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Geospatial tools address emerging issues in spatial ecology: a review and commentary on the Special Issue

Andrew K. Skidmore^{a*}, Janet Franklin^b, Terry P. Dawson^c and Petter Pilesjö^d

^aDepartment of Natural Resources, Faculty of Geoinformation Science and Earth Observation (ITC), University of Twente, Enschede, The Netherlands; ^bSchool of Geographical Sciences and Urban Planning, Arizona State University, Tempe, AZ, USA; ^cSchool of Geography, University of Southampton, Southampton, UK; ^dDepartment of Earth and Ecosystem Sciences, Lund University, Lund, Sweden

Spatial ecology focuses on the role of space and time in ecological processes and events from a local to a global scale and is particularly relevant in developing environmental policy and (mandated) monitoring goals. In other words, spatial ecology is where geography and ecology intersect, and high-quality geospatial data and analysis tools are required to address emerging issues in spatial ecology. In this commentary and review for the *International Journal of GIS* Special Issue on Spatial Ecology, we highlight selected current research priorities in spatial ecology and describe geospatial data and methods for addressing these tasks. Geoinformation research themes are identified in population ecology, community and landscape ecology, and ecosystem ecology, and these themes are further linked to the assessment of ecosystem services. Methods in spatial ecology benefit from explicit consideration of spatial autocorrelation, and applications discussed in this review include species distribution modeling, remote sensing of community and ecosystem properties, and models of climate change. The linkages of the Special Issue papers to these emerging issues are described.

Keywords: Spatial ecology; GIS; remote sensing; environmental change; temporal processes; species distribution models; biodiversity

1. Introduction

Spatial ecology focuses on the role of space and time in ecological processes and events and is applied to natural resource sciences including, for example, biology, forestry, conservation, agriculture, and environment. In other words, spatial ecology is where geography and ecology intersect. A principle underlying the field of spatial ecology is that the presence and abundance of organisms, their interactions with the environment, and other ecological processes form spatial patterns over geographical space and time. These patterns are the result of climate, environmental gradients and disjunctions, biotic interactions, and anthropogenic influences, creating variation in species, communities, and ecological processes and events at multiple scales in space and time (Dungan *et al.* 2002). For example, the availability of light, moisture, nutrients, and heat is spatially and temporally heterogeneous.

*Corresponding author. Email: skidmore@itc.nl

Patterns of disturbance (fire, wind, ocean temperature anomalies, and anthropogenic fragmentation of landscapes) are also heterogeneous as well as being spatially structured. Ecological processes not only occur on a template of a spatially heterogeneous environment, but many are also spatially explicit and generate spatial patterns – including dispersal and movement of organisms, interactions between species, and fluxes of matter and energy. Identifying, describing, and monitoring patterns over time are prerequisites to understanding ecological processes (Legendre *et al.* 2002, Liebhold and Gurevitch 2002). Furthermore, ecological models that account for spatial processes are more realistic and powerful than those that do not.

Spatial ecology examines the role of space and time in ecological processes and events at local to global scales and in this article, spatial ecology is not tied to a particular scale. Studies that label themselves as spatial ecology frequently address the population and community levels of ecological organization (Tilman and Kareiva 1997, Holyoak *et al.* 2005). Landscape ecology (Naveh and Lieberman 1994) considers processes and patterns at broader spatial scales encompassing landscapes or seascapes, on the order of 10s to 10,000s of km² (watersheds, ecoregions). Biogeography or ‘macro-ecology’ (Brown 1995) classically addresses patterns at even broader scales, encompassing entire species’ ranges, continents, or oceans and implicitly or explicitly considering processes that occur at geological time scales – adaptation, speciation, and species range changes in response to climate change.

Geospatial data and analysis tools are requisite to tackle emerging issues in spatial ecology from local to global scales. In addition to addressing basic research questions, geospatial data analysis provides background information as well as scenario testing of environmental policies and monitoring goals set by nation states as well as international conventions and agreements. For example, the importance of biodiversity was highlighted in the Millennium Development Goals (MDGs) coordinated by the United Nations Development Program (Sachs and MacArthur 2005). The MDGs are eight goals to be achieved by 2015 that respond to the world’s main development challenges, drawn from the actions and targets contained in the Millennium Declaration that was adopted by 189 nations in 2000 (www.un.org/millenniumgoals, accessed 30 January 2011). Of particular relevance for this article is MDG 7, which aims to ‘ensure environmental sustainability’. Targets 7a and 7b address quantitative environmental indicators to reduce biodiversity loss, such as protection of terrestrial and marine areas, reducing the number of species facing extinction, maintaining global forest cover, and reducing CO₂ emissions. International conventions, which bind signatory nations to specific environmental actions and outcomes, require information generated from spatial ecological data for monitoring and enforcement. Such conventions are diverse, ranging from maritime applications (such as the Convention on the Prevention of Marine Pollution by Dumping of Wastes and Other Matter (London Convention), 1972, and the International Convention for the Control and Management of Ships’ Ballast Water and Sediments, 2004) to conventions focusing on biodiversity (the Convention on Biological Diversity (year of coming into force: 1993), the Convention on Conservation of Migratory Species (also known as the Bonn Convention) (1983), the Convention on International Trade in Endangered Species of Wild Fauna and Flora (1975), the International Treaty on Plant Genetic Resources for Food and Agriculture (2004), the Ramsar Convention on Wetlands (1971), and the World Heritage Convention (1972)). Other examples of international conventions relevant to spatial ecology are the United Nations Convention to Combat Desertification and the United Nations Framework Convention on Climate Change. Some conventions can be considered subsets of the Convention on Biological Diversity, such as the Convention on the Conservation of European Wildlife and Natural Habitat (Bern Convention), the International Plant

Protection Convention; the Convention for the Protection and Development of the Marine Environment of the Wider Caribbean Region (Cartagena Convention) and its protocols, including the protocol concerning Specially Protected Areas and Wildlife and the Mediterranean Action Plan (Barcelona Convention).

The Millennium Ecosystem Assessment (MEA) was initiated in 2001 by the United Nations with the objective of assessing the consequences of ecosystem change for human well-being and the scientific basis for action needed to enhance the conservation and sustainable use of those systems and their contribution to human well-being (Corvalán 2005). Similar to the Intergovernmental Panel on Climate Change, the MEA assesses current knowledge, scientific literature, and data, rather than presenting new research findings. The main finding of the MEA is that over the past 50 years, humans have changed ecosystems more rapidly and extensively than in any comparable period of time in human history, largely to meet rapidly growing demands for food, fresh water, timber, fiber, and fuel (Carpenter *et al.* 2009). This has resulted in a substantial and largely irreversible loss in diversity of life on Earth.

To prepare, monitor, and achieve these assessments and goals, quality data and information must be registered accurately to both place and date. For example, the Global Earth Observation System of Systems provides information and decision-support tools to a wide variety of users through a flexible network of content providers (<http://www.earthobservations.org/>). Specifically the program provides funding and an international network to provide information for and about human-induced disasters, understand the environmental sources of health hazards, manage energy resources, respond to climate change and its impacts, safeguard water resources, improve weather forecasts, manage ecosystems, promote sustainable agriculture, and conserve biodiversity. In other words, the spatial and temporal data and information required for ecological and environmental analysis and assessment are increasingly embedded in the international community and its institutions. To satisfy international obligations for environmental reporting and monitoring, nations are investing heavily in spatial information provision and analysis at local, provincial, and national levels.

In this article an overview is provided of current themes and research priorities in spatial ecology (Section 2) and examples of geospatial data and methods for addressing these tasks are discussed (Section 3). This overview serves as a preface to the Special Issue on Spatial Ecology, and the linkages of the Special Issue papers to these emerging issues are described (Section 4). The overview is far from a comprehensive review of this burgeoning field and reflects the interests and biases of the authors, but the collection of papers included in the Special Issue illustrates the diversity of current research applying geospatial data and methods to spatial ecology problems.

2. Emerging issues in spatial ecology

Before discussing current research priorities in spatial ecology, the concepts of scale relevant to spatial ecology are reviewed (see Section 2.1). Geospatial data and tools are being used in innovative ways to address problems in spatial ecology at population, community/landscape, and ecosystem levels, and each level of ecological organization is discussed in Sections 2.2–2.4. Very broadly, many applications are aimed at supporting conservation of biological diversity: biodiversity elements (species, communities) as well as ecosystem processes (providing goods and services). Furthermore, geospatial analysis is currently being applied to assess the status of ecosystem services as mandated under a number of monitoring programs (Section 2.5).

2.1. Scale and geospatial data for ecology

Spatial scale has two components, grain and extent (Turner *et al.* 2001). Grain or sample resolution is the size of a single observation, for example, a 50-m radius bird survey plot, a 10-km grid cell for which averaged climate variables have been interpolated, or a 30-m image pixel (ground resolution element). Extent is the size of the study area domain. As discussed in the Introduction (Section 1), specializations within ecology are linked to extent, for example, a broader extent relates to biogeography or macro-ecology. Ecological studies are also characterized by temporal resolution (interval) and extent (time period, duration), though traditional spatial analyses often assume that time is static, with a study representing a 'snapshot' in time (as compared with the more recent studies cited in Sections 2.3 and 2.4 that explicitly model time). Finally, when considering how finely a system can distinguish differences of intensity, the radiometric resolution of imagery or spatial data becomes critical and is usually expressed as a number of levels or number of bits, for example, 8 bits or 256 levels is typical for computer image files.

Factors that control the spatial distribution of biotic elements have been described in a model by Mackey (1993) as the primary environmental regimes of radiation, thermal, moisture, and nutrients. Climate, topography, and geologic substrate control the distribution of these primary environmental regimes in complex ways, for example, through evapotranspiration, soil profile development, and the subsurface moisture regime in terrestrial ecosystems (Swanson *et al.* 1988, Franklin 1995, Wilby and Schimel 1999, Wilson and Gallant 2000). Maps describing the primary environmental regimes are often derived either from point measurements through interpolation (Skidmore 1996b, Varekamp *et al.* 1996) and physical models (Kumar *et al.* 1997) or from remote sensing (Clevers *et al.* 2002).

Drivers controlling these regimes are spatially nested (Franklin 1995). A nested hierarchy of spatial scales can be defined based on natural breaks in the distribution of the primary environmental resources (Mackey and Lindenmayer 2001). At a global (biogeography or macro-ecology) scale, latitudinal and seasonal patterns of incoming solar radiation drive regional weather and climate. At the meso-scale (i.e. landscape ecology scale), the interaction of weather with terrain affects precipitation, temperature, and radiation regimes, whereas geologic substrate and derived soil properties affect nutrient availability. At the topo-scale (i.e. population and community ecology scales), local topography controls the distribution of water and radiation (and therefore soil development and nutrient availability). Micro-scale is defined as the scale at which patches of vegetation affect the below-canopy microclimate. This concept of a spatially nested hierarchy has also been developed in wildlife ecology literature (Johnson 1980), where the four levels of habitat selection are described as the species' geographic range, home range, resource patches within the home range, and the selection of food items within the patches (e.g. Ciarniello *et al.* 2007). In this Special Issue, four papers investigate the role of scale in ecology, focusing on the environmental variables influencing ecological properties and processes, including species distribution modeling (SDM), biomass as well as ecosystem productivity (see Section 4 for details; Miller and Hanham (this issue), Leitão *et al.* (this issue), Propastin (this issue), and Svoray (this issue)). The interaction of biota with the physical environment is aided by global positioning system (GPS) and tracking technologies as outlined below.

2.2. Spatial processes in population ecology

Geospatial technologies have supported studies of populations and species autecology through the use of GPS and related technologies such as radio-, GPS-, and

satellite-telemetry for the precise mapping of individual organisms (Hays *et al.* 2001, Ropert-Coudert and Wilson 2005, Beck *et al.* 2008). GPS is now routinely used to record locations of ecological survey plots for plants (Stohlgren *et al.* 1997), animals, and other organisms, as well as specimen locations for natural history collection records (Graham *et al.* 2004). Telemetry is a primary source of data for defining an animal home range, as well as the area utilized by an individual (e.g. Walter *et al.* this issue), using spatial analysis techniques such as kernel density estimation (Seaman and Powell 1996, Berland *et al.* 2008). Advanced data and information systems allow telemetry data to be related to environmental data layers to determine individual patterns of habitat use and understand wildlife ecology (Coyne and Godley 2005).

Increased habitat fragmentation has important effects on the autecology of a species. The associated loss of connectivity will distort the meta-population arrangement within a region, with a likely increase in the number of, and respective isolation of, population clusters (Wang *et al.* 2010). However, because connectivity in most cases takes place across the whole landscape matrix, the importance of land management becomes crucial as certain landscape categories (irrespective of whether these are anthropogenic, seminatural, or natural) may become either corridors or barriers in the connection between those population clusters (see also Section 2.5, Zhang *et al.* (this issue), and van Langevelde and Grashof-Bokdam (this issue)). Spatial information about corridors and barriers has defined ecological networks linking high conservation value areas, such as the 'ecological networks' of northwest Europe (Bruinderink *et al.* 2003). The response of ecological networks to climate change (see Section 2.4) is being actively researched (Lebourgeois *et al.* 2010).

