Landscape ecology of mammals

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Recognition of the Anthropocene epoch formally acknowledges the pervasive and increasingly dominant effects of human activities on the world's biomes. A defining characteristic of the Anthropocene is habitat conversion (land-use change) for agricultural and urbanized land uses. Within this context, landscape ecology is of critical importance as it examines the influence of spatial heterogeneity on ecological patterns and processes at spatial and temporal extents that are larger than those traditionally studied in ecology. The application of landscape ecological approaches to mammalian populations, communities, and metacommunities began in and has increased steadily since the 1990s. Non-volant small mammals or bats are often the focus of landscape studies of communities, whereas carnivores or artiodactyls are commonly the focus of population-level studies cast within the domains of conservation or wildlife management. Research on the landscape ecology of mammals has primarily been conducted in Europe and North America, but with increasing frequency has been explored on other continents. Mammalian research has contributed significantly to the development of landscape ecology, demonstrating that responses to landscape structure are often taxon-, scale-, or context-dependent. Future research should consider hierarchical approaches that are scale-sensitive, with explicit linkage to contemporary hypotheses, thereby advancing theoretical understanding and informing management and conservation action.

La declaración formal del Antropoceno como época geológica implica el reconocimiento de la extensión y magnitud de los efectos de las actividades humanas sobre los biomas. Una característica definitoria del Antropoceno es la conversión de hábitats naturales a usos agrícolas o urbanos. En este contexto, la ecología del paisaje es de importancia crítica, ya se enfoca al estudio de la influencia de la heterogeneidad espacial sobre los patrones y procesos ecológicos a escalas espaciales y temporales mayores a las tradicionalmente estudiadas en ecología. La perspectiva de la ecología del paisaje aplicada a poblaciones, comunidades y metacomunidades de mamíferos se inicia en los años noventas y hoy, se encuentra en continuo desarrollo. Los pequeños mamíferos, voladores y no voladores, han sido a menudo el objeto de estudio en ecología del paisaje a nivel comunidad, en tanto que los carnívoros o artiodáctilos se han estudiado más bien a nivel poblacional en contextos de manejo y conservación. La investigación sobre ecología del paisaje aplicada a mamíferos tuvo sus inicios en Europa y Norteamérica, y de manera paulatina se ha venido desarrollando cada vez más en otros continentes. La investigación mastozoológica ha contribuido de manera considerable al desarrollo de la ecología del paisaje, demostrando que las respuestas a la estructura del paisaje a menudo dependen del taxón, la escala o el contexto de estudio. En el futuro, la investigación en este campo deberá contemplar aproximaciones jerárquicas que sean sensibles a la escala, y abordar hipótesis actuales, contribuyendo así tanto al desarrollo teórico de la disciplina como a la aplicación del conocimiento al manejo y conservación del paisaje.

The Anthropocene is a recently recognized epoch that acknowledges the pervasive and increasingly dominant effects of human activities on the nature of the world's biomes (Monastersky 2015). The defining human activities associated with the origins of the Anthropocene include a dramatic increase in carbon emissions (climate change) and habitat conversion (land-use change) for agricultural, urban, and suburban land uses. The rates of increase in these global change drivers are inextricably linked to increases in human population size (Jiang and Hardee 2011; Krausmann et al. 2013) and increasing per capita consumption (Kastner et al. 2012). As a consequence, habitat loss and fragmentation (Mantyka-pringle et al. 2012; Haddad et al. 2015) have resulted in a considerable loss of biodiversity (Newbold et al. 2015; Betts et al. 2017) and have altered biogeographical patterns of species distributions (Chen et al. 2011; Brown et al. 2016). Indeed, the loss of biodiversity is so severe as to represent the beginning of the Earth's sixth mass extinction (Ceballos et al. 2015). Understanding how changing landscapes affect populations, communities, and metacommunities is a grand challenge of the 21st century (NRC 2001), and the study of mammals has significantly contributed to our understanding of these dynamics.

Landscape Ecology

Landscape ecology is a relatively young discipline that examines the influence of spatial heterogeneity on ecological systems (populations, communities, or metacommunities interacting with matter and energy). The discipline focuses on spatial and temporal extents that are larger than those typically studied in ecology, and explicitly addresses the importance of landscape composition (the relative proportions of different land cover types within a focal area, without reference to their location or connectivity) and configuration (the spatial arrangement of land cover types within a focal area) in determining ecological patterns and processes (Table 1; Turner 1989; Dunning et al. 1992). We use landscape structure to collectively refer to compositional and configurational aspects of landscapes. Central to landscape ecology is the concept of the habitat patch: a relatively homogeneous area (e.g., forest patch, agricultural patch) that differs from its surroundings. All metrics of landscape composition and configuration use the patch as the focal unit of measure.

Unsurprisingly, ecological studies of landscapes emerged in the late 20th century as a paradigm for the study of biodiversity, concordant with unparalleled increases in the rate of habitat conversion and fragmentation (Fahrig 2003). Humans have reshaped over 77% of the terrestrial biosphere (Ellis et al. 2010), with over 40% used directly by humans for agriculture or settlements. The remaining area (~37%) includes natural (e.g., primary or mature forest) or seminatural (e.g., secondary forest) lands embedded within a mosaic of land converted for human use (Fig. 1). These embedded natural and seminatural areas comprise more land than do pristine areas (i.e., landscapes with no human impact; ~22%), and are prominent worldwide. Consequently, the success of conservation and management of ecosystem functions and services depends on understanding the value of heterogeneous landscapes to biota and the contributions of human-modified landscapes to conservation goals (Chazdon et al. 2009; Van de Perre et al. 2018).

In general, three processes associated with landscape modification affect patterns of the abundance and distribution of species: 1) loss of native vegetation, 2) fragmentation per se (i.e., formation of isolated patches of habitat), and 3) matrix (i.e., types of habitat that surround a patch) permeability or utility (Tscharntke et al. 2012). The loss of native vegetation and matrix effects are associated with the presence and proportion of natural and anthropogenically modified land cover types, independent of their spatial arrangement (i.e., landscape composition), whereas fragmentation per se affects connectivity and spatial arrangement (i.e., landscape configuration) of resource patches (Fahrig 2003; Bennett et al. 2006). In short, the fragmentation of habitat into patches is a landscape-level process that requires multiscale studies to understand biological dynamics in time and space (Fahrig 2003; Arroyo-Rodríguez and Mandujano 2009).

Comprehensive understanding of the effects of habitat loss and fragmentation, as well as the effects of matrix habitats (e.g., successional stages of habitat regeneration, agricultural fields, human settlements) on the biota requires explicit consideration

Table 1.—Common landscape metrics (McGarigal et al. 2012), their description, and classification (composition or configuration).

| Name	Description	Metric type
Focal patch size	Area of the focal habitat patch	Composition
Mean patch size	Average area of patches of a habitat type	Composition
Percent cover	Percent of landscape covered by a particular habitat type (e.g., forest, tall grass prairie, agriculture, developed land such as roads and housing)	Composition
Shannon diversity	Diversity measure based on the relative proportion of each land cover type	Composition
Edge density	Total length of the edge of all of the patches of a land cover type or of all land covers, divided by the area of the focal scale	Configuration
Mean shape	Average ratio of patch perimeter to area for a land cover type or of all land covers	Configuration
Mean proximity	Average isolation of patches of the same land cover type, weighted by patch size	Configuration
Contagion	Dispersion and interspersion of land cover types	Configuration
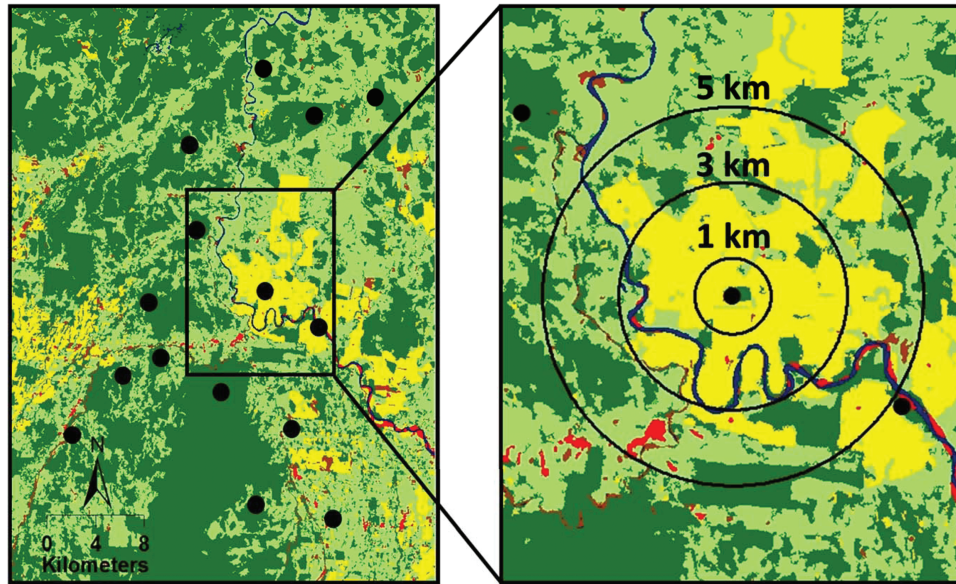
Fig. 1.—An example of sites distributed in a heterogeneous landscape subject to various forms of land use (left), and an example of multiple focal scales for evaluation of effects of landscape structure on populations, communities, or metacommunities in a focal patch (right). Black dots represent sampling locations, dark green is forest, light green is pasture, yellow is agriculture, blue is water, and red is human settlements.

of compositional and configurational characteristics of landscapes. Although patch area and isolation are important to the distribution of animals, including mammals, the quality of the matrix is of primary importance in determining interpatch dispersal and patch occupancy (Prugh et al. 2008). Consequently, improving the quality of the matrix may be a more effective conservation strategy than improving the quality of extant fragments in some circumstances. In general, there are two types of species: 1) those whose individuals primarily live within a patch, and 2) those whose individuals have large home ranges that include multiple patches and patch types (Sanderson et al. 2002). However, home range size, abundance, species composition, and species diversity of both types of species are affected by the composition and configuration of landscapes.

The popularity of investigating the relative importance of compositional versus configurational elements of landscapes was largely driven by the proposition that the amount and types of habitat in an area are a stronger influence on the abundance and distribution of species than is the spatial arrangement of those habitats (Andrén 1994). Moreover, landscape dynamics are inherently sensitive to scale because species perceive their environment at different spatiotemporal scales (Gorresen and Willig 2004; Gorresen et al. 2005; Betts et al. 2006; Ewers and Didham 2006; Smith et al. 2011; Klingbeil and Willig 2016). Consequently, a multiscale approach is necessary to ensure that the scale of response to landscape structure is included in experimental designs (Miguet et al. 2016; Fig. 1). In a pioneering study, Mönkkönen et al. (1997) used seven focal scales with radii ranging from 100 m to 10 km to investigate effects of landscape composition and configuration on the persistence of Siberian flying squirrels (*Pteromys volans*) in old-growth forests of Finland. Despite this early example of a multiscale assessment of landscape structure, the use of multiple focal

scales in landscape studies of small mammals remains uncommon (e.g., ~20 out of > 180 studies).

HISTORICAL AND GEOGRAPHICAL TRENDS IN LANDSCAPE RESEARCH

Concepts of landscape ecology emerged during the 1970s in Europe as scientists struggled to understand ecology in human-dominated environments and wished to inform land-use planning and conservation (Foreman 2015). Many foundational concepts in landscape ecology arose from the Theory of Island Biogeography (MacArthur and Wilson 1963) and were applied to habitat patches within a mainland context (e.g., Brown 1971; Terborgh 1974; Simberloff 1976; Brown and Kodric-Brown 1977; Diamond et al. 1980). Subsequently, landscape ecology as a distinct discipline crystalized in 1983 with the formation of the International Association of Landscape Ecology and its journal, *Landscape Ecology*, which debuted in 1987. Our review of the literature on the landscape ecology of mammals only considered publications that explicitly used characteristics of landscapes (i.e., estimates of habitat composition or configuration) as causative agents affecting spatial patterns of individuals, populations, communities, or metacommunities. We did not include studies that could be considered within the domain of island biogeography (patch-scale studies sensu Arroyo-Rodríguez and Fahrig 2014), which evaluated only effects of patch size or patch isolation from potential source populations. Moreover, we did not include studies (e.g., trophic cascades, habitat use, landscape of fear) that occur within the context of landscapes but that do not use attributes of landscape structure to understand responses—these generally fall within the domains of habitat selection or predator–prey dynamics (see Kelt et al. 2019; O'Connell and Hallett 2019).

