

REVIEW

The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology

Nathalie Pettorelli^{1,*}, Sadie Ryan², Thomas Mueller³, Nils Bunnefeld⁴,
Bogumiła Jędrzejewska⁵, Mauricio Lima⁶, Kyrre Kausrud⁷

¹Institute of Zoology, Zoological Society of London, Regent's Park, NW1 4RY London, UK

²National Center for Ecological Analysis and Synthesis (NCEAS), University of California, 735 State Street, Suite 300, Santa Barbara, California 93101-5504, USA

³Department of Biology, University of Maryland, College Park, Maryland 20742, USA

⁴Department of Wildlife, Fish, and Environmental Studies, Swedish University of Agricultural Sciences, 901 83 Umea, Sweden

⁵Mammal Research Institute, Polish Academy of Sciences, Waszkiewicza 1c, 17-230 Białowieża, Poland

⁶Center for Advanced Studies in Ecology and Biodiversity, Pontificia Universidad Católica de Chile, Casilla 114-D, Santiago CP 6513677, Chile

⁷Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology, University of Oslo, PO Box 1066 Blindern, 0316 Oslo, Norway

ABSTRACT: This review highlights the latest developments associated with the use of the Normalized Difference Vegetation Index (NDVI) in ecology. Over the last decade, the NDVI has proven extremely useful in predicting herbivore and non-herbivore distribution, abundance and life history traits in space and time. Due to the continuous nature of NDVI since mid-1981, the relative importance of different temporal and spatial lags on population performance can be assessed, widening our understanding of population dynamics. Previously thought to be most useful in temperate environments, the utility of this satellite-derived index has been demonstrated even in sparsely vegetated areas. Climate models can be used to reconstruct historical patterns in vegetation dynamics in addition to anticipating the effects of future environmental change on biodiversity. NDVI has thus been established as a crucial tool for assessing past and future population and biodiversity consequences of change in climate, vegetation phenology and primary productivity.

KEY WORDS: Satellite · Primary productivity · Remote sensing · Environmental change · NDVI

Resale or republication not permitted without written consent of the publisher

1. INTRODUCTION

As the human population and its resource requirements increase dramatically, major environmental changes are occurring at increasingly faster rates. Climate change is part of a suite of environmental changes characterizing the last hundred years, as human expansion translated into land use change, habitat degradation and habitat fragmentation (Reynolds & Stafford Smith 2002, Millennium Ecosystem Assessment 2005, World Meteorological Organization 2005, IPCC 2007). Our ability to anticipate the effects of such changes is

fundamental to designing appropriate adaptation and mitigation strategies (Millennium Ecosystem Assessment 2005). In order to assess and anticipate environmental change effects on biodiversity and ecosystem services, we require, among other things, a good understanding of how trophic levels and trophic interactions are impacted by such changes (Durant et al. 2005, Yang & Rudolf 2010).

Over the last decade, numerous studies have highlighted the potential key role of satellite data in ecology (Kerr & Ostrovsky 2003, Turner et al. 2003), and in particular the Normalized Difference Vegetation Index

(NDVI; Pettorelli et al. 2005a). The NDVI, computed as $(\text{NIR}-\text{Red})/(\text{NIR} + \text{Red})$ where NIR and Red are the amount of near-infrared and red light, respectively, reflected by a surface and measured by satellite sensors, was first reported by Rouse et al. (1974). The latter study primarily dealt with the transformed vegetation index (TVI) and contained no references to previous work using ratios of NIR/Red, such as Birth & McVey (1968), Jordan (1969), and Pearson & Miller (1972). Subsequently, Tucker (1977, 1979) and Deering (1978) employed the NDVI to estimate herbaceous biomass and Tucker et al. (1981) showed how frequent NDVI measurements were highly correlated to herbaceous total dry matter accumulation over the period of observation.

Green leaves absorb incoming solar radiation in the photosynthetically active radiation spectral region, which provides energy needed to power photosynthesis (Jensen 2007). More specifically, green leaves absorb incident solar radiation very strongly in the blue and red spectral regions and not as strongly in the green spectral region. In the near infrared spectral region, green leaves are highly reflective and no absorption occurs (Knipling 1970, Jensen 2007). Thus, green leaves have high visible light absorption together with high near-infrared reflectance, resulting in positive NDVI values. Bare soil, cloud, snow, and concrete have NDVI values close to zero, while water has negative NDVI values (Neigh et al. 2008). The NDVI has been shown to be highly correlated with photosynthetically active radiation absorbed by the plant canopy, photosynthetic capacity, net primary production, leaf area index (LAI), fraction of absorbed photosynthetically active radiation, carbon assimilation and evapotranspiration (Myneni et al. 1995, Buermann et al. 2002, Hicke et al. 2002, Wang et al. 2005). NDVI thus allows monitoring of vegetation photosynthesis through time and enables easy temporal and spatial comparisons (Myneni et al. 1997). It can be used to map, assess or predict the occurrence and impact of disturbances such as drought, fire, flood and frost (Pettorelli et al. 2005a), as well as helping to map and predict the extent of land degradation (Prince et al. 2009).

In 2005, Pettorelli et al. (2005a) provided an overview of the use of NDVI in wildlife management, highlighting how NDVI-based indices could be linked to animal distribution and abundance. The applications of the NDVI in ecology have continued to increase and expand, with new uses and advances arising every year (Table 1). This is illustrated by the number of ecological articles published over the last 5 years which refer to NDVI (282 articles published in 2005 or later with the topic NDVI and subject area ecology counted; ISI Web of Science search, 23rd of August 2010). This popularity can be partially explained by NDVI being a

widely available index with pre-processed NDVI data readily available from as early as 1981, and at various spatial scales. In comparison, access to pre-existing processed data for other vegetation indices at such temporal and spatial scales is reduced, and therefore presents a threshold for ecological studies in general (Pettorelli et al. 2005a). With this review we aim to update the overview provided in 2005 to acknowledge the great spectrum of possibilities associated with NDVI.

2. SUCCESS OF THE NDVI IN WILDLIFE MANAGEMENT

Much knowledge has been gained from coupling primary productivity distribution (as assessed by the NDVI) with species distribution and abundance (for recent examples, see Bro-Jørgensen et al. 2008, Evans et al. 2008, Pettorelli et al. 2009, St-Louis et al. 2009), but the greatest benefit of the NDVI comes from the access to large-scale primary production dynamics over time. Since NDVI also provides information on phenology (Fig. 1), it can be used to assess temporal aspects of vegetation development and quality (Pettorelli et al. 2007, Hamel et al. 2009). Such information has been shown to correlate with behaviour and life history traits of several species: in Norway, NDVI at vegetation onset was shown to be a strong predictor of red deer *Cervus elaphus* altitudinal migration date (Pettorelli et al. 2005b), while NDVI-based estimates of vegetation growth also proved to be helpful in understanding wildebeest *Connochaetes taurinus* migration in the Serengeti (Boone et al. 2006). In southern Africa, wet-season home-range sizes in elephants *Loxodonta africana* was shown to correlate with seasonal vegetation productivity as estimated by NDVI, while dry-season home-range sizes were best explained by heterogeneity in the distribution of vegetation productivity (Young et al. 2009). NDVI variation was also shown to correlate with elephant diet in Kenya (Wittemyer et al. 2009), while in Norway and France, NDVI in spring was shown to be a strong predictor of body mass in reindeer *Rangifer tarandus* and roe deer *Capreolus capreolus* (Pettorelli et al. 2005c, Pettorelli et al. 2006; see also Table 2).

