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A global assessment of primate responses to landscape structure

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ABSTRACT

Land-use change modifies the spatial structure of terrestrial landscapes, potentially shaping the distribution, abundance and diversity of remaining species assemblages. Non-human primates can be particularly vulnerable to landscape disturbances, but our understanding of this topic is far from complete. Here we reviewed all available studies on primates' responses to landscape structure. We found 34 studies of 71 primate species (24 genera and 10 families) that used a landscape approach. Most studies (82%) were from Neotropical forests, with howler monkeys being the most frequently studied taxon (56% of studies). All studies but one used a site-landscape or a patch-landscape study design, and frequently (34% of studies) measured landscape variables within a given radius from the edge of focal patches. Altogether, the 34 studies reported 188 responses to 17 landscape-scale metrics. However, the majority of the studies (62%) quantified landscape predictors within a single spatial scale, potentially missing significant primate–landscape responses. To assess such responses accurately, landscape metrics need to be measured at the optimal scale, i.e. the spatial extent at which the primate–landscape relationship is strongest (so-called 'scale of effect'). Only 21% of studies calculated the scale of effect through multiscale approaches. Interestingly, the vast majority of studies that do not assess the scale of effect mainly reported null effects of landscape structure on primates, while most of the studies based on optimal scales found significant responses. These significant responses were primarily to landscape composition variables rather than landscape configuration variables. In particular, primates generally show positive responses to increasing forest cover, landscape quality indices and matrix permeability. By contrast, primates show weak responses to landscape configuration. In addition, half of the studies showing significant responses to landscape configuration metrics did not control for the effect of forest cover. As configuration metrics are often correlated with forest cover, this means that documented configuration effects may simply be driven by landscape-scale forest loss. Our findings suggest that forest loss (not fragmentation) is a major threat to primates, and thus, preventing deforestation (e.g. through creation of reserves) and increasing forest cover through restoration is critically needed to mitigate the impact of land-use change on our closest relatives. Increasing matrix functionality can also be critical, for instance by promoting anthropogenic land covers that are similar to primates' habitat.

Key words: habitat fragmentation, habitat loss, landscape heterogeneity, matrix composition, monkeys, multi-scale design.

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I. INTRODUCTION

The advance of the agricultural frontier is rapidly converting natural ecosystems into human-modified landscapes (i.e. heterogeneous land areas composed of a mosaic of natural and anthropogenic land cover types). In recent decades, such conversion has been particularly noticeable in the tropics (Achard *et al.,* 2014; Taubert *et al.,* 2018), threatening the preservation of a large number of species (Newbold *et al.,* 2016). Yet the main drivers of species loss in human-modified landscapes remain poorly understood. This is because different species can show contrasting responses to habitat disturbance, making it difficult to identify general response patterns (Henle *et al.,* 2004). Furthermore, research has been focused primarily on a few local predictors, such as patch size (Prugh *et al.,* 2008; Arroyo-Rodríguez *et al.,* 2013*a*; Haddad *et al.,* 2015) and measures of forest edge (Tuff, Tuff & Davies, 2016; Pfeifer *et al.,* 2017). Nevertheless, as individuals usually move among habitat patches and interact with different landscape elements (Dunning, Danielson & Pulliam, 1992; Tscharntke *et al.,* 2012; Galán-Acedo *et al.,* 2019), assessing the response of species to landscape patterns is needed to understand the main drivers of species diversity better in human-modified landscapes (Fahrig *et al.,* 2019). Also, it is important to note that species responses to local patterns cannot be extrapolated at the landscape scale (Fahrig *et al.,* 2019), and thus, the current bias towards local factors has limited our knowledge of the landscape-scale drivers of biological populations and assemblages. Fortunately, the number of landscape studies has increased in recent decades, but there are important methodological caveats in landscape research (e.g. scale-dependence of landscape effects) that can impair the accuracy and reliability of landscape-scale inferences (Fahrig, 2003; Arroyo-Rodríguez *et al.,* 2013*a*). Therefore, a comprehensive review of landscape effects on biodiversity is urgently needed, not only accurately to assess theoretical models on species' responses to landscape structure (Dunning *et al.,* 1992; Tscharntke *et al.,* 2012; Villard & Metzger, 2014; Fahrig, 2017), but also to improve land-planning practices for biodiversity conservation in human-modified landscapes. This knowledge is particularly urgent for highly threatened taxa, such as primates (Estrada *et al.,* 2017).

Primates are of critical cultural and ecological importance and represent a key component of forest ecosystems (Estrada *et al.,* 2017). They are involved in numerous ecological processes, such as herbivory, seed dispersal, predation, and pest control (Stoner *et al.,* 2007; Mittermeier *et al.,* 2013; Estrada *et al.,* 2017; Andresen, Arroyo-Rodríguez & Ramos-Robles, 2018). Most primate species are forest specialists, and hence the rapid alteration of landscape structure caused by deforestation in tropical and subtropical regions (Taubert *et al.,* 2018) increasingly limits the distribution and abundance of primates in human-modified landscapes. This can have negative consequences for plant diversity (Stevenson & Aldana, 2008) and forest regeneration (Russo & Chapman, 2011; Marsh & Chapman, 2013; Andresen *et al.,* 2018). In fact, ~60% of the world's 504 primate species are threatened with extinction (Estrada *et al.,* 2017). Therefore, assessing the impact of landscape structure on primates is critical to improve conservation strategies, not only for primates, but also for the ecological processes in which they are involved.

Decades of research on primates' responses to habitat disturbance have been mainly focused on assessing the effects of forest patch size and isolation (Arroyo-Rodríguez *et al.,* 2013*a*). This bias is probably related to the deep influence of island biogeography theory and metapopulation theory in fragmentation research (Haila, 2002; Fahrig, 2013). However, patch size and isolation are spatial characteristics of focal patches, and should not be used to infer the effect of landscape-scale variables, such as forest cover and forest fragmentation, on population abundance and distribution (Fahrig, 2003, 2013; Fahrig *et al.,* 2019). Also, patch size and isolation effects may depend on matrix composition (Harcourt & Doherty, 2005; Prugh *et al.,* 2008). This can explain why patch size and isolation are poor predictors of patch occupancy for many vertebrate species (Prugh *et al.,* 2008), and weak predictors of primate presence and abundance in several studies (Onderdonk & Chapman, 2000; Arroyo-Rodríguez & Dias, 2010).

