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# Disturbance or propagule pressure? Unravelling the drivers and mapping the intensity of invasion of free-ranging dogs across the Atlantic forest hotspot

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## Abstract

**Aim**: Identifying the drivers of biological invasions is crucial to predict the risk of invasion across broad spatial scales and to devise strategies to prevent invasion impacts. Here, we explore the relative importance and synergies between two key drivers—propagule pressure and landscape disturbance—in determining the invasion of native forest remnants by dogs, one of the most abundant, widely distributed, and harmful invasive species worldwide.

**Location**: Brazilian Atlantic Forest.

**Methods**: Combining a camera trap dataset (96 sites in forest remnants) and censuses of populations of dogs raised by humans across 12 landscapes (2,830 ha each), we used $N$-mixture models that account for imperfect detection to confront alternative hypotheses of invasion drivers. We then used this empirical evidence to predict the intensity of dog invasion across the Atlantic Forest hotspot.

**Results**: Propagule pressure (density of raised dogs, positive effect) and landscape disturbance (forest cover, negative effect) were equally important drivers of dog invasion, presenting additive rather than synergistic effects. Dogs invade forest remnants far from their homes, making the density of raised dogs the key component of propagule pressure (relative to dog spatial distribution). Forest cover was more important than either the length or density of forest edges, suggesting that both reduced area of forested barriers to long-distance movements and increased proximity of forests to edges facilitate dog access to forests. Across the Atlantic Forest, the combination of high human population density and extensive deforestation makes dog invasion an additional and widespread threat.

**Main conclusion**: Combined with available maps of priority areas for biodiversity conservation, our spatial prediction of dog invasion can help target areas for integrated management actions. These actions should go beyond measures to control dog populations and encompass the maintenance and restoration of native forests and strategic planning of afforestation through planted forests.

KEYWORDS
abundance models, biotic homogenization, *Canis familiaris*, exotic species, habitat fragmentation, habitat loss, invasion risk, landscape structure, subsidized predator, tropical forest

## 1 | INTRODUCTION

Biological invasions are one of the principal threats to biodiversity on the planet (Bellard, Cassey, & Blackburn, 2016), influencing multiple levels of ecological organization (Mack et al., 2000). The intensification of human trade and transport (Seebens et al., 2015) contributes to both active and passive processes of introduction of potentially invasive species, leading to a global process of biotic homogenization (Liu, He, Chen, & Olden, 2017; Rosenblad & Sax, 2017). Given the widespread impacts of biological invasions, research on the subject has rapidly expanded (Lowry et al., 2013), fostering both conceptual controversies and advances. Debates on what defines an invasive species (Pereyra, 2016) arose in part from the ecological variability across invasive species and invaded environments, and the diverse roles humans play across invasion processes, leading to the claim that a unique definition is neither feasible nor desirable (Heger, Saul, & Trepl, 2013; Humair, Edwards, Siegrist, & Kueffer, 2014). Despite these controversies, the field has rapidly progressed, especially in terms of hypotheses about the drivers and the associated mechanisms of invasions.

Largely, these hypotheses assume that invasion success is related to species characteristics (e.g., high reproductive rate, early maturation) (Kolar & Lodge, 2001; Sakai et al., 2001), habitat conditions that increase susceptibility to invasion (Davis, Grime, Thompson, Davis, & Philip, 2000; Shea & Chesson, 2002) and/or the number or the spatial distribution of introduced individuals or introduction events—collectively termed propagule pressure (Lockwood, Cassey, & Blackburn, 2005; Simberloff, 2009). Although scattered evidence can be found for many of those hypotheses (Catford, Jansson, & Nilsson, 2009), the importance of both propagule pressure (Blackburn, Prowse, Lockwood, & Cassey, 2013; García-Díaz, Ross, Ayres, & Cassey, 2015; Lockwood et al., 2005; Simberloff, 2009) and disturbance (Byers, 2002; Crooks, Chang, & Ruiz, 2010; Gantchoff & Belant, 2015; Jauni, Gripenberg, & Ramula, 2015) has been frequently corroborated in a variety of studies.

Propagule pressure is related to the number of individuals released into a region and/or the number of introduction events (Lockwood et al., 2005). It also incorporates the spatial or temporal distribution of those individuals or events (Simberloff, 2009). Greater propagule pressure increases invasion success by increasing the chance of invasion (in a given area, and/or in a greater extension, of native habitat; Bossenbroek, Kraft, & Nekola, 2001), reducing the negative impacts of stochastic processes or Allee effects on population dynamics, and/or increasing genetic variability (Blackburn, Lockwood, & Cassey, 2015). Disturbances in turn are defined as environmental changes that transform a system on time-scales faster than the evolutionary responses of species (Byers, 2002). They vary widely in scale, ranging from local (e.g., canopy opening) to landscape disturbances (e.g., associated with native vegetation conversion at broader spatial scales; With, 2002). Disturbances facilitate invasion either by changing resources in a favourable way to invasive species (Davis et al., 2000) or by reducing native species abundance, and thus weakening the effects of negative interactions that native species may exert on invasive species (D'Antonio, Dudley, & Mack, 1999). In particular, landscape disturbances, such as habitat loss and fragmentation, affect species distribution and dispersal (Cornelius, Awade, Cândia-Gallardo, Sieving, & Metzger, 2017; Fahrig, 2003) and have been suggested to strongly facilitate and/or interact with biological invasions (Didham, Tylianakis, Gemmell, Rand, & Ewers, 2007).

Although many studies support the importance of disturbance and propagule pressure as drivers of invasions, relatively few have addressed these multiple drivers simultaneously (Lowry et al., 2013). Those that have often rely on limited quantifications of disturbance (commonly measured at the local scale or as a binary variable; Britton-Simmons & Abbott, 2008; Clark & Johnston, 2009; Eschtruth & Battles, 2009; Maron et al., 2013) and/or of propagule pressure (commonly measured indirectly; Vilà & Ibáñez, 2011). These limitations narrow our understanding of the synergies and relative importance between drivers, restricting our ability to predict the risk of invasion at broad scales and identify actions to prevent invasions. We address these gaps by focusing on one of the most widespread and harmful invasive species worldwide—the dog (*Canis familiaris*) (Bellard, Genovesi, & Jeschke, 2016; Doherty et al., 2017), and on a biodiversity hotspot—the Brazilian Atlantic Forest.

