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Review

Capturing the fugitive: Applying remote sensing to terrestrial animal distribution and diversity

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Abstract

Amongst many ongoing initiatives to preserve biodiversity, the Millennium Ecosystem Assessment again shows the importance to slow down the loss of biological diversity. However, there is still a gap in the overview of global patterns of species distributions. This paper reviews how remote sensing has been used to assess terrestrial faunal diversity, with emphasis on proxies and methodologies, while exploring prospective challenges for the conservation and sustainable use of biodiversity. We grouped and discussed papers dealing with the faunal taxa mammals, birds, reptiles, amphibians, and invertebrates into five classes of surrogates of animal diversity: (1) habitat suitability, (2) photosynthetic productivity, (3) multi-temporal patterns, (4) structural properties of habitat, and (5) forage quality. It is concluded that the most promising approach for the assessment, monitoring, prediction, and conservation of faunal diversity appears to be the synergy of remote sensing products and auxiliary data with ecological biodiversity models, and a subsequent validation of the results using traditional observation techniques.

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Keywords: Biodiversity; Animal species richness; NDVI; Habitat mapping; Habitat heterogeneity; Remote sensing

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1. Introduction

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The importance of biodiversity conservation is widely recognised, as there is a general concern about its current status and about the responses by society to present and future environmental changes (Gaston, 2000; Mace, 2005; Millennium Ecosystem Assessment, 2005). Biodiversity definitions include different levels of organisation of biological variation and richness, from genes and species to ecosystems. Noss (1990) expressed the variation at each of these hierarchical levels in terms of three spheres: composition (e.g. the genes of different cattle races), structure (e.g. the ratio of large versus small bodied animals), and function (e.g. forage consumption). However, this multi-faceted nature of the term biodiversity makes it a difficult concept to capture in one definition or description, so it cannot be measured in a single parameter (Noss, 1990; Wolfgang, 2003; Scholes and Biggs, 2005). The challenge to measure these levels and spheres of organisation of biological variation has led to the search of relevant biological indicators from which biodiversity could be measured. These indicators include species, habitats, and eco-regional characteristics, which can be sampled in the field, categorized, and interpreted.

Despite the efforts of scientists and policy makers to reduce the rate of species loss, there is still a gap in the overview of continental and global patterns of species distributions (Brooks et al., 2001; Ceballos et al., 2005). Remotely sensed data contribute to the assessment and monitoring of biodiversity from local to global scales (Murthy et al., 2003), and over time, with spatially continuous coverage. Since the 1980s, satellite multispectral imagery became a common tool, particularly in exploring the composition of biodiversity, i.e. species richness (e.g. Saxon, 1983; Nagendra, 2001). Several articles reviewed the potential and contribution of remote sensing data products to assess terrestrial vascular plant species diversity (e.g. Stohlgren et al., 1997; Gould, 2000; Griffiths et al., 2000; Nagendra, 2001). This review article has the purpose to summarise the historical development and prospective approaches in which remote sensing was used to assess and monitor terrestrial faunal diversity. While an important methodology of plant diversity consists in direct mapping of species and associations (Nagendra, 2001), the fugitive and secretive nature of animals requires approaches based on proxies and surrogates. Based on the currently applied methodologies, the following broad categories were identified, reflecting chronological approaches in this field: (1) habitat suitability mapping, relying on species-habitat associations, (2) spatial heterogeneity assessment based on primary productivity, (3) temporal heterogeneity assessment, (4) mapping of structural properties of habitat, and (5) mapping of plant chemical attractants, relying of the influence of land cover attractants on fauna, such as forage quality. These latter categories enclose the range from the most frequently used methodologies applied to terrestrial animal taxa to the latest approaches found in literature. In addition, direct and indirect measurements of species diversity and distribution are illustrated. Within each approach, the literature was, furthermore, grouped following the taxonomical system: mammals, avifauna, reptiles,

amphibians, and invertebrates. These taxonomic groups represent the most frequently studied taxa, and reflect different challenges to the application of remote sensing to assessing animal species presence. The discussion evaluates theory development and the potential use of remote sensing techniques for terrestrial animal ecology studies related to species diversity, and the prospective direction of remote sensing approaches applied to this field.

2. Assessing species richness through habitat suitability mapping

The most straightforward approach to estimate animal distribution or species richness from remotely sensed data is to identify and detect animal habitat suitability. A habitat is the local environment in which an organism normally lives and grows. In order to map habitat, knowledge of habitat preferences and the requirements of the species of interest is combined with airborne or satellite data, biophysical, geophysical data, and meteorological data.

For ecological biodiversity assessments, field surveys are usually executed to collect data on species distribution, habitat use or characteristics of nesting, breeding, or burrowing sites. Additionally, habitat use patterns can be derived from analysis of movements of radio or satellite collared individuals (e.g. Kanai et al., 1994; Bechtel et al., 2004). Using remote sensing, these local measurements can be extrapolated to cover a large region of interest, and estimate habitat suitability. After collecting field survey data, spectral in situ measurements at the locations of the ecological assessments or the spectral properties of the pixel corresponding to this location are used as training data to classify the imagery for a larger area. Resulting maps with spatially discrete habitat types can then be analysed using a wide array of statistical techniques to validate classified habitat with species population data. The main problem with this approach is the assumption that empirical conditions at the field survey point may be extrapolated over a large area. Such an assumption needs to be carefully tested otherwise the resulting maps will be biased by the sample points. In other words, habitats may not be described and stratified in ecologically meaningful terms, which could limit the predictive value of the relationships between reflectance data and species distribution within and beyond the study area.

The following sections demonstrate how widely remote sensing approaches are applied to estimating habitat suitability in terrestrial environments throughout many animal taxa.

2.1. Mammals

One of the earliest publication involving satellite imagery to detect mammalian species dates from 1980, when Löffler and Margules (1980) estimated the distribution of hairy nose wombat (Lasiorhinus latifrons) in southern Australia by identifying burrows and mounts from Landsat imagery. Also in Australia, Saxon (1983) used Landsat imagery to locate a habitat suitable for the re-introduction of rufous hare-wallabies Lagorchestes hirsutus. Later in the 1980s this approach of relating remotely sensed land cover types to habitat suitability, was used amongst others for assessment of the habitat of the giant panda, Ailuropoda melanoleuca (De Wulf et al., 1988), elk, Cervus elaphus (Eby and Bright, 1985) and white-tailed deer, Odocoileus virginianus borealis (Ormsby and Lunetta, 1987). The method of habitat mapping by means of signature classification was applied throughout the 1990s (e.g. Huber and Casler, 1990; Del Valle et al., 1997; Fuller et al., 1998; Cardillo et al., 1999; Richards, 1999) and is still used today (e.g. Oindo et al., 2003; Sharma et al., 2004).