We used the Web of Science to search for literature on the landscape ecology of mammals from 1983 through 2016. Our search included each possible pairwise combination that included one of seven landscape terms and one of 11 names of mammal groups. Landscape terms included "landscape ecolo*", "landscape comp*", "landscape config*", "landscape struct*", "landscape fragment*", "landscape patt*", and "landscape metri*", which represented forms of "landscape ecology", "landscape composition", "landscape configuration", "landscape structure", "landscape fragmentation", "landscape pattern", and "landscape metric". Search terms for mammal groups included "mammal*", "chiropter*", "rodent*", "insectivor*", "carnivor*", "primat*", "marsupia*", "artiodacty*", "perissodacty*", "ungulat*", and "lagomorph*", which represented forms of "mammal", "Chiroptera", "Rodentia", "Insectivora", "Carnivora", "Primates", "Marsupialia", "Artiodactyla", "Perissodactyla", "ungulate", and "Lagomorpha". We recognize that some of these taxonomic names are no longer in use, but these were valid during most of the time frame of the literature search and the search terms were abbreviated to detect common name representations that remain in use (e.g., marsupials, insectivores). This search returned 3,324 publications. We subsequently reviewed the content of each entry to identify those that represented research corresponding to our definition of "landscape ecology". This narrowed the list to 456 publications. Web of Science searches the full text of each document, resulting in inclusion of publications that do not focus on mammals or landscape ecology (e.g., a work could be included in the original search results if the text referred to "landscape ecology" once in the introduction and had "mammal" in the title of a reference). For this reason, we executed a detailed examination of all references returned by the search to retain only those that fulfilled our well-specified criteria.

The early literature on landscape ecology was dominated by considerations of concepts, scales, spatial patterns, metrics, models, and approaches to research that would ultimately define the discipline (Foreman 2015). It was not until the late 1990s that landscape ecology was commonly employed to study empirical effects of habitat composition and configuration on spatial patterns of mammals (Fig. 2). Interest in the landscape ecology of mammals has increased steadily since the inception of the discipline. Non-volant small mammals (127 studies on rodents, 21 on eulipotyphlans, and 37 on marsupials) and bats (66 studies) were frequently used as model systems for basic research on the landscape ecology of communities, whereas carnivores (136 studies) and artiodactyls (109 studies) were commonly the focus of population-level studies with a focus on conservation or wildlife management (Fig. 2). Nonetheless, the study of nearly every mammalian group, including xenarthrans and proboscideans, has benefited from the application of concepts and methodologies from landscape ecology. Research on the landscape ecology of mammals has primarily been conducted in Europe (149 studies) and North America (186 studies), which is not surprising as landscape ecology developed first in Europe and then grew into its modern form based on collaborations between European and North American ecologists (Fig. 3; Foreman 2015). Since the turn of the century, the landscape ecology of mammals from Asia, Africa, and Central and South America has been studied with increasing frequency.

Mammalian Review

An exhaustive review of the literature on the landscape ecology of mammals is beyond the scope of this article. Instead, we selectively and briefly highlight aspects of research on mammalian groups that illustrate past contributions to ecological understanding that have arisen because of an explicit focus on landscape composition and configuration.

Marsupialia

Arboreal marsupials in Australia require native habitats such as *Eucalyptus* forest. Pine plantations that occur in landscapes with eucalypt forests are not suitable habitat for any arboreal marsupial (Lindenmayer et al. 1999b). In heavily forested areas, including plantations, the most important predictor of the presence of arboreal marsupials, such as koalas (*Phascolarctos cinereus*), yellow-bellied gliders (*Petaurus australis*), and greater gliders (*Petauroides volans*), is the amount of native forest (Lindenmayer 1999a; Incoll et al. 2001; McAlpine et al. 2006). However, when forests are fragmented by conversion to urban or residential land, rather than to pine plantations, configuration of patches, proximity to eucalypt forest, and proximity to roads are important predictors of koala presence (McAlpine et al. 2006). Moreover, squirrel gliders (*Petaurus norfolcensis*) living in interior forest have significantly larger home ranges compared to individuals living near roads or residential areas (Brearley et al. 2011). In combination, these results suggest that plantations facilitate dispersal of arboreal marsupials among patches, even if such habitats cannot support populations on their own. Similarly, matrix attributes are important determinants of terrestrial mammal species richness in Australian forest fragments comprising nine small-to-medium-sized mammal species and three medium-to-large-sized macropod species. Specifically, intensity of human development in the matrix had a strong negative effect and structural complexity of matrix vegetation had a strong positive effect on species richness (Brady et al. 2011).

Chiroptera

Bat populations and communities have qualities that make them ideal for studying long- and short-term consequences of habitat loss and fragmentation. Bats are highly mobile and may travel long distances between roosts and foraging sites, making them efficient seed dispersers, pollinators, and predators of insects and small vertebrates (Findley 1993; Altringham 1996). Moreover, most bats are "landscape species" because individual home ranges include ecologically heterogeneous areas (i.e., individuals use multiple patch types in a landscape). In addition, bats comprise many foraging guilds (frugivores, nectarivores, carnivores, insectivores, sanguinivores, and
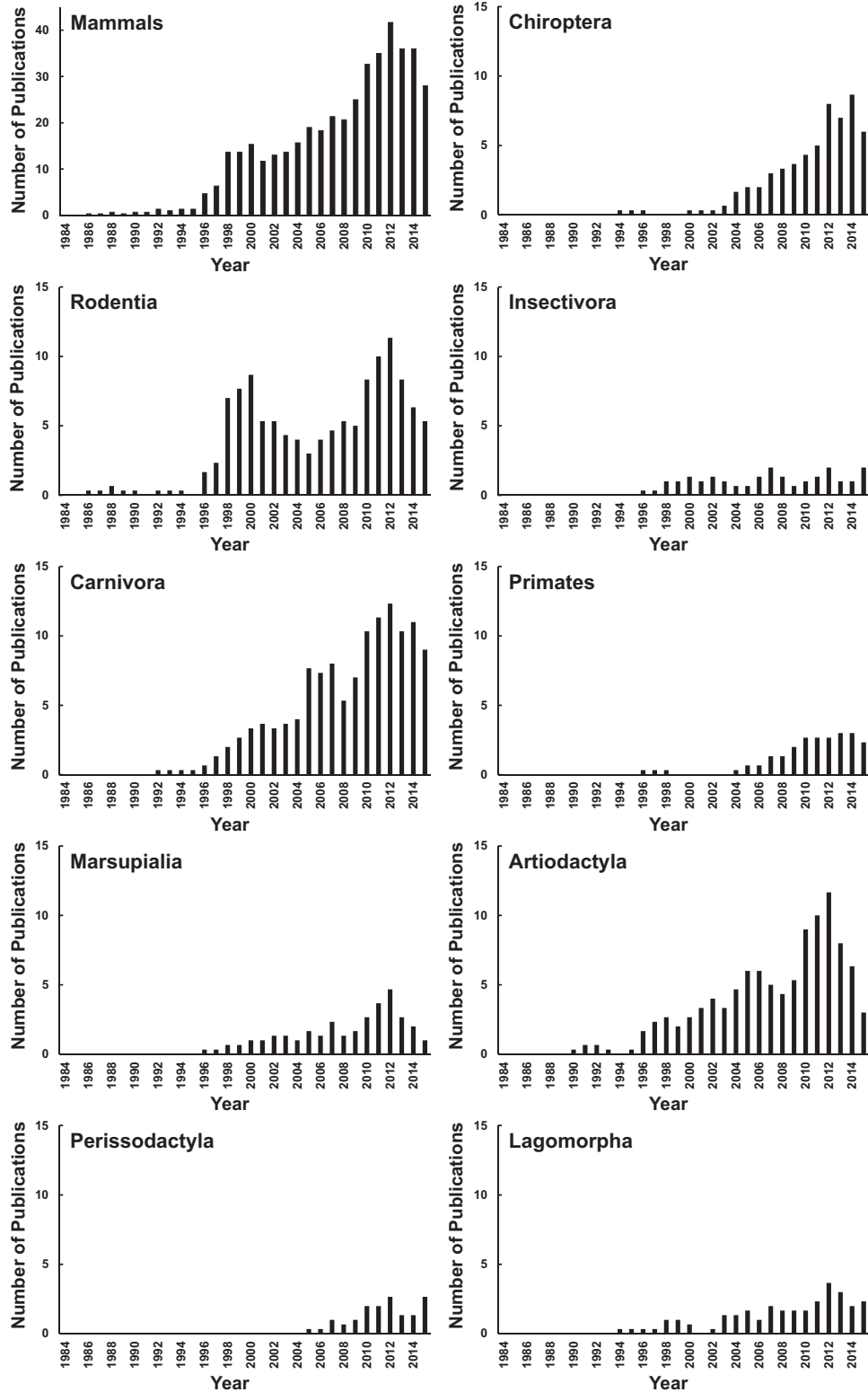
Fig. 2.—Running 3-year average (e.g., value for 1984 is the average number of publications for 1983, 1984, and 1985) for publications on mammalian landscape ecology from 1983 to 2016 for all mammals, and separately for each of nine groups of mammals.

