatF + Sav)	284.99	7.43	0.00	5	273.76
λ(MPSz + Sug + SugNDVI_sd)	284.99	7.44	0.00	5	273.77
λ(ManF + Past)	285.00	7.44	0.00	4	276.20
λ(ManF + Sug + SugNDVI_sd)	285.01	7.45	0.00	5	273.78
λ(Agr + Sug + SugNDVI_sd)	285.01	7.45	0.00	5	273.79
λ(MPSz + Past + Sug)	285.07	7.51	0.00	5	273.85
λ(ManF + Past + Sug)	285.09	7.53	0.00	5	273.86
λ(MPSz + ManF + Sav + SHDI)	285.09	7.54	0.00	6	271.34
λ(NatF + SugNDVI_sd)	285.10	7.54	0.00	4	276.30
λ(Agr + Past + Sug)	285.13	7.57	0.00	5	273.91
λ(MPSz + Sav + SHDI + SugNDVI_sd)	285.16	7.60	0.00	6	271.41
λ(MPSz + NatF + Sug)	285.17	7.61	0.00	5	273.94
λ(ManF + NatF + Sug)	285.17	7.61	0.00	5	273.94
λ(Agr + NatF + Sug)	285.17	7.61	0.00	5	273.95
λ(MPSz + Sav + SugNDVI_sd)	285.18	7.63	0.00	5	273.96
λ(MPSz + ManF + Sug)	285.18	7.63	0.00	5	273.96
λ(Agr + MPSz + Sug)	285.19	7.63	0.00	5	273.96
λ(MPSz + ManF + Sav)	285.20	7.64	0.00	5	273.97
λ(ManF + SugNDVI_sd)	285.21	7.65	0.00	4	276.41
λ(Agr + ManF + Sug)	285.22	7.66	0.00	5	274.00

Table S1 continued

Model	**AICc**	**ΔAICc**	**w**	**K**	**-2log(L)**
λ(MPSz + ManF)	285.24	7.68	0.00	4	276.44
λ(Past + SHDI)	285.38	7.83	0.00	4	276.58
λ(ManF + Sav + SugNDVI_sd)	285.39	7.84	0.00	5	274.17
λ(Agr + NatF + Past + Sav)	285.42	7.86	0.00	6	271.67
λ(Agr + NatF + SHDI)	285.42	7.86	0.00	5	274.20
λ(MPSz + NatF + SHDI)	285.43	7.87	0.00	5	274.20
λ(SHDI + SugNDVI_sd)	285.47	7.91	0.00	4	276.67
λ(Past + SugNDVI_sd)	285.56	8.01	0.00	4	276.76
λ(Agr + ManF + Sav + Sug)	285.59	8.03	0.00	6	271.84
λ(MPSz + Past)	285.60	8.04	0.00	4	276.80
λ(MPSz + SugNDVI_sd)	285.62	8.06	0.00	4	276.82
λ(ManF + Past + Sav + SHDI)	285.69	8.14	0.00	6	271.94
λ(Agr + MPSz + SHDI)	285.69	8.14	0.00	5	274.47
λ(Agr + Sav + Sug + SugNDVI_sd)	285.76	8.21	0.00	6	272.01
λ(Agr + Past + Sav + Sug)	285.77	8.22	0.00	6	272.02
λ(Agr + NatF + Sav + Sug)	285.80	8.24	0.00	6	272.04
λ(ManF + Sav + Sug + SugNDVI_sd)	285.80	8.24	0.00	6	272.05
λ(Agr + ManF + NatF + Sav)	285.80	8.24	0.00	6	272.05
λ(MPSz + ManF + Sav + Sug)	285.82	8.26	0.00	6	272.07
λ(Agr + MPSz + Sav + Sug)	285.83	8.27	0.00	6	272.08
λ(Past + Sav + SHDI + SugNDVI_sd)	285.83	8.28	0.00	6	272.08
λ(Agr + NatF + Sav + SugNDVI_sd)	285.89	8.33	0.00	6	272.14
λ(Agr + MPSz + NatF + Sav)	285.89	8.33	0.00	6	272.14
λ(ManF + NatF + Sav + Sug)	285.90	8.34	0.00	6	272.15
λ(ManF + Past + Sav + Sug)	285.92	8.36	0.00	6	272.17
λ(Agr + ManF + Past + Sav)	285.97	8.41	0.00	6	272.22
λ(Agr + SHDI + SugNDVI_sd)	285.98	8.42	0.00	5	274.75
λ(MPSz + Sav + Sug + SugNDVI_sd)	285.99	8.43	0.00	6	272.24
λ(Agr + Past + Sav + SugNDVI_sd)	285.99	8.43	0.00	6	272.24
λ(Past + Sav + Sug + SugNDVI_sd)	286.00	8.44	0.00	6	272.25
λ(Agr + MPSz + Past + Sav)	286.01	8.45	0.00	6	272.26

