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Influence of life-history traits on the occurrence of carnivores within exotic *Eucalyptus* plantations

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Abstract

Aim: The world's forested area has been declining, especially in developing countries. In contrast, forest plantations are increasing, particularly exotic *Eucalyptus* plantations, which cover nowadays over 20 million ha worldwide. This global landscape change affects native communities, especially those at higher trophic levels that are affected by bottom–up cascading effects, such as carnivores. We seek to identify the general life-history traits of mammalian carnivore species that use exotic *Eucalyptus* plantations.

Location: We reviewed 55 studies reporting carnivore presence in *Eucalyptus* plantations worldwide.

Methods: We consider seven species life-history traits (generation length, social behaviour, body mass, energetic trophic level, diet diversity, habitat generalist/specialist and locomotion mode) as candidate drivers. We used generalized linear mixed models, with life-history traits as fixed factors, and study as well as carnivore species as random factors. We obtained the carnivore occurrence data from the literature (detection of 42 different species, from seven families). We considered non-detected species those with an IUCN Red List of Threatened Species estimated distribution range overlapping with the study areas, but not recorded by the studies.

Results: While we found no evidence of an effect of any of the other life-history traits tested, our modelling procedure indicated that habitat generalist species are more likely to use *Eucalyptus* forests than specialist species.

Main conclusions: Our results, therefore, confirm an impoverishment of predator communities in disturbed environments, with the exclusion of the most specialist predators, leading to fragmentation of their populations and, ultimately contributing to their local extinction. The local extinction of specialist carnivores may lead to "functional homogenization" of communities within plantations, modifying ecosystem functioning with a negative impact on plantations' productivity, profitability and services.

KEYWORDS
Carnivora, habitat generalist species, mammals, predator's presence, production forest, tasmanian blue gum

1 | INTRODUCTION

By 2015, almost 4 billion hectares of the world's terrestrial systems were forests. However, since the 90s the world's forest area has been declining in some regions, particularly in developing countries, where most of the forest lands are being converted to other land uses, such as agriculture (FAO, 2015). This trend is of high concern among conservationists, natural resource managers, NGOs, the general public and even some political stakeholders (e.g. Sodhi, Koh, Brook, & Ng, 2004).

Forests are among the most important repositories of biodiversity, and their sustainable management is essential not only for conservation (e.g. Ribeiro et al., 2011; Tapia-Armijos, Homeier, Espinosa, Leuschner, & de la Cruz, 2015), but also for sustaining ecosystem functioning and thereby, the continued and healthy provision of ecosystem services, such as food production, or slowing climate change (FAO, 2018). However, while globally the area covered by natural forests is decreasing, planted forests are increasing in all climatic domains. Globally, forest plantations have increased by over 105 million hectares since 1990. The average annual rate of planted forests increase between 1990 and 2000 was 3.6 million ha. (FAO, 2015). In some parts of Asia, North America and Europe, this increase was due to large-scale afforestation programmes (including the establishment of plantations, many of which exotic) (FAO, 2018).

Production plantations are established with a commercial purpose associated with forestry activities, and the largest areas of planted forests are found in the temperate domain, accounting for 150 million ha, followed by the tropical and boreal domains with almost 60 million ha each (FAO, 2015). One of the most important forestry species in temperate and tropical regions are *Eucalyptus* spp., a Myrtaceae genus with a native distribution confined to the eastern region of the Wallace line (Coppen, 2002; Pryor, 1959), and exotic plantations covering over 20 million hectares (Forrester & Smith, 2012).

Exotic *Eucalyptus* plantations are mostly established to supply wood, pulp and paper industry (Klein & Luna, 2018). Several negative impacts of these plantations on natural ecosystems have been identified, ranging from soil erosion and acidification to eutrophication of water systems and biodiversity loss (da Silva et al., 2019; da Silva Vieira, Canaveira, da Simões, & Domingos, 2010). However, well-managed exotic plantations can still provide various forest goods, resources and services for some human and wildlife populations, or even have some value for biodiversity (although dependent on the original land cover; Bremer & Farley, 2010; Brockerhoff, Jactel, Parrotta, Quine, & Sayer, 2008), while contributing to reduce the pressure upon natural forests for primary commodities (FAO, 2015). Indeed, the certification principles of forest plantations aim on increasing their provision of ecosystem services and biodiversity conservation (FSC, 2015).

Recently, some ecological studies have targeted understanding the spatial patterns of mammal populations inhabiting exotic *Eucalyptus* plantations and found that the effects of plantation on vertebrate ecology were species and production cycle phase specific. For example, Martin, Gheler-Costa, Lopes, Rosalino, and Verdade (2012), in Brazil, concluded that the community composition of small mammals varies with plantation age, with generalist species being early colonizers of exotic *Eucalyptus* plantations and more habitat specialist species only appearing in latter production cycle stages, when those forests are more vertically structured. In Portugal, Teixeira et al. (2017) and Carrilho, Teixeira, Santos-Reis, and Rosalino (2017) also showed that plantations with a more complex structure (e.g. developed understory) harboured higher abundance of generalist small mammals.