Other authors tried to derive general patterns of species richness in relation to habitat (White et al., 1997; Mason et al., 2003). Fuller et al. (1998) combined field surveys of plants and animals with satellite remote sensing of broad vegetation types to map biodiversity in the Sango Bay area in Uganda. They identified 14 landcover classes from reflectance characteristics and validated the results with field surveys, recording 86% correspondence between field and map data. The field surveys included flowering plant species, dragonflies, butterflies, fish, amphibians, reptiles, birds, and mammals. These species data were used to generate biodiversity ratings, based on species 'richness' and 'rarity', which could be related to the vegetation cover. Similarly, Cardillo et al. (1999) predicted species richness and occurrences of terrestrial mammals from Principal Component Analysis (PCA) ordinated land cover variables from the Land Cover Map of Great Britain. Because of the high proportion of species with geographic distributions changing independently of land cover, the predictive strength of the land cover data for species richness assessment was however limited.

Heitkönig et al. (2003) directly correlated the distribution of large mammalian herbivores in the Okavango delta in Botswana with Landsat Thematic Mapper (TM) and Enhanced Thematic Mapper (ETM+) reflectance data. Animal distribution was sampled along field transects, while registering the locations with a Global Positioning System (GPS), and the recorded

animal presence was related to the spectral signature of the location. A multivariate approach allowed for the distinction of occurrence of several mammalian species, including elephant (Loxodonta africana), zebra (Equus burchelli), and impala (Aepyceros melampus). However, species with low densities in the field, including giraffe (Giraffa camelopardis) and wildebeest (Connochaetes taurinus), were not successfully distinguished. Bechtel et al. (2004) used a comparable method for woodland caribou (Rangifer tarandus caribou). Because habitat maps were incomplete for their study area, they correlated spectral information obtained from Landsat 5 TM satellite data with Global Positioning System (GPS) locations of satellite collared, and Very High Frequency Radio locations of collared animals. First, a statistical approach was used to automate the classification of each satellite imagery pixel to generate landscape classes based on characteristic spectral signatures. These classes were then regrouped corresponding to their relation with the GPS-registered animal presence. The resulting map indicated the woodland caribou use and avoidance of areas, based on corresponding identified spectral classes of the satellite imagery.

Coops and Catling (1997) used airborne multispectral videographic data to accurately predict the complexity of fauna habitat across forested landscapes. This video system provides a tool for stratifying the forest into fauna habitats to predict the composition, spatial distribution and abundance of faunal groups that are known to prefer the eucalypt forests (Coops et al., 1998; Catling et al., 2000). Coops and Catling (2002) then related habitat quality based on complexity scores, to predict future relative abundance of the long-nosed potoro (*Potorous tridactylus*) and the large wallabies (red-necked wallaby, *Macropus rofogriseus*, and swamp wallaby, *Wallabia bicolour*) across landscapes.

Mammals are relatively well studied and their habitat preference is quite well documented, which is of vital importance for successfully correlating mammal occurrence to remotely sensed habitat data. Many species however (e.g. generalist species) use more than a single distinct vegetation type, and non-herbivore species tend to have little direct association with a habitat or vegetation type that can be remotely sensed (e.g. Cardillo et al., 1999; Cowley et al., 2000). In other cases, there is a limitation to the use of remotely sensed data due to the animals' elusive nature. The predictive value of mammal-habitat relationships will also be limited for species for which the habitat preference changes with geographical position (e.g. Cardillo et al., 1999). Another issue that complicates the link between species presence and habitat characteristics is the sociobiology of the species. The predicted distribution of guanaco (*Lama guanicoe*), for example, proved to have little correlation with the real distribution and densities (Del Valle et al., 1997). The socio-biology of the species, classified as 'resource defence polygyny' (Franklin, 1983) where a dominant male will defend his territory against other males, in combination with interspecific competition with sheep and anthropogenic influences, was identified as the possible reason for the inaccuracy of the predictions.

2.2. Avifauna

Since the 1980s, remote sensing has been widely used in assessing and monitoring bird distribution and habitats (e.g. Baines et al., 1986; Perras et al., 1988; Minton et al., 2003; Venier et al., 2004). Habitat maps are aggregated from land cover maps that are generally produced from Landsat or radar imagery. The habitat maps are then combined with data from bird composition and abundance surveys, yielding distribution and density maps (e.g. Palmeirim, 1988; Schwaller et al., 1989; Avery and Haines-Young, 1990; Kanai et al., 1994; Morisson, 1997; Debinski et al., 1999; Osborne et al., 2001; Taft et al., 2003; Fuller et al., 2005; Prins et al., 2005).

Apart from Miller and Conroy (1990), who classified data from the Satellite Probatoire d'Observation de la Terre (SPOT) to predict Kirtland's warbler (Dendroica kirtlandii) occurrence in the Bahamas based on vegetation types, most studies applied Landsat TM data for the prediction of single bird species habitat suitability. Knowledge and ground studies on habitat preferences for nesting and feeding were combined with Landsat data for sedentary (e.g. Osborne et al., 2001; Johnson et al., 1998; Hurlbert and Haskell, 2003) as well as migratory birds (e.g. Green et al., 1987; Avery and Haines-Young, 1990; Sader et al., 1991). Environmental criteria (i.e. vegetation cover, landscape characteristics) derived from Landsat data were used to assess the location of nesting sites of buzzards, Buteo buteo (Austin et al., 1996) and great sandhill cranes, Grus canadensis, in Minnesota (Herr and Queen, 1993). Further, the probability of occurrence of 14 out of 23 species of land birds in Maine (Hepinstall and Sader, 1997), as well as winter distributions of sage grouse (Centrocercus urophasianus) in Utah (Homer et al., 1993) were successfully predicted using Landsat imagery. Kanai et al. (1994) analysed data of satellite collared red crowned cranes (Grus japonensis), hooded cranes (Grus monacha) and white-naped cranes (Grus vipio) to determine habitat use and species distribution. Subsequently, a combination of Landsat with Marine Observation Satellite-1 Multi-spectral

Electronic Self-scanning Radiometer (MOS1 MESSR) data was used to derive the characteristics of seven sites that were identified as crane habitat. The method proved very helpful, because the large crane habitats cannot easily be monitored through ground studies.