A demonstration of using the phenological signal in NDVI to understand the dynamics of an animal population is provided by Ryan (2006) and Ryan et al. (2007). In their 2007 study, the authors explored the relationship between seasonal NDVI patterns and birthing occurrence and synchrony for African buffalo *Syncerus caffer* living in a savanna environment. As the driver of this system appeared to be not simply the quantity of vegetation biomass, but rather the

Table 1. Examples of issues studied and sub-disciplines that benefitted from the availability of NDVI

Issue	Group/species	Sub-discipline	Source
Energy–abundance relationship	African ungulates Beetles	Macroecology	Pettorelli et al. (2009) Lassau & Hochuli (2008)
Energy–species richness relationship	Birds Beetles	Macroecology	Ding et al. (2006) Koh et al. (2006) Lassau & Hochuli (2008)
Energy–community composition relationship	Beetles	Macroecology	Lassau & Hochuli (2008)
Resource distribution, resource dynamics and space use	Brown bears Vervet monkeys Elk Mongolian gazelles Elephants Ptarmigans African buffalo	Habitat selection	Wiegand et al. (2008) Willems et al. (2009) Hebblewhite et al. (2008) Olson et al. (2009) Young et al. (2009) Pedersen et al. (2007) Winnie et al. (2008)
Resource quality vs. resource quantity in determining space use	Mongolian gazelles African buffalo	Habitat selection	Mueller et al. (2008) Ryan et al. (2006)
Resource quality vs. resource quantity in determining demographic parameters	Alpine ungulates African buffalo	Population dynamics	Pettorelli et al. (2007) Hamel et al. (2009) Ryan (2006)
Resource dynamics and population dynamics	Rodents Elephants	Population dynamics	Andreo et al. (2009a,b) Kausrud et al. (2007) Trimble et al. (2009)
Direct vs. indirect effect of climate on demographic parameters	Red deer Reindeer Moose Elephants	Population dynamics	Myserud et al. (2008) Pettorelli et al. (2005c) Herfindal et al. (2006a,b) Rasmussen et al. (2006)
Resource dynamics and migration patterns	Wildebeest Marsh harriers Saiga antelope	Movement ecology	Boone et al. (2006) Klaassen et al. (2010) Singh et al. (2010b)
Climatic variability and diet shifts	Elephants	Feeding ecology	Wittemyer et al. (2009)
Factors shaping sexual segregation	Eurasian wild sheep	Behavioural ecology	Singh et al. (2010c)
Climate, vegetation dynamics and past ecological processes	Plague outbreaks	Paleoecology	Kausrud et al. 2007

quality, a second study (S. Ryan et al. unpubl. data) was undertaken to examine the nutrient value of the vegetation, for which NDVI proved a useful proxy. Analyzing fecal samples and vegetation samples at feeding patches for buffalo, to measure the content of nitrogen (protein surrogate) and phosphorus (a limiting mineral in savanna landscapes, important in the metabolism of protein), they established correlative relationships between NDVI and nitrogen content, by season and landscape. No clear patterns were seen for phosphorus, likely obscured by metabolic interactions with nitrogen. However, the body condition of females was correlated, at a monthly lag—presumably the time it would take for sufficient quantities of high quality vegetation to demonstrate an effect—to NDVI, and NDVI to nitrogen at a similar time lag. This suggests that, in this savanna system, NDVI is a good proxy for the timing of high quality vegetation, which is the high-protein initial growth, rather than the formerly used simple measures of biomass.

In grassland habitats without trees, NDVI can sometimes be used as a direct proxy for resource availability: most grasses decline considerably in nutritional quality as they grow (Van Soest 1994). As grasses mature, they accumulate structural tissues and their fibre content increases, reducing their digestibility (McNaughton 1984, McNaughton 1985). Thus, mature grasslands may provide high vegetation productivity (i.e. high NDVI values), yet few resources to ungulates (Wilmshurst et al. 2000, Bergman et al. 2001, Payero et al. 2004, Hebblewhite et al. 2008). As a consequence of these trade-off relationships in grass quantity and quality, Mueller et al. (2008) showed that for Mongolian gazelles *Procapra gutturosa* in the Eastern Steppes of Mongolia, no monotonic relationship between NDVI and resource availability existed. Instead, an intermediate range of NDVI, allowing for sufficient forage quantity as well as quality, was associated with the highest resource availability to gazelles, and was a useful tool to delineate habitat dynamics for gazelles.

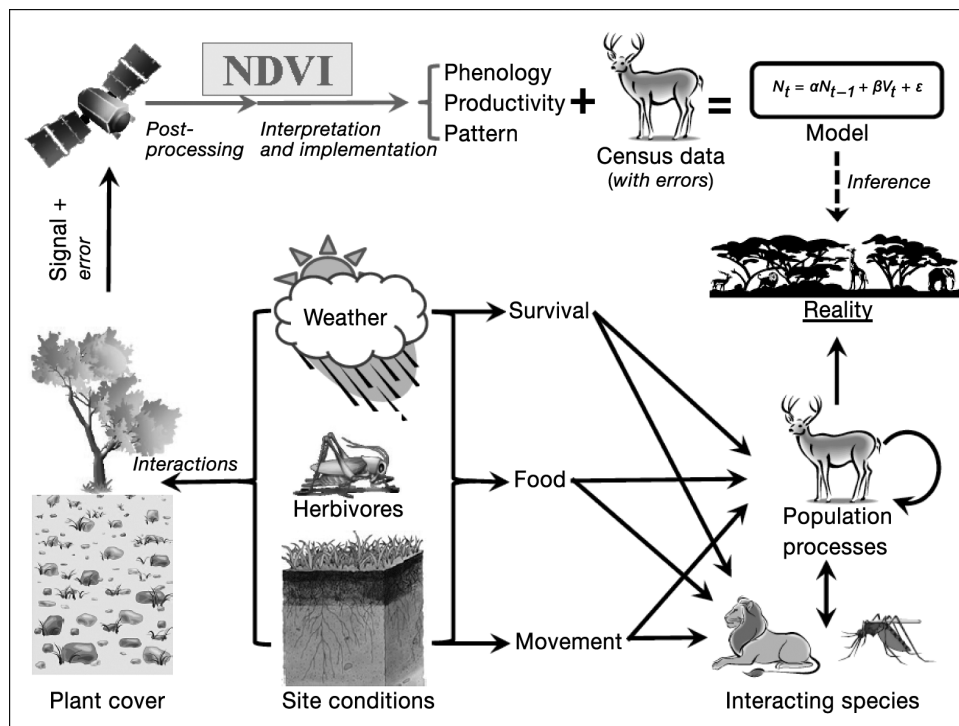


Fig. 1. Simplified schematic representing the advantages and pitfalls of NDVI. The effects of weather (e.g. precipitation or temperature), herbivory (including pests and pathogens) and site conditions (including interactions within the plant community and between plants and soil nutrients or water) interact to shape primary productivity. The resulting reflectance of the above-ground plant matter is then registered (with errors) by the satellite, and through post-processing one trades errors with spatiotemporal resolutions to determine the NDVI data available to users, which are interpreted and combined with data on the study organism to build an ecological model. NDVI data can give direct information on vegetation phenology and on primary productivity and its spatial distribution. However, multiple mechanisms can shape the observed population processes of the study organism, both directly through weather, productivity or site changes, and indirectly through e.g. effects mediated by interacting species. Moreover, several of these mechanisms are likely to induce a lagged response (with possible spatiotemporal lags) relative to NDVI variability. Thus, while the NDVI can give invaluable information on population processes that are hard to observe by ground-based methods, the validity of inference is reliant on correct assumptions and knowledge of the study system

Table 2. Examples where NDVI was not reported to significantly shape animal parameters

Link	Result	Taxa/Species	Source
Plant phenology variables and amount of fat deposited	Climatic variables describing spring conditions performed better than plant phenology variables	Raccoon	Melis et al. (2010)
Body mass and primary production	Not all populations examined displayed a correlation between body mass and NDVI	Red deer	Martinez-Jauregui et al. (2009)
	No correlation between NDVI and body mass	Roe deer Wild boar	Myserud et al. (2007) Pettorelli et al. (2006) (in Trois Fontaines)
Animal density and primary production	The correlation between animal density and primary production was a function of the NDVI spatial resolution	Topi	Bro-Jørgensen et al. (2008)
NDVI and animal distribution	Negligible effect of NDVI in predicting species presence	Iberian spider	Jimenez-Valverde & Lobo (2006)
NDVI and animal distribution	Presence not significantly related to NDVI	Gemsbok, eland, wildebeest and springbok	Verlinden & Masogo (1997)
NDVI and animal movement	NDVI not predictor of range size or chosen patch	African buffalo	Ryan et al. (2006)