However, few local scale studies have focused on how upper trophic level species cope with the landscape changes associated with exotic *Eucalyptus* plantations. Those studies did show a negative effect on some carnivores. The impact is less evident on generalist species (Cruz, Sarmento, & White, 2015), but all indicate some avoidance of pre-harvesting stands (Timo, Lyra-Jorge, Gheler-Costa, & Verdade, 2014). Nevertheless, a broader scale approach, in terms of taxonomy (carnivore families) and geographical scope, is still lacking. This limits our ability to efficiently assess how this global landscape change is influencing carnivore geographical ranges.

Carnivores are particularly important components of ecosystems, because they play crucial roles in maintaining their functioning (Mangas, Lozano, Cabezas-Díaz, & Virgós, 2008; Roemer, Gompper, & Van Valkenburgh, 2009), namely by controlling prey density (Salo, Banks, Dickman, & Korpimäki, 2010) and behaviour (Ferrero et al., 2011; Miller et al., 2001) and by dispersing seeds (Rosalino, Rosa, & Santos-Reis, 2010); both processes shape landscape structure and resilience (Roemer et al., 2009). Furthermore, they are "instruments of evolution" influencing the differentiation of new species (Caro, 2005). This mammalian group displays high morphological, ecological and behavioural diversity and is distributed on all continents, occupying different ecological niches (Hunter, 2011). These characteristics and the above-mentioned functional role in ecosystems, together with a wide continuum in the species threatened status (IUCN, 2018), make this group an excellent model to assess the impacts of *Eucalyptus* plantations on terrestrial vertebrate distribution. Specifically, their use as models allows identifying the life-history traits that permit wildlife to cope with the wide landscape changes associated with the implementation of exotic plantations worldwide. Such information and the assessment of general trait patterns are a crucial step towards sustainable production landscapes in a changing world (Sinclair, Fryxell, & Caughley, 2006).

Providing information to managers on what are the characteristics of the species that inhabit plantations will allow landowners to manage plantations in such a way that they may also provide resources that can fulfil the ecological requirements of a wider array of species.

In this paper, our objective was to: (a) identify the general life-history traits displayed by species that manage to use exotic *Eucalyptus* plantations worldwide; and (b) discuss, in light of those traits, how these forests may be managed to ensure they have a complementary role to native areas in wildlife conservation. To achieve this, and following Dochtermann and Jenkins (2011) suggestions for applying multiple hypothesis testing, we defined six working hypotheses about how life-history traits may influence the use of plantations by carnivores:

Hypothesis 1 *Larger/heavier species are less prone to use exotic plantations as these habitats provide less food resources (e.g. Ramírez & Simonetti, 2011);*

Hypothesis 2 *Habitat and diet generalist species are more prone to use exotic plantations, as they are able to use a wider range of environments/resources (e.g. Timo et al., 2014);*

Hypothesis 3 *Social species are more prone to use exotic plantations, as they may profit from group identification of resource location in such food limited habitats and from improved vigilance in environments with high human presence (e.g. Kumar & Singh, 2010);*

Hypothesis 4 *Terrestrial/cursorial species are more prone to use exotic plantations as this habitat has a less structured canopy (e.g. Cassano, Barlow, & Pardini, 2012);*

Hypothesis 5 *Carnivores with shorter generation times may adapt more rapidly to plantations temporal heterogeneity, and thus have a higher probability of using exotic* Eucalyptus *plantations (e.g. Beckmann & Berger, 2003; Rosalino, Verdade, & Lyra-Jorge, 2014);*

Hypothesis 6 *Species presence in* Eucalyptus *plantation is determined by the combination of variables coding distinct life-history traits (and tested separately in Hypothesis 1–5).*

2 | METHODS

2.1 | Literature review

We conducted a systematic review of published literature to identify studies detecting the presence of mammalian carnivore species within exotic *Eucalyptus* plantations all over the world. We excluded all information from countries where *Eucalyptus* trees are native species (e.g. Australia). The data search included published articles, reports and unpublished dissertations (such as undergraduate and postgraduate dissertations and theses), from all years up to August 2018. The terms "carnivor*" OR "predator*" AND "*Eucalyptus*" OR "plantation," both in paper title, abstract, keywords and full paper were searched in three databases: ISI Web of Knowledge (www.isiwebofknowledge.com), SCOPUS (www.scopus.com) and Google Scholar (https://scholar.google.com). Since some studies were published in languages other than English, especially from the neotropics and Iberian Peninsula, we conducted an additional search in Google Scholar using the same keywords in Portuguese and Spanish.