Table S1 continued

Model	**AICc**	**ΔAICc**	**w**	**K**	**-2log(L)**
λ(NatF + Sav + Sug + SugNDVI_sd)	286.04	8.48	0.00	6	272.29
λ(MPSz + Past + Sav + Sug)	286.07	8.52	0.00	6	272.32
λ(MPSz + NatF + Sav + Sug)	286.09	8.54	0.00	6	272.34
λ(NatF + Past + Sav + Sug)	286.12	8.56	0.00	6	272.37
λ(Agr + Past + SHDI)	286.13	8.57	0.00	5	274.90
λ(MPSz + NatF + Past + Sav)	286.15	8.59	0.00	6	272.40
λ(Agr + ManF + Sav + SugNDVI_sd)	286.17	8.61	0.00	6	272.42
λ(Agr + MPSz + ManF + Sav)	286.18	8.62	0.00	6	272.42
λ(NatF + Past + Sav + SugNDVI_sd)	286.21	8.65	0.00	6	272.46
λ(Agr + MPSz + Sav + SugNDVI_sd)	286.25	8.69	0.00	6	272.50
λ(MPSz + ManF + SHDI)	286.32	8.76	0.00	5	275.10
λ(NatF + Sav + SHDI + SugNDVI_sd)	286.32	8.77	0.00	6	272.57
λ(ManF + NatF + Past + Sav)	286.37	8.81	0.00	6	272.62
λ(Agr + MPSz + NatF + SHDI)	286.42	8.87	0.00	6	272.67
λ(ManF + NatF + Sav + SHDI)	286.45	8.90	0.00	6	272.70
λ(Agr + ManF + NatF)	286.51	8.95	0.00	5	275.28
λ(ManF + Past + SHDI)	286.56	9.00	0.00	5	275.33
λ(ManF + NatF + SHDI)	286.57	9.02	0.00	5	275.35
λ(Agr + NatF + SugNDVI_sd)	286.66	9.10	0.00	5	275.43
λ(ManF + NatF + Past)	286.67	9.11	0.00	5	275.44
λ(Agr + NatF + Past)	286.70	9.14	0.00	5	275.47
λ(Agr + MPSz + NatF)	286.71	9.16	0.00	5	275.49
λ(NatF + Past + SHDI)	286.78	9.23	0.00	5	275.56
λ(Agr + ManF + SugNDVI_sd)	286.85	9.29	0.00	5	275.62
λ(Agr + ManF + Past)	286.88	9.32	0.00	5	275.65
λ(Agr + ManF + NatF + SHDI)	286.89	9.33	0.00	6	273.14
λ(Agr + MPSz + ManF + SHDI)	286.91	9.36	0.00	6	273.16
λ(ManF + NatF + Past + Sug)	286.93	9.38	0.00	6	273.18
λ(Agr + MPSz + ManF)	286.93	9.38	0.00	5	275.71
λ(ManF + Sav + SHDI + SugNDVI_sd)	286.97	9.41	0.00	6	273.22
λ(ManF + SHDI + SugNDVI_sd)	286.97	9.41	0.00	5	275.75