In rural areas around the globe, the estimated dog population is ~600 million individuals and most of them are free ranging (Gompper, 2014). These large, free-ranging populations that are neither feral nor strictly owned are responsible for most reported impacts of dogs on native species (Young et al., 2011). As dogs are strongly associated with humans, the process of invasion is somewhat distinctive. In contrast to wild or feral species, free-ranging dogs do not establish sustainable populations, rather their populations depend strongly on human subsidies. Yet, individual dogs range freely through the landscape, commonly using native vegetation patches (e.g., Lessa, Corrêa, Bergallo, Cunha, & Vieira, 2016; Paschoal et al., 2016; Silva-Rodríguez & Sieving, 2012). In some areas, free-ranging dogs make up the most abundant carnivore in native vegetation (Paschoal et al., 2016), and their known impacts on wildlife include both lethal and sublethal effects of predator–prey interactions (Manor & Saltz, 2004; Silva-Rodríguez & Sieving, 2012; Young et al., 2011), interference and exploitative competition (Butler & du Toit, 2002; Vanak & Gompper, 2010), and disease transmission (Cleaveland et al., 2000; Curi et al., 2016).

We conducted an empirical study across 12 landscapes (2,830 ha each, varying from 10% to 50% in native forest cover), embedded in a 300,000-ha region of the Atlantic Forest biodiversity hotspot, to investigate the relative importance and synergies of key drivers—propagule pressure and landscape disturbance—on dog invasion in native forest remnants. We then model this empirical evidence to predict the intensity of invasion across the Atlantic Forest phytogeographical domain. To assess the relative importance and synergies of invasion drivers, we used a landscape study design (McGarigal & Cushman, 2002), combining a camera trap sampling within multiple forest remnants with a complete census of dogs raised by humans in each landscape. We considered measures of propagule pressure associated with both the number (density of raised dogs) and the spatial distribution (proportion of dogs raised near forests) of dogs, which should be positively related to dog invasion. We quantified landscape disturbance through metrics related to forest accessibility to dogs, considering both the distance of forests to edges (edge density between forest and open areas)—expected to increase dog invasion— and the perimeter (edge length between forest and open areas) and area (forest cover) of forested barriers to long-distance movements—expected to decrease dog invasion. We then used *N*-mixture models that address imperfect detection (Royle, 2004), and compared alternative hypotheses (models) about the drivers of dog abundance in native forests that consider only propagule pressure, only landscape disturbance, their additive effect or their interactive effect. To generate the map of invasion intensity, we then used the most parsimonious *N*-mixture model to predict dog invasion across Atlantic Forest landscapes that presented propagule pressure and landscape disturbance values within the range of the studied landscapes.

## 2 | METHODS

### 2.1 | Study region

The study was conducted in a 300,000-ha region in the Cantareira-Mantiqueira region of the Atlantic Plateau of São Paulo, Brazil (Figure 1), encompassing 10 municipalities. Mean annual rainfall is 1,513 mm and the mean of the minimum and maximum temperatures is 14.8 and 27.7°C in the warm-wet season (October to March) and 11.3 and 24.6°C in the cold-dry season (April to September) (www.cpa.unicamp.br). The region was originally covered by montane evergreen Atlantic Forest, although cattle pastures and eucalyptus forestry have now replaced much of the native vegetation.

The rural areas of the study region are densely populated (mean ± *SD*: 19.0 ± 19.2 people/km$^2$). Consequently, dog density is also high (11.6 ± 9.4 individuals/km$^2$; see Supporting Information Appendix S1: Figure S1.1). Approximately 75% of rural households raise dogs (range 1–21 individuals, 2.69 ± 1.99). Owners report that approximately 25% of dogs are castrated, 80% are vaccinated against rabies, but only 31% are vaccinated against other diseases, and 32% and 58% receive treatment for ecto- and endoparasites, respectively (Biffi, 2017). According to owners, 41% of dogs frequently leave the household surroundings on their own, 15% frequently search for food outside the household, 12% enter frequently into native forest and approximately 7% have already killed native animals, while 18% have already been injured by them (Biffi, 2017).

### 2.2 | Sampling design

We conducted a landscape study, using landscapes as sampling units and, hence, measuring both dog invasion and invasion drivers at the landscape scale (Fardila, Kelly, Moore, & McCarthy, 2017; McGarigal & Cushman, 2002). Although required to study the effects of processes that occurs at the landscape scale (such as landscape disturbances), this approach is still uncommon in the literature (Fardila et al., 2017). We selected 12 focal landscapes (2,830 ha) aiming at maximizing the variation in native forest cover while controlling for other variables (Supporting Information Appendix S1: Figure S1.1) and sampled each of them at eight native forest sites. As the size of the largest fragment is an important landscape characteristic nonlinearly related to habitat cover (Fahrig, 2003), we selected the eight sampling sites within each landscape (96 sites in total) using a stratified random sampling based on the proportion of native forest in the landscape contained in the largest fragment (Figure 1; Supporting Information Appendix S1).

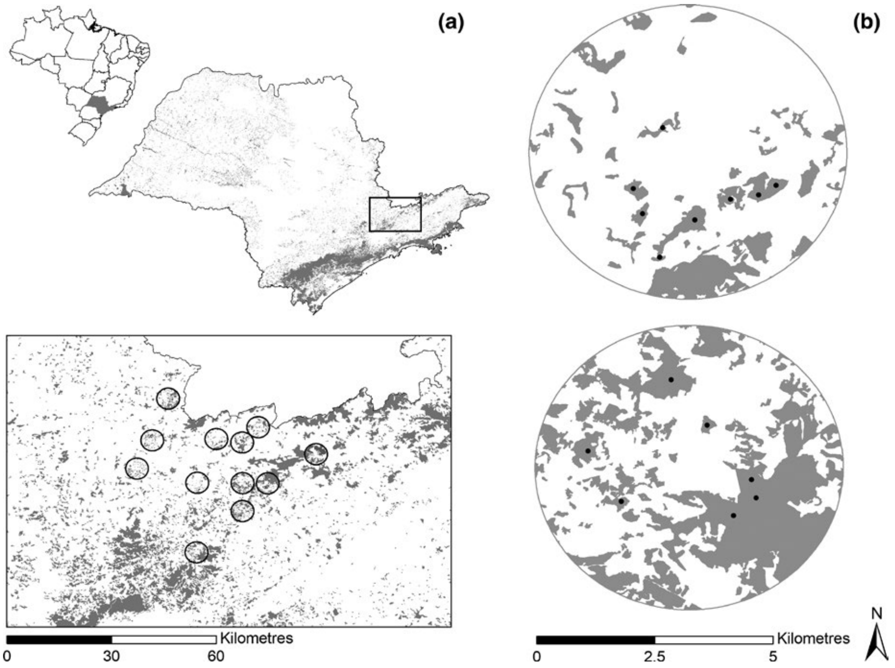

**FIGURE 1** Location of the study region and of the 12 focal landscapes. (a) Maps of Brazil and São Paulo state, highlighting the study region and the 12 focal landscapes. (b) Two of the focal landscapes, with high and low native forest cover, are shown in detail. Grey represents native forests remnants, and black dots the location of sampling sites