We first detected 323 papers that mentioned "carnivor*" OR "predator*" AND "*Eucalyptus*" OR "plantation." From those, we excluded studies that did not fit our major criterion; that is, studies sampling carnivores in *Eucalyptus* plantations. For example, we excluded from the analysis studies targeting non-carnivore mammals such as marsupials, primates, or plantations that were not composed by *Eucalyptus* sp. Therefore, from the initial 323 studies, only 70 presented data on carnivores in *Eucalyptus* plantations. Then, in a more detailed analysis of each study, we also excluded those for which *Eucalyptus* plantations were not the main habitat type or one of the most important within the study area. We assessed the importance of *Eucalyptus* plantations within the landscape area of each study using two criteria that could be utilized simultaneously: the study explicitly mentioned in the results that the carnivore(s) species was/were detected within the *Eucalyptus* plantations; or, when this was not explicitly stated, the *Eucalyptus* plantations was the dominant landcover type in the landscape (by explicitly referring to the percentage of cover or by stating that it was the main land cover in the region; Appendix S1). In total, we managed to collect data from 46 published and 9 unpublished studies, the majority being multispecies studies (the complete list is found in Appendix S1).

2.2 | Data compilation

For each study, we recorded the geographic location (country and administrative area—e.g. state/region/council—or latitude/longitude, when available) and the carnivores species detected.

We then collected information regarding the geographical range from all carnivores, including those that were detected in our review and those that were not, from the IUCN spatial data set (http://www.iucnredlist.org/technicaldocuments/spatial-data#mammals). We used the software QGIS (2019) to build a Geographical Information System (GIS), where the species polygon ranges were overlapped with the location of each study site, using the specific location mentioned on each study, or the countries' administrative regions (e.g. dividing Brazil by its 26 states) as geographical units, when no finer scale location was provided. This procedure allowed us to identify which species could *potentially* occur at each study site, which we then classified as either present (i.e. the study mentioned the detection of that species(1), or not detected (0)). Although the IUCN range maps are often based on limited knowledge and, therefore, the occupancy of sites by carnivores could be significantly overestimated, these spatial data are amply accepted as reference and have been widely used by vertebrate conservation ecologists, particularly in global-scale studies (Ferreira, Peres, Bogoni, & Cassano, 2018). Also, possible errors in the assignment of the potential occurrence of a species to a given site should be evenly distributed among the species life-history traits, and thus may not represent a significant bias to the present study [e.g. Alhajeri and Fourcade (2019) did not detect any variation between body mass—climate correlations estimated from IUCN range maps and other species distribution databases].

We characterized all carnivores that *potentially* occur at each site according to their life-history traits and ecological features. We assessed species generation length based on data published by Pacifici et al. (2013), defined by those authors as the mean age of parents of each cohort, which represents the rate of turnover of breeding individuals. We obtained data regarding carnivore body mass (average values), locomotion mode (terrestrial/cursorial = TE, scansorial = SC, semi-aquatic = SA or arboreal = AR) and social behaviour (not social = 0; social = 1) from literature databases, such as Paglia et al. (2012), Wilman et al. (2014), EOL (2018) and IUCN (2018). We also characterized the mean energetic trophic level and the diet diversity (Shannon–Wiener Index; Zar, 2010) for each species, based on the information published by Wilman et al. (2014), who compiled the proportion of dietary items for each species (i.e. invertebrates, vertebrates, fish, fruit, seeds, nectar, other plant parts and scavenge). We associated energetic trophic levels to each dietary category following an ordinal scale, as suggested in Bueno, Dantas, Henriques, and Peres (2018): folivores: consume mostly foliage = 1.0; frugivores: diet based on fruit pulp and nectar = 2.0; granivores: mostly seed predators = 3.0; insectivores/faunivores: prey mostly upon invertebrates = 4.0; and carnivores: diet based on vertebrate preys = 5.0. Finally, based on information available on the IUCN Red List of Threatened Species (IUCN, 2018), EOL (2018) and Hunter (2011), we characterized each species as habitat specialist or generalist.

2.3 | Data analysis

We used generalized linear mixed-effects models (GLMM; Zuur, Ieno, Walker, Saveliev, & Smith, 2009) with a binomial error distribution, and a logit link function, to model the influence of life-history traits and ecological features on the presence/non-detection of species within exotic *Eucalyptus* plantations, at different sites. Prior to model fitting, we standardized the continuous variables and assessed the explanatory variables for collinearity using Variance Inflation Factors (VIF; Zuur, Ieno, & Smith, 2007). To find a set of explanatory variables without substantial collinearity, we removed one variable at a time, recalculated the VIF values, and repeated this process until all VIF values were smaller than 5 (Zuur et al., 2009).

For modelling, we used the seven species life-history traits [Generation length, social behaviour, body mass, diet diversity (Shannon–Wiener Index), energetic trophic level, habitat specialist/generalist character and locomotion mode] as fixed factors. In addition, we included two random factors: (a) study, to control for any variation in sampling artefacts across studies leading to distinct detectability rates, resulting in studies that manage to detect more than one species; and (b) carnivore species, to account for any potential phylogenetic bias. Sampling unit was each species that potentially occur in each study site.