omnivores), providing many ecosystem functions and services. For example, bats are the sole or primary agents of pollination or seed dispersal for many early and mid-successional plant species (Galindo-González et al. 2000), promoting secondary succession and regeneration of disturbed areas (Gorchov et al. 1993), especially in the tropics, suggesting that use of landscapes by bats may influence temporal changes in landscape structure. Early studies of landscape ecology of bats primarily
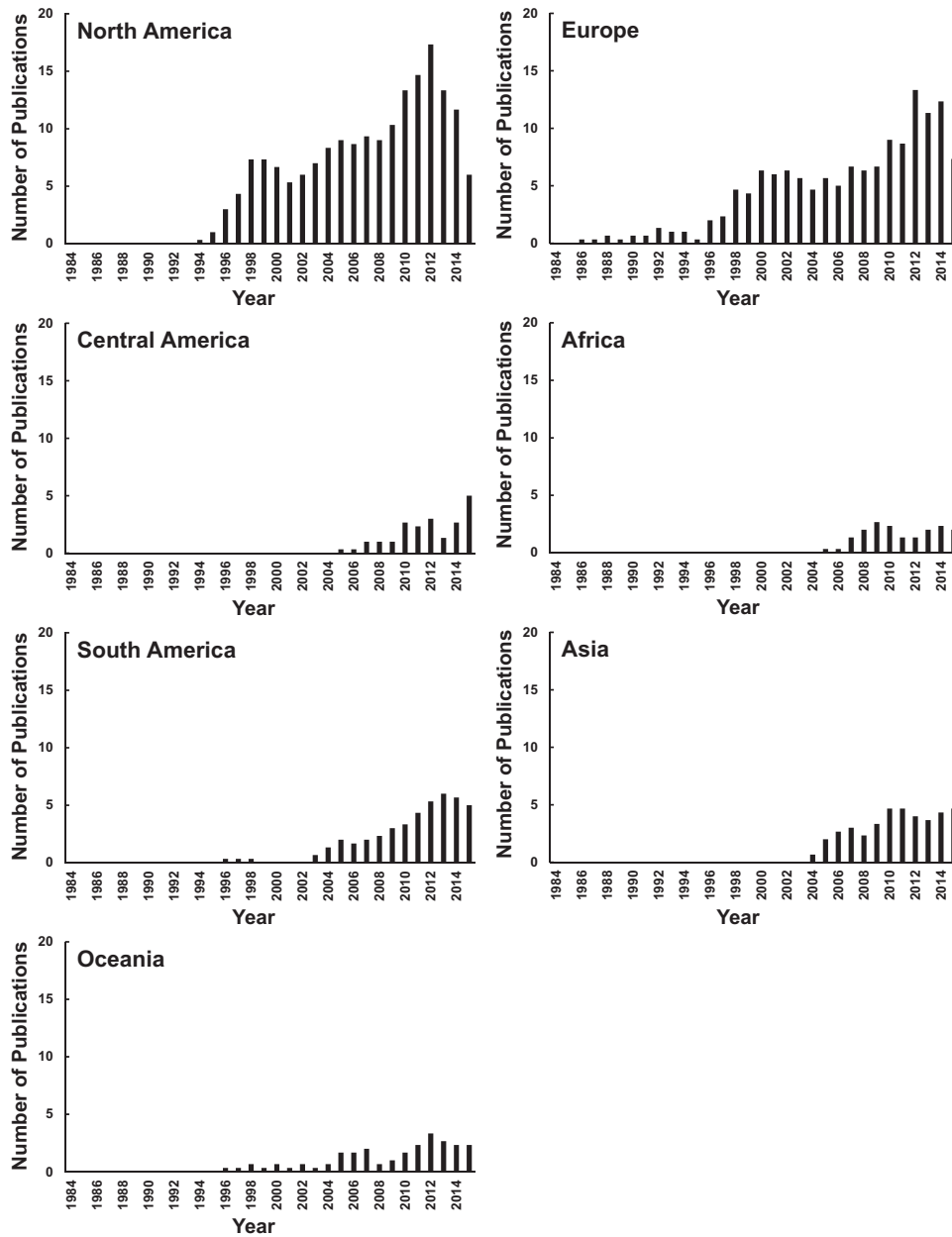
Fig. 3.—Running 3-year average (e.g., value for 1984 is the average number of publications for 1983, 1984, and 1985) for publications on mammalian landscape ecology from 1984 to 2015 for each of seven biogeographic regions.

focused on concerns associated with fragmentation of tropical forests (e.g., Cosson et al. 1999; Schulze et al. 2000; Estrada and Coates-Estrada 2002; Faria 2006) and generally emphasized the effects of forest area and isolation, essentially employing an island biogeographic approach that ignored effects of the surrounding landscape matrix. However, more recent studies have evaluated the importance of all habitat types and their spatial arrangements (Meyer et al. 2016).

Flying through fragmented landscapes.—Evidence from studies on moderately fragmented, lowland Amazonian Forest in Peru (Klingbeil and Willig 2009, 2010) and from highly fragmented Atlantic Forest in Paraguay (Gorresen and Willig 2004; Gorresen et al. 2005) suggests that species interact with their environment at multiple spatial scales. Moreover, species-,

guild-, and season-specific responses of phyllostomids were identified in Amazonian landscapes (Klingbeil and Willig 2009, 2010). During the dry season, abundances of frugivores responded primarily to variation in landscape composition (i.e., forest cover), whereas configurational metrics elicited the strongest responses during the wet season. In contrast, gleaning animalivores responded to landscape configuration during the dry season and to landscape composition during the wet season (Klingbeil and Willig 2010). In regions with tropical dry forest, frugivore abundance responds to riparian forest cover, whereas nectarivore abundance responds to dry forest cover (Avila-Cabadilla et al. 2012). In the Lacandona Rainforest of southern Mexico, abundance and diversity of frugivorous bats that forage in the canopy increase with cover of old-growth forest, whereas

abundance and diversity of frugivorous bats that forage in the understory increase with cover of secondary forest (Arroyo-Rodríguez et al. 2016). Each of these examples of season- and guild-specific responses to landscape structure likely are associated with seasonal and spatial variation in the abundance and diversity of foods as well as with energetic constraints associated with reproduction (Klingbeil and Willig 2010; Avila-Cabadilla et al. 2012; Arroyo-Rodríguez et al. 2016). Indeed, ecological function is associated with the form of response of phyllostomid bats to habitat fragmentation (Farneda et al. 2015). In general, body size and trophic level are the best predictors for sensitivity to habitat fragmentation; primary consumers often respond positively to fragmentation (i.e., increase in abundance), whereas secondary or tertiary consumers respond negatively (i.e., decrease in abundance) to fragmentation.

In highly fragmented Atlantic Forest, forest cover, patch size, and patch density were most strongly associated with variation in species abundances of phyllostomids. Phyllostomid abundances and species richness are commonly greatest in moderately fragmented landscapes (Gorresen and Willig 2004; Castro-Arellano et al. 2007; Willig et al. 2007). However, in regions with extensive tracts of undisturbed forest, responses of Neotropical bats to landscape structure can be highly species-specific. For example, abundances of 13 of 24 phyllostomid species were associated with landscape composition during the dry season; however, no measure of diversity (richness, evenness, dominance, rarity, and diversity) was associated with landscape composition (Klingbeil and Willig 2009). Diversity of bats of lowland Costa Rica was affected by landscape composition (patch density, pasture cover) during the dry season, but was unrelated to either landscape configuration or composition during the wet season (Cisneros et al. 2015a). However, functional diversity of lowland Costa Rican bats exhibited complex relationships with aspects of landscape composition (negative responses to forest cover, positive responses to pasture cover, positive responses to habitat diversity) and configuration (positive responses to proximity, negative responses to nearest patch). Nonetheless, the greatest diversity of bats, from abundance, functional, and phylogenetic perspectives, generally occurred in landscapes with high habitat diversity and large forest patches (Cisneros et al. 2015a).

In Neotropical forests, the area and configuration of old-growth forest are not the only important factors that affect the abundance or diversity of nectarivorous or frugivorous bats (García-Morales et al. 2013; Cisneros et al. 2015a). These bats forage on plants that commonly occur in early-successional forests or along forest edges. As such, a moderate amount of forest loss and fragmentation typically has a positive effect on these populations and communities (Willig et al. 2007; García-Morales et al. 2013). This has been observed in tropical rainforest (e.g., García-García and Santos-Moreno 2014; Arroyo-Rodríguez et al. 2016) and in tropical dry forest (Bolívar-Cimé et al. 2013) landscapes. Some frugivorous and nectarivorous Neotropical bats that are secondary forest or edge area specialists may now be more abundant than during pre-Columbian times, as they are well adapted for human-modified

landscapes. In contrast, gleaning insectivorous, aerial insectivorous, and carnivorous bats prefer well-preserved forests rather than disturbed sites (García-Morales et al. 2013), likely because disturbed habitats do not provide sufficient resources for members of these guilds to countermand the increased risk of predation while traversing open habitat (Presley et al. 2009).

Urban and suburban landscapes.—In habitats that have been highly fragmented by anthropogenic activities for centuries, some bats have adopted novel foraging behaviors to take advantage of resource distribution in human-dominated landscapes. In Luxembourg, greater horseshoe bats (*Rhinolophus ferrumequinum*) and Geoffroy's bats (*Myotis emarginatus*) prefer semi-open, traditional farmland habitats that have complex physical structure comprising orchards, pastures, and parklands compared to large patches of deciduous forests that historically covered the region (Dietz et al. 2013). The activity of these species is concentrated in areas of higher habitat diversity, with foraging behavior that takes advantage of resource availability and distribution associated with human activities. For example, *M. emarginatus* frequently preys on arthropods in cowsheds, and sometimes forages exclusively in these structures throughout the night (Dietz et al. 2013). Similarly, the gray-headed flying fox (*Pteropus poliocephalus*) established a colony in the middle of the Melbourne metropolitan area (Australia) in 1986, and the size of the colony has continued to increase over time (McDonald-Madden et al. 2005). These bats forage throughout the urban area on many plant genera that do not occur naturally in the region, essentially making use of human-planted resources that are widely distributed in a fragmented landscape. These bats are effectively "urbanized" (McDonald-Madden et al. 2005).

In the Sydney metropolitan area (Australia), bat activity is greater, but species richness is lower, than in nearby national parks (Basham et al. 2011). Species presence was most commonly associated with the amount of bushland and density of trees within 3 km of a site, whereas species richness was best predicted by area of bushland, tree hollow abundance, and average tree diameter. Species composition was different between urban areas and nearby forests (Basham et al. 2011). Suburban bat assemblages resemble those of forests rather than those in urban areas, likely due to the large number of trees in the suburbs that act as corridors for movement between suburban areas, forest remnants, and adjacent national parks. Importantly, the quality of the matrix (i.e., tree density) has a substantial effect on differences in bat activity, diversity, and composition between urban and suburban areas of Sydney. Nonetheless, urban areas may provide important roosting habitat in regions of intense agricultural activity, as natural roosting options may no longer exist in the surrounding landscape (Luck et al. 2013). However, the provisioning of such roosting habitat may have negative consequences to humans. The frequency of Indian flying fox (*Pteropus giganteus*) roosts in Bangladeshi villages increases with increasing forest fragmentation in the surrounding landscape (Hahn et al. 2014). *Pteropus giganteus* is a reservoir for Nipah virus, and its habit of roosting in human population centers has been linked to outbreaks of Nipah virus in central and northwestern Bangladesh (Hahn et al. 2014).

In general, urbanization has a negative effect on bat activity, abundance, and diversity (e.g., Fabianek et al. 2011; Hale et al. 2012; Luck et al. 2013). This is true on Montréal Island (Canada), where increasing urbanization has had a negative effect on bat activity and abundance (Fabianek et al. 2011). However, some species (e.g., *Eptesicus fuscus*, *Lasiurus cinereus*) use highly urbanized areas if suitable natural habitats or green spaces (parks, golf courses) are nearby. In an extensive urbanized area in the United Kingdom, all bat species responded negatively to urban density (Hale et al. 2012). However, the composition and structure of the urban areas mitigated these negative effects, suggesting that land-use planning and management of matrix quality to create tree networks may improve the resilience of some bat populations to urbanization. In general, species adapted to open areas are less affected by urbanization (Luck et al. 2013), whereas forest species rely more heavily on tree density and riparian corridors to support urban or suburban populations.

Roost locations in fragmented landscapes.—Landscape structure can limit suitable roost locations for bats. For example, red bats (*Lasiurus borealis*) in the eastern United States prefer roost locations in mature forests that are close to open water, riparian habitat, and forest trails, but roost away from roads, agricultural fields, pastures, or urban areas (Limpert et al. 2007). For vespertilionids in the southeastern United States, roost locations are associated with landscape characteristics at small spatial scales, exhibiting positive relationships with loblolly pine (*Pinus taeda*) forests, but negative associations with mixed pine-hardwoods or with immature pine forests (Perry et al. 2008). In some situations, different kinds of roosts (e.g., nursery roosts versus male roosts) are associated with different parts of the landscape. Nursery roosts of Daubenton's bat (*Myotis daubentonii*) occur in areas with more forest and open water, which represent better foraging habitats, compared to the locations of roosts used by males. This likely represents intraspecific competition for high-quality roost locations, with breeding females being dominant and defending favorable areas to increase offspring survival (Encarnação et al. 2005). Roost selection by the lesser horseshoe bat (*Rhinolophus hipposideros*) is based on landscape characteristics at a small spatial scale, as this species typically roosts in buildings that are close to forested areas (Tournant et al. 2013). However, the locations of maternity roosts are dependent on functional connectivity at larger spatial scales that facilitate travel among roost locations. Even the selection of overwintering roost locations can be affected by the surrounding landscape. In Poland, abundance and diversity of winter roosts were positively associated with amount of forest cover within 1 km as well as with forest proximity (Lesiński 2009).

