

## INTERDISCIPLINARY PERSPECTIVES

# Remote sensing of species dominance and the value for quantifying ecosystem services

Stephanie Pau<sup>1</sup> & Laura E. Dee<sup>2</sup><sup>1</sup>Department of Geography, Florida State University, Tallahassee, Florida 32306<sup>2</sup>Institute on the Environment, University of Minnesota, St. Paul, Minnesota 55108**Keywords**

Biodiversity monitoring, conservation, ecosystem functions, essential biodiversity variables, species abundance, species composition

**Correspondence**

Stephanie Pau, Department of Geography, Florida State University, Tallahassee, FL 32306.  
Tel: +1 850 644 1706; Fax: +1 850 644 5913;  
E-mail: spau@fsu.edu

**Funding Information**

L.D. was supported by a grant from the Institute on the Environment at University of Minnesota to P.B. Reich and S. Polasky.

Editor: Duccio Rocchini

Associate Editor: Martin Wegmann

Received: 28 February 2016; Revised: 29 May 2016; Accepted: 20 June 2016

doi: 10.1002/rse2.23

**Abstract**

Remote sensing (RS) is a powerful tool to measure and monitor Essential Biodiversity Variables (EBVs) and their environmental drivers. Despite this potential, stronger integration between remote sensing experts and the ecological community could better support biodiversity initiatives. Here we highlight opportunities to harness remote sensing technology to better understand biodiversity patterns, ecological processes and the consequences for ecosystem services (ESs). We argue that tracking many EBVs using remote sensing should prioritize the monitoring of dominant species, a scalable property across multiple EBV classes, for several reasons. First, a few dominant species in an ecological community disproportionately contribute to the satellite spectral signature. Second, a focus on dominance would enable a stronger links to ecological research, as dominance reflects the ecological community context (i.e. relative abundance of coexisting species). For example dominant species should be especially important contributors to many ecosystem functions and services that rely on abundance or biomass, such as carbon storage or nutrient cycling, because of their greater representation in a community. Furthermore, global change impacts on communities may be reflected in changing dominance structure before the losses of species, thus tracking dominance provides an early-warning sign of community change for EBVs. Finally, focusing on dominant species should improve understanding of spatial and temporal dynamics of dominance-driven ESs through RS mapping. Given the importance of dominant species to ecological communities and ESs, monitoring dominance under changing environmental conditions and human impacts should be a global priority.

**Introduction**

Global environmental change is rapidly transforming the Earth's ecosystems. The rate of biodiversity loss may have already crossed a threshold that will degrade ecosystem functions and have unexpected consequences on interrelated subsystems of the planet (Rockstrom et al. 2009). To capture the major dimensions of biodiversity change, monitoring efforts have recently identified a set of global Essential Biodiversity Variables (EBV). EBVs are measurements required for studying, reporting and managing biodiversity change (Pereira et al. 2013). The six broad classes of EBVs – genetic composition, species populations, species traits, community composition, ecosystem/habitat structure and ecosystem functions – are intended to complement each

other and observations of environmental change (Pereira et al. 2013). Remote sensing (RS) is a powerful tool to measure many EBVs and environmental change across time and space (O'Connor et al. 2015). Hundreds of satellites orbiting in space together provide global observations of the Earth's surface at repeated intervals. Increasing use of airborne sensors, unmanned aerial vehicles (UAVs) and in situ sensors also enhance the capability to detect changes in EBVs (Turner 2014). RS data should be complementary to time- and site-specific field observations by emphasizing scalable properties. By measuring scalable properties, RS can be used to extrapolate local data using models or proxies and provide information on how EBVs respond to environmental drivers (Pereira et al. 2013; Pettorelli et al. 2014a).

Despite the potential for RS to effectively monitor EBVs, recent calls for RS experts to better support biodiversity initiatives highlighted the need to form stronger links to the ecological community (Pereira et al. 2013; Pettorelli et al. 2014b; Skidmore et al. 2015). Discrepancies in scale between ecological data and pixel resolution, as well as incongruity between ecological metrics and satellite-derived proxies have been identified as barriers to integration (Turner et al. 2003; Skidmore et al. 2015). Rather than compromising to find overlap, efforts should aim for co-production of new knowledge beginning with the initial research questions. Toward that goal, here we highlight opportunities to integrate RS and ecology to address shared questions about biodiversity patterns, ecological processes and the consequences for ecosystem services (ESs). In particular, we argue that tracking many EBVs using RS should more explicitly focus on the causes and consequences of dominance, a scalable property across multiple EBV classes. Dominance reflects both species abundances and community composition (i.e. species that represent a disproportionate number of individuals and/or biomass in the community). Such a focus also enables spatially and temporally dynamic mapping of dominance-driven ecosystem functions and services (e.g. provisioning and regulating services).

In most optical RS applications, a few dominant species in an ecological community disproportionately contribute to the satellite spectral signature (Fig. 1). Dominance (or its counterpart, evenness) considers the abundance of species relative to the other species in a community (Hillebrand et al. 2008). Much of the biodiversity literature has focused on species richness – strictly the number of species within a community (Purvis and Hector 2000; Hillebrand et al. 2008). Yet, even in species-rich tropical forests, only a subset of species are large, emergent trees that comprise the canopy and thus the spectral signal of a pixel. Indeed, many advances in optical RS have focused on spectral mixture analysis, where the fraction of different surfaces contributing to the remotely sensed spectra is decomposed into linear combinations of pure spectra for each type of surface ('endmembers') (Roberts et al. 1998; Asner and Martin 2009). Spectrally mixed pixels can be a technical limitation of remote sensing that is problematic for studying local species richness and tracking losses of rare species; however, it provides an opportunity to link species dominance to EBVs. Given the highly skewed abundance of species in most natural systems (Whittaker 1975; Ricklefs 1990; Schwartz et al. 2000), focusing on dominance should enable a scalable, ecologically meaningful measure (rather than partitioning spectral endmembers) of EBVs using remotely sensed data.