Novel theoretical models challenge the use of patch-scale variables as predictors of biodiversity patterns, and highlight the key role played by landscape composition and configuration in moderating ecological patterns and processes (e.g. Tscharntke *et al.,* 2012; Fahrig, 2013; Mendenhall, Kappel & Ehrlich, 2013; Arroyo-Rodríguez *et al.,* 2017*b*). Such a role is related to the fact that habitat patches are open systems; that is, patch edges do not always represent real barriers to animal movements, and hence, rather than being driven by the characteristics of single habitat patches, plant and animal assemblages usually depend on environmental conditions present in the local landscape surrounding habitat patches (Dunning *et al.,* 1992; Benton *et al.,* 2002; Fahrig, 2013). In fact, the home range of primates (Arroyo-Rodríguez & Mandujano, 2009; Boyle *et al.,* 2013; Almeida-Rocha, Peres & Oliveira, 2017; Galán-Acedo *et al.,* 2019) and other animals (Mendenhall *et al.,* 2013; Ferreira *et al.,* 2018) can be composed of several habitat patches and different land-cover types (e.g. agricultural lands) and landscape elements (e.g. living fences, isolated trees), which can bring complementary and supplementary resources (Dunning *et al.,* 1992; Galán-Acedo *et al.,* 2019). Thus, to understand better the distribution and abundance of primates in these increasingly common landscapes, we need to assess species responses to landscape-scale patterns.

The number of studies that assess the effect of landscape structure on primates has increased in the last decade, but they also show contrasting results. For instance, the few studies that test the effect of forest fragmentation *per se* (i.e. controlling the effect of forest cover, *sensu* Fahrig, 2003) on primates demonstrate that fragmentation can have either positive (Arroyo-Rodríguez *et al.,* 2013*b*), negative (Thornton, Branch & Sunquist, 2011), or null (Ordóñez-Gómez *et al.,* 2015) effects, with different species showing contrasting responses to this variable (Thornton *et al.,* 2011). Similarly, some studies find weak responses to increasing landscape forest cover (Anzures-Dadda & Manson, 2007; Urquiza-Haas, Peres & Dolman, 2011; Benchimol & Venticinque, 2014), whereas others demonstrate that this landscape predictor can have significant positive effects on several primate species (Blanco & Waltert, 2013; Piel *et al.,* 2015). These apparently idiosyncratic responses to landscape structure can be related to differences among primate species in ecological traits, such as diet and home range size (Boyle & Smith, 2010). Nevertheless, such contrasting responses are not always explained by ecological traits (Onderdonk & Chapman, 2000), and can rather be related to differences in study designs, which can result in contradictions and results that are difficult to interpret (Fahrig, 2003; Arroyo-Rodríguez & Mandujano, 2009).

Herein we provide the first global assessment of all the studied primates' responses (e.g. distribution, abundance, and behaviour) to landscape structure. To do this, we first discuss some important concerns with study designs to identify potential shortfalls in primate studies on this topic. We then offer an updated summary of the literature and review all empirical evidence available to date. We describe the geographical distribution of studies and the study taxa, and assess the study designs commonly used in primate research. We finally evaluate the effect (positive or negative) of each landscape structure variable, separately assessing variables related to landscape composition and landscape configuration. As forest cover (i.e. a compositional variable) is usually significantly correlated with landscape configuration variables, when assessing the effect of configuration variables we separately assess the cases in which forest cover was controlled *versus* not controlled, as the latter case may lead to ambiguous responses to landscape configuration (Fahrig, 2003).

(1) Concerns in landscape studies

The 'landscape perspective' and its importance in ecology and conservation has been discussed elsewhere (Fahrig, 2005), especially for the case of primate research (Arroyo-Rodríguez & Fahrig, 2014); so only a brief overview is given here. In ecology, studies with a landscape perspective are those that assess ecological responses to landscape structure. As stated above, such a perspective is important because, when there are not enough resources in the habitat patches, primates can travel out of such patches in search of resources, interacting with different elements from the surrounding landscape. Thus, in many cases, they can be more strongly affected by the spatial structure of the surrounding landscape than by the characteristics of individual patches (Fahrig, 2013). Landscape structure (or heterogeneity) is defined by its spatial composition and configuration. The former refers to the types and proportions of different land covers in the landscape, such as the percentage of forest cover or the number of land cover types (Dunning *et al.,* 1992; McGarigal & Cushman, 2002). The latter describes the spatial arrangement of each land cover, such as the number of forest patches, mean patch size, or forest edge density (Dunning *et al.,* 1992; McGarigal & Cushman, 2002). Understanding the relative (independent) and interacting effects of these landscape attributes on species is an important challenge in ecology (Fahrig, 2005; Arroyo-Rodríguez & Fahrig, 2014). Therefore, we summarize below some methodological concerns that need to be considered to face such a challenge.

(2) Study design

The first and probably most important concern in studies with a landscape perspective is that the independent units of observation and analysis should be the landscapes, not the patches. Studies that measure both the ecological response (e.g. species abundance) and predictor variable (e.g. patch size) in independent habitat patches are called patch-scale studies (Fig. 1A), and should not be used to make landscape-scale inferences (Fahrig, 2003; Fahrig *et al.,* 2019). To make accurate landscape-scale inferences both the ecological response(s) and predictor variable(s) need to be measured in independent landscapes (Fig. 1B). To this end, we can use three different study designs depending on how response variables are measured, and thus on the research questions (Brennan *et al.,* 2002;