Some recent studies focus on avifaunal diversity, leading from single species assessments to diversity predictions for whole taxa. Nøhr and Jørgensen (1997) related avian diversity in northern Senegal to landscape diversity, while Debinski et al. (1999) categorized habitats in the Greater Yellowstone ecosystem based on Landsat data and then determined the relationship between habitat categorizations and plant, bird, and butterfly species distribution patterns. They found that sites of highest species richness coincided for plants, birds, and butterflies. This coincidence of 'hotspots' of different taxa shows those indicator taxa could be used to assess an areas' biodiversity status. Also in the Greater Yellowstone ecosystem Saveraid et al. (2001) assessed potential bird habitats for 11 types of montane meadows. Landsat imagery was further analyzed to identify habitats for migratory birds in Costa Rica (Sader et al., 1991), and to predict bird species richness in boreal agricultural-forest mosaics in south-western Finland (Luoto et al., 2004). Fuller et al. (1998) related the diversity of various taxa, including flowering plant species, dragonflies, butterflies, fish, amphibians, reptiles, birds and mammals in Uganda to vegetation cover derived from Landsat. Areas of bird endemism in East Africa were related to remotely sensed climatic variables by Johnson et al. (1998), to obtain general patterns of bird species richness. It was concluded that contemporary environmental conditions, ultimately determined by climate, appear to account for a substantial fraction of the observed variation in the distribution of endemic bird areas.

The above bird studies demonstrate that habitat classifications based on remote sensing data can be successful for sedentary and migratory birds, as well as bird communities. However, the spatial and spectral scale of the data appears to be a crucial factor in the prediction of bird occurrence patterns. Laurent et al. (2005) investigated the potential of using unclassified spectral data for predicting the distribution of three bird species by varying (1) the window size used to average spectral values in signature creation, and (2) the threshold distance for recording bird observations. Accuracy statistics for each species were affected by the detection distance of point count surveys used to stratify plots into presence and absence classes. Thus, the accuracy of wildlife occurrence maps classified from spectral data will differ given the species of interest, the spatial precision of occurrence records used as ground references and the number of pixels included in spectral signatures. Akin to mammal studies, a low number of bird records per habitat type decrease the power of the statistical tests to distinguish differences between habitat use and availability in bird studies (Garshelis, 2000).

2.3. Reptiles and amphibians

Only two studies on mapping reptilian or amphibian habitats using remote sensing data were identified, but both were innovative and successful. Raxworthy et al. (2003) assessed and predicted the distribution of known and unknown chameleon species in Madagascar, using a combination of satellite data (Moderate Resolution Imaging Spectroradiometer (MODIS) and historical and recent chameleon observations on the island). A generic algorithm for rule-set prediction (GARP) was used to delineate ecological niches, based on environmental geographical information system (GIS) data, and to predict geographical distributions of species. This study leads to the discovery of seven new species of chameleon.

Scribner et al. (2001) used in situ and remotely sensed data of the aquatic and terrestrial environment, to examine the correlation of habitat characteristics with population demographic and genetic characteristics of the common toad (*Bufo bufo*). This study was the only one (encountered) that focussed on the sub-species level. Allelic (i.e. genetic) richness, population size, and toad presence were mostly associated with terrestrial habitat variables, like pond density, availability of woodlands, hedgerows, and anthropogenic development.

While remotely sensed data for animal diversity assessment using habitat characteristics is increasingly used, its application to reptile and amphibian diversity remains poorly explored. Despite the success of the above-presented studies, there is still a gap between ecological theory and the application of remotely sensed data. One of the problems is that there is no clear understanding over which spatial scales the specieshabitat relationships apply for species of interest, specifically those of limited vagility. The complex life histories of amphibians and their secretive behaviour add to the challenge of successfully using remotely sensed data.

2.4. Invertebrates

Remotely sensed imagery is increasingly used to detect insect habitats or the effects of insects on their environment (Riley, 1989; Hay, 1997). Habitat patch characteristics essential for many insects, such as micro-variations in wetlands, grasslands and forests are too small to be identified using conventional imagery (Fisher, 1997; Cracknell, 1998). A recent study tackled the problem of sampling scale inherent to insect habitat mapping by comparing two satellite sensors with different spatial resolution (SPOT and Landsat) and, as a result, optimized insect species richness mapping at a landscape level (Chust et al., 2004).

One of the most common cases of insect habitat mapping deals with swarming insects that have the potential to destroy their habitat. Defoliating insects, once present in a food-endowed environment, quickly expand to a devastating outbreak consuming their primary resource. This allows a precise distribution mapping through classification of vegetation defoliation or discoloration using remote sensing. For instance, Joria et al. (1991) successfully classified gypsy moth (Choristoneura fumiferana) defoliation into three damage classes by delineating affected areas with Landsat data. Franklin and Raske (1994) differentiated four defoliation levels of spruce budworm (C. fumiferana) in a balsam fir forest analyzing SPOT HRV data. The spectral response of the Jack Pine (Pinus *banksiana*) canopy, attacked by the Jack Pine budworm (Choristoneura pinus pinus), was first described by Hall et al. (1995). Landsat TM images before and after defoliation were acquired to map the top-kill severity. Another aggressive defoliator actor widely documented is the mountain pine beetle (Dendroctonus ponderosa) which is primarily hosted by the lodgepole pine (Pinus contorta). Combinations of SPOT multispectral and panchromatic bands and PCA-transformations were evaluated by Sirois and Ahern (1988) to determine their ability to detect mountain pine beetle mortality ('red attack'). A conceptual model based on spectral brightness-greenness was developed and tested (Price and Jakubauskas, 1998) to relate beetle infestation to spectral properties. Similar examples are reported for pear thrips (Taeniothrips inconsequens) (Vogelmann and Rock, 1989); the black-headed budworm (Acleris variana) (Franklin et al., 2002; Luther et al., 1997); the aspen tortrix (Choristoneura conflictana) (Hall et al., 2003); and the Douglas-fir beetle (Dendroctonus pseudotsugae) (Lawrence and Labus, 2003).

In more diverse ecosystems, notable efforts to create habitat maps from remotely sensed data were made for butterfly and beetle species. Butterfly species are often host-specific and their diversity may correlate with underlying plant diversity. Thus, Debinski et al. (1999) reported that several rare butterfly species significantly correlated with remotely sensed habitat types in the Greater Yellowstone Ecosystem. The modelling of Luoto et al. (2002) supported the findings that specialist butterfly species distribution is closely related to remotely sensed habitat types. British ground (*Coleoptera*, *Carabidae*) (Eyre et al., 2003a) and water beetle (*Coleoptera* spec.) species pool distribution (Eyre et al., 2003b) strongly correlated with satellite-derived land cover data. Chust et al. (2004) successfully assessed woodland invertebrate taxa distribution based on satellite imagery.

Compared to other taxonomic groups, the ability of remote sensing data to contribute to the mapping and prediction of occurrence of invertebrate diversity appears to be poorly investigated. The current trend of studies on terrestrial invertebrates shows an emphasis on insects, whereas for other taxa there is no literature known to the authors. The majority of articles concentrated on insects that are considered pests, and their effects on crops or forests. However, very few studies deal with conservation efforts. Besides, the approach is limited to habitat-insect relationships using only beta diversity (i.e. local diversity, within-community component) whereas gamma diversity (i.e. total regional diversity) is not taken into account.