Table S1 continued

Model	**AICc**	**ΔAICc**	**w**	**K**	**-2log(L)**
λ(MPSz + ManF + NatF)	286.97	9.41	0.00	5	275.75
λ(MPSz + NatF + Past)	286.98	9.42	0.00	5	275.75
λ(MPSz + NatF + Sav + SugNDVI_sd)	287.00	9.44	0.00	6	273.25
λ(MPSz + ManF + NatF + Sav)	287.00	9.45	0.00	6	273.25
λ(MPSz + ManF + NatF + SHDI)	287.05	9.50	0.00	6	273.30
λ(NatF + Past + SugNDVI_sd)	287.06	9.51	0.00	5	275.84
λ(ManF + NatF + SugNDVI_sd)	287.12	9.56	0.00	5	275.89
λ(MPSz + Past + Sav + SugNDVI_sd)	287.12	9.56	0.00	6	273.37
λ(MPSz + NatF + SugNDVI_sd)	287.13	9.57	0.00	5	275.90
λ(NatF + SHDI + SugNDVI_sd)	287.13	9.57	0.00	5	275.90
λ(ManF + Past + Sav + SugNDVI_sd)	287.16	9.60	0.00	6	273.41
λ(MPSz + ManF + Past + Sav)	287.17	9.61	0.00	6	273.42
λ(NatF + Past + Sug + SugNDVI_sd)	287.22	9.67	0.00	6	273.47
λ(Agr + Past + SugNDVI_sd)	287.23	9.67	0.00	5	276.01
λ(Agr + MPSz + SugNDVI_sd)	287.24	9.68	0.00	5	276.02
λ(MPSz + SHDI + SugNDVI_sd)	287.25	9.69	0.00	5	276.03
λ(Agr + ManF + SHDI + SugNDVI_sd)	287.25	9.70	0.00	6	273.50
λ(MPSz + Past + SHDI)	287.28	9.73	0.00	5	276.06
λ(ManF + Past + SugNDVI_sd)	287.30	9.74	0.00	5	276.07
λ(Agr + MPSz + Past)	287.32	9.76	0.00	5	276.09
λ(Agr + ManF + Past + SHDI)	287.34	9.79	0.00	6	273.59
λ(Agr + NatF + Past + Sug)	287.36	9.80	0.00	6	273.61
λ(MPSz + NatF + Past + Sug)	287.38	9.82	0.00	6	273.63
λ(ManF + Past + Sug + SugNDVI_sd)	287.40	9.84	0.00	6	273.65
λ(MPSz + Past + Sug + SugNDVI_sd)	287.41	9.85	0.00	6	273.66
λ(MPSz + ManF + Past)	287.41	9.85	0.00	5	276.19
λ(ManF + NatF + Sav + SugNDVI_sd)	287.43	9.88	0.00	6	273.68
λ(Agr + Past + Sug + SugNDVI_sd)	287.45	9.89	0.00	6	273.70
λ(ManF + NatF + Sug + SugNDVI_sd)	287.50	9.94	0.00	6	273.74
λ(Agr + NatF + Sug + SugNDVI_sd)	287.50	9.94	0.00	6	273.75
λ(MPSz + NatF + Sug + SugNDVI_sd)	287.50	9.94	0.00	6	273.75