In an analysis of over 1,100 roost locations throughout the United Kingdom, roosts were most associated with proximity to forest, even for small forest patches (Boughey et al. 2011). In addition, livestock pastures were positively associated with roost locations, as these habitats have large populations of aerial insects compared to crop lands. In addition, roost locations were positively associated with amount of hedgerow. Linear elements, such as hedgerows or forest edges next to pasture or row crops, are important foraging habitat and dispersal corridors for insectivores in fragmented landscapes of Europe (e.g., Lundy and Montgomery 2010; Boughey et al. 2011; Haceková et al. 2014). Maintenance of these landscape features is important to enhance connectivity among forest patches and to maintain habitat diversity in landscapes.

Primates

Landscape connectivity and conservation.—Habitat loss, degradation, and fragmentation represent eminent threats to primate conservation. Nonetheless, a landscape perspective is rare in the primatological literature (Arroyo-Rodríguez and Fahrig 2014). Arboreal primates are at risk in changing landscapes as these mammals require trees and forest patches with particular characteristics to meet food, refuge, resting site, and reproductive needs (Pozo-Montuy et al. 2011). As primate habitat is lost, remnant populations are increasingly isolated in low-quality habitats, enhancing the likelihood of local extinction. Indeed, most fragments in which primate research is currently conducted are thought to be too small to maintain populations over the long term (Arroyo-Rodríguez and Mandujano 2009), making the incorporation of a landscape perspective into primate conservation plans of paramount importance (Arroyo-Rodríguez and Fahrig 2014).

Understanding how landscape connectivity affects the movement of individuals among habitat patches is critical to effective primate conservation (Estrada et al. 2012). However, this remains a challenge as structural connectivity (i.e., the physical arrangement of habitat patches) of the landscape may not accurately reflect the functional connectivity of the landscape (i.e., movement of individuals among habitat patches). For example, over a 23-year period (1987–2010) functional connectivity among gorilla (*Gorilla gorilla*) populations decreased by more than twice as much as structural connectivity (Imong et al. 2014). Consequently, a focus on structural connectivity could underestimate the negative effects of increasing physical isolation on gorilla populations.

In tropical areas (e.g., Indonesia, Sumatra), monospecific wood plantations are rapidly replacing natural forests, threatening local and regional biodiversity. Inclusion of wildlife corridors in landscape designs may mitigate effects of fragmentation on biodiversity loss (Nasi et al. 2008). In Sumatra, a well-connected network of natural forest corridors in landscapes dominated by monospecific wood plantations effectively maintains primate diversity compared to plantations that lack such corridors (Nasi et al. 2008). In southeastern Mexico, the ability of black howler monkeys (*Alouatta pigra*) to disperse among forest patches is contingent on the quality of matrix habitats (Pozo-Montuy et al. 2011), with *A. pigra* found most often in matrix habitats that include isolated trees, living fences (e.g., tree lines, hedge rows), *Eucalyptus* plantations, and orchards. In such cases, the quality of the matrix may be critical for long-term persistence of populations. In addition, the importance of matrix quality to the connectivity of primate populations and communities in forest fragments likely explains why traditional

estimates of fragment isolation have typically been ineffective predictors of primate demographics (Arroyo-Rodríguez and Mandujano 2009).

Patch size, patch shape, and spatial scale.—Patch size is the most important landscape characteristic for many primates. In southern Amazonia, patch size is the most common indicator of occupancy for many species as well as the primary determinant of species richness (Michalski and Peres 2005). The barbary macaque (*Macaca sylvanus*) lives in large social groups and persists in fragmented landscapes with an inhospitable agricultural matrix (Ménard et al. 2013). Population density increases with patch size, but has no relationship with patch shape, isolation, or connectivity. Populations in small patches go extinct and are not rescued because macaques do not cross agricultural habitats to disperse among forest patches (effective dispersal requires an entire social group to move between patches). Even when group fission occurs, both resultant groups remain in the same patch. Movement among patches is inhibited by the strong philopatry of female macaques, cohesiveness of groups, and reliance on mature forests with a sufficient number of large trees for the entire group to sleep or escape danger. Importantly, the necessary corridors for dispersal do not exist. This suggests that *M. sylvanus* likely will go extinct as human pressure on mature forests reduces the size and number of habitable patches (Ménard et al. 2013).

The West-African chimpanzee (*Pan troglodytes verus*) is one of the most endangered primates in the world because of anthropogenic habitat loss. Chimpanzees prefer old-growth forests, but their populations have continued to decline despite an increase in old-growth forest cover during the past 30 years. This indicates that increasing forest cover alone will not be an effective conservation strategy. An analysis of habitat use that considered compositional, configurational, and functional aspects of landscapes concluded that chimpanzees preferred old-growth patches with complex shapes and a high edge-to-area ratio (Torres et al. 2010). Importantly, forest edge provides most of the food resources for *P. t. verus* and is a habitat in which they spend a considerable amount of time foraging (Tweheyo et al. 2005). In contrast, Mexican mantled howler monkeys (*Alouatta palliata mexicana*) exhibit responses to forest loss and fragmentation that are closer to what one would expect for a forest species (Arroyo-Rodríguez et al. 2008). More specifically, forest patch occupancy increases with patch size, decreases with patch shape irregularity (i.e., more edge habitat per unit area), and increases with distance to human settlements.

The golden-headed lion tamarin (*Leontopithecus chrysomelas*) is endemic to Atlantic Forest, one of the most threatened tropical forests in the world. Both forest edge and interior forest habitats are important for populations of *L. chrysomelas*, which use many forest types, including degraded forests (Raboy et al. 2010). Unlike the chimpanzee, which frequently crosses nonforest habitats to move among forest patches, *L. chrysomelas* rarely traverses non-forested habitats. This behavior is corroborated by landscape analyses that find no relationship between *L. chrysomelas* and patch isolation; any distance between forest patches is an effective barrier to dispersal (Raboy et al. 2010). Importantly, in each of these examples, a landscape approach was required to understand the implications of habitat loss and fragmentation on primate populations, as well as to design effective conservation strategies.

The appropriate spatial scales to assess responses of primates to landscape composition and configuration are largely unknown (Arroyo-Rodríguez and Fahrig 2014). Identifying the appropriate scales of effect can be challenging for species with large home ranges or complex behaviors. For primates, responses to landscape features are generally species-specific, and different spatial scales may be required to evaluate different aspects of ecology for the same species. For example, the scale of effect differs for aspects of diet (fruit, leaves, wood) and behavior (e.g., time spent resting, feeding, or traveling) of spider monkeys (*Ateles geoffroyi*) in Mexico (Ordóñez-Gómez et al. 2015).

Carnivora

Although terrestrial species of Carnivora generally are members of the same functional group (i.e., have primarily carnivorous diets), the order exhibits a variety of responses to habitat loss and fragmentation. Understanding of landscape effects on carnivore ecology is evident in an extensive body of work on at least eight families (i.e., Mustelidae, Felidae, Canidae, Ursidae, Procyonidae, Mephitidae, Herpestidae, and Viverridae) from most biogeographic realms (i.e., Nearctic, Palearctic, Neotropical, Afrotropical, Indomalaysian, and Australasian). Nevertheless, this research has mostly focused on mustelids (25.5% of studies), felids (25.5% of studies), or canids (24% of studies), with most of the research occurring in the Nearctic (62.2% of studies), Palearctic (16% of studies), or Neotropical (13.4% of studies) regions. Population-level responses to landscape modification is the most pervasive theme, which often involves other large mammals (e.g., ungulates) that are easily surveyed using camera-trap technology (Ahumada et al. 2011; Garmendia et al. 2013; Magioli et al. 2016). Landscape studies of carnivores have contributed significantly to the development of theory in community ecology as well as to the advancement of conservation and management practices.

Boom or bust in human-modified landscapes.—The responses of carnivores to habitat loss and fragmentation differ greatly, with some species being highly sensitive to human land uses and some being generalists that thrive in landscapes with moderate amounts of human land use. In general, large-bodied species are most sensitive to habitat loss and fragmentation, as these species typically require expansive areas of contiguous habitat because of large home ranges and low population densities (Crooks 2002). In the Atlantic Forest and Cerrado of Brazil, species richness of mammal communities in large reserves was similar to that in habitat fragments; however, large seed dispersers, such as the southern muriqui (*Brachyteles arachnoides*), tapirs (*Tapirus terrestris*), and white-lipped peccaries (*Tayassu pecari*), as well as top predators, such as jaguars (*Panthera onca*), were absent from fragmented landscapes (Magioli et al. 2016), suggesting that the loss of important

ecosystem functions may occur with increasing fragmentation, even when no loss of species richness is apparent. Similarly, in the Lacandona Rainforest of Mexico, jaguars were recorded exclusively in large continuous forest (Garmendia et al. 2013). In Nearctic regions, densities of brown bears (*Ursus arctos*) declined with increasing forest edge density, decreasing mean forest patch size, and increasing densities of human developments and roads (Popplewell et al. 2003; Suring et al. 2006).

In addition to large carnivores, some species of small, specialized carnivores, such as martens (*Martes martes*, *M. americana*) and spotted skunks (*Spilogale* spp.), are highly sensitive to human land use (Crooks 2002; Lesmeister et al. 2013). For example, American martens (*M. americana*) establish home ranges in areas comprising > 60% forest cover and actively avoid crossing deforested areas in logged landscapes, regardless of increased foraging effort necessitated by staying in forested habitats (Cushman et al. 2011). Similarly, fishers (*Pekania pennanti*) establish home ranges in landscapes with large patches of mature forest, and with small amounts of open areas (e.g., > 50% connected mature forest patches with < 5% open areas—Sauder and Rachlow 2014). These strict aversions to habitat loss and fragmentation have consequences for population viability, as gene flow among populations of specialized carnivores is inhibited by anthropogenic land cover types and roads (Ruiz-González et al. 2014). This leads to increased risk of inbreeding depression and local extirpation.

In contrast to species affected negatively by human land use, medium-sized generalist carnivores (e.g., procyonids, canids) typically respond positively to increases in landscape diversity and thrive in areas with a mix of natural and human-dominated habitats (Oehler and Litvaitis 1996; Crooks 2002; Pita et al. 2009). For example, raccoons (*Procyon lotor*) increase in abundance with increasing cropland cover, density of forest edges, and water sources (Dijak and Thompson 2000; Chamberlain et al. 2007). Similarly, abundances of cats, foxes, and badgers exhibit positive relationships with cover of *Eucalyptus* and pine forest plantations in Mediterranean landscapes (Pita et al. 2009). Agricultural land may provide resources for carnivores directly via the crops themselves, and indirectly by supporting larger prey populations. In agriculturally dominated landscapes, adult black bears (*Ursus americanus*) without cubs supplement their diets considerably with crops (Ditmer et al. 2016). In Queensland, the frequency of occurrence of two invasive predators (i.e., *Felis catus* and *Vulpes vulpes*) increased in landscapes with cereal crops intermixed with forest patches because of increased prey populations that feed on grain (Graham et al. 2012). These opposing responses to habitat conversion may affect prey species via predator release or via intensification of predation rates. Consequently, responses of carnivore communities to landscape structure can result in trophic cascades with important repercussions for conservation and land management (Duffy et al. 2007).

Landscape composition and configuration.—A debate about the relative influence of habitat loss versus fragmentation characterizes landscape ecology (Villard and Metzger 2014). Understanding how each of these aspects of landscape structure

affect populations and communities can guide conservation strategies in terms of managing for habitat quality, landscape configuration, or matrix composition. Recent theory posits that habitat amount (measured by landscape composition) is most important when the landscape comprises large amounts of suitable habitat above a "fragmentation threshold" or when the amount of suitable habitat drops below an "extinction threshold" (Villard and Metzger 2014). In contrast, habitat fragmentation may play a larger role in species persistence when the amount of habitat is intermediate, as the arrangement of habitat patches will be most variable, with some arrangements facilitating functional connectivity among habitat patches better than do others. A fragmentation threshold of 20% forest cover was identified for European badgers (*Meles meles*) in central Spain (Virgós 2001), suggesting that habitat quality should be prioritized in landscapes with > 20% forest cover and that reducing forest patch isolation should be prioritized in landscapes with < 20% forest cover. Occurrences of Canada lynx (*Lynx canadensis*) increased with percent forest cover in landscapes with ≥ 40% forest cover, whereas the proportion of suitable habitat and habitat fragmentation were important in landscapes with moderate levels (30–35%) of forest cover. However, in landscapes with < 20% forest cover, lynx occurrences were not related to either habitat loss or habitat fragmentation, indicating behavioral plasticity in highly modified landscapes (Hornseth et al. 2014).

