

Flying high—assessing the use of the aerosphere by bats

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Synopsis Bats feature prominently among organisms that occupy the aerosphere as they extensively use this environment for foraging, but also for dispersal, migration, and behavioral interactions. Differential use of the aerosphere is an important factor structuring bat assemblages, with species exhibiting distinct morphological, physiological, and sensory adaptations to different habitat types. This necessitates comprehensive sampling methodologies such as combined ground-level and canopy-level mist netting as well as acoustic monitoring to assess the presence, diversity, and activity of different functional groups of species adequately. Recent technological advances in acoustic detection and in methods of analysis, coupled with the expansion of libraries of echolocation calls for species identification, now allow for the reliable quantification of species numbers and activity of the scarcely known group of aerial insectivorous bats, particularly in species-rich tropical assemblages. We provide a brief, exemplary overview of recent studies on bats conducted in Panamá to demonstrate the necessity of comprehensive sampling methods and application of new technologies in order to adequately depict assemblage composition and responses of bats to structural changes in habitats induced by fragmentation. In addition to acoustic methods, miniaturization of radio transmitters has provided new insights into the patterns of spatial use of the aerosphere by bats and has identified species-specific differences in mobility as one of the important traits that determines bats' reactions to anthropogenic alterations of the landscape. Following the goals of the symposium on aeroecology, we propose new avenues of research for probing the aerosphere. We discuss how integration of a diverse array of remote sensing tools with data on species distribution and species traits, such as mobility and edge-sensitivity, might provide novel opportunities for the development, and application of conservation-oriented monitoring systems.

Introduction

Habitat complexity, heterogeneity, and connectivity are driving forces that help create and maintain species diversity and functionality of ecosystems (Malanson and Cramer 1999; Tews et al. 2004; Fischer and Lindenmayer 2007). Structural characteristics of habitats, in particular the stratification and compartmentalization of space, i.e., aerosphere, are particularly relevant for flying organisms such as bats, birds, and insects, because their ability to fly from one patch of habitat to another largely determines their access to (micro)-habitats and hence spatial use on a local scale. Increasingly, disruption of habitats caused by changes in land use leads to patchiness of once continuous areas (Wade et al. 2003; Fischer and Lindenmayer 2007). The resulting habitat remnants differ in size, structural components, availability of resources, and degree of isolation (Ewers and Didham 2006; Kupfer et al. 2006).

For example, selective logging of forests and monocultures of commercially grown trees transform and simplify a formerly complex vertical gradient. Moreover, the distance and type of matrix separating habitat patches along with species-specific behavioral traits, such as mobility, profoundly affects the exchange of wildlife species in fragmented landscapes (Ricketts 2001; Debinski 2006; Kupfer et al. 2006). The degree to which animals can cope successfully with such habitat alterations determines their long-term survival in landscapes dominated by human activities.

Alterations of configurations and structural components of habitats and ecotones at local, regional, and global scales require the development and application of well-founded, conservation-oriented management plans to mitigate negative effects of disturbance. The significance of the aerosphere for volant organisms such as bats, birds, and insects represents one of the most challenging and least understood components of

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the biosphere, largely because methodological limitations still leave crucial gaps in our knowledge.

Focusing on the three central points put forward by Kunz et al. (this symposium) for probing and modeling the aerosphere as the next frontier in ecology, we selected bats (Chiroptera) as organisms that intensively use the aerosphere. Aerosphere encompasses the space between structural elements of habitats, ranging from wide open space high above the canopy and ground to small, stratified or compartmentalized spaces in the forest as well as spaces between habitat patches.

In our overview we focus on (1) comprehensive methods for the *detection* of presence, diversity, and activity of bats, (2) *quantification* of these variables as they relate to the use of the aerosphere, and (3) *detection* and *interpretation* of bats' responses to anthropogenic alterations of structural elements as well as configuration of habitats at different temporal and spatial scales. We argue that differential use of the aerosphere makes bats particularly well-suited organisms for the assessment of changes in landscape configuration and potential consequences relating to important ecosystem service. This, in turn, makes this group particularly relevant with regard to conservation issues.

Bats are the only mammals that have evolved powered flight. Adaptations in morphology (wing shape, body size), physiology, and sensory systems (vision, olfaction, passive listening, echolocation), as well as behavioral characteristics (i.e., foraging strategies), permit differential use of the aerosphere in time and space (Arita and Fenton 1997; Schnitzler and Kalko 2001; Schnitzler et al. 2003). Access to the aerosphere is constrained along vertical and horizontal axes by the ability of bats to cope with obstacles, i.e., vegetation clutter (Schnitzler and Kalko 2001; Schnitzler et al. 2003), and by their capability to navigate large, open spaces with few or no landmarks. Hence, disruption of previously continuous, vegetated habitats through isolation or hostile matrices may pose difficulties to those species that are adapted to navigate in cluttered space as opposed to species that are better adapted to exploit open space. Here, conservation issues are relevant that support establishment of habitat corridors to maintain landscape connectivity.

Bats are ecologically diverse and peak in abundance and species richness in tropical lowland forests where more than 100 species may coexist in local assemblages (Kalko 1998; Stevens and Willig 2002; Rex et al. in press). They fulfill crucial ecosystem services by contributing to plant recruitment and regeneration through pollination and seed dispersal

and by acting as control agents of arthropods through predation (Patterson et al. 2003; Kalka and Kalko 2006). Recent evidence suggests that those interactions include for example the massive reduction of pest insects in agricultural landscapes (Cleveland et al. 2006) and of herbivory in tropical forests (Kalka et al. 2008).

As with most wildlife, disruption of habitat by human activities increasingly affects the diversity and structure of bat assemblages. Thus, evaluating the significance and use of the aerosphere by bats is crucial if we are to understand and mitigate the effects of anthropogenic disturbance on biodiversity and preserve the functional roles of this species-rich and ecologically important group. To achieve this goal, methodologies are needed that permit comprehensive sampling of species assemblages and that give insights into the ecological, physiological, and behavioral adaptability, i.e., how well species can cope with anthropogenically induced habitat alterations including massive changes in structural components and resource availability.