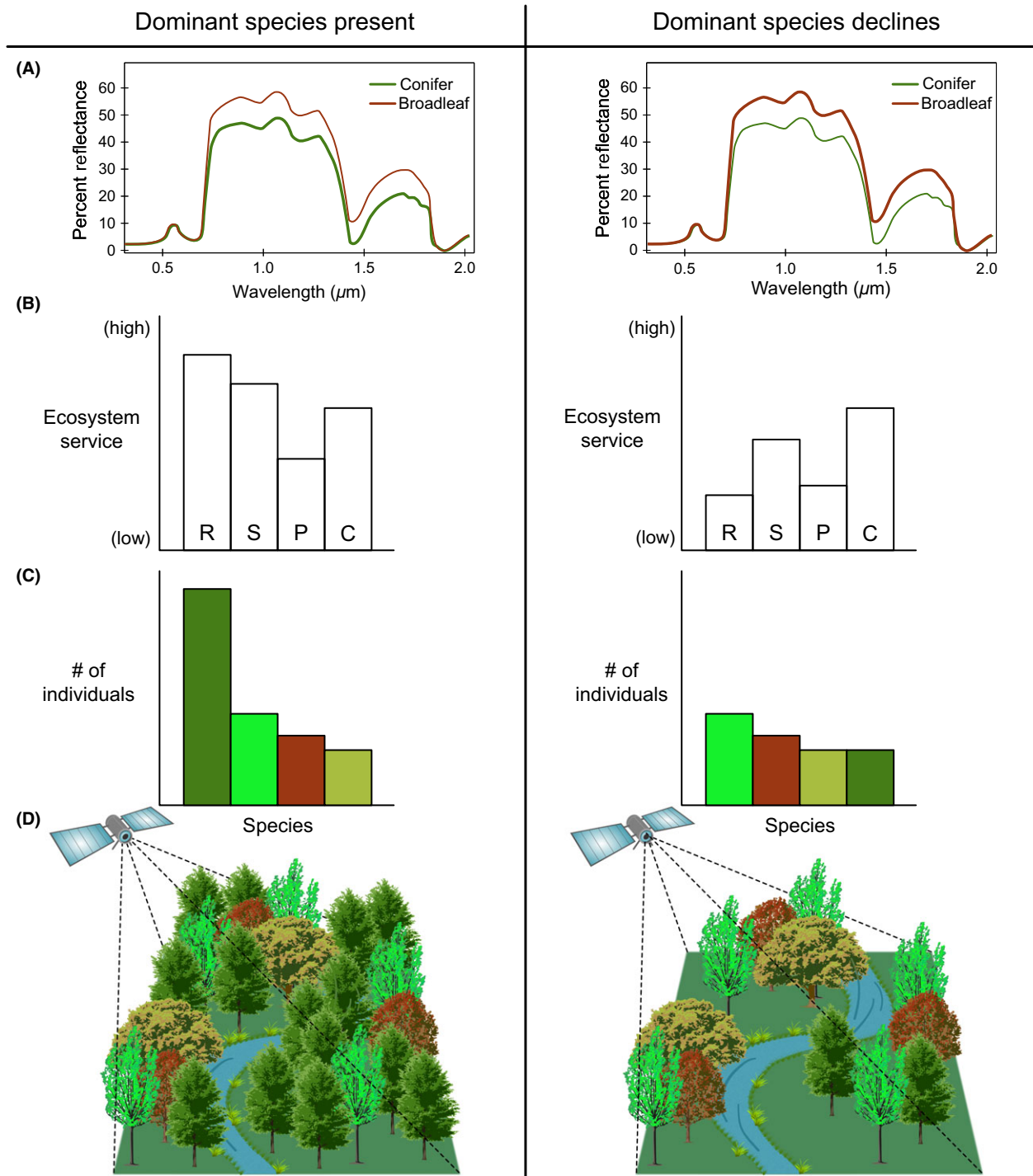
Despite the importance of dominant species to ecological communities and ecosystem functioning, there is

much to learn about the causes and consequences of dominance, especially under changing environmental conditions and human impacts (Hillebrand et al. 2008). RS is particularly well-suited to track changes in dominance over time and space and to quantify associated changes in ecosystem functions and services. In the following sections, we outline how a focus of RS on dominant species provides several insights for monitoring multiple classes of EBVs and better connects RS to ecological research priorities. Identifying which species are dominant in different locations or at different time periods should help inform our understanding of the environmental conditions that confer ecological success, and whether patterns and processes vary consistently across environmental gradients. Finally, individuals of dominant species are disproportionately represented in communities, often leading to a larger representation of their trait values and larger contributions to ecosystem structure and function (Hillebrand et al. 2008). Therefore, tracking dominant species in an ecosystem can provide a proxy for ES supply and greater insight into spatiotemporal dynamics of ESs.

## Remote Sensing of Biodiversity and Ecological Dominance

Several review papers identify various approaches for using remote sensing to track biodiversity and ecosystem functions (Nagendra 2001; Kerr and Ostrovsky 2003; Turner et al. 2003; Gillespie et al. 2008; Kuenzer et al. 2014; Skidmore et al. 2015). Many remote sensing studies have been devoted to detecting local species richness (i.e. alpha diversity). One approach is using land cover classifications and thematic mapping of habitats to monitor habitat extent and conversion. Habitat extent can then be used to estimate species loss based on species-area relationships (Turner et al. 2003). In addition to land-cover or habitat mapping, remote sensing provides various measures of habitat conditions, including proxies for habitat complexity (e.g. LAI; % tree cover) and primary productivity (e.g. NDVI). These proxies have been commonly used to indicate plant or bird species richness because of diverse resources provided by more productive and complex habitats (Waring et al. 2002; Gillespie 2005; Rompré et al. 2007; Phillips et al. 2010; Pau et al. 2012) or to test the species-energy hypothesis, which proposes that energy is a limiting resource to the number of species in an area (Currie and Paquin 1987; Hawkins et al. 2003).

Remote sensing has been widely used to understand species distributions (reviewed in He et al. 2015). Bioclimatic variables derived from satellites are increasingly included in species distribution models as environmental predictors of species occurrence (Bradley and Fleishman 2008; Buermann et al. 2008; Pau et al. 2013; Deblauwe et al. 2016).



**Figure 1.** Dominant species disproportionately contribute to the satellite spectral signature, whereas rare species, included in species richness counts, contribute relatively little (A). These dominant species are also primary contributors to abundance-driven ecosystem services (ESs) (B), often provisioning, regulating and supporting services ('P' = provisioning, 'R' = regulating, 'S' = supporting, and 'C' = cultural; Millennium Ecosystem Assessment 2005), because dominant species comprise more individuals and biomass in a community (C). Each species can potentially contribute to more than one type of service (e.g. carbon storage that regulates the climate as well as supporting biodiversity habitat). Rank abundance curves (C) showing an example of a dominant conifer species (left) and the loss of this dominant under changing conditions (right). Following the loss of a dominant species, the total biomass of a community (C) and total amount of some ESs (B) will be reduced, corresponding to different spectral signatures (A).

While species occurrence is the presence of a species in particular sites or locations, species turnover quantifies the replacement of one species by another species at different sites. Remote sensing has been particularly useful for understanding global patterns of species turnover by providing continuously observed data at a global extent (Gaston et al. 2007; Buckley and Jetz 2008; Qian and Ricklefs 2012). By examining environmental variation across large spatial gradients, these studies have disentangled the importance of environmental drivers (abiotic tolerances) from dispersal limitations and evolutionary histories in determining a species distribution. Another metric of biodiversity, beta diversity, is closely related to species turnover. Beta diversity can refer to a mathematical partitioning (additive) or scaling (multiplicative) of diversity between local (alpha) and landscape (gamma) scale diversity; or beta diversity can be a measure of community dissimilarity among paired sites (see Socolar et al. 2016 for a full discussion). It provides a useful measure for identifying how geographic or environmental gradients structure changes in species composition across sites, rather than turnover in individual species (e.g. Rocchini 2007). Dissimilarity metrics include abundance-weighted community composition or simply species presence-absence (Socolar et al. 2016). Species composition and abundance are thought to be more robust to satellite discrimination than species richness (Tuomisto et al. 2003; He et al. 2009; Oldeland et al. 2010; Rocchini et al. 2010).