We produced a set of candidate models representing all possible combinations of the independent variables within each working hypothesis (all including the two random factors), in order to test which of our hypotheses better captures the variability present in our data. We ranked the fitted models *per* hypothesis according to their AICc (Akaike's Information Criteria, corrected for small sample sizes; Burnham & Anderson, 2002). For each hypothesis, we considered as equally suitable those models with a ΔAICc < 2 (i.e. difference between the lowest AICc value in the set and the AICc value for each model) (Burnham & Anderson, 2002). When more than one model fitted this criterion, we applied a model averaging procedure (Burnham & Anderson, 2002) to the regression coefficients. We then estimated the 90% coefficients confidence intervals (CI90%). For every set of best models (*per* hypothesis), we selected the variables included in those average models whose CI90% did not included the zero (i.e. we could be sure of their impact on the dependent variable; positive or negative) to act as candidate variables to test Hypothesis 6, that is, the hypothesis stating that species presence is influenced by the combination of distinct life-history traits. Following Arnold (2010), besides the coefficient's confidence intervals (CI90%) we also estimated the relative variable importance (cumulative Akaike's Information Criterion weights—Σ wi—of each model parameter). This metric allowed us to identify those independent variables that may be informative, by determining with a high certainty, the direction (positive or negative) of their influence on carnivore's presence (Arnold, 2010). We compared the AICc of the best model of each hypothesis (Hypothesis 1–6) to determine which of them had greater support (i.e. lower AICc). Finally, we assessed overall best model predictive performance using the area under the curve (AUC) estimated from the receiver operating characteristic (ROC) curve (Hanley & McNeil, 1982). AUC values between 0.5 and 0.7 indicate low accuracy, while values between 0.7 and 0.9 indicate that models are able to predict species presence accurately and AUC > 0.9 indicates high accuracy (Manel, Williams, & Ormerod, 2001; Swets, 1988).

We used the glmer function in the "lme4" package (Bates, Mächler, Bolker, & Walker, 2015) for model fitting, the "MuMIn" package (Barton, 2014) for model averaging, and the "pROC" package (Robin et al., 2011) for AUC calculation, all within the R platform version 3.3.2 (R Core Team, 2017).

3 | RESULTS

We collected and analysed 847 carnivore data from the 55 identified studies that fulfilled our selection criteria (ranging from 1989 to 2018). These studies were carried out in nine countries distributed in South America (51%), Europe (42%), Asia (5%) and Africa (2%). The majority of papers were from Brazil (23), Spain (12) and Portugal (11), corresponding to 84% of all papers (Figure 1). Only 9% of the studies

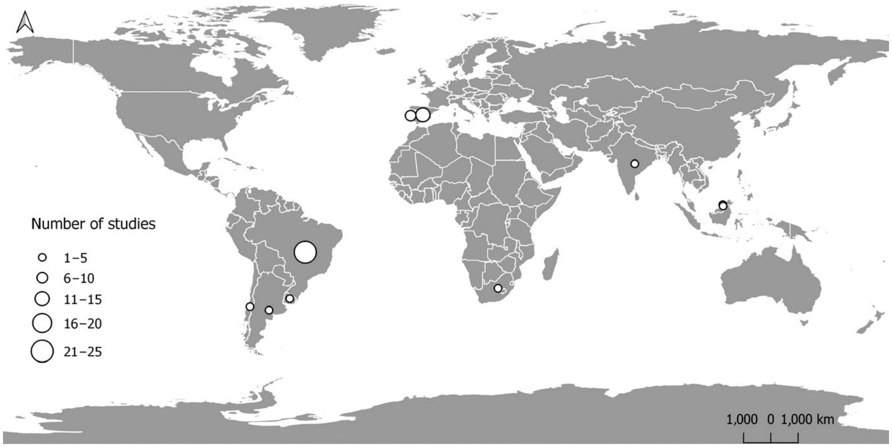

FIGURE 1 Number of studies identified in this study per country

focused solely on *Eucalyptus* plantations as the focal habitat. In the remaining 91%, *Eucalyptus* was one of the habitats sampled on the study areas (but always covering more than 25% of the study area), together with patches of other types.

The reviewed studies identified the presence of 42 carnivore species in exotic *Eucalyptus* plantations throughout the world, pertaining to seven families: Canidae ($N = 10$); Felidae ($N = 11$); Mustelidae ($N = 9$); Herpestidae ($N = 4$); Procyonidae ($N = 3$); Viverridae ($N = 3$); Mephitidae ($N = 2$) (Table 1). The majority of all these carnivore species have a habitat generalist character (nearly 90%). According to the species ranges reported by IUCN (IUCN, 2018), a total of 120 carnivore species have distribution ranges that *potentially* overlap the areas where the reviewed studies were carried (Appendix S1). Therefore, only 35% of the mammals whose *potential* range encompassed the studied areas were actually detected on *Eucalyptus* plantations, of which 70% were classified as Least Concern in the IUCN Red List of Threatened Species (IUCN, 2018 - Table 1).