Meta-population modeling, where subpopulations occupy discrete patches of habitat but may move between patches, is one spatial modeling framework that is often used in population viability analysis (PVA) (Akçakaya 2000). PVA is a framework for assessing threats to species persistence and ranking the effects of potential management actions (Akçakaya and Burgman 1995, Possingham *et al.* 2001, Beissinger and McCullough 2002). There are a number of well-established formulations for spatially explicit PVA (reviewed by Akçakaya and Regan 2002). When using meta-population structures or other spatial models, such as individual-based models or patch occupancy models, spatially explicit information about the distribution of habitat quality – the arrangement, size, and quality of habitat patches – is required (reviewed by Franklin 2010a). Models of landscape dynamics, in which landscape initial conditions are characterized using geospatial data, have been used to generate maps of suitable habitat over time for input to meta-population models (Akçakaya *et al.* 2004, 2005) (Figure 1). Patch occupancy models have been used to examine the effects of habitat fragmentation on species (Wilson *et al.* 2009), whereas individual-based models have predicted the impact of land use change on wildlife population trajectories (McRae *et al.* 2008). The paleoecological records provide some evidence of long-distance dispersal events, whereby plants have appeared to migrate significant distances during rapid climate transitions that cannot be explained by conventional seed dispersal mechanisms alone (Kullman 1996) and stochastic dispersal models based upon cellular automata (Figure 2) have been developed to explore the connectivity of habitat patches through long-distance dispersal mechanisms (Pearson and Dawson 2005).

2.3. Spatial and temporal processes in community and landscape ecology

At the community level of ecological organization, species that are found together in an area interact with each other, strongly or weakly, through competition and predation

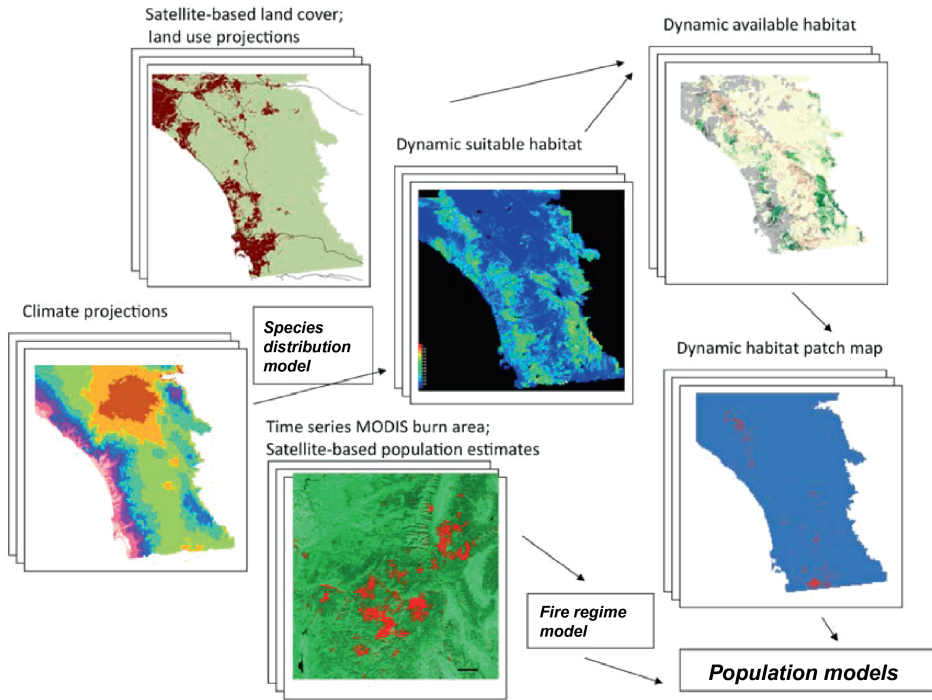


Figure 1. A conceptual overview of applications of and linkages between geospatial data (Section 3.3) on land cover, fire disturbance, and human population; model-based projections of future climate (Section 3.4) and land use; and species distribution models (Section 3.2) interpolated to generate dynamic habitat suitability for input to population viability models (Section 2.2) to forecast the impacts of environmental change on biological populations.

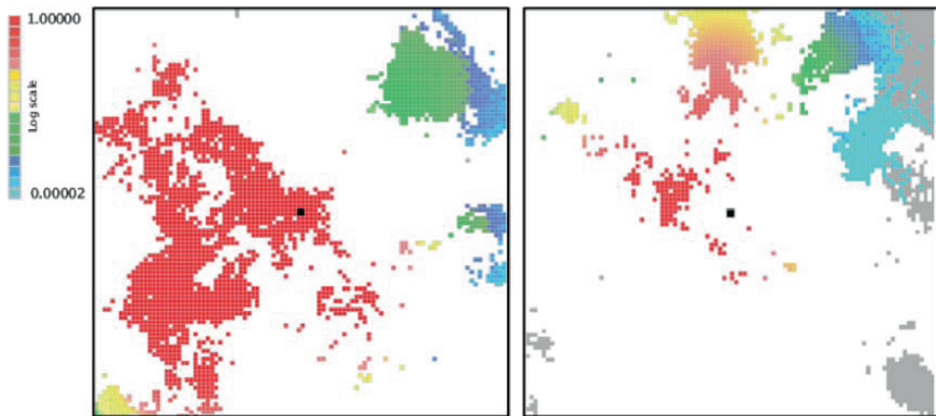


Figure 2. Cellular automata model of species dispersal generating two probabilistic species distributions on theoretical landscapes with varying degrees of fragmentation (Pearson and Dawson 2005). Initial populations are located at the center of each image (black grid). White is unsuitable habitat. Color scale indicated the probability that a species will reach a cell after a finite number of interactions.

as well as various forms of facilitation. These interactions occur at spatial scales determined in part by the mobility of the organisms. Interactions among plants and other sessile organisms (e.g., corals) are assumed to occur at local scales or close distances (Harper 1977). Geospatial data, technology, and analysis methods have supported the study of these community interactions. Point pattern analysis, spatial autocorrelation (SA) measures, and other spatial statistics have been used to test whether individuals of different species, age classes, and so on occur together (within specified distances) more (aggregation) or less (repulsion) often than would be expected by chance (reviewed in Franklin 2010b, see also Section 3.1). These patterns would suggest facilitation or competition, respectively, and multi-scale analysis would identify the scale at which they are operating. A commonly observed pattern in forest communities, for example, is for younger trees in a population to have a more clumped pattern and older trees a more uniform pattern (McDonald *et al.* 2003), which may be the result of density-dependent mortality caused by competition (Kenkel 1988), but can also occur if seedlings are more likely to be discovered by 'predators' (herbivores, fungal pathogens) when found near adult trees of the same species (Condit *et al.* 2000, Harms *et al.* 2000). Because different processes can yield the same observed pattern, spatial analysis cannot always conclusively confirm hypothesized ecological processes when used in isolation. However, advanced methods of spatial analysis provide powerful tools with which to address large and complex community datasets, containing errors and a variety of spatial scales (Franklin and Rey 2007, Lewison *et al.* 2009).

Describing the spatial pattern of ecological communities has long been a basic element of land inventory for resource management (in forestry, range management, and agriculture) and conservation planning (reserve design; see also Zhang *et al.* (this issue)) supported by remotely sensed and other geospatial data (e.g. Scott *et al.* 1993, Franklin *et al.* 2000). Some form of natural disturbance is typical for most ecosystems, and communities are also characterized by temporal dynamics (changes in composition and function) that unfold as a result of those disturbances, the life-history traits of species, and their interactions. Multi-temporal and hyper-temporal remote sensing and image analysis allow annual cycles, interannual variability, and state-changing anomalies caused by disturbance and succession in ecological communities to be tracked through biophysical measures of productivity, photosynthetic activity, foliar chlorophyll concentration, standing biomass, leaf area indices, vegetation species types, and so on (Wolter *et al.* 1995, Dechka *et al.* 2002, Dennison and Roberts 2003, Schmidt *et al.* 2004, Cho *et al.* 2007, Kalacska *et al.* 2007, Darvishzadeh *et al.* 2008, Huang and Geiger 2008). Change detection is the traditional approach used in remote sensing to map changes in land cover that result from natural or anthropogenic disturbances (Singh 1989, Woodcock *et al.* 2001, Rogan *et al.* 2003), but now many land surface attributes are monitored using moderate-resolution remote sensing (Justice *et al.* 1998, Justice *et al.* 2002, Turner *et al.* 2006), and land cover and other data products are routinely available (Strahler *et al.* 1994, Cohen *et al.* 2006). Such remote sensing and land cover data products are now used to spatially model ecological processes and events, for example, species invasion.

Exotic or alien species (nonnative to an area) are, by definition, invasive if they impact on other species, ecological communities, or ecosystem processes. If the invasive species is a pest or disease organism affecting plants, animals or humans, or its vector or host, then detecting its distribution serves public health goals and supports epidemiological studies. Remote sensing and SDM are increasingly being used to map invasive species including pathogens (Bradley and Mustard 2006, Roura-Pascual *et al.* 2006, Andrew and Ustin 2008, Hestir *et al.* 2008, Huang and Geiger 2008) as well as disease spread by predicting their

potential distributions (Kelly and Meentemeyer 2002, Underwood *et al.* 2004, Mohamed *et al.* 2006, Raso *et al.* 2006, Fleming *et al.* 2007, Meentemeyer *et al.* 2008). For example, when the light intensity requirements for an invasive species in Nepal (*Chromolaena odorata*) to germinate were understood, remote sensing and physical modeling could be used to predict the spatial distribution of present and future invasions (Joshi *et al.* 2006). Disease spread by migratory species (for example avian influenza by birds) or resident populations (such as Lyme disease by red deer) are topical public health issues, strongly underpinned by research in spatial ecology (Si *et al.* 2009, Walter *et al.* this issue).

Landscape ecology (at meso-scale) explicitly focuses on the impact of spatial patterns in landscapes on ecological processes, including population, community, and ecosystem processes. Landscape- (or meso-) scale modeling of plant community dynamics often requires spatially explicit information about the initial distribution of species or functional types comprising the community (He and Mladenoff 1999, Mladenoff and Baker 1999), derived from remote sensing (Wolter *et al.* 1995), species distribution models (Section 3.3), or forest survey databases (He *et al.* 1998, Ohmann and Gregory 2002). These models can simulate the impact of natural and anthropogenic disturbances on the dynamics of ecological communities and on ecosystem processes (Scheller and Mladenoff 2004) based on the life-history traits of the species that make up the community (Gustafson *et al.* 2004, Franklin *et al.* 2005, Scheller *et al.* 2005). For example, fire, logging, and climate change may have different or combined effects on the distribution of old-growth forests (He *et al.* 1999, Scheller and Mladenoff 2005, Xu *et al.* 2007). Spatial patterns of urban growth as well as a human-caused increase in fire frequency can lead to a decline in key plant functional types in a fire-prone Mediterranean-type ecosystem (Syphard *et al.* 2006, Syphard *et al.* 2007).

2.4. Spatial and temporal processes in ecosystem ecology

Ecosystem ecology addresses the interactions between organisms and the environment with an emphasis on the exchange and flow of matter and energy between biota, water, soil, and atmosphere (Chapin *et al.* 2002), for example, in biogeochemical cycles (Schlesinger 1991). Evaluating ecosystem services in support of sustainable ecosystem management often requires the use of models. Ecosystem modeling deals with relatively large spatial units; this makes the scaling of finer resolution data particularly relevant. Detailed, often point-based, nondistributed models describing a restricted spatial unit in a physically based manner, with high demands for accurate and extensive data, have to be extended in space as well as time. Traditionally, multiple point models are executed in a regular grid to cover larger areas. This approach, sometimes called spatially distributed modeling, has been used to model evapotranspiration and carbon fluxes (see e.g. Turner *et al.* 2006, Vazifedoust *et al.* 2009, Viviroli *et al.* 2009, Wang *et al.* 2009). However, to accommodate lateral fluxes, the modeling must be spatially explicit. User-friendly and sophisticated software has been developed to include these lateral fluxes (Tague *et al.* 2005), facilitating a better understanding of the processes in time and space (Lett *et al.* 2008).

Much of the impetus for spatially explicit ecosystem modeling is a response to anthropogenic CO₂ emissions and resulting global warming (climate change) on ecosystems, as well as the feedback from ecosystem fragmentation to climate (see Section 2.2). Here, the discussion will focus on models of the carbon cycle (see also Propastin (this issue) as well as Wilson *et al.* (this issue)) and the water cycle, with linkages to other biogeochemical cycles (e.g. nitrogen). To quantify the uptake and emission of carbon from different ecosystems, spatial and temporal information about climate, soils, emissions from industry, and

so on is required. Such datasets are becoming widely available in gridded form, covering extensive parts of the globe (Hickler *et al.* 2009). Availability of regional and global datasets has aided the development of advanced spatial modeling of ecosystems including available water and vegetation (Smith *et al.* 2001).

Because a substantial amount of carbon enters the terrestrial ecosystem without interacting with the atmosphere, the lateral modeling of carbon is an emerging issue (Cox *et al.* 2000). For example, sequestered carbon can be released into the atmosphere when ecosystems are disturbed by melting of permafrost, fires, or storms. Dynamic vegetation models (DVMs; Prentice *et al.* 2007) simulate monthly or daily dynamics of ecosystem processes, 'growing' vegetation types at a location using a time series of climate data (e.g. solar radiation, temperature and precipitation), given constraints of latitude, topography, and soil characteristics. These models can be tailored to individual plant species, including food crops such as wheat or maize, as well as tree species, to estimate productivity and yield and other physical characteristics. Alternatively, DVMs can model a simplified vegetation classification based upon plant functional types (Hickler *et al.* 2009), based on global biomes (Prentice *et al.* 1992, Haxeltine and Prentice 1996) and the response of the vegetation to competition as well as physiological responses to climate. For example, a DVM projected the impact of climate change on vegetation, carbon, and fire distributions in California (Lenihan *et al.* 2003), as well as the response of ecosystem structure and function to climate change (Cramer *et al.* 2001, Bonan *et al.* 2003, Sitch *et al.* 2003).

