

REVIEW

Mainstreaming remotely sensed ecosystem functioning in ecological niche models

Adrián Regos^{1,2,3,4} , João Gonçalves^{2,4} , Salvador Arenas-Castro^{2,4,5,6} , Domingo Alcaraz-Segura^{7,8} , Antoine Guisan^{9,10}  & João P. Honrado^{2,4,11} 

¹Departamento de Zooloxía, Xenética e Antropoloxía Física, Universidade de Santiago de Compostela, Santiago de Compostela, Spain

²BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, Vairão 4485-661 14, Portugal

³Centre Tecnològic i Forestal de Catalunya (CTFC), Ctra. St. Llorenç de Morunys km 2, Solsona 25280, Spain

⁴CIBIO-InBIO—Centro de Investigação em Biodiversidade e Recursos Genéticos, Laboratório Associado, Universidade do Porto, Campus de Vairão, Vila do Conde 4485-661, Portugal

⁵Área de Ecología, Dpto. de Botánica, Ecología y Fisiología Vegetal, Facultad de Ciencias, Universidad de Córdoba, Campus de Rabanales, Córdoba 14071, Spain

⁶Escola Superior Agrária, Instituto Politécnico de Viana do Castelo, Ponte de Lima 4990-706, Portugal

⁷Departamento de Botánica, Facultad de Ciencias, Universidad de Granada, Granada, Spain

⁸Andalusian Center for the Assessment and Monitoring of Global Change (CAESCG), Universidad de Almería, Almería, Spain

⁹Department of Ecology & Evolution, University of Lausanne, Biophore, Lausanne 1015, Switzerland

¹⁰Institute of Earth Surface Dynamics, University of Lausanne, Geopolis, Lausanne 1015, Switzerland

¹¹Departamento de Biologia, Faculdade de Ciências, Universidade do Porto, Porto 4169-007, Portugal

Keywords

Energy and water balance, habitat dynamics, habitat suitability modelling, heat dynamics, land surface temperature, model-assisted monitoring, primary productivity, radiative balance

Correspondence

Adrián Regos, Departamento de Zooloxía, Xenética e Antropoloxía Física, Universidade de Santiago de Compostela, Santiago de Compostela, Spain. E-mail: adrian.regos@usc.es

Editor: Kate He

Associate Editor: Justin Moat

Received: 19 February 2021; Revised: 6 December 2021; Accepted: 6 January 2022

doi: 10.1002/rse2.255

Abstract

Biodiversity is declining globally at unprecedented rates. Ecological niche models (ENMs) are one of the most widely used toolsets to appraise global change impacts on biodiversity. Here, we identify a variety of advantages of incorporating remotely sensed ecosystem functioning attributes (EFAs) into ENMs. The development of ENMs that explicitly incorporate ecosystem functioning will allow a more holistic and integrative perspective of the habitat dynamics. The synergies between the increasingly available open-access satellite images and cloud-based platforms for planetary-scale geospatial analysis offer an unprecedented opportunity to incorporate ecosystem processes and disturbances (such as fires, insect outbreaks or droughts) that have been so far largely neglected in ecological niche characterization and modelling. The most paradigmatic example of EFAs is the application of time series of spectral vegetation indices related to primary productivity and carbon cycle. EFAs related to surface energy balance and water cycles derived from remote sensing products such as land surface temperature or soil moisture enable a fine-scale characterization of the species' niche—eventually improving the predictive performance of ENMs. All these advantages confirm that a new generation of ENMs based on such EFAs would offer great perspectives to increase our ability to monitor habitat suitability trends and population dynamics. However, despite the technical advances and increasing effort of remote sensing community to develop integrative EFAs, ENMs have yet to make full profit of the most recent developments by integrating them in ENMs. A coordinated agenda for remote sensing experts and ecological modellers will be essential over the coming years to bridge the gap between remote sensing and ecology disciplines and to take full (and timely) advantage of the fast-growing body of Earth observation data and remote sensing technologies—with special emphasis on the development and testing of new variables related to key processes driving ecosystem functioning.

Introduction

Biodiversity is declining globally at unprecedented rates, with species extinctions accelerating (Tittensor et al., 2014). To address this challenge, ecological modellers need to improve their capacity to assess ongoing environmental changes. Methodological advances will play a critical role in this regard (IPBES, 2016). Ecological niche models (hereafter ENMs, also known as habitat suitability models or species distribution models; Sillero, 2011; Peterson & Soberón, 2012) are one of the most used toolsets to appraise global change impacts on biodiversity (Brotons, 2014), support decision-making and evaluate policies (Guisan et al., 2013; Villero et al., 2017). Still, despite all their applications, ENMs present important shortcomings that limit their 'real-world' applicability for conservation decision-making (Franklin, 2010). ENMs are based on the quantification of species–environment relationships (Guisan & Zimmermann, 2000). Since ENMs require ecologically meaningful predictor variables (Franklin, 1995), the lack of descriptors of key processes driving habitat dynamics can reduce their predictive power (Mod et al., 2016; Scherrer & Guisan, 2019). In addition, the changing nature of processes driving ecological changes highlights the need for long-term time series of data (Fisher et al., 2010). In this sense, Earth observation data and remote sensing technologies offer a new perspective on species' habitat dynamics (Hobi et al., 2017). Remote sensing variables are collected with highly systematic, repeatable and standardized procedures, presenting a global synoptic coverage at different spatial and temporal resolutions. The increasing availability of long-term time series of satellite data allows computing a broad range of new variables related to ecosystem functioning, that is the biogeochemical flow of energy and matter within ecosystems (see glossary in Table 1; Jax, 2005; Lovett et al., 2006).

In ENMs, environmental variables have traditionally informed about multiple dimensions of abiotic conditions such as soil, climate or topography (Mod et al., 2016). The inclusion of land-use/cover information into ENMs has gradually become more common to explicitly capture ecosystem and landscape composition and structure (Leitão & Santos, 2019; Randin et al., 2020). Including such satellite-based land-use/cover predictors is particularly key given that land-use changes are the primary driver of biodiversity erosion globally (Titeux et al., 2017, 2019). However, to date, most studies only relied on snapshots for specific time windows (e.g. land-use change analysis focused on two dates; Pellissier et al., 2013), accounting only for a small fraction of the species' habitat dynamics (Coops & Wulder, 2019), which might lead to a biased perception of the factors driving distributions and population dynamics. Moreover, remote sensing data have been proven valuable

Table 1. Glossary of concepts and key terms as used in this paper.

<i>Abrupt ecological change:</i>	Substantial changes in the mean or variability of a system that occur in a short period of time relative to typical rates of change (Ratajczak et al., 2018)
<i>Disturbance:</i>	Relatively discrete event in time that alters the biotic and/or abiotic components of an ecosystem (Ratajczak et al., 2018). Disturbances are a major driver of ecosystem dynamics influencing many structural and functional ecosystem properties such as vegetation and soil structure, species composition, water and CO ₂ fluxes, etc
<i>Ecological niche:</i>	N-dimensional hypervolume in environmental space within which populations of a species can persist (Hutchinson, 1957)
<i>Ecosystem functioning:</i>	The attributes related to the performance of an ecosystem as a whole that is the consequence of one or multiple ecosystem processes (Jax, 2005; Lovett et al., 2006)
<i>Gross Primary Productivity (GPP):</i>	The rate at which ecosystem's producers capture a provided amount of energy as biomass in a given time duration.
<i>Intra-annual variability:</i>	The annual seasonal behaviour of a process variable that can be measured in terms of quantity (i.e. centrality measure like the average, or area under the curve integral), seasonal variation or range (i.e. dispersion measure such as amplitude, inter-quartile range, std-dev.), phenology (i.e. timing of specific events such as the day of maximum/minimum value or length of time) and extreme values (i.e. minimum/maximum)
<i>Inter-annual variability:</i>	The temporal behaviour of a process variable in a period of time larger than a year, that allows detecting abrupt or monotonic changes across several years in regard to, for example, a reference value such as a long-term average (e.g. anomalies, Tukey outliers, breakpoints) or a long-term trend (e.g. Sen slope, Mann-Kendal tau)
<i>Land Surface Phenology:</i>	The seasonal pattern of variation in vegetated land surfaces observed from remote sensing. LSP dynamics reflect the response of vegetated surfaces of the earth to seasonal and annual changes in the climate and hydrologic cycle (Alemu & Henebry, 2017; De Beurs & Henebry, 2004)
<i>Phenology:</i>	The study of the timing of recurring biological events, the causes of their timing with regard to biotic and abiotic forces, and the interrelation among phases of the same or different species (Leith, 1974)
<i>Process variable:</i>	Current measured value of a particular part of a process which is being monitored or controlled
<i>Net Primary Productivity:</i>	How much carbon dioxide vegetation takes in during photosynthesis minus how much carbon dioxide the plants release during respiration (metabolizing sugars and starches for energy)
<i>Remotely sensed ecosystem functioning attributes (EFAs):</i>	Integrative descriptors of ecosystem functioning computed from intra-annual variability of remote sensing products related to different components of ecosystem functioning
<i>Seasonality:</i>	The presence of variations that occur at specific regular intervals shorter than a year, such as weekly, monthly or quarterly

Many of these terms are unfamiliar to non-specialists and experts in certain disciplines.

for modelling both animals and non-dominant plant species (i.e. rare, low-abundance specialist species; see e.g. Alcaraz-Segura et al., 2017; Arenas-Castro et al., 2019; Gonçalves et al., 2016). Such species often hold an indiscernible influence in energy-matter flows of ecosystems and hence do not blur the distinction between modelling potential distributions (or habitat suitability) and remotely sensed detection (Bradley et al., 2012). More caution is needed when modelling dominant plant species since spectral vegetation indices can be directly capturing the signal of the target species to be modelled.

From a niche theory perspective, the non-inclusion of ecosystem functioning attributes (hereafter: EFAs) such as annual primary productivity or seasonal heat dynamics could be constraining the real volume of species' niche experienced along its annual cycle (*sensu* Hutchinson's niche; Hutchinson, 1957) (see Fig. 1). For instance, a recent study found that long-distance bird migrants track vegetation greenness throughout their annual cycle (measured through the normalized difference vegetation index [NDVI]), adjusting the timing and direction of migratory movements with seasonal changes in resource availability (Mayor et al., 2017; Thorup et al., 2017). Another study found that the inter-annual dynamics in primary productivity significantly influences habitat colonization and occupancy dynamics of primary consumers (Fernández et al., 2016). This importance of primary productivity in determining the overall quantity and quality of food resources available to herbivores underlines the need of considering key regulatory functions determining the net energy fluxes driving trophic webs (Fernández et al., 2016; Ramírez et al., 2017; Regos et al., 2021; Wiegand et al., 2008).