As an example of a well-studied system, we focus on the results of studies conducted on Neotropical bats in Panamá to illustrate current knowledge, outline methodological and conceptual advances and constraints, and discuss future perspectives with regard to the use of the aerosphere by bats. The majority of studies were conducted at the 5400 ha-Barro Colorado Nature Monument (BCNM; 9°09' N, 79°51' W) consisting of Barro Colorado Island (BCI), a field station of the Smithsonian Tropical Research Institute, five adjacent mainland peninsulas, and a variety of islands in Gatún Lake, a reservoir created during the construction of the Panamá Canal. Forests in the study area are classified as lowland tropical moist forest (Holdridge 1967). The islands differ in size and degree of isolation and the forests vary in age, composition, and structural complexity (Leigh et al. 1993), conditions that are ideal for evaluating diversity patterns and spatial use of bats and their dependence on habitat heterogeneity including the differential use of the aerosphere as a prominent feature.

Studies on bats in the BCNM began in the 1950s, and since then have included long-term sampling at the community level in addition to a wealth of specific studies that employed a broad range of methods (mist netting, acoustic monitoring, radio tracking, behavioral experiments) and addressing a variety of topics (e.g., mobility in association with range size, habitat use, and foraging strategies). This comprehensive methodological approach, with emphasis on standardized sampling, has led to one of

the most comprehensive data bases on structure, dynamics, and functionality of a tropical bat assemblage at a single site in the Neotropics.

Putting the results of the exemplary studies from Panamá into a broader context, we provide an outlook of future avenues for exploring and probing of the aerosphere. Potentially, remote sensing technologies that permit continuous monitoring of important landscape features such as land cover, plant phenology as well as configuration and size of habitat patches may allow detection of changes in these features at an early stage and at an increasingly finer temporal and spatial scale than has been possible previously. The methodological advances in this field can potentially be used to create “early warning” systems to project, for instance, impending loss of habitat connectivity, and, in turn, to infer which species might be at risk from habitat modification, in particular when those transformations seriously affect structural components and hence the aerosphere.

Spatial use of the aerosphere by bats

One of the main factors structuring bat assemblages is the differential use of the aerosphere, which can be classified into three habitat types: (1) open space far away from obstacles or the ground, (2) edge space close to, but not within, vegetation or above water, and (3) narrow space within vegetation (Fig. 1). Each of these partitions of the aerosphere requires particular adaptations in shape of the wings and in design of echolocation calls (Norberg and Rayner 1987; Schnitzler and Kalko 2001; Schnitzler et al. 2003). Bats flying mostly in open space are characterized by long, narrow wings that permit fast flight. They usually emit low-frequency and narrowband echolocation calls that are an adaptation for long-range detection of insects. Bats hunting closer to obstacles are characterized by broader and somewhat shorter wings. Echolocation calls are higher in frequency and composed of two parts: a shallow-modulated component used in detection of flying insects and a short, steep frequency-modulated component related to ranging. Wing shapes of bats that mostly fly within the forest are broad and short, allowing skilful maneuvering around obstacles. In contrast to the echolocation signals of bats in open space and edge space, calls used in narrow space are rather stereotyped, mostly consisting of a short, broadband, multi-harmonic, and frequency-modulated component. Because of the difficulties in finding food in clutter by echolocation alone, bats foraging in narrow space also use information from other sensory modalities in addition to

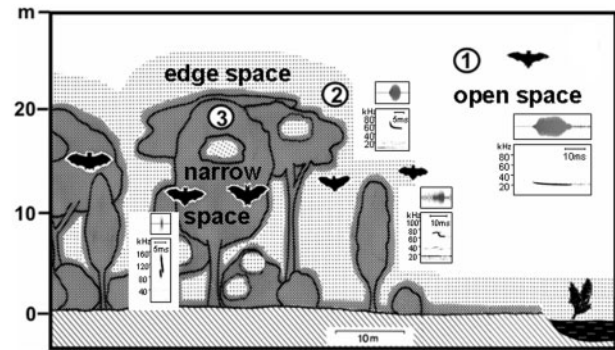


Fig. 1 Spatial habitat use of bats: 1, open space; 2, edge space; 3, narrow space. Typical echolocation calls are depicted as sonograms (frequency versus time) and time signal. Graph modified after Schnitzler and Kalko (2001) and Schnitzler et al. (2003).

echolocation, in particular olfaction when finding flowers and ripe fruits or passive listening when detecting calling katydids or frogs (Schnitzler and Kalko 2001; Korine and Kalko 2005).

Species richness of bats in the BCNM

To demonstrate the importance of comprehensive species inventories in association with the differential use of the aerosphere, we briefly summarize current knowledge from BCI. A total of 76 species have been documented using ground-level and canopy-level mist nets and acoustic monitoring in the BCNM (Table 1). Of those, 14 species are unlikely to reside permanently in the BCNM as they have been only captured at very low numbers (<5) throughout a period of several decades of comprehensive bat netting studies that started in the 1970s or as they have been recorded only a few times within the past 15-years after the successful introduction of bio-acoustic studies. Taking this into account, about 62 species are likely to reside permanently in the BCNM. BCI, part of the BCNM, harbors 74 species within an area of only 15.6 ha with an estimated 60 resident species.

Of the 76 species recorded for the BCNM, almost two thirds ($N=39$) are New World leaf-nosed bats (Phyllostomidae) that forage in narrow space and glean food from the vegetation or the ground, including fruit, nectar, pollen, leaves, invertebrates, small vertebrates, and blood. In contrast to tropical birds, vertical stratification does not appear to play a very prominent role in structuring assemblages of Neotropical bats, although some species are more likely to be captured in canopy nets than others (e.g., Kalko and Handley 2001; Rex et al. in press).

Table 1 Species list of bats known to occur in the BCNM, Panamá, based on a compilation of long-term mistnetting data, and acoustic recordings by E. Kalko and colleagues, including data from the literature