3. NDVI: NOT JUST FOR LARGE HERBIVORES

As NDVI provides information on vegetation distribution and dynamics, it is commonly thought that its applicability is limited to enhancing our understanding of large herbivore ecology. Yet a considerable number of studies have demonstrated that NDVI is a useful tool for investigating the ecology of other, sometimes non-herbivore species. In the case of non-herbivore species, the rationale behind the use of satellite-based indices of primary productivity is based on the assumption that primary productivity of an area influences its entire food web (McNaughton et al. 1989). NDVI can for example, help predict species richness, distribution, abundance, migration patterns or life history traits of birds (Saino et al. 2004a,b, Gordo 2007, Evans et al. 2008, St-Louis et al. 2009). Links between NDVI and bird populations can be found both through (1) higher primary productivity being linked to increased food abundance for birds (Gordo 2007), and (2) higher NDVI variance across pixels being linked to higher habitat variability (which is expected to influence species richness; St-Louis et al. 2009). In insectivorous barn swallow *Hirundo rustica* and insectivorous-carnivorous white stork *Ciconia ciconia*, temporal variation in ecological conditions (as reflected by NDVI in their winter quarters), for example, appeared to be a very important factor shaping breeding success and/or survival of birds in their European breeding ranges (Saino et al. 2004b, Schaub et al. 2005). In Svalbard, NDVI was shown to be a good predictor of the presence of territorial rock ptarmigan *Lagopus muta hyperborea* cocks (Pedersen et al. 2007). In East Asia (Oriental Region, Wallacea Subregion, and part of Palaearctic Region), average NDVI was the most important factor determining the variation in bird species richness, with a linear positive correlation between NDVI and bird species richness (Ding et al. 2006). Similarly, NDVI was the most powerful predictor of bird species richness at a markedly smaller spatial scale of northern Taiwan (the study again reported a linear positive correlation between NDVI and bird species richness; Koh et al. 2006).

For mammals, the relationship between NDVI and animal distribution has been recently explored for carnivorous and omnivorous animals (see also Table 2), with e.g. Wiegand et al. (2008) reporting that brown bears *Ursus arctos* selected areas with specific NDVI characteristics, or Basille et al. (2009) demonstrating that the preferred habitat of the lynx *Lynx lynx* includes areas of high plant productivity (as indexed by NDVI). Likewise, recent work on vervet monkey *Chlorocebus pygerythrus* home range location suggested that these monkeys prefer areas with elevated productivity and reduced seasonality—as indexed by

NDVI—with monthly NDVI values being shown to correlate with field measurements of leaf cover and food availability for vervet monkeys (Willems et al. 2009). NDVI has, so far, been little used in studies on small mammals. Yet, this direction of research seems to have a great conceptual and methodological potential, especially when it comes to the question of spatiotemporal dynamics of cyclic (or otherwise fluctuating) populations. Attempts to find the causal relationships between primary productivity and population density and/or fluctuations of rodents date go back to the years of the International Biological Programme. However, the studies conducted in the 1960s–1980s were performed at very small spatial scales (study sites usually encompassed one to a few hectares) as the methods of estimating habitat productivity relied on laborious direct sampling of vegetation (e.g. Grodziński 1971, Pelikan 1982). Since the 1980s, it has become more and more evident that patterns in small rodent abundance are better explained in macroecological scale, and several geographical gradients in vole population dynamics have been described (Hansson & Henttonen 1985, Mackin-Rogalska & Nagabło 1990, Tkadlec & Stenseth 2001). So far, successful attempts have been undertaken to relate those large-scale patterns in small mammal populations to habitat productivity, using such indices derived from ground sampling as standing crop and productivity of ground vegetation (Jędrzejewski & Jędrzejewska 1996) and crop yield index (Tkadlec et al. 2006), or ranks of forest productivity (Niedziałkowska et al. 2010). Examples of the great potential for using NDVI to study small rodents are provided by Andreo et al. (2009a,b), who investigated the relationships between small rodent population dynamics, climate and NDVI in an agricultural ecosystem in Central Argentina. For *Akodon azarae*, the authors highlighted that large changes in land use were quite well captured by NDVI, which was the sole variable able to explain the sudden collapse exhibited by this rodent population.

Vertebrates are not the only segment of biodiversity which can be successfully related to NDVI, as demonstrated by several studies carried out on insects. Lassau & Hochuli (2008) recently discovered positive relationships between NDVI and site-based beetle species richness and abundance, and NDVI was also useful for predicting differences in beetle composition in open canopy forests. Ground measures of moth larval density were found to correlate with a NDVI-based defoliation score in Fennoscandia (Jepsen et al. 2009), while de Beurs & Townsend (2008) concluded that NDVI data can be used to monitor insect defoliation on an annual time scale. NDVI was used to generate risk and distribution maps for diseases with arthropod vectors (Kalluri et al. 2007), as well as for temporal models of

disease outbreaks (Chretien et al. 2007). Malaria and other mosquito-borne diseases such as West Nile virus seem to receive the most frequent attention and be particularly amenable to modeling efforts involving spatiotemporal data such as NDVI, due to the close causal link between rainfall and both mosquito abundance and NDVI (Brooker et al. 2006, Gemperli et al. 2006, Ceccato et al. 2007, Britch et al. 2008, Brown et al. 2008). But other zoonoses like Hantaan virus (Yan et al. 2007), schistosomiasis (Clements et al. 2008, Wang et al. 2008), Ebola (Pinzon et al. 2004a), bubonic plague (Kausrud et al. 2007), leishmaniasis (Werneck et al. 2007), Rift Valley fever (Anyamba et al. 2009) and others have been found to have spatial and/or temporal components associated with NDVI variability.

4. SCALES OF ENVIRONMENTAL CHANGE AND ANIMAL MOVEMENT

The availability of data and methods to analyze animal movement has increased exponentially with the help of GPS-based technology, allowing the tracking of animals that cover large distances or are difficult to observe and follow. However, analyses of coupled data of animal movement and environmental variables in a unified framework are still lacking. Movement analyses of different taxa and species, such as mammals, birds, insects and amphibians, has largely been developed independently (Fryxell & Sinclair 1988, Alerstam et al. 2003, Grayson & Wilbur 2009). Also, movements at different spatial scales are often explained by different mechanisms such as migration versus feeding (Dingle 1996, 2006). The high temporal resolution of NDVI is particularly helpful in studying animal movements, since data on vegetation productivity can be linked to location data of individuals at the same time. Instead of traditional habitat selection analyses that use static habitat maps, dynamic landscape models based on NDVI allow the examination of movement decisions of individuals or populations as resource availability changes in time. For example, at broader scales, shifts in relative NDVI distribution can explain movement to and from seasonal ranges (e.g. Ito et al. 2006). On finer scales NDVI may be used to trace habitat choices of single individuals at a particular movement step (Hebblewhite et al. 2008). Thus, NDVI can be used to study movement patterns at different spatial scales in a unified framework (Nathan et al. 2008). Ryan et al. (2006) found that African buffalo had a reduced length of short-term ranging distances with increased values of NDVI, while it had no impact on estimated range size. The use of NDVI thus uncovered a behavior at a fine temporal scale that had not previously been explored. Wittemyer et al. (2009) found that

for African elephants, the peak in primary productivity matched the change from random movements to more directional movements. This study showed directional movement in relation to resources (food and water) during the dry season and more random movements during the wet season. By monitoring radio-collared Svalbard reindeer females, Hansen et al. (2009) were able to demonstrate that changes in forage abundance (as indexed by NDVI) can strongly influence winter habitat–space use interactions in predator-free systems, with females exhibiting more quality-based selection at the expense of quantity when forage abundance increased. NDVI was also useful in explaining an unusual mass aggregation of Mongolian gazelle: Olson et al. (2009) observed more than 200 000 gazelle that had all moved to the same region, and subsequently found that NDVI showed a temporary ‘green up’ of that particular location that perfectly aligned with the mass aggregation of gazelle. Importantly, dynamic landscape models based on NDVI can be used to gain a more mechanistic understanding of long distance animal movements: landscape models based on NDVI were key in explaining the wildebeest migration in the Serengeti. Boone et al. (2006) demonstrated in individual based models that NDVI was critical to ‘evolutionarily train’ model-organisms to reproduce patterns of wildebeest migration.

