

Habitat Fragmentation

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With rapid human population growth, food and biofuel production have shown a steep increase in recent decades, particularly in tropical developing countries. As a consequence, once-continuous tropical forests are being rapidly converted to fragmented landscapes, in which fragments of native vegetation are embedded in matrices of agricultural lands, cattle pastures, and human settlements. These landscapes are highly heterogeneous, and, hence, they can have different effects on biodiversity (reviewed by Fahrig 2003). Nevertheless, for primates, the available information on this topic is very scarce, as most studies in fragmented landscapes have been performed at the fragment scale, and do not assess, nor control for, the independent effects that loss of native vegetation and its subdivision (i.e., fragmentation) may have on these mammals (Arroyo-Rodríguez and Fahrig 2014). Evaluating the relative effect of fragmentation is required to design and implement effective management and conservation plans within human-modified landscapes (Fahrig 2003). This entry assesses how habitat fragmentation affects primates. To this end, it is necessary to define what habitat fragmentation is, discuss how its effects on primates should be measured, see what we know about the effects of habitat fragmentation on primates, and identify the main gaps of information on the topic.

Habitat Fragmentation and its Effects on Habitat Spatial Patterns

Habitat fragmentation is usually defined as a landscape-scale process in which a continuous habitat is broken apart into smaller pieces (fragments) of habitat scattered within a matrix of nonhabitat. This process modifies the landscape composition, that is, the types and proportions of different land covers across the landscape. For example, habitat fragmentation typically leads to the loss of habitat in the landscape. The composition of the matrix can also vary, from relatively simple and homogeneous matrices (Figure 1A–D) to highly heterogeneous ones (Figure 1E). In fact, the matrix can be composed of different elements, including riparian corridors, live fences, and isolated trees (Figure 1C), which increase the heterogeneity of the landscape.

The process of fragmentation also modifies the landscape configuration, that is, the spatial arrangement of each landscape composition (Figure 1). For example, by definition, fragmentation leads to an increase in the number (or density) of habitat fragments in the landscape. Yet, depending on the way habitat is removed, total habitat edge can be highly variable. In some cases, the remaining habitat fragments can show complex shapes (i.e., a very high perimeter to area ratio), thus increasing total habitat edge in the landscape (Figure 1D). In other cases, however, the remaining fragments show compact shapes, which reduce total habitat edge in the landscape (Figure 1E). Mean inter-fragment isolation and landscape connectivity can also be highly variable (see, for example, Figure 1A,B).

Overall, all these changes in landscape configuration and composition can have different effects on plants and animals, including primates, as these changes can determine the availability of resources in the landscape and the extent to which the landscape facilitates or impedes