Here, we provide a workflow connecting different components of ecosystem functioning derived from time series of remote sensing products (such as evapotranspiration, soil moisture, spectral indices or satellite band combinations; see Fig. 1) with ENMs. First, we highlight the technical advances of the remote sensing community in developing integrative descriptors of ecosystem functioning and then identify a variety of advantages of incorporating these descriptors into ENMs (both for species' niche characterization and model-based monitoring approaches). Second, we discuss the advantages of incorporating a more functional perspective into ENMs and review to what extent remotely sensed EFAs have been incorporated so far in ENM development and applications to identify gaps between the ENM and the remote sensing communities. Finally, we provide two case studies to illustrate how EFAs can be used for mapping species habitat trends.

Remote Sensing Offers New Descriptors of Ecosystem Functioning

A promising contribution of remote sensing to ENMs is the description of several components of ecosystem

functioning (Alcaraz-Segura et al., 2017; Leitão & Santos, 2019) (see remote sensing products in Fig. 1A). Ecosystem functioning can be understood as an umbrella term for the ensemble of processes related to the biogeochemical flow of energy and matter within ecosystems (Loreau, 2008). One of the most commonly used definitions of ecosystem functioning—the attributes related to the performance of an ecosystem as a whole that is the consequence of one or of multiple ecosystem processes' (Jax, 2005; Lovett et al., 2006)—explicitly relates ecosystem processes (e.g. evapotranspiration) to ecosystem functioning (e.g. climate regulation) (Pettorelli et al., 2018).

To successfully mainstream ecosystem functioning into ecological models, a joint effort from remote sensing and ENM communities in the development and application of global datasets of remotely sensed EFAs (expressing the temporal variability of different components of ecosystem functioning, as shown in Fig. 1B) is required—including the main factors influencing them (e.g. disturbance regimes). In this regard, remote sensing technologies have greatly advanced and are now able to inform—either directly or indirectly—on various components and attributes of ecosystem functioning (Pettorelli et al., 2018).

Spectral vegetation indices such as the well-known NDVI or the enhanced vegetation index (EVI) are positively correlated with aboveground net primary production, with the fraction of the photosynthetically active radiation (FAPAR) (Sellers et al., 1992) or with the leaf area index (Wang et al., 2005). The seasonal and intra-annual dynamics of these vegetation indices are closely related to fluxes of CO₂ in photosynthesis and respiration, and to atmospheric N deposition (Chen & Coops, 2009) (Fig. 3B), being increasingly used by the remote sensing communities as proxies for ecosystem functioning (Alcaraz et al., 2006; Fernández et al., 2010; Paruelo et al., 2001) (Figs. 1 and 2).

Among other metrics, the annual mean of these vegetation indices has been used as linear estimator of annual primary productivity; their seasonal range or standard deviation as descriptors of the differences in carbon and nitrogen gains between seasons; and the date of the maximum value of these vegetation indices as a phenological indicator of the growing season peak (see Figs. 1B and 2). Satellite-based phenological measures of the Earth's surface, calculated from time series of spectral vegetation indices, are perhaps one of the most active applications, with several measures proposed (Jönsson & Eklundh, 2004). For instance, temporal trends and spatial heterogeneity in NDVI seasonal dynamics were found to be affected by climate change (temperature and precipitation) and land-use/cover changes (land-use intensification) across the globe (Dieguez & Paruelo, 2017; Fensholt et al., 2012; Ichii et al., 2002; Piao, 2003). However, these

(A) ECOSYSTEM FUNCTIONING COMPONENTS

CARBON CYCLE

- Gross Primary Productivity (GPP)
- Net Primary Productivity (NPP)
- Leaf Area Index (LAI)
- Spectral Vegetation Indices (e.g., NDVI, EVI, SAVI, TCT greenness, ...)

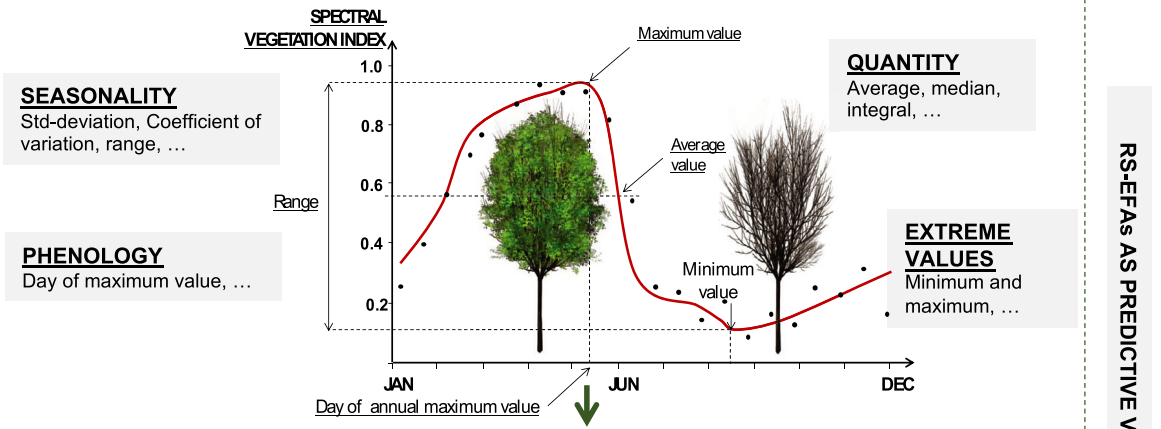
WATER CYCLE

- Evapotranspiration
- Soil Moisture
- Spectral Water Indices (e.g., NDWI, TCT 'wetness')
- Spectral Snow Indices (e.g., NDSI)

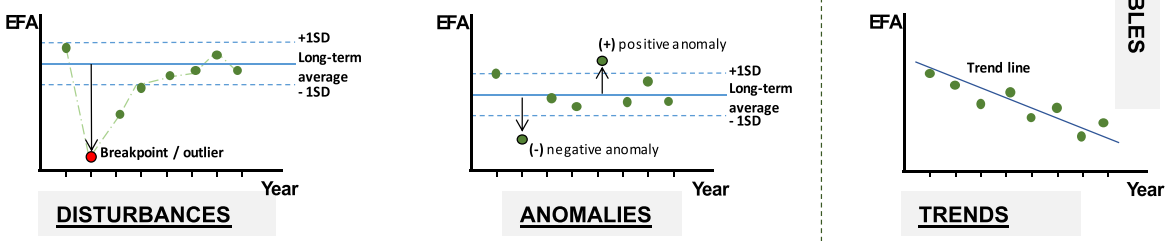
ENERGY BALANCE

- Land Surface Temperature
- Latent and Sensible Heat
- Evapotranspiration
- Albedo
- Surface reflectivity (e.g., TCT 'brightness')

(B) REMOTELY SENSED ECOSYSTEM FUNCTIONING ATTRIBUTES (RS-EFAs)



(C) INTER - ANNUAL VARIABILITY OF RS-EFAs



(D) ENM DEVELOPMENT

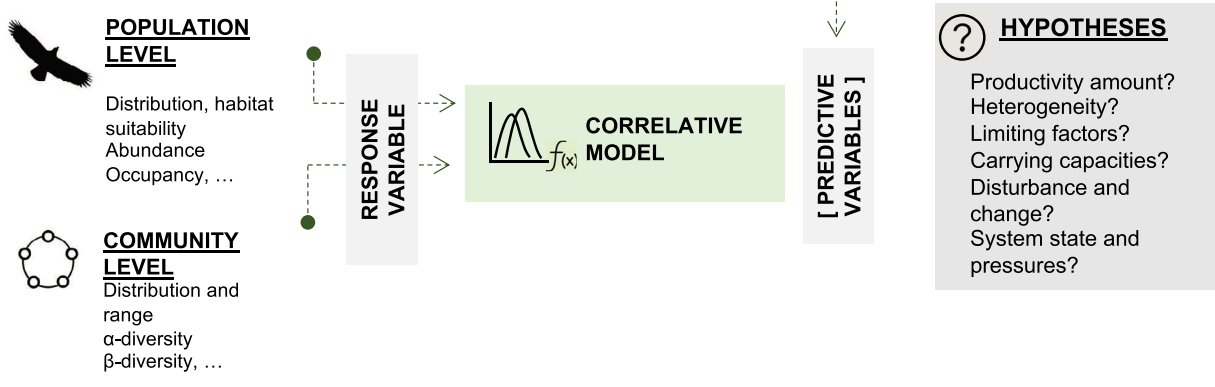


Figure 1. Pipeline connecting different ecosystem functioning components with remotely sensed ecosystem functioning attributes (RS-EFAs) and ecological niche models (ENMs). Different components of ecosystem functioning can be measured—either directly or indirectly—through various remote sensing products such as evapotranspiration, soil moisture, spectral indices or satellite band combinations (A). RS-EFAs are computed from intra-annual time series of these remote sensing products (e.g. the average annual value of NDVI time series as proxy of annual primary productivity) (B). The medium- and long-term variability of RS-EFAs can be computed from an inter-annual time series of RS-EFAs (e.g. the inter-annual trend in the annual primary productivity measured through RS-EFAs) (C). RS-EFAs computed for a specific year or longer periods can be incorporated as predictor variables in model development, according to the specific hypotheses and objectives of the model (D). NDVI, normalized difference vegetation index.

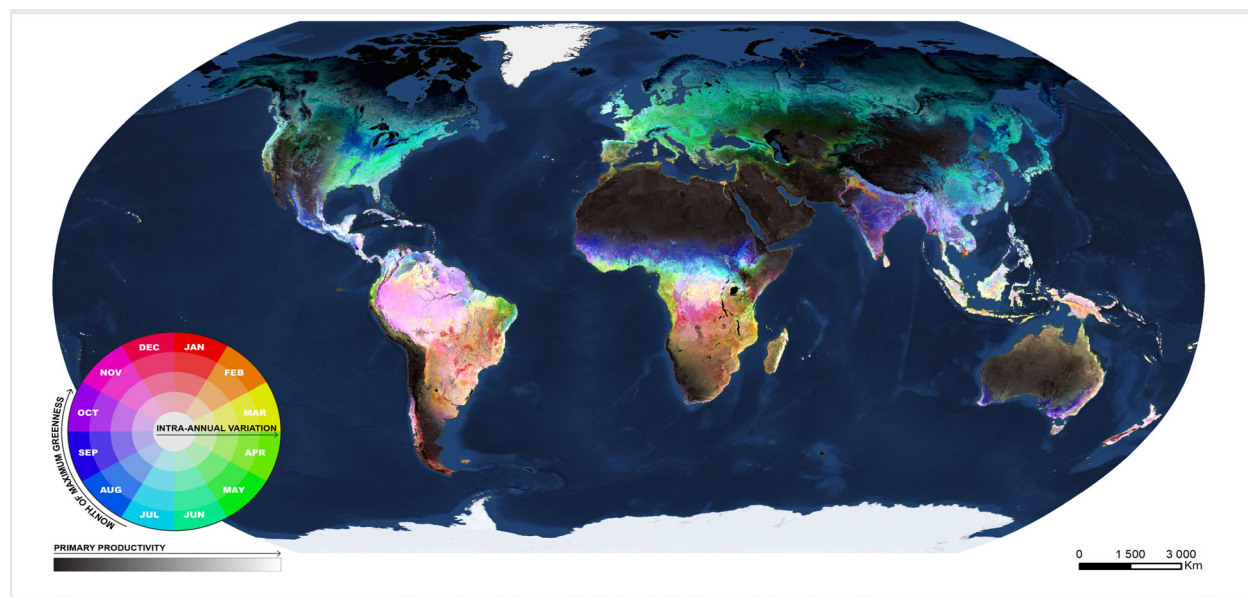


Figure 2. Hue-saturation-value (HSV colour space) image of annual vegetation productivity (annual average, value component), their seasonality or intra-annual variation (annual standard deviation, saturation component) and phenology (monthly maximum of EVI, in the hue circular component) computed for land areas (terrestrial ecosystems, excluding Greenland and Antarctic) in Google Earth Engine from the combination of MODIS EVI time series. EVI, enhanced vegetation index.