2.5. Summary

Habitat suitability is widely used as a remotely sensed proxy for species distribution and richness. It mainly covers the composition sphere of biodiversity. Though successful in many of the discussed examples, the micro-heterogeneity of an area required for many species does not always allow a discrete classification approach. Many species (e.g. generalist species) use more than a single distinct vegetation type and some non-herbivore species may show low strength of association with a habitat or vegetation type because many species, regardless of the degree of habitatspecificity, do not occupy the full extent of their preferred habitat type that can be remotely sensed (e.g. Cardillo et al., 1999; Cowley et al., 2000). Current habitat classification is based on discrete maps and the resulting representation of class boundaries may not capture the meaningful ecological functional variability for each species.

Correspondence between field data and remotely sensed imagery aimed at species communities was found to be high in some studies (Fuller et al., 1998; Bechtel et al., 2004), but limited in others (e.g. Cardillo et al., 1999; Heitkönig et al., 2003). One factor limiting the accuracy in this approach appears to be the application of proxies at inappropriate spatial, spectral,

and temporal resolutions. Remote sensing studies involving species diversity need to consider different levels of taxonomic resolution. Several studies used a higher or lower taxonomic resolution approach as proxy for estimating species richness for other taxa (Báldi, 2003; Olsgrad et al., 2003; Doerries and Van Dover, 2003; Sauberer et al., 2004; Ward and Larivière, 2004). Cross-taxon congruence in biodiversity across different groups of organisms was also investigated as potential surrogates for each other (Negia and Gadgil, 2002; Heino et al., 2005). However, correlations and congruencies in species richness among different taxonomic groups are difficult to generalise as they differ to environmental gradients. Accuracy of assessing species diversity in particular may further increase by adding environmental variables to the analysis. Moreover, despite the potential of remotely sensed data for habitat suitability analysis, ground survey data (e.g. species composition, abundance, and density maps) are essential to provide the basis for finding ecologically meaningful interpretations and for predicting species distribution and diversity.

3. Assessing species richness through spatial heterogeneity based on primary productivity

Spatial heterogeneity is one of the driving factors in the explanation of species richness (Stoms and Estes, 1993). It has long been accepted that environmental heterogeneity may support richer species assemblages compared to simple ecosystems (Simpson, 1949; MacArthur and Wilson, 1967; Lack, 1969; Huston, 1994) because of the creation of niche differentiation (Tilman et al., 1997; Loreau, 1998). This is of particular relevance for dealing with the structural sphere of biodiversity. Here, we are concerned not only with the species composition, but also with the relationships of species towards one another. Factors contributing to the environmental heterogeneity include the temporal and spatial variation in the biological, physical, and chemical features of the environment that create different conditions that species can preferentially exploit (Morin, 2000). In comparison with the previously discussed discrete classification approach, the biological, physical, and chemical features are represented in a continuous way. Depending on the spatial, spectral, temporal, and angular resolution of the remotely sensed data, different levels of differentiation are reached, while post-processing techniques (e.g. density slicing, thresholds) allow the assignment of a discrete class to every pixel, if necessary. Plant productivity and biomass of ecosystems vary in space and time, and the spatial

heterogeneity in productivity is hypothesized to influence species distribution and local abundance of individuals (Brown, 1988; Currie, 1991; Brown and Lomolino, 1998; Gaston and Blackburn, 2000; Oindo and Skidmore, 2002; Seto et al., 2004).

The most commonly used parameter for quantifying productivity and above-ground biomass of ecosystems is the Normalized Difference Vegetation Index (NDVI) (Tucker, 1979). It is based on the strong absorption of the incident radiation by chlorophyll in the red, and the contrasting high reflectance by plant cells in the Near infrared (NIR) spectral region. Because it is based on the normalized ratio of the reflectance in these two spectral bands (i.e. NDVI = (NIR - red)/(NIR + red)), it is an indicator of the greenness of vegetation canopies and able to separate vegetation from other materials. NDVI values proved to be a suitable indicator for vegetation parameters including biomass and aboveground primary productivity (e.g. Sellers, 1985, 1987; Tucker and Sellers, 1986; Box et al., 1989), and it is therefore often correlated to faunal species occurrence and diversity.

3.1. Mammals

Since the late 1990s, an increasing number of studies is analysing NDVI to predict wildlife habitat suitability. Verlinden and Masogo (1997) found a significant positive relationship between NDVI and grass greenness in the Kalahari of Botswana. The relationship between NDVI and animal distribution using animal census data turned out to be more complex. Results using presence/absence data indicated a significant selection for higher NDVI signatures only for ostrich (Struthio camelus) and wildebeest (C. taurinus), the latter only when present in high numbers. The gemsbok (Oryx gazelle), the less abundant eland (Taurotragus oryx), and the locally concentrated springbok (Antidorcas masupialis) did not show significant relationships with greenness and NDVI. Musiega and Kazadi (2004) found, that the great seasonal migration of herds of wildebeest (C. taurinus) in the Serengeti-Mara ecosystem is primarily driven by green vegetation availability, as detected using NDVI. In another African case, Zinner et al. (2001) described habitat quality in central Eritrea through NDVI derived from Landsat MSS satellite data for three baboon species (Papio hamadryas hamadryas, Papio hamadryas anubis and Chlorocebus aethiops). Hamadryas (P. h. hamadryas) and olive baboons (P. h. anubis) tended to select better quality habitats, characterized by a higher NDVI than the average in four out of five ecogeographical zones in Eritrea. Moreover, Hamadryas baboons showed a greater ecological plasticity than olive baboons, which are confined to riverbeds with extended gallery forest.

Although successful in some studies (e.g. Zinner et al., 2001), difficulties in correlating NDVI with the mammal distribution of less abundant species (Verlinden and Masogo, 1997) remain unsolved. Results suggest that relationships between less abundant species and greenness might become insignificant because of a large number of unoccupied suitable habitats. Moreover, the biomass-based approach is successful only with herbivorous species that are sensitive to differences in vegetation characteristics across an area.