Nitrogen has been recognized as a limiting factor in carbon sequestration (see e.g. Hutchings *et al.* 2007, Thornton *et al.* 2007, Bonan 2008, Gerber *et al.* 2010, Zaehle *et al.* 2010). However, nitrogen is difficult to model, though recent work indicates that the concentration of foliar nitrogen, as well as other biochemicals such as polyphenols, can be simultaneously estimated using hyperspectral remote sensing (Skidmore *et al.* 2010; Figure 3). The amount of nitrogen is dependent on temperature and soil and is linked to lateral hydrological fluxes. Because water movement is closely linked to a large number of other processes, there has been a steady development in hydrological models (see, Pilesjö *et al.* 1998, Pilesjö *et al.* 2006, Pilesjö 2008).

Key challenges to modeling spatial and temporal processes in ecosystem ecology are the inclusion of individual species or functional types in ecosystem modeling and models linked to carbon (De Deyn *et al.* 2009), for example, how species range might expand or shift under climate change in large ecosystems such as the Siberian tundra (Delbart and Picard 2007). The role of nitrogen as a limiting factor in vegetation modeling (Schubert *et al.* 2010, Zaehle *et al.* 2010) and the melting of permafrost affect the carbon emissions from the arctic and subarctic ecosystems (Christensen *et al.* 2004, Johansson *et al.* 2006). Translation across spatial scales is of specific interest in these studies. When moving from detailed models on a 1-m scale to global models on a 1-km scale (see also Sections 1 and 2.1), lateral movements have not been stressed (Gedney and Cox 2003, Merot *et al.* 2003). As the grid cells may be large in relation to fluxes, every cell is often treated as an isolated system. However, more comprehensive models in combination with increasing data quality and availability have rapidly increased the demand for 'truly' distributed models (Prentice *et al.* 2007). When modeling ecosystems, the influence of different natural and anthropogenic disturbances (Pickett *et al.* 1989) such as agriculture, urbanization, forest management, fire, and storms on, for example, carbon sequestration is of interest (Lindroth *et al.* 2009). Characterizing patterns of disturbance requires geospatial data and data processing such as Moderate Resolution Imaging Spectroradiometer (MODIS) global fire mapping and land cover products (Friedl *et al.* 2002, Cohen *et al.* 2006, Hawbaker *et al.* 2008). In many areas fire is the most important type of natural (and/or human) disturbance

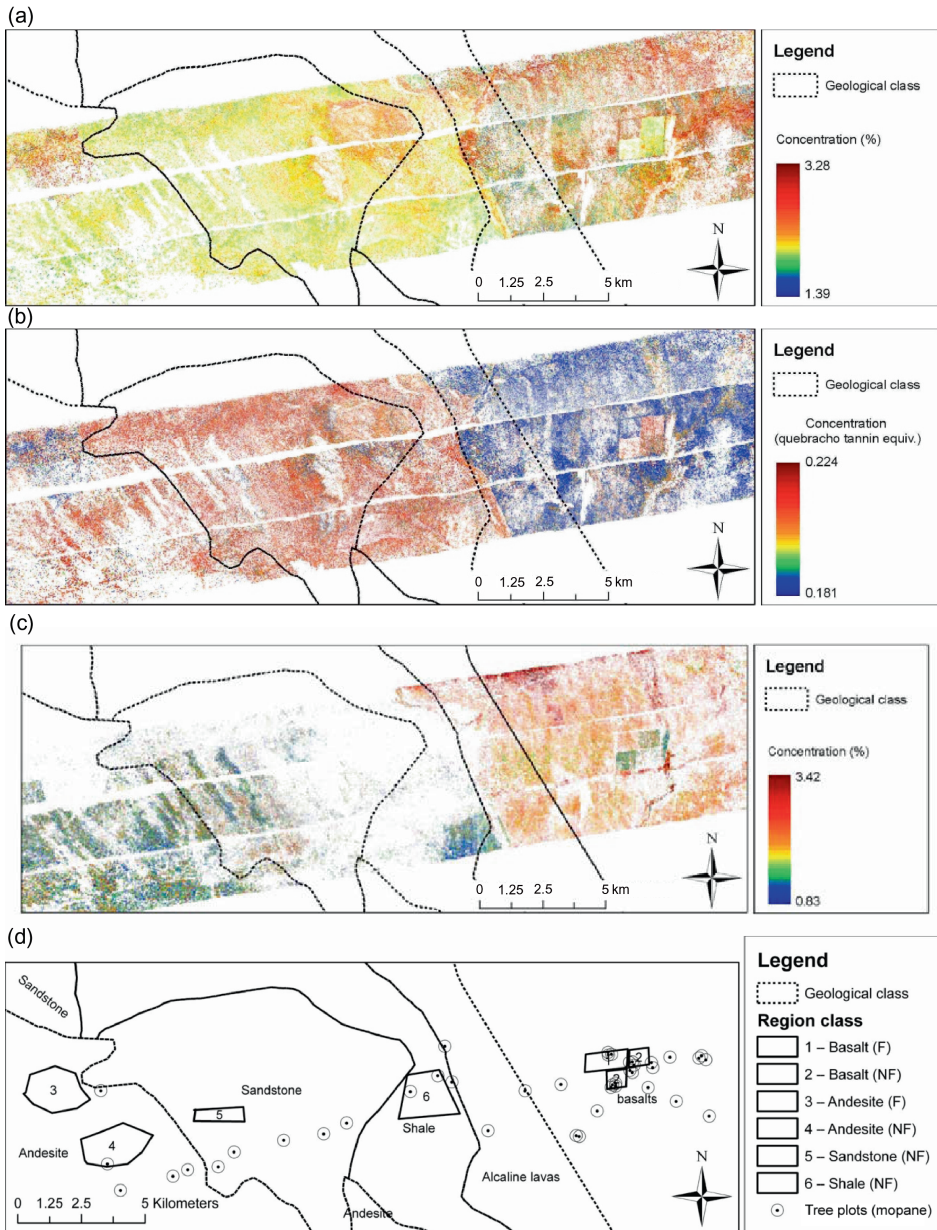


Figure 3. Hyperspectral mapping of savanna forage quality. (a) Foliar nitrogen concentration for mopane trees and shrubs (percent). The white areas represent the 'grass' pixels. (b) Total polyphenol concentration for mopane trees and shrubs (quebracho polyphenol equivalents in gg^{-1}). The white areas represent the 'grass' pixels. (c) Foliar nitrogen concentration in grass (percent). The white areas in this map represent the 'tree' pixels. (d) Homogeneous areas with respect to parent material and fire (F, fire; NF, no fire), overlaid on a map of parent material. The lines are geological class boundaries and are shown in all maps. From Skidmore *et al.* (2010).

affecting biogeochemical cycles and we have many examples of researchers incorporating fire modules in DGVMs (e.g. Thonicke *et al.* 2001, Venevsky *et al.* 2002). However, disturbance processes are often difficult to model. Fire depends not only on commonly used datasets such as temperature, vegetation, and topography but also on wind and fire breaks, natural and anthropogenic. Human disturbance, such as logging and other forms of land use/land cover change, is beginning to be addressed in ecosystem models as well (Shevliakova *et al.* 2009). In turn, human disturbance impacts on the quality and provision of ecosystem goods and services.

2.5. Measures of ecosystem goods and services

Assessing the status of ecosystem goods and services, provided by the regulation, habitat, production, and information functions of ecosystems, is required to support the MEA (Section 1) and similar mandates. These goods and services include provisioning (food and fiber, dependent on the productivity of the land, freshwater, and sea), regulating (climate, water, and air quality), cultural (spiritual, aesthetic, and recreation), and supporting (primary productivity and soil formation) functions. Assessment is almost always an inherently spatial exercise and relies on geospatial data and methods. Although definition, valuation, and assessment of these services are challenging (de Groot *et al.* 2002), there are large-scale examples of ecological integrity being characterized in support of ecosystem management and using proxies derived from geospatial data, for example, the extent and configuration of different land covers (Quigley *et al.* 2001) as well as operational state of environment reporting and analysis, such as undertaken on a regular basis by the Australian government (<http://www.environment.gov.au/soe/index.html>).

Habitat loss and fragmentation resulting from human land use, and increasingly from the effects of anthropogenic climate change, are the primary causes of biodiversity loss (Wilson 1992, Vitousek *et al.* 1997, Thomas *et al.* 2004, van Langevelde and Grashof-Bokdam (this issue)). In turn, climate change poses challenges to the integrity and viability of existing ecological networks (Lebourgeois *et al.* 2010). Consequently, predicting the impact of habitat loss on biodiversity elements and ecosystem processes is an important scientific contribution to conservation and ecosystem management (Ferrier 2002, Burgman *et al.* 2005, Heikkinen *et al.* 2006, Zhang *et al.* (this issue)). Landscape ecology has seen the development of a suite of metrics for describing the spatial arrangement of landscape elements to characterize landscape disturbance, habitat fragmentation, and other patterns and processes (O'Neill *et al.* 1988, Haines-Young and Chopping 1996, Gustafson 1998, McGarigal 2002). These measures are applied to geospatial data that describe the Earth's surface. Typically these include measures describing landscape patch characteristics applied to categorical maps (discrete polygons and classes of land cover) such as class area, patch size characteristics, patch shape characteristics (relative amount of patch edge vs. interior), and patch arrangement (measures of connectivity or distribution of distances among patches). Widely used spatial statistics and geostatistics can also be applied to continuous measures of landscape properties, such as remotely sensed indices of ecosystem productivity or plant canopy structure (Jupp *et al.* 1988, Cohen and Spies 1990, Johansen and Phinn 2006, Tarnavsky *et al.* 2008) as well as the community ecology of endangered species (Wang *et al.* 2010).

Landscape pattern measures of fragmentation have been designated as indicators of sustainable ecosystem management (Loyn and McAlpine 2005). It has been shown in practice that identifying metrics that adequately describe the impacts of fragmentation on biodiversity to meet regional reporting requirements can be challenging (McAlpine and

Eyre 2002, McAlpine *et al.* 2002). Using advanced metrics such as wavelets to describe fragmentation, coupled with indicators of biodiversity, demonstrates that when the degree of fragmentation passes a tipping point, particular ecosystem goods and services disappear (Murwira and Skidmore 2005).

3. Emerging data and methods for spatial ecology

3.1. *Spatial autocorrelation and spatial ecology*

Classical statistical models used in ecology assume that observations of the response and predictor variables are independent. However, it is the ‘first law of geography’ (Tobler 1979) and well-known in ecology (Legendre and Fortin 1989, Fortin and Dale 2005) that near things are similar because they are likely to either be influenced by the same pattern generating processes and/or influence each other. SA is defined as the covariation of properties with distance so that values of a variable are related, either positively or negatively, as a function of proximity (Cressie 1991, Anselin *et al.* 2004). The application of spatial statistics to ecological data has a rich tradition (Pielou 1977, Diggle 1983) and has become a very active area of research (Legendre 1993, Borcard *et al.* 2004, Wagner and Fortin 2005, Hoeting *et al.* 2006, Ives and Zhu 2006).

SA may be considered a nuisance in statistical analyses, but when dealing with spatially explicit data, especially dense data from remote sensing and other geospatial technologies, it is fruitful to consider SA as a potential source of information about underlying processes. For example, measuring SA at different resolutions (spatial lags) using geostatistical or other approaches can yield insights about the scale at which the property being measured interacts with, or is affected by, the same processes (Webster and Oliver 1990, Varekamp *et al.* 1996).

3.2. *Species distribution models*

SDM is the development of quantitative rules linking a species occurrence or abundance to environmental variables, usually based on statistical or machine learning models (Austin 2002). Applying these rules to maps of environmental predictors yields a map of the potential distribution of a species. Spatial realizations of biotic distributions (species or functional types) are required for a number of the emerging applications in spatial ecology already discussed, including modeling meta-population and landscape dynamics (Figure 1) as well as ecosystem processes. In addition, these predictive maps are used, often in combination with other models or spatial data, for a growing number of applications in environmental planning and management including conservation planning and reserve design, environmental risk assessment, predicting the risk of pathogen and exotic species invasion, and targeting areas for species reintroduction (Franklin 2009), as described in Section 2.3.

A number of modeling strategies for predicting the distribution of species have been developed, often focusing on the identification of a species’ ‘bioclimate envelope’ or ‘niche space’ (see Pearson and Dawson 2003, Elith and Leathwick 2009, Franklin 2009 for comprehensive reviews). Computational methods include machine learning approaches (Fielding 1999, Olden *et al.* 2008), such as artificial neural networks (Skidmore *et al.* 1997), genetic algorithms (Genetic Algorithm for Rule-set Production (GARP); Anderson, *et al.* 2003), expert systems (Schmidt *et al.* 2004), nonparametric techniques (Skidmore *et al.* 1996a), and maximum entropy (Phillips *et al.* 2006) as well as statistical inference and ordination approaches. Random forests (Breiman 2001, Prasad *et al.* 2006, Cutler *et al.*

2007) is a machine learning method, developed from the cartographic and regression tree approaches (see Skidmore *et al.* 1996a), that uses model averaging to generate ensemble predictions.

SDM has generally used either (a) inductive and empirical techniques (based on inductive logic – see Skidmore 2002) that correlate the distribution of a species with climate and other environmental variables that vary across space and time (Morin and Lechowicz 2008) or (b) physiologically based approaches (based on deductive logic – see Skidmore 2002), including DVMs described in Section 2.4. Correlative models have been criticized for ignoring biotic interactions and assume that the relationship of a species distribution to its niche space is in equilibrium (Hampe 2004, Pearson and Dawson 2004), although species and land use/cover change (LUCC) interactions, together with dispersal and migration processes, are now being incorporated (Thuiller *et al.* 2004, Pearson and Dawson 2005, Lawson *et al.* 2010, reviewed in Franklin 2010a).