Remote sensing also provides data on species themselves (reviewed in He et al. 2015). Images with high spatial resolution can directly detect species by delineating individual tree crowns or through traits associated with particular species (e.g. Weisberg et al. 2007; Palace et al. 2008; He et al. 2011). This is generally most successful for species or functional types with distinct growth forms, phenologies or biochemical traits. For example woody encroachment along a forest-savanna boundary (Mitchard et al. 2009) or into tundra biomes (Stow et al. 2004) has been detected by distinguishing woody versus non-woody species. Distinct phenologies have been used to quantify an upward shift of a hardwood (deciduous)-boreal (evergreen) forest ecotone (Beckage et al. 2008) and to detect the relative abundance of functional groups, such as C<sub>3</sub> and C<sub>4</sub> grass species (Goodin and Henebry 1997; Davidson and Csillag 2003; Foody and Dash 2010). Phenological differences are also commonly used to identify invasive species (Bradley 2014). For example the distinct annual phenology of cheatgrass was used to quantify the extent it is replacing native perennial grasses and shrubs (Bradley and Mustard 2006). Similarly, species-specific leaf biochemical properties, detected using hyperspectral reflectance data (>100 spectral bands), has helped identify

species invasions (e.g. Asner et al. 2008; Asner and Martin 2009; He et al. 2011).

While large advances have been made using remote sensing to address different measures of biodiversity, a body of RS studies centered on the causes and consequences of dominance is lacking. An explicit focus on dominance, as we advocate here, would facilitate methodological and conceptual advances in the study of dominance. This focus would enable stronger links to the ecological community because most communities are dominated by only a few species (Whittaker 1975; Ricklefs 1990; Schwartz et al. 2000). Dominance is also ecologically relevant because species dominance reflects biotic and abiotic ecological relationships (e.g. Lohbeck et al. 2014) and many ecosystem functions (EF) and associated ESs depend heavily on dominant species (e.g. Walker et al. 1999; Schwartz et al. 2000; Smith and Knapp 2003; Dangles and Malmqvist 2004; Hillebrand et al. 2008; Kleijn et al. 2015). For example aboveground net primary productivity was reduced in a tallgrass prairie when dominant species abundances were experimentally altered, whereas declines of less common species did not affect productivity (Smith and Knapp 2003). Importantly, species richness and dominance (or evenness) do not always co-vary and thus dominance provides independent information on ecological functioning (Stirling and Wilsey 2001).

Some of the RS studies reviewed above illustrate remote sensing's ability to detect shifting species dominance, such as those addressing biomes shifts (shifting dominant vegetation), species invasions (increasing dominance of a new species) and beta diversity (when using abundance-weighted composition). Other work may implicitly address species dominance by identifying range distributions where species are assumed to have the highest density in the core of their range. However, these studies do not address which species in a community is more abundant or has greater biomass than coexisting species. Furthermore, relationships between species occurrence and dominance can be inconsistent depending on species and spatial scale (Schroeder et al. 2010). The most robust methods for using RS to detect dominant species will require ground-based field surveys of relative abundance. These data can be used as training data for classification approaches that allow extrapolation across space and time when RS provides data on species themselves (in contrast to RS providing data on environmental or ecological predictors). Moderate to coarse resolution multi-spectral RS will be more effective discriminating structurally and functionally distinct species (i.e. conifer vs. broadleaf; Fig. 1A); although pixel dissimilarity is also linked to abundance-weighted species turnover (e.g. Tuomisto et al. 2003; He et al. 2009; Oldeland et al. 2010).

In addition to detecting and characterizing communities based on dominant species, RS can help elucidate drivers of dominance by identifying how communities change along environmental gradients. RS provides valuable observations of environmental gradients and drivers that can influence dominance, including primary productivity, land-use/land cover and disturbances, in addition to climatic variables (see Table 1). More deliberately tracking dominance across environmental gradients should help inform our understanding of the relative importance of environmental drivers of ecological success (e.g. climate, land-use, disturbances) in comparison to biotic factors (competition or consumption), life-history strategies (dispersal and colonization) or historical processes (e.g. relict populations). The role of each of these drivers may change with spatial and temporal scale (i.e. grain size and extent), highlighting further how RS could facilitate new research directions in understanding species dominance. In the next section, we outline the value of remotely sensing dominant species for quantifying ESs.

## Remote Sensing of Ecosystem Services

There is increasing evidence that dominant species are important contributors to many ESs that rely on abundance or biomass. For instance in many natural forests, dominant species store most above-ground carbon under current conditions (Balvanera et al. 2005; Ngo et al. 2013; Fauset et al. 2015). In the Amazon, a 'hyperdominant' 1% of all estimated 16 000 tree species provide around 50% of total tree carbon storage (ter Steege et al. 2013; Fauset et al. 2015). Recent syntheses show a similar pattern for pollination services: the most abundant pollinators provide the bulk of crop pollination services across several crop types and continents (Kleijn et al. 2015; Winfree et al. 2015). Similarly, in coastal ecosystems, the biomass of salt marsh vegetation and its density/complexity contribute to coastal protection by stabilizing the shoreline and attenuating wave energy (Sullivan and Zedler 1999; Zedler et al. 2001; Callaway et al. 2003; Sullivan et al. 2007; Shepard et al. 2011). As for these services, when the amount of an ES depends on abundance or biomass, tracking dominant species with RS offers a proxy for ES supply. ES supply refers to the amount of that ES that an ecological community can provide (also known as its capacity; Villamagna et al. 2013). Supply differs from how much people use or demand a service (known as ES 'flow'; Martínez-Harms and Balvanera 2012).

RS can track changes in populations of dominant species across changing conditions (Fig. 1), providing a scalable measure to monitor ESs. Some provisioning services (e.g. timber and food production) are derived directly

from these populations, and regulating services depend on the EFs that populations support (e.g. carbon storage by tree populations). RS can estimate the size or extent of dominant populations or habitats/land-uses defined by dominant species, providing quantitative measures of ES supply (Table 1; Fig. 1). In the case of wetlands, which are characterized by their dominant vegetation (Zedler and Kercher 2005; Frieswyk et al. 2007), water regulation or flood control is associated with the size and distribution of the wetland (Troy and Wilson 2006). One study showed that freshwater wetlands (defined by the % cover of indicator species) yielded the highest ecosystem values compared to other habitats when their extents were mapped (Troy and Wilson 2006). Remote sensing of species' traits is another approach for detecting dominance-driven EFs and ESs. The effect of dominant species on EFs and ESs can be mediated through their respective traits, many of which are observable from space (reviewed in Jetz et al. 2016). Trait values of dominant species are disproportionately represented in communities leading to larger contributions to EFs and ESs like productivity (Smith and Knapp 2003 add Mason et al. 2016) and carbon storage (Fauset et al. 2015). However, some ESs, for example supporting or cultural services, are often provided by ecosystem integrity rather than functional traits of particular species.