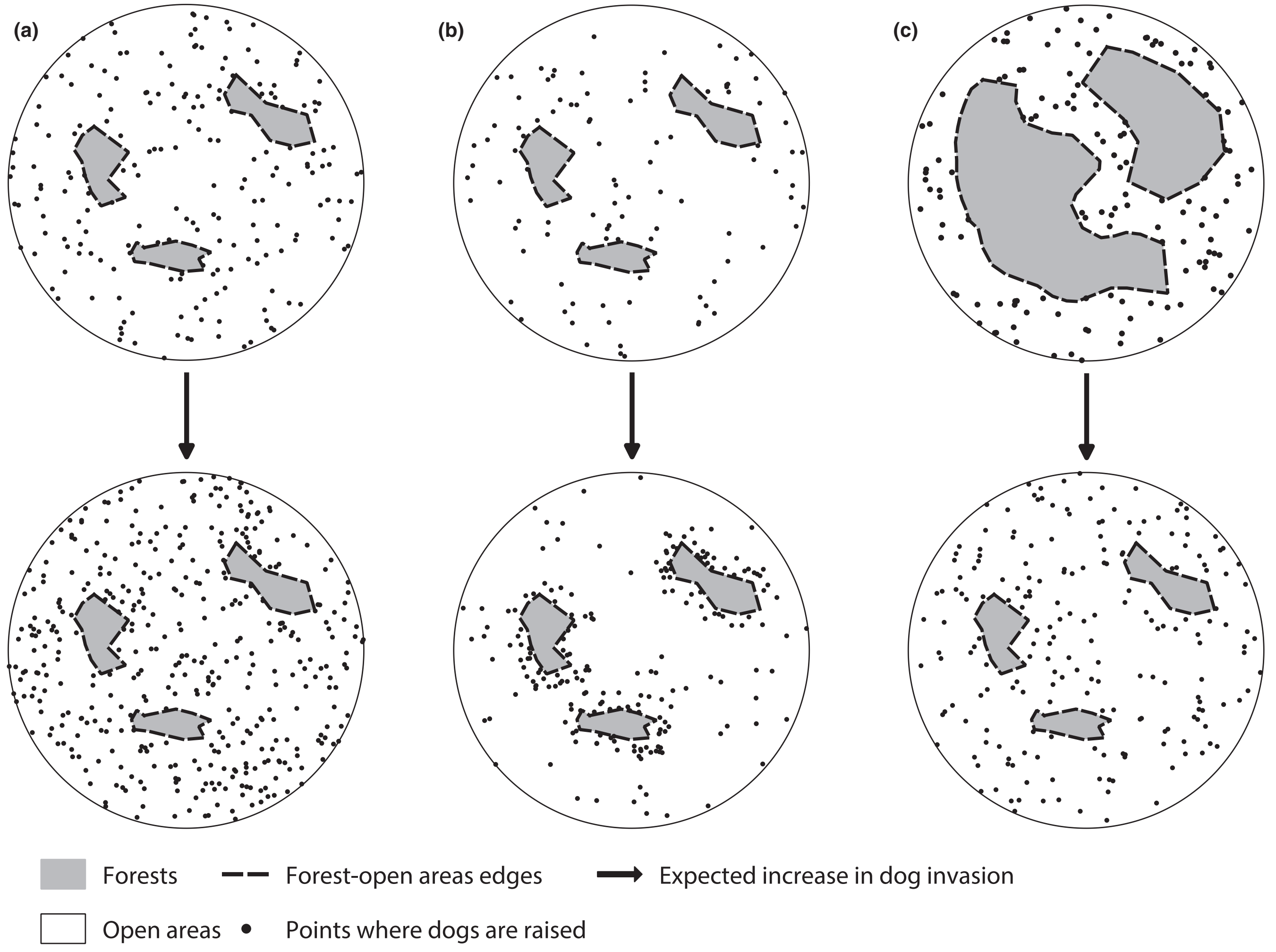

**FIGURE 2** Expected effects of propagule pressure (a-b) and landscape disturbance (c) variables on dog invasion. (a) As the density of raised dogs or (b) the aggregation (percentage) of dogs raised near forests increases, dog invasion increases. These propagule pressure variables are independent: it is possible to increase the density of raised dogs without increasing the aggregation (percentage) of dogs raised near forests, and vice-versa. (c) As forest cover decreases, edge length between forests and open areas decreases, but edge density (edge length divided by forest cover) increases, increasing dog invasion. These landscape disturbance variables are then interdependent. Moreover, as forest cover decreases, the absolute number of raised dogs in the landscape tends to increase because open areas where dogs are raised increase. However, this does not necessarily mean increased propagule pressure because the density of raised dogs and the number of dogs surrounding forest sites may be maintained (that is why we measured propagule pressure as density instead of the absolute number of raised dogs)

## 2.3 | Dogs in native forests

At each sampling site, we set a single camera trap (Trophy Cam HD 119537c, Bushnell), resulting in eight traps per landscape (Supporting Information Appendix S1). Data were collected between February and July 2015, and the cameras were active between 42 and 45 consecutive days (43.6 ± 0.7) at each sampling site. We sampled four landscapes simultaneously and three groups of four landscapes consecutively. Due to occasional camera malfunctioning, final sampling effort varied between 293 and 351 camera days per landscape, totalling 4,006 cameras-days across all landscapes. We identified individual dogs photographed by the cameras using features of coat colour and body size (Supporting Information Appendix S1: Figure S1.2) and compared them with photographs of the dogs raised in the landscapes (see below).

## 2.4 | Propagule pressure

To quantify the number of dogs raised by the human population, we first mapped the locations of all visible houses and roads in the 12 focal landscapes using Google Earth images (Digital Globe satellites 2015). During the camera trap sampling period, we visited the mapped houses (and checked for the existence of other houses by searching along accessible roads), and in each house, we interviewed residents to obtain the number of raised dogs and photograph them. In a subset of eight of the 12 focal landscapes (1,512 dogs, 38% of the total), we applied a more detailed questionnaire to dog owners to obtain information on dog living conditions and management (see Study area; Biffi, 2017).

We quantified propagule pressure in each landscape in two ways, considering both the density and the spatial distribution (aggregation within five distances from forest) of raised dogs (Lockwood et al., 2005; Simberloff, 2009), totalling six variables. Higher density or aggregation of raised dogs near forests should increase dog invasion, as forest sites are surrounded by larger numbers of raised dogs or larger numbers of dogs are raised closer to forest sites, respectively (Figure 2a,b).

These measures were considered appropriate to quantify propagule pressure because (a) populations of raised dogs around forest remnants (regardless of whether individuals are born there or brought from outside) are controlled by human demand (Morters et al., 2014); (b) given the particular characteristics of free-ranging dogs (neither feral nor strictly owned; see Introduction), we measure dog invasion as the number of raised dogs that use forest remnants, defining the invasion process as a subset of raised dogs including forest remnants in their home ranges; and (c) observations during the 7 months of continuous fieldwork indicate that the number of stray or feral dogs (i.e., not raised by humans) was low.