3.2. Avifauna

Jørgensen and Nøhr (1996) and Nøhr and Jørgensen (1997) used a combination of satellite image analysis and ornithological surveys to assess avian biodiversity in the Sahel. A Landsat image was used to derive landscape diversity and NDVI, the latter being an indicator for the annual biomass production. Both variables were significant factors in a multiple regression model explaining species diversity. Hurlbert and Haskell (2003) analysed avian species richness in relation to primary productivity and habitat heterogeneity in America. They found that NDVI was a good predictor of seasonal species richness at fine spatial scales, whereas habitat heterogeneity best predicted richness at coarser spatial resolutions. Hawkins (2004) and Hawkins et al. (2003) showed that productivity indicators (NDVI and actual evapotranspiration) correlated well with bird diversity data in North America. A positive correlation between NDVI and bird and butterfly species richness was found by Seto et al. (2004), though this relation did not have a definite functional shape. The relationship between NDVI and species richness of butterflies was strongest at high spatial resolutions, whilst that of birds was better at a lower resolution. In a comparable study, Bailey et al. (2004) distinguished between both habitat primary productivity and habitat heterogeneity by using estimated maximum NDVI and the spatial variation therein. This, in turn, was correlated with species richness of birds and butterflies. They found positive linear relationships between maximum NDVI and the number of functional guilds of birds and species richness of neotropical migrant birds, but a negative association between NDVI and the number of functional guilds of birds and species richness of resident birds. Alternatively, Lee et al. (2004) found a humpshaped relationship between NDVI and bird species

richness in Taiwan, but this became insignificant when effects of roads and elevation were accounted for.

Generally, NDVI proves to be a suitable proxy reflecting primary production or heterogeneity. Nevertheless, the correlations with bird species diversity were positive, hump-shaped, or even negative. The differences in results suggest that a functional link between NDVI and diversity remains elusive, underpinning the importance of ground truth data and validation. Results from several studies (e.g. Bailey et al., 2004; Cushman and McGarigal, 2004) suggest that taxa related scale issues are to be considered when setting up a monitoring scheme using remote sensing

3.3. Reptiles and Amphibians

In a study on two genetically differentiated forms of the Golden-striped salamander (*Chioglossa lusitanica*) in Portugal, Arntzen and Alexandrino (2004) applied GIS-based rules in addition to NDVI data, and found that the southern form of the salamander tended to encounter harsher environmental conditions, with lower precipitation, air humidity, summer temperatures and NDVI, but with a higher number of frost months than the northern form. This is the only study on amphibians using NDVI to assess or monitor species richness.

3.4. Invertebrates

Very few studies use remote sensing data to assess or predict invertebrate species richness beside cases cited above as pests or acting as disease vectors. Nevertheless, Seto et al. (2004) and Bailey et al. (2004) found strong correlations between NDVI values and butterfly species' richness in the Great Basin of western North America.

Insect outbreaks may result in such a dramatic reduction in standing biomass, that it enables vegetation indices to precisely indicate the affected location. Amongst the earliest reports on remote insect detection, Nelson (1983) analysed Landsat data for detecting significant forest canopy alteration caused by gipsy moth (Lymantria dispar) defoliation. The author found that the transformed vegetative index difference (VID = NIR - red) most accurately delineated forest change, and thus was able to map gypsy moth outbreak. More recently, MODIS NDVI data was successfully analysed to map a locust (Locust migratoria manilensis) plague in China (Ma et al., 2005). The NDVI difference image between the data before and after the peak damage of the locust plague accurately mapped the geographical extent and severity of the affected areas.

Many invertebrate studies used NDVI in combination with the reflectance in the middle infrared, land surface temperature, and rainfall to predict abundance, distribution and seasonality of diseases transmitted by an invertebrate vector. Robinson et al. (1997) used satellite data to make predictions of the probable distribution of tsetse fly (Glossina spp.) species in southern Africa. For some subspecies (e.g. Glossina morsitans centralis) the distribution was best correlated with NDVI and the average maximum temperature (75% correct predictions). Relative abundances of the midge Culicoides inicola, the vector of bluetongue virus and African horse sickness virus, at various sites in Morocco and Spain, were compared with climatic variables, altitude and NDVI of the same sites (Baylis and Rawlings, 1998). No significant correlations were found, although wind speed and NDVImin explained over 50% of the variance in abundance. Using broadband NOAA AVHRR data, Hay et al. (1998) successfully correlated NDVI-series with malaria presence in Kenya, and malaria admissions could be predicted across Kenya in an average year with regression analysis. NOAA AVHRR data of a site in Brazil (Bavia et al., 2001) and sub-Saharan Africa (Kristensen et al., 2001; Malone et al., 2001) was similarly used to produce NDVI maps, and analyzed for relationships with the prevalence of schistosomiasis, hosted by snails. Results indicated that NDVI, together with climate data, predicted snail distributions accurately enough for schistosomiasis risk assessment.

As in the case of habitat characteristics used to predict species distribution, the use of NDVI has a strong emphasis on insects considered a pest and those that act as vector diseases, thus there is a lack of conservation-oriented studies for species which are not considered as pests. The use of NDVI has proven to be successful, however it depends directly on the species life history and ecology whether NDVI can act as a surrogate itself or in combination to other remotely sensed data.

3.5. Summary

The approach of assessing species distribution and richness through spatial heterogeneity based on primary production, can be considered as a functional, nondiscrete correlation. Here, animal occurrence and diversity are related to terrestrial features by means of an ecological link. The link emphasised in this review is a trophic one (i.e. food-related), e.g. the case of herbivore animals being correlated with local vegetation biomass or primary productivity (Oindo, 2002; Seto et al., 2004), and heterogeneity therein. The heterogeneity hypothesis affirms a positive relationship between ecosystems diversity and biological diversity (Simpson, 1949; MacArthur and Wilson, 1967; Lack, 1969; Huston, 1994). The spatial and temporal heterogeneity in primary productivity is an explanatory variable to assess species occurrence and richness.

Although successful in some studies (Zinner et al., 2001; Ito et al., 2005), difficulties to correlate NDVI and animal distribution of less abundant mammal species (Verlinden and Masogo, 1997) remains unsolved. Moreover, the biomass-based approach is successful only with species sensitive to differences across an area. More elaborate studies, including additional explanatory environmental variables together with primary productivity heterogeneity (e.g. landscape diversity, evapotranspiration, land surface temperature, rainfall, altitude), explained considerable variation in species richness, but - here too - the explanatory power of each variable differed among spatial scales (Robinson et al., 1997; Baylis and Rawlings, 1998; Hurlbert and Haskell, 2003; Hawkins et al., 2003; Hawkins, 2004; Bailey et al., 2004).

One of the factors influencing the accuracy of predictions of species richness using primary productivity indicators (NDVI) is scale or resolution, where the variation of species diversity - within and between taxa - is better explained using a specific scale, e.g. finer spatial resolution, whereby other variables explains more of the variation at another scale, e.g. coarser spatial resolution (Bailey et al., 2004; Cushman and McGarigal, 2004; Hawkins et al., 2003; Lee et al., 2004; Hurlbert and Haskell, 2003). Another aspect leading to ambiguous accuracy is that the results are based on NDVI and other environmental variables, such as (e.g. average maximum temperature, rainfall, altitude) where the independent marginal effect of each variable is unknown. However, this conditional effect can be as high as 50 to 75% of the explained variation (Baylis and Rawlings, 1998; Robinson et al., 1997).