5. SPARSELY VEGETATED AREAS

It has been previously acknowledged that the relationship between NDVI and vegetation can be biased in low vegetated areas, unless the soil background is taken into account (Huete 1988). Asrar et al. (1984), for example, demonstrated that for a LAI below 3, NDVI was mainly influenced by soil reflectance. Such results led to a common belief that NDVI could not be used in semi-arid, arid and desert areas, as well as polar environments—where vegetation is sparse and growing season short. Yet several recent studies have shown that NDVI could provide useful information even in sparsely vegetated areas: in the Kerguelen archipelago, Santin-Janin et al. (2009) demonstrated how NDVI correlates with ground-based measurements of plant biomass; in north-central Chile, De la Maza et al. (2009) demonstrated that NDVI could be related to ground-truthed measures of vegetation productivity, allowing exploration of the relationship between rainfall patterns and vegetation cover and productivity related to El Niño phenomenon. Using NDVI data, it was possible to determine that rainfall not only influences plant productivity, but also has a strong effect on plant phenology, determining the length of the growing season, which in turn contributed to increased bio-

mass formation in semi-arid Chile (De la Maza et al. 2009). During high rainfall years (El Niño), there is an earlier start of plant growth, and this earlier greening season—and delayed timing of plant productivity peaks—influences the timing of greater food availability for herbivores, and thus, their breeding dates and the length of their reproductive period (De la Maza et al. 2009). NDVI was also successfully used to monitor the vegetation response to rainfall in both Egypt and Israel (Dall'Olmo & Karnieli 2002). This again scales up to the level of consumers: desert mule deer *Odocoileus hemionus eremicus* distribution in the Sonoran Desert was shown to correlate with high NDVI values in 3 out of 4 seasons (Marshall et al. 2006); likewise the dynamics of great gerbils *Rhombomys opimus* in the arid Kazakhstan steppe was shown to be influenced by annual variability captured by spring NDVI (Kausrud et al. 2007).

6. IMPORTANCE OF TIME LAGS IN POPULATION DYNAMICS

Climate impacts on population dynamics will often be visible with a time lag mediated through the endogenous dynamics of the system. However, the relative importance of different time lags is often not known when the data are gathered, creating a need for continuous data coverage when analyzing the data in retrospect (Norris & Taylor 2006). Moreover, in species that range over wide areas, such as migratory birds, large predators and some ungulates, the relevant climate impact may not take place where the population is sampled. In these cases, the global and continuous nature of the NDVI data are extremely valuable as it allows ecologists to assess climate variability at a different time and place than where the population was sampled. A good example of this is provided by Couturier et al. (2009), who demonstrated that reindeer birth mass—which was positively affected by NDVI in June—positively correlated with population productivity (in terms of number of calves produced per 100 females) 3 and 4 yr later (which corresponds to the beginning of reproduction for females).

7. PAST PROCESSES

A major obstacle to using the NDVI to explore the link between climatic variation and ecological processes is the lack of data for any significant period prior to mid-1981. Not only do many interesting ecological data sets extend much further back in time, but to draw robust conclusions about effects of climate variation on some system, longer time series and/or other time

periods than provided by the NDVI are often needed. However, the large-scale spatial variability in NDVI values depend to a large extent on interactions between local variation in soil types, terrain morphology, and macro-gradients such as latitude, elevation, elevational rain shadows, or continental vs. oceanic influences (Zhang et al. 2009). These factors change slowly on ecological time scales, making it possible to use non-spatial measurements or reconstructions of climate to extend NDVI data or related aspects as proxies back in time (Jicheng & Xuemei 2006, Rutishauser et al. 2007, Leavitt et al. 2008, Neerinckx et al. 2008). Surprisingly, this has rarely been done in ecology, but in cases where spatiotemporal ecological data exist before and after 1980, it offers a means of testing whether predictions from ecological models built using NDVI data are consistent with earlier climate variability (Kausrud et al. 2007).

Although such approaches represent significant opportunities to ecologists, a few caveats should be pointed out. Firstly, human impact is the main challenge for ecosystem persistence and consequently, knowing how NDVI and vegetation have changed in the past without incorporating changes in human impact could be of reduced interest. Secondly, one needs to keep in mind that these extrapolations (and their associated reliability) are linked to the quality and the spatio-temporal resolution of the climatic data entered in the model.

8. ROLE IN CONSERVATION AND ENVIRONMENTAL MANAGEMENT

As well as being highly valuable for detecting and mapping large-scale impacts of global climate change (Breshears et al. 2005, Soja et al. 2007), NDVI can help assess population and biodiversity consequences of future change in vegetation phenology and primary productivity. As NDVI provides a measurable index of primary productivity, links between climate, vegetation and animals can be explored and quantified at various spatial and temporal scales. For example, climatic models predict a decrease of rainfall in semiarid Chile by between 15 and 40% of present conditions. Despite this dramatic reduction in annual rainfall, De la Maza et al. (2009) predicted that primary production in protected semiarid areas of Chile will decrease only between 2 and 9%. In systems where NDVI reflects important resource variation, it can be used to create spatially explicit and realistic models simulating key processes of the system, incorporating adaptive behavior and spatial autocorrelation. Such links enable development of a framework wherein potential consequences of environmental change can be assessed

(Kausrud et al. 2007). For example, by demonstrating that the timing of vegetation onset is key to red deer and reindeer performance in Norway (Pettorelli et al. 2005b,c) and incorporating the knowledge that climate change projections for Norway suggest earlier and later vegetation onsets than at present at low and high altitudes, respectively, one can predict a beneficial effect of climate change on red deer and a detrimental effect on mountain reindeer populations. A positive effect of early onset of spring on one population during a limited number of years does not, however, necessarily tell the complete story of how climate change will affect the species as a whole. For example, Herfindal et al. (2006a,b) showed similar positive effects of early onset of spring on moose *Alces alces* performance when looking at year to year-variation in body mass. However, when looking at geographical differences in population performance, populations in areas with an overall early onset of spring had lower body masses than populations in areas with a late onset of spring.

Several climatic models aimed at predicting spatio-temporal changes in NDVI have been developed (see e.g. Anyamba et al. 2006, Funk & Brown 2006). These may be useful in conjunction with current studies of habitat selection and distribution to help understand future range requirements and restrictions for many species. This is particularly important to protected area planning and reserve design (Alcaraz-Segura et al. 2009). For species currently in protected areas at the edges of their ranges, range shift predictions are fundamental to assessing whether they will be able to migrate and adapt. In a study on the critically endangered saiga antelope *Saiga tatarica*, Singh et al. (2010a,b) showed that in the past, the seasonal migration and distribution as well as the selection of calving sites could be explained by NDVI. However, the saiga population has collapsed by >90% in the last decade, and the current distribution is largely influenced by human disturbance and development restricting the range and movement of saigas. NDVI can be helpful to predict suitable habitat for future spatiotemporal patterns of saiga antelope distribution under scenarios of population recovery, anti-poaching efforts and climate change. These scenarios in turn can be informative for the development of saiga antelope protected areas, whether in terms of size or spatial extent.

NDVI is potentially a cheap, systematic, repeatable, and verifiable monitoring method for environmental management. In particular, it has recently been proposed that the monitoring of remotely assessed ecosystem functional attributes through NDVI provides an excellent opportunity to assess the effectiveness of management practices as well as the effects of global environmental change (Alcaraz-Segura et al. 2009).

9. CONCLUSIONS

Over the last few decades, ecology has increasingly relied on the wealth of opportunities and information provided by new technological developments as exemplified by animal tracking devices such as GPS, camera traps or increased computational speed for sophisticated analyses such as Bayesian analyses. Remote sensing data and NDVI in particular are among those technological advances useful for ecology: mostly freely available, with global coverage across several decades, and high temporal resolution, NDVI opens the possibility of addressing questions on scales inaccessible to ground-based methods alone.

In 2005, Pettoelli et al. (2005a) highlighted how NDVI might represent a key tool to assess the consequences of environmental change on wildlife, allowing ecologists to couple climate, vegetation and animal distribution and performance at both large spatial and temporal scales. Five years later, we highlight how NDVI provides significant opportunities in behavioural ecology, habitat selection studies, movement ecology, environmental conservation and paleo-ecology—areas that were not envisaged in 2005 (Table 1). Across sub-disciplines, ranging from macroecology and species niche modeling to evolution, NDVI can provide critical information about vegetation dynamics that allow the investigation of relationships between animal populations and environmental variability. Large-scale and long-term data sets are increasingly available in many disciplines, such as macroecology, population dynamics and biodiversity. These data sets are often spatially explicit and, coupled with NDVI, are ideally suited to the study of climate change impacts and the development of more reliable future scenarios.