A number of LUCC patterns, and particularly habitat fragmentation, are leading to species reductions and extinctions (see also Sections 2.4 and 3.6, as well as Zhang *et al.* (this issue) and van Langevelde and Grashof-Bokdam (this issue)). In particular, agricultural conversion of natural landscapes to managed crop or pastureland results in wild species habitat loss and fragmentation, which can lead to reductions in total genetic variation, barriers to dispersal, and, for plants, the potential loss of key biotic interactions with pollinators and dispersal agents (Kerr and Currie 1995). Spatial ecology can also be used to reconstruct and understand historical landscapes in the United States (Yoo and Trgovnac (this issue)). Another example, from the United Kingdom, demonstrated that the range distribution of 21 farmland birds has contracted over three decades due to changes in management practices, including intensification (Chamberlain and Fuller 2000). Loss of hedgerows and field margins and increased use of insecticides and herbicides all contribute to biodiversity loss. Although birds and other animals are highly mobile, their specific foraging, breeding, and nesting requirements can make them highly sensitive to LUCC and management regimes at a landscape scale (van Langevelde and Grashof-Bokdam (this issue)).

With regard to the correlative approach based on empirical methods, there are several classes of models that have now been extensively tested for SDM. Generalized regression approaches include generalized linear models, generalized additive models, and multivariate adaptive regression splines, and are commonly used in SDM because they allow alternative distributions to be modeled, specifically binomial distributions (logistic regression) that are appropriate for species presence/absence data (Venables and Ripley 1994, Hastie *et al.* 2001, Guisan *et al.* 2002, Austin *et al.* 2006). Most statistical and machine learning methods are discriminative, that is, they require data characterizing both the presence and the absence of a species. However, they can be applied to environmental background locations to prepare so-called pseudo-absences, if generated appropriately (Manly *et al.* 2002). Other approaches quantify the environmental conditions associated with species presence and have been called ‘profile methods’ (Pearce and Boyce 2006) or use the taxonomy of Skidmore (2002) termed inductive/deterministic models. These include one of the first SDM systems, BIOCLIM/BIOMAP (Nix 1986; Busby 1986, 1991), which used a simple ‘hyper-box’ classifier of independent climatic variables to define the potential range of a species.

Maximum entropy (maxent) is a principle from a statistical mechanics and information theory that states that a probability distribution with maximum entropy (the most spread out, closest to uniform), subject to known constraints, approximates an unknown distribution because it agrees with everything we know, but avoids assuming anything we do not

know. Maximum entropy is a recently developed software application for SDM (Phillips *et al.* 2006) that only requires presence data plus environmental background data, as it generates pseudo-absence data from the background (Phillips and Dudík 2008).

Some heuristics are now emerging from extensive comparisons of these modeling methods. Machine learning methods, and especially those that incorporate model averaging such as random forests (Breiman 1996, 2001), as well as curve-fitting regression methods such as generalized additive models, tend to perform with higher accuracy than simple decision trees or parametric statistical methods such as generalized linear models (Segurado and Araújo 2004, Lawler *et al.* 2006, Prasad *et al.* 2006). However, the difference in performance may be small, especially for those species to which reasonably high-performing models can be fitted by most techniques (Leathwick *et al.* 2006, Elith and Leathwick 2009, Syphard and Franklin 2010). Less than 20% of SDM studies addressed SA (Dormann 2007) (see also Section 3.1), and SA has become an active area of research in SDM (recently reviewed by Dormann *et al.* 2007, Miller *et al.* 2007 and is a topic explored in papers in this Special Issue by Miller and Hanham, Svoray and Lvne, Leitão *et al.*, as well as Propastin).

SDM methods are most useful, for interpolating biotic patterns in data-poor regions, as well as for extrapolating habitat suitability to novel places and future environments (Barry and Elith 2006), when they can cope well with data-poor situations, such as biased, small samples of presence-only species occurrence data. Model comparisons further suggest that distance- and envelop-based methods tend to perform poorly in this situation (Segurado and Araújo 2004, Elith *et al.* 2006, Hijmans and Graham 2006, Pearson *et al.* 2006) whereas maximum entropy has higher accuracies in comparison with other techniques (e.g. Wisz *et al.* 2008, Elith and Leathwick 2009). However, further research is required to generate firm heuristics about the optimal SDM method to use under specific conditions, based on factors including the species characteristics (generalist or specialist), the independent variables used in the model, the scale, SA, and multicollinearity.

3.3. Remote sensing of biodiversity hotspots and ecosystem properties

Traditionally, ecologists characterize biodiversity at community level, using metrics such as species richness (the number of species in an area) and various measures of evenness (richness scaled by relative abundance) such as the Shannon index (Pielou 1975) (see also Section 1). There has been a close connection between the development of remote sensing and biodiversity mapping (Franklin 1995, Leyequien *et al.* 2007). Digital environmental data layers (terrain, geology, soils) were incorporated as ‘ancillary’ data into early efforts to map ecological communities from Landsat imagery (Strahler 1981, Hutchinson 1982). Remote sensing has since seen the development of data products from a plethora of passive and active airborne and satellite-borne sensors, in particular hyperspectral (Ustin *et al.* 2004) and hyper-spatial (Culvenor 2002, Wulder *et al.* 2004) imaging. These new data have been used to move far beyond general plant community mapping to quantifying biodiversity at multiple levels of ecological organization – from mapping individual organisms to modeling species’ distributions, community composition, and species diversity at global to regional to landscape scales (Stoms and Estes 1993, Nagendra 2001, Turner *et al.* 2003). Specifically, numerous studies have used remotely sensed variables to directly estimate species richness or other diversity measures, thus providing spatially explicit information about biodiversity. These landscape- to continental-scale studies use data ranging from low resolution (MODIS, Advanced Very High Resolution Radiometer (AVHRR)) to multispectral, moderate resolution (Landsat) to airborne hyperspectral (Airborne Visible InfraRed

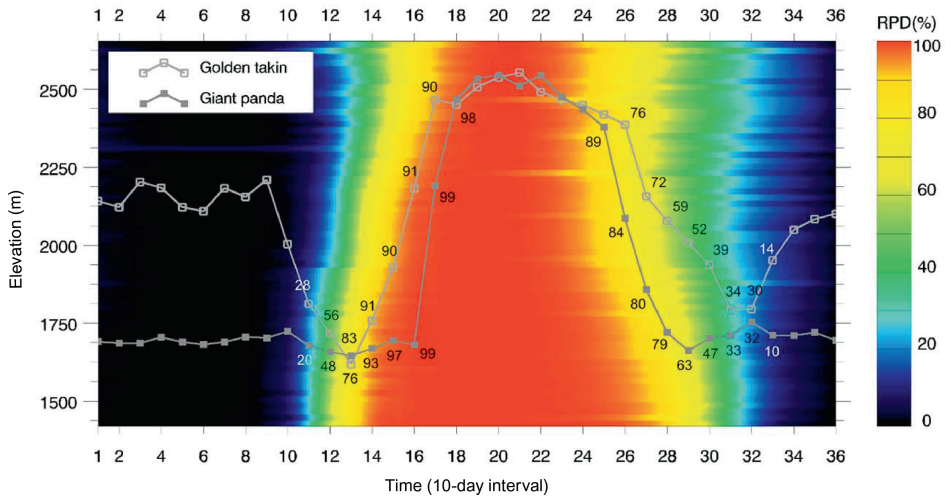


Figure 4. Altitudinal migration patterns of the giant panda (solid squares) and the golden takin (open squares) as estimated from the average elevations of radio-tracking data in Foping Nature Reserve, China. The movement is shown against a background of the vegetation's relative phenological development (RPD) throughout the year, where each interval represents a period of 10 days. The RPD is estimated using the satellite-based Normalized Difference Vegetation Index and ranges from 0% for minimum greenness to 100% for maximum greenness. Key migration times are tagged with RPD values for both the giant panda (above the solid squares) and the golden takin (below the open squares) to show the differences of altitudinal migration in response to vegetation phenology. From Wang *et al.* (2010).

Imaging Spectrometer (AVIRIS)), and they have shown that spectral measures of productivity, water and nutrient status, vegetation structure, phenology, and biochemical diversity are correlated with biodiversity measures (Oindo *et al.* 2001, Gillespie 2005, St-Louis *et al.* 2006, Waring *et al.* 2006, Carlson *et al.* 2007, Goetz *et al.* 2007, Rocchini *et al.* 2007, Saatchi *et al.* 2008). Reflectance, surface temperature, Normalized Difference Vegetation Index, and other spectral indices from a variety of sensors and platforms have also been used to estimate habitat quality (Figure 4) as well as species richness for different taxonomic groups, in particular, plants and birds (Hurlbert and Haskell 2003, Oindo *et al.* 2003, Fairbanks and McGwire 2004, Levin *et al.* 2007).

The rapid technological development of remote sensors is continuously increasing possibilities to derive spatial data. Hyperspectral data (Kumar *et al.* 2001, Wu *et al.* 2007) and radar imagery (Paloscia *et al.* 2010, Tanase *et al.* 2010) are used for detailed mapping of environmental factors as diverse as the concentration of foliar biochemicals, temperature, soil moisture, water content, fire damage, hazards such as landslides and coastal inundation, as well as water quality and biomass. Topography and terrain, as well as vegetation density and height, can be detected directly by the use of Lidar data (Guo *et al.* 2010).

Effective analysis of time-series ecological data remains a challenge, but a number of novel signal-processing techniques developed from telecommunications engineering are emerging. Fourier analysis is a signal-processing technique that can be applied to a time series of satellite images to examine the frequency distribution of the multi-temporal signal, for example, to evaluate the interannual climate response of vegetation phenology (Beck *et al.* 2006) or seasonal patterns of land use (Andresa *et al.* 1994). The technique involves the decomposition of time-series data into a sum of sinusoidal components to illustrate any harmonic regression. Indeed, many ecological systems exhibit periodic

behavior, in time and space, and has been examined using Fourier analysis (Scharlemann *et al.* 2008). Wavelet analysis, involving a transform from a one-dimensional time series (or frequency spectrum) to a diffuse two-dimensional time–frequency image, is becoming increasingly popular in spatial pattern analysis (Dale and Mah 1998). The advantage of wavelet analysis over Fourier transform is that the former does not assume stationarity of the underlying data series as the use of a variable-length moving window along the sequence provides insight into the spatial properties of a two-dimensional image, for example, to evaluate deforestation (Galford *et al.* 2008) or changes in an elephant population in response to increasing landscape fragmentation (Murwira and Skidmore 2005).

3.4. *Environmental change and spatial ecology*

As the human global population continues to grow, with predictions that there will be 9 billion people on Earth by 2050 (United Nations Department of Economic and Social Affairs, Population Division, <http://www.un.org/esa/population/unpop.htm>, accessed 10 October 2010), scientists have raised concerns that we are entering into a new geological epoch named the Anthropocene (Crutzen 2006) in which human impacts on our biological systems and biogeochemical cycles significantly dominate natural processes. Human impact upon biodiversity and ecosystems occurs through several mechanisms. These include extraction from the wild (hunting and fishing), land use/land cover change (LUCC), pollution, and introduction of alien species. The greatest change and impact of the anthropogenic modification of landscapes is through the conversion of natural habitats into agricultural land or through urbanization, which results in habitat loss and fragmentation (van Langevelde and Grashof-Bokdam (this issue) and Zhang *et al.* (this issue)). Habitat fragmentation effects were discussed in Sections 2.2 and 2.3, whereas the impact of climate change on the environment is discussed below.

General circulation (or global climate) models (GCMs) are mathematical models of the circulation of the Earth's atmosphere and oceans based upon equations describing the physics of fluid mechanics and thermodynamics. Because climate is a complex system, driven by solar energy, it is useful to break it down into five components: the atmosphere, ocean, biosphere, cryosphere, and lithosphere. A GCM models these components using a three-dimensional gridded sphere in which the atmosphere and the oceans, for example, have several layers representing different heights and depths, respectively. Each grid cell describes a quantity of mass, energy, and chemical materials transferred from adjacent cells in a horizontal or a vertical direction through wind or ocean currents. GCMs simulate the global climate system using temperature, water, and energy fluxes to drive the 'climate forcing' effects of atmospheric concentrations of greenhouse gases, such as CO₂ and methane, Earth's surface albedo, and clouds. Feedbacks between climate change and ecosystems are pertinent to spatial ecology. Linking GCMs to DGVMs (also see Section 2.4), including physical and carbon cycle coupling of the atmosphere and biosphere, has shown that carbon-cycle feedbacks could significantly accelerate climate change over the twenty-first century (Cox *et al.* 2000, Gedney *et al.* 2000, Prentice *et al.* 2007).

Regional climate models have become increasingly sophisticated with a focus on land surface–climate interactions (Gustafsson *et al.* 2003). Here, again, scale is problematic but central. We have to ask ourselves what scale is relevant and be sure that ancillary data used in the modeling, such as topography, spatial distribution of trees within a stand, and temperature, match this scale. Scale and data availability play crucial roles in the development of spatial ecology applications. Detailed site-specific field measurements, such as the approximately 500 sites included in the FLUXNET global network of CO₂ and water measured

from instruments mounted on towers (www.daac.ornl.gov/FLUXNET/fluxnet.html), have to be integrated with less detailed but globally distributed remotely sensed data relating to both processes and scale (Olofsson *et al.* 2007).

3.5. Spatial data infrastructure and databases

The development of spatial data infrastructure has increased during recent decades (De Man 2006, Mohammadi *et al.* 2010). As just one example, the Global Biodiversity Information Facility (<http://www.gbif.org/>) is working to make the world's biodiversity data globally accessible through Internet and data-sharing protocols. This database comprises over 216 million records of individual species (accessed 12 October 2010). Many, but not all of these, are georeferenced; older records that predate GPS technology have only a general description of location. Most of these records are compiled from natural history collections, databases, and large-scale species monitoring programs.