No variables displayed high collinearity in our set of explanatory variables (i.e. VIF ≥ 5), and consequently, we did not remove any of the initial variables from the analysis, leaving all seven variables to be used for model building (generation length, social behaviour, body mass, energetic trophic level, Shannon–Wiener Index, locomotion mode and habitat generalist/specialist character) (see Appendix S2 for variables variation).

We produced one, eight, one, one and one GLMM candidate models for Hypothesis 1–5, respectively, but only one to four models were considered best models for each hypothesis (ΔAICc < 2; Table 2). From those, only one variable was selected to test Hypothesis 6, as they were the only ones with a CI90% that did not include 0: "Habitat generalist/specialist character" (Appendix S3). Thus, as only one variable fulfils our criteria, the model that could be produced for Hypothesis 6 was already included in the Hypothesis 2 model set. Therefore, we excluded Hypothesis 6. The hypothesis that revealed to have a high support from the data (i.e. that included the best models) was Hypothesis 2—carnivore occurrence was influenced by the generalist/specialist character of the species (Table 2).

The estimated best overall average model included three variables: habitat generalist/specialist character; energetic trophic level; and Shannon–Wiener Index. But from those only one ("Habitat generalist/specialist character") had a 90% confidence interval that did not overlap with zero, evidencing their influence on carnivore presence in *Eucalyptus* plantations (Table 3). For the remaining variables, we could not assess how they influence carnivore occurrence as the 90% confidence interval included positive and negative values. Thus, according to these results, habitat generalists have a higher probability of occurring in *Eucalyptus* plantations (Table 3). Finally, we tested the significance of the random effects (using a likelihood ratio test) and we detected a significant effect of including random effects ($\chi^2 = 148.32$, $p < .001$; Random effect (Species) intercept: variance = 2.011, $SD = 1.418$; Random effect (Study) intercept: variance = 1.190, $SD = 1.091$). The best models presented good predicting capacity, with an AUC value of 0.883 (Manel et al., 2001).

4 | DISCUSSION

Identifying the patterns and underlying drivers of upper trophic level organisms' occurrence in anthropic environments, namely plantations, is crucial to understand and predict changes in community structure associated to anthropogenic habitat changes (Dunning et al., 1995). Indeed, by studying the occurrence of carnivores in *Eucalyptus* plantations, it became apparent that communities were mostly dominated by species with a habitat generalist character.

Habitat generalist character was key for carnivore occurrence in *Eucalyptus* plantations, thus partially supporting our second hypothesis, that is, habitat generalist species are more prone to use exotic plantations, as they are able to use a wider range of environments/resources (e.g. Timo et al., 2014). Other alternative hypotheses based on carnivore's body mass, generation length, generalist feeding behaviour, locomotion mode and social behaviour had no support from our data.

Landscape fragmentation/degradation and disturbance often affect more deeply habitat specialist species (Devictor, Julliard, & Jiguet, 2008), due to their dependence on one or few habitat/resource types, especially those more temporally stable (Futuyma & Moreno, 1988), and because specialization decreases the ability of a species to cope with specific resource scarcity (e.g. by changing its distribution range) (Brook, Sodhi, & Bradshaw, 2008). Almost

TABLE 1 Carnivore species detected in exotic *Eucalyptus* plantations throughout the world, countries where they were detected and their threat status according to the IUCN Red List of Threatened Species (IUCN, 2018) (the complete list of papers that detected each species in *Eucalyptus* plantations is presented in Appendix S1)