Habitat patch size and matrix amount are compositional characteristics that frequently influence the abundances of carnivore species in human-modified landscapes. Habitat patch size had a positive effect on large-bodied species, such as grizzly bears (*Ursus arctos horribilis*—Popplewell et al. 2003) and giant pandas (*Ailuropoda melanoleuca*—Wang et al. 2010), as well as on smaller species, such as stone martens (*Martes foina*—Virgós and García 2002), white-nosed coatis (*Nasua narica*), and ocelots (*Leopardus pardalis*—Garmendia et al. 2013). Amount of agricultural cover can have positive effects on carnivore populations; however, such effects only manifest if sufficient natural habitat is present. For example, den sites of raccoons are situated in landscapes with many agricultural patches that also contain extensive patches of forest characterized by large amounts of forest-grass edge (Henner et al. 2004).

Characteristics of landscape configuration (e.g., patch dispersion, patch shape, edge density) play a significant role in structuring carnivore populations in temperate and tropical landscapes that have been modified by humans. In Neotropical landscapes, amount of forest edge negatively affects highly mobile carnivores (*Canis brachyurus*, *Puma concolor*, *L. pardalis*—Lyra-Jorge et al. 2010), but benefits the smallest cat in the Americas, the kodkod (*Leopardus guigna*—Fleschutz et al. 2016). In temperate landscapes, abundances of wild felids have generally increased with increasing amounts of habitat edge. In southern Idaho, home ranges of *P. concolor* comprised at least a moderate amount of habitat edge during the summer, presumably providing hunting habitat (Laundré and Loxterman 2007). Similarly, bobcats (*Lynx rufus*) respond positively to three configurational characteristics: their space use increases

with increasing edge contrast, increasing dispersion of habitat patches, and decreasing patch shape complexity (Constible et al. 2006). Given these diverse effects of human-modified landscapes on carnivores, conservation strategies must balance considerations of habitat loss, landscape configuration, and matrix quality.

At the community level, carnivore richness or diversity generally increases with landscape diversity (i.e., the number and relative cover of habitat types), a pattern observed for carnivore communities in Nearctic (Oehler and Litvaitis 1996), Palearctic (Pita et al. 2009; Herrera et al. 2016), and Afrotropical (Ramesh et al. 2016) regions. Alternatively, a combination of compositional (e.g., habitat patch size, number of matrix patches) and configurational (e.g., edge density, habitat patch dispersion, habitat patch shape) characteristics may collectively represent a landscape heterogeneity gradient that influences carnivore diversity. For example, in the Lacandona Rainforest of Mexico, species richness increased with increasing patch shape complexity, patch size, and matrix quality (Garmendia et al. 2013). As such, species richness effectively increased as the landscape became more diverse.

Artiodactyla

Some of the most notable species that thrive in human-modified landscapes are artiodactyls (e.g., *Odocoileus virginianus*, *Capreolus capreolus*—Jepsen and Topping 2004; Hurley et al. 2012), as heterogeneous landscapes comprising forest edge, agriculture, and early-successional environments provide abundant forage for these generalist species (i.e., species that can adapt to a wide range of environmental conditions and habitat types). High densities of artiodactyls can result in increased human–wildlife interactions (e.g., wildlife-vehicle collisions—Girardet et al. 2015) as well as intensified herbivory that dramatically alters native plant communities (Augustine and Jordan 1998), creating major management concerns throughout much of the world (Fig. 2). Accordingly, understanding responses of artiodactyls to landscape structure is primarily based on studies of habitat-generalist deer species (i.e., 86% of artiodactyl studies) in Nearctic and Palearctic regions (i.e., 53% and 39% of artiodactyl studies, respectively).

Behavioral plasticity in a changing landscape.—Landscape structure can affect the quantity and quality of food resources available for deer. The success of species in dynamic human-dominated landscapes depends on the ability of individuals to reach isolated resource patches or to use a diversity of resources that are available in highly modified landscapes. For example, roe deer (*C. capreolus*) exhibit plastic feeding behavior by supplementing their diets with cultivated seeds and consuming less native forest browse as crop availability increases (Abbas et al. 2011; Serrano Ferron et al. 2012). The diet in agriculture-dominated landscapes is nutritionally superior to that of their counterparts in forested landscapes during non-mast years (Abbas et al. 2011). The ability to exploit resources in human-dominated landscapes has given these populations access to reliable and high-energy resources (Serrano Ferron et al. 2012).

Deer-friendly human-modified landscape characteristics.—For many species of deer, home range sizes decrease with increasing landscape heterogeneity. Home ranges of mule deer (*Odocoileus hemionus*) are smaller in landscapes with a large amount of habitat edge, irregular forest patch shapes, and many land cover types (Kie et al. 2002). White-tailed deer (*O. virginianus*) use less space in landscapes with small patches of many land cover types that are highly interspersed (Dechen Quinn et al. 2013), and home range sizes of roe deer decrease with increasing edge density (Said and Servanty 2005). Each of these species use multiple land cover types for different resources. As such, home ranges can be smaller when patches that provide different types of resources occur within a small area. This idea is further supported by responses of *O. virginianus* to the spatial arrangement of food-rich balsam fir stands. Home range sizes decrease as the density of food-rich balsam fir increases, but when balsam fir coverage is low, home ranges are established in heterogeneous parts of the landscape (Massé and Cote 2012).

Although heterogeneous landscapes with agricultural land cover types can increase abundance of artiodactyls, not all landscape features are beneficial, and some landscape characteristics associated with human activity (e.g., settlements, roads) negatively affect species abundance and behavior (e.g., roe deer, moose [*Alces alces*], sika deer [*Cervus nippon*], white-tailed deer—Hewison et al. 2001; Sirkia et al. 2010; Uzal et al. 2013; Magle et al. 2014). In the Chicago metropolitan area, the quintessential habitat-generalist *O. virginianus* more frequently occupied sites with lower housing, human, and dog densities (Magle et al. 2014). In these same landscapes, occupancy of deer and coyote were strongly and positively correlated, suggesting that a lack of high-quality habitat in urban areas may cause these species to co-occur despite potential predation of fawns by coyotes (Magle et al. 2014).

Landscape and deer-vehicle collisions.—An overabundance of deer can cause considerable economic loss and human injuries via vehicular collisions (Girardet et al. 2015). The incidence of vehicular collisions with deer is related to landscape composition and configuration (Danks and Porter 2010; Girardet et al. 2015), indicating that movement between habitat patches as well as the quantity of resources near roadsides likely affect collision rates. Collisions with roe deer are associated with the proportions of forest and cultivated fields (i.e., landscape composition associated with forage availability) as well as with landscape connectivity (Girardet et al. 2015). Similarly, moose-vehicle collisions increase with increasing percent cover of preferred foraging habitats (cleared forest and coniferous forest) next to roadsides as well as with decreasing interspersion of cover types, suggesting that moose must travel longer distances between types of habitat patches and cross roads more frequently (Danks and Porter 2010). Managing landscape structure could be an effective tactic to moderate negative effects of overabundance of deer on native and agricultural plants as well as on the frequency of vehicular collisions.

Rodentia

Experimental approaches.—Much of the early field research in landscape ecology focused on experimental approaches using small mammals as model taxa and old fields or successional habitats as model systems (Barrett and Peles 1999). The combination of small home range sizes (< 0.2 ha), short dispersal distances (< 200 m), generation times shorter than a growing season, and the ability to experimentally manipulate landscape features (i.e., to create landscapes comprising patches of different sizes, shapes, and arrangements) offered a way to test predictions derived from simulation models and observational studies (Bowers and Barrett 1999). These approaches facilitated the study of effects of habitat fragmentation on population dynamics, how movement among focal patches occurs in landscapes, and the effects of patch configuration, habitat edges, and corridors on dispersal. Many studies compared individuals within populations as well as populations of different species, relying on mark-recapture or radiotelemetry approaches (e.g., Diffendorfer et al. 1999; Peles et al. 1999; Schweiger et al. 1999). Additionally, translocations were a common approach to study the movements of small mammals in fragmented landscapes. Experiments identified that gap crossing by forest mammals such as chipmunks (*Tamias striatus*—Bowman and Fahrig 2002) or red squirrels (*Tamiasciurus hudsonicus*—Bakker and Van Vuren 2004) could not be explained by the size of clear-cut areas. Moreover, corridors did not increase cotton rat (*Sigmodon bispidus*) movements in connected fragments versus isolated fragments (Bowne et al. 1999). This suggests that landscape configuration did not have isolating effects on chipmunks or cotton rats because the matrix did not represent a barrier to dispersal for these species (Bowne et al. 1999; Bowman and Fahrig 2002). In contrast, landscape configuration was the primary factor in determining if *T. hudsonicus* were more likely to cross clear-cut areas or follow forest edges to return to home territories (Bakker and Van Vuren 2004). Enclosure experiments were also used to study edge sensitivity, matrix effects, and the influence of isolation and corridors on *Microtus oeconomus* in Norway and *Microtus canicaudus* in Oregon (Ims and Andreassen 1999; Lidicker and Peterson 1999). Both species are sensitive to edges and to the extent of matrix, with individuals willing to cross 1 m distances but not 9 m distances between habitat patches.

These early experiments, which explicitly tested effects of spatial configuration, helped differentiate the young field of landscape ecology from more established fields like metapopulation biology and island biogeography that focus on extinction and colonization, consider patches and dispersal ability to be of equal importance, and consider the matrix to be inhospitable. Furthermore, they helped to shape the direction of the discipline as an applied science that investigates spatial processes and patterns to address contemporary environmental problems (Pickett and Cadenasso 1995; Bowers and Barrett 1999).

Disease dynamics.—The study of infectious diseases, particularly those spread, transmitted, or harbored by rodents, has benefited from multiscale assessments of landscape structure (e.g., Allan et al. 2003; Ostfeld and LoGiudice 2003).

Landscape structure may affect infectious disease dynamics by altering the composition of ecological communities or the movement of individuals, thereby modifying ecological interactions associated with pathogen transmission. For example, forest fragmentation in the northeastern United States results in mammalian communities dominated by *Peromyscus leucopus*, the most competent reservoir for the spirochete that causes Lyme disease. This effect of landscape structure has significantly increased disease risk to humans (e.g., Allan et al. 2003; Ostfeld and LoGiudice 2003). Forest patch area is negatively correlated with the density of vectors and with pathogen prevalence in vectors. These two factors increase risk of Lyme disease in humans that live near small forest fragments (Allan et al. 2003). Similarly, the prevalence, intensity of infection, and average number of *Baylisascaris procyonis* larvae (a roundworm parasite of raccoons, *P. lotor*) that are pathogenic to numerous small vertebrates were significantly higher in fragmented landscapes than in contiguous forests (Page et al. 2001).

Landscape composition and configuration significantly influence the prevalence of Sin Nombre virus in *Peromyscus maniculatus* across Canada (Langlois et al. 2001). Landscape structure has stronger effects on virus incidence than do other factors often used in epidemiological models of Sin Nombre virus (e.g., climate, season). This suggests that models should account for variation in landscape structure on the demographics of host populations (Langlois et al. 2001). Finally, plague occurrence in prairie dog colonies is significantly related to landscape context in both rural and urban settings. Roads, streams, and lakes serve as barriers to plague transmission among black-tailed prairie dog (*Cynomys ludovicianus*) colonies, with relationships between landscape structure and plague occurrence being most evident at larger spatial scales (Collinge et al. 2005).