*(a) density of raised dogs (Den):* As the open areas (e.g., agropastoral areas) of these originally forested landscapes are where households and raised dogs are concentrated (Supporting Information Appendix S1: Figure S1.1), they can be understood as a vector of propagule pressure, and the areal extent of this vector varies as a function of forest cover. Thus, density of raised dogs in each landscape is a measure of propagule pressure independent of forest cover when calculated as the number of raised dogs divided by the area of the landscape occupied by open areas (Figure 2c). Density of raised dogs varied between 4 and 66 dogs/km$^2$ among the 12 focal landscapes (Supporting Information Appendix S1: Figure S1.3).

*(b) aggregation of raised dogs near native forests (Ag):* To quantify the spatial component of propagule pressure, we calculated the proportion of dogs raised in each landscape within five distances (50, 100, 150, 200 and 250 m) from the nearest native forest. Aggregation near forest is independent from density of raised dogs (Figure 2a,b), and distance classes were chosen based on radio tracking studies that recorded most dog sightings within 250 m from households where they are raised (Ruiz-Izaguirre et al., 2015; Sepúlveda, Pelican, Cross, Eguren, & Singer, 2015). The aggregation of raised dogs varied widely at each distance class among the 12 focal landscapes (50 m: 9%–38%, 100 m: 14%–70%, 150 m 25%–88%, 200 m: 30%–91%, 250 m: 35%–98%) (Supporting Information Appendix S1: Figure S1.3).

## 2.5 | Landscape disturbance

Dogs moving long distances prefer to move across open areas (Sepúlveda et al., 2015), suggesting that forests may act as barriers to these movements. Therefore, the higher the forest cover and the edge length between forests and open areas (i.e., the greater the area and the perimeter of potential barriers to dog movements), the more limited the excursions of dogs through the landscape should be, decreasing the chance of a given forest site being reached by multiple dogs raised across the landscape, and thus the number of dogs per forest area in a landscape. When dogs do enter forests, they are more common at forest edges than forest interiors (Srbek-Araujo & Chiarello, 2008). Hence, the greater the edge density (i.e., the proportion of edge length between forests and open areas in relation to forest cover), the more accessible forest interiors are to dogs, and the number of dogs per forest area in a landscape should increase. Although these metrics represent distinct aspects of landscape structure, their variation across landscapes is not independent. As forest cover is reduced below 50%, edge length decreases (Fahrig, 2003; Villard & Metzger, 2014) and edge density (edge length divided by forest cover) increases (Liu, He, & Wu, 2016; Neel, McGarigal, & Cushman, 2004) (Figure 2c). Thus, reductions in forest cover potentially lead to an increase in forest accessibility to dogs by decreasing the area (forest cover) and the perimeter (edge length) of forested barriers, and simultaneously decreasing the distance of forests to edges (edge density) (Figure 2c). As our focal landscapes contain not only native forests but also planted eucalyptus forests, we considered the possibility that forest plantations act in the same way as native forests (barriers) by calculating six variables to represent the expected effects of landscape disturbance on dog invasion.

*(a) forest cover (FC):* We calculated the proportion of each landscape covered by native forest (NFC) (range 10%–48% among the 12 focal landscapes), and the proportion of each landscape covered by either native or planted forests (TFC) (range 20%–67%; Supporting Information Appendix S1: Figure S1.3).

*(b) edge length between forests and open areas (E):* We calculated edge length between native forests and open areas (NE) (range 63–184 km among the 12 focal landscapes), and edge length between any forest (native or planted) and open areas (TE) (128–246 km; Supporting Information Appendix S1: Figure S1.3).

*(c) edge density (ED):* We calculated edge density between native forests and open areas (NED; edge length between native forests and open areas divided by native forest cover; range 73–363 km/ha among the 12 focal landscapes), and edge density between any forest (native or planted) and open areas (TED; edge length between any forest type and open areas divided by total forest cover; range 74–265 km/ha) (Supporting Information Appendix S1: Figure S1.3).

## 2.6 | Sampling effort, seasons and blocks

Finally, we defined three temporal variables that could affect the detection of dogs in native forests.

*(a) sampling effort:* Sum of active days across the eight cameras in each landscape and sampling occasion.

*(b) sampling season:* Warm (February and March) and cool (between April and July). Dog activity is often reduced at high temperatures (Ruiz-Izaguirre et al., 2015).

*(c) sampling blocks*: Group or block of landscapes sampled simultaneously and thus subjected to similar weather conditions during sampling.

**TABLE 1** *N*-mixture models of the number of dogs using native forests as a function of propagule pressure and landscape disturbance. Models are ordered from the lowest to the highest AICc values, and only models with Akaike weights ≥0.01, plus the first-ranked model with the abundance parameter constant (i.e., the first-ranked reference model), are presented. Information regarding the number of model parameters (*K*), Akaike information criterion corrected for small samples (AICc), AICc difference from the first-ranked model (ΔAICc), Akaike weight ($\omega_i$), log likelihood (LL), intercept and covariates coefficients with standard errors is provided

| | | | | | | Intercept and coefficients for covariables of the parameter abundance $\lambda$ | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Model** | ***K*** | **AICc** | **ΔAICc** | $\omega_i$ | **LL** | **Intercept (*SE*)** | **Disturbance covariate (*SE*)** | **Propagule pressure covariate (*SE*)** | **Interaction (*SE*)** |
| p(E) $\lambda$(TFC+Den) | 5 | 347.17 | 0.00 | 0.635 | −163.58 | 2.8129 (0.4109) | −0.3365 (0.0950) | 0.5725 (0.0892) | – |
| p(E+S) $\lambda$(TFC+Den) | 6 | 350.89 | 3.72 | 0.099 | −161.04 | 3.0948 (0.5767) | −0.3458 (0.0877) | 0.4752 (0.0942) | – |
| p(E) $\lambda$(TE+Den) | 5 | 351.58 | 4.41 | 0.07 | −165.79 | 2.8112 (0.3809) | −0.3886 (0.1454) | 0.7191 (0.1265) | – |
| p(E) $\lambda$(NFC+Den) | 5 | 352.29 | 5.12 | 0.049 | −166.14 | 2.6623 (0.3332) | −0.2754 (0.1090) | 0.5324 (0.0896) | – |
| p(E) $\lambda$(Den) | 4 | 352.37 | 5.20 | 0.047 | −169.33 | 2.5309 (0.2694) | – | 0.4628 (0.0817) | – |
| p(E) $\lambda$(TED+Den) | 5 | 353.73 | 6.57 | 0.024 | −166.87 | 2.5932 (0.3078) | 0.2292 (0.1022) | 0.4702 (0.0840) | – |
| p(E) $\lambda$(NED+Den) | 5 | 354.37 | 7.21 | 0.017 | −167.19 | 2.5842 (0.3007) | 0.1969 (0.0929) | 0.4856 (0.0855) | – |
| p(E) $\lambda$(TE*Den) | 6 | 354.87 | 7.71 | 0.013 | −163.04 | 3.1805 (0.5152) | −0.4027 (0.1297) | 0.9208 (0.1388) | −0.2293 (0.0946) |
| p(E) $\lambda$(TFC*Den) | 6 | 355.26 | 8.10 | 0.011 | −163.23 | 2.8502 (0.4245) | −0.3151 (0.0973) | 0.6143 (0.1008) | −0.0781 (0.0919) |
| p(E+S) $\lambda$(.) | 4 | 366.23 | 19.06 | 0.000 | −176.26 | 2.4803 (0.2142) | – | – | – |