Geoscience data may be visualized and analyzed using new systems such as the Integrated Data Viewer (<http://www.unidata.ucar.edu/software/idv/>) from Unidata, which is an open-source Java™-based software framework. The Integrated Data Viewer offers the ability to display and work with satellite imagery, gridded data, surface observations, balloon soundings, National Oceanic and Atmospheric Administration (NOAA)

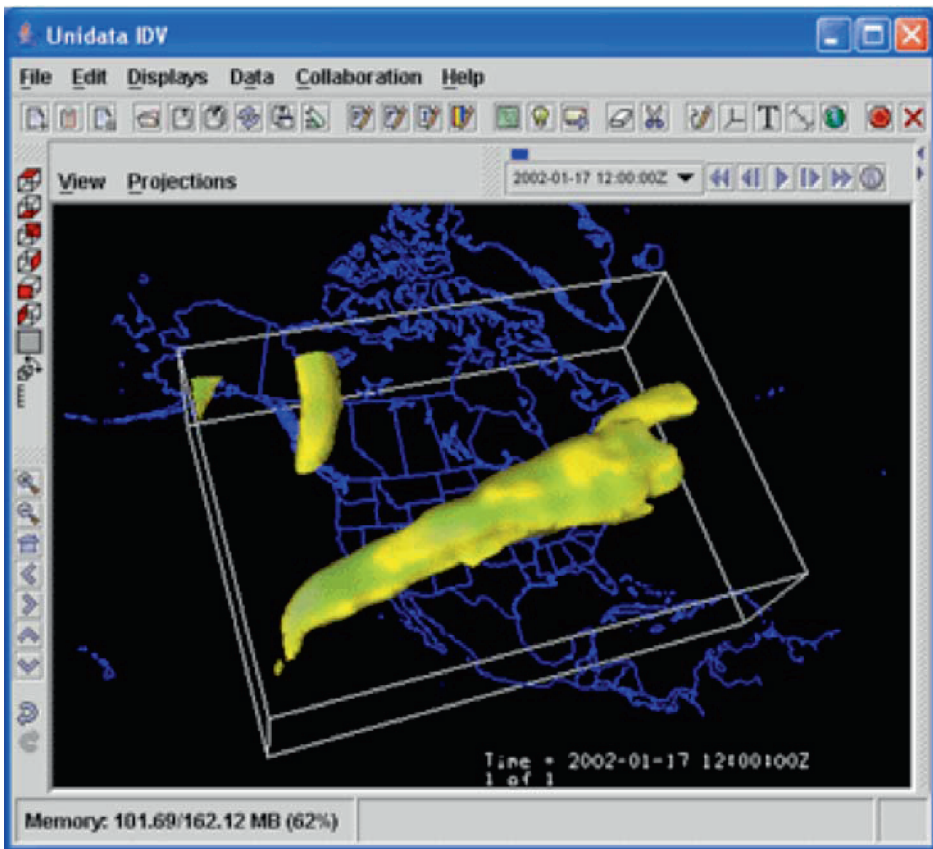


Figure 5. This view is a screen shot illustrating the use of the Integrated Data Viewer (IDV; <http://www.unidata.ucar.edu/software/idv/>) from Unidata, an open-source Java™-based software framework for analyzing and visualizing geoscience data.

National Weather Service (NWS) WSR-88D Level II and Level III radar data, and NOAA National Profiler Network data, all within a unified interface (Figure 5).

Although there are still examples of researchers, communities, and even nations reluctant to share data and knowledge freely, tremendous resources have been allocated to the development of spatial data infrastructures and the accessibility of data has increased. One example is the European INSPIRE initiative (<http://www.inspire-geoportal.eu/>), where the 27 member states of the European Union have established and operated a standardized infrastructure for spatial data and information. However, the data providers in many cases are not economically compensated for standardizing and delivering the data. For example, though Sweden provided 2000 different datasets for standardization, the input of data into the spatial databases is delayed.

Error assessment in spatial ecology is often neglected, for otherwise excellent studies. Many datasets and databases have limited or no documentation regarding quality, and all too often it appears that the applied GIS community does not acknowledge the importance of including metadata about uncertainty. All geospatial modeling results should be presented with confidence intervals, and standard tools for error propagation should be used. There are many examples and reviews of accuracy assessment and error propagation with application to spatial ecology (Heuvelink and Burrough 1993, Franklin 1998, Skidmore 1999, Holmes *et al.* 2000, Foody 2002, Hijmans *et al.* 2005, Svoray and Livne (this issue)).

4. Current research in spatial ecology – themes of the Special Issue

As noted in Section 2.2, the analysis and management of the entire landscape matrix is crucial to biodiversity conservation and management because certain landscape features can act as either corridors or barriers for the movement of individuals and the connectivity of populations. The study by van Langevelde and Grashof-Bokdam (this issue), using a spatially explicit, individual-based model, demonstrated that the intersections of (linear) habitat features (e.g. hedgerows) have higher biodiversity and act as refuges for local populations of organisms (bird species) with limited movement ability in human-dominated landscapes. These findings can be used as input to conservation strategies about poorly dispersing species in, for example, agricultural landscapes. The study is also interesting in that it is ‘deductive’, in other words it draws specific conclusions from a set of ecological propositions (Skidmore 2002). The other studies comprising this Special Issue on Spatial Ecology are ‘inductive’ and derive a conclusion from facts and data that serve as evidence for the conclusion (Skidmore 2002).

Walter *et al.* (this issue) also addressed wildlife management in human-dominated landscapes but did not target species of conservation concern. Rather, their study focused on the risk of disease transmission (see also Section 2.3) within populations of overabundant white-tailed deer as a function of their overlapping use of space (likelihood of coming into contact) in urban landscapes. Using radio-telemetry (Section 2.2) they found that overlapping use of space varied by age, sex, season, and time of day and was greatest for young males at night and during the nongrowing season. The techniques demonstrated by Walter *et al.* (this issue) provide strategies for controlling disease transmission within wildlife populations, as well as the human population (e.g. Lyme disease).

Spatial conservation prioritization (Moilanen *et al.* 2009) is an important area of applied spatial ecology whereby optimal networks of conservation areas are designed according to principles discussed in this article, for example, increasing the viability of biological populations by minimizing habitat fragmentation (Section 2.5). Zhang *et al.* (this issue) have improved the geographical realism of one of the most widely used software

systems for reserve design, Marxan (Ball *et al.* 2009), by incorporating proximity into the parcel selection process based on distance-to-edge, not the currently implemented distance-to-centroid of other parcels. The distance-to-edge method is unaffected by the shape or size of the existing reserve portfolio. These authors raise the important issue that minimizing distances between parcels not only increases the connectivity of the reserve, and therefore is likely to improve the viability of species targeted for conservation, but also has benefits for management. A more compact reserve system is likely to be cheaper and easier to monitor and manage. In other words, land use planning is improved by using a new distance cost function, and new nature conservation areas may be added to reserve systems in an efficient and effective manner.

In ecosystem management on a landscape scale, historical data can be used to describe baseline reference conditions for ecological communities (Section 2.3). Yoo and Trgovnac (this issue) used optimal geostatistical techniques (specifically blocked indicator kriging) to develop maps of historical forest vegetation in Minnesota from a classic land survey dataset by spatial interpolation. Such studies are critical for predicting the historical condition of landscapes, as well as the response of landscapes to climate change or other human-induced modifications such as landscape fragmentation.

As noted by Miller and Hanham (this issue), SDM (Section 3.2) has become a fertile area for research that is at the confluence of spatial ecology and geographic information science. In spatial statistics, a process such as the relationship between *X* and *Y* is stationary if it is invariant (homogeneous and isotropic) over space. Their study used geographically weighted regression (Fotheringham *et al.* 2002) to explore how stationarity of species–habitat relationships varies with scale (Section 2.1). Some of their results were as expected, for example, climate and elevation have greater influence on species distribution at broader scales, whereas terrain and topographic variables (e.g. slope, aspect) become influential at finer scales. However, they found much greater variability in these patterns between species than was expected.

A well-designed study by Leitão *et al.* (this issue) also addressed methodological issues in SDM. Their paper illustrates the importance of using an unbiased sample when developing a species distribution model, and of carefully interpreting models of species–habitat relationships, as well as spatial predictions resulting from them, when they are based on a biased sample. Leitão *et al.* (this issue) also highlighted that an inappropriate choice of environmental variables when undertaking SDM significantly reduces the prediction accuracy of species.

Propastin (this issue), like Miller and Hanham (this issue), explored issues of scale-dependent spatial stationarity in relationships between biotic and abiotic variables. Whereas Miller and Hanham investigated the distribution of species, Propastin examined another ecosystem property (Section 2.4), aboveground biomass, in an Indonesian rainforest. The relationship between biomass and elevation was found to be nonstationary, with coefficients actually varying from positive to negative values with elevation or topography (topography being a surrogate that is strongly related to the primary environmental regimes of light, moisture, heat, and nutrients; see Section 2.1). His analysis allowed strata within the study region to be defined, within which the relationship was stationary. The scale (grain) of environmental variables is related to aboveground biomass, and these relationships exhibit significant interaction effects. For example, aboveground biomass increases with elevation, whereas at lower elevations temperature and solar radiation correlate to higher biomass.

Svoray and Livne (this issue) used Monte Carlo simulation to quantify uncertainty and error propagation (Section 3.5) in a model of ecosystem productivity implemented for a

semiarid landscape in Israel (Section 2.4). Their aim was to partition the effects of topographic error, classification error, and location error on the ecosystem model, and they found that topographic error, and not parent material, was the largest contributor to model uncertainty. Specifically, primary topographic variables (e.g. slope, aspect) contribute more to the error than secondary topographic variables (e.g. solar radiation). As discussed in Section 3.5, the works of Svoray and Livne (this issue) and of Propastin (this issue) confirm that environmental variables become important at different scales depending on which particular ecosystem property is being modeled, whether this is the distribution of species, biomass, or ecosystem productivity.

The use of remotely sensed data to estimate measures of ecosystem productivity (Section 2.3) has long formed a central link between geospatial information and spatial ecology (e.g. Tucker 1979). Wilson *et al.* (this issue) used hierarchical Bayesian modeling in an innovative way to explore scale dependence in the well-established relationship between ecosystem productivity (as measured by Normalized Difference Vegetation Index (Section 3.3), a remotely sensed index) and biomass. They used this approach to integrate upwards from the scale of ecological field plots (centimeter to meters) to coarse-grained satellite imagery.

References

- Akçakaya, H.R. 2000. Viability analyses with habitat-based metapopulation models. *Population Ecology*, 42, 45–53.
- Akçakaya, H.R. and Burgman, M. 1995. PVA in theory and practice. *Conservation Biology*, 9, 705–707.
- Akçakaya, R.H. and Regan, H.M. 2002. Population models: individual-based. In: R.A. Pastorok, *et al.*, eds. *Ecological modeling in risk assessment: chemical effects on populations, ecosystems and landscapes*. Boca Raton, FL: Lewis Publishers, 83–95.
- Akçakaya, H.R., *et al.*, 2004. Integrating landscape and metapopulation modeling approaches: viability of the sharp-tailed grouse in a dynamic landscape. *Conservation Biology*, 18, 526–537.
- Akçakaya, H.R., *et al.*, 2005. Viability of Bell's sage sparrow (*Amphispiza belli* ssp. *belli*) under altered fire regimes. *Ecological Applications*, 15, 521–531.
- Anderson, R.P., Lew, D., and Peterson, A.T. 2003. Evaluating predictive models of species' distributions: criteria for selecting optimal models. *Ecological Modelling*, 162 (211), 232.
- Andres, L., Salas, W.A., and Skole, D. 1994. Fourier analysis of multi-temporal AVHRR data applied to a land cover classification. *International Journal of Remote Sensing*, 15, 1115–1121.
- Andrew, M.E. and Ustin, S.L. 2008. The role of environmental context in mapping invasive plants with hyperspectral image data. *Remote Sensing of Environment*, 112, 4301–4317.
- Anselin, L., Florax, R.J.G.M., and Rey, S.J. 2004. *Advances in spatial econometrics: methodology, tools and applications*. Berlin: Springer.
- Austin, M.P. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling*, 157, 101–118.
- Austin, M.P., *et al.*, 2006. Evaluation of statistical models used for predicting plant species distributions: role of artificial data and theory. *Ecological Modelling*, 199, 197–216.
- Ball, I.R., Possingham, H.P., and Watts, M. 2009. Marxan and relatives: software for spatial conservation prioritisation. In: A. Moilanen, K.A. Wilson, and H.P. Possingham, eds. *Spatial conservation prioritisation: quantitative methods and computational tools*. Oxford, UK: Oxford University Press, Chapter 14: 185–195.
- Barry, S. and Elith, J. 2006. Error and uncertainty in habitat models. *Journal of Applied Ecology*, 43, p. 14 413–423.
- Beck, P.S.A., *et al.*, 2006. Improved monitoring of vegetation dynamics at very high latitudes: a new method using MODIS NDVI. *Remote Sensing of Environment*, 100, 321–334.
- Beck, P.S.A., *et al.*, 2008. Displaying remotely sensed vegetation dynamics along natural gradients for ecological studies. *International Journal of Remote Sensing*, 29, 4277–4283.
- Beissinger, S.R. and McCullough, D.R., ed., 2002. *Population viability analysis*. Chicago, IL: The University of Chicago Press.