Table S1 continued

Model	AICc	ΔAICc	w	K	-2log(L)
λ(MPSz + ManF + Sug + SugNDVI_sd)	287.51	9.96	0.00	6	273.76
λ(Agr + MPSz + Sug + SugNDVI_sd)	287.51	9.96	0.00	6	273.76
λ(MPSz + ManF + Past + Sug)	287.53	9.97	0.00	6	273.78
λ(Agr + ManF + Sug + SugNDVI_sd)	287.53	9.97	0.00	6	273.78
λ(MPSz + NatF + Past + SHDI)	287.55	10.00	0.00	6	273.80
λ(MPSz + ManF + SugNDVI_sd)	287.58	10.02	0.00	5	276.35
λ(Agr + MPSz + Past + Sug)	287.60	10.04	0.00	6	273.84
λ(Agr + ManF + Past + Sug)	287.61	10.06	0.00	6	273.86
λ(MPSz + NatF + SHDI + SugNDVI_sd)	287.65	10.09	0.00	6	273.90
λ(Agr + NatF + SHDI + SugNDVI_sd)	287.65	10.10	0.00	6	273.90
λ(Past + SHDI + SugNDVI_sd)	287.66	10.11	0.00	5	276.44
λ(MPSz + ManF + NatF + Sug)	287.68	10.12	0.00	6	273.93
λ(Agr + MPSz + NatF + Sug)	287.68	10.13	0.00	6	273.93
λ(Agr + ManF + NatF + Sug)	287.68	10.13	0.00	6	273.93
λ(MPSz + ManF + Sav + SugNDVI_sd)	287.70	10.14	0.00	6	273.95
λ(Agr + MPSz + ManF + Sug)	287.71	10.15	0.00	6	273.96
λ(Agr + NatF + Past + SHDI)	287.83	10.27	0.00	6	274.08
λ(MPSz + Past + SugNDVI_sd)	287.93	10.38	0.00	5	276.71
λ(ManF + NatF + Past + SHDI)	288.01	10.45	0.00	6	274.26
λ(Agr + MPSz + SHDI + SugNDVI_sd)	288.08	10.52	0.00	6	274.33
λ(Agr + MPSz + Past + SHDI)	288.21	10.66	0.00	6	274.46
λ(Agr + Past + SHDI + SugNDVI_sd)	288.50	10.94	0.00	6	274.75
λ(MPSz + ManF + Past + SHDI)	288.50	10.94	0.00	6	274.75
λ(MPSz + ManF + SHDI + SugNDVI_sd)	288.69	11.13	0.00	6	274.94
λ(Agr + ManF + NatF + Past)	288.81	11.25	0.00	6	275.06
λ(ManF + NatF + SHDI + SugNDVI_sd)	288.85	11.29	0.00	6	275.10
λ(ManF + Past + SHDI + SugNDVI_sd)	288.87	11.31	0.00	6	275.12
λ(Agr + ManF + NatF + SugNDVI_sd)	288.88	11.32	0.00	6	275.13
λ(ManF + NatF + Past + SugNDVI_sd)	288.97	11.41	0.00	6	275.22
λ(Agr + MPSz + ManF + NatF)	288.98	11.43	0.00	6	275.23

Table S1 continued

Model	AICc	ΔAICc	w	K	-2log(L)
λ(NatF + Past + SHDI + SugNDVI_sd)	288.99	11.43	0.00	6	275.24
λ(Agr + NatF + Past + SugNDVI_sd)	289.04	11.48	0.00	6	275.29
λ(MPSz + ManF + NatF + Past)	289.05	11.49	0.00	6	275.29
λ(Agr + MPSz + NatF + SugNDVI_sd)	289.10	11.54	0.00	6	275.35
λ(Agr + MPSz + NatF + Past)	289.13	11.58	0.00	6	275.38
λ(Agr + ManF + Past + SugNDVI_sd)	289.31	11.75	0.00	6	275.55
λ(MPSz + NatF + Past + SugNDVI_sd)	289.33	11.77	0.00	6	275.58
λ(MPSz + ManF + NatF + SugNDVI_sd)	289.36	11.80	0.00	6	275.61
λ(Agr + MPSz + ManF + SugNDVI_sd)	289.37	11.81	0.00	6	275.61
λ(Agr + MPSz + ManF + Past)	289.39	11.83	0.00	6	275.64
λ(MPSz + Past + SHDI + SugNDVI_sd)	289.68	12.13	0.00	6	275.93
λ(Agr + MPSz + Past + SugNDVI_sd)	289.76	12.20	0.00	6	276.01
λ(MPSz + ManF + Past + SugNDVI_sd)	289.82	12.26	0.00	6	276.07

AICc = Akaike Information Criterion for small samples; ΔAICc = AICc of each model *i* minus the lowest AICc; w = Akaike weights; K = number of parameters; -2log(L) = twice the negative log-likelihood. NatF = % of Native Forest; Sav = % of Savanna; ManF = % of Managed Forests; Sug = % of Sugarcane crops; Past = % of Pastures; Agr = % of other Agriculture; SHDI = Shannon's Diversity Index; MPSz = Mean Patch Size; SugNDVI_sd = Sugarcane NDVI standard deviation.