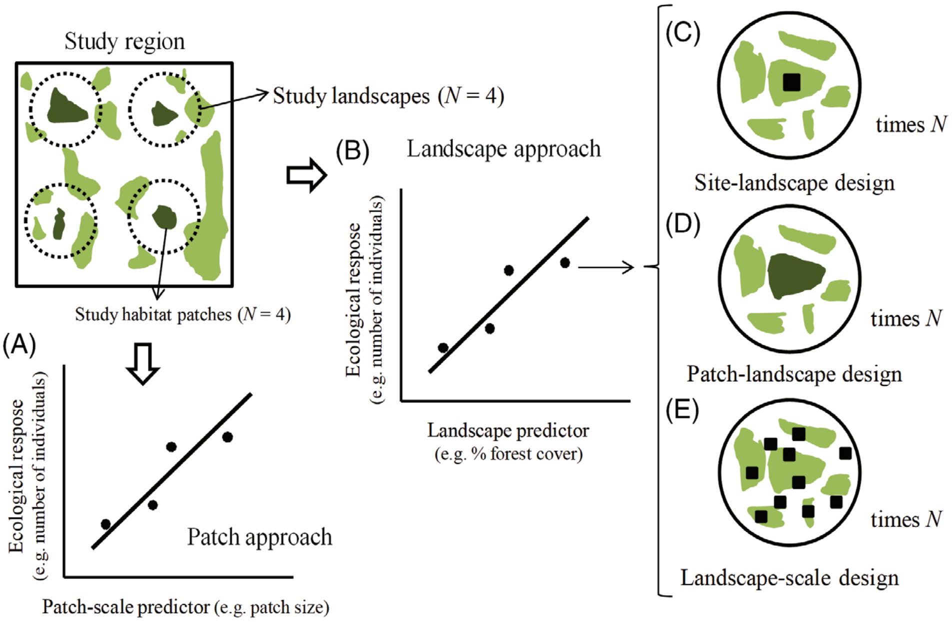

Fig. 1. Patch and landscape approaches in ecological studies. In patch-scale studies (A), both ecological responses and predictor variables are measured in different (and independent) focal patches distributed across the study region. Studies with a landscape approach (B) are those that assess the effect of landscape variables on ecological responses. The responses can be measured in three ways: within equal-sized sample sites at the centre of each landscape (i.e. site-landscape design; (C), within focal patches at the centre of each landscape (i.e. patch-landscape design; (D) or within several sample sites or patches across the landscape (i.e. landscape-scale design; (E). In site- and patch-landscape designs, landscape variables are measured within a specified radius from the centre of the sites/patches. In all cases, multiple landscapes need to be sampled in order to ask questions about the influence of landscape structure on an ecological response. Note that in landscape-scale studies, the sites or patches located near the edge of the landscape can be affected by the landscape context beyond the bounds of the sample landscape. For simplicity of illustration, habitat patches (green polygons) are embedded in a homogeneous (white areas) anthropogenic matrix (modified from Arroyo-Rodríguez & Fahrig, 2014; Andresen *et al.*, 2018).

McGarigal & Cushman, 2002; Arroyo-Rodríguez & Fahrig, 2014): (*i*) site-landscape (Fig. 1C); (*ii*) patch-landscape (Fig. 1D); and (*iii*) landscape-scale designs (Fig. 1E). Site- and patch-landscape studies measure response variables in equal-sized sample sites (e.g. transects) or habitat patches, respectively, and predictor variables (landscape attributes) are measured within a specified radius from each focal site or patch (McGarigal & Cushman, 2002), i.e. in the surrounding landscape. In landscape-scale studies, response variables are measured in several sample sites within the landscape, and a single data point for analysis corresponds to the combined response data from all sample sites within the landscape, along with the landscape composition/configuration predictor variable of that landscape (Brennan *et al.*, 2002).

Site- and patch-landscape study designs are useful to evaluate the effects of landscape context on an ecological response and are particularly recommended to assess mobile organisms such as primates (Arroyo-Rodríguez & Fahrig, 2014). Also, as the response variables are measured in focal sites/patches located in the centre of study landscapes, the cost (time and money) of these study designs can be similar to patch-scale studies (Brennan *et al.*, 2002). Another advantage of these designs is that they allow one to assess the scale of effect (Jackson & Fahrig, 2012) – an important step to evaluate accurately the influences of landscape context on the ecological response of interest (see Section II.4). Landscape-scale studies, on the other hand, are particularly useful to assess ecological processes such as metapopulation dynamics and species turnover across space (Arroyo-Rodríguez & Fahrig, 2014). Note that multiple landscapes are still needed here to answer questions about the effects of landscape structure on metapopulation dynamics or species turnover. In any case, special care should be taken when selecting the focal sample sites/patches in landscape-scale studies, because if they are located near the edge of the study landscape, they can be strongly affected by the larger landscape context outside the study landscape (Andresen *et al.*, 2018; Fig. 1E).

(3) Constant landscape size and shape

In site- and patch-landscape study designs, the distance within which landscape variables are measured should be measured from the centre of each focal site/patch (Fig. 1) and not from their patch edges (Arroyo-Rodríguez, Galán-Acedo & Fahrig, 2017*a*). In the latter case, different sample landscapes would have different sizes and shapes depending on the sizes and shapes of focal patches. This could lead to a confounding of landscape structure effects with landscape size and shape effects.

(4) Spatial overlap

As discussed above, a landscape approach implies that both response variables and their potential predictors are measured in independent sample landscapes. Such independence implies that the value of a variable in a given landscape does not affect the value of this same variable in other landscapes. In this sense, independence between landscapes can be violated when landscapes overlap in space at the relevant spatial extent, i.e. at the scale of effect (Eigenbrod, Hecnar & Fahrig, 2011). The effects of such lack of independence are not well studied. There is evidence that it can decrease parameter estimates in regression models (Eigenbrod *et al.,* 2011; Jackson & Fahrig, 2012), although other studies do not find significant effects on statistical models (Zuckerberg *et al.,* 2012). In any case, to prevent potential confounding effects of overlapping landscapes on study findings, we suggest selecting sample sites that are sufficiently separated to avoid spatial overlap at the likely scale of effect, to increase the likelihood of spatial independence.

(5) Scale of effect

Species–landscape relationships depend on the spatial extent (i.e. landscape size) within which landscape variables are measured (Jackson & Fahrig, 2015; Miguet *et al.,* 2016; Martin, 2018), and this has specifically been shown in primate research (e.g. Ordóñez-Gómez *et al.,* 2015; Galán-Acedo *et al.,* 2018). Significant species–landscape relationships may be undetected (i.e. high likelihood of type II statistical error) if the landscape variables are measured at the incorrect scale (Fahrig, 2013; Jackson & Fahrig, 2015). Therefore, landscape studies should measure landscape variables across several spatial extents (i.e. within different-sized radii) to identify the scale(s) that yield the strongest response–landscape relationship (so-called 'scale of effect'; Jackson & Fahrig, 2012). It is important to note, however, that the scale of effect usually differs among response variables (e.g. patch occupancy, species abundance, diet), as each response is related to drivers acting across different spatio-temporal scales (Thogmartin & Knutson, 2007; Bradter *et al.,* 2011; Miguet *et al.,* 2016; Martin, 2018). Thus, in practice, a multiscale approach is needed to assess the effect of each landscape variable on each ecological response. This is not trivial, as measuring landscape variables at the incorrect scale can decrease the variance explained by the models and other statistical caveats that can lead to wrong interpretations of results (de Knegt *et al.,* 2010). To assess the scale of effect accurately, the range of spatial extents tested should be selected based on species traits (e.g. vagility, home range size), because the scale of effect is thought to be a function of such species traits (Jackson & Fahrig, 2012; Miguet *et al.,* 2016). Furthermore, it is crucial to choose a wide range of scales, both smaller than and larger than the scale thought likely to contain the true scale(s) of effect (Jackson & Fahrig, 2015). When the range of scales is too narrow, studies can find that the optimal scale is the smallest or the largest scale evaluated, which suggests that the correct scale of effect is outside the selected range (Jackson & Fahrig, 2015).