applications mostly focus on the timing of specific events related to the carbon and nitrogen cycles (e.g. growing season peak or duration). These metrics can in fact be applied to other ecosystem attributes (e.g. soil moisture or land surface temperature [LST]; see Fig. 1A and B; Table S1.1). They can be computed from spectral indices related to the water cycle such as the Normalized Difference Water Index (NDWI; Gao, 1996) or the Land Surface Water Index (Jönsson & Eklundh, 2004), among others, to inform about the dynamics of water content in vegetation or soil (Rickebusch et al., 2008; Fig. 1). Evapotranspiration is a key component of the global water cycle, closely tied to carbon and surface energy exchanges. The biophysical meaning and properties encapsulated in remote sensing products such as Evapotranspiration or Soil Moisture enhance our capabilities for monitoring water and energy cycles across scales (Rodríguez-Fernández et al., 2019; Zhang et al., 2016), including their

intra- and inter-annual dynamics and feedbacks with anthropogenic global change (see Fig. 1B and C).

A key advantage of remotely sensed EFAs is their sensitivity to environmental changes, including: (1) regular fluctuations, mostly driven by inter-annual climatic variability; (2) abrupt ecological changes, caused by extreme events or disturbances such as droughts, floods or wildfires; or even (3) long-term gradual or monotonic trends linked to processes such as urban sprawl, post-fire recovery or ecological succession (see Fig. 1C). For instance, disturbances such as wildfires, which represent a critical exchange of energy and matter between the land and the atmosphere *via* combustion, can affect dramatically these biophysical descriptors of ecosystem functioning (Kasischke et al., 1995). In terms of the land surface energy balance, fires initially reduce surface albedo due to the production of charcoal (Archibald et al., 2018). The subsequent dynamics will depend on the albedos of pre- and

post-fire vegetation and land surface (Archibald et al., 2018), and the rate at which different species and vegetation types recover (Torres et al., 2018).

In conclusion, EFAs measured through time series of satellite images can be considered integrative descriptors of environmental status and change, as they can timely inform about intra- and inter-annual variability of different components of ecosystem functioning. Their incorporation into ENMs therefore holds strong advantages for both biodiversity modelling and monitoring.

Advantages of Incorporating Ecosystem Functioning into ENMs

Remotely sensed EFAs improve species' niche characterization

Remotely sensed EFAs have been used as proxies for ecosystem functioning in different types of models to predict species distributions, abundances and diversity (Cabello et al., 2012; Coops et al., 2009; Hobi et al., 2017; Radeloff et al., 2019). Remotely sensed EFAs are closely related to abiotic and biotic conditions experienced by organisms on the ground. Thus, EFAs allow us to better characterize species ecological niche than with macroclimatic datasets and thus enhance our capacity to model their habitat dynamics through time. As mentioned above, the most paradigmatic example of EFAs measured from space is the application of time series of spectral vegetation indices related to primary productivity (Fig. 2).

For instance, the 'Gerês lily' (*Iris boissieri*)—a narrow-ranged endemic plant—tends to occur in areas characterized by cool temperatures and high precipitation during the summer season, which translates into maximum primary productivity in summer and minimum in winter (measured from EVI time series; see Fig. 3A). The aerial part of the plant disappears as the summer advances, and only the underground part (i.e. bulb) remains in a latent state during the less favourable season, favoured by deposits of organic matter of the soil in open, fire-prone scrublands (Arenas-Castro et al., 2018, 2019) (Fig. 3A). Some mammals such as the European badger (*Meles meles*) prefer mosaic landscapes consisting of fruit orchards and natural vegetation, which provide shelter and food resources (Requena-Mullor et al., 2014). In the south-eastern Iberian Peninsula, badger diet depends on fruit orchards and other derived food resources (e.g. insects) (Fig. 3B). Ecosystem functioning variables related to primary productivity derived from EVI time series were used as proxies for the spatial and temporal variability of food resources for badgers in these environments. In fact, models calibrated with these EFAs outperformed models built with land-cover variables, and their

combination resulted significantly increased model accuracy (see Requena-Mullor et al., 2014 for details).

Differences between characterizing the species' niche exclusively with compositional or structural descriptors (e.g. forest cover) or adding EFAs (e.g. primary productivity) are likely more important for those species dependent on the seasonal dynamics of such attributes (see examples in Fig. 3). In addition, EFAs related to LST or soil moisture can better characterize the species' niche than macroclimate sets inferred from interpolation, since they provide information more closely related to the 'real' conditions experienced by organisms at ground level (e.g. microclimate; see Lembrechts et al., 2018). This may translate into an improvement in ENM performance (Amiri et al., 2020), especially important for species living in areas with steep environmental gradients (e.g. mountain regions) (Bramer et al., 2018).

Remotely sensed EFAs improve ENM and monitoring

Recent research showed how ENMs based on remotely sensed EFAs can provide early warnings of range shifts and predictions of short-term fluctuations in suitable conditions for plant species of conservation concern (Alcaraz-Segura et al., 2017). For instance, considering *Scrophularia grandiflora* (a narrow endemic forb from central Portugal), climate- and EFA-based models were equally accurate. However, while climate-based models forecasted expansion under near-future climate conditions, EFA-based models estimated contractions of habitat availability, capturing habitat suitability dynamics at finer scales associated with observed land-use changes (Alcaraz-Segura et al., 2017). These findings support the need of global EFA databases to boost the development of process-based models that enable future projections of key ecosystem functioning components (e.g. carbon cycle) under climate and land-use scenarios (e.g. dynamic global vegetation models such as the LPJ-GUESS; <https://web.nateko.lu.se/lpj-guess/>).

EFAs related to carbon cycle dynamics were useful descriptors of plant species distributions and abundance at different scales, independent of their range and life form (Arenas-Castro et al., 2018, 2019). A recent study modelling the abundance of 'Gerês lily' revealed that the species' abundance is mainly influenced by annual minimum green-up days, related to late winter–early spring precipitation, and by low vegetation productivity during the winter–early spring (see Fig. 3)—ecosystem attributes linked to sparsely vegetated landscape mosaics dominated by crawling scrub and grasslands (Arenas-Castro et al., 2019). In another study, inter-annual changes in seasonal marine productivity influenced seabird fitness in the

Arctic. The increasing temporal lag in sea ice melting—which is the physical process driving the annual bloom of sea ice algae and pelagic phytoplankton—resulted in rapidly decreasing breeding performance for little auks and Brünnich's guillemots (Ramírez et al., 2017). In Spain, habitat selection of brown bears (*Ursus arctos*)—a species showing hyperphagia and hibernation as evolutionary adaptation to seasonal peaks and bottlenecks in ecosystem productivity—was related to ecosystem properties and functioning, measured through seasonal patterns of NDVI (Wiegand et al., 2008). Recent studies also found that MODIS-derived gross primary productivity and net primary productivity (NPP) were highly correlated with bird

species richness across different scales (Nieto et al., 2015; Phillips et al., 2008; Radeloff et al., 2019; Toszogyova & Storch, 2019)—an issue that is especially relevant in the light of species-energy theory and the role of energy variability (Carrara & Vázquez, 2010; Hurlbert, 2004).

In addition, recent studies also suggest that the incorporation of descriptors of the water cycle into ENMs can support decision-making in wildlife conservation and management (e.g. in species recovery planning; Regos, Vidal, et al., 2020), since these variables can indirectly provide information, not only on habitat availability and quality, but also on spatial and temporal variations in resource availability (Requena-Mullor et al., 2014; Wiegand

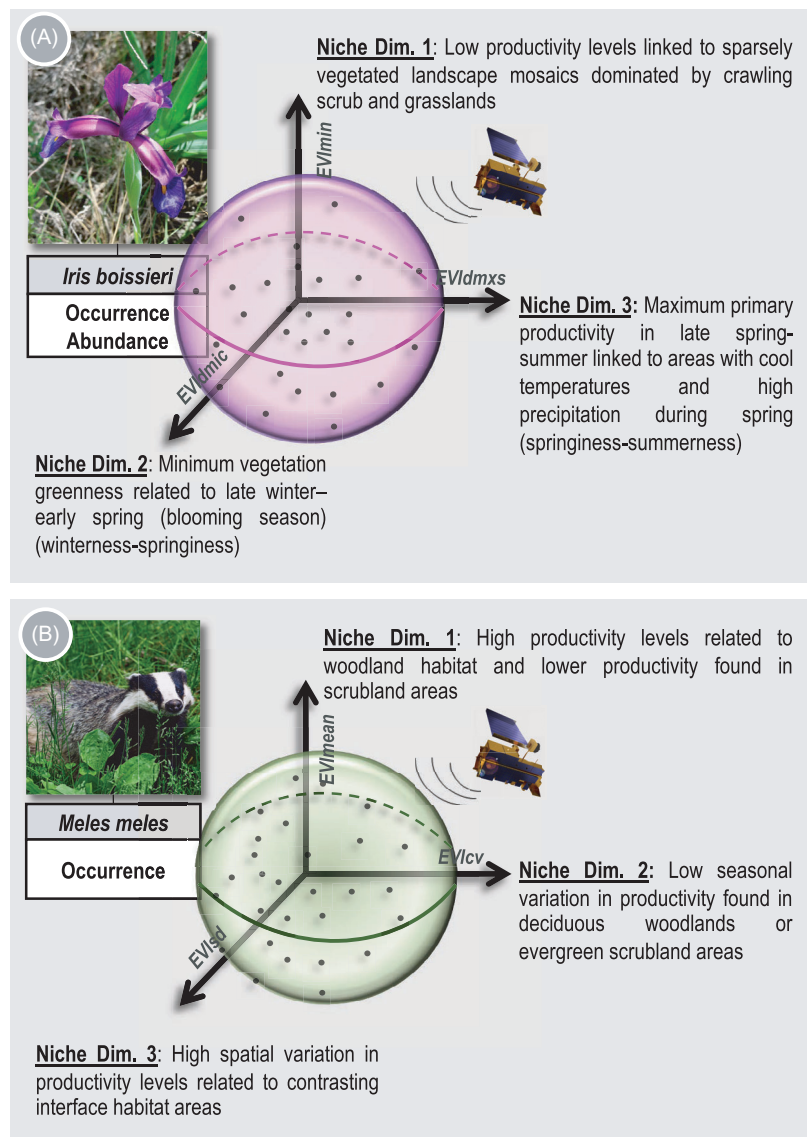


Figure 3. Examples of ecological niche characterization for 'Gerès lily' (*Iris boissieri*) and European badger (*Meles meles*) from ecosystem functioning attributes computed from the seasonal variation of the enhanced vegetation index (EVI).