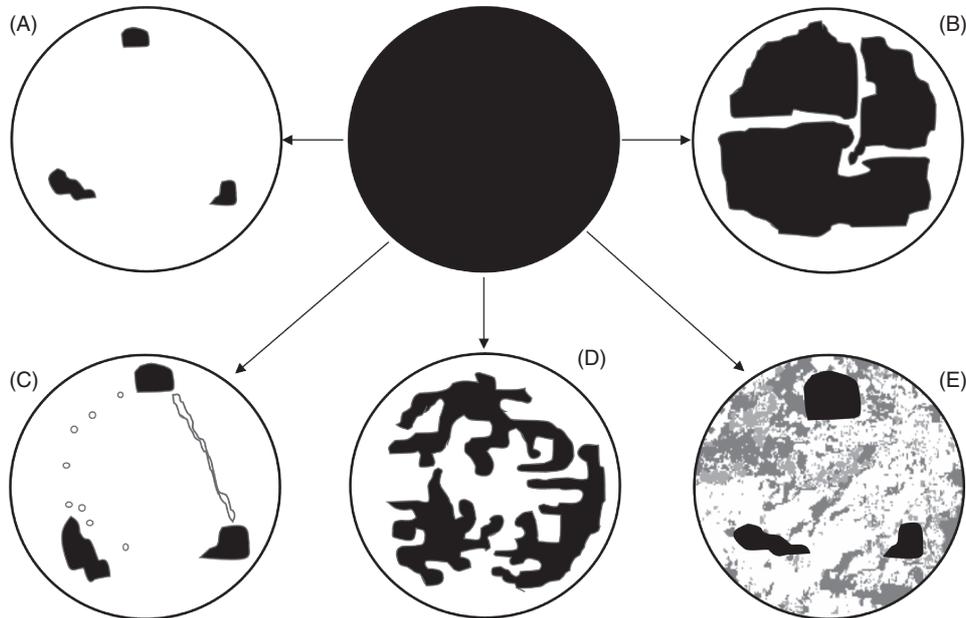


Figure 1 Five possible scenarios in which habitat loss increases the number of habitat fragments in the landscape. All landscapes (circles) show the same degree of habitat fragmentation, defined as the number of fragments (here, three), but differ notably in other aspects of landscape composition and configuration. In A–D, remaining habitat fragments (black polygons) are surrounded by the same matrix (e.g., a monoculture sugarcane plantation), whereas habitat fragments in E are surrounded by a heterogeneous matrix composed of sugarcane plantations (white), secondary forests (dark gray), and cocoa plantations (light gray). In C we also find a riparian vegetation corridor and several isolated trees in the matrix, which can be used by primates as stepping stones to move between habitat fragments. Mean interfragment isolation distance is also highly variable, as is total habitat edge. Additional examples of changes in habitat spatial patterns in fragmented landscapes can be found in Arroyo-Rodríguez et al. (2013a).

ecological flows or functionality (Arroyo-Rodríguez and Mandujano 2009; Marsh 2003; see also “Further Reading”). Nevertheless, to assess the relative effects of fragmentation per se on primates, it is necessary to test the independent effects of habitat subdivision, while controlling for the effects of other changes in landscape composition and configuration, such as habitat loss (Fahrig 2003). Such habitat subdivision can encompass the abundance or density of habitat fragments in the landscape, as well as related indices (e.g., landscape division index, splitting index, and effective mesh size; reviewed by Jaeger 2000).

How can the Effects of Fragmentation per se on Primates be Measured?

A discussion on how to measure the effects of fragmentation per se on biodiversity (e.g., Fahrig 2003) and primates (Arroyo-Rodríguez and Mandujano 2009; Arroyo-Rodríguez et al. 2013a; Arroyo-Rodríguez and Fahrig 2014) has been detailed elsewhere; hence only a brief description of some important considerations is given here. First of all, as habitat fragmentation is a landscape-scale process, a landscape perspective is required to test the impact of this factor on primates. A “landscape perspective” implies using landscapes as the independent units of observation and analysis. To this end, there are three