The major drawback of using vegetation NDVI, however, is the asymptotical approach to a saturation level above a certain biomass density and leaf area index (Tucker, 1977; Sellers, 1985; Todd et al., 1998; Gao et al., 2000;), and has therefore limited value in assessing biomass during, for example, the peak of seasons (Thenkabail et al., 2000). This problem could be overcome by using more recent remote sensing products and techniques, such as the enhanced vegetation index (EVI) from the MODIS product suite (Huete et al., 2002). The EVI was developed to optimize the vegetation signal with improved sensitivity in high

biomass regions and improved vegetation monitoring through a de-coupling of the canopy background signal and a reduction in atmosphere influences. Further, several studies explored the possibilities of narrow band vegetation indices for biomass estimation at high canopy density: Todd et al. (1998) and Clevers and Jongschaap (2001) reported a widening and deepening of the red absorption pit with an increase in biomass. Mutanga and Skidmore (2004a) successfully estimated biomass based on band depth analysis for densely vegetated areas where NDVI values reached an asymptote. In a similar approach it was demonstrated that imaging spectrometer data enhance the estimation of forest stand variables (leaf area index and crown volume) compared to broadband multispectral data (Schlerf et al., 2005).

As indicated above, novel indices developed as proxies for biomass and primary productivity, which are based on spectrometer data, encompass the capability of moving beyond conventional NDVI analysis, particularly suitable for identifying habitats in heterogeneous, densely vegetated areas.

4. Assessing species richness through temporal heterogeneity

Ecoclimatic dynamics are highly complex, ranging from the impact of changing weather, seasonal variation in climate, including interannual cycles, to climate changes such as the global Pleistocene glacial periods. Seasonal variations in climate govern differences in plant species growth and establishment patterns, leading to changes in species composition and distributions (Hobbs, 1990). Consequently, annual variations in vegetation can induce changes in the spatial distribution of plant phenology and growth (Tucker and Sellers, 1986). Therefore, analysis of multiannual land cover data potentially provides a key to understanding the influence of climate variability on shaping ecosystems-which form the overarching hierarchical layer in biodiversity assessment. Continuous data to study ecoclimatic dynamics are available from 1980, with the establishment of the AVHRR meteorological satellite series. The coefficient of variation of AVHRR-derived NDVI data for a number of years indicates the relative variability of the vegetation cover for a given region. Consequently, regions with a high coefficient of variation should reflect large variations in vegetation composition and growth, following unstable and unpredictable climatic conditions over a number of years. On the other hand, low coefficients of variation should indicate regions with small variations in vegetation composition and growth. The use of temporal heterogeneity as a proxy is limited to a small number of studies, therefore all taxa are treated within the same chapter.

Species richness and abundance of large mammals in Kenya were correlated with yearly variation in vegetation, as assessed by the interannual variation of the maximum AVHRR-derived NDVI (Oindo, 2002). In line with the findings above, maximum numbers of species were found in regions with current ecoclimatic stability. These studies support the hypothesis that high species diversity occurs in stable, predictable environments (Sanders and Hessler, 1969; Fjeldså and Lovett, 1997).

Fjeldså et al. (1997) correlated interannual variability of NDVI with biodiversity 'hotspots' of tropical Africa, linking local endemism with local ecoclimatic stability. Similarly, Fjeldså et al. (1999) correlated interannual differences in NDVI with endemism of 789 Andean bird species, thereby linking biodiversity with short-term and long-term ecoclimatic stability. Their results suggest that high ecoclimatic stability allows species to 'accumulate' in an area, whereas large interannual variation limits the community to species able to withstand large fluctuations in habitat quality resulting from interannual climatic variation.

Rodríguez et al. (2005) used regression analyses to examine the relationship between reptile and amphibian species richness and a set of environmental variables related to five hypotheses for geographical patterns of species richness based on productivity, ambient energy, water-energy balance, habitat heterogeneity, and climatic variability. For reptiles, annual potential evapotranspiration (an index of atmospheric energy) explained 71% of the variance. For amphibians, annual actual evapotranspiration (an index of the joint availability of energy and water in the environment), and the global vegetation index derived from satellite data, both described about 60% of the variance. Their results were consistent with reptile and amphibian environmental requirements, where the former depend strongly on solar energy, and the latter on both warmth and moisture for reproduction. On a somewhat different vein, Carey et al. (2001) attempted to identify the causes of amphibian declines around the globe. Four relatively undisturbed areas in northeastern Australia, Costa Rica-Panama, central Colorado, and Puerto Rico were chosen for examination of environmental correlates coincident with mass mortalities at these localities. They compiled a database including descriptions of 120 localities, both at which declines have been documented and at which no declines were known at the time. For each locality,

the number of species, dates and degree of declines, habitat characteristics, and other factors were provided. The authors then used data predicted by models or collected by satellites, airplanes, or direct sampling on the ground to evaluate variations over time in temperature, precipitation, wind direction, UV-B radiation, and concentrations of contaminants. They considered the variation in certain environmental variables unlikely to have directly caused amphibian deaths, but suggested that correlations between these environmental changes and the occurrence of amphibian dic-offs need further investigation into synergistic interactions among environmental variables and possible indirect causal relationships.

4.1. Summary

This approach assesses species richness based on temporal heterogeneity, The multi-temporality of habitat heterogeneity, indicated through the heterogeneity in NDVI, was suggested to be an appropriate proxy to predict species richness patterns (Sanders and Hessler, 1969; Fjeldså and Lovett, 1997). The literature review showed that temporal studies were mostly performed across large regional areas. Further, conflicting results highlight the need to select relevant taxa (refer to taxonomic resolution) and to tune the methodology (Oindo and Skidmore, 2002). Even though NOAA-AVHRR data currently offer the longest time series, they are limited in their spatial and spectral resolution. The variability in vegetation cover as assessed using AVHRR data is the result of multiple influences: intrinsic characteristics of climate such as interannual variability in rainfall and temperature, longterm climate trends, vegetation succession, anthropogenic land-cover changes, and variability in the state of atmosphere (Fjeldså et al., 1997). However, the prospective for the temporal analysis is promising as alternative long-term satellite data series evolve. In the future, the combination of multitemporal satellite data with historical meteorological, ecological and paleological data has the potential of describing interactions among seasonal, annual and long-term climate variability to understand species diversity. Multi-temporal data offer possibilities to overcome the limitations of 'static' habitat studies needed for conservation purposes. Given the fact that many species are extremely mobile over time, e.g. migratory species, single-date studies do not cover the complete range of their habitats. In such cases only multitemporal data can provide a more complete assessment of the species' occurrence and distribution.