Appendix K – Chapter III: European hare conditional occupancy covariate

Conditional occupancy is the probability that a species occupies a site, given the detection history at that site. The conditional occupancy probability equals 1 when the species' is detected at a site (confirmed presence) and varies from 0 to 1 when the species is not detected. See MacKenzie et al., 2018 (p. 133-134) for detailed calculation. We obtained the European hare conditional occupancy probability from our previous study that investigated the main driver of the European hare invasion in southeastern Brazil (Pasqualotto et al. 2021). This previous study used the same sampling design (same sampled sites) and was conducted simultaneously to our study. Specifically, we used the most parsimonious model that accounted for potential track misidentification of European hare to obtain the conditional occupancy probability for each site using the program PRESENCE (Hines 2006).

Appendix L – Chapter III: Correlation among covariates

Table S1. Correlations (Pearson or Spearman, depending on the covariate pair under analysis) among the covariates used to investigate the Brazilian cottontail habitat use in the northeast of São Paulo state, southeastern Brazil.

	Sug	**ManF**	**Past**	**NatF**	**Sav**	**StrD**	**FED**	**FDist**	**H**
Sug	1								
ManF	-0.39	1							
Past	-0.13	-0.13	1						
NatF	-0.19	-0.52	-0.22	1					
Sav	-0.21	-0.20	-0.06	-0.22	1				
StrD	-0.15	-0.08	0.26	-0.10	0.32	1			
FED	-0.06	-0.11	0.19	0.08	0.28	**0.72**	1		
FDist	-0.05	0.05	-0.11	0.17	-0.16	-0.28	-0.47	1	
H	0.15	0.17	0.30	-0.36	-0.12	-0.11	-0.06	0.02	1

Sug = % of Sugarcane; ManF = % of Managed Forest; Past = % of Pastures; NatF = % of Native Forest; Sav = % of Savanna; StrD = Stream Density; FED = native Forest Edge Density; FDist = Farmhouse Distance; H = European hare conditional occupancy probability.

Appendix M – Chapter III: Evidence for footprint misidentification

We empirically investigated the existence of false positive detections of the Brazilian cottontail using uncertain (footprints) and certain (camera photos) detection-nondetection data by fitting two competing models: 1) a misidentification model (Miller et al. 2011) where the false positive detection probability (p_{10}) was explicitly estimated for transect surveys, and 2) a single-season model (MacKenzie et al. 2002), assuming no false positive errors for either survey method (p_{10} forced to be zero). The two models were fitted using the a general ψ structure where cottontail occupancy was modeled as an additive function of managed forest, distance to nearest farmhouse, and conditional occupancy of European hare – i.e., ψ(ManF + FDist + H). We found evidence that the footprint identification of the Brazilian cottontail likely contains false positive detections. The misidentification model, $p_{10}(.)\ p_{11}{=}r_{11}(.)$, was four times better supported than the single-season model (see below Table S1). The single-season model estimated an occupancy probability ($\hat{\bar{\psi}} = 0.15$, $SE = 0.04$) over 36% higher than the misidentification model ($\hat{\bar{\psi}} = 0.11$, $SE = 0.04$).

Table S1. Model selection results for the preliminary analysis used to investigate false positive detections during the footprint identifications of the Brazilian cottontail in the northeast of São Paulo state, southeastern Brazil. The misidentification model [$p_{10}(.)\ p_{11}{=}r_{11}(.)$] was better supported than the model that estimated no false positive (i.e, p(.), the single-season model). The two models included a general ψ structure – i.e., ψ(ManF + FDist + H).