et al., 2008). For instance, one of these studies showed that seasonal variation of water content, measured by the standard deviation of the NDWI computed from Sentinel-2, was the most important habitat descriptor at local scale of a waterbird species—the common snipe (*Gallinago gallinago*) (Regos, Vidal, et al., 2020). Model-based response curves showed that wet grasslands with either low or high seasonal variability throughout the breeding season do not provide habitat because fluctuations of the water content of vegetation are either too small (i.e. areas with no water) or too high (i.e. areas with a steep decrease in water content). The limited amount of water content in this period of the species' biological cycle is critical and relates to soil penetrability and invertebrate density (i.e. prey availability) (Regos, Vidal, et al., 2020). In addition, EFAs based on NDWI seasonality were also found to boost modelling performance of several oak species (Vila-Viçosa et al., 2020).

Other authors computed different satellite-based metrics of seasonal dynamics from LST and albedo as predictor variables to incorporate energy balance into ENMs (Amiri et al., 2020; Arenas-Castro et al., 2018; Cord & Rödder, 2011; Regos, Gómez-Rodríguez, et al., 2020). For instance, surface temperature during the coldest month (an energy balance EFA) was a more relevant predictor for explaining the distribution of the threatened plant 'Gerês lily' at coarse scale than EFAs related to the carbon cycle (Arenas-Castro et al., 2018). The distribution of birds nesting in rocky cavities such as the common raven (*Corvus corax*), the common rock thrush (*Monticola saxatilis*) or the Eurasian crag martin (*Ptyonoprogne rupestris*) was correlated with sensible heat dynamics and radiative balance—measured from minimum or maximum Albedo and mean or standard deviation of LST time series (Regos, Gómez-Rodríguez, et al., 2020). Finally, novel applications of remote sensing time series have recently been described to model animal and plant phenology. For instance, the phenology of two moth species (*Orthosia gothica* and *Ectropis crepuscularia*) was related to snow melt-off date (from MODIS daily snow maps) and greening date (using MODIS NDWI)—processes driving the water cycle dynamics (Pöyry et al., 2017; Fig. 1). In China, ENMs developed with land surface phenology, captured by high-temporal resolution remotely sensed imagery, allowed for characterizing and monitoring the habitat of the giant panda (*Ailuropoda melanoleuca*) (Tuanmu et al., 2011).

Synergies Between Ecological Modelling and Remote Sensing Communities

EFA-based ENMs in the support of global biodiversity monitoring

Over the last years, several authors have called the attention of the great potential of remote sensing for ENM

(Bradley & Fleishman, 2008; He et al., 2015; Leitão & Santos, 2019; Randin et al., 2020). The synergies between the increasingly available open-access satellite images (e.g. Terra/MODIS, Landsat, Sentinel) (Wulder et al., 2016) and cloud-based platforms for planetary-scale geospatial analysis (e.g. Google Earth Engine (GEE), EOS Engine, CODE-DE) (Gorelick et al., 2017) in the Era of Big Data (e.g. Earth observation Data Cube) (Lewis et al., 2016) are enabling new approaches to old problems (Casu et al., 2017). Despite the progressive integration of remote sensing variables into ENMs over the last decades (Estes et al., 2010; He et al., 2015; Pottier et al., 2014) (Fig. 4), the ENM community is still far from embracing its full potential, especially regarding the incorporation of the ecosystem functioning dimension (Fig. 4) (He et al., 2015). A quick search in the ISI Web of Knowledge shows the modest role that ecosystem functioning variables have played so far in ENM development and applications, in contrast to the increasing availability of remote sensing products capturing features of ecosystem functioning at several spatio-temporal scales (Fig. 4; Tables S1.1 and 1.2). This quick search evidenced that many ecosystem processes and properties that are ecologically relevant for species (e.g. NPP or evapotranspiration) have been neglected in ENM. There may be various reasons for this, but a lack of technology to develop spatially explicit variables related to ecosystem functioning does not seem to be one (Fig. 4).

This gap between the ENM and the remote sensing communities potentially holds important consequences for conservation decision-making and environmental management. For instance, habitat loss and degradation caused by land-use changes are one of the main threats to biodiversity in the Anthropocene (Newbold et al., 2015; WWF ZSL, 2016). In the last decade, the number of studies including land-use/cover change in ENMs has increased (but see Titeux et al., 2016). The interplay of climate and land-use change has been predicted to strongly affect the distribution of a wide range of species across different taxa (Barbet-Massin et al., 2012; Marshall et al., 2017; Smith et al., 2016). However, while habitat loss and degradation caused by land-use conversions (e.g. from land abandonment; Pellissier et al., 2013) can be easily integrated into ENMs (e.g. through land-cover time series; Bradley et al., 2012; Pellissier et al., 2013), other processes and disturbances are much more difficult to incorporate. Forest defoliation processes favoured by the concomitant effects of insect outbreaks and extreme climatic events (e.g. droughts), or changes caused by shorter harvesting timing or increased extracting rates are examples of how changes within—and not only between—landscape features can dramatically affect ecosystem functioning and, in turn, species diversity, abundance and/or

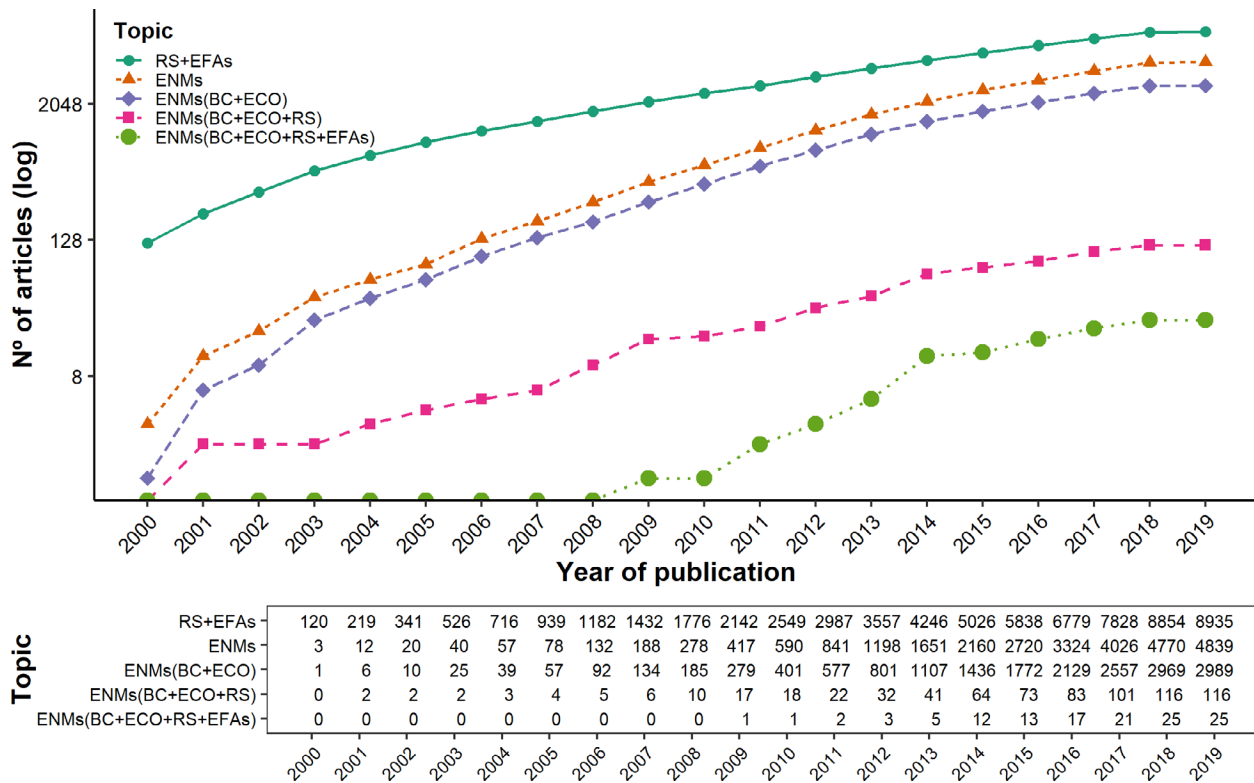


Figure 4. The delayed response of the ecological niche modelling community to the ever-increasing availability of data and methods provided by the RS community that is progressively offering new variables related to ecosystem functioning (see Table S2 for details). RS, remote sensing; ENMs, ecological niche models; EFAs, ecosystem functioning attributes; BC, biodiversity and conservation; ECO, environmental sciences and ecology. Despite the outstanding development of remote sensing products related to ecosystem functioning (olive green colour line) and the increasing applicability of ENMs in Biodiversity and Ecology journals, the number of studies incorporating remotely sensed EFAs into ENMs has only increased slightly (<30 papers in 2019, light green line).

distribution (James et al., 2010; Laliberté et al., 2010; Venier & Holmes, 2010). Such habitat changes would not be captured by land cover data, thus preventing an accurate prediction of the subsequent dynamics of species. Ecological disturbances—such as wildfires that involve a large exchange of matter and energy—can impact species distributions in many different ways depending on the intensity, recurrence or time since the disturbance took place (Griffiths et al., 2015; Kelly et al., 2020; Taillie et al., 2018). As a result, potential impacts of natural (or anthropogenic) disturbances on species distributions are hard to predict (Vallecillo et al., 2009), especially when interacting with other drivers (e.g. climate change), and require more dynamic approaches involving large amounts of data describing environmental conditions over long time series (Shang et al., 2004).

