COMMENTARY

Why is a Landscape Perspective Important in Studies of Primates?

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With accelerated deforestation and fragmentation through the tropics, assessing the impact that landscape spatial changes may have on biodiversity is paramount, as this information is required to design and implement effective management and conservation plans. Primates are expected to be particularly dependent on the landscape context; yet, our understanding on this topic is limited as the majority of primate studies are at the local scale, meaning that landscape-scale inferences are not possible. To encourage primatologists to assess the impact of landscape changes on primates, and help future studies on the topic, we describe the meaning of a "landscape perspective" and evaluate important assumptions of using such a methodological approach. We also summarize a number of important, but unanswered, questions that can be addressed using a landscape-scale study design. For example, it is still unclear if habitat loss has larger consistent negative effects on primates than habitat fragmentation *per se*. Furthermore, interaction effects between habitat area and other landscape effects (e.g., fragmentation) are unknown for primates. We also do not know if primates are affected by synergistic interactions among factors at the landscape scale (e.g., habitat loss and diseases, habitat loss and climate change, hunting, and land-use change), or whether landscape complexity (or landscape heterogeneity) is important for primate conservation. Testing for patterns in the responses of primates to landscape change will facilitate the development of new guidelines and principles for improving primate conservation. Am. J. Primatol. 76:901–909, 2014.

Key words: habitat fragmentation; habitat loss; landscape scale; landscape structure; patch scale; patch-landscape approach

INTRODUCTION

Primates are among the most studied free-ranging mammals in the wild, but it has only been in the last two decades that primatologists have focused their attention on understanding the response of primates to landscape changes. For example, a SCOPUS database search showed a steep increase in the number of publications on this topic from one in 1976 to >300 in 2013 (Fig. 1). This may be related to the fact that rapid human population growth [81 million persons annually between 2005 and 2013; United Nations, 2012] has resulted in the alteration of more than three quarters of the terrestrial biosphere into anthropogenic biomes [Ellis, 2013], in which the persistence of primate populations is compromised [Marsh et al., 2013]. In fact, more than half of the world's primate species are currently threatened by extinction [Chapman & Peres, 2001], principally as consequence of land-use intensification [Marsh et al., 2013]. Thus, the future of primates and their habitats will depend on our ability to design and implement effective management and conservation plans within human-modified landscapes.

To this end, understanding the responses of primates to landscape change is of paramount importance. Unfortunately, despite the amount of information published on primates during the last several decades (Fig. 1), which includes several books [e.g., Cowlishaw & Dunbar, 2000; Estrada et al., 2006a; Marsh, 2003; Marsh & Chapman, 2013], we

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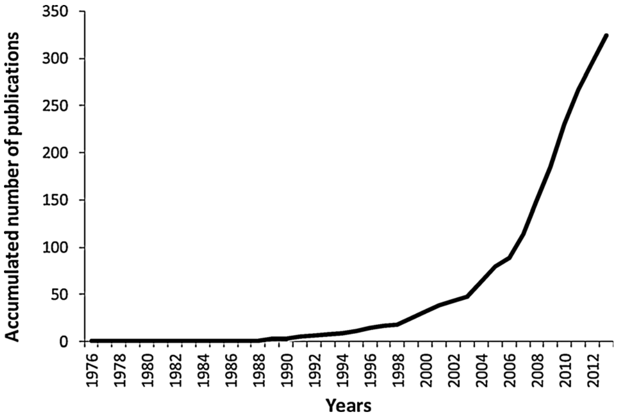

Fig. 1. Accumulated number of publications found in the SCOPUS database up to November 2013 containing "primates" and "habitat fragmentation" or "land-use change" or "landscape change" or "deforestation" in the title, abstract, and/or keywords ($n = 324$ papers).