Recent research shows the importance of considering spatiotemporal dynamics of ESs, rather than considering ES supply as static (Renard et al. 2015). While many ES studies consider static maps (Tallis et al. 2008), which generate an average ES value based on different land-cover types, considering spatiotemporal dynamics can lead to the different conclusions about the amount of an ES or trade-offs among multiple ESs (Bennett et al. 2009; de Groot et al. 2010; Renard et al. 2015; Tomscha and Gergel 2016). For instance Renard et al. (2015) analyze the spatiotemporal dynamics of livestock production, recreation, hunting, flood control and carbon sequestration, revealing not only that the magnitude of these ESs differs over time but also that trade-offs or synergies among ESs can fade or increase. Inaccurate estimates of ES value or of trade-offs among multiple ESs can result in suboptimal management decisions.

Despite the importance of considering spatiotemporal dynamics to account for and manage ESs, these data are costly and difficult to collect in the field. RS can aid these efforts by providing greater sampling and coverage. Remote sensing is especially useful for detecting changes in ESs (or ES proxies) relative to previous measurements. For example RS has reliably estimated annual food production from crop yields of the dominant crop species. Consecutive years of crop extent, yield, and planting dates were modeled for wheat fields in an intensive agricultural



**Table 1.** Commonly used remotely sensed proxies for, or abiotic/biotic predictors of, ecosystem functions (modified from He et al. 2015). Some proxies measure biomass or abundance-driven ecosystem functions (e.g. plant productivity or standing tree biomass; forest structural complexity) that support ecosystem services (ESs; e.g. carbon storage and ultimately climate regulation; biodiversity habitat associated with dominant vegetation), while other proxies more directly estimate ESs (e.g. crop provisioning). Some variables could be considered both abiotic and biotic (land-use/land cover and land surface temperature) depending on the surface of interest (we note that the concept of a niche acknowledges that species alter their own environment; Holt 2009). Examples of ESs are listed according to the Millennium Ecosystem Assessment (2005) classifications (R = regulating, S = supporting, P = provisioning, C = cultural).

Predictor or proxy for ecosystem functions and services	Abiotic variables	Sources
<ul style="list-style-type: none"> <li>• Agriculture (P,C)</li> <li>• Standing tree biomass (R,S)</li> <li>• Biodiversity habitat (S,C)</li> <li>• Recreation, sense of place &amp; esthetics (C)</li> </ul>	Land-use/Land cover (biotic)	MODIS, Landsat, Landsat ETM+
<ul style="list-style-type: none"> <li>• Flood control (R)</li> </ul>	Topography, elevation, slope	SRTM, LiDAR, WorldView-2,
<ul style="list-style-type: none"> <li>• Climate regulation (R)</li> <li>• Biodiversity habitat (S,C)</li> </ul>	Land Surface Temperature (LST)	ASTER, GTOPO30, GMTED2010, UAVs Landsat-8, MODIS
<ul style="list-style-type: none"> <li>• Plant productivity (S)</li> <li>• Climate regulation (R)</li> </ul>	Cloud cover and frequency, quality	MODIS, GOES, ISCCP
<ul style="list-style-type: none"> <li>• Freshwater input as groundwater recharge or surface water (R,S,P,C)</li> </ul>	Rainfall	TRMM, GPM, MODIS, NASA SMAP
<ul style="list-style-type: none"> <li>• Plant productivity (S)</li> <li>• Biodiversity habitat (S,C)</li> </ul>	Soil moisture	NASA SMAP
<ul style="list-style-type: none"> <li>• Biodiversity habitat (S,C)</li> </ul>	Fire (presence/burned area, frequency)	MODIS
	Biotic variables	
<ul style="list-style-type: none"> <li>• Plant productivity (S)</li> <li>• Crop yield (P)</li> </ul>	Normalized Difference Vegetation Index (NDVI)	AVHRR, Landsat, MODIS, Quickbird
<ul style="list-style-type: none"> <li>• Plant productivity (S)</li> <li>• Crop yield (P)</li> </ul>	Vegetation phenology	MODIS, Landsat
<ul style="list-style-type: none"> <li>• Plant productivity (S)</li> <li>• Biodiversity habitat (S,C)</li> </ul>	Leaf Area Index (LAI)	MODIS
<ul style="list-style-type: none"> <li>• Plant productivity (S)</li> <li>• Biodiversity habitat (S,C)</li> <li>• Climate regulation (R)</li> <li>• Carbon storage (R)</li> <li>• Recreation, sense of place &amp; esthetics (C)</li> </ul>	fPAR (fraction of absorbed photosynthetically active radiation) Percent tree cover	MODIS, Landsat MODIS VCF
<ul style="list-style-type: none"> <li>• Biodiversity habitat (S,C)</li> <li>• Climate regulation (R)</li> <li>• Carbon storage (R)</li> </ul>	Canopy/tree height	LiDAR, RADAR, MODIS VCF
<ul style="list-style-type: none"> <li>• Biodiversity habitat (S,C)</li> <li>• Carbon storage (R)</li> </ul>	Stem density	LiDAR, RADAR
<ul style="list-style-type: none"> <li>• Microclimate (S)</li> </ul>	Canopy moisture	Hyperspectral sensors, QSCAT
<ul style="list-style-type: none"> <li>• Biodiversity habitat (S,C)</li> </ul>	Canopy roughness/surface complexity	QSCAT
<ul style="list-style-type: none"> <li>• Biodiversity habitat (S,C)</li> <li>• Carbon storage (R)</li> </ul>	3-D habitat structural profile	LiDAR, RADAR
<ul style="list-style-type: none"> <li>• Productivity (S)</li> </ul>	Leaf water content	Hyperspectral sensors
<ul style="list-style-type: none"> <li>• Productivity (S)</li> <li>• Nutrient cycling (R)</li> </ul>	Leaf nitrogen content	Hyperspectral sensors

region in northwest Mexico (Lobell et al. 2003). Such changes in quantity can then be associated with different drivers, like variation in abiotic conditions (e.g. climate), human impacts or management changes (e.g. land-use change and deforestation rates) (De Araujo Barbosa et al. 2015). For instance RS enabled global mapping of cropland distribution and their sensitivity to climate change (Ramankutty and Foley 1998; Ramankutty et al. 2002; Leff et al. 2004). Carbon stocks in tropical forests were estimated using RS measures of tree height and forest structure and then extrapolated across three continents based on their relationships with environmental predictors (i.e. NDVI, LAI, canopy roughness and topography; Saatchi et al. 2011). Assessing the effects of management and policy changes, Griffiths et al. (2012) used a Landsat time-series to examine how changing forest ownership and natural factors affected forest disturbance and recovery rates in Romania, with important implications for several ESs (e.g. carbon, water quality, timber production).