Remotely sensed EFAs allow incorporating a more functional and dynamic perspective of ecosystem/habitat conditions into ENMs, going beyond often used structural and compositional attributes. As described above, feeding EFA-related variables as predictors in ENMs holds several

advantages for understanding species diversity patterns and predicting responses to environmental changes: (1) EFAs allow adding niche descriptors complementary to those traditionally used, thus providing a more complete view of the species' ecological niche (Fig. 3); (2) EFAs allow incorporating intra- and inter-annual variability of ecosystem functioning (Fig. 1B and C); (3) EFAs can be measured systematically through remote sensing technologies at different spatio-temporal scales, facilitating a cross-scale, standardized, repeatable and cost-effective model-assisted monitoring (see e.g. Alcaraz-Segura et al., 2017; Arenas-Castro et al., 2019; Regos, Gómez-Rodríguez, et al., 2020); and (4) long-term data archives such as those provided by Landsat or Terra/Aqua satellites offer the possibility to assess decadal changes in ecosystem functioning at a resolution suitable for species modelling applications to conservation (Fig. 1B) (Berry et al., 2007; Cabello et al., 2012). Many of these advantages are requirements for being selected as essential biodiversity variables (EBVs) (see Pettorelli et al., 2016 and reference therein).

Illustrative case studies—mapping species habitat trends driven by ecosystem functioning

To illustrate how remotely sensed EFAs can be incorporated into ENMs (Fig. 1), we modelled two emblematic species: the whooping crane (*Grus americana*) and the snow leopard (*Panthera uncia*) (details in Appendix S2). Records were compiled for the whole distribution range available from GBIF. Satellite data from MODIS were used to calculate EFA variables (Fig. 1A). We computed several metrics describing the intra-annual properties of each product listed in Table S1.1: the average (as a descriptor of quantity), the minimum and the maximum annual values (descriptors of extreme conditions) and the standard deviation (intra-annual seasonal variation or ‘seasonality’) (Fig. 1B). These statistical measures were calculated for each complete year from 2001 to 2018. To capture multi-year conditions of EFA variables, we computed the average (Fig. 1C). All calculations were performed in GEE (Gorelick et al., 2017). A total of 40 EFA variables were generated as candidate predictors for modelling (Fig. 1D).

Due to the lack of previous knowledge in species–environment relationships regarding each EFA variable and the target species, we applied a model-driven procedure to select the best predictors. First, we performed a preliminary round of models which included all available variables and was based on the Random Forest algorithm—known for handling well large numbers of variables and multicollinearity. Second, an iterative selection of variables was performed to decrease multicollinearity based on pairwise correlation and the importance rank (details in Table S1.2) which retained the best five predictors by species. Note that multicollinearity problems must be also tested before modelling when combining EFAs with other environmental predictors such as bioclimatic variables (see e.g. Alcaraz-Segura et al., 2017; Arenas-Castro et al., 2018; Regos et al., 2019; Vila-Viçosa et al., 2020 for comparison between climate-based and EFA-based ENMs), and that should be selected according to the ecological requirements of the target species (see some examples for birds in Regos, Gómez-Rodríguez, et al., 2020).

To deal with model uncertainty, we implemented an ensemble/consensus model with eight different algorithms (biomod2 R package; Thuiller et al., 2016). The ensemble models were then projected to the EFA conditions for each year, between 2001 and 2018, to obtain annual

projections of habitat suitability and assess its change. Finally, to assess the habitat suitability trends between 2001 and 2018, we computed the Theil–Sen estimator based on annual habitat suitability projections. This method allowed assessing the change sign (increase or decrease), its magnitude and the trend statistical significance (Fig. 5).

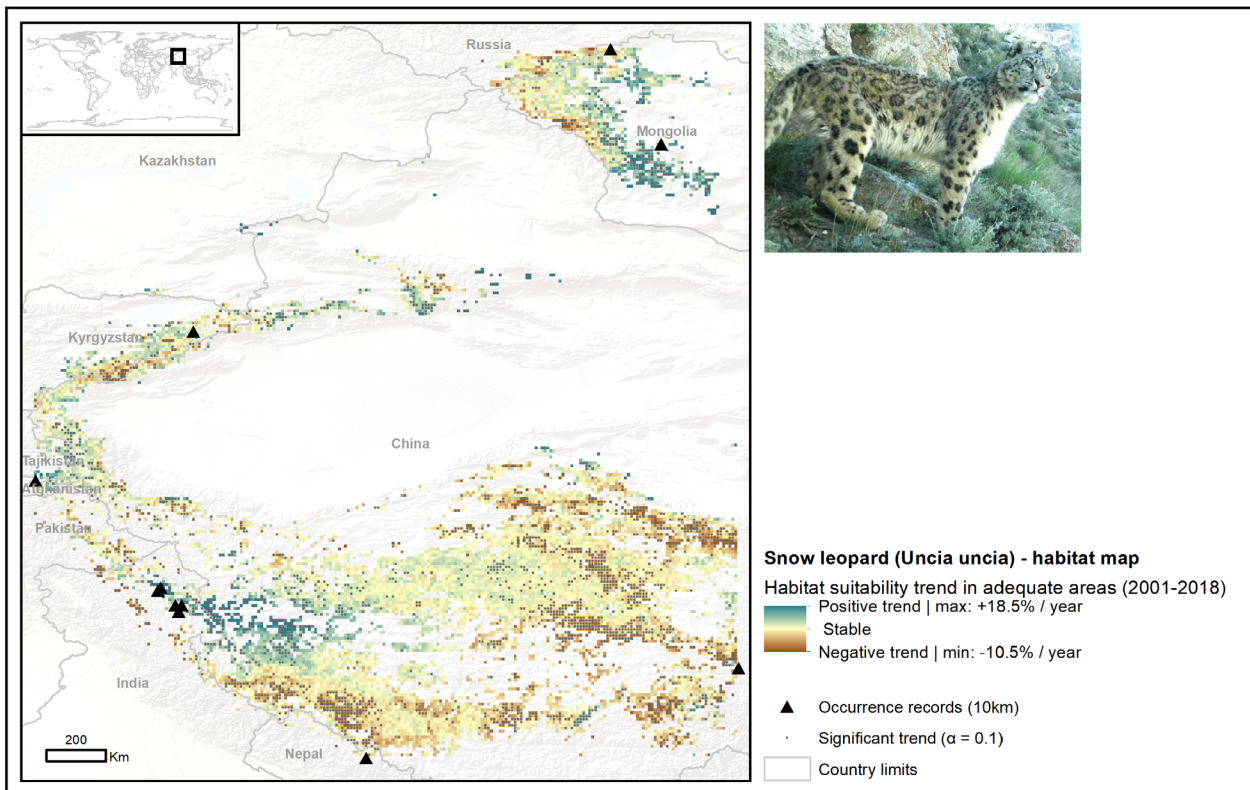
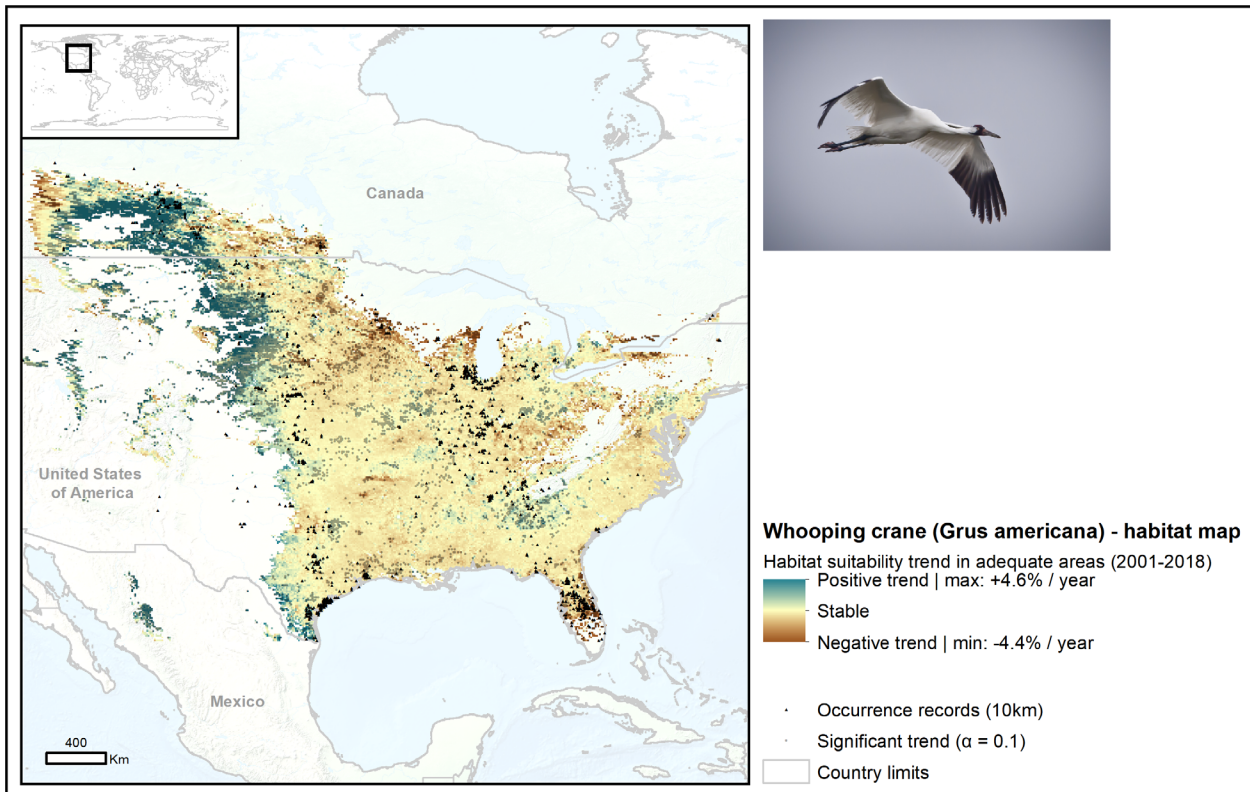
The illustrated workflow clearly identifies some advantages in relation to more ‘classical’ approaches based on static habitat features or bioclimatic variables. Although in these examples we have calibrated the ENMs based on multi-year averaged EFA variables (which was needed given the timespan of presence records), we encourage modellers to characterize the species niche with the inter-annual variability of the EFA variables, which can increase model performance, as shown for climate niche models (see Perez-Navarro et al., 2020).

Concluding Remarks

Despite the many technical advances and the increasing effort by the remote sensing community to develop integrative descriptors of ecosystem functioning, ENM have yet to make full profit of the most recent developments by integrating them in ENM pipelines (see Fig. 4). The synergies between the increasingly available open-access satellite images (e.g. Sentinel missions) (Wulder et al., 2016) and cloud-based platforms for planetary-scale geospatial analysis (such as GEE) (Gorelick et al., 2017) offer an unprecedented opportunity for ecologists to incorporate ecosystem processes and properties that have been so far largely neglected in ecological niche characterization and modelling. Remotely sensed EFAs are characterized by an increasingly higher spatial and temporal resolution that can complement traditional environmental variables extracted from interpolated macroclimate data or describing static habitat features (Coops & Wulder, 2019; Mod et al., 2016)—thereby potentially improving ecological niche characterization and the predictive performance of ENMs. In addition, EFAs can be measured systematically and synoptically through Earth Observation data and remote sensing technologies, facilitating cross-scale, standardized, repeatable and cost-effective biodiversity monitoring.