Taxon	Ensemble			Sampling method	
	Food	Foraging mode	Habitat	Mistnet	Acoustic
Phyllostomidae					
Carollinae					
<i>Carollia brevicauda</i> ^a	FRUG	GLEAN	NARROW	X	
<i>Carollia castanea</i>	FRUG	GLEAN	NARROW	X	
<i>Carollia perspicillata</i>	FRUG	GLEAN	NARROW	X	
Desmodontinae					
<i>Desmodus rotundus</i>	SANG	GLEAN	NARROW	X	
<i>Diaemus youngi</i>	SANG	GLEAN	NARROW	X	
Glossophaginae					
<i>Glossophaga commissarisi</i> ^a	NECT	GLEAN	NARROW	X	
<i>Glossophaga soricina</i>	NECT	GLEAN	NARROW	X	
<i>Lonchophylla robusta</i> ^a	NECT	GLEAN	NARROW	X	
Phyllostominae					
<i>Lamproncyteris brachyotis</i>	ANIM	GLEAN	NARROW	X	
<i>Lophostoma brasiliense</i> ^a	ANIM	GLEAN	NARROW	X	
<i>Lophostoma silvicolum</i>	ANIM	GLEAN	NARROW	X	
<i>Macrophyllum macrophyllum</i>	ANIM	GLEAN	EDGE		X
<i>Mimon crenulatum</i>	ANIM	GLEAN	NARROW	X	
<i>Micronycteris hirsuta</i>	ANIM	GLEAN	NARROW	X	
<i>Micronycteris microtis</i>	ANIM	GLEAN	NARROW	X	
<i>Micronycteris schmidtorum</i>	ANIM	GLEAN	NARROW	X	
<i>Phylloderma stenops</i>	FRUG	GLEAN	NARROW	X	
<i>Phyllostomus discolor</i>	NECT	GLEAN	NARROW	X	
<i>Phyllostomus hastatus</i>	OMNI	GLEAN	NARROW	X	
<i>Trachops cirrhosus</i>	ANIM	GLEAN	NARROW	X	
<i>Trinycteris nicefori</i>	ANIM	GLEAN	NARROW	X	
<i>Tonatia saurophila</i>	ANIM	GLEAN	NARROW	X	
<i>Vampyrum spectrum</i>	ANIM	GLEAN	NARROW	X	
Stenodermatinae					
<i>Ametrida centurio</i> ^a	FRUG	GLEAN	NARROW	X	
<i>Artibeus hartii</i> ^a	FRUG	GLEAN	NARROW	X	
<i>Artibeus jamaicensis</i>	FRUG	GLEAN	NARROW	X	
<i>Artibeus lituratus</i>	FRUG	GLEAN	NARROW	X	
<i>Artibeus phaeotis</i>	FRUG	GLEAN	NARROW	X	
<i>Artibeus watsoni</i>	FRUG	GLEAN	NARROW	X	
<i>Centurio senex</i>	FRUG	GLEAN	NARROW	X	
<i>Chiroderma trinitatum</i> ^a	FRUG	GLEAN	NARROW	X	
<i>Chiroderma villosum</i>	FRUG	GLEAN	NARROW	X	
<i>Mesophylla macconelli</i> ^a	FRUG	GLEAN	NARROW	X	
<i>Platyrrhinus helleri</i>	FRUG	GLEAN	NARROW	X	
<i>Sturnira luisi</i> ^a	FRUG	GLEAN	NARROW	X	
<i>Uroderma bilobatum</i>	FRUG	GLEAN	NARROW	X	
<i>Uroderma magnirostrum</i> ^a	FRUG	GLEAN	NARROW	X	
<i>Vampyrodes caraccioli</i>	FRUG	GLEAN	NARROW	X	

(Continued)

Table 1 Continued

Taxon	Ensemble			Sampling method	
	Food	Foraging mode	Habitat	Mistnet	Acoustic
<i>Vampyressa nymphaea</i>	FRUG	GLEAN	NARROW	X	
<i>Vampyressa pusilla</i>	FRUG	GLEAN	NARROW	X	
Thyropteridae					
<i>Thyroptera discifera</i> ^a	INS	AER-GLEAN	EDGE	X	
<i>Thyroptera tricolor</i>	INS	AER-GLEAN	EDGE	X	
Natalidae					
<i>Natalus stramineus</i> ^a	INS	AER-GLEAN	EDGE	X	
Emballonuridae					
<i>Centronycteris centralis</i>	INS	AER	EDGE		X
<i>Cormura brevirostris</i>	INS	AER	EDGE		X
<i>Cyttarops alecto</i>	INS	AER	EDGE		X
<i>Diclidurus albus</i>	INS	AER	OPEN		X
<i>Peropteryx kappleri</i>	INS	AER	EDGE		X
<i>Peropteryx macrotis</i>	INS	AER	EDGE		X
<i>Rhynchonycteris naso</i>	INS	AER	EDGE		X
<i>Saccopteryx bilineata</i>	INS	AER	EDGE		X
<i>Saccopteryx leptura</i>	INS	AER	EDGE		X
Molossidae					
<i>Cynomops greenhalli</i>	INS	AER	OPEN		X
<i>Eumops auripendulus</i>	INS	AER	OPEN		X
<i>Eumops glaucinus</i>	INS	AER	OPEN		X
<i>Eumops hansae</i>	INS	AER	OPEN		X
<i>Eumops underwoodi</i>	INS	AER	OPEN		X
<i>Molossus sinaloae</i> ^a	INS	AER	OPEN		X
<i>Molossus bondae</i>	INS	AER	OPEN		X
<i>Molossus molossus</i>	INS	AER	OPEN		X
<i>Nyctinomops laticaudatus</i>	INS	AER	OPEN		X
<i>Promops centralis</i>	INS	AER	OPEN		X
Mormoopidae					
<i>Pteronotus gymnonotus</i>	INS	AER	EDGE		X
<i>Pteronotus parnellii</i>	INS	AER	NARROW	X	X
<i>Pteronotus personatus</i>	INS	AER	EDGE		X
Noctilionidae					
<i>Noctilio albiventris</i>	ANIM	GLEAN	EDGE		X
<i>Noctilio leporinus</i>	ANIM	GLEAN	EDGE		X
Vespertilionidae					
<i>Eptesicus brasiliense</i> ^a	INS	AER	EDGE		X
<i>Eptesicus furinalis</i>	INS	AER	EDGE		X
<i>Lasiurus blossevillii</i>	INS	AER	EDGE		X
<i>Lasiurus ega</i>	INS	AER	EDGE		X
<i>Myotis albescens</i>	INS	AER	EDGE		X
<i>Myotis nigricans</i>	INS	AER	EDGE		X
<i>Myotis riparius</i>	INS	AER	EDGE		X
<i>Rhogeessa tumida</i>	INS	AER	EDGE		X

Sampling method refers to the method by which a species is most reliably sampled. Species are assigned to ensembles (sensu Fauth et al. 1996) based on diet, foraging mode and habitat type. Taxonomic designations follow Simmons (2005). FRUG, frugivore; SANG, sanguivore; NECT, nectarivore; ANIM, animalivore; INS, insectivore; GLEAN, gleaning; AER, aerial; NARROW, narrow space; EDGE, edge space; OPEN, open space.

^aVery low sample size, suggesting that species may not occur permanently in the study area.