continue to lack the data needed to develop general management plans for primate conservation, particularly at the landscape scale [Arroyo-Rodríguez et al., 2013a; Marsh et al., 2013]. This situation is related to several factors. First, most studies are at the local scale (i.e., the home range of individual groups), meaning that landscape-scale inferences are not possible [Arroyo-Rodríguez & Mandujano, 2009; Arroyo-Rodríguez et al., 2013a; Fahrig, 2003]. Second, human-modified landscapes are highly heterogeneous, with many confounding factors, challenging our ability to identify key proximate (direct) causes and the underlying species-specific behavioral, social, and ecological responses that drive these forces [Arroyo-Rodríguez et al., 2013a; Fahrig, 2003; Villard & Metzger, 2014]. For example, fragmented landscapes can strongly differ in economic activities, demographic change, sociopolitical factors, and cultural and religious factors [Millennium Ecosystem Assessment, 2005], which can play critical roles in determining the specific nature of habitat loss and fragmentation [e.g., Duvall, 2008; García-Frapolli et al., 2007; Ormsby & Edelman, 2010]. Third, primate responses to landscape change only may be evident within certain ranges of landscape change [Arroyo-Rodríguez et al., 2008; Pardini et al., 2010; Villard & Metzger, 2014]. Finally, the response of populations to landscape change is complex and highly variable among species [Boyle & Smith, 2010; Pyritz et al., 2010; Vetter et al., 2011]. For example, the presence of primates in fragmented forests has been negatively related to the total proportion of fruit in diet and to home range size [Boyle & Smith, 2010].

In this paper, we argue that most of these limitations may be solved using a landscape perspective, which is almost absent from the primatological literature [Arroyo-Rodríguez et al., 2013a]. Therefore, we first describe the meaning of a "landscape perspective." We then assess some important assumptions in using this methodological approach to help researchers in future studies to assess the effects of landscape change on primates. Finally, to highlight the importance of adopting a landscape perspective in studies of primates, we summarize a number of hypotheses that can be tested using a landscape-scale (or patch-landscape, see below) study design. We argue that these hypotheses need to be tested in order to improve management and conservation strategies in human-modified landscapes.

The Meaning of "Landscape Perspective"

Although there are many different interpretations of the term "landscape," from an ecological point of view, a landscape can be defined as a heterogeneous land area containing a mosaic of patches or land cover types (e.g., forest patches, agricultural lands, pasturelands, vegetation corridors, and human settlements). The landscape spatial heterogeneity (or landscape structure) is thus described by its composition and configuration, where composition refers to the types and proportions of different forms of land cover across the landscape, and configuration refers to the spatial arrangement of a given landscape composition [Dunning et al., 1992; Fahrig, 2005]. Thus, in contrast to patch-scale studies, where the response variable (e.g., primate abundance, species richness, behavior) is related to attributes of the patches in which the primates are found (e.g., patch size, patch quality; Fig. 2A), a "landscape perspective" or "landscape approach" assesses the impacts of the composition and/or configuration of the landscape on individual response variables singly or as part of a multifactorial analysis (Fig. 2B,C).

There are two main types of landscape studies, as described by McGarigal and Cushman [2002]. First, in "patch-landscape studies" the response variable is measured in individual "focal" patches, and the explanatory variables include landscape composition and/or configuration information such as area of forest cover, number of patches of each habitat, and matrix quality, which can be defined using indices that relate the percentage of each land cover type within the landscape matrix to their relative ability to provide food resources or cover, as well as opportunities to disperse among food patches [see e.g., Arroyo-Rodríguez et al., 2013b; Garmendia et al., 2013]. These variables are assessed within a specified radius from each of the focal patches (Fig. 2B). Patch-landscape studies also have been called "focal patch landscape studies" [Brennan et al., 2002]. One version of the patch-landscape study evaluates the response variable not in patches but in equal-sized sample sites, with the landscape variables measured within a specified radius of these sample sites [Fahrig, 2013]. In patch-landscape studies, each data point in an analysis corresponds to