Family	Species	Country	IUCN threat category 2018 IUCN (2018)
Canidae	*Cerdocyon thous*	Brazil	Least Concern
Canidae	*Chrysocyon brachyurus*	Brazil	Near Threatened
Canidae	*Cuon alpinus*	India	Endangered
Canidae	*Lycalopex culpaeus*	Chile	Least Concern
Canidae	*Lycalopex fulvipes*	Chile	Endangered
Canidae	*Lycalopex griseus*	Chile	Least Concern
Canidae	*Lycalopex gymnocercus*	Brazil and Uruguay	Least Concern
Canidae	*Lycalopex vetulus*	Brazil	Least Concern
Canidae	*Vulpes bengalensis*	India	Least Concern
Canidae	*Vulpes vulpes*	Portugal	Least Concern
Felidae	*Caracal caracal*	South Africa	Least Concern
Felidae	*Herpailurus yagouaroundi*	Brazil	Least Concern
Felidae	*Leopardus geoffroyi*	Uruguay and Argentina	Least Concern
Felidae	*Leopardus guigna*	Chile	Vulnerable
Felidae	*Leopardus pardalis*	Brazil	Least Concern
Felidae	*Leopardus tigrinus*	Brazil	Vulnerable
Felidae	*Leopardus wiedii*	Brazil and Uruguay	Near Threatened
Felidae	*Lynx pardinus*	Spain	Endangered
Felidae	*Panthera onca*	Brazil	Near Threatened
Felidae	*Panthera pardus*	India	Vulnerable
Felidae	*Puma concolor*	Brazil and Chile	Least Concern
Herpestidae	*Herpestes fuscus*	India	Least Concern
Herpestidae	*Herpestes ichneumon*	Portugal and Spain	Least Concern
Herpestidae	*Herpestes semitorquatus*	Malaysia	Near Threatened
Herpestidae	*Herpestes vitticollis*	India	Least Concern
Mephitidae	*Conepatus chinga*	Brazil and Uruguay	Least Concern
Mephitidae	*Conepatus semistriatus*	Brazil	Least Concern
Mustelidae	*Eira barbara*	Brazil	Least Concern
Mustelidae	*Galictis cuja*	Brazil and Uruguay	Least Concern
Mustelidae	*Galictis vittata*	Brazil	Least Concern
Mustelidae	*Lontra longicaudis*	Brazil and Uruguay	Near Threatened
Mustelidae	*Lutra lutra*	Portugal	Near Threatened
Mustelidae	*Martes foina*	Portugal and Spain	Least Concern
Mustelidae	*Meles meles*	Portugal and Spain	Least Concern
Mustelidae	*Mustela nivalis*	Portugal	Least Concern
Mustelidae	*Mustela putorius*	Portugal and Spain	Least Concern
Procyonidae	*Nasua nasua*	Brazil	Least Concern
Procyonidae	*Potos flavus*	Brazil	Least Concern
Procyonidae	*Procyon cancrivorus*	Brazil and Uruguay	Least Concern
Viverridae	*Genetta genetta*	Portugal and Spain	Least Concern
Viverridae	*Paradoxurus hermaphroditus*	Malaysia	Least Concern
Viverridae	*Viverricula indica*	India	Least Concern

TABLE 2 Best GLMMs (ΔAICc < 2) per hypothesis, ranked by their ΔAICc values, showing their degrees of freedom (*df*), Akaike's Information Criterion corrected for small sample sizes (AICc), the difference between the lowest AICc value in the set and the AICc value for each model (ΔAICc) and the probability of each model being the best among the set of candidate models (Akaike weight)

Hypothesis	Model	Df	AICc	ΔAICc	Akaike weight	Overall ΔAICc
	Full Model	13	777.7			6.8
	Null Model	2	774.0			3.1
Hypothesis 1 (Body size)	Bdy_mss	2	775.9	0.00	1.000	5.0
Hypothesis 2 (Generalist/ specialist character)	**Habitat + Shn**	**5**	**770.9**	**0.00**	**0.268**	**0.0**
	Habitat	**4**	**771.0**	**0.07**	**0.259**	**0.1**
	Shn	**4**	**772.3**	**1.41**	**0.133**	**1.4**
	Habitat + Trp_lvl	**5**	**772.7**	**1.76**	**0.111**	**1.8**
Hypothesis 3 (Social Behaviour)	Social	4	775.9	0.00	1.000	5.0
Hypothesis 4 (Locomotion mode)	Lcm	6	773.7	0.00	1.000	2.8
Hypothesis 5 (Generation time)	Gen_time	4	775.5	0.00	1.000	4.6

Note: The full and null models are also presented, and the hypothesis with more support is highlighted in bold type.

Abbreviations: Bdy_mss, body mass; Gen_time, generation time; Habitat, habitat generalist/specialist character; Lcm, locomotion mode; Shn, Shannon–Wiener Index; Social, social Behaviour; Trp_lvl, energetic trophic level.

90% of the carnivore species found in these studies are habitat generalists, a pattern in line with the previous arguments and partially supporting our Hypothesis 2 (as no diet diversity effect was detected) (i.e. "generalist species are more prone to use exotic plantations, as they are able to use a wider range of the resources available"; Timo et al., 2014). Indeed, some studies highlighted that ecologically generalist species should benefit from environments that are temporally heterogeneous where resource availability is linked to production cycles, often originating a mast availability of resource in one period (e.g. refuge availability will be higher just prior to plantation's harvest) and a complete shortage in others (e.g. after harvest, refuge availability will be null, when plantations are reduced to bare soil), along vast geographical areas, as in forestry plantations (Futuyma & Moreno, 1988; Kassen, 2002; Marvier, Kareiva, & Neubert, 2004; Östergård & Ehrlén, 2005). Such resource instability in plantations will probably increase competition, which may be biased towards generalist and less threatened, and often more abundant, species. Interspecific competition due to resource shortage is less intense in natural environments habitat (even if abundance is higher) than in anthropic ecosystem (e.g., Manor & Saltz, 2008).