(6) Confounding variables

Another important concern in landscape studies is that landscape variables can be significantly inter-correlated. In particular, forest cover (i.e. a proxy of habitat amount for forest-dependent species such as most primates) is strongly related to several landscape configuration variables (e.g. mean inter-patch distance, mean patch size, edge density, and number/density of forest patches; Fahrig, 2003; Villard & Metzger, 2014). Studies on the effect of landscape configuration variables that do not control for the effect of forest cover may lead to ambiguous responses to landscape configuration (Fahrig, 2003, 2017). Therefore, to assess the effect of landscape configuration accurately, the effect of forest cover needs to be controlled. This is particularly important when assessing the effect of forest fragmentation on biodiversity. As the breaking apart of forest (i.e. fragmentation) is followed by forest loss, the effect of fragmentation needs to be measured independently from the effect of forest loss (i.e. so-called 'fragmentation *per se*'; Fahrig, 2017). Such control can be achieved by selecting landscapes with similar forest cover but different configuration or by including forest cover as a covariate within multiple regression analyses (Fahrig, 2017). Note that, in principle, when assessing the effects of composition variables such as forest amount, we should control for correlated configuration variables. However, studies that include both composition and configuration variables generally find that composition is more important than configuration (Fahrig, 2003). This means that we are more likely to misinterpret a configuration effect when composition has not been controlled for, than the reverse. Keeping all these issues in mind, below we review the available literature on primates to assess what we know so far.

II. METHODS

(1) Literature search

We systematically reviewed all available articles on primates' responses to changes in landscape structure. To this end, we carried out a search in the *SCOPUS* (www.scopus.com) and *Google Scholar* (https://scholar.google.com/) databases on 21 July 2018 for research articles containing the following search terms in all reference topics: [(primate* OR monk*) AND ('radius' AND/OR 'radii' AND/OR 'forest cover' AND/OR 'buffer' AND/OR 'multiscale' AND/OR 'landscape' AND/OR 'multi-scale' AND/OR 'landscape metric*' AND/OR 'landscape variable*' AND/OR 'landscape scale' AND/OR 'percentage' AND/OR 'forest' AND/OR 'percentage of forest' AND/OR 'landscape heterogeneity' AND/OR 'landscape predictors' AND/OR

Table 1. Landscape composition and configuration variables assessed in landscape studies of primates. The number of study responses per predictor is also indicated, as is the percentage of significant ones

Predictor variables	Definition	Responses (% significant)
Landscape composition		
Agroforest cover	Percentage of agroforest in the landscape	1 (0%)
Corridor length	Sum of the lengths of wooded corridors within the landscape	2 (0%)
Forest cover	Proportion/percentage/area of forest in the landscape	99 (32%)
Land cover richness	Number of land cover types in the landscape	1 (100%)
Landscape quality indices	Areas or numbers of pixels of different land covers in the landscape weighted by their overall suitability for primates and averaged over the landscape	8 (37%)
Logged forest cover	Percentage of logged forest in the landscape	1 (0%)
Matrix cover	Percentage of matrix habitats (i.e. open areas, secondary vegetation and riparian vegetation) in the landscape	1 (100%)
Matrix permeability	Percentage of each land cover type within the landscape matrix weighted by their suitability for primates travelling and averaged over the landscape	6 (17%)
Secondary forest cover	Proportion of secondary forest in the landscape	1 (0%)
Sugar cane cover	Percentage of sugar cane in the landscape	1 (0%)
Landscape configuration[a]		
Area-weighted mean patch fractal dimension	Patch size-weighted average of the fractal dimensions of all forest patches in the landscape	2 (0%)
Corridor abundance	Corridor abundance in the landscape	2 (50%)
Edge density	Sum of forest-matrix edge length divided by landscape area	9 (11%)
Fragmentation	Number/density of forest patches, including the splitting index	33 (24%)
Mean inter-patch distance	Mean of all pairwise edge-to-edge distances between forest patches in the landscape	15 (33%)
Mean patch size	Arithmetic mean of forest patch sizes	2 (0%)
Road abundance	Road abundance in the landscape	4 (0%)

The classification of compositional or configurational variables was based on McGarigal et al. (2002).
[a]These variables can be highly correlated with forest cover.

'landscape structure')]. We limited our review to studies that explicitly assessed the response of primates to landscape composition and/or configuration variables, excluding 'grey literature'. We also excluded studies on biophysical variables, such as elevation, terrain aspect, and soil properties.

(2) **Data extraction**

From each article, we recorded the species' name, genus and the country where the study was conducted – which we classified into four main regions (Asia, Madagascar, Mainland Africa and Neotropics) following Estrada *et al.* (2017). We also recorded the study design considering the three major designs described above: site-landscape, patch-landscape or landscape-scale designs (Arroyo-Rodríguez & Fahrig, 2014). Regarding the spatial scale, we recorded the number of scales (buffers) included in the study, and whether the study estimated or not the scale of landscape effect. When the scale of effect was evaluated, we recorded whether the reported scale of effect was equal to the smallest or to the largest scale evaluated and we also recorded the scale range (i.e. largest scale divided by the smallest scale). To assess whether the scales were arbitrarily selected, we also recorded whether the authors offered a biological explanation for the selected scales. Finally, we recorded whether studies avoided spatial overlap between study landscapes, and thus, potential spatial dependence (i.e. pseudoreplication; Eigenbrod *et al.,* 2011).

We classified landscape variables into compositional and configurational metrics (Table 1) following McGarigal & Cushman (2002). Response variables included: abundance-related variables (i.e. encounter rate, total or mean abundance, and total/mean density), species composition, number of roads crossed by primates, diet diversity, feeding time, resting time, travelling time, species richness, species diversity (Simpson), functional diversity, total biomass, immature-to-female ratio, number of males/females/juveniles, sex ratio, infant survival rate, group size, lambda growth rate, occurrence-related variables (e.g. presence/absence), frequency of dispersal events, and hunting pressure (usually measured through interviews). We then synthesized the results, recording if there was a significant effect or not, and the direction of significant effects (positive or negative). We did not carry out a formal meta-analysis because we are not attempting to estimate the overall effect size of each landscape variable on each response, but only summarize the number (and direction) of significant effects documented to date.