*Notes.* $\lambda$: abundance, *p*: detection probability, + additive function, * interactive function, E: sampling effort, S: sampling season, Den: density of raised dogs, Ag50: proportion of raised dogs aggregated within 50 m from forests, TFC: total forest cover (native and planted), NFC: native forest cover, TE: edge length between any forest (native or planted) and open areas, NED: edge density between native forest and open areas, TED: edge density between any forest (native or planted) and open areas.

## 2.7 | Data analysis

To evaluate dog invasion in forest remnants, we used single-season *N*-mixture abundance models (Royle, 2004). These models estimate two parameters from the count of individuals across sampling occasions (*j*) in each sampling unit (*i*): ($\lambda_i$) abundance in sampling unit *i*, and ($p_{ij}$) detection probability in sampling unit *i* and occasion *j*. We defined a sampling occasion as six consecutive days, resulting in seven consecutive occasions. In all occasions, we were able to distinguish how many individuals the cameras recorded. Given our landscape study (see Sampling design), we defined a sampling unit as each of the focal landscapes, pooling data from the eight cameras located in each landscape.

Given the small size of the area sampled by each camera compared to the size of dog home ranges, we interpreted the parameter abundance as the number of dogs in each landscape with home ranges overlapping at least one of the eight sampling sites (Joseph, Elkin, Martin, & Possingham, 2009). We assume that the closure assumption of single-season *N*-mixture models was met, given the short sampling period (42–45 consecutive days) compared to the longevity of dogs and to the low rates of gains and losses of individuals within such short period in rural dog populations reported elsewhere (Morters et al., 2014; Villatoro, Sepúlveda, Stowhas, & Silva-Rodríguez, 2016). The assumption that detection probability is constant across individual dogs is difficult to assert. However, assumption violation does not affect the estimates of the effects of covariables on abundance (Barker, Schofield, Link, & Sauer, 2018), which is the focus of our results and interpretations.

We defined six possibilities to model the parameter detection probability: one with constant detection, three with detection as a function of either sampling effort, sampling season or sampling block and two with detection as an additive function of sampling effort and either sampling season or sampling block. We also defined 85 possibilities to model the parameter abundance, considering either abundance constant, as a function of each of the 12 variables individually (six of propagule pressure and six of landscape disturbance), or as an additive or interactive function of two variables (considering all possible combinations between one variable of propagule pressure and one variable of landscape disturbance). We then combined the possibilities of modelling detection with those of modelling abundance, which resulted in a candidate model set with 510 models (Supporting Information Appendix S1: Table S1.1). All 12 propagule pressure and landscape disturbance variables were standardized, and collinearity between those used together in the same models was acceptably low (VIF < 3.1) (Supporting Information Appendix S1: Figure S1.4).

Models were compared using Akaike information criterion corrected for small samples (AICc), considering that models with AICc ≤ 2 in relation to the first-ranked, most parsimonious model are equally plausible (Burnham & Anderson, 2002). We then used Akaike weights (Burnham & Anderson, 2002) to compare the relative importance in determining the number of dogs using native forests among individual variables (sum of weights of models containing each variable), and among groups of variables, either propagule pressure or landscape disturbance (sum of weights of models containing any of the variables of each group). We also choose the most appropriate abundance distribution, assessed the goodness-of-fit of the models and examined the influence of the number and duration of sampling occasions on the results (Supporting Information Appendix S1: Tables S1.2, S1.3, and Figure S1.5). All analyses were performed in the R environment version 3.3.2 (R Development Core Team 2016), using the package “unmarked” (Fiske & Chandler, 2011).

## 2.8 | Mapping the intensity of invasion across the Atlantic forest hotspot

We combined three spatial datasets—on native and planted forests and human population density—to calculate the covariates total forest cover and density of raised dogs (present in the most parsimonious *N*-mixture model; Table 1) across landscapes (2,750-ha each; similar in area to our focus landscapes) of the Atlantic Forest domain (Supporting Information Appendix S1). We then used the most parsimonious model to predict the number of dogs using forest remnants across Atlantic Forest landscapes. To generate reliable results, we restricted the prediction to Atlantic Forest landscapes with total forest cover and density of raised dogs within the range of variation of these covariates observed across our 12 focal landscapes.

# 3 | RESULTS

We identified a total of 144 dogs using native forests across the 12 focal landscapes. Dogs were recorded in forests in all focal landscapes, and in 51 of the 96 sampling sites (53%). The number of detected dogs within forests ranged from 0 to 12 across sampling sites and from 5 to 27 across focal landscapes (Figure 3a–b). By comparing photographs from camera traps and census of raised dogs, we were able to identify the origin of 59 dogs (41%) of the 144 dogs detected in native forests. This relatively low proportion is due mainly to the difficulty of discerning details of individual characteristics in camera trap photographs compared to photographs from raised dogs taken during census, and the high number of raised dogs, many of which present similar characteristics. These 59 individuals were recorded in 272 events in native forests (the number of events represents the sum of the records of distinct individuals plus the records of the same individual in distinct days or distinct cameras). The distances of these excursions to native forests (straight line distance from where dogs were raised and forest sites where they were detected) varied between 100 and 3043 m (mean ± *SD*: 381.50 ± 309.42; Figure 3d).