All these advantages strongly suggest that a new generation of ENMs based on such EFAs would offer great perspectives to increase our ability to monitor habitat suitability trends and population dynamics (Gonçalves

Figure 5. Habitat suitability trends between 2001 and 2018 for two emblematic species: whooping crane (*Grus americana*) (area under the ROC curve [AUC] of 0.972 and true skill statistic [TSS] of 0.820) and snow leopard (*Uncia uncia*) (AUC of 0.999 and TSS of 0.995), computed from ecological niche models based exclusively on remotely sensed EFA variables (see details in Appendix S2). Photographs taken from Wikipedia with Public domain license. EFA, ecosystem functioning attribute.



et al., 2016) (Figs. 1 and 5) and to predict species distributional shifts under global change (Regos et al., 2019; Tuanmu et al., 2011). The development of new global datasets supporting the implementation of EBVs relevant for monitoring ecosystem functioning is a priority for the Group on Earth Observations Biodiversity Observation Network (GEOBON; see Working Group ‘Ecosystem function’, <http://geobon.org/working-groups/ecosystem-function/>) (Skidmore et al., 2015), with great potential for ‘Species Population EBVs’ through their incorporation into ENMs (see Working Group ‘Species Populations’, <https://geobon.org/ebvs/working-groups/species-populations/>). Freely available and continuously updated global datasets of RS-EFAs will boost research in conservation biogeography and macroecology—as already happened in the history of ENMs in the context of climate datasets and climate change scenarios after the release of the first special report on emission scenarios (SRES) by the Intergovernmental Panel on Climate Change (IPCC) and the development of global climate datasets (e.g. WorldClim) (Titeux et al., 2017). The development of models and scenarios that explicitly incorporate ecosystem functioning will allow the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) (Díaz et al., 2015) to assess global change impacts on biodiversity in more integrative way, by including ecosystem processes and disturbances often neglected in global assessments.

A coordinated agenda for remote sensing experts and ENM will be essential over the coming years to bridge the gap between remote sensing and ecological disciplines, and to take full (and timely) advantage of the fast-growing body of Earth observation data (Skidmore et al., 2015)—with special emphasis on the development and testing of new variables related to key features of ecosystem functioning.

Acknowledgements

Part of this work was funded by the EU H2020 Project 641762 ‘ECOPOTENTIAL: Improving Future Ecosystem Benefits through Earth Observations’, from which many valuable thoughts originated. A.R. was funded by the Xunta de Galicia (post-doctoral fellowship ED481B2016/084-0) and currently by ‘Juan de la Cierva’ fellowship program funded by the Spanish Ministry of Science and Innovation (IJC2019-041033-I). J.G. was funded by the Individual Scientific Employment Stimulus Program (2017) by the Portuguese Foundation for Science and Technology (FCT CEECIND/02331/2017/CP1423/CT0012). S.A.-C. was funded by the PORBIOTA - Portuguese e-Infrastructure for Information and Research on Biodiversity (POCI-01-0145-FEDER-022127) project grant and is currently supported by

the ‘María Zambrano’ program funded by the Spanish Ministry of Universities and the EU-NextGenerationEU fund.

Funding information

Part of this work was funded by the EU H2020 Project 641762 ‘ECOPOTENTIAL: Improving Future Ecosystem Benefits through Earth Observations’, from which many valuable thoughts originated. A.R. was funded by the Xunta de Galicia (post-doctoral fellowship ED481B2016/084-0) and currently by ‘Juan de la Cierva’ fellowship program funded by the Spanish Ministry of Science and Innovation (IJC2019-041033-I). J.F.G. was funded by the Individual Scientific Employment Stimulus Program (2017) by the Portuguese Foundation for Science and Technology (FCT CEECIND/02331/2017/CP1423/CT0012). S.A.-C. was financially supported by PORBIOTA—E-Infraestrutura Portuguesa de Informação e Investigação em Biodiversidade (POCI-01-0145-FEDER-022127).

References

- Alcaraz, D., Paruelo, J. & Cabello, J. (2006) Identification of current ecosystem functional types in the Iberian Peninsula. *Global Ecology and Biogeography*, **15**, 200–212. <https://doi.org/10.1111/j.1466-822X.2006.00215.x>
- Alcaraz-Segura, D., Lomba, A., Sousa-Silva, R., Nieto-Lugilde, D., Alves, P., Georges, D. et al. (2017) Potential of satellite-derived ecosystem functional attributes to anticipate species range shifts. *International Journal of Applied Earth Observation and Geoinformation*, **57**, 86–92. <https://doi.org/10.1016/j.jag.2016.12.009>
- Alemu, W.G. & Henebry, G.M. (2017) Land surface phenology and seasonality using cool earthlight in croplands of Eastern Africa and the linkages to crop production. *Remote Sensing*, **9**. <https://doi.org/10.3390/rs9090914>
- Amiri, M., Tarkesh, M., Jafari, R. & Jetschke, G. (2020) Bioclimatic variables from precipitation and temperature records vs. remote sensing-based bioclimatic variables: which side can perform better in species distribution modeling? *Ecological Informatics*, **57**, 101060. <https://doi.org/10.1016/j.ecoinf.2020.101060>
- Archibald, S., Lehmann, C.E.R., Belcher, C., Bond, W.J., Bradstock, R.A., Daniau, A.-L. et al. (2018) Biological and geophysical feedbacks with fire in the Earth system. *Environmental Research Letters*, **13**, 033003. <https://doi.org/10.1088/1748-9326/aa9ead>
- Arenas-Castro, S., Gonçalves, J., Alves, P., Alcaraz-Segura, D. & Honrado, J.P. (2018) Assessing the multi-scale predictive ability of ecosystem functional attributes for species distribution modelling. *PLoS One*, **13**, e0199292. <https://doi.org/10.1371/journal.pone.0199292>
- Arenas-Castro, S., Regos, A., Gonçalves, J.F., Alcaraz-Segura, D. & Honrado, J.P. (2019) Remotely sensed variables of

- ecosystem functioning support robust predictions of abundance patterns for rare species. *Remote Sensing*, **11**, 2086.
- Barbet-Massin, M., Thuiller, W. & Jiguet, F. (2012) The fate of European breeding birds under climate, land-use and dispersal scenarios. *Global Change Biology*, **18**, 881–890. <https://doi.org/10.1111/j.1365-2486.2011.02552.x>
- Berry, S., Mackey, B. & Brown, T. (2007) Potential applications of remotely sensed vegetation greenness to habitat analysis and the conservation of dispersive fauna. *Pacific Conservation Biology*, **13**, 120–127.
- Bradley, B.A. & Fleishman, E. (2008) Can remote sensing of land cover improve species distribution modelling? *Journal of Biogeography*, **35**, 1158–1159. <https://doi.org/10.1111/j.1365-2699.2008.01928.x>
- Bradley, B.A., Olsson, A.D., Wang, O., Dickson, B.G., Pelech, L., Sennie, S.E. et al. (2012) Species detection vs. habitat suitability: are we biasing habitat suitability models with remotely sensed data? *Ecological Modelling*, **244**, 57–64. <https://doi.org/10.1016/j.ecolmodel.2012.06.019>
- Bramer, I., Anderson, B.J., Bennie, J., Bladon, A.J., De Frenne, P., Hemming, D. et al. (2018) Advances in monitoring and modelling climate at ecologically relevant scales. *Advances in Ecological Research*, **58**, 101–161.
- Brotons, L. (2014) Species distribution models and impact factor growth in environmental journals: methodological fashion or the attraction of global change science. *PLoS One*, **9**, e111996. <https://doi.org/10.1371/journal.pone.0111996>
- Cabello, J., Fernández, N., Alcaraz-Segura, D., Oyonarte, C., Piñeiro, G., Altesor, A. et al. (2012) The ecosystem functioning dimension in conservation: insights from remote sensing. *Biodiversity and Conservation*, **21**, 3287–3305. <https://doi.org/10.1007/s10531-012-0370-7>
- Carrara, R. & Vázquez, D.P. (2010) The species-energy theory: a role for energy variability. *Ecography*, **33**, 942–948. <https://doi.org/10.1111/j.1600-0587.2009.05756.x>
- Casu, F., Manunta, M., Agram, P.S. & Crippen, R.E. (2017) Big Remotely Sensed Data: tools, applications and experiences. *Remote Sensing of Environment*, **202**, 1–2. <https://doi.org/10.1016/j.rse.2017.09.013>
- Chen, B. & Coops, N.C. (2009) Understanding of coupled terrestrial carbon, nitrogen and water dynamics - an overview. *Sensors*, **9**, 8624–8657. <https://doi.org/10.3390/s91108624>
- Coops, N.C., Waring, R.H., Wulder, M.A., Pidgeon, A.M. & Radeloff, V.C. (2009) Bird diversity: a predictable function of satellite-derived estimates of seasonal variation in canopy light absorbance across the United States. *Journal of Biogeography*, **36**, 905–918. <https://doi.org/10.1111/j.1365-2699.2008.02053.x>
- Coops, N.C. & Wulder, M.A. (2019) Breaking the Habit(at). *Trends in Ecology & Evolution*, **34**, 585–587. <https://doi.org/10.1016/j.tree.2019.04.013>
- Cord, A. & Rödder, D. (2011) Inclusion of habitat availability in species distribution models through multi-temporal remote sensing data? Towards multifunctional agricultural landscapes in Europe: assessing and governing synergies between food production, biodiversity, and ecosystem. *Ecological Applications*, **21**, 3285–3298. <https://doi.org/10.2307/41417127>
- De Beurs, K.M. & Henebry, G.M. (2004) Land surface phenology, climatic variation, and institutional change: analyzing agricultural land cover change in Kazakhstan. *Remote Sensing of Environment*, **89**, 497–509. <https://doi.org/10.1016/j.rse.2003.11.006>
- Díaz, S., Demissew, S., Carabias, J., Joly, C., Lonsdale, M., Ash, N. et al. (2015) The IPBES Conceptual Framework—connecting nature and people. *Current Opinion in Environment Sustainability*, **14**, 1–16. <https://doi.org/10.1016/j.cusust.2014.11.002>
- Dieguez, H. & Paruelo, J.M. (2017) Disentangling the signal of climatic fluctuations from land use: changes in ecosystem functioning in South American protected areas (1982–2012). *Remote Sensing in Ecology and Conservation*, **3**, 177–189. <https://doi.org/10.1002/rse2.39>
- Estes, L.D., Reillo, P.R., Mwangi, A.G., Okin, G.S. & Shugart, H.H. (2010) Remote sensing of structural complexity indices for habitat and species distribution modeling. *Remote Sensing of Environment*, **114**, 792–804. <https://doi.org/10.1016/j.rse.2009.11.016>
- Fensholt, R., Langanke, T., Rasmussen, K., Reenberg, A., Prince, S.D., Tucker, C. et al. (2012) Greenness in semi-arid areas across the globe 1981–2007 - an Earth Observing Satellite based analysis of trends and drivers. *Remote Sensing of Environment*, **121**, 144–158. <https://doi.org/10.1016/j.rse.2012.01.017>
- Fernández, N., Paruelo, J.M. & Delibes, M. (2010) Ecosystem functioning of protected and altered Mediterranean environments: a remote sensing classification in Doñana, Spain. *Remote Sensing of Environment*, **114**, 211–220. <https://doi.org/10.1016/j.rse.2009.09.001>
- Fernández, N., Román, J. & Delibes, M. (2016) Variability in primary productivity determines metapopulation dynamics. *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20152998. <https://doi.org/10.1098/rspb.2015.2998>
- Fisher, J.A.D., Frank, K.T. & Leggett, W.C. (2010) Dynamic macroecology on ecological time-scales. *Global Ecology and Biogeography*, **19**, 1–15. <https://doi.org/10.1111/j.1466-8238.2009.00482.x>
- Franklin, J. (1995) Predictive vegetation mapping: geographic modelling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography*, **19**, 474–499.
- Franklin, J. (2010) Moving beyond static species distribution models in support of conservation biogeography. *Diversity and Distributions*, **16**, 321–330.
- Gao, B.C. (1996) NDWI – a normalized difference water index for remote sensing of vegetation liquid water from space.