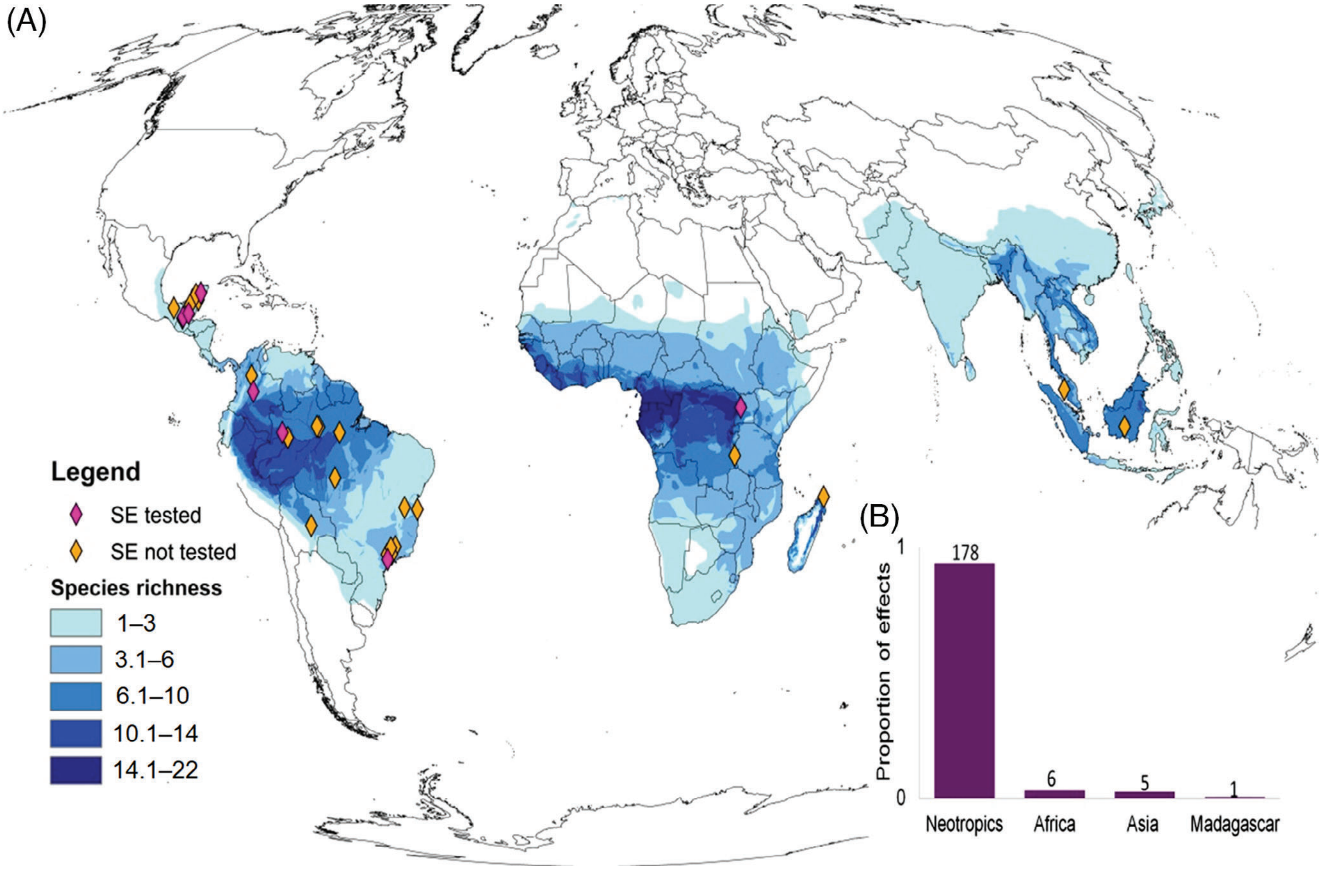

Fig. 2. (A) Global distribution of primate studies with a landscape approach (diamonds). Pink and orange diamonds refer to studies that assess or do not assess the scale of landscape effects (SE) on primates, respectively. Primate species richness is represented in blue (based on Pimm *et al.*, 2014). (B) The proportion and absolute number (above each column) of individual effects tested per geographic region.

III. RESULTS AND DISCUSSION

(1) Distribution of landscape studies

We found 34 studies of 71 primate species (24 genera and 10 families) that used a landscape perspective (Fig. 2; see online Supporting information, Table S1). Studies were distributed worldwide, but most studies (82%) were carried out in the Neotropics (Fig. 2). The most studied genera were *Alouatta* (56% of studies), followed by *Callicebus* and *Ateles* (both assessed in 35% of studies), and *Sapajus* (26%), all Neotropical primates. Thus, our findings indicate that there is an important gap in research, especially regarding Asian and African primates. Filling this gap is urgently needed given the rapid loss and fragmentation of Paleotropical forests (Taubert *et al.*, 2018), and the threats facing primates from this geographic realm (Estrada *et al.*, 2017).

(2) Potential methodological caveats

The vast majority of studies used either a site-landscape design (18 studies, 53% of studies) or a patch-landscape design (14 studies, 41%) (Fig. 3). One study was a review that included studies with site-landscape and patch-landscape designs (Benchimol & Peres, 2014), and only one study used a landscape-scale design (Prist, Michalski & Metzger, 2012). Eleven of 32 site- or patch-landscape studies (34%) measured landscape variables within radii taken from the edge of focal patches, and not from the centre of the site/patch where the response variables were measured. This suggests that landscape structure effects could be confounded with landscape size and/or landscape shape effects in these studies (Arroyo-Rodríguez *et al.*, 2017*a*), but the consequences of such potential confounding effects are unclear, and need to be assessed in future studies.

Landscapes overlapped in space in eight of 34 studies, suggesting that almost a quarter of studies may have violated the assumption of independence between replicate landscapes, and that the true parameters (slopes) may be different from those estimated in these studies (Eigenbrod *et al.*, 2011). Worryingly, 14 studies (38%) did not show information on spatial overlap between study landscapes, suggesting that pseudoreplication problems in landscape studies of primates may be higher than recorded here. However, as stated above, the effect of such pseudoreplication on statistical models is not well understood (Zuckerberg *et al.*, 2012), so this represents another interesting avenue for future research.

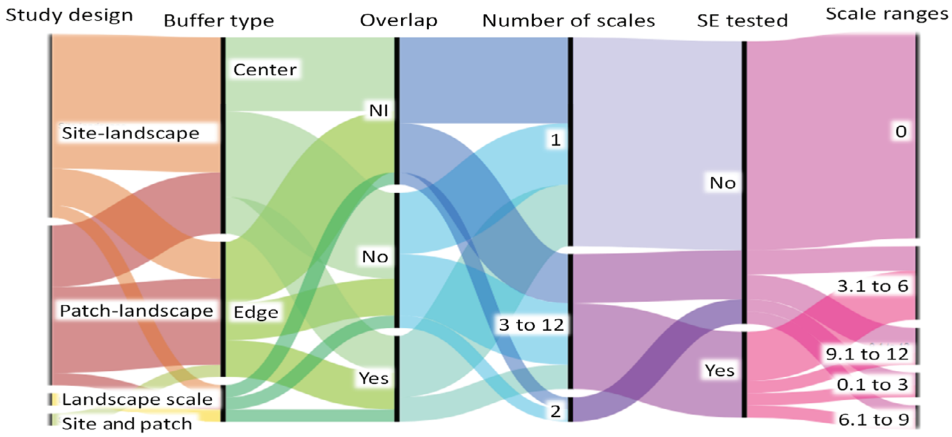

Fig. 3. Designs of published primate studies that use a landscape approach ($N = 34$ studies). The proportion (represented by the size of black vertical lines) of studies with different study designs is indicated, as is the type of buffer used to determine the extents of the replicate landscapes (site- and patch-landscape study designs only), the presence/absence of spatial overlap between landscapes, the number of scales within which landscape variables were measured, the cases in which the scale of effect (SE) was tested, and the range of scales tested. The latter was measured as the largest scale divided by the smallest scale. 'Site and patch' in the first column refers to a review that used both site-landscape and patch-landscape study designs. NI = no information available, which includes studies that do not specify the buffer type and one landscape-scale study where this information was not applicable.