Three species form the ensemble of edge space trawlers. They use the aerosphere above water, including the two species of bulldog bats (Noctilionidae) and the Neotropical leaf-nosed bat, *Macrophyllum macrophyllum*, the only phyllostomid bat known to take food from the surface of the water (Weinbeer and Kalko 2007). The sucker-footed bats, genus *Thyroptera*, and the funnel-eared bat, *Natalus stramineus* presumably use a mixed strategy for hunting in narrow space, slowly flying along the vegetation and scooping up arthropods in flight with their tail membrane. The mustached bat, *Pteronotus parnellii* is a narrow space aerial insectivore and the only species at BCNM that forages on the wing in dense vegetation for flying insects. It emits long, constant-frequency echolocation calls that are an adaptation to detect moving prey in a cluttered background. This echolocation and foraging strategy has evolved twice and is found in a large number of rhinolophids and hipposiderids (Jones and Holderied 2007), two unrelated families of bats in the Old World tropics.

Until recently, approximately one-third of all bat species ($N=29$) that hunt for insects on the wing in edge space ($N=18$) and open space ($N=11$) had been difficult or impossible to sample with mist nets in the BCNM. Consequently, although the extensive mist-netting data provide an excellent background, adequate data on presence, activity, and habitat use of aerial insectivores had still been mostly lacking for the BCNM. Recording and identification of echolocation calls with ultrasound recording devices and custom-made identification keys has substantially increased our knowledge of bat species richness at BCNM (Jung et al. 2007). With a broader application of this methodology we are likely to achieve a much better understanding of the geographical distributions of many of the species foraging either in edge or open space at the local, regional, and global scale.

As the exemplary results from the BCNM underline, comprehensive sampling of bats requires combined methodologies (i.e., mist netting, acoustic monitoring) depending on the differential use of the aerosphere by the respective species. Species adapted to narrow space are best sampled with mist nets, whereas species flying in edge and open space are documented best by acoustic methods. Further development of automated ultrasound recording-stations, automated analysis methods, and expansion of libraries of echolocation calls for species identification (Jung et al. 2007) are needed to improve the quality and efficiency of inventories for species difficult to monitor with mist nets and to integrate aerial insectivores into conservation programs as

hardly anything is currently known about their abundance and ecological function other than their insect-eating habits.

Moreover, monitoring needs to be expanded to include those parts of the aerosphere that are out of reach for mist nets and acoustic studies conducted from the ground, or, at best, with microphones in the canopy. Here, the use of radio microphones suspended from tethered helium balloons and kites as outlined by McCracken et al. (this volume) provides a unique method to access this part of the aerosphere. In addition, modern radar technology increasingly permits better in-depth studies on volant organisms, including birds, bats, and insects in the aerosphere which had been impossible before (for summaries see other symposium contributions).

Effects of habitat disruption on the structure of bat assemblages

Changes in the configuration and size of habitats through fragmentation lead to profound alterations in structural components, such as creation of extensive edge space at the border of forest patches and open space as well as loss of connectivity due to isolation. Given the differential use of the aerosphere by bats and the associated adaptations in wing shape and foraging strategies, alterations in structural features are likely to lead to marked changes in the composition and dynamics of species assemblages. This has been confirmed in a 2-year mist netting study of phyllostomid bats, where species richness and relative abundance of bats were compared at six mainland sites in the BCNM and on 11 islands in Gatún Lake (Meyer and Kalko 2008). In their study, Meyer and Kalko (2008) used a standardized sampling protocol and a combination of ground-level and subcanopy-level mist netting, which resulted in more than 8400 captures and an inventory estimated to be >90% complete. As expected, isolation had a strong effect on the local assemblages. “Far” islands (i.e., distance > ca. 1.5 km from the mainland) had lower species richness (15 species) than did “near” islands (< ca. 500 m; 21 species) or the mainland (30 species; Fig. 2A). Phyllostomid assemblages on “far” islands differed markedly in species composition from the mainland, and were numerically dominated by a few species of medium to large frugivores with good dispersal abilities. The three frugivorous species, *Artibeus jamaicensis*, *Artibeus lituratus*, and *Uroderma bilobatum* accounted for almost 90% of all captures on “far” islands, emphasizing their importance in the local forests as seed dispersers and, depending on season, also as pollinators. In general,

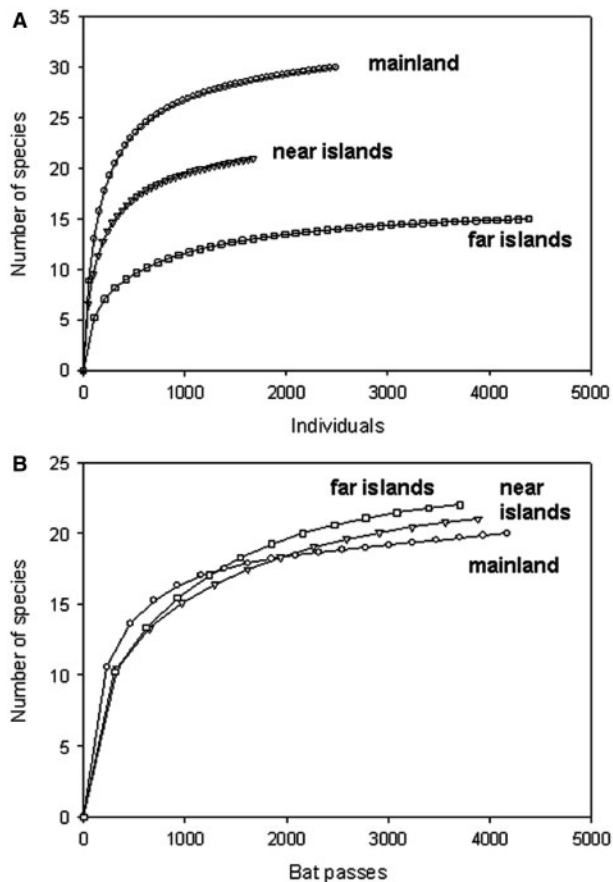


Fig. 2 Species accumulation curves for (A) phyllostomid bats (modified after Meyer and Kalko 2008) and (B) aerial insectivores sampled in the BCNM and on Gatún Lake islands, Panamá. The sample order was randomized 1000 times to smooth curves.

capture rates of bats were greatest on “far” islands compared to the mainland and “near” islands. Large frugivores such as *A. jamaicensis* and *A. lituratus*, seemingly are unaffected by fragmentation as long as resources on islands abound. High mobility with nightly commutes of several kilometers (Morrison 1980) promote use of the abundant fruit resources on islands, where density of some bat-dispersed trees, including figs and others, often is higher than on the mainland (C. Meyer, personal observation). The ability to cover vast stretches of open space likely explains the observed patterns of distribution and abundance of large frugivores on “far” islands (Meyer and Kalko 2008).