The specialist character is frequently highlighted as promoter of extinction rate (Pearson et al., 2014), often acting synergistically with other species characteristics, such as sensitivity to disturbance or population density, or human population density (Brook et al., 2008; Cardillo et al., 2005). Most studies reporting carnivore species in *Eucalyptus* plantations were carried out in Brazil and Iberian Peninsula (Portugal and Spain), where plantations were implemented in already disturbed landscapes (e.g. conversion of cattle grazing areas in Brazil—Martin et al., 2012; or in areas where human presence and activities occurred millennia ago in the Iberian Peninsula—Blondel, 2006). Thus, these areas might be occupied mostly by more habitat generalist species, and those more specialist were already locally extinct. Therefore, the range of potentially occurring species might be already a subset of species that could originally be present in each region, as a result of historical extinctions of

TABLE 3 Coefficients (Coef; full average), standard errors (*SE*), *z*-values, significance level [Pr (>|*z*|)], 90% confidence intervals (CI 90%) and relative importance of the variables included in the best models explaining the carnivore's presence in Eucalyptus plantations (ΔAIC < 2)

Model-averaged coefficients	Coef	*SE*	*z*-value	Pr (>|*z*|)	CI 90%		Relative Importance
Intercept	−3.620	1.141	3.169	0.002	−5.499	−1.742	
Habitat (generalist)	**1.613**	**0.858**	**1.879**	**0.060**	**0.201**	**3.025**	**0.638**
Shannon–Wiener	0.678	0.430	1.573	0.116	−0.031	1.387	0.401
Trophic level	−0.208	0.360	0.579	0.563	0.800	0.383	0. 111

Note: Variables in bold type have CI 90% that do not include 0.

Abbreviations: Habitat, Habitat generalist/specialist character; Shannon–Wiener, Shannon–Wiener Index; Trophic level, Energetic trophic level.

bigger species (especially in landscapes historically used by humans) due to the combined effect of lower population density and growth, and disproportionately higher exploitation rate by humans (Cardillo et al., 2005). This absence of habitat specialist species in *Eucalyptus* plantations is a worldwide pattern, as different specialist species taxa are declining throughout the world in most of the ecosystems (Clavel, Julliard, & Devictor, 2011), for example plants (Fischer & Stöcklin, 1997; Rooney, Wiegmann, Rogers, & Waller, 2004); some insects as butterflies (Warren et al., 2001), carabid beetles (Kotze & O'Hara, 2003) and bumblebees (Goulson, Hanley, Darvill, Ellis, & Knight, 2005); coral reef fish (Munday, 2004); birds (Julliard, Jiguet, & Couvet, 2004); and marsupials (Fisher, Blomberg, & Owens, 2003). The replacement of specialized species by generalists, together with the loss of threatened carnivores, will create a "functional homogenization" of communities inhabiting plantations, which can modify the ecosystem functioning, leading to a decline of ecosystem productivity, profitability and services (Clavel et al., 2011). This loss of specialist/threatened species is particularly important in carnivores, due to their crucial role in ecosystems structuring and functioning. When a change in the carnivore community occurs (e.g. loss of specialist), important ecosystem services and functions that predators provide might be menaced. For example, several studies have detected that a change in predator communities may lead to a decrease in the efficiency of important agriculture pests control (e.g. Schmitz, Hamback, & Beckerman, 2000), a change in prey population dynamics (e.g. Berger & Conner, 2008), an indirect influence on vegetation structure (Beschta & Ripple, 2016) and to an increase of invasive domestic species in the wilderness (e.g. Carvalho et al., 2019). In a landscape oriented for production, the increase in the abundance of some of potential carnivores' prey may affect tree productivity due to predator depletion/change (e.g. insect pests or rodents; Freer-Smith & Webber, 2017; Paquette & Messier, 2011), and may impact plantation's profitability. Therefore, the maintenance of a healthy carnivore's community should be viewed by landowners as a crucial management strategy. But, since *Eucalyptus* plantations rarely host specialist species, the benefits of these environments can only be complementary to other conservation strategies, such as the establishment of protected areas, where specialist species may be conserved accordingly.

Diet specialization and energetic trophic level did not have an effect on the use of *Eucalyptus* plantations by carnivores. Therefore, the ability of carnivores to use these environments is more related to an ability to exploit a large array of environments than to exploit alternative food sources or specific food sources. We also did not detect any significant influence of the social/solitary character, body size, locomotion mode and generation time on carnivore's presence in *Eucalyptus* plantations. Life in group is favoured by several aspects, including more access to mating partners, better protection against predators and improved detection of food resources (Krause & Ruxton, 2002). However, life in group is also disfavoured by some aspects, such as competition for food (Krause & Ruxton, 2002). Consequently, life in group is more viable when the food resources are distributed in patches (Macdonald & Johnson, 2015). Thus, our hypothesis may not have been confirmed due to the spatial homogeneity of *Eucalyptus* plantations, which does not allow resource patchiness, disfavouring life in group. The lack of relationship of the locomotion mode with the probability of presence in *Eucalyptus* plantations may be related to the fact that scansorial species may be as suited to exploit these plantations as terrestrial/cursorial species (Piña, Carvalho, Rosalino, & Hilário, 2019). Since these two locomotion modes represent 84% of the species in our sample, even a complete absence of other locomotion modes (i.e. semi-aquatic and arboreal) within the plantations would not represent a significant effect in the models. Regarding the generation time, probably the time since implementation of most plantations and the time in which the studies were carried was not enough to adaptive responses to occur. Finally, it is not clear why we did not find a relationship between body size and the probability of presence in *Eucalyptus* plantations. Since larger species demand higher amounts of resources, we expected that these species were less prone to occur in *Eucalyptus* plantations. However, this relationship was also not detected in another previous study (Ramírez & Simonetti, 2011). This may be due to body size interactions with other variables, such as energetic trophic level and generalist/specialist character, but further research is needed to assess those relationships.