Regarding the scale of analysis, more than half of studies (21 of 34) measured landscape predictors within only a single spatial extent, two studies (6%) considered two different-sized scales, and only 11 studies (32%) included three or more scales (Fig. 3). This is alarming, as an increasing number of studies demonstrate that if landscape variables are not measured at the optimal scale, species responses to landscape predictors can be poorly estimated or missed altogether, potentially leading to erroneous conclusions about the effects of landscape structure on species (Holland, Fahrig & Cappuccino, 2005; de Knegt *et al.,* 2010; Jackson & Fahrig, 2012; Miguet *et al.,* 2016; Galán-Acedo *et al.,* 2018; Gestich *et al.,* 2019).

Regarding this issue, four of 11 multi-scale studies (36%) did not test the scale of effect, but measured landscape variables across several scales to select the scale that prevented strong correlations between predictor variables (Benchimol & Peres, 2015), or simply for descriptive purposes (Pyritz *et al.,* 2010). Only seven studies (21%) provided information on the scales of landscape effects for 19 primate species. Yet, approximately half of the studies that assessed the scale of effect reported scales of effect equal to the smallest or to the largest scale, thus suggesting that the actual scales of effect were outside the range of scales tested (Jackson & Fahrig, 2015). This can be related to at least two factors: (*i*) the small range of scales included in the analysis; and (*ii*) the lack of a biological/ecological justification when selecting the range of scales (Jackson & Fahrig, 2015). In agreement with this idea, most studies that tested the scale of effect (five of seven multi-scale studies, 71%) used scale ranges ≤ 6, and only one study used a scale range > 10, i.e. greater than one order of magnitude (Fig. 3). In addition, only two of the seven multi-scale studies (29%) offered a biological explanation for the selected scales; these were the home range requirements and dispersal distances of the study species (Ordóñez-Gómez *et al.,* 2015; Carretero-Pinzón *et al.,* 2017).

Those studies that assessed the scale of effect reported scales ranging from 0.39-km (Ordóñez-Gómez *et al.,* 2015) to 5.5-km radius (Rabelo *et al.,* 2017). The cause of such differences remains poorly understood, but following previous studies (e.g. Jackson & Fahrig, 2012; Miguet *et al.,* 2016) it is probably related to the huge differences in ranging behaviours and foraging-area requirements among species (e.g. home range size can vary from 0.1 ha to >5,000 ha; Mittermeier *et al.,* 2013). Studies of primates also suggest that the scale of effect differs among landscape predictors, with forest cover showing larger (Gestich *et al.,* 2019) or smaller (Galán-Acedo *et al.,* 2018) scale of effect, depending on the response variable and regional context. This is not surprising, as theoretical models suggest that the response variable and regional context can also drive the scale of effect (Miguet *et al.,* 2016). Thus, in practice, studies on landscape effects on primates need to use a multiscale approach to ensure that landscape–species associations are correctly evaluated (Jackson & Fahrig, 2015).

(3) Primate responses to landscape structure

In total, the 34 studies reported 188 individual effects relating to 17 landscape metrics (Table 1; Table S1). From these, 121 (64%) effects were responses to landscape composition and only 39 (21%) to landscape configuration *per se* (i.e. after controlling for the effect of forest cover). We found 28 (15%) additional responses to landscape configuration, but as they came from studies that did not control for forest cover effects, we classified these effects as ambiguous responses to landscape configuration (see Section IV.3*b*). Although 23 of 34 studies (68%) reported at least one significant effect of landscape composition or configuration on primates, null

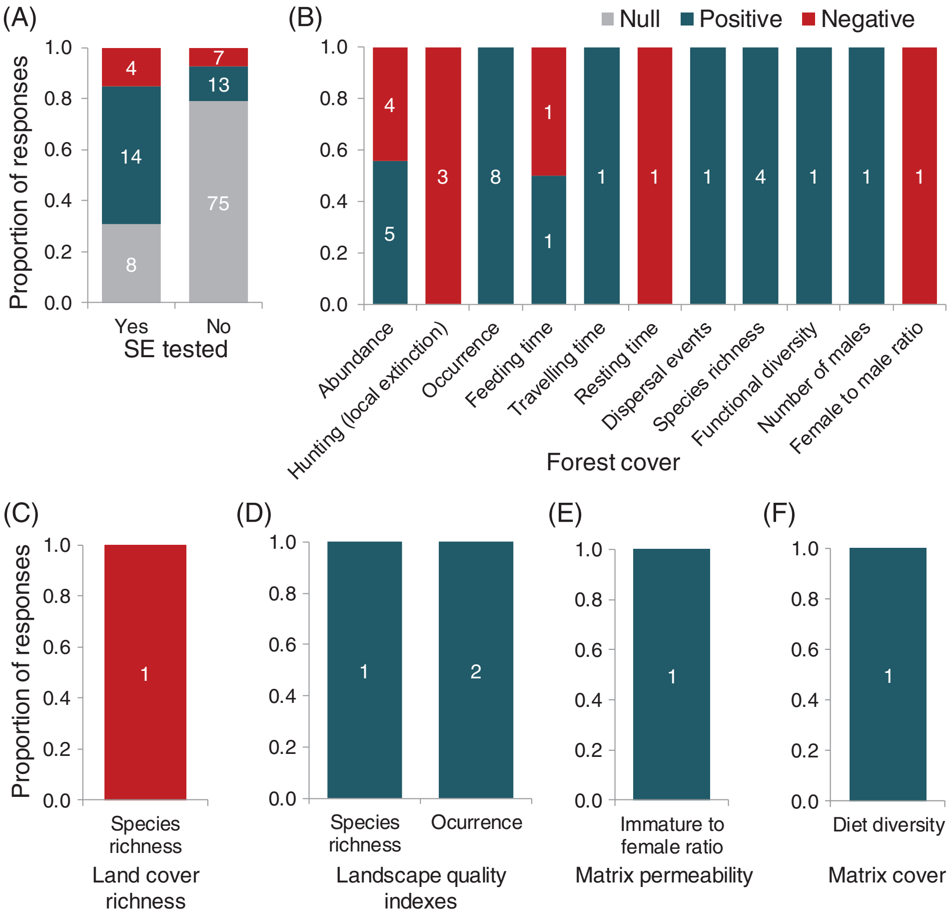

Fig. 4. Proportions (and numbers in bars) of positive, negative and null responses ($N = 121$ responses from 34 studies) of primates to landscape composition variables (defined in Table 1). (A) Studies that evaluated or did not evaluate the scale of landscape effect (SE). (B–F) The proportion of positive and negative significant responses showing the impact of forest cover (B), land cover richness (C), landscape quality indexes (D), matrix permeability (E) and matrix cover (F).

responses were most common (135 of 188 responses, 72%). This does not necessarily indicate that landscape structure has weak effects on primates, as the methodological problems indicated above may have reduced the likelihood of studies finding significant effects. For example, the percentage of significant responses to landscape compositional variables was 3.3 times higher in those studies that considered the scale of effect (69% of responses) than in those that did not consider the scale of effect (21%) (Fig. 4A). This highlights the importance of assessing the scale of landscape effect.