- Berland, A., *et al.*, 2008. The impact of landscape disturbance on grizzly bear habitat use in the Foothills Model Forest, Alberta, Canada. *Forest Ecology and Management*, 256, 1875–1883.
- Bonan, G. 2008. Carbon cycle fertilizing change. *Nature Geoscience*, 1, 645–646.
- Bonan, G.B., *et al.*, 2003. A dynamic global vegetation model for use with climate models: concepts and description of simulated vegetation dynamics. *Global Change Biology*, 9, 1543–1566.
- Borcard, D., *et al.*, 2004. Dissecting the spatial structure of ecological data at multiple scales. *Ecology*, 85, 1826–1832.
- Bradley, B.A. and Mustard, J.F. 2006. Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. *Ecological Applications*, 16, 1132–1147.
- Breiman, L. 1996. Bagging predictors. *Machine Learning*, 26, 123–140.
- Breiman, L. 2001. Random forests. *Machine Learning*, 45, 15–32.
- Brown, J.H. 1995. *Macroecology*. Chicago, IL: The University of Chicago Press.
- Bruinderink, G.G., *et al.*, 2003. Designing a coherent ecological network for large mammals in northwestern Europe. *Conservation Biology*, 17, 549–557.
- Burgman, M.A., Lindenmayer, D.B., and Elith, J. 2005. Managing landscapes for conservation under uncertainty. *Ecology*, 86, 2007–2017.
- Busby, J.R. 1986. A biogeoclimatic analysis of *Nothofagus cunninghamii* (Hook.) Oerst. in south-eastern Australia. *Australian Journal of Ecology*, 11, 1–7.
- Busby, J.R. 1991. BIOCLIM – a bioclimatic analysis and prediction system. In: C.R. Margules and M.P. Austin, eds. *Nature conservation: cost effective biological surveys and data analysis*. East Melbourne, Australia: CSIRO, 64–68.
- Carlson, K.M., *et al.*, 2007. Hyperspectral remote sensing of canopy biodiversity in Hawaiian lowland rainforests. *Ecosystems*, 10, 536–549.
- Carpenter, S.R., *et al.*, 2009. Science for managing ecosystem services: Beyond the Millennium Ecosystem Assessment. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 1305–1312.
- Chamberlain, D.E. and Fuller, R.J. 2000. Local extinctions and changes in species richness of lowland farmland birds in England and Wales in relation to recent changes in agricultural land-use. *Agriculture, Ecosystems and Environment*, 78, 1–17.
- Chapin, F.S., III, Matson, P.A., and Mooney, H. 2002. *Principles of terrestrial ecosystem ecology*. New York: Springer.
- Cho, M.A., *et al.*, 2007. Estimation of green grass/herb biomass from airborne hyperspectral imagery using spectral indices and partial least squares regression. *International Journal of Applied Earth Observation and Geoinformation*, 9, 414–424.
- Christensen, T.R., *et al.*, 2004. Thawing sub-arctic permafrost: effects on vegetation and methane emissions. *Geophysical Research Letters*, 31 (L04501), 4 pp.
- Ciarniello, L.M., *et al.*, 2007. Grizzly bear habitat selection is scale dependent. *Ecological Applications*, 17, 1424–1440.
- Clevers, J., *et al.*, 2002. Derivation of the red edge index using the MERIS standard band setting. *International Journal of Remote Sensing*, 23, 3169–3184.
- Cohen, W.B. and Spies, T.A. 1990. Remote sensing of canopy structure in the Pacific Northwest. *The Northwest Environmental Journal*, 6, 415–418.
- Cohen, W.B., *et al.*, 2006. MODIS land cover and LAI collection 4 product quality across nine sites in the western hemisphere. *IEEE Transactions on Geoscience and Remote Sensing*, 44, 1843–1857.
- Condit, R., *et al.*, 2000. Spatial patterns in the distribution of tropical tree species. *Science*, 288, 1414–1418.
- Corvalán, C.F. 2005. *Ecosystems and human well-being [electronic resource]: a report of the millennium ecosystem assessment*. Geneva: World Health Organization.
- Cox, P.M., *et al.*, 2000a. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. *Nature*, 408, 184–187.
- Coyne, M.S. and Godley, B.J. 2005. Satellite tracking and analysis tool (STAT): an integrated system for archiving, analyzing and mapping animal tracking data. *Marine Ecology – Progress Series*, 301, 1–7.
- Cramer, W., *et al.*, 2001. Global response of terrestrial ecosystem structure and function to CO₂ and climate change: results from six dynamic global vegetation models. *Global Change Biology*, 7, 357–373.
- Cressie, N. 1991. *Statistics for spatial data*. New York: Wiley.
- Crutzen, P. 2006. The ‘Anthropocene’. In: E. Ehlers and T. Krafft, eds. *Earth system science in the anthropocene*. Berlin, Heidelberg: Springer, 13–18.

- Culvenor, D.S. 2002. TIDA: an algorithm for the delineation of tree crowns in high spatial resolution remotely sensed imagery. *Computers & Geosciences*, 28, 33–44.
- Cutler, D.R., et al., 2007. Random forests for classification in ecology. *Ecology*, 88, 2783–2792.
- Dale, M.R.T. and Mah, M. 1998. The use of wavelets for spatial pattern analysis in ecology. *Journal of Vegetation Science*, 9, 805–814.
- Darvishzadeh, R., et al., 2008. LAI and chlorophyll estimation for a heterogeneous grassland using hyperspectral measurements. *ISPRS Journal of Photogrammetry and Remote Sensing*, 63, 409–426.
- De Deyn, G.B., et al., 2009. Vegetation composition promotes carbon and nitrogen storage in model grassland communities of contrasting soil fertility. *Journal of Ecology*, 97, 864–875.
- de Groot, R.S., Wilson, M.A., and Boumans, R.M.J. 2002. A typology for the classification, description and valuation of ecosystem functions, goods and services. *Ecological Economics*, 41, 393–408.
- De Man, W.H.E. 2006. Understanding SDI; complexity and institutionalization. *International Journal of Geographical Information Science*, 20, 329–343.
- Dechka, J.A., et al., 2002. Classification of wetland habitat and vegetation communities using multi-temporal Ikonos imagery in southern Saskatchewan. *Canadian Journal of Remote Sensing*, 28, 679–685.
- Delbart, N. and Picard, G. 2007. Modeling the date of leaf appearance in low-arctic tundra. *Global Change Biology*, 13, 2551–2562.
- Dennison, P.E. and Roberts, D.A. 2003. Endmember selection for multiple endmember spectral mixture analysis using endmember average RMSE. *Remote Sensing of Environment*, 87, 123–135.
- Diggle, P. 1983. *Statistical analysis of spatial point patterns*. London: Academic Press.
- Dormann, C.F. 2007. Effects of incorporating spatial autocorrelation into the analysis of species distribution data. *Global Ecology and Biogeography*, 16, 129–138.
- Dormann, C.F., et al., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, 30, 609–628.
- Dungan, J.L., et al., 2002. A balanced view of scale in spatial statistical analysis. *Ecography*, 25, 626–640.
- Elith, J. and Leathwick, J.R. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution and Systematics*, 40, 677–697.
- Elith, J., et al., 2006. Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29, 129–151.
- Fairbanks, D.H.K. and McGwire, K.C. 2004. Patterns of floristic richness in vegetation communities of California: regional scale analysis with multi-temporal NDVI. *Global Ecology and Biogeography*, 13, 221–235.
- Ferrier, S. 2002. Mapping spatial pattern in biodiversity for regional conservation planning. Where to from here? *Systematic Biology*, 51, 331–363.
- Fielding, A.H., ed., 1999. *Machine learning methods for ecological applications*. Boston, MA: Kluwer.
- Fleming, G., van der Merwe, M., and McFerren, G. 2007. Fuzzy expert systems and GIS for cholera health risk prediction in southern Africa. *Environmental Modelling & Software*, 22, 442–448.
- Foody, G.M. 2002. Status of land cover classification accuracy assessment. *Remote Sensing of Environment*, 80, 185–201.
- Fortin, M.-J. and Dale, M.R.T. 2005. *Spatial analysis: a guide for ecologists*. Cambridge, UK: Cambridge University Press.
- Fotheringham, A.S., Brunson, C., and Charlton, M. 2002. *Geographically weighted regression: the analysis of spatially varying relationships*. Chichester: Wiley.
- Franklin, J. 1995. Predictive vegetation mapping: geographic modeling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography*, 19, 474–499.
- Franklin, J. 1998. Predicting the distribution of shrub species in southern California from climate and terrain-derived variables. *Journal of Vegetation Science*, 9, 733–748.
- Franklin, J. 2009. *Mapping species distributions: spatial inference and prediction*. Cambridge, UK: Cambridge University Press.
- Franklin, J. 2010a. Moving beyond static species distribution models in support of conservation biogeography. *Diversity and Distributions*, 16, 321–330.
- Franklin, J. 2010b. Spatial point pattern analysis of plants. In: S.J. Rey and L. Anselin, eds. *Perspectives on spatial data analysis*. New York: Springer, 113–123.

- Franklin, J. and Rey, S.J. 2007. Spatial patterns of tropical forest trees in Western Polynesia suggest recruitment limitations during secondary succession. *Journal of Tropical Ecology*, 23, 1–12.
- Franklin, J., Woodcock, C.E., and Warbington, R. 2000. Multi-attribute vegetation maps of forest service lands in California supporting resource management decisions. *Photogrammetric Engineering and Remote Sensing*, 66, 1209–1217.
- Franklin, J., *et al.*, 2005. The effects of altered fire regimes on patterns of plant succession in the foothills and mountains of southern California. *Ecosystems*, 8, 885–898.
- Friedl, M.A., *et al.*, 2002. Global land cover mapping from MODIS: algorithms and early results. *Remote Sensing of Environment*, 83, 287–302.
- Galford, G.L., *et al.*, 2008. Wavelet analysis of MODIS time series to detect expansion and intensification of row-crop agriculture in Brazil. *Remote Sensing of Environment*, 112, 576–587.
- Gedney, N. and Cox, P.M. 2003. The sensitivity of global climate model simulations to the representation of soil moisture heterogeneity. *Journal of Hydrometeorology*, 4, 1265–1275.
- Gedney, N., *et al.*, 2000. Characterizing GCM land surface schemes to understand their responses to climate change. *Journal of Climate*, 13, 3066–3079.
- Gerber, S., *et al.*, 2010. Nitrogen cycling and feedbacks in a global dynamic land model. *Global Biogeochemical Cycles*, 24 (GB1001), 15 pp.
- Gillespie, T.W. 2005. Predicting woody-plant species richness in tropical dry forests: a case study from south Florida, USA. *Ecological Applications*, 15, 27–37.
- Goetz, S., *et al.*, 2007. Laser remote sensing of canopy habitat heterogeneity as a predictor of bird species richness in an eastern temperate forest, USA. *Remote Sensing of Environment*, 108, 254–263.
- Graham, C.H., *et al.*, 2004. New developments in museum-based informatics and applications in biodiversity analysis. *Trends in Ecology & Evolution*, 19, 497–503.
- Guisan, A., Edwards, T.C. Jr., and Hastie, T. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling*, 157, 89–100.
- Guo, Q.H., *et al.*, 2010. Effects of topographic variability and Lidar sampling density on several DEM interpolation methods. *Photogrammetric Engineering and Remote Sensing*, 76, 701–712.
- Gustafson, E.J. 1998. Quantifying landscape spatial pattern. What is the state of the art? *Ecosystems*, 1, 143–156.
- Gustafsson, D., *et al.*, 2003. Boreal forest surface parameterization in the ECMWF model – 1D test with NOPEX long-term data. *Journal of Applied Meteorology*, 42, 95–112.
- Gustafson, E.J., *et al.*, 2004. Influence of forest management alternatives and land type on susceptibility to fire in northern Wisconsin, USA. *Landscape Ecology*, 19, 327–341.
- Haines-Young, R. and Chopping, M. 1996. Quantifying landscape structure: a review of landscape indices and their application to forested landscapes. *Progress in Physical Geography*, 20, 418–445.
- Hampe, A. 2004. Bioclimatic envelope models: what they detect and what they hide. *Global Ecology & Biogeography*, 13, 469–471.
- Harms, K.E., *et al.*, 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*, 404, 493–495.
- Harper, J.L. 1977. *Population biology of plants*. London: Academic Press.
- Hastie, T., Tibshirani, R., and Friedman, J. 2001. *The elements of statistical learning: data mining, inference and prediction*. New York: Springer.
- Hawbaker, T.J., *et al.*, 2008. Detection rates of the MODIS active fire product in the United States. *Remote Sensing of Environment*, 112, 2656–2664.
- Haxeltine, A. and Prentice, I.C. 1996. BIOME3: an equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types. *Global Biogeochemical Cycles*, 10, 693–709.
- Hays, G.C., *et al.*, 2001. The implications of location accuracy for the interpretation of satellite-tracking data. *Animal Behaviour*, 61, 1035–1040.
- He, H.S. and Mladenoff, D.J. 1999. Spatially explicit and stochastic simulation of forest-landscape fire disturbance and succession. *Ecology*, 80, 81–90.
- He, H.S., *et al.*, 1998. Integration of GIS data and classified satellite imagery for regional forest assessment. *Ecological Applications*, 8, 1072–1083.
- He, H.S., Mladenoff, D.J., and Crow, T.R. 1999. Linking an ecosystem model and a landscape model to study forest species response to climate warming. *Ecological Modelling*, 114, 213–233.
- Heikkinen, R.K., *et al.*, 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. *Progress in Physical Geography*, 30, 751–777.