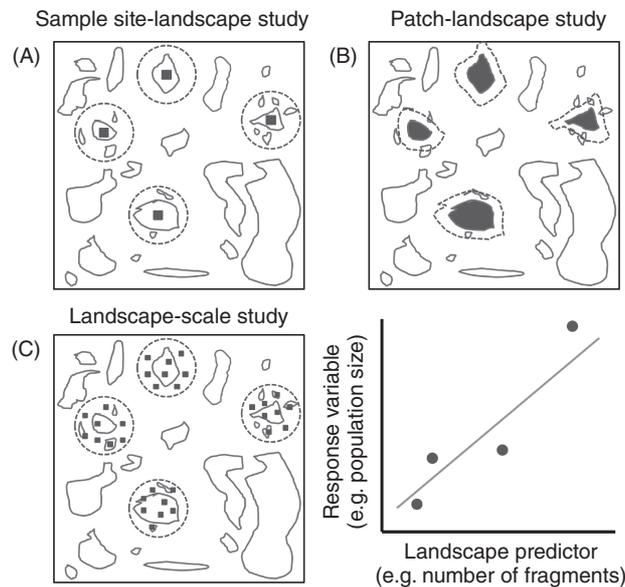


Figure 2 Study designs with a landscape perspective. Response variables (e.g., population size) can be measured in: (A) equal-sized sampling units (red squares), (B) individual “focal” fragments (red polygons), or (C) several sampling units (or fragments) within each landscape. In all cases, response variables are then related to landscape composition/configuration attributes of the surrounding landscapes (dashed circles). Note that in landscape-scale studies (C), each data point will correspond to the combined response data from all sample sites within the landscape (e.g., average, sum). Also note that there are two ways of measuring landscape characteristics in patch-landscape studies. The most common way is considering the landscape surrounding the fragment, that is out to a distance (a “buffer”) from the edge of each fragment (B). Yet, based on such a study design, landscape size and shape will vary depending on the size and shape of each fragment. As landscape configuration can vary depending on landscape size/shape, studies based on such a study design can lead to confusing results, as there is an uncontrolled effect of landscape size/shape within the analyses. In this sense, patch-landscape studies should control for the effect of landscape size/shape, for example by considering landscape attributes measured within a specified radius from the geographic center of each focal fragment (Arroyo-Rodríguez et al. 2013a). Then, depending on the research question, different landscape variables can be measured within this radius, including the percentage of the landscape covered by old-growth forest, the number/density of old-growth forest fragments, forest edge density, and the percentage of the matrix composed by each land cover type.

main types of study designs, which basically differ in the way the response variable is measured (Figure 2). In “sample site-landscape studies” and “fragment-landscape studies” the response variable is measured in only one location in the landscape (at its center); in the first case, it is measured in equal-sized sample sites (e.g., using plots, transects, or other sampling units), whereas in the second case it is measured at the fragment scale. In both cases, the explanatory variables include landscape attributes assessed within a specified radius from each of the focal

sites/fragments. Based on these study designs, each data point in the analyses corresponds to the response in a single sample site or fragment, along with the landscape composition/configuration attributes of its surrounding landscape (Figure 2). The third type is the “landscape-scale study,” in which the response variable is measured in several sample sites (or fragments) within each landscape, and, hence, a single data point for analysis corresponds to the combined response data from all sample sites/fragments within the

landscape, along with the landscape composition/configuration attributes of that landscape (Figure 2).

Although the selection of the most appropriate study design will depend on the research questions to be addressed, it is important to note that landscape-scale studies have two important caveats when applied to the study of mobile organisms, such as primates. First, within this approach, sample sites (or fragments) located nearer to the edge of the landscape will be affected not only by the landscape within which the fragments/sites have been studied, but also by the landscape outside of that border (Arroyo-Rodríguez and Fahrig 2014). Second, landscape-scale studies are generally more costly than fragment-landscape (or sample site-landscape) studies, as it is very difficult to sample the response variable at the landscape scale (i.e., at many sites within each landscape) and to sample a sufficient number of landscapes to conduct powerful statistical tests. Thus, in general, fragment-landscape and sample site-landscape approaches will usually be the best option for assessing the effects of landscape structure on primates. In fact, the costs (in time, effort, and money) for obtaining the response variables (e.g., population size, species richness, behavior) within these two approaches are similar to those invested within fragment-scale studies.

As described above, fragmented landscapes are highly heterogeneous, and, hence, to accurately test the effects of fragmentation per se on primates, we need to control for the effects of as many confounding variables as possible (e.g., habitat amount, matrix type, habitat edge density, landscape connectivity). Such control can be done through experimental design (e.g., by selecting landscapes with the same habitat amount or matrix type). Nevertheless, as it is very difficult to control for all these possible confounding factors at the landscape scale in “real-world” scenarios of habitat fragmentation, we suggest measuring, including, and hence controlling these factors in statistical models, such as multiple regression or generalized linear models (e.g., Arroyo-Rodríguez et al. 2013b). In this sense, to perform reliable landscape studies it is recommended to investigate as many

landscapes as possible. Therefore a fragment-landscape (or sample site-landscape) approach is preferred because, as indicated above, they are generally less costly than landscape-scale studies (Arroyo-Rodríguez and Fahrig 2014).