Model	**AICc**	**ΔAICc**	**w**	**K**	**-2log(L)**
$p_{10}(.)\ p_{11}{=}r_{11}(.)$	429.56	0.00	0.80	6	417.14
p(.)	432.34	2.78	0.20	5	422.04

AICc = Akaike Information Criterion corrected for small samples; ΔAICc = AICc of each model *i* minus the lowest AICc; w = Akaike weights; K = number of parameters; -2log(L) = twice the negative log-likelihood.

Appendix N – Chapter III: Detection hypotheses and model selection results

Table S1. List of models fit during the first step of occupancy modeling of the Brazilian cottontail in the northeast of São Paulo state, southeastern Brazil. All models included the general structure for cottontail probability of use – i.e., ψ (ManF + FDist + H).

Number	Model	Method effect
1	$p_{10}(.)\ p_{11}=r_{11}(.)$	No
2	$p_{10}(.)\ p_{11}=r_{11}(\text{Sav})$	No
3	$p_{10}(.)\ p_{11}=r_{11}(\text{Past})$	No
4	$p_{10}(.)\ p_{11}=r_{11}(\text{Sug})$	No
5	$p_{10}(.)\ p_{11}=r_{11}(\text{ManF})$	No
6	$p_{10}(.)\ p_{11}=r_{11}(\text{NatF})$	No
7	$p_{10}(.)\ p_{11}=r_{11}(\text{StrD})$	No
8	$p_{10}(.)\ p_{11}=r_{11}(\text{FED})$	No
9	$p_{10}(.)\ p_{11}=r_{11}(\text{FDist})$	No
10	$p_{10}(.)\ p_{11}=r_{11}(\text{H})$	No
11	$p_{10}(.)\ p_{11}=r_{11}(\text{t})$	No
12	$p_{10}(.)\ p_{11}=r_{11}(\text{T})$	No
13	$p_{10}(.)\ p_{11}=r_{11}(\text{Sq\_T})$	No
14	$p_{10}(.)\ p_{11}=r_{11}(\text{Rainf})$	No
15	$p_{10}(.)\ p_{11}=r_{11}(\text{MinTemp})$	No
16	$p_{10}(.)\ p_{11}=r_{11}(\text{S})$	No
17	$p_{10}(.)\ p_{11}=r_{11}(\text{Y})$	No
18	$p_{10}(\text{TS})\ p_{11}=r_{11}(.)$	No
19	$p_{10}(\text{TS})\ p_{11}=r_{11}(\text{Sav})$	No
20	$p_{10}(\text{TS})\ p_{11}=r_{11}(\text{Past})$	No
21	$p_{10}(\text{TS})\ p_{11}=r_{11}(\text{Sug})$	No
22	$p_{10}(\text{TS})\ p_{11}=r_{11}(\text{ManF})$	No
23	$p_{10}(\text{TS})\ p_{11}=r_{11}(\text{NatF})$	No
24	$p_{10}(\text{TS})\ p_{11}=r_{11}(\text{StrD})$	No
25	$p_{10}(\text{TS})\ p_{11}=r_{11}(\text{FED})$	No
26	$p_{10}(\text{TS})\ p_{11}=r_{11}(\text{FDist})$	No
27	$p_{10}(\text{TS})\ p_{11}=r_{11}(\text{H})$	No
28	$p_{10}(\text{TS})\ p_{11}=r_{11}(\text{t})$	No

Table S1 continued

Number	Model	Method effect
29	p_{10}(TS) p_{11}=r_{11}(T)	No
30	p_{10}(TS) p_{11}=r_{11}(Sq_T)	No
31	p_{10}(TS) p_{11}=r_{11}(Rainf)	No
32	p_{10}(TS) p_{11}=r_{11}(MinTemp)	No
33	p_{10}(TS) p_{11}=r_{11}(S)	No
34	p_{10}(TS) p_{11}=r_{11}(Y)	No
35	p_{10}(.) p_{11}(.) r_{11}(.)	Yes
36	p_{10}(.) p_{11}(.) r_{11}(CT_pos)	Yes
37	p_{10}(.) p_{11}(.) r_{11}(CT_eff)	Yes
38	p_{10}(.) p_{11}(TS) r_{11}(.)	Yes
39	p_{10}(.) p_{11}(TS) r_{11}(CT_pos)	Yes
40	p_{10}(.) p_{11}(TS) r_{11}(CT_eff)	Yes
41	p_{10}(TS) p_{11}(.) r_{11}(.)	Yes
42	p_{10}(TS) p_{11}(.) r_{11}(CT_pos)	Yes
43	p_{10}(TS) p_{11}(.) r_{11}(CT_eff)	Yes
44	p_{10}(TS) p_{11}(TS) r_{11}(.)	Yes
45	p_{10}(TS) p_{11}(TS) r_{11}(CT_pos)	Yes
46	p_{10}(TS) p_{11}(TS) r_{11}(CT_eff)	Yes