- Remote Sensing of Environment*, **58**, 257–266. [https://doi.org/10.1016/S0034-4257\(96\)00067-3](https://doi.org/10.1016/S0034-4257(96)00067-3)
- Gonçalves, J., Alves, P., Pôças, I., Marcos, B., Sousa-Silva, R., Lomba, Â. et al. (2016) Exploring the spatiotemporal dynamics of habitat suitability to improve conservation management of a vulnerable plant species. *Biodiversity and Conservation*, **25**, 2867–2888. <https://doi.org/10.1007/s10531-016-1206-7>
- Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D. & Moore, R. (2017) Google Earth Engine: planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment*, **202**, 18–27. <https://doi.org/10.1016/j.rse.2017.06.031>
- Griffiths, A.D., Garnett, S.T. & Brook, B.W. (2015) Fire frequency matters more than fire size: testing the pyrodiversity – biodiversity paradigm for at-risk small mammals in an Australian tropical savanna. *Biological Conservation*, **186**, 337–346. <https://doi.org/10.1016/j.biocon.2015.03.021>
- Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T. et al. (2013) Predicting species distributions for conservation decisions. *Ecology Letters*, **16**(11), 424–435. <https://doi.org/10.1111/ele.12189>
- Guisan, A. & Zimmermann, N.E. (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.
- He, K.S., Bradley, B.A., Cord, A.F., Rocchini, D., Tuanmu, M.-N., Schmidlein, S. et al. (2015) Will remote sensing shape the next generation of species distribution models? *Remote Sensing in Ecology and Conservation*, **1**, 4–18. <https://doi.org/10.1002/rse2.7>
- Hobi, M.L., Dubinin, M., Graham, C.H., Coops, N.C., Clayton, M.K., Pidgeon, A.M. et al. (2017) A comparison of Dynamic Habitat Indices derived from different MODIS products as predictors of avian species richness. *Remote Sensing of Environment*, **195**, 142–152. <https://doi.org/10.1016/j.rse.2017.04.018>
- Hurlbert, A.H. (2004) Species-energy relationships and habitat complexity in bird communities. *Ecology Letters*, **7**, 714–720. <https://doi.org/10.1111/j.1461-0248.2004.00630.x>
- Hutchinson, G. (1957) Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 415–427.
- Ichii, K., Kawabata, A. & Yamaguchi, Y. (2002) Global correlation analysis for NDVI and climatic variables and NDVI trends: 1982–1990. *International Journal of Remote Sensing*, **23**, 3873–3878. <https://doi.org/10.1080/01431160110119416>
- Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). (2016) *The methodological assessment report on scenarios and models of biodiversity and ecosystem services*. Bonn, Germany: Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, p. 348.
- James, P.M.A., Fortin, M.-J., Sturtevant, B.R., Fall, A. & Kneeshaw, D. (2010) Modelling spatial interactions among fire, spruce budworm, and logging in the Boreal forest. *Ecosystems*, **14**, 60–75. <https://doi.org/10.1007/s10021-010-9395-5>
- Jax, K. (2005) Function and “functioning” in ecology: what does it mean? *Oikos*, **111**, 641–648. <https://doi.org/10.1111/j.1600-0706.2005.13851.x>
- Jönsson, P. & Eklundh, L. (2004) TIMESAT - a program for analyzing time-series of satellite sensor data. *Computational Geosciences*, **30**, 833–845. <https://doi.org/10.1016/j.cageo.2004.05.006>
- Kasischke, E.S., Christensen, N.L. & Stocks, B.J. (1995) Fire, global warming, and the carbon balance of boreal forests. *Ecological Applications*, **5**, 437–451.
- Kelly, L.T., Giljohann, K.M., Duane, A., Aquilué, N., Archibald, S., Battlori, E. et al. (2020) Fire and biodiversity in the Anthropocene. *Science*, **370**, eabb0355. <https://doi.org/10.1126/science.abb0355>
- Laliberté, E., Wells, J.A., DeClerck, F., Metcalfe, D.J., Catterall, C.P., Queiroz, C. et al. (2010) Land-use intensification reduces functional redundancy and response diversity in plant communities. *Ecology Letters*, **13**, 76–86. <https://doi.org/10.1111/j.1461-0248.2009.01403.x>
- Leitão, P.J. & Santos, M.J. (2019) Improving models of species ecological niches: a remote sensing overview. *Frontiers in Ecology and Evolution*, **7**, 9. <https://doi.org/10.3389/FEVO.2019.00009>
- Leith, H. (1974) *Phenology and seasonality modeling*. New York, NY: Springer.
- Lembrechts, J., Nijs, I. & Lenoir, J. (2018) Incorporating microclimate into species distribution models. *Ecography*, 1–13. <https://doi.org/10.1111/ecog.03947>
- Lewis, A., Lymburner, L., Purss, M.B.J., Brooke, B., Evans, B., Ip, A. et al. (2016) Rapid, high-resolution detection of environmental change over continental scales from satellite data – the Earth Observation Data Cube. *International Journal of Digital Earth*, **9**, 106–111. <https://doi.org/10.1080/17538947.2015.1111952>
- Loreau, M. (2008) Biodiversity and ecosystem functioning: the mystery of the deep sea. *Current Biology*, **18**, 126–128. <https://doi.org/10.1016/j.cub.2007.12.001>
- Lovett, G.M., Jones, C.G., Turner, M.G. & Weathers, K.C. (2006) *Ecosystem function in heterogeneous landscapes, ecosystem function in heterogeneous landscapes*. New York, NY: Springer.
- Marshall, L., Biesmeijer, J.C., Rasmont, P., Vereecken, N.J., Dvorak, L., Fitzpatrick, U. et al. (2017) The interplay of climate and land use change affects the distribution of EU bumblebees. *Global Change Biology*. <https://doi.org/10.1111/gcb.13867>
- Mayor, S.J., Guralnick, R.P., Tingley, M.W., Otegui, J., Withey, J.C., Elmendorf, S.C. et al. (2017) Increasing phenological asynchrony between spring green-up and arrival of

- migratory birds. *Scientific Reports*, **7**, 1–10. <https://doi.org/10.1038/s41598-017-02045-z>
- Mod, H.K., Scherrer, D., Luoto, M. & Guisan, A. (2016) What we use is not what we know: environmental predictors in plant distribution models. *Journal of Vegetation Science*, **27**, 1308–1322. <https://doi.org/10.1111/jvs.12444>
- Newbold, T., Hudson, L.N., Hill, S.L., Contu, S., Lysenko, I., Senior, R.A. et al. (2015) Global effects of land use on local terrestrial biodiversity. *Nature*, **520**, 45–50. <https://doi.org/10.1038/nature14324>
- Nieto, S., Flombaum, P. & Garbulsky, M.F. (2015) Can temporal and spatial NDVI predict regional bird-species richness? *Global Ecology and Conservation*, **3**, 729–735. <https://doi.org/10.1016/j.gecco.2015.03.005>
- Paruelo, J.M., Burke, I.C. & Lauenroth, W.K. (2001) Land-use impact on ecosystem functioning in eastern Colorado. *Global Change Biology*, **7**, 631–639.
- Pellissier, L., Anzini, M., Maiorano, L., Dubuis, A., Pottier, J., Vittoz, P. et al. (2013) Spatial predictions of land-use transitions and associated threats to biodiversity: the case of forest regrowth in mountain grasslands. *Applied Vegetation Science*, **16**, 227–236. <https://doi.org/10.1111/j.1654-109X.2012.01215.x>
- Perez-Navarro, M.A., Broennimann, O., Esteve, M.A., Moya-Perez, J.M., Carreño, M.F., Guisan, A. et al. (2020) Temporal variability is key to modelling the climatic niche. *Diversity and Distributions*, 1–12. <https://doi.org/10.1111/ddi.13207>
- Peterson, A.T. & Soberón, J. (2012) Species distribution modeling and ecological niche modeling: getting the concepts right. *Nature Conservation*, **10**, 102–107. <https://doi.org/10.4322/natcon.2012.019>
- Pettorelli, N., Schulte to Bühne, H., Tulloch, A., Dubois, G., Macinnis-Ng, C., Queirós, A.M. et al. (2018) Satellite remote sensing of ecosystem functions: opportunities, challenges and way forward. *Remote Sensing in Ecology and Conservation*, **4**, 71–93. <https://doi.org/10.1002/rse2.59>
- Pettorelli, N., Wegmann, M., Skidmore, A., Múcher, S., Dawson, T.P., Fernandez, M. et al. (2016) Framing the concept of satellite remote sensing essential biodiversity variables: challenges and future directions. *Remote Sensing in Ecology and Conservation*, **2**, 122–131. <https://doi.org/10.1002/rse2.15>
- Phillips, L.B., Hansen, A.J. & Flather, C.H. (2008) Evaluating the species energy relationship with the newest measures of ecosystem energy: NDVI versus MODIS primary production. *Remote Sensing of Environment*, **112**, 4381–4392. <https://doi.org/10.1016/j.rse.2008.08.002>
- Piao, S. (2003) Interannual variations of monthly and seasonal normalized difference vegetation index (NDVI) in China from 1982 to 1999. *Journal of Geophysical Research*, **108**, 4401. <https://doi.org/10.1029/2002JD002848>
- Pottier, J., Malenovsky, Z., Psomas, A., Homolová, L., Schaeppman, M.E., Choler, P. et al. (2014) Modelling plant species distribution in alpine grasslands using airborne imaging spectroscopy. *Biology Letters*, **10**. <https://doi.org/10.1098/rsbl.2014.0347>
- Pöyry, J., Böttcher, K., Fronzek, S., Gobron, N., Leinonen, R., Metsämäki, S. et al. (2017) Predictive power of remote sensing versus temperature-derived variables in modelling phenology of herbivorous insects. *Remote Sensing in Ecology and Conservation*. <https://doi.org/10.1002/rse2.56>
- Radeloff, V.C., Dubinin, M., Coops, N.C., Allen, A.M., Brooks, T.M., Clayton, M.K. et al. (2019) The Dynamic Habitat Indices (DHIs) from MODIS and global biodiversity. *Remote Sensing of Environment*, **222**, 204–214. <https://doi.org/10.1016/j.rse.2018.12.009>
- Ramírez, F., Tarroux, A., Hovinen, J., Navarro, J., Afán, I., Forero, M.G. et al. (2017) Sea ice phenology and primary productivity pulses shape breeding success in Arctic seabirds. *Scientific Reports*, **7**, 4500. <https://doi.org/10.1038/s41598-017-04775-6>
- Randin, C.F., Ashcroft, M.B., Bolliger, J., Cavender-Bares, J., Coops, N.C., Dullinger, S. et al. (2020) Remote Sensing of Environment Monitoring biodiversity in the Anthropocene using remote sensing in species distribution models. *Remote Sensing of Environment*, **239**(111), 626. <https://doi.org/10.1016/j.rse.2019.111626>
- Ratajczak, Z., Carpenter, S.R., Ives, A.R., Kucharik, C.J., Ramiadantsoa, T., Stegner, M.A. et al. (2018) Abrupt change in ecological systems: inference and diagnosis. *Trends in Ecology & Evolution*, **33**, 513–526. <https://doi.org/10.1016/j.tree.2018.04.013>
- Regos, A., Gagne, L., Alcaraz-Segura, D., Honrado, J.P. & Domínguez, J. (2019) Effects of species traits and environmental predictors on performance and transferability of ecological niche models. *Scientific Reports*, **9**, 4221. <https://doi.org/10.1038/s41598-019-40766-5>
- Regos, A., Gómez-Rodríguez, P., Arenas-Castro, S., Tapia, L., Vidal, M. & Domínguez, J. (2020) Model-assisted bird monitoring based on remotely sensed ecosystem functioning and atlas data. *Remote Sensing*, **12**, 2549.
- Regos, A., Tapia, L., Arenas-Castro, S., Gil-Carrera, A. & Domínguez, J. (2021) Ecosystem Functioning Influences Species Fitness at Upper Trophic Levels. *Ecosystems*, <https://doi.org/10.1007/s10021-021-00699-5>.
- Regos, A., Vidal, M., Lorenzo, M. & Domínguez, J. (2020) Integrating intraseasonal grassland dynamics in cross-scale distribution modeling to support waterbird recovery plans. *Conservation Biology*, **34**, 494–504. <https://doi.org/10.1111/cobi.13415>
- Requena-Mullor, J.M., López, E., Castro, A.J., Cabello, J., Virgós, E., González-Miras, E. et al. (2014) Modeling spatial distribution of European badger in arid landscapes: an ecosystem functioning approach. *Landscape Ecology*, **29**, 843–855. <https://doi.org/10.1007/s10980-014-0020-4>
- Rickebusch, S., Thuiller, W., Hickler, T., Araújo, M.B., Sykes, M.T., Schweiger, O. et al. (2008) Incorporating the effects of changes in vegetation functioning and CO₂ on water