In contrast to the large frugivores, animalivorous gleaners were most strongly affected by habitat fragmentation. They were substantially reduced in abundance (“near” islands) or went extinct (“far” islands). This pattern likely is caused by a combination of reduced availability of resources on islands and comparatively low mobility due to adaptations in wing morphology to cluttered habitats

(broad, short wings) that make regular commutes across open space energetically costly. Consequently, most species of animalivorous gleaner probably are not able to maintain stable populations on islands. Furthermore, several species were sensitive to edges as revealed by reduced numbers at the transition zones between forest and open space.

Overall, in an analysis assessing ecological correlates of sensitivity to fragmentation, mobility was one of the species traits most strongly associated with the occurrence and abundance of species of bats on islands (Meyer et al. 2008). These findings suggest that maintenance or re-establishment of habitat connectivity through management of vegetation cover is essential to maintain species-rich assemblages of bats in tropical forest systems, in particular for the preservation of fragmentation-sensitive groups of bats like animalivorous gleaners (Meyer and Kalko 2008; Meyer et al. 2008).

The study on land-bridge islands represents a worst-case scenario due to the hostile matrix (water) separating habitat patches. However, such a scenario with reduced or no connectivity between habitat patches is more and more likely to dominate many fragmented landscapes throughout the tropics given the rapid changes in land use with vast areas dedicated to intensive monoculture of soybeans, corn, and other agricultural products as well as cattle ranching. Other mist netting studies in the Neotropics conducted in systems with a terrestrial matrix largely support the main findings of Meyer et al. on phyllostomid bats, particularly with regard to the sensitivity of gleaning animalivorous species towards fragmentation or disturbance or the relative tolerance of larger, mobile canopy frugivores (Estrada and Coates-Estrada 2002; Faria 2006; Willig et al. 2007). However, in fragmented landscapes where the matrix confers higher connectivity and provides additional food resources than in Meyer and Kalko’s (2008) study, for instance where forest regrowth surrounds habitat remnants, contrasting abundance patterns are often observed for certain groups of species such as understory frugivores, which often dramatically increase in abundance following fragmentation (Faria 2006). This highlights the modulating influence matrix quality can have on the intensity of observed fragmentation effects (Ewers and Didham 2006).

Whereas mist netting studies in the Neotropics have substantially increased our knowledge of phyllostomid bats, we lack almost any information on aerial insectivores in the tropics. Recently, complementing the mist netting study by Meyer and Kalko 2008, effects of forest fragmentation have been assessed for

the first time in a systematic way for aerial insectivores using bioacoustic methods (Estrada, Meyer, and Kalko, unpublished data). Preliminary results based on more than 12,000 recordings of echolocation calls within a 3-months period and an estimated level of sampling completeness of > 85% at the same sites used in the mist netting study (Meyer and Kalko 2008) showed contrasting responses to fragmentation by aerial insectivorous species of bats compared to phyllostomids. Species accumulation curves for aerial insectivores on the mainland and on both groups of islands were almost identical in shape (Fig. 2B), and rank abundance curves and site ordinations pointed to a high degree of similarity in species composition. As one might expect, this was especially the case for open space species and trawling bats, whereas for edge space species that depend on forest as hunting habitat there was a trend indicative of an isolation effect and an influence of vegetation structure on species composition. Contrary to the pattern found for phyllostomid islands, (23 species) even exceeded the mainland (20 species) in species richness of aerial insectivores. Overall activity, expressed in number of bat passes, which is a surrogate for relative abundance, was not significantly different among site categories although some differences were apparent on the species level.

In general, aerial insectivores appeared much less affected by fragmentation than phyllostomids. The larger stretches of edge space surrounding small islands compared to the mainland sites coupled with potentially higher insect availability at the forest edges close to water may contribute to the observed pattern of species richness. As our study was designed to target aerial insectivores that depend primarily on forest for foraging, part of the high-flying open space species could not be reliably detected. Several studies are currently underway that examine species richness, activity, and distribution of open space aerial insectivores across the Isthmus of Panamá where echolocation call sequences are systematically recorded from canopy towers, high-rises, and from boats (Barboza and Jung, personal communication). Preliminary results suggest that some of the open space aerial insectivores adapt well to urban settlements and profit from extensive open space as well as artificial lights attracting insects. Other species are highly dependent on forest. Highest species richness occurs in heterogeneous landscapes with extensive edge space, open space, and richly structured forest areas where up to 20–25 species of aerial insectivores may coexist.

In conclusion, phyllostomid bats and aerial insectivores show differential responses to forest

fragmentation, probably depending primarily on species-specific differences in the use of the aerosphere in conjunction with differences in resource availability. A thorough understanding of the bats' vagility combined with an analysis of their differential use of the aerosphere is essential to predict and mitigate effects of anthropogenic habitat disruption on species composition and ecosystem services such as predation, pollination, and seed dispersal. If the effects of isolation through fragmentation become strong, gleaning insectivorous bats may be reluctant to regularly cross large, open space between forest patches. If gleaning insectivores decline in numbers and, in a worst-case scenario, go locally extinct, it is likely that the part of the herbivory rates of insects that is usually controlled by bats, increases. A recent study revealed that bats and birds significantly reduce herbivory rates in Neotropical lowland forest and that bats have even a stronger effect than birds (Kalko et al. 2008).

Spatial use of bats assessed by radio tracking

Studies on the effects of fragmentation in the land-bridge island system in Panamá have revealed distinct differences in species richness and abundance of phyllostomid bats and differential responses comparing phyllostomid bats and aerial insectivores. A better understanding of the underlying causes for the observed patterns requires knowledge of the ecological requirements and adaptability of bats to environmental changes. Thorough studies on species' mobility are key as this determines the ability of bats to either use open space primarily for foraging or to regularly commute between habitat patches.

Although morphological characteristics like wing shape permit a first assessment of whether bats are more likely to fly above the canopy or whether they are adapted to fly in cluttered habitats, extensive radio tracking studies of a variety of bat species in the BCNM that assessed home range size, habitat use, activity patterns, and foraging strategies revealed the necessity of detailed, species-specific studies of the use of the aerosphere. Contrary to the assumption that similar-sized bats are characterized by similar movement patterns and home range size, two small (< 15 g) bats, the frugivorous *Artibeus watsoni* and the gleaning animalivorous *Miconycteris microtis* (Phyllostomidae) exhibited marked differences in home range size and mobility (Albrecht et al. 2007). Home range size of *A. watsoni* was highly variable (~ 2–18 ha), and it regularly flew between islands, thereby crossing open water (Fig. 3).