Another advantage of using a fragment-landscape (or sample site-landscape) approach is that it allows to test the scale of landscape effects on primates. The response of populations to landscape change is complex and highly variable among species and may be only evident within certain distances of a sample site or fragment. To accurately assess the impacts of landscape structure on primates, we need to measure landscape structure at the correct scale. To this end, a multiscale approach is necessary. That is, we should study different landscapes of different sizes to identify the scale(s) at which the landscape context most strongly affects primates’ responses (see Ordóñez-Gómez et al. 2015).

An important assumption in fragmentation studies is that “habitat fragments” are correctly defined in the study landscapes. “Habitat” is a species-specific concept, as it refers to the range of environments suitable for a given species; hence the definition of habitat fragments should be species-specific (Arroyo-Rodríguez and Mandujano 2009; Figure 3). Therefore care should be taken when assessing the impact of habitat fragmentation at the community level, as different species can have different habitat requirements. As most primate species inhabit forest ecosystems, almost all studies on primates in fragmented landscapes equate habitat with native forest, that is, broad vegetation types such as tropical rainforest and tropical dry forest. Thus such studies typically define habitat fragments by simply considering structural characteristics of vegetation, such as canopy continuity. Nevertheless, such definition can result in an inaccurate estimation of habitat availability and configuration, as habitat requirements can differ among species. In fact, most species can use resources from a range of forest ages and types, as well as other land cover types in the landscape, thus making it difficult to define habitat fragments in many cases. Therefore, when possible, it is more appropriate to use a definition of habitat fragments based on the specific habitat requirements of the species/population of interest, that is, use a functional definition

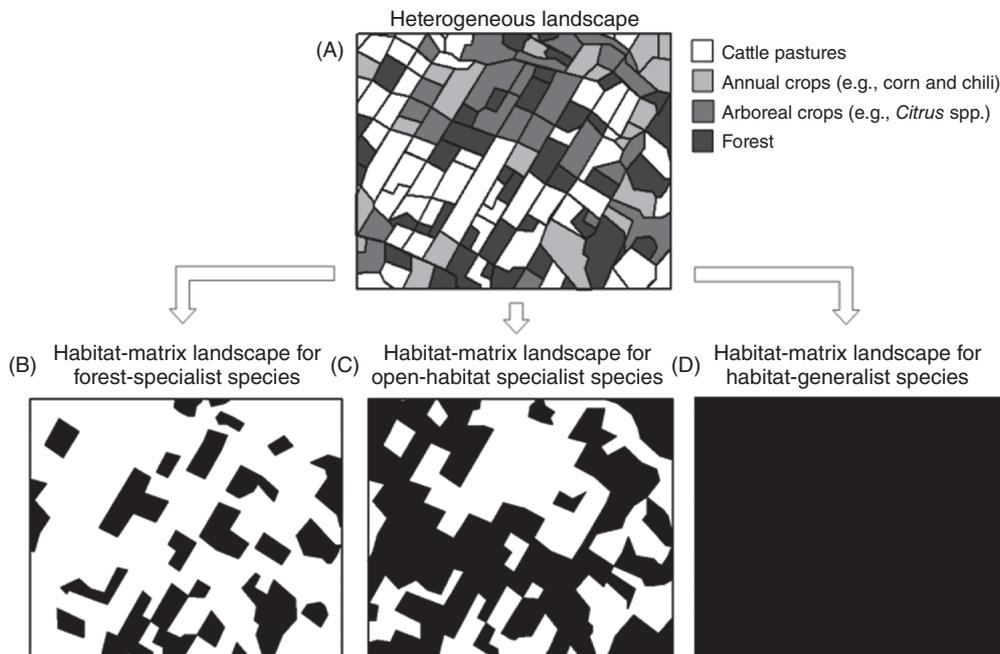


Figure 3 In heterogeneous landscapes (A), the definition of habitat fragments (black polygons in B, C, and D) to construct habitat-matrix landscapes depends on the species' habitat requirements. Note that the landscape shows a lower habitat amount and a higher degree of fragmentation for forest-specialist species (B) than for open-habitat specialists (C). The landscape is not fragmented for habitat-generalist species, as they can use all land cover classes (D).

of habitat (Arroyo-Rodríguez and Mandujano 2009).