- Hestir, E.L., *et al.*, 2008. Identification of invasive vegetation using hyperspectral remote sensing in the California delta ecosystem. *Remote Sensing of Environment*, 112, 4034–4047.
- Heuvelink, G.B.M. and Burrough, P.A. 1993. Error propagation in cartographic modelling using Boolean logic and continuous classification. *International Journal of Geographical Information Systems*, 7, 231–246.
- Hickler, T., *et al.*, 2009. An ecosystem model-based estimate of changes in water availability differs from water proxies that are commonly used in species distribution models. *Global Ecology and Biogeography*, 18, 304–313.
- Hijmans, R.J. and Graham, C.H. 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology*, 12, 2272–2281.
- Hijmans, R.J., *et al.*, 2005. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965–1978.
- Hoeting, J.A., *et al.*, 2006. Model selection for geostatistical models. *Ecological Applications*, 16, 87–98.
- Holmes, K.W., Chadwick, O.A., and Kyriakidis, P.C. 2000. Error in a USGS 30-meter digital elevation model and its impact on terrain modeling. *Journal of Hydrology*, 233, 154–173.
- Holyoak, M., Liebold, M.A., and Holt, R.D., ed., 2005. *Metacommunities: spatial dynamics and ecological communities*. Chicago, IL: The University of Chicago Press.
- Huang, C.Y. and Geiger, E.L. 2008. Climate anomalies provide opportunities for large-scale mapping of non-native plant abundance in desert grasslands. *Diversity and Distributions*, 14, 875–884.
- Hurlbert, A.H. and Haskell, J.P. 2003. The effect of energy and seasonality on avian species richness and community composition. *American Naturalist*, 161, 83–97.
- Hutchings, N.J., *et al.*, 2007. Modelling spatial heterogeneity in grazed grassland and its effects on nitrogen cycling and greenhouse gas emissions. *Agriculture Ecosystems & Environment*, 121, 153–163.
- Hutchinson, C.F. 1982. Techniques for combining Landsat and ancillary data for digital classification improvement. *Photogrammetric Engineering and Remote Sensing*, 48, 123–130.
- Ives, A.R. and Zhu, J. 2006. Statistics for correlated data: phylogenies, space, and time. *Ecological Applications*, 16, 20–32.
- Johansen, K. and Phinn, S. 2006. Linking riparian vegetation spatial structure in Australian tropical savannas to ecosystem health indicators: semi-variogram analysis of high spatial resolution satellite imagery. *Canadian Journal of Remote Sensing*, 32, 228–243.
- Johansson, T., *et al.*, 2006. Decadal vegetation changes in a northern peatland, greenhouse gas fluxes and net radiative forcing. *Global Change Biology*, 12, 2352–2369.
- Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, 61, 65–71.
- Joshi, C., *et al.*, 2006. Indirect remote sensing of a cryptic forest understorey invasive species. *Forest Ecology and Management*, 225, 245–256.
- Jupp, D.L.B., Strahler, A.H., and Woodcock, C.E. 1988. Autocorrelation and regularization in digital images. I. Basic theory. *IEEE Transactions on Geoscience and Remote Sensing*, 26, 463–473.
- Justice, C.O., *et al.*, 1998. The moderate resolution imaging spectroradiometer (MODIS): land remote sensing for global change research. *IEEE Transactions on Geoscience and Remote Sensing*, 36, 1228–1249.
- Justice, C.O., *et al.*, 2002. An overview of MODIS land data processing and product status. *Remote Sensing of Environment*, 83, 3–15.
- Kalacska, M., *et al.*, 2007. Ecological fingerprinting of ecosystem succession: estimating secondary tropical dry forest structure and diversity using imaging spectroscopy. *Remote Sensing of Environment*, 108, 82–96.
- Kelly, M. and Meentemeyer, R.K. 2002. Landscape dynamics of the spread of sudden oak death. *Photogrammetric Engineering and Remote Sensing*, 68, 1001–1009.
- Kenkel, N.C. 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. *Ecology*, 69, 1017–1024.
- Kerr, J.T. and Currie, D.J. 1995. Effects of human activity on global extinction risk. *Conservation Biology*, 9, 1528–1538.
- Kullman, L. 1996. Norway spruce present in the Scandes Mountains, Sweden at 8000 BP: new light on holocene tree spread. *Global Ecology and Biogeography*, 5, 94–101.
- Kumar, L., Skidmore, A.K., and Knowles, E. 1997. Modelling topographic variation in solar radiation in a GIS environment. *International Journal of Geographical Information Science*, 11, 475–497.

- Kumar, L., *et al.*, 2001. Imaging spectroscopy and vegetation science. In: F.D. van der Meer and S.M. de Jong, eds. *Imaging spectrometry: basic principles and prospective applications*. Dordrecht: Kluwer Academic Publishers, 1–52.
- Lawler, J.J., *et al.*, 2006. Predicting climate-induced range shifts: model differences and model reliability. *Global Change Biology*, 12, 1568–1584.
- Lawson, D.M., *et al.*, 2010. Cumulative effects of land use, altered fire regime and climate change on persistence of *Ceanothus verrucosus*, a rare, fire dependent plant species. *Global Change Biology*, 16, 2518–2529.
- Leathwick, J.R., Elith, J., and Hastie, T. 2006. Comparative performance of generalized additive models and multivariate adaptive regression splines for statistical modelling of species distributions. *Ecological Modelling*, 199, 188–196.
- Lebourgeois, F., *et al.*, 2010. Simulating phenological shifts in French temperate forests under two climatic change scenarios and four driving global circulation models. *International Journal of Biometeorology*, 54, 563–581.
- Legendre, P. 1993. Spatial autocorrelation: problem or new paradigm. *Ecology*, 74, 1659–1673.
- Legendre, P. and Fortin, M.J. 1989. Spatial pattern and ecological analysis. *Vegetatio*, 80, 107–138.
- Legendre, P., *et al.*, 2002. The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography*, 25, 601–615.
- Lenihan, J.M., *et al.*, 2003. Climate change effects on vegetation distribution, carbon and fire in California. *Ecological Applications*, 13, 1667–1681.
- Lett, C., *et al.*, 2008. A Lagrangian tool for modelling ichthyoplankton dynamics. *Environmental Modelling & Software*, 23, 1210–1214.
- Levin, N., *et al.*, 2007. Predicting mountain plant richness and rarity from space using satellite-derived vegetation indices. *Diversity and Distributions*, 13, 692–703.
- Lewison, R.L., Soykan, C., and Franklin, J. 2009. Mapping the bycatch seascape: multi-species and multi-scale spatial patterns of fisheries bycatch. *Ecological Applications*, 19, 920–930.
- Leyequien, E., *et al.*, 2007. Capturing the fugitive: applying remote sensing to terrestrial animal distribution and diversity. *International Journal of Applied Earth Observation and Geoinformation*, 9, 1–20.
- Liebold, A.M. and Gurevitch, J. 2002. Integrating the statistical analysis of spatial data in ecology. *Ecography*, 25, 553–557.
- Lindroth, A., *et al.*, 2009. Storms can cause Europe-wide reduction in forest carbon sink. *Global Change Biology*, 15, 346–355.
- Loyn, R.H. and McAlpine, C.A. 2005. Spatial patterns and fragmentation: indicators for conserving biodiversity in forested landscapes. In: R.J. Raison, A.G. Brown, and D.W. Flinn, eds. *Criteria and indicators for sustainable forest management*. Wallingford, Oxon: CAB International.
- Mackey, B.G. 1993. A spatial analysis of the environmental relations of rainforest structural types. *Journal of Biogeography*, 20, 303–336.
- Mackey, B.G. and Lindenmayer, D.B. 2001. Towards a hierarchical framework for modeling the spatial distribution of animals. *Journal of Biogeography*, 28, 1147–1166.
- Manly, B.F.J., *et al.*, 2002. *Resource selection by animals: statistical design and analysis for field studies*. 2nd ed. New York: Kluwer Press.
- McAlpine, C.A. and Eyre, T.J. 2002. Testing landscape metrics as indicators of habitat loss and fragmentation in continuous eucalypt forests (Queensland, Australia). *Landscape Ecology*, 17, 711–728.
- McAlpine, C.A., *et al.*, 2002. Mapping glider habitat in dry eucalypt forests for Montreal process indication 1.1e: fragmentation of forest types. *Australian Forestry*, 64, 232–241.
- McDonald, R.I., Peet, R.K., and Urban, D. 2003. Spatial pattern of *Quercus* regeneration limitations and *Acer rubrum* invasion in a Piedmont forest. *Journal of Vegetation Science*, 14, 441–450.
- McGarigal, K. 2002. Landscape pattern metrics. In: A.H. El-Shaarawi and W.W. Piergorsch, eds. *Encyclopedia of environmetrics*. Sussex: Wiley, 1135–1142.
- McRae, B.H., *et al.*, 2008. A multi-model framework for simulating wildlife population response to land-use and climate change. *Ecological Modelling*, 219, 77–91.
- Meentemeyer, R.K., *et al.*, 2008. Early detection of emerging forest disease using dispersal estimation and ecological niche modeling. *Ecological Applications*, 18, 377–390.
- Merot, P., *et al.*, 2003. Testing a climato-topographic index for predicting wetlands distribution along an European climate gradient. *Ecological Modelling*, 163, 51–71.
- Miller, J., Franklin, J., and Aspinall, R. 2007. Incorporating spatial dependence in predictive vegetation models. *Ecological Modelling*, 202, 225–242.

- Mladenoff, D.J. and Baker, W.L. 1999. Development of forest and landscape modeling approaches. In: D.J. Mladenoff and W.L. Baker, eds. *Spatial modeling of forest landscape change: approaches and applications*. Cambridge, UK: Cambridge University Press, 1–13.
- Mohamed, K.L., et al., 2006. Global invasion potential of 10 parasitic witchweeds and related Orobanchaceae. *Ambio*, 35, 281–288.
- Mohammadi, H., Rajabifard, A., and Williamson, I.P. 2010. Development of an interoperable tool to facilitate spatial data integration in the context of SDI. *International Journal of Geographical Information Science*, 24, 487–505.
- Moilanen, A., Wilson, K.A., and Possingham, H.P., eds., 2009. *Spatial conservation prioritization: quantitative methods and computational tools*. New York: Oxford University Press.
- Morin, X. and Lechowicz, M.J. 2008. Contemporary perspectives on the niche that can improve models of species range shifts under climate change. *Biology Letters*, 4, 573–576.
- Murwira, A. and Skidmore, A.K. 2005. The response of elephants to the spatial heterogeneity of vegetation in a Southern African agricultural landscape. *Landscape Ecology*, 20, 217–234.
- Nagendra, H. 2001. Using remote sensing to assess biodiversity. *International Journal of Remote Sensing*, 22, 2377–2400.
- Naveh, Z. and Lieberman, A. 1994. *Landscape ecology: theory and applications*. 2nd ed. New York: Springer.
- Nix, H.A. 1986. A biogeographic analysis of Australian Elapid Snakes. In: R. Longmore, ed. *Atlas of Elapid Snakes of Australia, Australian Flora and Fauna Series Number*. Canberra: Australian Government Publishing Service, 4–15.
- Ohmann, J.L. and Gregory, M.J. 2002. Predictive mapping of forest composition and structure with direct gradient analysis and nearest neighbor imputation in coastal Oregon, USA. *Canadian Journal of Forest Research*, 32, 725–741.
- Oindo, B.O., Skidmore, A.K., and Prins, H.H.T. 2001. Body size and abundance relationship: an index of diversity for herbivores. *Biodiversity and Conservation*, 10, 1923–1931.
- Oindo, B.O., Skidmore, A.K., and de Salvo, P. 2003. Mapping habitat and biological diversity in the Maasai Mara ecosystem. *International Journal of Remote Sensing*, 24, 1053–1069.
- Olden, J.D., Lawler, J.J., and Poff, N.L. 2008. Machine learning methods without tears: a primer for ecologists. *Quarterly Review of Biology*, 83, 171–193.
- Olofsson, P., et al., 2007. Estimating net primary production for Scandinavian forests using data from Terra/MODIS. *Advances in Space Research*, 39, 125–130.
- O’Neill, R.V., et al., 1988. Indices of landscape pattern. *Landscape Ecology*, 1, 153–162.
- Paloscia, S., et al., 2010. Generation of soil moisture maps from ENVISAT/ASAR images in mountainous areas: a case study. *International Journal of Remote Sensing*, 31, 2265–2276.
- Pearce, J.L. and Boyce, M.S. 2006. Modelling distribution and abundance with presence-only data. *Journal of Applied Ecology*, 43, 405–412.
- Pearson, R.G. and Dawson, T.P. 2003. Predicting the impacts of climate change on the distribution of species: Are bioclimatic envelope models useful? *Global Ecology and Biogeography* 12, 361–371.
- Pearson, R.G. and Dawson, T.P. 2004. Bioclimate envelope models: what they detect and what they hide – response to Hampe (2004). *Global Ecology & Biogeography*, 13, 471–473.
- Pearson, R.G. and Dawson, T.P. 2005. Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change. *Biological Conservation*, 123, 389–401.
- Pearson, R.G., et al., 2006. Model-based uncertainty in species range prediction. *Journal of Biogeography*, 33, 1704–1711.
- Phillips, S.J., Anderson, R.P., and Schapire, R.E. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190, 231–259.
- Phillips, S.J. and Dudík, M. 2008. Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, 31, 161–175.
- Pickett, S.T.A., Amesto, J.J., and Collins, S.L. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos*, 54, 129–136.
- Pielou, E. 1977. *Mathematical ecology*. New York: Wiley.
- Pielou, E.C. 1975. *Ecological diversity*. New York: Wiley.
- Pilesjö, P. 2008. An integrated raster-TIN surface flow algorithm. In: Q. Zhou, B. Lees, and G. Tang, eds. *Advances in digital terrain analysis*. Berlin: Springer, 458.
- Pilesjö, P., Zhou, Q., and Harrie, L. 1998. Estimating flow distribution over digital elevation models using a form-based algorithm. *Annals of GIS*, 4, 44–51.