The only selected, most parsimonious model presented a high weight of evidence ($\omega i = 0.63$) and contained density of raised dogs and total forest cover (native and planted forests) as covariates of abundance ($\lambda$). It indicates that a higher number of dogs use native forests in landscapes with higher densities of raised dogs, and lower total forest cover (Table 1; Supporting Information Appendix S1:

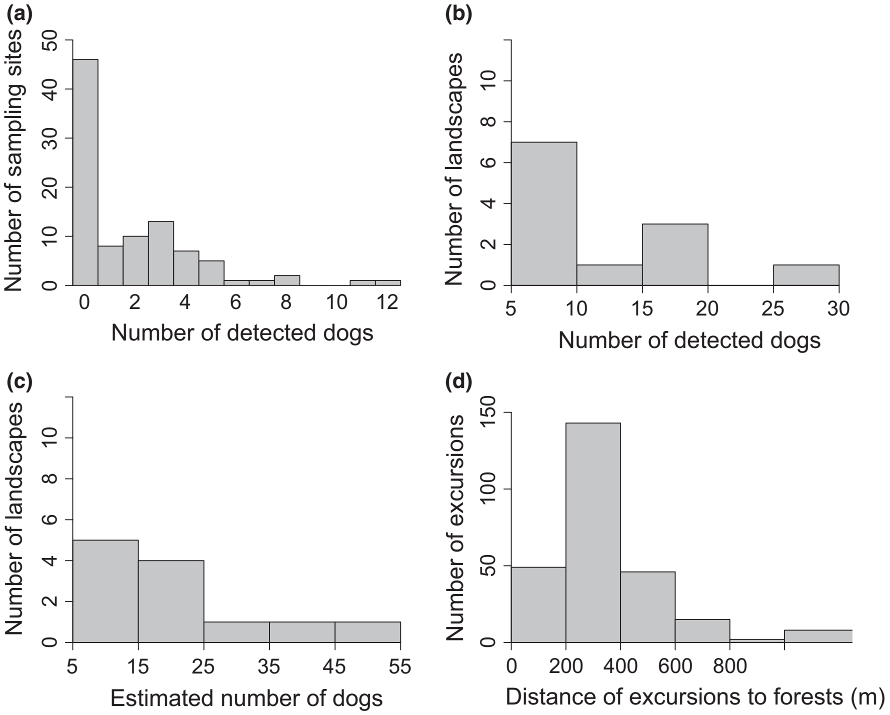

**FIGURE 3** Histograms of dog numbers and excursion distances across the 12 focal landscapes. Histograms of (a) the number of detected dogs per native forest site, (b) the number of detected dogs in native forest per landscape, (c) estimated number of dogs using native forests per landscape (parameter abundance λ from first-ranked model in Table 1) and (d) distances of excursions to forest (estimated by the straight line distance between where dogs were raised and sampling sites where they were detected) for 59 dogs for which origin was identified

Figure S1.6). Estimates (parameter λ) of dogs using native forests from this model varied from 7 to 46 individuals across landscapes (mean ± *SD*: 20.2 ± 13.3) (Figure 3c). The model also indicates that dog detection probability increases with sampling effort (mean ± *SD* 0.18 ± 0.03).

All nine top-ranked models also contained density of raised dogs as a covariate of abundance (Table 1). In this group of models, the effects of landscape disturbance variables on the number of dogs using forests were as expected: a positive effect of edge density and a negative effect of forest cover and edge length. Models containing covariates considering any forest type (including both native and planted) performed better than models containing covariates considering only native forest (Table 1). However, the model containing native forest cover and density of raised dogs as covariates of abundance was the third-ranked model and was more plausible than the first-ranked model with abundance constant (i.e., the first-ranked reference model; Table 1).

Summed Akaike weights of models containing propagule pressure variables and of models containing variables of landscape disturbances were similar (Table 2), indicating that both drivers are equally important for dog invasion in native forests. Among propagule pressure variables, only models containing density of raised dogs had considerable weights (Table 2). Among landscape disturbance variables, models containing total forest cover had greater weights than the remaining variables (Table 2).

By restraining the prediction to landscapes with propagule pressure and landscape disturbance values within the range of the 12 focal landscapes, we were able to predict the number of dogs per forest area (i.e., dogs using an area of forest equivalent to the area sampled by the 8 cameras in our focal landscapes) for 39% of the current Atlantic Forest remnants (i.e., for 10,169 of the 47,043 landscapes that contained forest remnants; Figure 4). We estimate that at least 5–105 dogs use native forest remnants across Atlantic Forest landscapes (mean ± *SD*: 17.18 ± 10.61). Fourteen per cent of Atlantic Forest remnants are within the 25% of landscapes predicted to have the smallest number of dogs per forest area (<12 dogs), while 8% are within the 25% of landscapes predicted to have the highest number (more than 18 dogs) (Figure 4).

## 4 | DISCUSSION

We combined a landscape-scale design, metrics of disturbance measured at broad spatial scales and a direct quantification of propagule pressure to explore the relative importance and synergies between landscape disturbance and propagule pressure as drivers of invasions by dogs—a widely distributed invasive species that severely impacts native fauna (Doherty et al., 2017). Our results are in accordance with both theory and previous empirical studies that indicate that greater invasion intensity is associated with higher propagule pressure and disturbance (Jauni et al., 2015; Simberloff, 2009). Most importantly, our results indicate that landscape disturbance and propagule pressure are equally important drivers of dog invasions and suggest that the effects of these drivers are additive rather than synergistic. Moreover, we found that the density of raised dogs was more important than their spatial distribution and that forest cover was more important than the length or the density of forest edges, in determining dog invasion. Finally, we linked these results to spatial data on human population density and forest cover to generate a map of invasion intensity across the Atlantic Forest. Our results suggest that dog invasion is a pervasive threat in vast areas of this biodiversity hotspot.

Previous studies reporting evidence of positive interactions between propagule pressure and disturbance focused on local disturbances and on plants (Britton-Simmons & Abbott, 2008; Eschtruth & Battles, 2009; Warren, Bahn, & Bradford, 2012) or sessile organisms (Clark & Johnston, 2009). In these cases, interactions should be expected because local disturbances can amplify propagule pressure effects by increasing the probability of propagule establishment and/or survival. In our system, landscape disturbances are unlikely to amplify propagule pressure effects, because while less forest cover at broad scales may facilitate access to native forests, it should not strongly influence dog survival, as dogs are subsidized by humans through food (Morters et al., 2014) and, at a lesser extent, veterinary care, effectively decoupling fitness effects from landscape disturbances. In contrast, for invasive species that are not subsidized by humans, it is indeed possible that broad scale disturbances may affect not only the access to native habitats, but also the survival or establishment of propagules, by altering the quality of the remaining habitat through edge effects (Laurance et al., 2007). Future studies should evaluate possible synergies between landscape disturbance and propagule pressure on the invasion of animal species not subsidized by humans.

Because we contrasted the relative influence of multiple, distinct measures of propagule pressure and disturbance, our results allow us to propose hypotheses concerning the processes underlying the effects of these drivers. Regarding propagule pressure, density of raised dogs was far more important than the spatial distribution of dogs in driving dog invasion. This is in agreement with both the fact that dogs are able to perform long-distance movements (Ruiz-Izaguirre et al., 2015; Sepúlveda et al., 2015; our study) and the idea that larger populations of an invasive species are more likely to contain individuals possessing traits that facilitates invasion (Blackburn et al., 2015). Indeed, previous studies suggest that sex (males; Dürr, Dhand, Bombara, Molloy, & Ward, 2017; Sparkes, Körtner, Ballard, Fleming, & Brown, 2014), age (young adults; Van Bommel & Johnson, 2014), as well as breed and health conditions (Meek, 1999) are related to larger movements and home ranges of free-ranging dogs. Thus, irrespective of the distribution of the households where dogs are raised, the larger the density of dogs, the higher the number of dogs with attributes related to larger movements, and thus the higher the probability of native forests invasion.