NDVI has been established as a crucial tool for assessing past and future population and biodiversity consequences of change in climate, vegetation phenology and primary productivity. The possibilities and limitations of satellite-based ecological data such as the NDVI (Fig. 1, Box 1) are however suggested to be of crucial interest when assessing and understanding the effects of multiple, large-scale environmental changes. As Pinzon et al. (2004b) noted, 'users [...] are strongly encouraged to validate their results using independent data' (p. 18). This is rarely seen in NDVI-based studies of animal ecology, and may point to a lack of collaboration between those who generate satellite-based indices such as NDVI and those who use it. We recommend increased multidisciplinary links between ecology, geophysics and remote sensing as crucial to promoting a better use of satellite data in ecological research (Skidmore & Ferwerda 2008). We also believe that increased emphasis must be placed on methodology when teaching ecology

Box 1. Caveats and limits of NDVI usefulness in animal ecology

NDVI is a crude estimate of vegetation health and a means of monitoring changes in vegetation over time (Pettorelli et al. 2005a). NDVI integrates the composition of species within the plant community, vegetation form, vigour, and structure, the vegetation density in vertical and horizontal directions, reflection, absorption, and transmission within and on the surface of the vegetation or ground, and the reflection, absorption, and transmission by the atmosphere, clouds, and atmospheric contaminants (Markon et al. 1995). The ability of NDVI to monitor variations in primary productivity can, however, be negatively affected (Markon & Peterson 2002). In tropical ecosystems, for example, the radiation data reaching the satellite sensor may be contaminated by atmospheric variations such as cloud cover and smoke, and NDVI values may therefore provide inexact representations of the vegetation status on the ground in such cases (Tanre et al. 1992, Achard & Estreguil 1995). Saleska et al. (2007) demonstrated that reduced rainfall resulted in satellite-based primary productivity estimates that are higher than observed values during the wet season in a South American wet tropical region. Garonna et al. (2009) highlighted the same pattern: with clouds being more likely to bias NDVI estimates in wet months than in dry months, and with more light reaching the canopy during the dry season, higher NDVI values were reported during the dry season in the Solomon Islands.

To eliminate the noise in the data, different types of processing have been applied to the raw data (Markon & Peterson 2002, Tucker et al. 2005). However, eliminating the noise means inevitably removing variation from the raw data that could be due to environmental variation that is of particular interest in the detection of environmental change. Alcaraz-Segura et al. (2010) compare different processing schemes of the same raw data (Advanced Very High Resolution Radiometer, AVHRR sensor) and show that spatial and temporal inconsistencies exist between processing schemes. Baldi et al. (2008) evaluated the detection probability of land cover change and found differences between processing methods. More research into the effect of different image processing on detection of environmental change is needed to optimize removal of noise from the data, while retaining valuable variation stemming from actual environmental variability in the image.

The quality of the information regarding primary productivity variation and food availability for herbivores encompassed in NDVI values is therefore a function of several factors (see Fig. 1) such as the type of processing applied to the raw data; the spatial location of the study (e.g. the linear correlation between NDVI and the leaf area index, does not hold in very arid and in very densely vegetated areas; Huete 1988); the behaviour and dietary preferences of the study animals (e.g. high rainfall areas tend to be less nutritious and therefore available only to certain large herbivores which can tolerate lower plant nutrient content; Olff et al. 2002); and the scale of the study (e.g. some large herbivore species may seek high productivity 'patches' at very large spatial scales, but select low productivity patches within this landscape matrix at the local scale).

The most commonly used data (e.g. data derived from the satellite pour l'Observation de la Terre, SPOT, from the Moderate Resolution Imaging Spectroradiometer, MODIS, and from the AVHRR) are then generally aggregated at a temporal resolution of 10–15 d, which means that it is not possible to precisely date phenological phenomena. Moreover, these datasets generally cover spatial resolutions spanning from 250 m to 8 km, which may be too coarse, depending on the biological system considered. Although higher spatial resolution data exist, these data have a low temporal resolution (e.g. Landsat TM; see Pettolelli et al. 2005a). In areas with vegetational inactive periods such as deserts, a substantial part of the year is not informed by NDVI. Yet such periods may be important for animals, and other variables, such as average temperature, may represent key variables for animal movement, space use, performance or abundance. Finally, other vegetation indexes might be more appropriate than NDVI, especially for particular situations. In sparsely vegetated areas the soil-adjusted vegetation index (SAVI; Huete 1988) may perform better than NDVI (see Despland et al. 2004 for an example that uses SAVI). The Enhanced Vegetation Index (EVI; Huete et al. 2002) is meant to take full advantage of MODIS' new, state-of-the-art measurement capabilities (see Wallace & Thomas 2008 for an example of application of the EVI in the Mojave Desert). Importantly, this index does not become saturated as easily as the NDVI when viewing rainforests and other areas of the Earth with large amounts of green material, meaning that EVI may perform better than NDVI in densely vegetated areas.

students, who commonly lack the mathematical and factual knowledge needed to make use of satellite-derived data. Further, because NDVI is shaped by factors such as climate and topography, its use as an explanatory variable should not necessarily lead to the exclusion of these environmental variables. For example, the relative importance of the direct and indirect effects of climate on animal population dynamics is expected to be spatiotemporally variable. Failing to integrate climatic variables with NDVI when assessing the consequences of change in climate on animals could lead to erroneous results, as NDVI may only partially capture the role of indirect effect of climate change on animals (see e.g. Mysterud et al. 2008). Finally, considering the possibilities

linked to the use of satellite-based data, it is important that the scientific community keep such data products homogenous, free, and readily available.

Acknowledgements: This work is the result of a symposium entitled 'The use of satellite-based data in assessing ecological responses to environmental change' organized by N.P. during the 10th International Mammal Conference in Mendoza, Argentina. N.P. was supported by the Royal Society to attend the conference. S.R. worked on this study as a postdoctoral associate at the National Center for Ecological Analysis and Synthesis, a Center funded by the National Science Foundation (Grant #EF-0553768), the University of California, Santa Barbara, and the State of California. The authors are grateful to Jim Tucker and 2 other anonymous referees for their valuable inputs.