Although depleted from more specialist top predators, *Eucalyptus* plantations still are used by a wide carnivore community (ca. 35% of the community that could potentially use the areas). Even though they are dominated by generalist species, such community could be enriched with the implementation of management actions that allow for the development of a complex vegetation structure (i.e. dense understory) within plantations, together with the sustainable use of agro-chemicals and mechanical treatments (i.e. restricted to specific seasons non-overlapping with carnivores reproductive season) (Teixeira et al., 2017; Timo et al., 2014).

Due to the evident decline in global biodiversity (McGill, Dornelas, Gotelli, & Magurran, 2015), the development of appropriate management practices that allow species survival, without significantly compromising business profitability, is imperative and a major challenge for conservation biology (Fuller, Oliver, & Leather, 2008). Several management schemes have proven to be more sustainable than an intensive approach, benefiting species survival by acting as supplementary environments to natural systems, in a landscape approach (e.g. Carnus et al., 2006; Fischer, Lindenmayer, & Manning, 2006). Since we manage to identify that habitat generalist species are more prone to use *Eucalyptus* plantations, some management actions might be implemented to promote its use by other carnivores. Timo et al. (2014) identified the most critical phase of plantation's cycle is harvesting, a period when most carnivores avoid using plantations. Thus, by implementing a harvesting scheme that favours a rotation in wood-cutting activities across stands (and not a harvesting the entire plantation in a single moment) will allow managers to create conditions for species which are more susceptible to disturbance (i.e. habitat specialists species that need low disturbance areas; Irwin et al., 2010) to find refuge and resources in non-disturbed stands while part of the plantation is being harvested. As habitat specialist are avoiding *Eucalyptus* plantations, by creating several native habitat patches throughout the landscape (e.g. using well preserved riparian areas as corridors/connectors or patches that provide resources and act as stepping stones; e.g. Archibald et al., 2011; Mazzolli, 2010), landowners can manage plantations in such a way that they may also provide resources that can fulfil the ecological requirements of more habitat specialist species, and thus enhance plantations' carnivore richness.

5 | CONCLUSION

This worldwide review of carnivore occurrence in exotic plantations, and the assessment of the drivers shaping those patterns, highlights that the global landscape changes associated with forestry plantations induce changes in carnivore communities, which are currently composed mostly by habitat generalist species. These global changes led to an impoverished community encompassing 35% of the species with ranges overlapping with the monitored areas with plantations.

Such pattern found for carnivores that inhabit *Eucalyptus* plantations reinforce the scale of the impact caused by the expansion of human activities on natural ecosystems and communities. This is another piece of information supporting that the loss of natural habitat to human uses or the conversion of extensive regime agroecosystems to more intensive exploitation schemes is one of the most recurrent promoters of species extinction risk at local, regional and even global scales (see Brummitt et al., 2015; Estrada et al., 2017). Based on these results, to overcome such community changes it is suggested that managers should create heterogeneity (i.e. to include less disturbed areas) within plantations, through rotation in wood-cutting activities across stands and by promoting native habitat patches throughout the landscape. These approaches will allow more habitat specialist species to use plantations, assuring a higher landscape functionality.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analysed in this study. All the data used in the manuscript analysis were retrieved from already published documents (papers, Master dissertations, PhD thesis or Reports).

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BIOSKETCH

The authors are interested in investigating the patterns of occupancy, abundance and richness of mammals in anthropogenic landscapes, and understanding how different land uses affect mammals in space and time. Our focus is to achieve a balance between the necessary productive activities and biodiversity conservation, which are a goal of the sustainable development. Furthermore, their research is also focused on wildlife monitoring and species distribution modelling. Links to the authors CVs or webpages: Daniela Teixeira - www.cesam.ua.pt/danielateixeira; Gurutzeta Guillera-Arroita - http://ceed.edu.au/ceed-researchers/all-members/261-dr-gurutzeta-guillera-arroita.html; Renato Hilário: http://lattes.cnpq.br/8431052349581155; Carlos Fonseca http://www.cesam.ua.pt/cfonseca; Luís M. Rosalino - https://ce3c.ciencias.ulisboa.pt/member/luismiguelrosalino

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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