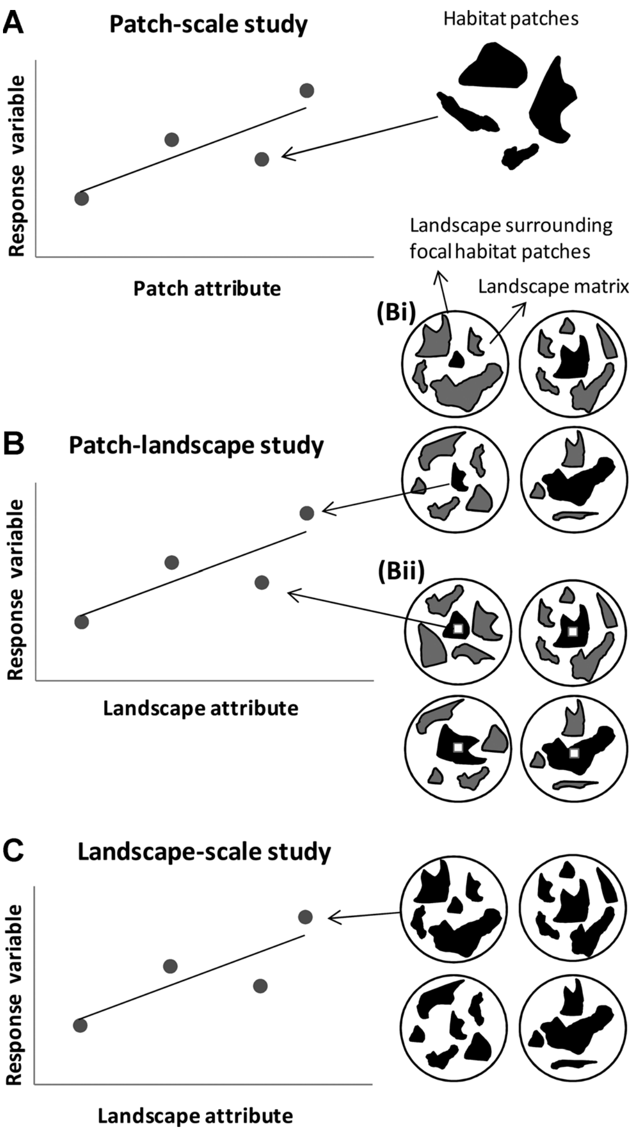

Fig. 2. Experimental designs in fragmentation studies. In patch-scale studies (**A**) individual patches are the experimental units. Response variables (e.g., population size) are related to attributes of the patches (e.g., patch size, patch isolation, and food availability). In patch-landscape studies (**B**) the response variables are measured either in widely dispersed individual "focal" patches (**Bi**: black polygons) or sample sites (**Bii**: gray squares within black polygons). In both cases, the landscape attributes (e.g., forest cover) are assessed within a specified radius (buffer) from these focal patches (Bi) or sampled sites (Bii). Finally, in landscape-scale studies (**C**) both the response and the predictor variables are measured across individual landscapes (i.e., entire patch mosaics). The response variables are measured in several sample sites (or patches) within each landscape, and are then related to landscape composition/configuration attributes of that landscape.

the response in a single patch (or sample site), along with the landscape composition/configuration attributes of its surrounding landscape (the landscape predictor variables). An important advantage of patch-landscape studies is that they are generally no more costly to conduct than patch-scale studies, if the landscape structure variables can be obtained using remotely-sensed (satellite) imagery [Brennan et al., 2002]. Secondly, in "landscape-scale studies" the response variable is measured in several sample sites (or patches) within each landscape (Fig. 2C). In this case, a single data point for analysis corresponds to the combined response data from all sample sites within a landscape, along with the landscape composition/configuration attributes of that landscape (again, the landscape predictor variables). In both study types, the unit of replication is the landscape, with the difference being that in the first case the response variable is measured in only one location within that landscape (its center).

In all cases, the most appropriate study design depends on the question to be addressed and the system studied [McGarigal & Cushman, 2002]. Patch-scale studies are particularly useful to study patch-level processes (e.g., diet selectivity), and can provide insightful information for understanding some of the mechanisms contributing to landscape-scale patterns (e.g., forest patch occupancy). In this sense, metapopulation theory [Hanski, 1999], which has been rarely tested in primate research [reviewed by Arroyo-Rodríguez & Mandujano, 2009], assesses patterns of colonization and extinction of local populations in habitat patches, and can be useful to identify habitat suitability for the long-term persistence of primate species in fragmented landscapes [e.g., Chapman et al., 2003; Swart & Lawes, 1996]. Accurately testing the impact of landscape-scale patterns and processes on species and populations requires adopting a landscape perspective.