- availability in plant habitat models. *Biology Letters*, **4**, 556–559. <https://doi.org/10.1098/rsbl.2008.0105>
- Rodríguez-Fernández, N., Al Bitar, A., Colliander, A. & Zhao, T. (2019) Soil moisture remote sensing across scales. *Remote Sensing*, **11**, 190. <https://doi.org/10.3390/rs11020190>
- Scherrer, D. & Guisan, A. (2019) Ecological indicator values reveal missing predictors of species distributions. *Scientific Reports*, **9**, 3061. <https://doi.org/10.1038/s41598-019-39133-1>
- Sellers, P.J., Berry, J.A., Collatz, G.J., Field, C.B. & Hall, F. (1992) Canopy reflectance, photosynthesis, and transpiration. III. A reanalysis using improved leaf models and a new canopy integration scheme. *Remote Sensing of Environment*, **42**, 187.
- Shang, B.Z., He, H.S., Crow, T.R. & Shifley, S.R. (2004) Fuel load reductions and fire risk in central hardwood forests of the United States: a spatial simulation study. *Ecological Modelling*, **180**, 89–102. <https://doi.org/10.1016/j.ecolmodel.2004.01.020>
- Sillero, N. (2011) What does ecological modelling model? A proposed classification of ecological niche models based on their underlying methods. *Ecological Modelling*, **222**, 1343–1346. <https://doi.org/10.1016/j.ecolmodel.2011.01.018>
- Skidmore, A.K., Pettorelli, N., Coops, N.C., Geller, G.N., Hansen, M., Lucas, R. et al. (2015) Environmental science: agree on biodiversity metrics to track from space. *Nature*, **523**, 403–405. <https://doi.org/10.1038/523403a>
- Smith, A., Schoeman, M.C., Keith, M., Erasmus, B.F.N., Monadjem, A., Moilanen, A. et al. (2016) Synergistic effects of climate and land-use change on representation of African bats in priority conservation areas. *Ecological Indicators*, **69**, 276–283. <https://doi.org/10.1016/j.ecolind.2016.04.039>
- Taillie, P.J., Burnett, R.D., Roberts, L.J., Campos, B.R., Peterson, M.N. & Moorman, C.E. (2018) Interacting and non-linear avian responses to mixed-severity wildfire and time since fire. *Ecosphere*, **9**. <https://doi.org/10.1002/ecs2.2291>
- Thorup, K., Tøttrup, A.P., Willemoes, M., Klaassen, R.H.G., Strandberg, R., Vega, M.L. et al. (2017) Resource tracking within and across continents in long-distance bird migrants. *Science Advances*, **3**, e1601360. <https://doi.org/10.1126/sciadv.1601360>
- Thuiller, W., Engler, R., Breiner, F.T., 2016. biomod2: ensemble platform for species distribution modeling. R package version 3.3–7. <https://CRAN.R-project.org/package=biomod2> [Accessed 15 November 2020].
- Titeux, N., Brotons, L. & Settele, J. (2019) IPBES promotes integration of multiple threats to biodiversity. *Trends in Ecology & Evolution*, **34**, 969–970. <https://doi.org/10.1016/j.tree.2019.07.017>
- Titeux, N., Henle, K., Mihoub, J.-B., Regos, A., Geijzendorffer, I.R., Cramer, W. et al. (2016) Biodiversity scenarios neglect future land use change. *Global Change Biology*, **22**, 2505–2515. <https://doi.org/10.1111/gcb.13272>
- Titeux, N., Henle, K., Mihoub, J.-B., Regos, A., Geijzendorffer, I.R., Cramer, W. et al. (2017) Global scenarios for biodiversity need to better integrate climate and land use change. *Diversity and Distributions*, **23**, 1231–1234. <https://doi.org/10.1111/ddi.12624>
- Tittensor, D.P., Walpole, M., Hill, S.L.L., Boyce, D.G., Britten, G.L., Burgess, N.D. et al. (2014) A mid-term analysis of progress toward international biodiversity targets. *Science*, **346**, 241–244. <https://doi.org/10.1126/science.1257484>
- Torres, J., Gonçalves, J., Marcos, B. & Honrado, J. (2018) Indicator-based assessment of post-fire recovery dynamics using satellite NDVI time-series. *Ecological Indicators*, **89**, 199–212. <https://doi.org/10.1016/j.ecolind.2018.02.008>
- Toszogyova, A. & Storch, D. (2019) Global diversity patterns are modulated by temporal fluctuations in primary productivity. *Global Ecology and Biogeography*, 1–12. <https://doi.org/10.1111/geb.12997>
- Tuanmu, M.-N., Viña, A., Roloff, G.J., Liu, W., Ouyang, Z., Zhang, H. et al. (2011) Temporal transferability of wildlife habitat models: implications for habitat monitoring. *Journal of Biogeography*, **38**, 1510–1523. <https://doi.org/10.1111/j.1365-2699.2011.02479.x>
- Vallecillo, S., Brotons, L. & Thuiller, W. (2009) Dangers of predicting bird species distributions in response to land-cover changes. *Ecological Applications*, **19**, 538–549. <https://doi.org/10.1890/08-0348.1>
- Venier, L.A. & Holmes, S.B. (2010) A review of the interaction between forest birds and eastern spruce budworm. *Environmental Reviews*, **18**, 191–207. <https://doi.org/10.1139/A10-009>
- Vila-Viçosa, C., Arenas-Castro, S., Marcos, B., Honrado, J., García, C., Vázquez, F.M. et al. (2020) Combining satellite remote sensing and climate data in species distribution models to improve the conservation of Iberian White oaks (*Quercus L.*). *ISPRS International Journal of Geo-Information*, **9**, 735. <https://doi.org/10.3390/ijgi9120735>
- Villero, D., Pla, M., Camps, D., Ruiz-Olmo, J. & Brotons, L. (2017) Integrating species distribution modelling into decision-making to inform conservation actions. *Biodiversity and Conservation*, **26**, 251–271. <https://doi.org/10.1007/s10531-016-1243-2>
- Wang, Q., Adiku, S., Tenhunen, J. & Granier, A. (2005) On the relationship of NDVI with leaf area index in a deciduous forest site. *Remote Sensing of Environment*, **94**, 244–255. <https://doi.org/10.1016/j.rse.2004.10.006>
- Wiegand, T., Naves, J., Garbulsky, M.F. & Fernández, N. (2008) Animal habitat quality and ecosystem functioning: exploring seasonal patterns using NDVI. *Ecological Monographs*, **78**, 87–103. <https://doi.org/10.1890/06-1870.1>
- Wulder, M.A., White, J.C., Loveland, T.R., Woodcock, C.E., Belward, A.S., Cohen, W.B. et al. (2016) The global Landsat archive: status, consolidation, and direction. *Remote Sensing of Environment*, **185**, 271–283. <https://doi.org/10.1016/j.rse.2015.11.032>
- WWF ZSL. (2016) *Living Planet Report 2016. Risk and resilience in a new era*. Gland, Switzerland: WWF International.

Zhang, K., Kimball, J.S. & Running, S.W. (2016) A review of remote sensing based actual evapotranspiration estimation. *Wiley Interdisciplinary Reviews Water*, 3, 834–853. <https://doi.org/10.1002/wat2.1168>

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1.1. List of process variables used in EFA calculation.

Table S1.2. Selected variables used for modelling each species after the two-step selection procedure.

Appendix S1. Methodological details of the two illustrative case studies.

Table S2. Summary of systematic literature survey performed on the Web of Sciences (WOS) database.