Landscape connectivity and spatial scale.—Although gray squirrels (*Sciurus carolinensis*) are ubiquitous in urban parks and suburban landscapes, this may be the result of behavioral adaptations by particular populations and not a reflection of the species in general (e.g., "synurbanization" sensu Parker and Nilon 2012). Populations of *S. carolinensis* in forested landscapes that have been fragmented by agriculture are limited by individual area requirements and dispersal ability (Goheen et al. 2003), generally requiring continuous forest sites and large patches (> 4.6 ha) adjacent to other wooded habitats (Nupp and Swihart 2000). This contrasts with the occurrences of red (*T. hudsonicus*) or fox (*S. niger*) squirrels, which were related to patch size, but not to landscape connectivity (Nupp and Swihart 2000). *Sciurus niger* were found in most forest fragments, and translocation experiments demonstrated that *S. niger* require less time to move from fencerows to forest patches compared to the situations for *S. carolinensis* or *T. hudsonicus*. *Sciurus carolinensis* were the least successful at moving from fencerows across the agricultural matrix to forest (Goheen et al. 2003), despite their successful colonization of parks and suburban residential areas throughout their geographical distribution.

North American (*T. hudsonicus*) and Eurasian (*Sciurus vulgaris*) red squirrels exhibit context-specific responses to

landscape structure. *Tamiasciurus hudsonicus* were insensitive to landscape configuration in temperate forests that are fragmented by agricultural lands (Nupp and Swihart 2000; Patterson and Malcolm 2010). In contrast, the effects of landscape composition and configuration on the occurrence of *T. hudsonicus* in Canadian boreal forest were scale-, time-, and context-dependent (Fisher et al. 2005). In fragmented forests of Sweden, only the proportion of spruce trees in a fragment predicted density of *S. vulgaris*. However, patch size, quality, and isolation influenced presence of *S. vulgari* in wooded patches embedded within an urban matrix, with significant improvements in explanatory power observed when matrix resistance was added to models (Verbeylen et al. 2003).

Northern (*Glaucomys sabrinus*) and Siberian (*P. volans*) flying squirrels are indicator species for ecosystem management of forests in western North America (Carey 2000) and Finland (Reunanen et al. 2000), respectively. *Pteromys volans* prefer large contiguous forest patches that are connected by habitats suitable for gliding (Reunanen et al. 2000). In managed forests, the best predictor of occupancy was a negative relationship with the number of clear-cuts surrounding sites (Mönkkönen et al. 1997). In fragmented forest landscapes, connectivity of patches increased the probability of *P. volans* occurrence and a high level of connectivity enabled lower quality patches to be occupied (Reunanen et al. 2002). Similarly, *G. sabrinus* occurrence is positively related to patch size and area of contiguous forest (Patterson and Malcolm 2010; Walpole and Bowman 2011; Shanley et al. 2013). However, *G. sabrinus* respond negatively to connectivity. They are less likely to be found in landscapes comprising small patches that are highly connected compared to those that contain large unconnected patches (Walpole and Bowman 2011). Nonetheless, the effects of structural connectivity on *G. sabrinus* are scale-specific: high connectivity is favored at local scales and selected against at larger scales (Shanley et al. 2013).

Outbreaks, crop damage, and zoonosis.—Changes in agricultural practices throughout Europe have led to an increase in connectivity of grasslands, resulting in outbreaks of grassland rodents, such as the fossorial water vole (*Arvicola terrestris scherman*), whose populations undergo travelling waves on a multiyear cycle (Giraudoux et al. 1997). High population densities of *A. t. scherman* cause severe crop damage, substantial economic losses (Meylan 1977; Jacob and Tkadlec 2010), and a greater prevalence of alveolar echinococcosis in humans, which is a lethal parasitic disease transmitted via a fox–small mammal cycle (Viel et al. 1999). At a regional scale (~2,500 km^2), percent grassland is the primary driver of fluctuations in population densities and outbreaks of *A. t. scherman* (Giraudoux et al. 1997), whereas at the landscape scale (~25 km^2) differences in landscape structure exist between outbreak epicenters and diffusion areas (locations of minor outbreaks that occur in years following the initial outbreak). Epicenters occur in open landscapes with little forest and in unfragmented grasslands, whereas diffusion areas have more woodland patches and hedgerow networks that fragment grasslands, suggesting a negative effect of fragmentation on rodent breakouts (Duhamel et al. 2000).

Effects of landscape structure on arvicoline rodents (i.e., voles and lemmings) are pervasive. Landscape composition and configuration (e.g., percent cover of grassland, density of hedgerow networks, forest boundary shape) influence population fluctuations of *Microtus arvalis* (Delattre et al. 1992, 1996). Landscape connectivity affects the likelihood that ponds are colonized (or recolonized) by water voles (*Arvicola sapidus*), whereas local habitat composition around ponds affect the persistence of populations (Fedriani et al. 2002). Densities of the gray red-backed vole (*Myodes rufocanus*) in boreal forests of Sweden are primarily associated with landscape configuration (distance between habitat patches, patch interspersion, and spatial contiguity) rather than habitat composition (Ecke et al. 2006). In contrast, landscape structure is unrelated to distributional patterns of endemic Lusitanian (*Microtus lusitanicus*) or Mediterranean pine voles (*Microtus duodecimcostatus*) in Portugal (Santos et al. 2011).

Matrix quality.—Although no consistent pattern characterizes community-level relationships of small mammals with landscape structure, a unifying theme is the importance of matrix quality. In fragmented temperate rain forests, species richness of old-growth forest mammals was not correlated with fragment area or with simple geographic measures of isolation, but was associated with the amount of old-growth forest and secondary forest in the matrix (Lomolino and Perault 2001). Species richness, composition, and abundance of small mammal communities comprising 13 rodent and 13 marsupial species in Amazonian rainforest fragments were primarily affected by the quality of the open-habitat matrix of cattle pastures, rather than by forest patch metrics such as fragment size and shape (Santos-Filho et al. 2012). Similarly, small mammal abundance in Atlantic Forest was greater in matrix habitats containing some tree cover than in structurally simplified anthropogenic grasslands (Umetsu and Pardini 2007). Furthermore, distributions of small mammals in Atlantic Forest remnants are best predicted by models that include matrix quality (Umetsu et al. 2008). In forested areas that were fragmented by agricultural lands in central North America, forest patch size, distance between patches, and fractal dimension are the best predictors of small mammal species richness (Nupp and Swihart 2000). However, species of rodents differ in sensitivity to forest fragmentation in agriculturally dominated landscapes. Species that easily move through matrix habitats (e.g., *P. leucopus*, *S. niger*) are relatively insensitive to fragmentation, whereas species that find agricultural lands to be barriers to dispersal (e.g., *Glaucomys volans*, *S. carolinensis*, *T. striatus*) are highly sensitive to fragmentation.

Lagomorpha

Context-dependent responses.—Like most rabbits and hares, responses of the brown hare (*Lepus europaeus*) to landscape structure are complex and context-dependent, resulting in a general lack of congruence of landscape-level responses among studies (Panek and Kamieniarz 1999; Kamieniarz et al. 2013). For example, effects of pasture cover depend on the type of livestock in the field, and the impact of the grazing regime on

plant community composition. Similarly, effects of agricultural edges differ between landscapes in which adjacent agricultural fields have direct contact and landscapes in which strips of permanent vegetation (e.g., hedgerows, tree lines) define field edges. Finally, the effects of particular habitat types depend on other landscape characteristics (i.e., effects of forest area in diverse landscapes are different than those in landscapes with large agricultural monocultures).

In Poland, abundance of *L. europaeus* is negatively associated with the number of forest patches and with amount of forest edge, but is positively associated with permanent grassland cover (Panek and Kamieniarz 1999). Red foxes (*V. vulpes*) are a primary predator of *L. europaeus* and are found commonly in fields that abut forest. Survival of young hares declines in field-forest mosaics compared to forest-free landscapes due to fox predation associated with the presence of forest (Wasilewski 1991). In contrast, survival of adult hares is greater in forest-field mosaics, as forests act as shelter when harvesting occurs in agricultural fields. These effects have increased over time (from 1984 to 1995) as fox abundances have increased regionally, causing an overall decline in hare abundances in mosaic landscapes (Panek and Kamieniarz 1999).

The eastern cottontail (*Sylvilagus floridanus*) is a habitat generalist and does well in disturbed areas and successional vegetation. Cottontails are most abundant in patchy landscapes that have a mix of row crops, grasslands, and woodland edge habitats with low contagion (Roseberry 1998), as these landscapes provide the necessary shelter and dietary components for high reproductive and survival rates. Habitat models that evaluated the suitability of landscapes for *S. floridanus* were effective at identifying unsuitable landscapes; however, about equal amounts of apparently suitable landscapes had high or low cottontail densities (Roseberry 1998). This discrepancy occurs because remote-sensing technology has not yet been able to effectively distinguish among important small-scale habitat components (i.e., brush piles, briar patches, narrow strip cover between habitat types) that occur independently of landscape structure and that affect cottontail abundance. Interestingly, cottontails are most abundant in areas with soil fertility and terrain that allow for an intermediate amount of agriculture. Ideal areas for agriculture lack sufficient grassland and woodland edges, whereas areas unsuitable for agriculture are covered by too much forested habitat to support high densities of cottontails.

European wild rabbits (*Oryctolagus cuniculus*) and *S. floridanus* exhibit similar responses to landscape composition and configuration, reaching greater densities in heterogeneous landscapes comprising agriculture, grasslands, scrub habitats, and large amounts of edge (Calvete et al. 2004; Jiménez-García et al. 2006). Optimal landscapes for *O. cuniculus* have cereal crops near natural cover (grass or shrublands), providing safe access to abundant high-quality food and protection from predation (Calvete et al. 2004). However, *O. cuniculus* prefer to establish warrens away from edge areas, usually within larger patches of natural cover (Dellafiore et al. 2008). Landscape

features affect the distribution and movements of carnivores, with greater perimeter-to-edge ratio (i.e., irregularly shaped or narrow patches) and degraded habitat (e.g., row crops), exposing rabbits to greater risk of predation (Brown and Litvaitis 1995).

For both American and European rabbits, concerns exist about patterns of regional land use that result in landscape structures that isolate populations (e.g., Roseberry 1998; Calvete et al. 2004). Major highways and rivers can limit gene flow among rabbit populations, whereas corridors of habitat along roads, railways, and utilities facilitate gene flow among populations (Fenderson et al. 2014). However, the relative effects of these barriers and facilitators of gene flow depend on the composition and configuration of the surrounding landscape. Moreover, barriers to dispersal are most important at large spatial scales, effectively isolating populations, whereas structures that facilitate gene flow are most important at the local scale, enabling dispersal of individuals among suitable habitat patches (Fenderson et al. 2014).

METACOMMUNITY STRUCTURE IN A LANDSCAPE CONTEXT

Few studies have evaluated effects of landscape structure on the composition of mammal communities or on their metacommunity structure. A metacommunity is a set of ecological communities occurring at sites along an environmental gradient that are potentially connected by dispersal. Metacommunity structure is an emergent property that describes the relationships among species' distributions across a gradient (Leibold and Mikkelson 2002; Presley et al. 2010). In human-modified landscapes, the a priori assumption is that metacommunities will be nested, with more heavily modified landscapes harboring communities that are perfect subsets of communities from less disturbed landscapes. However, this assumption has not been confirmed for bats in Costa Rica (Cisneros et al. 2015b) or for non-volant small mammals in Atlantic Forest (de la Sancha et al. 2014). Phyllostomid bats exhibited Gleasonian structure (coherent species distributions and range turnover, with species-specific responses to gradients) during the dry season and Clementsian structure (coherent species distributions and range turnover, with coincident range boundaries) during the wet season (Cisneros et al. 2015b). Variation in distances between forest patches structured metacommunities during the dry season, whereas variation in forest edge density structure metacommunities during the wet season. Similarly, small mammals in Atlantic Forest exhibited Clementsian and Gleasonian structures, with fragment size being associated with differences in species composition (de la Sancha et al. 2014). Differences in small mammal community composition were associated with locations of historical refugia and vicariance events associated with large rivers. Despite intensive and extensive deforestation throughout the Atlantic Forest, species distributions and community composition retain historical signals that can be detected in metacommunity structures.