Another important assumption in fragmentation studies of primates is that separate landscapes represent independent samples in statistical analyses. In this sense, landscapes (e.g., buffers at the appropriate scale) should not overlap in space, and they should be separated by a sufficient distance to avoid spatial autocorrelation (dependency). The independence among landscape samples can be solved experimentally, for instance, by selecting landscapes separated by geographical features (e.g., large rivers, lakes, and other natural barriers that impede the exchange of individuals between landscapes), or using statistical methods to test and correct for spatial autocorrelation (see further details in Arroyo-Rodríguez and Fahrig 2014).

Finally, to correctly assess the effects of fragmentation on primates, it is necessary to control for the influence of possible confounding factors on the response variables. To this end, a sufficient

number of predictor variables should be considered from the potential range of landscape predictors. Yet, as these predictors can be correlated among each other, it is important to test and control for collinearity problems in the multivariate models. Otherwise, we can misidentify relevant predictors in our analyses (Arroyo-Rodríguez and Fahrig 2014).

Impact of Habitat Fragmentation on Primates

Primates may be particularly vulnerable to habitat fragmentation (Marsh 2003). Unfortunately, as most studies on the topic have been performed at the fragment scale (Arroyo-Rodríguez et al. 2013a), it is still difficult to draw general conclusions on the impacts that habitat fragmentation may have on primates. Yet, by combining the results of fragment-scale studies with a few landscape-scale studies and theoretical models,

we can shed some light on the possible effects of habitat fragmentation on primates.

Fragmentation per se results in smaller habitat fragments (Fahrig 2003). Although we are still unable to identify which species are more threatened in such small remnants (reviewed by Marsh et al. 2013), we can predict that the availability of food resources is reduced in smaller habitat fragments, potentially limiting the number of individuals that a fragment can sustain. In this sense, many studies have demonstrated that the abundance of primates increases with fragment size (e.g., Anzures-Dadda and Manson 2006), but other studies have found that fragment size is a poor predictor of primate presence and abundance (e.g., Onderdonk and Chapman 2000). Some primates seem to be relatively resistant to the initial phases of disturbance, concentrating in small and isolated forest fragments (Pattanaivibool and Dearden 2002; reviewed by Marsh 2003). As a consequence, the population density of some species can increase in smaller habitat remnants, particularly in recently fragmented landscapes (e.g., Arroyo-Rodríguez et al. 2013b)—a situation that can have negative consequences for the long-term persistence of primates. In particular, higher population densities in small fragments can limit resource availability and increase inter- and intraspecific competition for resources, increasing the physiological stress of primates (Marsh and Chapman 2013). Endoparasite loads can also increase in fragments, sustaining hyperdense populations (Marsh and Chapman 2013). Such postfragmentation threats, together with the lower abundance of individuals in small remnants, can increase the probability of extinction that results from demographic and environmental stochasticity. All these population changes are, however, expected to be more pronounced in species with a greater proportion of fruit in their diet and with larger home range requirements (Boyle and Smith 2010; Marsh and Chapman 2013; but see Onderdonk and Chapman 2000), as fruit availability in small fragments is very scarce. In fact, primate species with such characteristics tend to disappear from small fragments (Boyle and Smith 2010; Pattanaivibool and Dearden 2002), thus explaining why primate species richness is often positively related to fragment size (Harcourt and Doherty 2005; Pattanaivibool and Dearden 2002).

Based on the positive relationship between fragment size and primates' species richness, Harcourt and Doherty (2005) conclude that "fragmentation of habitat clearly threatens the survival of primates." Yet fragment size is an ambiguous predictor of fragmentation effects, as both habitat loss alone and fragmentation per se results in smaller forest fragments (Fahrig 2003). Thus the effects of fragment size cannot be considered as synonymous with fragmentation effects (Arroyo-Rodríguez et al. 2013a). Furthermore, the response of primates to variations in fragment size is complex and, as stated above, it can vary widely among species (Onderdonk and Chapman 2000). In fact, some studies have reported that fragment size is not always related to primates' species richness (Harcourt and Doherty 2005). These apparently contradictory results are probably related to the lack of consideration of the landscape context in which habitat fragments are embedded.

