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Monitoring biodiversity in the Anthropocene using remote sensing in species distribution models

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Abstract

In the face of the growing challenges brought about by human activities, effective planning and
decision-making in biodiversity and ecosystem conservation, restoration, and sustainable

development are urgently needed. Ecological models can play a key role in supporting this need and helping to safeguard the natural assets that underpin human wellbeing and support life on land and under water (United Nations Sustainable Development Goals; SDG 14 & 15). The urgency and complexity of safeguarding forest (SDG 15.2) and mountain ecosystems (SDG 15.4), for example, and halting decline in biodiversity (SDG 15.5) in the Anthropocene requires a re-envisioning of how ecological models can best support the comprehensive assessments of biodiversity and its change that are required for successful action.

A key opportunity to advance ecological modeling for both predictive and explanatory purposes arises through a collaboration between ecologists and the Earth observation community to achieve a close integration of remote sensing and species distribution models. Remote sensing data products have the capacity to provide continuous spatiotemporal information about key factors driving the distribution of organisms, therefore improving both the use and accuracy of these models for management and planning.

Here we first survey the literature on remote sensing data products available to ecological modelers interested in improving predictions of species range dynamics under global change. We specifically explore the key biophysical processes underlying the distribution of species in the Anthropocene including climate variability, changes in land cover, and disturbance. We then discuss potential synergies between the ecological modeling and remote sensing communities, and highlight opportunities to close the data and conceptual gaps that currently impede a more effective application of remote sensing for the monitoring and modeling of ecological systems. Specific attention is given to how potential collaborations between the two communities could lead to new opportunities to report on progress towards global agendas such as the Agenda 2030 for sustainable development of the United Nations or the Post-2020 Global Biodiversity Framework of the Convention for Biological Diversity, and help guide conservation and management strategies towards sustainability.

1. Introduction

Human society in the Anthropocene has emerged as a global driver rapidly transforming ecosystems (Ellis, 2015, 2011; Waters et al., 2016). Anthropogenic transformation affects the distribution of species and habitats through a range of drivers and processes including land-use and land-cover change, climate change, pollution, (over-)exploitation (Benítez-López et al., 2019), and biological invasions (Chaudhary et al., 2015; Lenzen et al., 2009; Newbold et al., 2016, 2015; Pekin and Pijanowski, 2012; Pereira et al., 2012). Importantly, the existence of global supply chains that interconnect human societies implies that local anthropogenic impact can also be driven by consumptive demands thousands of kilometers away (Chaudhary and Kastner, 2016; Marques et al., 2019; Meyfroidt et al., 2013; Rudel, 2007; Verburg et al., 2015). Furthermore, novel disturbance regimes are emerging, such as altered frequency and intensity of extreme climatic and fire events (IPCC, 2014; Mahecha et al., 2017; Ummenhofer and Meehl, 2017). Such events impact the state, structure, functionality, and evolution of biological systems at different scales, potentially increasing vulnerability to further changes in climate variability (Dirzo et al., 2014; IPCC, 2014).

The challenges posed by anthropogenic impact on the environment are increasingly recognized at national and international levels. This has resulted in large integrated monitoring and reporting frameworks. At the global level, such frameworks include the United Nations' Sustainable Development Goals (2030 Agenda) and the Aichi biodiversity targets of the Convention on Biological Diversity (Strategic Plan for Biodiversity 2011-2020). For example, UN goal 15.5 aims to 'Take urgent and significant action to ... halt the loss of biodiversity and, by 2020, protect and prevent the extinction of threatened species', whilst the closely related Aichi target 12 focuses on improving the conservation status of threatened species. These targets are used to monitor progress, inform actions, and evaluate alternative options for governance and decision-making. Meeting the SDGs and Aichi targets requires a suite of monitoring strategies for the acquisition of

high quality data and a thorough understanding of current and emerging pressures acting on species and ecosystems (Chen et al., 2011; Lenoir et al., 2019; Lenoir and Svenning, 2015; Mirtl et al., 2018). Monitoring programs should help conservation and management strategies based on explanatory as well as predictive models and support the regular evaluation of the effectiveness of policy interventions (Haase et al., 2018).