**TABLE 2** Summed Akaike weights of *N*-mixture models of the number of dogs using native forests as a function of different propagule pressure and landscape disturbance variables. The values represent a measure of the importance of covariates

| Propagule pressure | Summed ωi |
|---|---|
| Density of raised dogs (Den) | 0.999 |
| Proportion of dogs aggregated within 50 m from native forests (Ag50) | <0.001 |
| Proportion of dogs aggregated within 100 m from native forests (Ag100) | <0.001 |
| Proportion of dogs aggregated within 150 m from native forests (Ag150) | <0.001 |
| Proportion of dogs aggregated within 200 m from native forests (Ag200) | <0.001 |
| Proportion of dogs aggregated within 250 m from native forests (Ag250) | <0.001 |
| **Total** | **0.999** |
| Landscape disturbance | |
| Total forest cover (native and planted, TFC) | 0.746 |
| Native forest cover (NFC) | 0.060 |
| Edge length between any forest (native or planted) and open areas (TE) | 0.085 |
| Edge length between native forests and open areas (NE) | 0.004 |
| Edge density between any forest (native or planted) and open areas (TED) | 0.026 |
| Edge density between native forest and open areas (NED) | 0.018 |
| **Total** | **0.939** |

Regarding the metrics used to quantify landscape disturbance, forest cover was a relevant driver of dog invasion, irrespective of the variation in factors, such as trails and roads that may also facilitate the access to forest and were not controlled for. Particularly, forest cover was more important in explaining dog invasion than the length or the density of forest edges. As the reduction of forest cover within the range observed across our 12 focal landscapes implies a decrease in edge length and an increase in edge density (Liu et al., 2016; Neel et al., 2004), our results suggest that both mechanisms of increased accessibility of forests to dog are relevant to determine dog invasion. On the one hand, forest cover reduction decreases the area of forested barriers and should increase the accessibility of forest to a higher number of dogs raised across the landscapes, as dogs are known to perform long-distance excursions in open areas (Sepúlveda et al., 2015). On the other hand, forest cover reduction decreases the distances of forest to the edges, making forests more accessible to dogs, as they are more common at edges compared to forest interiors (Srbek-Araujo & Chiarello, 2008). However, testing these mechanisms directly depend on studies focusing on movement ecology, and estimating the distance travelled and path sinuosity of dogs across different landscapes. For invasive species that are not subsidized by humans, though, mechanisms underlying the negative effects of forest cover on invasions may encompass also demographic besides dispersal/movement processes. In those cases, it is possible that the expansion of open areas caused by forest conversion increases habitat quality and resource availability, leading to larger and more connected populations of the invasive species across open areas (Umetsu & Pardini, 2007). This in turn could either increase rates of spillover from open areas into native forests (Tscharntke et al., 2012) or facilitate source-sink dynamics between open areas and forests (Pulliam, 1988; Thomson, 2007), increasing invasion intensity.

Our study also suggests the potential importance of non-native forests as barriers to dog movements. Metrics that considered both planted (eucalyptus) and native forests performed better than metrics considering native forests alone. Thus, it may be possible to