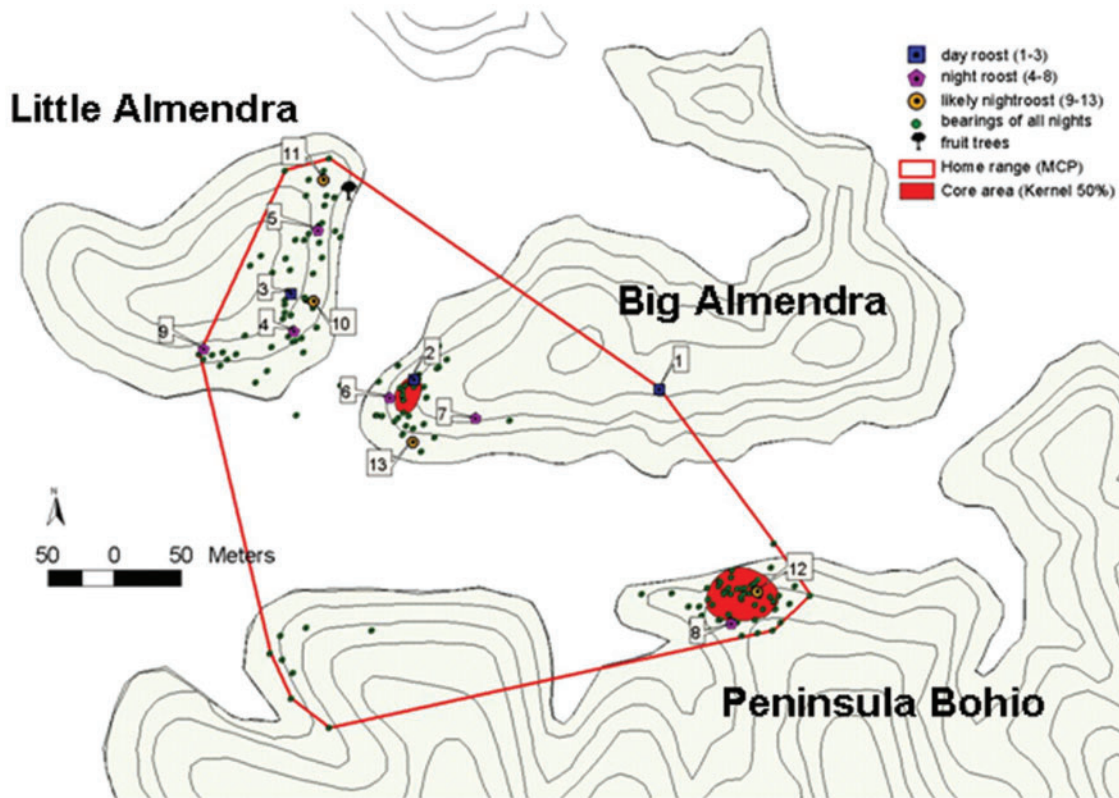


Fig. 3 Spatial use of a male *A. watsoni* tracked throughout 5 nights on two islands (Little and Big Almendra) in Gatún Lake and the adjacent mainland (Peninsula Bohio), Panamá. Each bearing is depicted as a tracking point. Day and night roosts are numbered. Home range (red line) is given as Minimum Convex Polygon. For further details see Albrecht et al. (2007).

In contrast, *M. microtis* consistently used smaller home ranges (1.6–7.5 ha), and remained on small islands where it had established resident colonies (Fig. 4). Interestingly, *M. microtis* was the only gleaner animalivore present on almost all islands, regardless of island size or degree of isolation, and with an overall abundance exceeding that observed at the mainland sites (Meyer and Kalko 2008). It is likely that this species has evolved a highly efficient foraging strategy that permits exploitation of resources even on small islands where habitat suitability and prey availability is very low for other, larger gleaners.

Furthermore, a radio tracking study of the small gleaner animalivore *Lamproncycteris brachyotis* on BCI revealed frequent long-distance commutes, some individuals flew several kilometers from their day roost across the island to their foraging sites (Fig. 5) (Weinbeer and Kalko 2004). This study suggested also that *L. brachyotis* does not glean insects in the forest understory but forages on the wing for insects above or next to tree crowns, a behavior that had previously not been documented for phyllostomid bats.

Finally, the small trawling phyllostomid, *M. macrophyllum*, flew even longer distances on a nightly basis and had more extensive home ranges compared to the other three small phyllostomids (Meyer et al. 2005). Typically, these bats foraged over water, using a combination of gleaning and aerial hawking to capture insects from or near the water surface (Weinbeer et al. 2006). Average nightly flight times were 3.5 h, with the bats covering estimated total distances of 30–50 km/night. Clearly, vagility and movement patterns cannot be fully predicted from morphological traits such as body mass alone, but require a thorough understanding of the bats' behavior (Meyer et al. 2005; Weinbeer et al. 2006). Improvement of existing radio tracking techniques through automated tracking systems (see Wikelski, this volume), advances in transmitter technology, and novel algorithms to assess and evaluate the spatial use of habitat by bats open up new avenues of research to fully appreciate the crucial role of movement patterns of bats with regard to habitat connectivity. The latter is of great importance in the development of meaningful conservation programs targeted at maintaining diversity and functionality of ecosystems at various scales.