A Diversity of Responses and Common Themes in Mammal Landscape Ecology

Mammals exhibit a great deal of diversity in how they respond to variation in human land use and landscape structure. Some species exhibit behavioral adaptations to urban environments that take advantage of novel dietary resources (e.g., gray-headed flying fox—McDonald-Madden et al. 2005; greater horseshoe bats and Geoffroy's bat—Dietz et al. 2013; gray squirrels—Parker and Nilon 2012) or roosting habitat (e.g., Indian fly fox—Hahn et al. 2014), whereas most species avoid areas of human habitations (e.g., bats—Fabianek et al. 2011; Hale et al. 2012; Luck et al. 2013; artiodactyls—Hewison et al. 2001; Sirkia et al. 2010; Uzal et al. 2013; Magle et al. 2014). Some species respond positively to a moderate amount of human land use because they specialize on resources that are abundant in newly created edge habitats (e.g., West-African chimpanzees—Torres et al. 2010; Neotropical bats—Willig et al. 2007; García-Morales et al. 2013; García-García and Santos-Moreno 2014; Arroyo-Rodríguez et al. 2016; eastern cottontails—Jiménez-García et al. 2006; Bolívar-Cimé et al. 2013; European wild rabbits—Calvete et al. 2004), whereas other species exhibit only negative responses to habitat loss (e.g., carnivorous bats—Klingbeil and Willig 2009; Mexican mantled howler monkeys—Arroyo-Rodríguez et al. 2008). Some species are unaffected by habitat fragmentation (e.g., red squirrels—Bakker and Van Vuren 2004; frugivorous bats—Gorresen and Willig 2004; Gorresen et al. 2005; Castro-Arellano et al. 2007; Willig et al. 2007; Klingbeil and Willig 2009, 2010; Cisneros et al. 2015a, 2015b), whereas even short distances between patches can represent significant barriers to dispersal for others (e.g., golden-headed lion tamarins—Raboy et al. 2010; barbary macaques—Ménard et al. 2013). Nonetheless, some common themes exist in the responses of mammals to landscape structure.

Perhaps paradoxically, context-dependent responses may be the most common theme to describe mammal responses to landscape structure. How abundance or diversity respond to landscape may depend on spatial scale (e.g., Gorresen and Willig 2004; Gorresen et al. 2005; Betts et al. 2006; Ewers and Didham 2006; Smith et al. 2011; Ordóñez-Gómez et al. 2015), season (e.g., Fisher et al. 2005; Klingbeil and Willig 2009, 2010; Abbas et al. 2011; Serrano Ferron et al. 2012; Cisneros et al. 2015a, 2015b), foraging guild (e.g., Klingbeil and Willig 2009, 2010; Avila-Cabadilla et al. 2012; Arroyo-Rodríguez et al. 2016), or even type of livestock in a pasture (Kamieniarz et al. 2013).

For many groups, landscape structure affects choice of roost or den locations. Despite exceptional vagility, roost selection by bats is affected by proximity to forest or water (Encarnação et al. 2005; Limpert et al. 2007; Tournant et al. 2013; Boughey et al. 2011). Similarly, European wild rabbits (Dellafiore et al. 2008) and raccoons (Henner et al. 2004) choose den sites in response to proximity to large patches of forest cover.

Finally, an emerging consensus in landscape ecology is the importance of matrix permeability or utility (Tscharntke et al. 2012) for understanding responses to landscape structure, with mammalian groups well represented among these studies. Improved matrix quality or permeability has positive effects on species richness of marsupials in Australian forest fragments (Brady et al. 2011); small mammal diversity in the Amazonian (Santos-Filho et al. 2012), Atlantic (Umetsu et al. 2008), and temperate (Lomolino and Perault 2001) rainforests; activity and diversity of bats in Australia (Luck et al. 2013) and Europe (Hale et al. 2012); occupancy by black howler monkeys in Mexico (Pozo-Montuy et al. 2011); species richness of carnivores in North America (Oehler and Litvaitis 1996), Central America (Garmendia et al. 2013), Europe (Pita et al. 2009; Herrera et al. 2016), and Africa (Ramesh et al. 2016); and density of Eurasian red squirrels (Verbeylen et al. 2003).

The Future of Mammalian Landscape Ecology

Because terrestrial mammals range in size over seven orders of magnitude (from the 1.8-g Etruscan shrew [*Suncus etruscus*] to the 10.4-metric-ton African bush elephant [*Loxodonta africana*]), can be habitat specialists (e.g., koala, giant panda) or generalists (e.g., raccoon, white-tailed deer), and may be highly mobile (e.g., bats and reindeer [*Rangifer tarandus*]) to rather sedentary (e.g., three-toed sloths [*Bradypus* spp.]), the class represents a model taxon for exploring the comparative roles of habitat and landscape structure on population, community, and metacommunity dynamics. Although mammalian research has contributed significantly to the development of the discipline, future research would benefit from the application of a hierarchical approach that is scale-sensitive with an explicit linkage to a series of contemporary hypotheses.

Hierarchical and scale-sensitive designs linked to theory.— From a landscape perspective, the size of a core habitat patch (e.g., forest), the amount of core habitat within a focal scale, the configuration of focal habitat within a focal scale (Fahrig 2013), or the identity, diversity, and configuration of all habitat types within the focal scale (Ewers and Didham 2006; Kupfer et al. 2006) may mold characteristics of diversity. The most basic landscape structure hypothesis (i.e., Patch Area Hypothesis) was derived from the Theory of Island Biogeography and posits that the characteristics of diversity in a patch are determined by the area of that patch (Fig. 4A). The Habitat Amount Hypothesis challenges assumptions that patches are natural units for the measurement or evaluation of characteristics of diversity or that patch size and isolation have distinct effects (Fahrig 2013). This hypothesis proposes that the amount of focal habitat in a landscape is the underlying characteristic that molds patterns of diversity (Fig. 4B). Consequently, diversity should increase with the amount of area represented by the focal habitat and should be independent of the size of the local patch in which diversity is measured. An alternative conceptual model (the Habitat Configuration Hypothesis) integrates the amount of habitat with configuration of habitat patches in the landscape (Fig. 4C). This hypothesis proposes that configuration, in addition to the amount of focal habitat, should have a strong influence
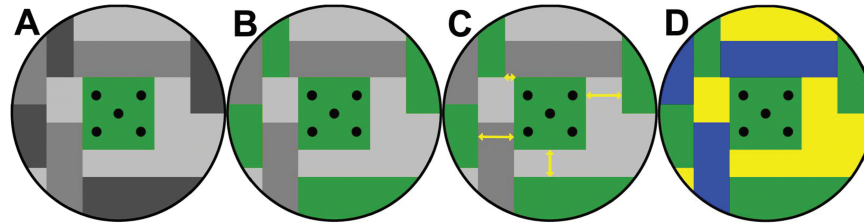
Fig. 4.—Diagrammatic representations of landscape characteristics that relate to the (A) Patch Area Hypothesis, (B) Habitat Amount Hypothesis, (C) Habitat Configuration Hypothesis, and (D) Multi-Habitat Hypothesis. Shades of gray represent attributes of the landscape that are ignored for particular hypotheses. Patches are represented by polygons; land cover is represented by a color (green, blue, or yellow). Black dots represent sampling locations. Yellow arrows indicate the distance of a focal patch from other patches of the same land use.

on diversity (Villard and Metzger 2014), particularly at intermediate amounts of focal habitat, and requires quantification of metrics (e.g., patch shape, contagion, edge density) beyond habitat area. Finally, the Multi-Habitat Hypothesis predicts that local diversity is influenced by the composition and configuration of all land cover types (Fig. 4D), with more heterogeneous landscapes supporting greater diversity than less heterogeneous landscapes. In sum, these theoretical aspects of landscape ecology predict that characteristics of diversity of a focal patch may be a function of: 1) focal patch size (Fig. 4A); 2) the total area of focal habitat in a landscape (Fig. 4B); 3) both the amount of focal habitat in a landscape and the configuration of those habitat patches (Fig. 4C, arrows represent distances between focal habitat patches); or 4) heterogeneity, diversity, and configuration of all land cover types (Fig. 4D). Complicating matters is that the spatial scale with which landscape composition or configuration affects attributes of diversity likely depends on species-specific life history characteristics of the biota, necessitating analyses at multiple spatial scales (Fahrig 2003; Miguet et al. 2016). Research on mammals that focus on these contrasting hypotheses represent fertile grounds for attaining predictive understanding of the effects of landscape characteristics on biodiversity.

Technological advancements.—Radiotelemetry has long been used to monitor movements of individuals to understand how they use habitats in native and human-dominated landscapes (e.g., Brøseth and Pedersen 2000; Cagnacci et al. 2010). Automated recording devices such as camera traps and acoustic recorders represent useful options for collecting data on populations, communities, and metacommunities within a landscape context. Acoustic monitors can be used to record presence and activity, reducing observer bias, creating a permanent verifiable record, and enabling simultaneous recording of data at many sites and for extended time periods with limited personnel (Tegeler et al. 2012; Klingbeil and Willig 2015). Camera traps are trigged by animal movement or body heat and are a common tool used for species inventories, detection of elusive species, conservation assessments, wildlife management, and monitoring population dynamics (Rowcliffe and Carbone 2008; Beaudrot et al. 2016). However, an underused application of camera traps is the monitoring of large mammals within the context of landscape studies (Kinnaird et al. 2003; Michalski and Peres 2007).

Over the past several decades, remote-sensing technology has increasingly been used to measure human land use, habitat coverage, productivity, and the quality of vegetation throughout terrestrial biomes (Horning et al. 2010). Data captured by Landsat, the Terra and Aqua Earth Observing System, and the Polar-orbiting Operational Environmental satellites are publicly available, affordable, cover large areas, and are updated regularly (Strand et al. 2007). The archive of terrestrial satellite imagery from the Landsat system spans more than four decades, facilitating long-term research in landscape ecology. Moreover, very high spatial resolution (pixel size < 10 m^2) commercial optical sensors provide new opportunities for habitat mapping at finer spatial scales than previously possible (Nagendra et al. 2013). Hyperspectral imagery allows for the identification of plant species and assessment of habitat conditions (Clark et al. 2005). Synthetic aperture radar (SAR) and light detection and ranging (LiDAR) are increasingly being used in ecology and natural resource management to estimate aboveground biomass and the structure of woody vegetation (Vierling et al. 2008).

The amount and types of information available will continue to increase as space agencies that are members of the Committee on Earth Observation Satellites have missions planned over the next decade associated with over 200 Earth observation satellite missions (Pettorelli et al. 2014). The primary challenges for remote-sensing technology are associated with increasing its use and utility for natural resource management (Strand et al. 2007). New technologies and software that could benefit environmental sciences as well as theoretical and applied ecology remain underused (e.g., fractional vegetation cover products, radar and hyperspectral imagery, differential interferometry algorithms—Pettorelli et al. 2014). Continued development of collaborations between the ecological and remote-sensing communities is needed to ensure that society realizes the full benefits that remote sensing offers in terms of conservation, land management, and sustainable use.

Quantitative approaches.—Landscape ecology of mammals benefits from incorporation of a variety of multivariate approaches, especially given the degree of correlation among characteristics representing habitat or landscape structure and the extent of spatial autocorrelation in such characteristics. Hereafter, we highlight a few approaches that are promising additions to the arsenal of tools used by those studying the landscape ecology of mammals.