Ecosystem responses to external drivers are often nonlinear and exhibit threshold dynamics (Scheffer and Carpenter 2003; DeFries et al. 2004; Rockstrom et al. 2009). Species abundances and population dynamics are commonly characterized by population crashes or periodic irruptions that in turn alter their environment and population trajectories (Holt 2009). These unexpected and rapid changes will have important consequences for quantifying ESs (Gordon et al. 2008). RS can contribute to our ability to track nonlinear or threshold responses by providing independent information on the driver and/or response, which importantly can operate on different spatial and temporal scales. Forest insects and pathogens have resulted in massive disturbances affecting forest structure, function and ESs (Kurz et al. 2008). In the case of mountain pine beetles, the spatial and temporal characteristics of outbreaks are the result of complex feedbacks between beetle population sizes (endemic, epidemic, post-epidemic) and tree mortality or damage, which affect the spread of the beetle. Remote sensing can map and quantify the spatial, temporal and spectral damage from these outbreaks, such as lagged effects of different types of foliage damage (Wulder et al. 2006). The increasing frequency of extreme climatic events will also result in nonlinear and threshold ecosystem response (Jentsch et al. 2007). As just one example, RS allowed the tracking of mangroves across the east coast of Florida over several decades (Cavanaugh et al. 2014). This work showed that mangroves (dominated by one to three species) were insensitive to mean annual temperature and precipitation; rather, their distribution exhibited a threshold response to fewer cold events. This implies that associated ESs provided by mangroves – wood production, coastal protection and habitat for commercially harvested

fish and invertebrates – might also exhibit nonlinear responses to environmental change.

Remotely sensing dominant species can detect early signs of future changes in ecological communities and the ESs they supply. Reorganization of ecological communities following global change may more immediately manifest as altered patterns of dominance and evenness rather than changes in species richness (Hillebrand et al. 2008). Climate warming, altered biogeochemical cycles, the addition or removal of species and land-use change all alter dominance structure (Walker et al. 2006; Hillebrand et al. 2008; Naeem 2009; Kardol et al. 2010; Forrester et al. 2015). Therefore, detecting changes in dominant species may provide insight into future changes in both an ecological community and the ES it provides – before species losses, species turnover or changes in beta diversity occur. Furthermore, RS can measure flows and rates of ecosystem processes (e.g. change over space or time), offering early signs of changes in a population or future trends in ES supply.

The proposed focus on dominant species complements a growing body of work applying remote sensing to map and quantify ESs (reviewed in Ayanu et al. 2012; De Araujo Barbosa et al. 2015). One approach uses RS to derive biophysical parameters associated with an EF or ES in radiative transfer models, which establish relationships between an EF or ES proxy and how satellite measured radiation is transferred through different atmospheric and canopy conditions. Alternatively, an ES or EF is empirically linked to RS data using regression models. RS proxies can be used to map an ES, or provide information on predictors of an ES (e.g. abiotic variables and land-use change; Table 1; Ayanu et al. 2012). In particular, studies have linked RS data on ecosystem functions or species' traits, such as productivity, leaf biochemistry or growth forms, to field measurements (e.g. biomass and carbon storage) and ultimately to ESs (Table 1; Feng et al. 2010; Ayanu et al. 2012; De Araujo Barbosa et al. 2015). Empirical relationships between an ES and RS data can be modeled continuously: for each pixel, a unit change in RS data (e.g. % reflectance, land surface temperature (Kelvin); fire frequency (counts)) is associated with a unit change in an ES. More commonly, pixels with similar spectral information are grouped into classes to create thematic maps of land-use/land cover classifications (e.g. habitat type). Often studies map ESs by assigning an average amount of an ES to land cover type, or using land cover information as inputs into models that estimate ES supply for a location (Chan et al. 2006; Troy and Wilson 2006; Naidoo et al. 2008; Nelson et al. 2009a; Feng et al. 2010; Martínez-Harms and Balvanera 2012; Costanza et al. 2014; see Tallis and Polasky 2009 for a detailed explanation). For instance Nelson et al. (2009)

generated maps of soil conservation as a function of land-use/land-cover and other inputs that determine soil retention (i.e. soil type, topography, rainfall). Despite the value of these existing studies, future work should develop and test meaningful RS proxies and RS drivers of dominance, and their link to ESs, to effectively contribute to ES assessments.

## Conclusions

Rapid global change creates an urgent need for biodiversity monitoring to inform conservation and the management of ESs. Here we argue that RS can better support biodiversity monitoring by matching RS metrics with dominant species. We argue that dominance is an ecologically relevant and scalable measure (of population abundance, community composition, traits and ecosystem function), can provide an early-warning sign of ecological change, and overwhelmingly contributes to some biomass-driven ESs. RS metrics can be used as a response or predictors of EFs and ESs, or provide environmental correlates or predictors of dominance. Considering changes in dominant species is a new research agenda that extends current work on RS mapping of ESs.

RS mapping of dominance-driven ESs is a promising new direction to quantify how ESs change across space and time in an increasingly dynamic world. Focusing on dominant species contributes to ES assessments by harnessing the inherent bias of dominant species in optical RS, and providing cost-effective and near-continuous data to extrapolate point measurements. Indeed, RS can detect changes in dominance due to global change, which furthers our understanding of what structures ecological communities (e.g. biotic, abiotic, dispersal limitation) as well as the consequences for the supply of EFs and ESs. It is important to note that not all EFs and ESs are biomass or abundance-driven. A diversity of species, including rare species, are highly valued for various EFs and ESs, thus our proposition here should complement other EBV monitoring efforts.

## Acknowledgments

We thank three anonymous reviewers for their helpful comments on a previous version of this paper. L.D. was supported by a grant from the Institute on the Environment at University of Minnesota to P.B. Reich and S. Polasky.

## Conflict of Interest

None declared.