Detection structures in each model include the following parameters: p_{10} = false positive detection for the uncertain method (transect); r_{11} = true positive detection for certain method (camera trapping); and p_{11} = true positive detection for uncertain method (transect) and are modeled as a function of the following covariates: Sug = % of Sugarcane; ManF = % of Managed Forest; Past = % of Pastures; NatF = % of Native Forest; Sav = % of Savanna; StrD = Stream Density; FED = native Forest Edge Density; FDist = Farmhouse Distance; H = European hare conditional occupancy probability; t = Time; T = Trend; Sq_T = Squared Trend; Rainf = Rainfall; MinTemp = Daily Minimum Temperature; S = Seasonality; Y = year; CT_pos = Camera-trap Position; CT_eff = Camera-trap Effort; TS = Transect Surveys.

Table S2. Model selection results for the 46 models that differ in the structures of three detection parameters (p_{10}, p_{11}, and r_{11}) for the Brazilian cottontail in the northeast of São Paulo state, southeastern Brazil. All models included the general ψ structure – i.e., ψ (ManF + FDist + H).

Model	**AICc**	**ΔAICc**	**w**	**K**	**-2log(L)**
p_{10}(.) $p_{11}=r_{11}$(S)	423.32	0.00	0.31	7	408.75
p_{10}(.) p_{11}(.) r_{11}(CT_pos)	424.52	1.20	0.17	8	407.78
p_{10}(TS) $p_{11}=r_{11}$(S)	425.44	2.12	0.11	8	408.71
p_{10}(TS) p_{11}(.) r_{11}(CT_pos)	426.62	3.30	0.06	9	407.70
p_{10}(.) p_{11}(TS) r_{11}(CT_pos)	426.68	3.36	0.06	9	407.75
p_{10}(.) $p_{11}=r_{11}$(Sq_T)	427.68	4.36	0.04	8	410.94
p_{10}(.) $p_{11}=r_{11}$(FED)	428.69	5.37	0.02	7	414.12
p_{10}(TS) p_{11}(TS) r_{11}(CT_pos)	428.83	5.51	0.02	10	407.70
p_{10}(.) $p_{11}=r_{11}$(StrD)	428.85	5.53	0.02	7	414.28
p_{10}(.) $p_{11}=r_{11}$(MinTemp)	428.93	5.61	0.02	7	414.36
p_{10}(.) $p_{11}=r_{11}$(.)	429.56	6.24	0.01	6	417.14
p_{10}(TS) $p_{11}=r_{11}$(Sq_T)	429.84	6.52	0.01	9	410.91
p_{10}(.) $p_{11}=r_{11}$(t)	430.12	6.80	0.01	11	406.75
p_{10}(.) p_{11}(.) r_{11}(.)	430.64	7.32	0.01	7	416.07
p_{10}(.) $p_{11}=r_{11}$(NatF)	430.78	7.46	0.01	7	416.21
p_{10}(.) $p_{11}=r_{11}$(ManF)	430.79	7.47	0.01	7	416.22
p_{10}(TS) $p_{11}=r_{11}$(FED)	430.84	7.52	0.01	8	414.10
p_{10}(.) $p_{11}=r_{11}$(T)	430.84	7.52	0.01	7	416.27
p_{10}(TS) $p_{11}=r_{11}$(StrD)	431.01	7.69	0.01	8	414.27
p_{10}(.) $p_{11}=r_{11}$(Sug)	431.07	7.75	0.01	7	416.50
p_{10}(TS) $p_{11}=r_{11}$(MinTemp)	431.07	7.75	0.01	8	414.34
p_{10}(.) p_{11}(.) r_{11}(CT_eff)	431.14	7.82	0.01	8	414.41
p_{10}(.) $p_{11}=r_{11}$(Y)	431.26	7.94	0.01	7	416.69
p_{10}(.) $p_{11}=r_{11}$(Rainf)	431.37	8.05	0.01	7	416.80
p_{10}(.) $p_{11}=r_{11}$(Sav)	431.58	8.27	0.01	7	417.02
p_{10}(.) $p_{11}=r_{11}$(Past)	431.67	8.35	0.00	7	417.10
p_{10}(TS) $p_{11}=r_{11}$(.)	431.67	8.36	0.00	7	417.11
p_{10}(.) $p_{11}=r_{11}$(FDist)	431.68	8.36	0.00	7	417.11
p_{10}(.) $p_{11}=r_{11}$(H)	431.70	8.38	0.00	7	417.13
p_{10}(TS) $p_{11}=r_{11}$(t)	432.34	9.02	0.00	12	406.72