To evaluate the effects of landscape structure on mobile organisms such as primates, the patch (or site)-landscape design is generally preferred to the landscape-scale design, for two reasons. First, the spatial extent within which the landscape affects a population (the "scale of effect" of the landscape) is related to the dispersal range of a species of interest [Jackson & Fahrig, 2012]. Therefore, landscape structure variables should be measured within the distance from a sample patch or site that corresponds to the scale of effect of the landscape (see below). For example, Eigenbrod et al. [2008] find that automobile traffic density is negatively related to the abundance of anurans, with the strongest effects being apparent at landscapes with a radius of 500 m; thus, the impact of this landscape variable (traffic density) should be assessed at this scale. This creates a problem for landscape-scale studies. In such studies, sample sites (or patches) located nearer to the edge of the landscape will be affected not only by the landscape within which the patches/sites have been studied but also by the landscape outside of that border. Therefore, for mobile species, the landscape-scale design does not accurately pair the area over which the landscape predictors are measured to the appropriate area for measuring the species response, that is, the area within which the species is expected to respond to those predictors. In contrast, this pairing is explicit in the patch/site-landscape design.

We note that this caveat may not apply in cases where populations are bounded by natural barriers (e.g., large rivers, canyons), and where these barriers are used to delineate separate landscapes in the study. However, even in such cases patch (or site)-landscape studies may be preferred over landscape-scale studies because they are generally less costly than landscape-scale studies [Brennan et al., 2002]. As argued by Arroyo-Rodríguez et al. [2013a], given the spatial scale that is relevant for primate research, and the time required to accurately sample certain variables (e.g., diet and behavior) it is difficult to sample the response variable at the landscape scale (i.e., at many sites within each landscape) or to sample a sufficient number of landscapes to conduct powerful statistical tests. Thus, a patch–landscape approach is normally the best option for assessing the effects of landscape patterns on primates [e.g., Anzures-Dadda & Manson, 2007; Arroyo-Rodríguez et al., 2013b; Thornton et al., 2011a; approach reviewed in Thornton et al., 2011b]. As mentioned above, if the landscape variables are obtained from existing spatial data (e.g., derived from satellite imagery), such a study design is not more expensive (in time and money) or more difficult than a patch-scale study, and has the added advantage that it allows the evaluation of the association between patch-scale (or site-scale) response variables and landscape-scale attributes.

Assumptions of Patch-Landscape and Landscape-Scale Studies

A basic premise of patch-scale, patch-landscape, and landscape-scale studies is that we can accurately identify and measure "habitat" according to the cover types actually used by the species under study [Arroyo-Rodríguez & Mandujano, 2009; Fahrig, 2013]. As described above, a landscape can be composed of different types of land cover. Because native vegetation is important for many species, fragmentation studies on primates usually equate habitat with native vegetation (e.g., tropical rainforest, tropical dry forest, and cloud forest), and hence, habitat usually refers to areas of primary forest, secondary forest, or more specialized habitats such as swamp forest or bamboo forest [Arroyo-Rodríguez & Mandujano, 2009]. However, all primates exploit forests characterized by a variety of microhabitats and therefore in human-modified landscapes, primates are likely to use resources from multiple cover types, such as secondary forests, forest edge, and agricultural lands [e.g., Angola black-and-white colobus, *Colobus angolensis palliates*: Anderson et al., 2007; chimpanzees, *Pan troglodytes*: Duvall, 2008;]. Thus, one needs to consider all used cover types as habitat, of varying quality (i.e., with different resources' availability and different connectivity) [see a detailed discussion for primates in Arroyo-Rodríguez & Mandujano, 2009, and a general discussion in Fahrig, 2013].