Mammals respond to environmental variation in a scale-sensitive fashion including local factors (e.g., foliage height diversity, canopy openness, litter depth, diversity or biomass of trees) as well as landscape composition and configuration.

Effects of local factors may be contingent on landscape composition and configuration, and effects of landscape configuration may be contingent on composition (Borcard et al. 1992; Legendre 2008). Variance partitioning addresses such issues by quantifying the proportion of variation in a biota (e.g., community composition represented by a site × species abundance matrix) that can be attributed to suites of different types of environmental components (e.g., measures of landscape composition, landscape configuration, or local habitat), as well as the proportion of variation associated with shared components (e.g., a joint response to landscape composition and configuration). For example, variation partitioning can identify unique responses to landscape composition (Fig. 5A) as the primary driver of variation in mammal species composition, with local habitat, landscape configuration, or their shared effects (overlapping areas) being of little importance. Alternatively, variation partitioning could show that species composition is primarily determined by a shared response to both landscape composition and configuration (overlapping region of these two partitions in Fig. 5B), with only small unique effects associated with local habitat, landscape composition, or landscape configuration. However, variation partitioning cannot isolate effects associated a particular environmental characteristic. Hierarchical partitioning is a complementary approach that identifies unique responses to each environmental characteristic (e.g., patch size, patch shape, edge density) that are independent of responses to all other characteristics (Chevan and Sutherland 1991). Finally, classification and regression trees are ideal for analysis of complex data, such as those found in studies of landscape ecology. Regression trees are flexible, do not require linear relationships, and are robust with respect to missing values and high-order interactions (De'ath and Fabricius 2000). Regression trees explain variation of a single response variable (e.g., species richness, abundance) by repeatedly subdividing the data into more homogeneous, mutually exclusive groups (i.e., groups that are similar in terms of species richness or abundance), using combinations of environmental factors (e.g., landscape measure, abiotic characteristics) that may be categorical or continuous. After each step, the splitting procedure is applied separately to each group, with the goal of optimizing the level of homogeneity within each group and maintaining the smallest possible number of branches in the tree. For example, evaluation of effects of landscape structure on species richness using regression tree analysis could divide communities into two groups based on responses to forest cover, with high species richness occurring in landscape with > 60% forest cover and low-to-moderate species richness occurring in landscapes with < 60% forest cover. Subsequently, low-to-moderate species richness sites could be divided into two groups, with low species richness occurring in landscapes with low connectivity (and forest cover < 60%) and moderate species richness occurring in landscapes with high connectivity (and forest cover < 60%). Regression trees can be used for data exploration or hypothesis testing, and represent an alternative to many traditional statistical techniques, such as multiple regression, analysis of variance, logistic regression,
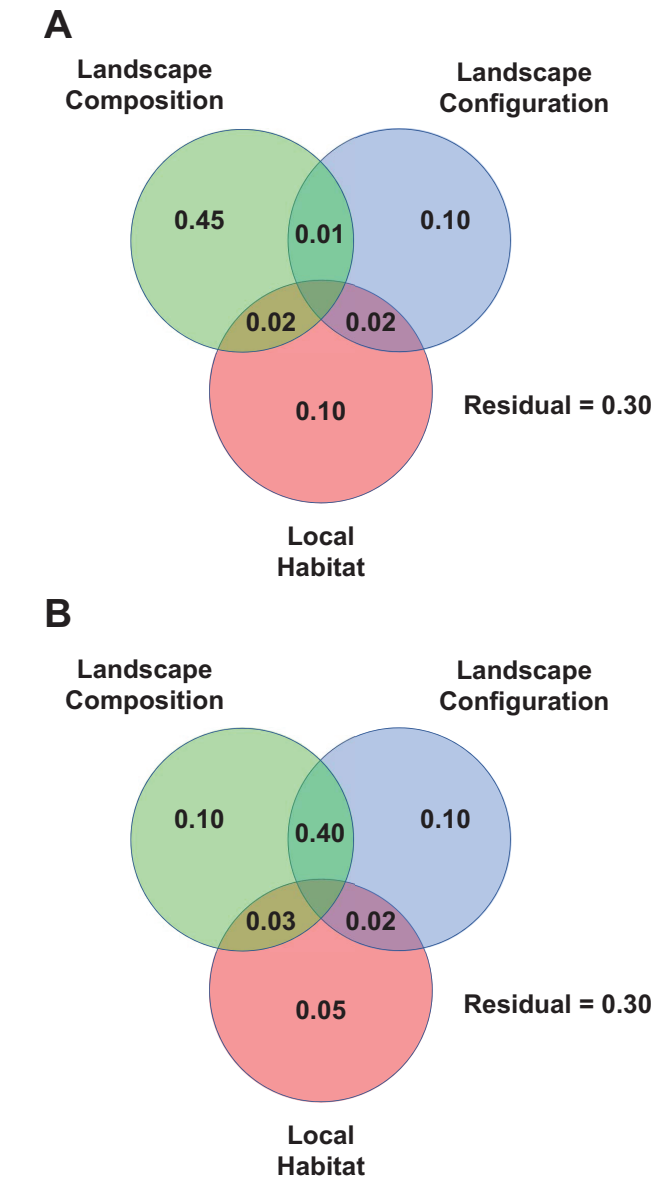

Fig. 5.—Illustrations of two hypothetical results of variation partitioning on species composition with respect to landscape composition, landscape configuration, and local habitat. (A) Results indicate that variation in species composition is primarily driven by landscape composition (45% of explained variation), while landscape configuration and local habitat each account for 10% of the variation, and the overall model explains 70% of variation. (B) Results indicate that variation in species composition is primarily driven by a combination of landscape composition and configuration (40% of explained variation), whereas unique effects associated with landscape composition (10%), configuration (10%), and local habitat (5%) are each small.

log-linear models, linear discriminant analysis, and survival models (De'ath and Fabricius 2000).

Structural equation modeling (SEM) and path analysis (Mitchell 1993; Grace 2006) offer powerful tools for evaluating multifactor causal pathways that involve suites of landscape characteristics and aspects of diversity (e.g., species abundance, species richness, abundance diversity, phylogenetic diversity,

or functional diversity). Unlike multiple regression approaches, SEM requires delineation of well-specified cause and effect or correlative associations between factors, and facilitates the detection of direct and indirect effects of characteristics. Moreover, it is sufficiently flexible to allow an assessment of differences in the form or parameterization of causal pathways related to multiple groups, where groups can be different species, different communities or guilds, or different geographic or ecological settings (Fig. 6). Finally, analyses can be conducted using a number of software programs, including those that are based on graphical interfaces that facilitate construction and analysis of path diagrams (Arbuckle and Wothke 1999).

CONCLUDING REMARKS

Climate change and land-use change will continue to alter the composition and configuration of landscapes in the coming decades. In this context, the study of mammals is positioned to make significant contributions that will 1) advance the theoretical and empirical underpinnings of the discipline, 2) catalyze comparative studies based on differences among groups in life history or phylogenetic characteristics, and 3) contribute multiscale ecological understanding to guide and inform conservation and management in a changing world. The emergence of new technologies to detect animals, including those that are secretive or active at night, the improvement of satellite
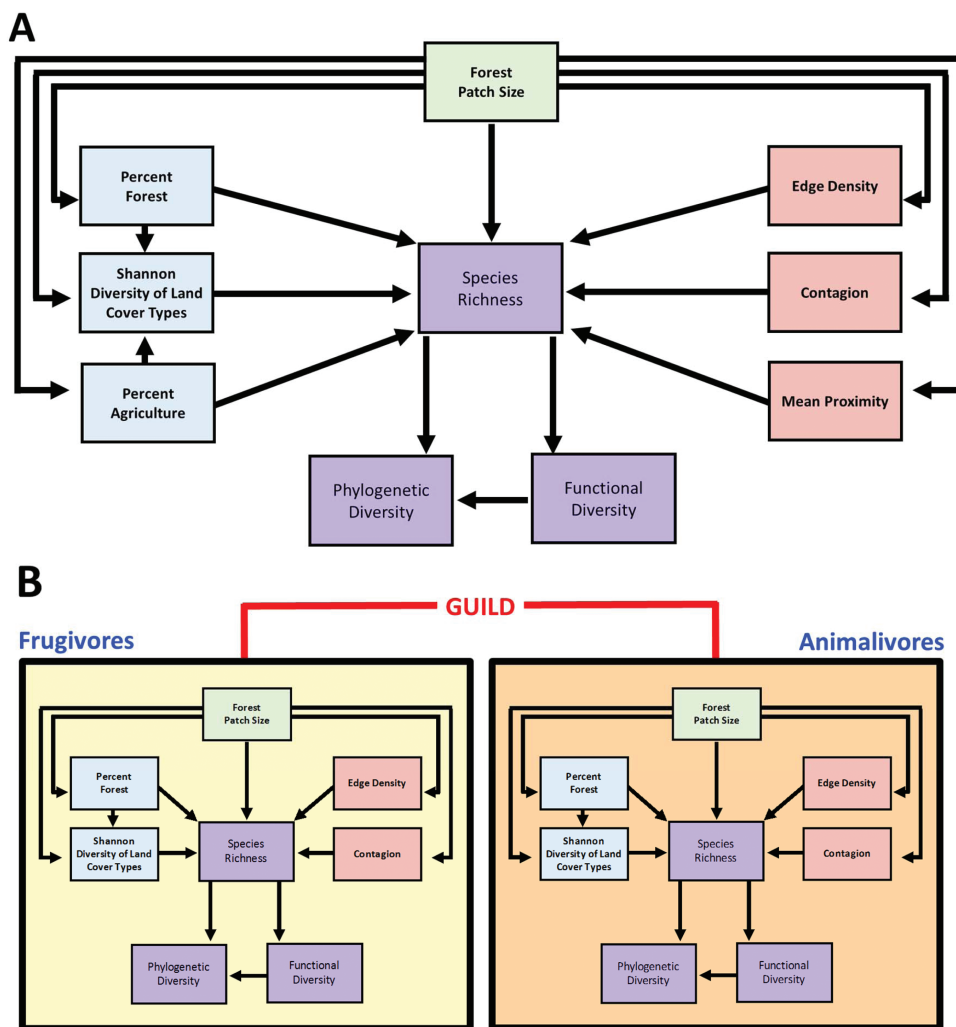

Fig. 6.—Path diagrams that reflect complex causal models in the landscape ecology of mammals, to evaluate questions about landscape composition (blue shading), landscape configuration (red shading), or patch size (an island biogeographic metric, green shading), on characteristics of diversity (purple shading). Arrows represent causal pathways; focal land use is forest. In Panel A, patch size is hypothesized to have a direct effect on species richness, as well as multiple indirect effects mediated by each of three compositional metrics and three configurational metrics. Moreover, Shannon diversity of land cover types, a measure of land cover heterogeneity, is hypothesized to be affected by two other compositional characteristics in the model (i.e., percent forest and percent agriculture). Finally, the effect of species richness on phylogenetic diversity is hypothesized to be direct as well as indirect, mediated by functional diversity. In Panel B, the overarching hypothesis is that the two models of how patch size and landscape characteristics affect attributes of diversity are indistinguishable between the frugivore and animalivore guilds of bats. This hypothesis can be discarded if the form of the models differs between groups (e.g., forest patch size has a large significant effect on frugivore richness but not on animalivore richness) or if the parameterizations differ, even if the models are the same for the two guilds (e.g., metrics of landscape configuration have a significant negative effect on species richness of frugivores, but a significant positive effect on species richness of animalivores).

imaging in terms of habitat resolution and spatial precision, and the advancement of new quantitative approaches for analyzing highly correlated data combine to suggest that research on the landscape ecology of mammals will accelerate greatly over the coming years. The anticipated changes in landscape structure associated with anthropogenic activities heightens the need to combine such approaches to effectively manage and conserve mammals, as well as contribute to the theoretical advancement of the discipline of landscape ecology.

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