Table S2 continued

Model	AICc	ΔAICc	w	K	-2log(L)
$p_{10}(.)\ p_{11}(TS)\ r_{11}(.)$	432.74	9.42	0.00	8	416.00
$p_{10}(TS)\ p_{11}(.)\ r_{11}(.)$	432.77	9.45	0.00	8	416.04
$p_{10}(TS)\ p_{11}=r_{11}(ManF)$	432.85	9.54	0.00	8	416.12
$p_{10}(TS)\ p_{11}=r_{11}(NatF)$	432.87	9.55	0.00	8	416.14
$p_{10}(TS)\ p_{11}=r_{11}(T)$	432.95	9.64	0.00	8	416.22
$p_{10}(TS)\ p_{11}=r_{11}(Sug)$	433.21	9.89	0.00	8	416.47
$p_{10}(.)\ p_{11}(TS)\ r_{11}(CT\_eff)$	433.25	9.93	0.00	9	414.32
$p_{10}(TS)\ p_{11}(.)\ r_{11}(CT\_eff)$	433.31	9.99	0.00	9	414.38
$p_{10}(TS)\ p_{11}=r_{11}(Y)$	433.42	10.10	0.00	8	416.68
$p_{10}(TS)\ p_{11}=r_{11}(Rainf)$	433.51	10.19	0.00	8	416.77
$p_{10}(TS)\ p_{11}=r_{11}(Sav)$	433.72	10.40	0.00	8	416.99
$p_{10}(TS)\ p_{11}=r_{11}(Past)$	433.81	10.49	0.00	8	417.07
$p_{10}(TS)\ p_{11}=r_{11}(FDist)$	433.82	10.50	0.00	8	417.08
$p_{10}(TS)\ p_{11}=r_{11}(H)$	433.84	10.52	0.00	8	417.10
$p_{10}(TS)\ p_{11}(TS)\ r_{11}(.)$	434.92	11.60	0.00	9	416.00
$p_{10}(TS)\ p_{11}(TS)\ r_{11}(CT\_eff)$	435.46	12.14	0.00	10	414.32

AICc = Akaike Information Criterion corrected for small samples; ΔAICc = AICc of each model *i* minus the lowest AICc; w = Akaike weights; K = number of parameters; -2log(L) = twice the negative log-likelihood; Sug = % of Sugarcane; ManF = % of Managed Forest; Past = % of Pastures; NatF = % of Native Forest; Sav = % of Savanna; StrD = Stream Density; FED = native Forest Edge Density; FDist = Farmhouse Distance; H = European hare conditional occupancy probability; t = Time; T = Trend; Sq_T = Squared Trend; Rainf = Rainfall; MinTemp = Daily Minimum Temperature; S = Seasonality; Y = year; CT_pos = Camera-trap Position; CT_eff = Camera-trap Effort; TS = Transect Surveys.