Another important premise of patch-landscape and landscape-scale studies is that landscapes are of an appropriate size, that is, that we are using an appropriate spatial scale of analysis [Fahrig, 2013; Jackson & Fahrig, 2012]. An increasing number of studies have demonstrated that the measured impact of landscape change on populations and communities depends on landscape size, and hence, landscape structure needs to be measured at the appropriate scale (called the "scale of effect") [see Eigenbrod et al., 2008; Martin & Fahrig, 2012; Smith et al., 2011]. Unfortunately, the scale of effect has not been tested for primates. There is only one study, on black howler monkeys (*Alouatta pigra*), that assesses population responses to landscape metrics measured at two spatial scales (within 100 and 500 ha landscapes). This study found that howler monkey density was more strongly affected by metrics at the smaller spatial scale, such as fragment size, than by landscape metrics measured at the 500 ha scale [Arroyo-Rodríguez et al., 2013b]. Another recent study by Thornton et al. [2011a] evaluated the relative impact of habitat loss and fragmentation on the distribution of several terrestrial mammals in Guatemala, and found that the occurrence of spider monkeys (*Ateles geoffroyi*) was positively related to the percentage of remaining forest cover in the landscape and negatively related to fragmentation (i.e., density of forest fragments in the landscape), and that these effects were particularly strong when measured within 500-ha landscapes. Thus, further studies are required to identify the scale(s) at which landscape context most strongly affects primate responses, to accurately assess the impacts of landscape structure on primates.

An additional assumption of patch-landscape and landscape-scale studies is that landscapes represent independent samples. In this sense, landscapes (i.e., buffers) should not overlap in space [Eigenbrod et al., 2011] and they should be separated by a sufficient distance to avoid spatial autocorrelation (dependency) [Pasher et al., 2013]. There are several statistical methods that can be used to test (and correct) for spatial autocorrelation between the response variable and landscape location [Dormann et al., 2007].

Two other statistical assumptions that are often violated are those associated with sub-optimal study designs, such as using only a few predictor variables from the potential range of landscape predictors and failing to account for collinearity among predictors [Eigenbrod et al., 2011]. The former is related to the lack of control of confounding factors, and the latter is associated with the lack of independence among predictor variables. Both problems can result in misidentification of relevant predictors and/or cause a switch in the sign of the inferred relationship between a species response and landscape structure [see details in Dormann et al., 2012; Eigenbrod et al., 2011]. Thus, care should be taken with study design to ensure methods are suitable for development of robust generalizations in landscape studies.

DISCUSSION

Why is a landscape perspective important in studies of primates? We hypothesize that landscape context affects primate abundance, distribution, and survivorship. To test this hypothesis, a landscape perspective is needed. If such tests support the hypothesis, then a landscape perspective will be further needed to incorporate the results in effective management and conservation strategies for primates [Fahrig, 2005].

Within this broad hypothesis there are numerous more specific hypotheses that can be tested using a landscape approach. First, it is probable that, as demonstrated in a review of fragmentation papers [Fahrig, 2003], habitat loss has larger consistent negative effects on primates than habitat fragmentation per se (i.e., the effect of the breaking apart of habitat while controlling for the effect of habitat amount). To our knowledge, however, only three studies on primates have tested this hypothesis, using a patch-landscape approach. First, Anzures-Dadda and Manson [2007] found that patch occupancy by howler monkeys (*A. palliata*) was positively related to both landscape forest cover and fragmentation (i.e., number of forest patches). Thornton et al. [2011a] found that the probability of patch occupancy by *A. pigra* was associated significantly with neither forest cover nor fragmentation (i.e., density of forest patches) in the landscape, whereas the occurrence of spider monkeys (*Ateles geoffroyi*) was positively related to landscape forest cover and negatively related to fragmentation. Finally, Arroyo-Rodríguez et al. [2013b] found that the density of *A. pigra* populations in forest patches was more strongly related (positively) to the degree of fragmentation (i.e., number of forest patches in the landscape) than to forest cover. Given such contrasting findings, further studies are required to improve our understanding on the relative effects of habitat loss and fragmentation on primates.