## References

- Asner, G. P., and R. E. Martin. 2009. Airborne spectranomics: mapping canopy chemical and taxonomic diversity in tropical forests. *Front. Ecol. Environ.* **7**, 269–276.
- Asner, G. P., R. F. Hughes, P. M. Vitousek, D. E. Knapp, T. Kennedy-Bowdoin, J. Boardman, et al. 2008. Invasive plants transform the three-dimensional structure of rain forests. *Proc. Natl Acad. Sci. USA* **105**, 4519–4523.
- Ayanu, Y., C. Conrad, T. Nauss, M. Wegmann, and T. Koellner. 2012. Quantifying and mapping ecosystem services supplies and demands: a review of remote sensing applications. *Environ. Sci. Technol.* **46**, 8529–8541.
- Balvanera, P., C. Kremen, and M. Martínez-Ramos. 2005. Applying community structure analysis to ecosystem function: examples from pollination and carbon storage. *Ecol. Appl.* **15**, 360–375.
- Beckage, B., B. Osborne, D. G. Gavin, C. Pucko, T. Siccama, and T. Perkins. 2008. A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proc. Natl Acad. Sci. USA* **105**, 4197–4202.
- Bennett, E. M., G. D. Peterson, and L. J. Gordon. 2009. Understanding relationships among multiple ecosystem services. *Ecol. Lett.* **12**, 1394–1404.
- Bradley, B. A. 2014. Remote detection of invasive plants: a review of spectral, textural and phenological approaches. *Biol. Invasions* **16**, 1411–1425.
- Bradley, B. A., and E. Fleishman. 2008. Can remote sensing of land cover improve species distribution modelling? *J. Biogeogr.* **35**, 1158–1159.
- Bradley, B. A., and J. F. Mustard. 2006. Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. *Ecol. Appl.* **16**, 1132–1147.
- Buckley, L. B., and W. Jetz. 2008. Linking global turnover of species and environments. *Proc. Natl Acad. Sci. USA* **105**, 17836–17841.
- Buermann, W., S. Saatchi, T. B. Smith, B. R. Zutta, J. A. Chaves, B. Milá, et al. 2008. Predicting species distributions across the Amazonian and Andean regions using remote sensing data. *J. Biogeogr.* **35**, 1160–1176.
- Callaway, J. C., G. Sullivan, and J. B. Zedler. 2003. Species-rich plantings increase biomass and nitrogen accumulation in a wetland restoration experiment. *Ecol. Appl.* **13**, 1626–1639.
- Cavanaugh, K. C., J. R. Kellner, A. J. Forde, D. S. Gruner, J. D. Parker, W. Rodriguez, et al. 2014. Poleward expansion of mangroves is a threshold response to decreased frequency of extreme cold events. *Proc. Natl Acad. Sci. USA* **111**, 723–727.
- Chan, K. M. A., M. R. Shaw, D. R. Cameron, E. C. Underwood, and G. C. Daily. 2006. Conservation planning for ecosystem services. *PLoS Biol.* **4**, 2138–2152.
- Costanza, R., R. de Groot, P. Sutton, S. van der Ploeg, S. J. Anderson, I. Kubiszewski, et al. 2014. Changes in the global



- value of ecosystem services. *Glob. Environ. Change* **26**, 152–158.
- Currie, D., and V. Paquin. 1987. Large-scale biogeographical patterns of species richness of trees. *Nature* **329**, 326–327.
- Dangles, O., and B. Malmqvist. 2004. Species richness-decomposition relationships depend on species dominance. *Ecol. Lett.* **7**, 395–402.
- Davidson, A., and F. Csillag. 2003. A comparison of three approaches for predicting C4 species cover of northern mixed grass prairie. *Remote Sens. Environ.* **86**, 70–82.
- De Araujo Barbosa, C. C., P. M. Atkinson, and J. A. Dearing. 2015. Remote sensing of ecosystem services: a systematic review. *Ecol. Ind.* **52**, 430–443.
- Deblauwe, V., V. Droissart, B. Sonke, J.-C. Svenning, J. Wieringa, B. R. Ramesh, et al. 2016. Remotely sensed temperature and precipitation data improve species distribution modelling in the tropics. *Glob. Change Biol.* **25**, 443–453.
- DeFries, R. S., J. A. Foley, and G. P. Asner. 2004. Land-use choices: balancing human needs and ecosystem function. *Front. Ecol. Environ.* **2**, 249–257.
- Fauset, S., M. O. Johnson, M. Gloor, T. R. Baker, M. A. Monteagudo, R. J. Brienen, et al. 2015. Hyperdominance in Amazonian forest carbon cycling. *Nat. Commun.* **6**, 6857.
- Feng, X., B. Fu, X. Yang, and Y. Lü. 2010. Remote sensing of ecosystem services: an opportunity for spatially explicit assessment. *Chin. Geogr. Sci.* **20**, 522–535.
- Foody, G. M., and J. Dash. 2010. Estimating the relative abundance of C3 and C4 grasses in the Great Plains from multi-temporal MTCI data: issues of compositing period and spatial generalizability. *Int. J. Remote Sens.* **31**, 351–362.
- Forrestel, E. J., M. J. Donoghue, and M. D. Smith. 2015. Functional differences between dominant grasses drive divergent responses to large herbivore loss in mesic savanna grasslands of North America and South Africa. *J. Ecol.* **103**, 714–724.
- Frieswyk, C. B., C. A. Johnston, and J. B. Zedler. 2007. Identifying and characterizing dominant plants as an indicator of community condition. *J. Great Lakes Res.* **33**, 125–135.
- Gaston, K. J., R. G. Davies, C. D. L. Orme, V. A. Olson, G. H. Thomas, T. S. Ding, et al. 2007. Spatial turnover in the global avifauna. *Proc. Biol. Sci.* **274**, 1567–1574.
- Gillespie, T. W. 2005. Predicting woody-plant species richness in tropical dry forests: a case study from south Florida, USA. *Ecol. Appl.* **15**, 27–37.
- Gillespie, T. W., G. M. Foody, D. Rocchini, A. P. Giorgi, and S. Saatchi. 2008. Measuring and modelling biodiversity from space. *Prog. Phys. Geogr.* **32**, 203–221.
- Goodin, D. G., and G. M. Henebry. 1997. Monitoring ecological disturbance in tallgrass prairie using seasonal NDVI trajectories and a discriminant function mixture model. *Remote Sens. Environ.* **61**, 270–278.
- Gordon, L. J., G. D. Peterson, and E. M. Bennett. 2008. Agricultural modifications of hydrological flows create ecological surprises. *Trends Ecol. Evol.* **23**, 211–219.
- Griffiths, P., T. Kuemmerle, R. E. Kennedy, I. V. Abrudan, J. Knorn, and P. Hostert. 2012. Using annual time-series of Landsat images to assess the effects of forest restitution in post-socialist Romania. *Remote Sens. Environ.* **118**, 199–214.
- de Groot, R. S., R. Alkemade, L. Braat, L. Hein, and L. Willemen. 2010. Challenges in integrating the concept of ecosystem services and values in landscape planning, management and decision making. *Ecol. Complex.* **7**, 260–272.
- Hawkins, B., R. Field, H. Cornell, D. Currie, J. Guegan, D. Kaufman, et al. 2003. Energy, water, and broad-scale geographic patterns of species richness. *Ecology* **84**, 3105–3117.
- He, K. S., J. Zhang, and Q. Zhang. 2009. Linking variability in species composition and MODIS NDVI based on beta diversity measurements. *Acta Oecol.* **35**, 14–21.
- He, K. S., D. Rocchini, M. Neteler, and H. Nagendra. 2011. Benefits of hyperspectral remote sensing for tracking plant invasions. *Divers. Distrib.* **17**, 381–392.
- He, K. S., B. A. Bradley, A. F. Cord, D. Rocchini, M. N. Tuanmu, S. Schmidlein, et al. 2015. Will remote sensing shape the next generation of species distribution models? *Remote Sens. Ecol. Conserv.* **1**, 4–18.
- Hillebrand, H., D. M. Bennett, and M. Cadotte. 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* **89**, 1510–1520.
- Holt, R. D. 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proc. Natl Acad. Sci.* **106**, 19659–19665.
- Jentsch, A., J. Kreyling, and C. Beierkuhnlein. 2007. A new generation of climate change experiments: events, not trends. *Front. Ecol. Environ.* **5**, 365–374.
- Jetz, W., J. Cavender-Bares, R. Pavlick, D. Schimel, F. W. Davis, G. P. Asner, et al. 2016. Monitoring plant functional diversity from space. *Nat. Plants* **2**, 16024.
- Kardol, P., C. E. Campany, L. Souza, R. J. Norby, J. F. Weltzin, and A. T. Classen. 2010. Climate change effects on plant biomass alter dominance patterns and community evenness in an experimental old-field ecosystem. *Glob. Change Biol.* **16**, 2676–2687.
- Kerr, J. T., and M. Ostrovsky. 2003. From space to species: ecological applications for remote sensing. *Trends Ecol. Evol.* **18**, 299–305.
- Kleijn, D., R. Winfree, I. Bartomeus, L. G. Carvalheiro, M. Henry, R. Isaacs, et al. 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nat. Commun.* **6**, 7414.
- Kuenzer, C., M. Ottinger, M. Wegmann, and H. Guo. 2014. Earth observation satellite sensors for biodiversity monitoring: potentials and bottlenecks. *Int. J. Remote Sens.* **35**, 6599–6647.