For instance, landscape connectivity increases with greater landscape forest cover, thus increasing the total population size and facilitating interfragment movements and resource availability (reviewed by Arroyo-Rodríguez and Mandujano 2009). The presence of live fences, isolated trees, and tree crops in the matrix can also increase landscape connectivity and resource availability, particularly when such landscape elements contain food resources for primates (Arroyo-Rodríguez and Mandujano 2009). In fact, primates in fragments can supplement their diet by using resources located outside such habitat fragments, a process called "landscape supplementation." Although this process can be of key relevance for population survival in fragmented landscapes, little is known about the ability of most primate species to move through the matrix and feed from different landscape elements. Thus further studies are required to assess the relative impact of fragment size, for example, by controlling for the effects of the landscape context (Marsh et al. 2013).

The few studies that test the impact of fragmentation per se on primates demonstrate that fragmentation can have either positive, negative, or neutral effects on primates. To our knowledge, the only study that reports negative effects of fragmentation on primates indicates that the occurrence of spider monkeys (*Ateles*

geoffroyi) in fragments is positively related to landscape forest cover and negatively related to fragmentation (i.e., density of forest fragments in the landscape) in a Guatemalan tropical forest (Thornton, Branch, and Sunquist 2011). This species is highly frugivorous and has very large home range requirements (more than 100 ha); life history attributes that increase the vulnerability of species to fragmentation (Boyle and Smith 2010). Nevertheless, Ordóñez-Gómez et al. (2015) report that the number of forest fragments in the landscape is poorly related to the diet and activity pattern of *A. geoffroyi* in the Lacandona rainforest, Mexico, thus suggesting that the negative effect of fragmentation on the probability of monkeys inhabiting fragments is not mediated by changes in such behaviors, but by changes in other processes (e.g., limited dispersal patterns and lower reproductive success).

Howler monkeys are known to be a relatively tolerant taxon to habitat disturbance, as they are present in fragments where other Neotropical primate species cannot persist. The success of howler monkeys in coping with habitat degradation has been related to their capacity to feed on many different plant species, adapt their diet to the species available in the habitat, increase the amount of leaves in their diet relative to fruits, consume exotic and secondary species abundant in disturbed habitats, use small home ranges, and minimize energy expenditure by adjusting their activity patterns. All these attributes allow this species to inhabit fragmented landscapes and feed from resources present in different landscape elements, such as forest fragments, vegetation corridors, live fences, isolated trees, secondary forests, and tree crops. These feeding behaviors can explain why fragmentation per se seems to have neutral (Thornton et al. 2011) or even positive effects (Arroyo-Rodríguez et al. 2013b) on black howler monkeys (*Alouatta pigra*). Similarly, Anzures-Dadda and Manson (2007) demonstrate that fragments surrounded by a higher density of fragments have a greater probability of being occupied by mantled howler monkeys (*Alouatta palliata*) in a Mexican rainforest. This result can also be related to the fact that landscapes with the same habitat amount but with higher degree of fragmentation (i.e., with higher fragmentation per se; *sensu* Fahrig 2003) show lower mean

interfragment isolation distances, thus facilitating fragment colonization (Fahrig 2003). Other positive effects of fragmentation are summarized by Arroyo-Rodríguez and Fahrig (2014), such as increasing access to resources in forest edges in more highly fragmented landscapes, and increasing number of subpopulations, thus enhancing metapopulation dynamics and persistence.

Such apparently advantageous effects of fragmentation will depend on other aspects of the landscape pattern. For instance, we might expect negative effects of fragmentation if habitat fragments are too small to support viable populations, particularly when such populations are bounded by fragments and the matrix does not contain potential resources for primates. In contrast, through “landscape supplementation,” primates can persist in very small fragments if they are able to supplement their diet with resources located in the matrix (Arroyo-Rodríguez and Mandujano 2009). This situation is expected to be particularly evident in heterogeneous landscapes, in which different land cover types (e.g., tree crops, secondary forests) and landscape elements (e.g., isolated trees, live fences) can offer a large amount of food resources to these primates, as well as refuges and opportunities to disperse throughout the landscape. Thus the effects of fragmentation may depend on the landscape matrix, but no study to date has tested if there is an interaction effect between fragmentation per se and matrix quality. This assessment constitutes a very important avenue for future research.