(*a*) *Effects of landscape composition*

Only 38 of 121 responses (31%) to landscape composition were significant (Fig. 4A), probably because most studies do not assess the scale of effect. Yet significant responses to landscape forest cover were mostly positive (69% of significant responses) (Fig. 4B). For example, the probability of habitat occupancy by *Leontopithecus chrysomelas* in Brazil increased with increasing forest cover (Cassano, Barlow & Pardini, 2014). Also, in Tanzania, forest sites surrounded by higher forest cover can show more individuals of *Pan troglodytes* (Piel *et al.*, 2015), and a higher number of primate species (Blanco & Waltert, 2013). Ordóñez-Gómez *et al.* (2015) also demonstrate that Geoffroyi's spider monkeys (*Ateles geoffroyi*) spent more time travelling and feeding in landscapes with more forest cover (Fig. 4B). These findings are not surprising, as habitat amount in a landscape is expected to be positively related to landscape connectedness and resource availability (Fahrig, 2003, 2013), which may explain why habitat amount has positive effects on species richness (Gurd, Nudds & Rivard, 2001; Arroyo-Rodríguez *et al.*, 2016), population distribution and abundance (Gibbs, 1998), and genetic diversity (Gibbs, 2001) of several taxa. Although forest cover was negatively related to hunting pressure of *Lagothrix cana*, *L. poeppigii* and *L. lagothricha* in Amazonia (Parry & Peres, 2015), this represents evidence of a positive effect of forest cover on primate populations because it suggests that hunting can be reduced or prevented by increasing forest cover in the landscape. This is likely related to the fact that primates are more easily located and hunted in landscapes with lower forest cover and smaller forest patches (Laurance, Vasconcelos & Lovejoyo, 2000).

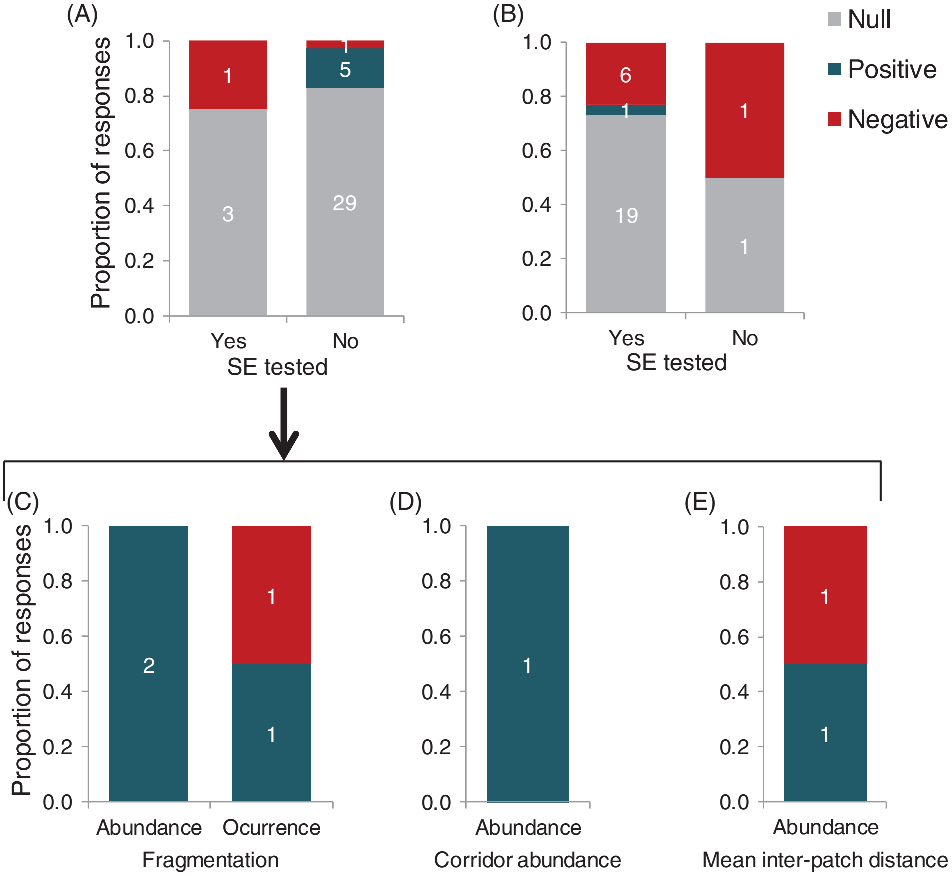

Fig. 5. Proportions (and number in bars) of positive, negative and null responses ($N = 39$ responses from 9 studies) of primates to landscape configuration. (A, B) Studies that assessed or did not assess the scale of effect (SE). Responses from studies that control (A) or not (B) the effect of forest cover are shown separately, because the latter case may lead to ambiguous responses to landscape configuration (Fahrig, 2003). Considering only the studies that assess the effect of configuration variables *per se* (A), we indicate primate responses to habitat fragmentation (C), corridor abundance (D) and mean inter-patch distance (E).

Land cover richness was negatively related to primate species richness in one study (Adila *et al.,* 2017; Fig. 4C). As suggested by the authors of that study, this pattern can be related to increasing human–primate conflicts in landscapes with more anthropogenic land covers in Peninsular Malaysia (Adila *et al.,* 2017). However, different land covers in the landscape can provide complementary and supplementary resources for primates (Dunning *et al.,* 1992; Watling *et al.,* 2011; Tscharntke *et al.,* 2012; Ferreira *et al.,* 2018). This can explain why when considering the suitability of different land covers to primates, all studies report positive responses to increasing landscape and matrix quality (Fig. 4D, E). For instance, the occurrence of *Ateles geoffroyi* and *Alouatta pigra* was positively related to the suitability of different land covers in a tropical forest from southeastern Mexico (Urquiza-Haas, Peres & Dolman, 2009). Some primate species can benefit from moving and/or feeding in some anthropogenic land covers, especially in those that are more similar to the original habitat of primates (Anderson, Rowcliffe & Cowlishaw, 2007; Watling *et al.,* 2011; Blanco & Waltert, 2013; Galán-Acedo *et al.,* 2019), thus highlighting the importance of improving matrix quality for biodiversity persistence in human-modified landscapes (Dunning *et al.,* 1992; Benton, Vickery & Wilson, 2003; Tscharntke *et al.,* 2012).