LITERATURE CITED

- Achard F, Estreguil C (1995) Forest classification of Southeast Asia using NOAA AVHRR data. *Remote Sens Environ* 54: 198–208
- Alcaraz-Segura D, Cabello J, Paruelo JM, Delibes M (2009) Use of descriptors of ecosystem functioning for monitoring a national park network: a remote sensing approach. *Environ Manage* 43:38–48
- Alcaraz-Segura D, Elisa L, Siham T, José P, Javier C (2010) Evaluating the consistency of the 1982–1999 NDVI trends in the Iberian Peninsula across four time-series derived from the AVHRR sensor: LTDR, GIMMS, FASIR, and PAL-II. *Sensors* 10:1291–1314
- Alerstam T, Hedenstrom A, Akesson S (2003) Long-distance migration: evolution and determinants. *Oikos* 103:247–260
- Andreo V, Lima M, Provencal C, Priotto J, Polop J (2009a) Population dynamics of two rodent species in agro-ecosystems of central Argentina: intra-specific competition, land-use, and climate effects. *Popul Ecol* 51:297–306
- Andreo V, Provencal C, Scavuzzo M, Lamfri M, Polop J (2009b) Environmental factors and population fluctuations of *Akodon azarae* (Muridae: Sigmontinae) in central Argentina. *Austral Ecol* 34:132–142
- Anyambaa A, Chretien JP, Small J, Tucker CJ and others (2009) Prediction of a Rift Valley fever outbreak. *Proc Natl Acad Sci USA* 106:955–959
- Asrar G, Fuchs M, Kanemasu ET, Hatfield JL (1984) Estimating absorbed photosynthetic radiation and leaf area index from spectral reflectance in wheat. *Agron J* 76:300–306
- Baldi G, Noretto MD, Aragón MR, Aversa F, Paruelo JM, Jobbagy EG (2008) Long-term satellite NDVI datasets: Evaluating their ability to detect ecosystem functional changes in South America. *Sensors* 8:5397–5425
- Basille M, Herfindal I, Santin-Janin H, Linnell JDC and others (2009) What shapes Eurasian lynx distribution in human dominated landscapes: selecting prey or avoiding people? *Ecography* 32:683–691
- Bergman CM, Fryxell JM, Cormack Gates C, Fortin D (2001) Ungulate foraging strategies: energy maximizing or time minimizing? *J Anim Ecol* 70:289–300
- Birth GS, McVey GR (1968) Measuring color of growing turf with a reflectance spectrophotometer. *Agron J* 60:640–645
- Boone RB, Thirgood SJ, Hopcraft JGC (2006) Serengeti wildebeest migratory patterns modeled from rainfall and new vegetation growth. *Ecology* 87:1987–1994
- Breshears DD, Cobb NS, Rich PM, Price KP and others (2005) Regional vegetation die-off in response to global-change-type drought. *Proc Natl Acad Sci USA* 102:15144–15148
- Britch SC, Linthicum KJ, Anyamba A, Tucker CJ and others (2008) Satellite vegetation index data as a tool to forecast population dynamics of medically important mosquitoes at military installations in the continental United States. *Mil Med* 173:677–683
- Bro-Jørgensen J, Brown M, Pettorelli N (2008) Using NDVI to explain ranging patterns in a lek-breeding antelope: the importance of scale. *Oecologia* 158:177–182
- Brooker S, Leslie T, Kolaczinski K, Mohsen E and others (2006) Spatial epidemiology of *Plasmodium vivax*, Afghanistan. *Emerg Infect Dis* 12:1600–1602
- Brown H, Diuk-Wasser M, Andreadis T, Fish D (2008) remotely-sensed vegetation indices identify mosquito clusters of West Nile Virus vectors in an urban landscape in the Northeastern United States. *Vector Borne Zoonotic Dis* 8:197–206
- Buermann W, Wang YJ, Dong JR, Zhou LM and others (2002) Analysis of a multiyear global vegetation leaf area index data set. *J Geophys Res Atm* 107:4646 doi:10.1029/2001JD000975
- Ceccato P, Ghebremeskel T, Jaiteh M, Graves PM and others (2007) Malaria stratification, climate, and epidemic early warning in Eritrea. *Am J Trop Med Hyg* 77:61–68
- Chretien JP, Anyamba A, Bedno SA, Breiman RF and others (2007) Drought-associated chikungunya emergence along coastal East Africa. *Am J Trop Med Hyg* 76:405–407
- Clements A, Brooker S, Nyandindi U, Fenwick A, Blair L (2008) Bayesian spatial analysis of a national urinary schistosomiasis questionnaire to assist geographic targeting of schistosomiasis control in Tanzania, East Africa. *Int J Parasitol* 38:401–415
- Couturier S, Côté SD, Otto RD, Weladji RB, Huot J (2009) Variation in calf body mass in migratory caribou: the role of habitat, climate, and movements. *J Mammal* 90: 442–452
- Dall'Olmo G, Karnieli A (2002) Monitoring phenological cycles of desert ecosystems using NDVI and LST data derived from NOAA-AVHRR imagery. *Int J Remote Sens* 23:4055–4071
- de Beurs KM, Townsend PA (2008) Estimating the effect of gypsy moth defoliation using MODIS. *Remote Sens Environ* 112:3983–3990
- De la Maza M, Lima M, Meserve PL, Gutierrez JR, Jaksic FM (2009) Primary production dynamics and climate variability: ecological consequences in semiarid Chile. *Glob Change Biol* 15:1116–1126
- Deering DW (1978) Rangeland reflectance characteristics measured by aircraft and spacecraft sensors. PhD Dissertation, Texas A & M University, College Station, TX
- Despland E, Rosenberg J, Simpson SJ (2004) Landscape structure and locust swarming: a satellite's eye view. *Ecography* 27:381–391
- Ding TS, Yuan HW, Geng S, Koh CN, Lee PF (2006) Macro-scale bird species richness patterns of the East Asian mainland and islands: energy, area and isolation. *J Biogeogr* 33:683–693
- Dingle H (1996) *Migration: the biology of life on the move*. Oxford University Press, New York.
- Dingle H (2006) Animal migration: Is there a common migratory syndrome? *J Ornithol* 147:212–220
- Durant JM, Hjermand DØ, Anker-Nilssen T, Beaugrand G, Coulson T, Pettorelli N, Stenseth NC (2005) Timing and abundance as key mechanisms affecting trophic interactions in variable environments. *Ecol Lett* 8:952–958
- Evans KL, Newson SE, Storch D, Greenwood JJD, Gaston KJ (2008) Spatial scale, abundance and the species-energy relationship in British birds. *J Anim Ecol* 77:395–405
- Fryxell JM, Sinclair ARE (1988) Causes and consequences of migration by large herbivores. *Trends Ecol Evol* 3:237–241
- Funk CC, Brown ME (2006) Intra-seasonal NDVI change projections in semi-arid Africa. *Remote Sens Environ* 101: 249–256
- Garonna I, Fazey I, Brown M, Pettorelli N (2009) Rapid primary productivity change in one of the last coastal rainforests: the case of Kahua, Solomon Islands. *Environ Conserv* 36:253–260
- Gemperli A, Vounatsou P, Sogoba N, Smith T (2006) Malaria mapping using transmission models: application to survey data from Mali. *Am J Epidemiol* 163:289–297
- Gordo O (2007) Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Clim Res* 35:37–58
- Grayson KL, Wilbur HM (2009) Sex- and context-dependent migration in a pond-breeding amphibian. *Ecology* 90: 306–312