Testing this hypothesis is not simply an academic exercise, as the management strategies for mitigating the two threats are quite different. If the density of a given primate species is more strongly related to the loss of habitat in the landscape than its fragmentation, we should conserve as much habitat as possible, irrespective of its spatial arrangement. If species are negatively impacted by fragmentation [e.g., Thornton et al., 2011a], management actions should focus on increasing landscape connectivity, for instance by creating vegetation corridors. Alternatively, species can be positively affected by fragmentation [e.g., Anzures-Dadda & Manson, 2007; Arroyo-Rodríguez et al., 2013b]. In this case, management actions will depend on the causes of such a relationship, as the positive effects of fragmentation can be related to different processes [reviewed by Fahrig, 2003]. For example, positive effects of fragmentation have been related to increasing access to resources in edges in more highly fragmented landscapes [see Thornton et al., 2011a]. In this case, increasing edge density in the landscape (e.g., by creating vegetation corridors), would favor the persistence of certain species. However, positive effects can be related to increasing number of patches, for example, because of increasing metapopulation persistence [Hanski, 1999], or because more patches imply better access from the patches to other resources in the landscape, augmenting landscape supplementation and complementation [Dunning et al., 1992; Fahrig et al., 2011]. In this case, management actions should be focused on increasing the number of patches in the landscape. Furthermore, if the amount of particular habitats in the landscape is held constant, increasing the number of patches will reduce inter-patch distances [see Fahrig, 2003], favoring between-patch dispersal movements [Tischendorf & Fahrig, 2000], and influencing metapopulation dynamics [Chapman et al., 2003; Swart & Lawes, 1996].

A second landscape prediction that should be tested for primates is whether the response of animal and plant biodiversity to landscape spatial change depends on the amount of habitat remaining in the landscape [Andrén, 1994; Pardini et al., 2010; Villard & Metzger, 2014]. Interaction effects between habitat amount and other landscape effects (e.g., fragmentation) are unknown for primates, and hence this should be a major focus of future studies with primates. To demonstrate an interaction effect, for example between habitat amount and habitat fragmentation, one would need to show that the effect of fragmentation per se is stronger within some range of habitat amount (usually hypothesized to be the lowest range) than within other ranges [e.g., Trzcinski et al., 1999].

Related to the question of interaction effects, a topic of growing concern is the potential existence of synergistic effects among factors at the landscape scale [Ewers & Didham, 2006; Fischer & Lindenmayer, 2007]. For example, emerging infectious diseases may be a more important threat to primates in fragmented landscapes, increasing their vulnerability to extinction. However, the information on this topic is limited [but see a review for howler monkeys in Arroyo-Rodríguez & Dias, 2010]. Another synergistic outcome may result from the interaction between broad-scale climate change and habitat loss, as dispersal movements required to cope with regional climatic variation may be limited (or even interrupted) if the landscape is largely deforested [Ewers & Didham, 2006]. Fragmentation also can interact with several chronic post-fragmentation disturbances (e.g., logging, hunting), as such disturbances may be more common in landscapes that are more fragmented [reviewed by Ewers & Didham, 2006]. Thus, the maintenance of primate populations in fragmented landscapes can be determined by a complex set of patterns and processes that interact within and between scales [also see Didham et al., 2012]. Of course, testing synergistic effects by controlling collinearity represents a challenging, but achievable exercise [see empirical examples reviewed in Ewers & Didham, 2006].

Tscharntke et al. [2012] describe other relevant hypotheses of how the landscape could moderate biodiversity patterns and processes. Among them, the "landscape-moderated insurance hypothesis" is particularly relevant for primate conservation. This hypothesis postulates that landscape complexity can provide spatial and temporal insurance (i.e., higher resilience and stability of ecological processes in changing environments) [Tscharntke et al., 2012]. Evidence indicates that some patch-dwelling primates (both Neotropical and Paleotropical species) are able to supplement their food intake by using resources from the surrounding matrix, including neighboring small patches, vegetation corridors, secondary vegetation, isolated trees, and even agricultural fields [Asensio et al., 2009; Chaves et al., 2012; Estrada et al., 2006b, 2012; Pozo-Montuy et al., 2013], a process named "landscape supplementation" [sensu Dunning et al., 1992]. Landscape supplementation may be a key process for population survival in highly fragmented landscapes, and it is expected to be particularly evident in more complex landscapes. However, little is known about the ability of most primate species to move through such a matrix and feed from different landscape elements, and so far no one has tested for a relationship between landscape complexity (also called heterogeneity) and primate population or community responses [but see Anderson et al., 2007]. This assessment is particularly needed given that large-scale movements through the landscape entail not only the benefit derived from access to new types of resource but also significant costs associated with increased vulnerability to anthropogenic threats in the matrix (e.g., hunting, being hit by vehicles when crossing roads, electrocution when climbing on power lines, and predation by domestic carnivores) [reviewed in Fahrig, 2007].