(*b*) *Effects of landscape configuration*

Regarding the effect of landscape configuration variables, we found a higher number of responses (39 responses) from studies that control for forest cover effect (Fig. 5A) than from studies that do not control for such effects (28 responses, Fig. 5B). The latter group of responses can be considered ambiguous responses to configuration because landscape configuration variables are frequently correlated to forest cover (Fahrig, 2003, 2013), and thus we suggest caution with interpretation of these results.

Considering only studies on landscape configuration *per se*, most responses (32 of 39) were not significant (Table 1; Fig. 5A). Yet, in concordance with Fahrig (2017), we found that most (3 of 4, 75%) significant responses to habitat fragmentation *per se* are positive (Fig. 5C). In particular, the presence of *Alouatta palliata* (Anzures-Dadda & Manson, 2007), and the abundance of *Alouatta pigra* (Arroyo-Rodríguez *et al.,* 2013*b*) in Mexico, and the abundance of *Sapajus* *nigritus* in Brazil (Hendges *et al.,* 2017) usually increases with increasing number/density of habitat patches in the landscape. This is not surprising because fragmentation *per se* decreases mean inter-patch isolation distances and favours landscape complementation and supplementation dynamics, thus increasing resource availability for forest-dwelling species at the landscape scale (Dunning *et al.,* 1992; Fahrig, 2017). This can explain why other mammal species, such as tayras (*Eira barbara*), northern tamanduas (*Tamandua mexicana*), and gray-tailed voles (*Microtus canicaudus*) respond positively to increasing fragmentation *per se* in human-modified landscapes (Wolff, Schauber & Edge, 1997; Thornton *et al.,* 2011). Yet, there is evidence that fragmentation can have negative effects on spider monkeys (*Ateles geoffroyi*), and other terrestrial mammals (*Leopardus wiedii*, *Nasua narica*, *Dasypus novemcinctus*, and *Urocyon cinereoargenteus*) – a finding that could be associated with higher exposure to risks in the matrix (e.g. predation, hunting; Thornton *et al.,* 2011). Therefore, additional studies with a larger number of species are needed to identify which species and under which regional context forest fragmentation *per se* can have positive or negative effects to better manage this landscape metric in conservation plans.

Responses of primates to patch isolation were variable, with some population parameters increasing with patch isolation, and others decreasing. For example, mean inter-patch distance was negatively related to population size of *Alouatta pigra*, but positively related to population density in the Lancadona rainforest, Mexico, probably because these monkeys can be relatively resistant to the initial phase of deforestation, concentrating in isolated forest patches (Arroyo-Rodríguez *et al.,* 2013*b*; Fig. 5E). In fact, Anzures-Dadda & Manson (2007) showed that the abundance of *A. palliata* is positively related to the number of vegetation corridors in a strongly deforested landscape from southeastern Mexico (Fig. 5D). Therefore, as most (84%) primate species have arboreal locomotion, maintaining landscape elements such as vegetation corridors and arboreal crops can play a key role in primate conservation. These landscape elements are not only used for travelling, but they can also provide valuable complementary food resources (Asensio *et al.,* 2009; Tscharntke *et al.,* 2012; Galán-Acedo *et al.,* 2019).

IV. CONCLUSIONS

(1) We found a significant geographical and taxonomic bias in landscape studies of primates, which are mainly focused on Neotropical forests, and especially on the genus *Alouatta*. Our understanding of the effect of landscape structure on Asian and African primates remains extremely poor.

(2) Despite this information gap, we found an increasing number of studies on the impact of landscape structure on primates, with important theoretical and conservation implications. Nevertheless, we first need to consider limitations in study designs, which can make interpretation of the available evidence difficult.

(3) Of particular concern is the fact that the majority of the studies quantified landscape predictors within a single spatial scale, potentially missing significant primate–landscape responses (i.e. a high likelihood of type II statistical error). To assess such responses accurately, landscape metrics need to be measured at the optimal scale, i.e. the spatial extent at which the primate–landscape relationship is strongest (so-called 'scale of effect'). Only 21% of studies calculated the scale of effect using multiscale approaches. This may explain the large number of null responses to landscape structure, as the vast majority of studies that do not assess the scale of effect report mainly null effects of landscape structure, while most studies that optimized the scale found significant responses.

(4) Significant responses to landscape structure were primarily to landscape composition variables rather than to landscape configuration variables. In particular, primates generally show positive responses to increasing forest cover, landscape quality indices and matrix permeability, whereas responses to landscape configuration were generally weak. This is consistent with evidence from studies with several taxa (Fahrig, 2003, 2017; Garmendia *et al.,* 2013; Carrara *et al.,* 2015), and suggests that forest loss (not fragmentation) is an important threat to primates.

(5) Unfortunately, half of studies showing significant responses to landscape configuration metrics did not control for the effect of forest cover. As landscape configuration variables are usually strongly correlated to forest cover (Fahrig, 2003, 2013), such impacts may simply be driven by landscape-scale forest loss. Therefore, additional studies on the effect of landscape configuration *per se* are needed to understand the effect of these variables better on primates. This represents another important information gap that needs to be filled in future research.

(6) Although weaker, the impact of landscape configuration *per se* on primates should not be overlooked. For example, the effect of forest fragmentation is mostly positive, thus highlighting the very high conservation value of small habitat patches for primates and other taxa in human-modified landscapes (Fahrig, 2017). Small patches not only provide important complementary and supplementary resources for primates (Asensio *et al.,* 2009; Pozo-Montuy *et al.,* 2013), but can also decrease inter-patch isolation distances, thus contributing to prevent the negative impact of habitat isolation that we found herein.

(7) Despite the limitations described above, the available findings on primate's responses to landscape structure can be used to guide conservation strategies in human-modified landscapes. First, the maintenance of native habitats for primates (e.g. through creation of reserves) and increasing habitat amount through restoration should be considered priorities in the conservation agenda for primates. Second, such conservation and restoration programs should not give a lower value to small habitat patches, as these patches can actually have a higher conservation value

than the same area in a larger patch. Thus, increasing the number of habitat patches in the landscape through 'reverse fragmentation' (i.e. establishment of habitat patches in degraded areas; *sensu* del Castillo, 2015) is highly valuable for biodiversity conservation. Third, complementing this with other land-management strategies to improve overall landscape quality is also of paramount importance. This includes matrix enrichment with food-plant species and creation of wooded corridors (Galán-Acedo *et al.,* 2019). Finally, environmental education programs can also be critical to reduce harmful activities in the matrix (e.g. killing or hunting primates in anthropogenic land covers). Taken together, these management strategies can help to mitigate the negative impacts of land-use change on our closest relatives.

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VII. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.
Table S1. Data extracted from all published studies of primates with a landscape perspective in human-modified landscapes.

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