5. Assessing species richness through heterogeneity based on landscape structural properties

Brokaw and Lent (1999) stated that, in general, the more vertically diverse a forest is, the more diverse is its biota. Remote sensing has the potential to estimate structural properties and assess their heterogeneity. Most studies relating remote sensing derived structural properties to animal diversity relied on height measuring technologies such as airborne lasers (i.e. airborne LiDAR) and Synthetic Aperture Radar (SAR). They are tools to map vegetation height and its variability, field boundary height, shape of individual agricultural fields, fractional vegetation cover, and aboveground biomass (e.g. Ritchie et al., 1995; Blair et al., 1999; Lefsky et al., 2002; Lim et al., 2003; Mason et al., 2003; Santos et al., 2003; Lefsky et al., 2005).

Recently, Nelson et al. (2005) analyzed LiDAR measurements and video to identify and locate forested sites that might potentially support populations of a mammal, the Delmarva fox squirrel (*Sciurus niger cinereus*). Results indicated that the largest part of the area (78%) met certain minimum length, height, and canopy closure criteria to support squirrel populations. This is the only study addressing a faunal taxa other than the avifauna.

Beier and Drennan (1997) demonstrated that Northern Goshawks (Accipiter gentilis) selected foraging sites based on structure rather than on prey abundance, while (Jansson and Andrén, 2003) found that forest structure is related to species richness. Imhoff et al. (1997) used SAR and aerial photography to map vegetation heterogeneity and relate this to field studies of bird abundances in Australia's Northern Territory. The abundances of individual species changed significantly across floristic and structural gradients, implying that bird habitat can be predicted from SAR data. Hinsley et al. (2002) and Hill et al. (2003) used an airborne laser scanning (ALS) system to map forest structure and related canopy heights to chick mass (i.e. nestling weight), a surrogate for breeding success, which, in turn, is a function of 'territory quality'. They found that, for one species, chick mass increased with increasing forest canopy height, and for a second species, chick mass decreased. Hence, Hill et al. (2003) concluded that airborne laser scanning data can be used to predict habitat quality and to map species distributions as a function of habitat structure. Davenport et al. (2000) devised a technique to measure the height of crops in farmland fields using LiDAR scanning, as crop height is an important predictor of bird species

population and, in turn, can be used as a proxy for bird suitability. Using a population model of skylark (*Alauda arvensis*) they concluded that the achieved structural accuracy – less than 10 cm – would be sufficient to discriminate suitable from unsuitable habitat from LiDAR data. Incorporating high resolution multispectral images, these techniques can be used over large geographical areas and could therefore have wide application in ecological monitoring of change in habitat structures and the associated effects on wildlife (Mason et al., 2003).

5.1. Summary

The fourth approach, assessing species richness through heterogeneity based on landscape structural properties, involves the assessment of species diversity using structural properties of habitat heterogeneity. This is a more complicated approach that not only relies on primary productivity and its heterogeneity, but also on structural properties of ecosystems. Vegetation height, height variability, percent canopy cover, and aboveground biomass are structural properties defining habitat heterogeneity (e.g. Ritchie et al., 1995; Blair et al., 1999; Lefsky et al., 2002, 2005; Lim et al., 2003; Santos et al., 2003). Such structural habitat properties were successfully correlated to species distributions (Imhoff et al., 1997; Brokaw and Lent, 1999; Hinsley et al., 2002; Jansson and Andrén, 2003; Hill et al., 2003). In addition to the applied laser and radar systems, optical multiangular sensor products (e.g. from the Multiangular Imaging SpectroRadiometer (MISR)) describing structural properties, such as the leaf area index and leaf angle distribution have the potential to contribute to the assessment and monitoring of terrestrial faunal species richness. In addition to more traditional approaches, the use of structural characteristics of habitats, their change and influence on faunal species distribution has a high potential for further studies covering large geographical areas (Nelson et al., 2005).

6. Assessing species richness through heterogeneity based on plant chemical constituents

Animal species have a preference for the spatial and structural composition of habitat, but another attractant is the forage quality that an animal perceives in that habitat. Studies in the African savannah demonstrated that the occurrence and spatial distribution of many wildlife species is influenced by the variation in grass quality (Grant et al., 2002; Heitkönig and Owen-Smith, 1998; McNaughton, 1988). Techniques that can estimate canopy quality on a large scale appear relevant in understanding wildlife diversity. Broadband satellites such as Landsat TM or SPOT lack the potential to capture detailed spectral features needed to detect or estimate the concentration of chemical constituents. Alternatively, imaging spectrometers can measure canopy reflectance in narrow and contiguous spectral bands in a wide wavelength range (e.g. 400-2500 nm). A wide range of plant compounds and their concentration can be identified from the many subtle absorption features of the spectrometer data (Curran, 1989; Elvidge, 1990). The relationships with spectral properties and foliar chemicals, nitrogen amongst others, have been studied from dried and fresh leaves (e.g. Grossman et al., 1996; Dury and Turner, 2001), to entire canopies (e.g. Jago et al., 1999; Curran et al., 2001). However, there are many complicating factors to consider when estimating biochemicals of entire canopies. These include the masking effect of leaf water absorption (Fourty and Baret, 1998), the complexity of the canopy architecture, variation in leaf internal structure and directional, atmospheric and background effects. Several methods were developed to maximize sensitivity to the vegetation characteristics while minimizing confounding factors, including band ratios, difference indices, and derivative analysis (e.g. Huang et al., 2004; Schmidt and Skidmore, 2004).

Regarding forage quality assessment as proxies for animal studying, McIlwee et al. (2001) investigated the utility of in situ reflectance spectroscopy as a means of rapidly assaying chemical constituents of leaves of four Eucalyptus species to predict herbivory by greater gliders (Petauroides volans) and common ringtail possums (Pseudocheirus peregrinus). Resulting concentrations of nitrogen, neutral detergent fibre, condensed tannins and total phenolics, and thus leaf palatability, were predicted accurately and were consistent with documented food preferences of greater gliders. Dury et al. (2001) estimated concentrations of nutrients in Eucalypt tree foliage using airborne imaging spectrometer data. They determined secondary compounds of the group diformylphloroglucinols known to be deterrents for herbivores. Consequently, they derived palatability of Eucalypt leaves for foliovorous marsupials to map potential koala and possum habitats.

Mutanga et al. (2004a) investigated the ability of field spectroscopy to discriminate different levels of sodium concentration in grass, as sodium is a scarce

element needed and sought by mammals (e.g. Brady et al., 2002; Grant et al., 2002). Using field spectrometer measurements of pasture grass, they were able to detect several sodium concentrations. They concluded that with the knowledge of grass species distribution, imaging spectrometer data would help to understand the distribution of mammals in nutrient limited savannas. This approach was successfully applied to large geographical areas linking forage quality to species richness and distribution particularly in areas with limited nutrients (Ferwerda, 2005).