- Pilesjö, P., Persson, D.A., and Harrie, L. 2006. Digital elevation data for estimation of potential wetness in ridged fields – comparison of two different methods. *Agricultural Water Management*, 79, 225–247.
- Possingham, H.P., Lindermyer, D.B., and McCarthy, M.A. 2001. Population viability analysis. *Encyclopedia of Biodiversity*, 4, 831–843.
- Prasad, A.M., Iverson, L.R., and Liaw, A. 2006. Newer classification and regression techniques: bagging and random forests for ecological prediction. *Ecosystems*, 9, 181–199.
- Prentice, C.I., et al., 2007. Dynamic global vegetation modelling: quantifying terrestrial ecosystem responses to large-scale environmental change. In: J. Canadell, D.E. Pataki, and L.F. Pitelka, eds. *Terrestrial ecosystems in a changing world*. Berlin: Springer, 175–192.
- Prentice, I.C., Guiot, J., and Harrison, S.P. 1992. Mediterranean vegetation, lake levels and paleoclimate at the last glacial maximum. *Nature*, 360, 658–660.
- Quigley, T.M., Haynes, R.W., and Hann, W.J. 2001. Estimating ecological integrity in the interior Columbia river basin. *Forest Ecology and Management*, 153, 161–178.
- Raso, G., et al., 2006. An integrated approach for risk profiling and spatial prediction of *Schistosoma mansoni*-hookworm coinfection. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 6934–6939.
- Rocchini, D., Ricotta, C., and Chiarucci, A. 2007. Using satellite imagery to assess plant species richness: the role of multispectral systems. *Applied Vegetation Science*, 10, 325–331.
- Rogan, J., et al., 2003. Land cover change monitoring in southern California using multitemporal Landsat TM and ancillary data. *Photogrammetric Engineering and Remote Sensing*, 69, 793–804.
- Ropert-Coudert, Y. and Wilson, R.P. 2005. Trends and perspectives in animal-attached remote sensing. *Frontiers in Ecology and the Environment*, 3, 437–444.
- Roura-Pascual, N., et al., 2006. Niche differentiation and fine-scale projections for Argentine ants based on remotely sensed data. *Ecological Applications*, 16, 1832–1841.
- Saatchi, S., et al., 2008. Modeling distribution of Amazonian tree species and diversity using remote sensing measurements. *Remote Sensing of Environment*, 112, 2000–2017.
- Sachs, J.B. and MacArthur, J.W. 2005. The Millennium Project: a plan for meeting the Millennium Development Goals. *The Lancet*, 365, 347–353.
- Scharlemann, J.P.W., et al., 2008. Global data for ecology and epidemiology: a novel algorithm for temporal Fourier processing MODIS data. *PLoS ONE*, 3, e1408.
- Scheller, R.M. and Mladenoff, D.J. 2004. A forest growth and biomass module for a landscape simulation model, LANDIS: design, validation, and application. *Ecological Modelling*, 180, 211–229.
- Scheller, R.M. and Mladenoff, D.J. 2005. A spatially interactive simulation of climate change, harvesting, wind, and tree species migration and projected changes to forest composition and biomass in northern Wisconsin, USA. *Global Change Biology*, 11, 307–321.
- Scheller, R.M., et al., 2005. Simulating the effects of fire reintroduction versus continued fire absence on forest composition and landscape structure in the boundary waters canoe area, northern Minnesota, USA. *Ecosystems*, 8, 396–411.
- Schlesinger, W.H. 1991. *Biogeochemistry, an analysis of global change*. San Diego, CA: Academic Press.
- Schmidt, K.S., et al., 2004. Mapping coastal vegetation using an expert system and hyperspectral imagery. *Photogrammetric Engineering and Remote Sensing*, 70, 703–715.
- Schubert, P., et al., 2010. Impact of nutrients on peatland GPP estimations using MODIS time series data. *Remote Sensing of Environment*, 114, 2137–2145.
- Scott, J.M., et al., 1993. Gap analysis: a geographical approach to protection of biological diversity. *Wildlife Monographs*, 123, 1–41.
- Seaman, D.E. and Powell, R.A. 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, 77, 2075–2085.
- Segurado, P. and Araújo, M.B. 2004. An evaluation of methods for modelling species distributions. *Journal of Biogeography*, 31, 1555–1568.
- Shevliakova, E., et al., 2009. Carbon cycling under 300 years of land use change: importance of the secondary vegetation sink. *Global Biogeochemical Cycles*, 23 (GB2022), 16 pp.
- Si, Y.L., et al., 2009. Spatio-temporal dynamics of global H5N1 outbreaks match bird migration patterns. *Geospatial Health*, 4, 65–78.
- Singh, A. 1989. Digital change detection techniques using remotely-sensed data. *International Journal of Remote Sensing*, 10, 989–1003.

- Sitch, S., et al., 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, 9, 161–185.
- Skidmore, A.K., Gauld, A., and Walker, P. 1996a. Classification of kangaroo habitat distribution using three GIS models. *International Journal of Geographical Information Systems*, 10, 441–454.
- Skidmore, A.K. 1999. Accuracy assessment of spatial information. In: A. Stein, F. van der Meer, and B. Gorte, eds. *Spatial statistics for remote sensing*. Dordrecht: Kluwer Academic Publishers, 197–209.
- Skidmore, A.K. 2002. *Environmental modeling using GIS and remote sensing*. London: Taylor & Francis.
- Skidmore, A.K., et al., 1996b. An operational expert system for mapping forest soils. *Photogrammetric Engineering and Remote Sensing*, 62, 501–511.
- Skidmore, A.K., et al., 1997. Performance of a neural network: mapping forests using GIS and remotely sensed data. *Photogrammetric Engineering and Remote Sensing*, 63, 501–514.
- Skidmore, A.K., et al., 2010. Forage quality of savannas – simultaneously mapping foliar protein and polyphenols for trees and grass using hyperspectral imagery. *Remote Sensing of Environment*, 114, 64–72.
- Smith, B., Prentice, I.C., and Sykes, M.T. 2001. Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. *Global Ecology and Biogeography*, 10, 621–637.
- St-Louis, V., et al., 2006. High-resolution image texture as a predictor of bird species richness. *Remote Sensing of Environment*, 105, 299–312.
- Stohlgren, T.J., et al., 1997. Rapid assessment of plant diversity patterns: a methodology for landscapes. *Environmental Monitoring and Assessment*, 48, 25–43.
- Stoms, D. and Estes, J.E. 1993. A remote sensing research agenda for mapping and monitoring biodiversity. *International Journal of Remote Sensing*, 14, 1839–1860.
- Strahler, A.H. 1981. Stratification of natural vegetation for forest and rangeland inventory using Landsat digital imagery and collateral data. *International Journal of Remote Sensing*, 2, 15–41.
- Strahler, A.H., Moody, A., Lambin, E., et al., 1994. *MODIS land cover product algorithm technical basis document, NASA document for MODIS product No. 11, Parameter Nos. 2669 and 2671*. Washington, DC: NASA.
- Swanson, F.J., et al., 1988. Landform effects on ecosystem patterns and processes. *Bioscience*, 38, 92–98.
- Syphard, A.D. and Franklin, J. 2010. Species' traits affect the performance of species' distribution models for plants in southern California. *Journal of Vegetation Science*, 21, 177–189.
- Syphard, A.D., Franklin, J., and Keeley, J.E. 2006. Simulating the effects of frequent fire on southern California coastal shrublands. *Ecological Applications*, 16, 1744–1756.
- Syphard, A.D., Clarke, K.C., and Franklin, J. 2007. Simulating fire frequency and urban growth in southern California coastal shrublands, USA. *Landscape Ecology*, 22, 431–445.
- Tague, C.L., Band, L.E., and Franklin, J. 2005. Terrestrial ecosystems. In: M.G. Anderson, ed. *Encyclopedia of hydrological sciences*. New York: Wiley, Chapter 103, 14 pp.
- Tanase, M.A., et al., 2010. TerraSAR-X data for burn severity evaluation in Mediterranean forests on sloped terrain. *IEEE Transactions on Geoscience and Remote Sensing*, 48, 917–929.
- Tarnavsky, E., Garrigues, S., and Brown, M.E. 2008. Multiscale geostatistical analysis of AVHRR, SPOT-VGT, and MODIS global NDVI products. *Remote Sensing of Environment*, 112, 535–549.
- Thomas, C.D., et al., 2004. Extinction risk from climate change. *Nature*, 427, 145–148.
- Thonicke, K., et al., 2001. The role of fire disturbance for global vegetation dynamics: coupling fire into a dynamic global vegetation model. *Global Ecology and Biogeography*, 10, 661–677.
- Thornton, P.E., et al., 2007. Influence of carbon-nitrogen cycle coupling on land model response to CO₂ fertilization and climate variability. *Global Biogeochemical Cycles*, 21 (GB4018), 15 pp.
- Thuiller, W., et al., 2004. Effects of restricting environmental range of data to project current and future species distributions. *Ecography*, 27, 165–172.
- Tilman, D. and Kareiva, P., eds., 1997. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton, NJ: Princeton University Press.
- Tobler, W. 1979. Cellular geography. In: G.O.S. Gale, ed. *Philosophy in geography*. Dordrecht: Reidel, 379–389.
- Tucker, C.J. 1979. Red and infrared linear combinations for monitoring vegetation. *Remote Sensing of Environment*, 8, 127–150.

- Turner, D.P., *et al.*, 2006. Evaluation of MODIS NPP and GPP products across multiple biomes. *Remote Sensing of Environment*, 102, 282–292.
- Turner, M.G., Gardner, R.H., and O'Neill, R.V. 2001. *Landscape ecology in theory and practice*. New York: Springer.
- Turner, W., *et al.*, 2003. Remote sensing for biodiversity science and conservation. *Trends in Ecology & Evolution*, 18, 306–314.
- Underwood, E.C., Klinger, R., and Moore, P.E. 2004. Predicting patterns of non-native plant invasions in Yosemite National Park, California, USA. *Diversity and Distributions*, 10, 447–459.
- Ustin, S.L., *et al.*, 2004. Using imaging spectroscopy to study ecosystem processes and properties. *Bioscience*, 54, 523–534.
- Varekamp, C., Skidmore, A.K., and Burrough, P.A.B. 1996. Using public domain geostatistical and GIS software for spatial interpolation. *Photogrammetric Engineering and Remote Sensing*, 62, 845–854.
- Vazifedoust, M., *et al.*, 2009. Assimilation of satellite data into agrohydrological models to improve crop yield forecasts. *International Journal of Remote Sensing*, 30, 2523–2545.
- Venables, W.M. and Ripley, B.D. 1994. *Modern applied statistics with S-Plus*. New York: Springer.
- Venevsky, S., *et al.*, 2002. Simulating fire regimes in human-dominated ecosystems: Iberian Peninsula case study. *Global Change Biology*, 8, 984–998.
- Vitousek, P.M., *et al.*, 1997. Human domination of Earth's ecosystems. *Science*, 277, 494–499.
- Viviroli, D., *et al.*, 2009. An introduction to the hydrological modelling system PREVAH and its pre- and post-processing-tools. *Environmental Modelling & Software*, 24, 1209–1222.
- Wagner, H.H. and Fortin, M.J. 2005. Spatial analysis of landscapes: concepts and statistics. *Ecology*, 86, 1975–1987.
- Wang, L., *et al.*, 2009. Development of a distributed biosphere hydrological model and its evaluation with the Southern Great Plains Experiments (SGP97 and SGP99). *Journal of Geophysical Research-Atmospheres*, 114 (D08107), 15 pp.
- Wang, T.J., *et al.*, 2010. Characterizing the spatial distribution of giant pandas (*Ailuropoda melanoleuca*) in fragmented forest landscapes. *Journal of Biogeography*, 37, 865–878.
- Wang, T.J., *et al.*, (2010). Migration patterns of two endangered sympatric species from a remote sensing perspective. *Photogrammetric Engineering and Remote Sensing*, 76, 1343–1352.
- Waring, R.H., *et al.*, 2006. MODIS enhanced vegetation index predicts tree species richness across forested ecoregions in the contiguous USA. *Remote Sensing of Environment*, 103, 218–226.
- Webster, R. and Oliver, M.A. 1990. *Statistical methods in soil and land resource survey*. New York: Oxford University Press.
- Wilby, R.L. and Schimel, D.S. 1999. Scales of interaction in eco-hydrological relations. In: A.J. Baird and R.L. Wilby, eds. *Eco-hydrology: plants and water in terrestrial and aquatic environments*. London: Routledge, 39–77.
- Wilson, E.O. 1992. *The diversity of life*. New York: Norton.
- Wilson, J. and Gallant, J. 2000. *Terrain analysis: principles and applications*. New York: Wiley.
- Wilson, R.J., Davies, Z.G., and Thomas, C.D. 2009. Modelling the effect of habitat fragmentation on range expansion in a butterfly. *Proceedings of the Royal Society B: Biological Sciences*, 276, 1421–1427.
- Wisz, M.S., *et al.*, 2008. Effect of sample size on the performance of species distribution models. *Diversity and Distributions*, 14, 763–773.
- Wolter, P.T., *et al.*, 1995. Improved forest classification in the Northern Lake states using multi-temporal Landsat imagery. *Photogrammetric Engineering and Remote Sensing*, 61, 1129–1143.
- Woodcock, C.E., *et al.*, 2001. Monitoring large areas for forest change using Landsat: generalization across sensors, space and time. *Remote Sensing of Environment*, 78, 194–203.
- Wu, G.F., *et al.*, 2007. Concurrent monitoring of vessels and water turbidity enhances the strength of evidence in remotely sensed dredging impact assessment. *Water Research*, 41, 3271–3280.
- Wulder, M.A., *et al.*, 2004. High spatial resolution remotely sensed data for ecosystem characterization. *Bioscience*, 54, 511–521.
- Xu, C.G., Gertner, G.Z., and Scheller, R.M. 2007. Potential effects of interaction between CO₂ and temperature on forest landscape response to global warming. *Global Change Biology*, 13, 1469–1483.
- Zachle, S., *et al.*, 2010. Carbon and nitrogen cycle dynamics in the O-CN land surface model: 2. Role of the nitrogen cycle in the historical terrestrial carbon balance. *Global Biogeochemical Cycles*, 24 (GB1006).