- Kurz, W. A., C. C. Dymond, G. Stinson, G. J. Rampley, E. T. Neilson, A. L. Carroll, et al. 2008. Mountain pine beetle and forest carbon feedback to climate change. *Nature* **452**, 987–990.
- Leff, B., N. Ramankutty, and J. A. Foley. 2004. Geographic distribution of major crops across the world. *Global Biogeochem. Cycles* **18**, 1009.
- Lobell, D. B., G. P. Asner, J. I. Ortiz-Monasterio, and T. L. Benning. 2003. Remote sensing of regional crop production in the Yaqui Valley, Mexico: estimates and uncertainties. *Agric. Ecosyst. Environ.* **94**, 205–220.
- Lohbeck, M., L. Poorter, M. Martínez-Ramos, J. Rodríguez-Velázquez, M. van Breugel, and F. Bongers. 2014. Changing drivers of species dominance during tropical forest succession. *Funct. Ecol.* **28**, 1052–1058.
- Martínez-Harms, M. J., and P. Balvanera. 2012. Methods for mapping ecosystem service supply: a review. *Int. J. Biodiv. Sci. Ecosys. Serv. Manage.* **8**, 17–25.
- Mason, N. W., K. Orwin, S. Lambie, S. L. Woodward, T. McCready, and P. Mudge. 2016. Leaf economics spectrum-productivity relationships in intensively grazed pastures depend on dominant species identity. *Ecol. Evol.* **6**, 3079–3091.
- Millennium Ecosystem Assessment. 2005. *Ecosystems and human well-being: synthesis*. Island Press, Washington, DC.
- Mitchard, E. T. A., S. S. Saatchi, F. F. Gerard, S. L. Lewis, and P. Meir. 2009. Measuring woody encroachment along a forest-savanna boundary in Central Africa. *Earth Interact.* **13**, 1–29.
- Naem, S. 2009. Gini in the bottle. *Nature* **458**, 2–3.
- Nagendra, H. 2001. Using remote sensing to assess biodiversity. *Int. J. Remote Sens.* **22**, 2377–2400.
- Naidoo, R., A. Balmford, R. Costanza, B. Fisher, R. E. Green, B. Lehner, et al. 2008. Global mapping of ecosystem services and conservation priorities. *Proc. Natl Acad. Sci.* **105**, 9495–9500.
- Nelson, E., G. Mendoza, J. Regetz, S. Polasky, H. Tallis, D. R. Cameron, et al. 2009. Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. *Front. Ecol. Environ.* **7**, 4–11.
- Ngo, K. M., B. L. Turner, H. C. Muller-Landau, S. J. Davies, M. Larjavaara, N. F. Bin Nik Hassan, et al. 2013. Carbon stocks in primary and secondary tropical forests in Singapore. *For. Ecol. Manage.* **296**, 81–89.
- O'Connor, B., C. Secades, J. Penner, R. Sonnenschein, A. Skidmore, N. D. Burgess, et al. 2015. Earth observation as a tool for tracking progress towards the Aichi Biodiversity Targets. *Remote Sens. Ecol. Conserv.* **1**, 19–28.
- Oldeland, J., D. Wesuls, D. Rocchini, M. Schmidt, and N. Jürgens. 2010. Does using species abundance data improve estimates of species diversity from remotely sensed spectral heterogeneity? *Ecol. Ind.* **10**, 390–396.
- Palace, M., M. Keller, G. P. Asner, S. Hagen, and B. Braswell. 2008. Amazon forest structure from IKONOS satellite data and the automated characterization of forest canopy properties. *Biotropica* **40**, 141–150.
- Pau, S., T. W. Gillespie, and E. M. Wolkovich. 2012. Dissecting NDVI-species richness relationships in Hawaiian dry forests. *J. Biogeogr.* **39**, 1678–1686.
- Pau, S., E. J. Edwards, and C. J. Still. 2013. Improving our understanding of environmental controls on the distribution of C3 and C4 grasses. *Glob. Change Biol.* **19**, 184–196.
- Pereira, H. M., S. Ferrier, M. Walters, G. N. Geller, R. H. G. Jongman, R. J. Scholes, et al. 2013. Essential biodiversity variables. *Science* **339**, 277–278.
- Pettorelli, N., W. F. Laurance, T. G. O'Brien, M. Wegmann, H. Nagendra, and W. Turner. 2014a. Satellite remote sensing for applied ecologists: opportunities and challenges. *J. Appl. Ecol.* **51**, 839–848.
- Pettorelli, N., K. Safi, and W. Turner. 2014b. Satellite remote sensing, biodiversity research and conservation of the future. *Phil. Trans. R. Soc. Biol. Sci.* **369**, 1–5.
- Phillips, L. B., A. J. Hansen, C. H. Flather, and J. Robison-Cox. 2010. Applying species-energy theory to conservation: a case study for North American birds. *Ecol. Appl.* **20**, 2007–2023.
- Purvis, A., and A. Hector. 2000. Getting the measure of biodiversity. *Nature* **405**, 212–219.
- Qian, H., and R. E. Ricklefs. 2012. Disentangling the effects of geographic distance and environmental dissimilarity on global patterns of species turnover. *Glob. Ecol. Biogeogr.* **21**, 341–351.
- Ramankutty, N., and J. A. Foley. 1998. Characterizing patterns of global land use: an analysis of global croplands data. *Global Biogeochem. Cycles* **12**, 667–685.
- Ramankutty, N., J. A. Foley, J. Norman, and K. McSweeney. 2002. The global distribution of cultivable lands: current patterns and sensitivity to possible climate change. *Glob. Ecol. Biogeogr.* **11**, 377–392.
- Renard, D., J. M. Rhemtulla, and E. M. Bennett. 2015. Historical dynamics in ecosystem service bundles. *Proc. Natl Acad. Sci. USA* **112**, 13411–13416.
- Ricklefs, R. E. 1990. *Ecology*, 3rd ed. Freeman, New York.
- Roberts, D. A., M. Gardner, R. Church, S. Ustin, G. Scheer, and R. O. Green. 1998. Mapping chaparral in the Santa Monica mountains using multiple spectral mixture models. *Remote Sens. Environ.* **65**, 267–279.
- Rocchini, D. 2007. Distance decay in spectral space in analysis ecosystem  $\beta$ -diversity. *Int. J. Remote Sens.* **28**, 2635–2644.
- Rocchini, D., N. Balkenhol, G. A. Carter, G. M. Foody, T. W. Gillespie, K. S. He, et al. 2010. Remotely sensed spectral heterogeneity as a proxy of species diversity: Recent advances and open challenges. *Ecol. Inform.* **5**, 318–329.
- Rockstrom, J., W. Steffan, K. Noone, A. Persson, F. S. Chapin, E. F. Lambin, et al. 2009. A safe operating space for humanity. *Nature* **461**, 472–475.
- Rompré, G., W. D. Robinson, A. Desrochers, and G. Angehr. 2007. Environmental correlates of avian diversity in lowland Panama rain forests. *J. Biogeogr.* **34**, 802–815.