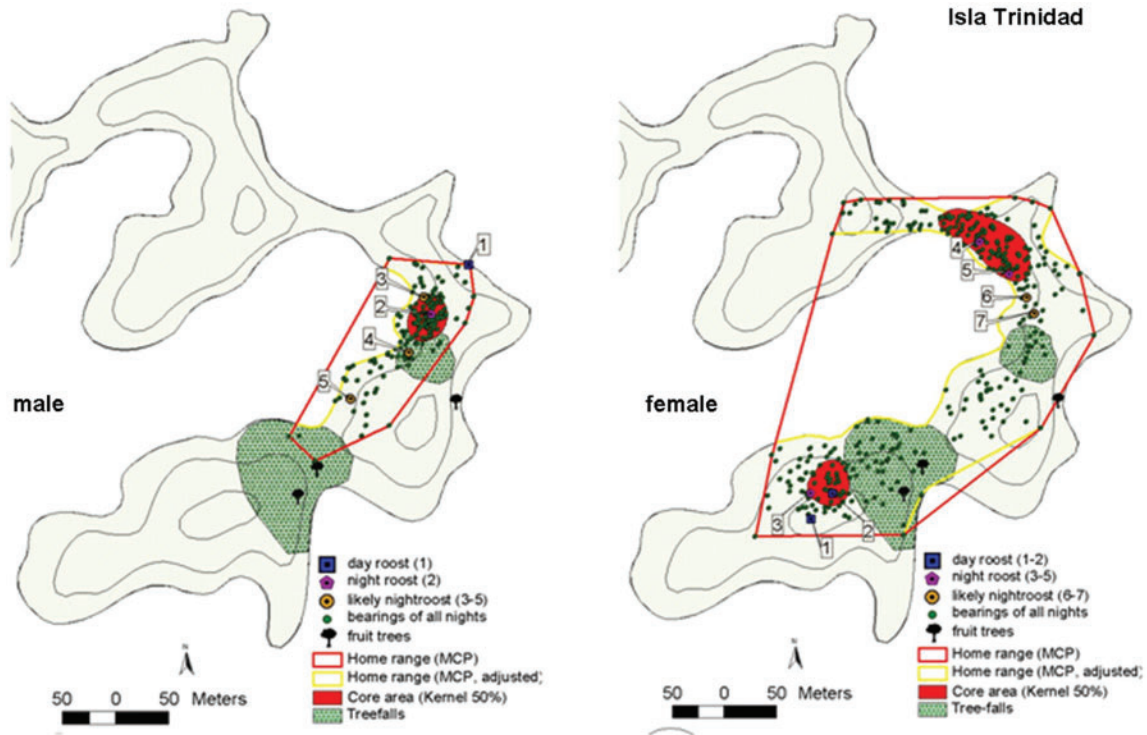


Fig. 4 Spatial use of a male and a female *M. microtis* tracked throughout 4 and 4.5 nights, respectively, on Trinidad island, Gatún Lake, Panamá. Each bearing is depicted as a tracking point. Day and night roosts are numbered. Home range (red line) is given as Minimum Convex Polygon. For further details see Albrecht et al. (2007).

Future perspectives: combining data on diversity patterns and behavior of mobile animals with remote sensing

In recent years, remote sensing has greatly advanced, leading to a set of novel tools well suited for research on biodiversity. New sensor technologies with improved resolution offer the opportunity to integrate data sets on land cover, land use, and structural components of habitats, i.e. classification of forest types or canopy closure reflecting among others differences in resource distribution and the atmosphere, with patterns of species' distributions. This data integration has the potential to form the basis for the establishment of detailed monitoring programs of biodiversity on several spatial scales. As basic distributional and ecological information becomes available for an increasing number of species, the improved resolution of remote sensing data sets with the possibility to gather information on patch size, habitat types, or amount of edge space provides novel opportunities for studies integrating information on landscape structure with distributional and behavioral information of bats such as mobility.

Currently, three major satellite systems are available that are equipped with medium-resolution

sensors (60–300 m): the American MODIS (Moderate Resolution Imaging Spectroradiometer), the European MERIS (Medium Resolution Imaging Spectrometer) and the Indian IRS-P6 (Indian Remote Sensing Satellite). The three systems offer daily to 3-day global coverage and give a consistent view over continents and regions (Tucker et al. 2005). These instruments permit for the first time detailed analysis of time series. Time series have the potential to deliver data for the establishment of long-term monitoring programs depicting, for instance, spatiotemporal changes in the configuration of landscapes which then can be linked to predictions on possible changes in species distributions based on ecological and mobility data of the animals (Colditz et al. 2006). New data sets obtained with those technologies include the Global Inventory Modeling and Mapping Studies (GIMMS), which features a normalized difference vegetation index (NDVI) available for a 22-year period spanning from 1981 to 2003. The GIMMS data set has been corrected for a number of adverse effects and delivers now a consistent view over larger regions and continents. Additionally, since 2000, MODIS and MERIS provide data on biotic and abiotic parameters like NPP (Net Primary Productivity), LAI (Leaf Area Index), and LST (Land Surface

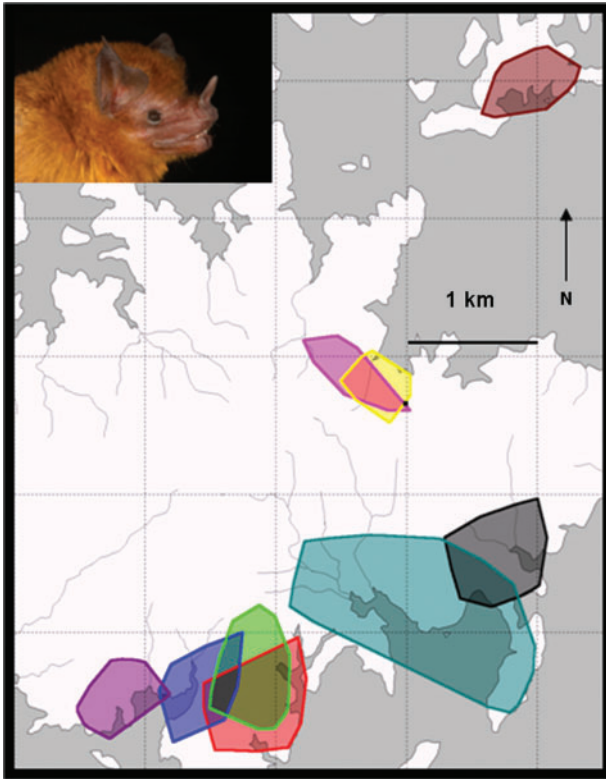


Fig. 5 Tracking data of eight individuals of *L. brachyotis* on BCI, Panamá. Home range of each individual throughout the tracking time is color-coded and calculated as Minimum Convex Polygon. For further details see Weinbeer and Kalko (2004). Photo credit: M. Tschapka.

Temperature), all of which are seen as important drivers of biodiversity.

MODIS and MERIS deliver data at a resolution of 250–1000 m for all terrestrial surfaces. In the higher resolution range of 10–30 m, sensors like SPOT (Satellites Pour l'Observation de la Terre) or the Indian LISS-4 (Linear Imaging Self Scanner) have emerged and even in the very high resolution range (0.4–5 m), sensors (Orbview, IKONOS, Quickbird, Worldview, TerraSAR-X) have become available that facilitate direct integration of field data and remote sensing data with Google Earth as a highly integrative portal for the use and understanding of remote sensing datasets.