What is the best scenario for the long-term survival of a primate species? Is it living in smaller isolated populations that depend on dispersal between patches or living in a larger single population within which individuals may disperse between social units without being exposed to the risks of moving through the matrix? These questions are related to the single large or several small (SLOSS) debate. Although this debate started in the 1970s [e.g., Diamond, 1975], we still have very little empirical evidence on primate responses to answer these questions. This is why we are encouraging primatologists to assess the impact of landscape changes on primate behavior, ecology, demography, reproduction, and survivorship.

CONCLUSIONS

An increasing proportion of global biodiversity, including primates, is located in human-modified landscapes. Hence, primate conservation will depend on our ability to maintain and conserve their populations in such environments. Adopting a landscape perspective will allow us to develop an understanding of the impacts of the landscape context on primates, and to use this understanding to develop effective predictive models at the landscape scale. Such models are particularly needed given that even protected areas in the world's major tropical forest regions are experiencing erosion of taxonomic diversity, including primate diversity [Laurance et al., 2012], and hence, we need to design more effective conservation programs outside these protected areas.

Primatologists face a great challenge, as to date their primary focus has been on developing a solid understanding of the biology and ecology of a small number of primate social groups or populations, through intensive long-term studies. For example, in a recent review of 100 fragmentation studies of primates, Arroyo-Rodríguez et al. [2013a] found that all were patch-scale studies, and almost 40% studied fewer than five patches (median = 6 patches). Future landscape studies addressing the important questions outlined above will require a reduction in sampling effort per group/population to allow assessment of a larger number of groups/populations located in different landscapes. This will require a significant shift in the culture of primatological research. Alternatively, primatologists should be encouraged to share their data to collate primary datasets on primates in fragments into a comprehensive database to be used in patch- and landscape-scale analyses. This is the idea of BIOFRAG (http://biofrag.wordpress.com), a new project that is looking for fragmentation effects on biodiversity in a global analysis [see further details in Pfeifer et al., 2014]. Generating a global database on primates in fragments would help primatologists to address most of the methodological problems described above.

To perform reliable landscape studies we recommend investigating as many landscapes as possible. There is no single adequate sample size for all such studies, since the sample size needed to detect a landscape effect will depend on the number of landscape variables assessed and the number of potentially confounding variables that can be controlled in the study design. Work on temperate mammals indicates that as few as 14 landscapes can provide adequate statistical power when only a single landscape variable is studied and all known potential confounding variables are controlled for through sample site selection [e.g., Rytwinski & Fahrig, 2007]. For primates, existing patch-landscape studies [Anzures-Dadda & Manson, 2007; Arroyo-Rodríguez et al., 2013b] could be used in retrospective power analyses to estimate the minimum number of sample populations needed in future studies and in estimating the effects of particular landscape variables on primate responses [see Christensen & Ringvall, 2013]. As discussed above, the need for samples in multiple landscapes also is an important reason for using the patch-landscape approach, where the primate response is measured in widely dispersed sample sites and the landscape variables are measured in the area surrounding each of the primate sample sites (Fig. 2Bii). Such sample sites need to be adequately separated to ensure independence among landscapes. We also should consider that fragmented landscapes are highly heterogeneous in terms of composition, spatial configuration, and history (e.g., economic activity, demographic and sociopolitical factors, cultural, and religious characteristics), so we need to control (or measure) the impact of these confounding factors when adopting a landscape perspective. Finally, since different response variables (e.g., patch occupancy, population size, diet, and behavior) are likely affected by landscape variables at different spatial scales, researchers also need to evaluate the scale of effect within their study system by conducting multi-scale analyses. In conclusion, although these recommendations represent a significant shift in primatological research, we expect such a shift to deliver large pay-offs in the quality of information relevant to landscape-scale protection of primate diversity.

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