- Saatchi, S. S., N. L. Harris, S. Brown, M. Lefsky, E. T. Mitchard, W. Salas, et al. 2011. Benchmark map of forest carbon stocks in tropical regions across three continents. *Proc. Natl. Acad. Sci. USA* **108**, 9899–9904.
- Scheffer, M., and S. R. Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol. Evol.* **18**, 648–656.
- Schroeder, T. A., A. Hamann, T. Wang, and N. C. Coops. 2010. Occurrence and dominance of six Pacific Northwest conifer species. *J. Veg. Sci.* **21**, 586–596.
- Schwartz, M. W., C. A. Brigham, and J. D. Hoeksema. 2000. Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia* **122**, 297–305.
- Shepard, C. C., C. M. Crain, and M. W. Beck. 2011. The protective role of coastal marshes: a systematic review and meta-analysis. *PLoS One* **6**, e27374.
- Skidmore, A. K., N. Pettorelli, N. C. Coops, G. N. Geller, M. Hansen, R. Lucas, et al. 2015. Agree on biodiversity metrics to track from space. *Nature* **523**, 403–405.
- Smith, M. D., and A. K. Knapp. 2003. Dominant species maintain ecosystem function with non-random species loss. *Ecol. Lett.* **6**, 509–517.
- Socolar, J. B., J. J. Gilroy, W. E. Kunin, and D. P. Edwards. 2016. How should beta-diversity inform biodiversity conservation? *Trends Ecol. Evol.* **31**, 67–80.
- ter Steege, H., N. C. A. Pitman, D. Sabatier, C. Baraloto, R. P. Salomão, J. E. Guevara, et al. 2013. Hyperdominance in the Amazonian tree flora. *Science* **342**, 1243092.
- Stirling, G., and B. Wilsey. 2001. Empirical relationships between species richness, evenness, and proportional diversity. *Am. Nat.* **158**, 286–299.
- Stow, D. A., A. Hope, D. McGuire, D. Verbyla, J. Gamon, F. Huemmrich, et al. 2004. Remote sensing of vegetation and land-cover change in Arctic tundra ecosystems. *Remote Sens. Environ.* **89**, 281–308.
- Sullivan, G., and J. B. Zedler. 1999. Functional redundancy among tidal marsh halophytes: a test. *Oikos* **84**, 246–260.
- Sullivan, G., J. C. Callaway, and J. B. Zedler. 2007. Plant assemblage composition explains and predicts how biodiversity affects salt marsh functioning. *Ecol. Monogr.* **77**, 569–590.
- Tallis, H., and S. Polasky. 2009. Mapping and valuing ecosystem services as an approach for conservation and natural-resource management. *Ann. N. Y. Acad. Sci.* **1162**, 265–283.
- Tallis, H., P. Kareiva, M. Marvier, A. Chang, and A. H. Mwinyi. 2008. An ecosystem service framework to support both practical conservation and economic development. *Proc. Natl. Acad. Sci. USA* **105**, 9457–9465.
- Tomscha, S. A., and S. E. Gergel. 2016. Ecosystem service trade-offs and synergies misunderstood without landscape history. *Ecol. Soc.* **21**, 43.
- Troy, A., and M. A. Wilson. 2006. Mapping ecosystem services: practical challenges and opportunities in linking GIS and value transfer. *Ecol. Econ.* **60**, 435–449.
- Tuomisto, H. A., A. D. Poulsen, K. Ruokolainen, and R. Moran. 2003. Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. *Ecol. Appl.* **13**, 352–371.
- Turner, W. 2014. Sensing biodiversity. *Science* **346**, 301–302.
- Turner, W., S. Spector, N. Gardiner, M. Fladeland, E. Sterling, and M. Steininger. 2003. Remote sensing for biodiversity science and conservation. *Trends Ecol. Evol.* **18**, 306–314.
- Villamagna, A. M., P. L. Angermeier, and E. M. Bennett. 2013. Capacity, pressure, demand, and flow: a conceptual framework for analyzing ecosystem service provision and delivery. *Ecol. Complex.* **15**, 114–121.
- Walker, B., A. Kinzig, and J. Langridge. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* **2**, 95–113.
- Walker, M. D., C. H. Wahren, R. D. Hollister, G. H. R. Henry, L. E. Ahlquist, J. M. Alatalo, et al. 2006. Plant community responses to experimental warming across the tundra biome. *Proc. Natl. Acad. Sci. USA* **103**, 1342–1346.
- Waring, R. H., N. C. Coops, J. L. Ohmann, and D. A. Sarr. 2002. Interpreting woody plant richness from seasonal ratios of photosynthesis. *Ecology* **83**, 2964–2970.
- Weisberg, P. J., E. Lingua, and R. B. Pillai. 2007. Spatial patterns of Pinyon–Juniper woodland expansion in central Nevada. *Rangeland Ecol. Manag.* **60**, 115–124.
- Whittaker, R. H. 1975. *Communities and ecosystems*, 2nd ed. MacMillan, New York.
- Winfree, R., J. W. Fox, N. M. Williams, J. R. Reilly, and D. P. Cariveau. 2015. Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecol. Lett.* **18**, 626–635.
- Wulder, M. A., C. C. Dymond, J. C. White, D. G. Leckie, and A. L. Carroll. 2006. Surveying mountain pine beetle damage of forests: a review of remote sensing opportunities. *For. Ecol. Manage.* **221**, 27–41.
- Zedler, J. B., and S. Kercher. 2005. Wetland resources: status, trends, ecosystem services, and restorability. *Ann. Rev. Environ. Res.* **30**, 39–74.
- Zedler, J. B., J. C. Callaway, and G. Sullivan. 2001. Declining biodiversity: why species matter and how their functions might be restored in Californian tidal marshes. *Bioscience* **51**, 1005.