Improved resolution permits integration of more fine-grained, field-based data and it delivers an urgently needed, better understanding of the effects of scale on spatial patterns, a problem inherent in remote sensing as well as field data sets as well as with data on species diversity (Rahbeck 2005). The latter can obviously lead to markedly different patterns and conclusions, which is particularly important to consider when dealing with the impacts of habitat modification on faunal assemblages (Hill

and Hamer 2004). Currently, the direct relation of species-related field samples to remote sensing signals is still difficult. The main difficulties lie in the different approaches of counting versus measuring. Species data are usually based on a classification process involving the perception and pattern recognition capacity of the researcher while remote sensing data are based on direct measurements of surface parameters. Whereas field data, like a 1 m² sample of vegetation or a mapped 50 × 5 m transect containing a complete mapping of all plant species, cannot be related directly to remote sensing data, characteristics of surface structures (i.e., canopy) are best recorded by remote sensing. Technical improvements and the combined analysis of patterns covering the range of the sensors' spatial resolution and the distribution patterns of organisms over larger regions are likely to greatly improve our abilities to link data sets gathered in the field to remote sensing, thereby bridging the gap between patterns based on sampling of species on the local level and patterns of species distributions projected onto the regional or continental scale. Integration of remote sensing data and field data across several spatial scales is particularly relevant for a better understanding of the role of the atmosphere in influencing diversity patterns.

As an example, current remote sensing technology allows selection of a dataset from Google Earth for a given region and to overlay it with data collected in the field, e.g., on functional types and distribution of plants and indices of leaf area. Processing of the remote sensing data sets by using differences in the measured surface reflectance and subsequent synthesis combination of the data leads to data sets that show, for example, heterogeneity of canopy cover as one value, fragmentation of habitats as another, and vegetation type as a third. If one joins this 30 × 30 km sample together with a data set at lower resolution (30 m) but with coverage of a larger area (180 × 180 km) and transforms it accordingly, a new data set is produced that contains values for the degree of habitat fragmentation as well as the *density* of vegetation types. This enlarged data set can then be combined into a medium-resolution (500 m) wide-area coverage (1200 × 1200 km) data set covering a whole country or even larger regions. Furthermore, this process can be applied over a longer temporal scale, e.g., several months or years, thus creating a time series.

This method allows comparison of data on species occurrence obtained by sampling in the field with specific surface parameters documented with remote sensing. Combined data analysis of samples collected

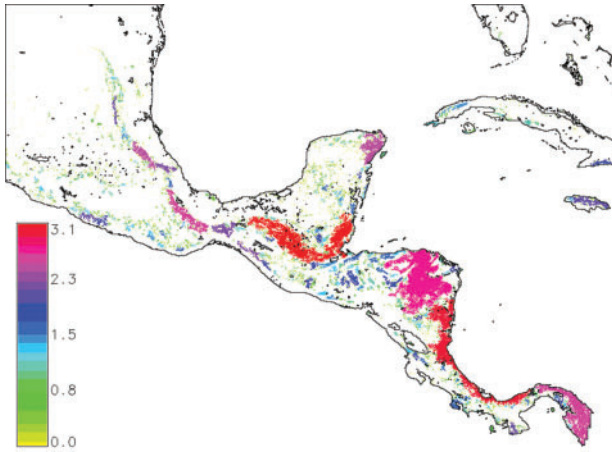


Fig. 6 Complexity SHAPE Index (log transformed) of forest fragments across Central America with compact patches in yellow and complex patches in red. Based on a NOAA AVHRR landcover product (Hansen et al. 2000).

over longer periods of time are likely to highlight rather detailed patterns and dynamics of species occurrence and their intricate association with certain environmental parameters. The use of time series overcomes the prevailing problem of relating time of field samples with the time environmental parameters have been recorded with remote sensing. New sensors allow hourly to daily coverage (polar orbits of MODIS or constellations like RapidEye record data sets every 4 to 24 hours) and thus permit the full integration of samples collected in the field with reflectance values measured by remote sensing. The temporal stability of most environmental parameters makes a direct relation of field data with remote sensing data feasible. Furthermore, this approach promotes research where dynamics and changes in ecosystems over time are monitored.

In this context, comprehensive, local species inventories of bats can be combined and integrated into a multi-dimensional space in order to identify areas of similar surface characteristics and vegetation features. Thus, areas likely to harbor similar sets of species may be identified and scrutinized in further field surveys and high-resolution remote sensing imagery. The combined analysis of very high resolution data sets (1 m spatial resolution) with data sets of larger coverage (60 m spatial resolution) offers the chance to transcribe effects from a local to a regional scale.

One envisioned result of such an analysis could be the assessment of the impact of habitat fragmentation (see example of patch complexity in Fig. 6) on biodiversity or species' distribution (Fahrig 2003; Ewers and Didham 2006). Although it is indispensable to always include ground-truthing in the

field as a control, the development of new modeling tools is likely to permit predictions of expected change in species composition through extrapolation of ecological requirements and dispersal patterns of highly mobile species, such as bats, from the local scale onto the landscape level and regional scale (Townsend et al. 2002). Depending on the scale and taxa examined, it seems likely that indices can be developed in which features such as habitat connectivity and patch size play central roles in predicting the potential effects of fragmentation on animals differing in mobility (Bender et al. 2003) and hence on ecosystem services by pollinators, seed dispersers, and predators of insects. It seems likely that an improved spatial resolution of several meters as it will be delivered in the near future by some of the sensors and these will permit the integration of fine-scale radio tracking of species' mobility onto the landscape. This requires quality data on the use of the atmosphere by bats.

Furthermore, the combination of spatial use and resource distribution is likely to lead to important and new results in our understanding of factors driving biodiversity. For example, recent studies have shown that diversity in fruit-eating birds in Africa is largely determined by food plant diversity (Kissling et al. 2007). Hence, the improved quality of broad-scale data on vegetation and habitat types obtained through remote sensing is likely to form the basis of refined approaches for a better understanding of biodiversity, including questions about the use of the atmosphere by bats and potential effects of human-induced change on structural components of species assemblages.

The new developments in satellite sensors, further improvements in data assessment as well as improved analysis and synthesis capabilities are highly likely to facilitate our understanding of biodiversity patterns and associated processes at a broad range of spatial and temporal scales even more. Inter-disciplinary research in a variety of disciplines, including geography and biology, combined with the new remote sensing technologies, are likely to lead to the development of novel products that potentially can also be applied in conservation.

New data sets delivered by remote sensing with a high relevance for conservation and management of biodiversity could, for instance, include time-series analysis of selected regions focusing on changes in landscape characteristics and habitat configurations. Continuous monitoring of certain habitat types including different structural features such as vegetation, canopy structure, and boundary layers between vegetation types potentially permits the establishment

of “early warning systems”, pointing out, for instance, loss of connectivity through fragmentation and its possible consequences for species diversity and ecosystem functioning.

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