6.1. Summary

This last approach is based on the use of plant chemical constituents to define habitat heterogeneity and ultimately assess and predict species richness. Attractants and deterrents related to the structural and trophic composition of habitat are important criteria to be considered in habitat-species associations. These attractants can be forage quality (Grant et al., 2002; Heitkönig and Owen-Smith, 1998; McNaughton, 1988). Consequently the estimation of forage quality is essential to understand species richness patterns. Imaging spectroscopy with its ability to record reflected radiance in narrow spectral bands, allows the detection and quantification of canopy biochemical components. The overview of these initial studies demonstrated the utility of imaging spectrometer data to map foliar nutrient concentration in savannas and woody ecosystems. The above mentioned studies provide a first step towards understanding the movement and distribution of wildlife, particularly in areas where herbivorous wildlife is known to be limited by nutrients. The correlations between animal presence-abundance/habitat and forage quality were consistent with results derived from imaging spectroscopy; McIlwee et al., 2001; Mutanga et al., 2004a,b), whilst other studies successfully upscaled those correlations to large geographical areas (Dury et al., 2001; Mutanga and Skidmore, 2004b), particularly in areas with limited nutrients (Ferwerda, 2005).

Some authors recommended that future studies should focus on monitoring seasonal changes in foliar nutrient concentration as well as extending the method to predict other macro nutrients (P, K, Na, Mg, Ca) and secondary compounds in both grass and tree canopies. Nevertheless, a major constraint remains that foliar chemicals contribute only a little to the canopy optical properties. Radiative transfer models incorporating the involved optical mechanisms at varying complexity have some success at biochemical parameter retrieval (e.g. Jacquemoud et al., 2000; Kötz et al., 2004); however, typically many inputs of canopy parameters are required. At the current stage extensive in situ investigations on spectral features of attractants and deterrents of forage and their influence on faunal species distributions is a prerequisite to successfully upscale these findings to large areas for monitoring and conserving faunal species.

7. Conclusion

It is important for conservation purposes to generate consistent and reliable information about species distribution and diversity in order to develop plans for species protection and sustainable use (Riede, 2000). Remote sensing is generally regarded to be able to contribute to this aim, mainly by its ability to provide continuous spatial information. It is rapidly developing, capable of coping with environmental heterogeneity – and thus biodiversity – in its broadest range, by measuring increasingly detailed variation on a spatial, temporal, and structural scale, and recently by measuring variation in biochemical composition. This development is clearly highlighted in the presented review.

A major issue complicating the assessment of species occurrence and richness across all techniques is the mobility of faunal species, especially migrants which can move long distances occupying a wide range of natural and anthropogenic habitats. Techniques used in plant oriented diversity studies are generally based on characteristic spectral reflectance features of plant species or plant communities. For this purpose, objects need to be sessile to be accurately assessed. The techniques of remote sensing that have aided the studies on plant species distribution and diversity cannot be applied to animal studies in a similar fashion. Although commercial satellites with 61 cm pixel size are now capable of locating elephants in Kenya's Amboseli National Park and surrounding ecosystem (see, e.g. http://media.digitalglobe.com/file.php/binaries/51/

AmboseliF.pdf), most animal species remain undetectable. The often cryptic existence of fauna poses an additional general problem, akin to that of undergrowth species in vegetation.

Table 1 presents a summary of the various approaches discussed in this paper, including aspects of methodology, data requirements, techniques involved, and the biodiversity aspects covered. Most of the earlier studies on the application of remote sensing to biodiversity research were published in ecological, rather than remote sensing journals. This review is mainly based on peer-reviewed literature.

Aim	Approach	Field data	RS data	Biodiv. sphere	Biodiv. level
Discrete mapping Spatial Habitat suitability mapping (single species and species richness) based on reflectance of landscape characteristics	Image classification of expected habitat correlated with in situ species data	 Knowledge of, or ground studies on habitat preferences Ground truth data of reflectance characteristics Ancillary data (e.g. ecological and/or meteorological data) 	 Multispectral imagery (e.g. Landsat, SPOT) Videographic tracking 	Composition	Species, community
Continuous mapping Spatial Species distribution or diversity prediction and mapping based on variation in primary productivity	NDVI, or other vegetation indices correlated with in situ species data	 Species distribution data Ancillary data (e.g. ecological and/or meteorological data) 	 Multispectral imagery (e.g. Landsat, SPOT, MODIS) 	Composition Function	(Sub)species, community Production
Temporal Species diversity prediction and mapping based on eco-climatic stability in productivity	Interannual NDVI variability correlated with in situ species data	 Species distribution data Ancillary data (e.g. long-term meteorological data) 	 Meteorological imagery: NOAA-AVHRR 	Composition Function	Species, community Production
Structural Habitat suitability mapping (single species and species richness) based on structural habitat characteristics	Structural characteristics estimation using radar or laser altimetry correlated with species data	 Validation data structural characteristics Species distribution data Data of proxy (e.g. bird nests) 	RadarLiDAR	Composition Function	Species Production
Biochemical Species distribution or diversity prediction and mapping based on biochemical compounds of canopy (in the future)	Estimation of biochemical compounds of canopy correlated with in situ species data	 Validation data biochemical compounds Signature library Species distribution data 	 Imaging spectroscopy 	Composition Function	Species Production, quality

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Two main biases can be identified in the selected studies: a strong emphasis on NDVI-based approaches and on spaceborne sensor data. The development and application of new remote sensing techniques and products appears to undergo a lag time before they enter the realm of ecological research. We acknowledge that new methodologies (e.g. narrow-band vegetation indices), and less operational systems (e.g. airborne imaging and in situ spectroradiometers, lidar) have a high potential to provide a new generation of vegetation products representing proxies to estimate animal distribution.

A more recent – and most promising – development in terms of methodology was observed in the assimilation of remote sensing data in ecological species distribution models. Although the reviewed papers mostly emphasise the composition and functional part of animal biodiversity and distribution, rather than population structures, for instance, it is expected that the approaches described here, particularly those with an emphasis on functional ecological relationships, will aid in the ultimate goal of biodiversity conservation.

Finally, this review has focussed on the use of remote sensing for estimating terrestrial animal distribution and diversity. Geostatistical methods are more and more being used incorporating remote sensing and field measurements. The use of ancillary data such as climate, terrain, soils, human infrastructure and footprint, access to water and so on, have been extensively used in geographic information systems. Many of these GIS modelling exercises also incorporate remotely sensed imagery. Corsi et al. (2000) provide an overview of these models and ancillary data sources.

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