- Grodziński W (1971) Energy flow through populations of small mammals in the Alaskan taiga forest. *Acta Theriol (Warsz)* 16:231–275
- Hamel S, Garel M, Festa-Bianchet M, Gaillard JM, Côté SD (2009) Spring normalized difference vegetation index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. *J Appl Ecol* 46: 582–589
- Hansen BB, Aanes R, Herfindal I, Sæther BE, Henriksen S (2009) Winter habitat-space use in a large arctic herbivore facing contrasting forage abundance. *Polar Biol* 32: 971–984
- Hansson L, Henttonen H (1985) Gradients in density variations in small rodents: the importance of latitude and snow cover. *Oecologia* 67:394–402
- He J, Shao X (2006) Relationships between tree-ring width index and NDVI of grassland in Delingha. *Chin Sci Bull* 51:1106–1114
- Hebblewhite M, Merrill E, McDermid G (2008) A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. *Ecol Monogr* 78:141–166
- Herfindal I, Solberg EJ, Sæther BE, Hogda KA, Andersen R (2006a) Environmental phenology and geographical gradients in moose body mass. *Oecologia* 150:213–224
- Herfindal I, Sæther BE, Solberg EJ, Andersen R, Hogda KA (2006b) Population characteristics predict responses in moose body mass to temporal variation in the environment. *J Anim Ecol* 75:1110–1118
- Hicke JA, Asner GP, Randerson JT, Tucker C and others (2002) Trends in North American net primary productivity derived from satellite observations, 1982–1998. *Global Biogeochem Cycles* 16:1018–1032
- Huete AR (1988) A soil-adjusted vegetation index (SAVI). *Remote Sens Environ* 25:295–309
- Huete AR, Didan K, Miura T, Rodriguez E (2002) Overview of radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sens Environ* 83:195–213
- Indeje M, Ward NM, Ogallo LJ, Davies G, Anyamba A (2006) Predictability of the normalized difference vegetation index in Kenya and potential applications as an indicator of Rift Valley fever outbreaks in the greater Horn of Africa. *J Clim* 19:1673–1687
- IPCC (Intergovernmental Panel on Climate Change) (2007) Climate change 2007: synthesis report. Fourth Assessment Report of the Intergovernmental Panel on Climate Change. www.ipcc.ch/pdf/assessment-report/ar4/syr/ar4_syr.pdf
- Ito TY, Miura N, Lhagvasuren B, Enkhbileg D, Takatsuki S, Tsunekawa A, Jiang Z (2006) Satellite tracking of Mongolian gazelles (*Procapra gutturosa*) and habitat shifts in their seasonal ranges. *J Zool (Lond)* 269:291–298
- Jędrzejewski W, Jędrzejewska B (1996) Rodent cycles in relation to biomass and productivity of ground vegetation and predation in the Palearctic. *Acta Theriol (Warsz)* 41:1–34
- Jensen JR (2007) Remote sensing of the environment: an earth resource perspective, 2nd edn. Prentice Hall, Upper Saddle River, NJ
- Jepsen JU, Hagen SB, Hogda KA, Ims RA, Karlsen SR, Tommervik H, Yoccoz NG (2009) Monitoring the spatio-temporal dynamics of geometrid moth outbreaks in birch forest using MODIS-NDVI data. *Remote Sens Environ* 113:1939–1947
- Jimenez-Valverde A, Lobo JM (2006) Distribution determinants of endangered Iberian spider *Macrothele calpeiana*. *Environ Entomol* 35:1491–1499
- Jordan CF (1969) Derivation of leaf-area index from quality of light on forest floor. *Ecology* 50:663–666
- Kalluri S, Gilruth P, Rogers D, Szczur M (2007) Surveillance of arthropod vector-borne infectious diseases using remote sensing techniques: a review. *PLoS Pathog* 3:e116
- Kausrud KL, Viljugrein H, Frigessi A, Begon M and others (2007) Climatically-driven synchrony of gerbil populations allows large-scale plague outbreaks. *Proc Biol Sci* 274: 1963–1969
- Kerr JT, Ostrovsky M (2003) From space to species: ecological applications for remote sensing. *Trends Ecol Evol* 18: 299–305
- Klaassen RHG, Strandberg R, Hake M, Olofsson P, Tottrup AP, Alerstam T (2010) Loop migration in adult marsh harriers *Circus aeruginosus*, as revealed by satellite telemetry. *J Avian Biol* 41:200–207
- Knipling EB (1970) Physical and physiological basis for the reflectance of visible and near infrared radiation from vegetation. *Remote Sens Environ* 1:155–159
- Koh CN, Lee PF, Lin RS (2006) Bird species richness patterns of northern Taiwan: primary productivity, human population density, and habitat heterogeneity. *Divers Distr* 12:546–554
- Lassau SA, Hochuli DF (2008) Testing predictions of beetle community patterns derived empirically using remote sensing. *Divers Distr* 14:138–147
- Leavitt SW, Chase TN, Rajagopalan B, Lee E, Lawrence PJ (2008) Southwestern U.S. tree-ring carbon isotope indices as a possible proxy for reconstruction of greenness of vegetation. *Geophys Res Lett* 35:L12704 doi: 10.1029/2008GL033894
- Mackin-Rogalska R, Nabagło L (1990) Geographical variation in cyclic periodicity and synchrony in the common vole, *Microtus arvalis*. *Oikos* 59:343–348
- Markon CJ, Peterson KM (2002) The utility of estimating net primary productivity over Alaska using baseline AVHRR data. *Int J Remote Sens* 23:4571–4596
- Markon CJ, Fleming MD, Binnian EF (1995) Characteristics of vegetation phenology over the Alaskan landscape using AVHRR time-series data. *Polar Rec (Gr Brit)* 31:179–190
- Marshall JP, Bleich VC, Krausman PR, Reed ML, Andrew NG (2006) Factors affecting habitat use and distribution of desert mule deer in an arid environment. *Wildl Soc Bull* 34:609–619
- Martinez-Jauregui M, San Miguel-Ayaz A, Mysterud A, Rodriguez-Vigal C, Clutton-Brock T, Langvatn R, Coulson T (2009) Are local weather, NDVI and NAO consistent determinants of red deer weight across 3 contrasting European countries? *Glob Change Biol* 15:1727–1738
- McNaughton SJ (1984) Grazing lawns: animals in herds, plant form and coevolution. *Am Nat* 124:863–886
- McNaughton SJ (1985) Ecology of a grazing ecosystem: the Serengeti. *Ecol Monogr* 55:259–294
- McNaughton SJ, Oesterheld M, Frank DA, Williams KJ (1989) Ecosystem-level patterns of primary productivity and herbivory in terrestrial habitats. *Nature* 341:142–144
- Melis C, Herfindal I, Kauhala K, Andersen R, Hogda KA (2010) Predicting animal performance through climatic and plant phenology variables: the case of an omnivore hibernating species in Finland. *Mamm Biol* 75:151–159
- Millennium Ecosystem Assessment (2005) Ecosystems and human well-being: synthesis. Island Press, Washington, DC
- Mueller T, Olson KA, Fuller TK, Schaller GB, Murray MG, Leimgruber P (2008) In search of forage: predicting dynamic habitats of Mongolian gazelles using satellite-based estimates of vegetation productivity. *J Appl Ecol* 45: 649–658
- Myneni RB, Hall FG, Sellers PJ, Marshak AL (1995) The interpretation of spectral vegetation indexes. *IEEE Trans Geosci Rem Sens* 33:481–486

- Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386:698–702
- Mysterud A, Tryjanowski P, Panek M, Pettorelli N, Stenseth NC (2007) Inter-specific synchrony of 2 contrasting ungulates: wild boar and roe deer. *Oecologia* 151:232–239
- Mysterud A, Yoccoz NG, Langvatn R, Pettorelli N, Stenseth NC (2008) Hierarchical path analysis of deer responses to direct and indirect effects of climate in northern forest. *Philos Trans R Soc Lond, B* 363:2359–2368
- Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE (2008) Movement ecology paradigm for unifying organismal movement research. *Proc Natl Acad Sci USA* 105:19052–19059
- Neerinckx SB, Peterson AT, Gulinck H, Deckers J, Leirs H (2008) Geographic distribution and ecological niche of plague in sub-Saharan Africa. *Int J Health Geogr* 7:54. doi:10.1186/1476-072X-7-54
- Neigh CSR, Tucker CJ, Townshend JRG (2008) North American vegetation dynamics observed with multi-resolution satellite data. *Remote Sens Environ* 112:1749–1772
- Niedziakowska M, Kończak J, Czarnomska S, Jędrzejewska B (2010) Species diversity and abundance of small mammals in relation to forest productivity in northeastern Poland. *Ecoscience* 17:109–119
- Norris DR, Taylor CM (2006) Predicting the consequences of carry-over effects for migratory populations. *Biol Lett* 2: 148–151
- Olff H, Ritchie ME, Prins HHT (2002) Global environmental controls of diversity in large herbivores. *Nature* 415: 901–904
- Olson KA, Mueller T, Bolortsetseg S, Leimgruber P, Fagan WF, Fuller TK (2009) A mega-herd of more than 200000 Mongolian gazelles *Procapra gutturosa*: a consequence of habitat quality. *Oryx* 43:149–153
- Payero JO, Neale CMU, Wright JL (2004) Comparison of eleven vegetation indices for estimating plant height of alfalfa and grass. *Appl Eng Agric* 20:385–393
- Pearson RL, Miller LD (1972) Remote mapping of standing crop biomass for estimation of the productivity of the shortgrass prairie. In: *Proc Eight Int Symp on Remote Sens Environ*, October 2–6, 1972, ERIM, Ann Arbor, MI, p. 1357–1381
- Pedersen AO, Jepsen JU, Yoccoz NG, Fuglei E (2007) Ecological correlates of the distribution of territorial Svalbard rock ptarmigan. *Can J Zool* 85:122–132
- Pelikan J (1982) *Microtus arvalis* on mown and unmown meadows. *Acta Sc Nat Brno* 16:1–36
- Pettorelli N, Vik JO, Mysterud A, Gaillard JM, Tucker CJ, Stenseth NC (2005a) Using the satellite-derived Normalized Difference Vegetation Index (NDVI) to assess ecological effects of environmental change. *Trends Ecol Evol* 20:503–510
- Pettorelli N, Mysterud A, Yoccoz NG, Langvatn R, Stenseth NC (2005b) Importance of climatological downscaling and plant phenology for red deer in heterogeneous landscapes. *Proc Biol Sci* 272:2357–2364
- Pettorelli N, Weladji R, Holand Ø, Mysterud A, Breie H, Stenseth NC (2005c) The relative role of winter and spring conditions: linking climate and landscape-scale plant phenology to alpine reindeer body mass. *Biol Lett* 1:24–26
- Pettorelli N, Gaillard JM, Mysterud A, Duncan P, Stenseth NC, Delorme D, Van Laere G (2006) Using a proxy of plant productivity (NDVI) to track animal performance: the case of roe deer. *Oikos* 112:565–572
- Pettorelli N, Pelletier F, Von Hardenberg A, Festa-Bianchet M, Cote SD (2007) Early onset of vegetation growth versus rapid green-up: impacts on juvenile mountain ungulates. *Ecology* 88:381–390
- Pettorelli N, Bro-Jørgensen J, Durant SM, Blackburn T, Carbone C (2009) Energy availability and density estimates in African ungulates. *Am Nat* 173:698–704
- Pinzon JE, Wilson JM, Tucker CJ, Arthur R, Jahrling PB, Formenty P (2004a) Trigger events: enviroclimatic coupling of Ebola hemorrhagic fever outbreaks. *Am J Trop Med Hyg* 71:664–674
- Pinzon JE, Brown ME, Tucker CJ (2004b) Monitoring seasonal and interannual variations in land-surface vegetation from 1981–2003 using GIMMS NDVI. ftp://landval.gsfc.nasa.gov/Documentation/GIMMS_NDVI_8km_doc.pdf
- Prince SD, Becker-Reshef I, Rishmawi K (2009) Detection and mapping of long-term land degradation using local net production scaling: application to Zimbabwe. *Remote Sens Environ* 113:1046–1057
- Rasmussen HB, Wittemyer G, Douglas-Hamilton I (2006) Predicting time-specific changes in demographic processes using remote-sensing data. *J Appl Ecol* 43:366–376
- Reynolds JF, Stafford Smith M (2002) *Global desertification: Do humans create deserts?* Dahlem University Press, Berlin
- Rouse JW, Haas RH, Schell JA, Deering DW (1974). Monitoring vegetation systems in the Great Plains with ERTS. *Proc Third Earth Resources Technology Satellite-1 Symp*, December 10–15 1974, Greenbelt, MD, 3:301–317, NASA, Washington, D.C.
- Rutishauser T, Luterbacher J, Jeanneret F, Pfister C, Wanner H (2007) A phenology-based reconstruction of interannual changes in past spring seasons. *J Geophys Res* 112: G04016. doi:10.1029/2006JG000382
- Ryan SJ (2006) *Spatial ecology of African buffalo and their resources in a savanna landscape*. PhD Dissertation, University of California at Berkeley
- Ryan SJ, Knechtel CU, Getz WM (2006) Range and habitat selection of African buffalo in South Africa. *J Wildl Manag* 70:764–776
- Ryan SJ, Knechtel CU, Getz WM (2007) Ecological cues, gestation length, and birth timing in African buffalo. *Behav Ecol* 18:635–644
- Saino N, Szep T, Ambrosini R, Romano M, Moller AP (2004a) Ecological conditions during winter affect sexual selection and breeding in a migratory bird. *Proc Biol Sci* 271: 681–686
- Saino N, Szep T, Romano M, Rubolini D, Spina F, Moller AP (2004b) Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecol Lett* 7:21–25
- Saleska SR, Didan K, Huete AR, Rocha HRD (2007) Amazon forests green-up during 2005 drought. *Science* 318:612
- Santin-Janin H, Garel M, Chapuis JL, Pontier D (2009) Assessing the performance of NDVI as a proxy for plant biomass using non-linear models: a case study on the Kerguelen archipelago. *Polar Biol* 32:861–871
- Schaub M, Kania W, Koppen U (2005) Variation in primary production during winter indices synchrony in survival rates in migratory white storks. *J Anim Ecol* 74:656–666
- Singh NJ, Grachev IA, Bekenov AB, Milner-Gulland EJ (2010a) Saiga antelope calving site selection is increasingly driven by human disturbance. *Biol Conserv* 143: 1770–1779
- Singh NJ, Grachev IA, Bekenov AB, Milner-Gulland EJ (2010b) Tracking greenery across a latitudinal gradient in central Asia—the migration of the saiga antelope. *Div Distrib* 16:663–675
- Singh NJ, Bonenfant C, Yoccoz NG, Cote SD (2010c) Sexual segregation in Eurasian wild sheep. *Behav Ecol* 21:410–418