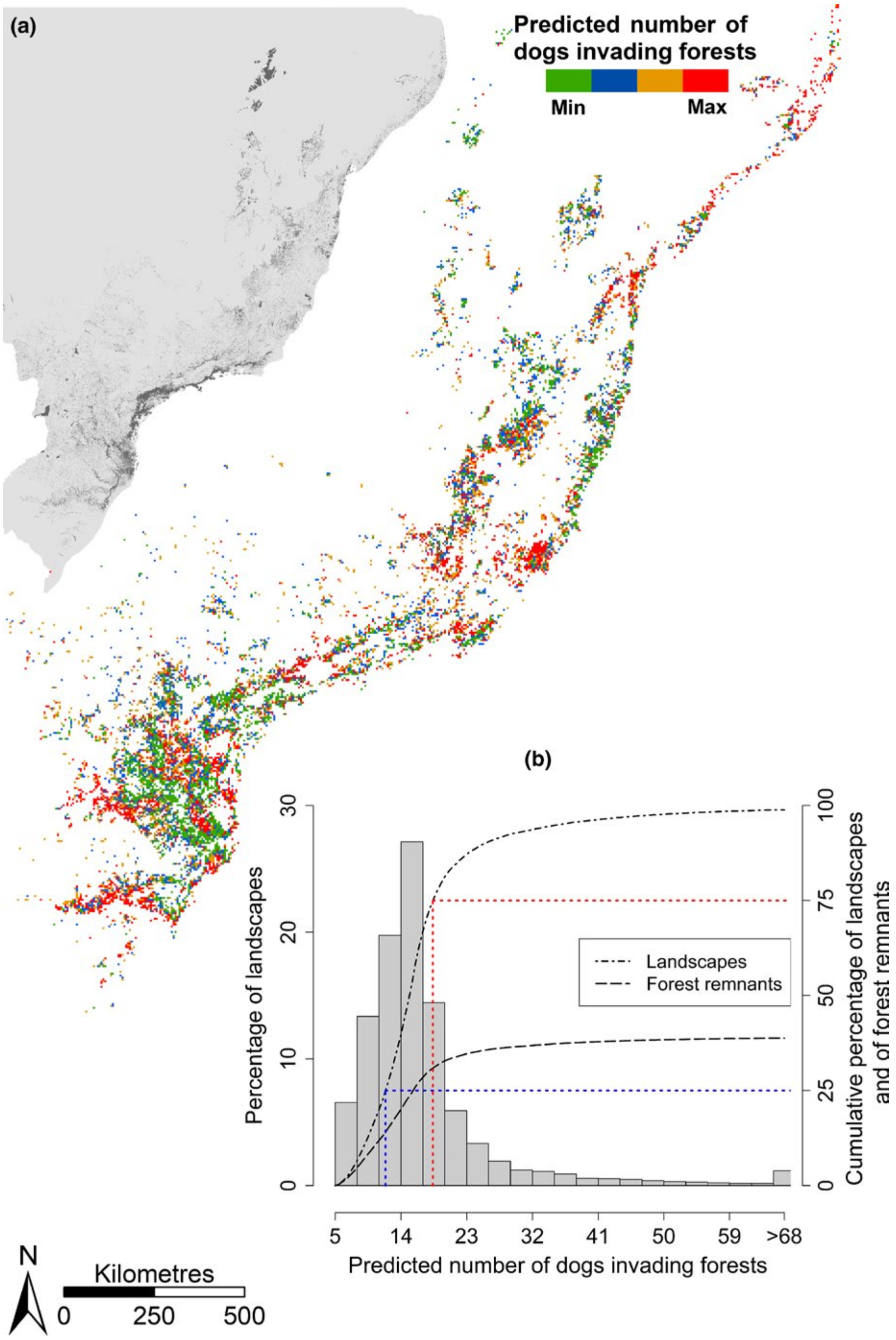

**FIGURE 4** Map of the intensity of dog invasion across the Atlantic Forest hotspot. (a) Distribution of current Atlantic Forest remnants (top left) and predicted number of dogs invading forest remnants across Atlantic Forest landscapes. (b) Percentage of landscapes (left axis, grey bars) and cumulative percentage (right axis, lines) of landscapes or forest remnants, across classes of predicted number of dogs invading forest remnants. The first (blue line) and the third (red line) quartiles of landscapes predicted to have the lowest and the highest number of dogs invading forest remnants are highlighted [Colour figure can be viewed at wileyonlinelibrary.com]

control dog invasions by either the restoration of native forests or by planning the distribution of planted forests to increase the distance of native forest to open areas. However, studies comparing dog movements or dog invasion in landscapes with similar forest cover but different spatial distribution or different proportions of planted forests in relation to native forests are necessary to test this hypothesis. It is noteworthy though that the model considering native forest cover instead of total forest cover performed better than models with the parameter abundance constant, highlighting the positive relationship of native habitat loss and dog invasion.

To our knowledge, this is the first study to describe the invasion of dogs through estimates of abundance and to predict the intensity of invasion over a large extent of a phytogeographical domain. These advancements were possible because of our landscape-scale design, identification of individual dogs, use of *N*-mixture models and a complete census of dog populations. These characteristics of our empirical dataset allowed us to predict invasion using human population and forest cover data over large areas of the Atlantic Forest. The numbers we obtained are impressive, both across the focal landscapes and across the Atlantic Forest in general. In the studied landscapes, we observed up to 27, and estimated up to 46, individual dogs invading forests in a single landscape. These numbers certainly make dogs the most abundant carnivore in native forests of the study region. Previous studies have also found that dogs are common in protected areas (Lessa et al., 2016) and are the most common carnivore species in other Atlantic Forest regions (Paschoal et al., 2016; Srbek-Araujo

& Chiarello, 2008). Our prediction exercise indeed suggests that invasion by dogs is high across most Atlantic Forest landscapes, where dogs certainly represent one more widespread threat to wildlife beyond the well-known impacts of habitat loss (Beca et al., 2017) and hunting (Cullen, Bodmer, & Valladares-Padua, 2001).

Given that dogs negatively impact wildlife, these numbers are also alarming. Multiple lines of evidence from around the world link dogs to predation on wildlife across the spectrum of body sizes (e.g., rodents to deer; Young et al., 2011). The sublethal effects of predator–prey interactions may be even more damaging than direct mortality (Preisser, Bolnick, & Benard, 2005), contributing to landscapes of fear (Laundré, Hernandez, & Ripple, 2010) and causing changes in physiology and behaviour, with potential implications for fitness (e.g., Sheriff, Krebs, & Boonstra, 2009; Silva-Rodríguez & Sieving, 2012). Such sublethal effects are likely to be more important when predators are subsidized by humans and have high population densities (Gompper & Vanak, 2008) or are highly vocal like dogs. Indeed, many owners reported that dogs chase native animals and/or have been injured by wildlife in our study region (Biffi, 2017). Other negative impacts of dogs on native animals include competition (Butler & du Toit, 2002; Vanak & Gompper, 2010) and disease transmission (Cleaveland et al., 2000; Curi et al., 2016). Given their movements between domestic/agropastoral areas and native forests, dogs may occupy a relatively unique role in disease transmission both to wildlife and to humans (Macpherson, 2005), particularly given the low rates of reported preventative (vaccination) and therapeutic (parasite treatment) care of dogs by owners across our study region (Biffi, 2017).

Lastly, it is important to highlight that our study has limitations. As a trade-off of the landscape-scale design, which is rare, yet key for addressing landscape-level processes (Fardila et al., 2017), the sample size was relatively low (12 landscapes). This is because we invested in sampling multiple sites within each landscape for capturing heterogeneity within landscapes. This may have limited the power to detect synergies between drivers of dog invasion. However, as argued above, the absence of synergies between propagule pressure and landscape disturbance is indeed expected in the case of invasion by subsidized predators. In addition, although our analyses are robust for estimating the effects of covariates and therefore to evaluate the relative importance of drivers of dog invasion and to predict invasion intensity across the Atlantic Forest, the absolute estimates of the number of dogs in forests should be used with caution. This comes from the susceptibility of these estimates to the violation of the assumptions of *N*-mixture models. However, because the observed (not only the estimated) numbers of dogs are high, this limitation does not affect our conclusion that dogs represent a strong and widespread threat to native fauna.

## 4.1 | Implications for conservation

Given the importance of forest cover on dog invasion, we suggest that conservation mechanisms stimulating the maintenance and restoration of native forests are more relevant for controlling dog invasion than currently recognized. Besides favouring native species through increased connectivity and population size, forests can also reduce the negative effects of biological invasions. In contrast, traditional alternatives (neutering and lethal control) that target the decrease in propagule pressure may be fruitless, as human-mediated immigration is a key factor controlling dog populations (Morters et al., 2014; Villatoro et al., 2016). Consequently, changes in the beliefs and attitudes towards dog management may be more effective to reduce the effects of propagule pressure. Population control strategies should then consider social components and be integrated with conservation and restoration of native forests and with an appropriate planning of the spatial distribution of planted forests to reduce dog invasion. Combined with already available maps of priority areas for biodiversity conservation, our spatial prediction of dog invasion can help targeting areas for these integrated and complementary management actions aiming at preventing the impact of dogs.

Our findings also raise the hypothesis that the direct effects of habitat loss and overexploitation on native fauna, especially large-bodied mammals, may have been overestimated. Besides being considered the most important threat to biodiversity (Foley et al., 2005), landscape disturbances, such as habitat loss and fragmentation, can also be an important driver of invasions, as demonstrated here, and part of the negative effects attributed to them may be indirectly mediated by dog invasion. The same may also be true for hunting pressure, an important threat to mammals (Gonzalez-Suarez & Revilla, 2014) that is associated with human population density and, therefore, to dog density. Most studies that investigate biodiversity decline are limited to the examination of individual threats (Murphy & Romanuk, 2014), but these threats are often correlated and interact with each other (Brook, Sodhi, & Bradshaw, 2008). Our results suggest caution in the assumption that our current understanding of the mechanisms related to fauna decline is complete, as dog invasion is associated with multiple recognized threats to wildlife.

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## BIOSKETCH

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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