Theoretical models suggest that the probability of colonization of a fragment will decline with increasing interfragment distances (e.g., Island Biogeography Theory and Metapopulation Theory). Yet the impact of fragment isolation on primates is largely unknown, as it depends on many factors, including the ability of the species to use the matrix, the spatial configuration of habitat fragments, and the placement, number, and connectivity of vegetation corridors. In fact, studies assessing the impact of fragment isolation on primates have resulted in contrasting results, with positive, negative, and neutral effects of fragment isolation commonly reported in the literature (Arroyo-Rodríguez and Mandujano 2009). In fact, in their global meta-analysis, Harcourt and Doherty (2005) did not find a significant effect of isolation (i.e., distance of

fragment from main forest block) on species richness. However, many different types of isolation metrics have been proposed, each showing stronger or weaker impacts on species. The most commonly used distance-based isolation metric in fragmentation studies with primates is the Euclidean distance between habitat fragments (Arroyo-Rodríguez and Mandujano 2009), but this metric can underestimate the effects of isolation because it does not consider the presence of very small vegetation remnants (stepping stones), live fences, and other elements (e.g., isolated trees) in the matrix, which can provide food and facilitate interfragment movements. Thus further studies assessing alternative isolation metrics, such as those based on habitat area, are required to have a better understanding of the impact that fragment isolation may have on primates. Similar to fragment size, fragment isolation is also a poor descriptor of fragmentation effects, as fragment isolation increases exponentially in landscapes with lower habitat amount, so isolation is more correctly viewed as an indicator of habitat loss than of fragmentation (Fahrig 2003). Thus inferences on the impact of fragmentation should not be made from studies analyzing the effects of fragment isolation (Fahrig 2003).

Conclusions and Future Directions

Despite the large amount of information published on primates in habitat fragments during recent decades (e.g., Marsh and Chapman 2013), most studies have been performed at the fragment scale, and have been biased towards Neotropical primates (particularly from Mexico and Brazil). Hence the hypothesis that habitat fragmentation affects primate distribution, abundance, health, and/or survivorship has not been adequately tested. Using the available literature on the topic, it seems evident that the effects of fragmentation will be highly variable among species, depending on life history traits such as home range requirements, diet, and vagility. In particular, fragmentation may have neutral or positive effects on species with smaller home range requirements, a generalist diet, and the ability to move and use resources from different land cover types, especially if the fragmented landscapes are composed of a heterogeneous

matrix and have a large percentage of habitat remaining in the landscape. In contrast, species with a specialized diet, large home range requirements, and without the ability to move and use resources from the anthropogenic matrix would be negatively affected by fragmentation, particularly when fragmented landscapes are composed of homogeneous and inhospitable matrices that limit interfragment animal movements.

The impact of fragmentation likely also depends on other landscape attributes, including landscape connectivity and percentage of habitat amount, but no study to date has tested these possible interaction effects. Thus performing additional studies at the landscape scale is imperative to accurately assess the impact of fragmentation on primates. This assessment is particularly needed for Asian and African primates, as well as for those Neotropical primates that have been less studied (reviewed in Arroyo-Rodríguez et al. 2013a). Such studies are required to improve management and conservation strategies. Complementarily, more information is needed about the ability of primates to move through the matrix and feed from different landscape elements. Such studies are needed to understand the mechanisms that contribute to the positive, negative, or neutral effects of fragmentation.

SEE ALSO: Agroecosystems; Anthropogenic Landscapes; Biological Corridors; Deforestation; Ecological Knowledge; Environmental Stress; Habitat Conservation; Hunting and Habitat Degradation; Logging

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