- Skidmore AK, Ferwerda JG (2008) Resource distribution and dynamics: mapping herbivore resources. In: Prins HHT, Van Langevelde F (eds) *Resource Ecology, spatial and temporal dynamics of foraging*. Springer, Dordrecht, p 57–77
- Soja AJ, Tchepakova NM, French NHF, Flannigan MD and others (2007) Climate-induced boreal forest change: predictions versus current observations. *Global Planet Change* 56:274–296
- St-Louis V, Pidgeon AM, Clayton MK, Locke BA, Bash D, Radloff VC (2009) Satellite image texture and a vegetation index predict avian biodiversity in the Chihuahuan desert of New Mexico. *Ecography* 32:468–480
- Tanre D, Holben BN, Kaufman YJ (1992) Atmospheric correction algorithm for NOAA-AVHRR products: theory and application. *IEEE Geosci Rem Sens* 30:231–248
- Tkadlec E, Stenseth NC (2001) A new geographical gradient in vole population dynamics. *Proc Biol Sci* 268:1547–1552
- Tkadlec E, Zboril J, Losik J, Gregor P, Lisická L (2006) Winter climate and plant productivity predict abundances of small herbivores in central Europe. *Clim Res* 32:99–108
- Trimble MJ, Ferreira SM, van Aarde RJ (2009) Drivers of megaherbivore demographic fluctuations: inference from elephants. *J Zool (Lond)* 279:18–26
- Tucker CJ (1977) Spectral estimation of grass canopy variables. *Remote Sens Environ* 6:11–26
- Tucker CJ (1979) Red and photographic infrared linear combinations for monitoring vegetation. *Remote Sens Environ* 8:127–150
- Tucker CJ, Holben BN, Elgin JH, McMurtrey JE (1981) Remote sensing of total dry-matter accumulation in winter wheat. *Remote Sens Environ* 11:171–189
- Tucker CJ, Pinzon JE, Brown ME, Slayback DA and others (2005) An extended AVHRR 8-km NDVI data set compatible with MODIS and SPOT vegetation NDVI data. *Int J Remote Sens* 26:4485–4498
- Turner W, Spector S, Gardiner N, Fladeland M, Sterling E, Steininger M (2003) Remote sensing for biodiversity science and conservation. *Trends Ecol Evol* 18:306–314
- Van Soest PJ (1994) *Nutritional Ecology of the Ruminant*, 2nd edn. Cornell University Press, Ithaca, NY
- Verlinden A, Masogo R (1997) Satellite remote sensing of habitat suitability for ungulates and ostrich in the Kalahari of Botswana. *J Arid Environ* 35:563–574
- Wallace CSA, Thomas KA (2008) An annual plant growth proxy in the Mojave Desert using MODIS-EVI data. *Sensors* 8:7792–7808
- Wang Q, Adiku S, Tenhunen J, Granier A (2005) On the Relationship of NDVI with leaf area index in a deciduous forest site. *Remote Sens Environ* 94:244–255
- Wang XH, Zhou XN, Vounatsou P, Chen Z and others (2008) Bayesian spatio-temporal modeling of *Schistosoma japonicum* prevalence data in the absence of a diagnostic gold standard. *PLoS Negl Trop Dis* 2:e250
- Werneck G, Costa C, Walker A, David J, Wand M, Maguire J (2007) Multilevel modelling of the incidence of visceral leishmaniasis in Teresina, Brazil. *Epidemiol Infect* 135:195–201
- Wiegand T, Naves J, Garbulsky MF, Fernandez N (2008) Animal habitat quality and ecosystem functioning: exploring seasonal patterns using NDVI. *Ecol Monogr* 78:87–103
- Willems EP, Barton RA, Hill RA (2009) Remotely sensed productivity, regional home range selection, and local range use by an omnivorous primate. *Behav Ecol* 20:985–992
- Wilmshurst JF, Fryxell JM, Bergman CM (2000) The allometry of patch selection in ruminants. *Proc Biol Sci* 267:345–349
- Winnie JA, Cross P, Getz W (2008) Habitat quality and heterogeneity influence distribution and behavior in African buffalo. *Ecology* 89:1457–1468
- Wittemyer G, Cerling TE, Douglas-Hamilton I (2009) Establishing chronologies from isotopic profiles in serially collected animal tissues: an example using tail hairs from African elephants. *Chem Geol* 267:3–11
- World Meteorological Organization (2005) *Climate and land degradation*. WMO, Geneva
- Yan L, Fang L, Huang H, Zhang L and others (2007) Landscape elements and Hantaan virus-related hemorrhagic fever with renal syndrome, People's Republic of China. *Emerg Infect Dis* 13:1301–1306
- Yang LH, Rudolf VHW (2010) Phenology, ontogeny and the effects of climate change on the timing of species interactions. *Ecol Lett* 13:1–10
- Young KD, Ferreira SM, van Aarde RJ (2009) Elephant spatial use in wet and dry savannas of southern Africa. *J Zool (Lond)* 278:189–205
- Zhang Y, Xu M, Chen H, Adams J (2009) Global pattern of NPP to GPP ratio derived from MODIS data: effects of ecosystem type, geographical location and climate. *Glob Ecol Biogeogr* 18:280–290

Editorial responsibility: Nils Chr. Stenseth, Oslo, Norway

*Submitted: January 14, 2010; Accepted: September 11, 2010
Proofs received from author(s): January 13, 2011*