The development of monitoring design and management strategies that account for the scale, pace, and complexity of anthropogenic impacts on species and ecosystems (Ceballos et al., 2017; Dirzo et al., 2014; Kim et al., 2018) requires assessments of past and current biodiversity changes as well as robust projections of the potential future distributions of species and ecosystems (i.e., satisfactory accuracy and precision of models transferred to novel conditions. Species Distribution Models (SDMs, *sensu* Guisan and Thuiller, 2005; Guisan and Zimmermann, 2000, Box 1) provide a powerful explanatory and predictive modeling framework in this context. In conservation and decision-making, SDMs can for example be used as explanatory models (*sensu* Shmueli, 2009) to identify critical environmental variables for species or communities (e.g. Droz et al., 2019), or for interpolating and extrapolating potential geographic distributions from available observations of species or communities (McShea, 2014). These predicted ranges can then be used in conservation planning to minimize the impact of development (Guisan et al., 2013) and may be linked to biodiversity monitoring through frameworks such as Essential Biodiversity Variables¹ (EBVs, Fernandez et al., 2019; Pereira et al., 2013). SDMs have further evolved to provide scenarios for past and future species distributions and community composition, based on the use of environmental variables such as climate, land cover and biotic constraints. This allows stakeholders to identify the natural resources they want to sustain and assess the projected effects of environmental policy options on the distribution of threatened, rare, flagship or invasive species (e.g. Cianfrani et al., 2018, 2015; Esselman and Allan, 2011). SDM projections can also

¹ a minimum set of biodiversity state variables required to study, report, and manage multiple facets of biodiversity change (Pereira et al., 2013)

154 indicate whether current protected areas or networks of protected sites match with likely future
155 species and community distributions (e.g. Araujo et al., 2004; Bolliger et al., 2007; Droz et al.,
156 2019). Collectively, these applications illustrate the high relevance of SDMs for biodiversity
157 conservation and hence for meeting the SDGs and the Aichi targets.

158 However, there are numerous criticisms of current implementations of SDMs, in particular when
159 applied to assist biodiversity monitoring. Such criticisms originate primarily from the reliance of
160 both correlative and process-based SDMs (see Box 1) on long-term, averaged, and interpolated
161 spatial climate variables, routinely used without accounting for their temporal variability
162 (Zimmermann et al., 2009). Moreover, correlative models are calibrated on statistical relationships
163 that fail to capture the actual biological processes underlying the geographical distributions of
164 species and biodiversity (Dormann et al., 2012). Finally, projections from both correlative and
165 process-based SDMs are often based on calibration datasets with limited spatial and temporal
166 extent, which restricts transferability of model projections (Werkowska et al., 2017; Yates et al.,
167 2018). Although hybrid and process-based distribution models (see Box 1) address flaws such as
168 the causality between the response and the predictors as well as the spatiotemporal
169 transferability, these models are data intensive (and thus limited to few species) and typically rely
170 on climate interpolations.

171 The development of free, open, easily accessible remote sensing data provide opportunities for
172 resolving some of the limitations of SDMs. For example, a large variety of products derived from
173 various satellite sensors are available to assess key natural systems and environmental
174 conditions as well as extremes affecting the land surface in a contiguous spatial and temporal
175 fashion (Mahecha et al., 2017), thereby capturing the environmental processes underlying
176 species, and thus biodiversity, distribution. For example, these products allow assessment of land
177 use and cover (e.g. Verburg et al., 2011), forest cover (e.g. Hansen et al., 2008; Klein et al., 2015),
178 vegetation structure (e.g. Schneider et al., 2014), vegetation productivity and phenology (e.g. de
179 Jong et al., 2013; Garonna et al., 2018; Jolly et al., 2005), snow (e.g. Hüsler et al., 2014; Xie et

al., 2017), temperature (e.g. Ibrahim et al., 2018), and precipitation (e.g. Naumann et al., 2012). Additionally, continuous time series deliver observations over large spatial extents and at ecologically relevant time scales, improving the transferability of model projections and at least partially solving data sparsity with respect to spatial and temporal resolution.

Some remote sensing data products are already used in SDMs (see Franklin, 1995 for an early review), mostly as abiotic and biotic predictor variables and occasionally as response variables (see He et al., 2015 for a comprehensive review). However, remote sensing and species distribution modeling are still quite distinct fields that have not typically overlapped extensively, resulting in a lack of awareness of potential opportunities. Accordingly, we argue that remote sensing-derived data products are not yet used to their full potential and that they can contribute more to the development of SDMs for biodiversity monitoring and policy.

Here, we² first discuss how current developments in remote sensing may improve our understanding and projections of species distributions (see section 2: Modeling species distribution using remote sensing data: state-of-the-art). This discussion is based on a selection of processes and a prioritization of relevant literature, which by no means aims to be exhaustive. We then suggest synergistic activities between the ecological modeling and remote sensing communities (see section 3: Modeling species distribution using remote sensing data: closing gaps and moving forward). These activities may serve to fill data and conceptual gaps and develop remote sensing data products that can effectively contribute to the monitoring and modeling of ecological systems and ultimately guide and inform conservation and management strategies towards sustainability. Unlike previous contributions (e.g. He et al., 2015), this paper is organized around some of the key biophysical dimensions and processes (Mackey and Lindenmayer, 2001; Pearson and Dawson, 2003) underlying the distribution of species in the

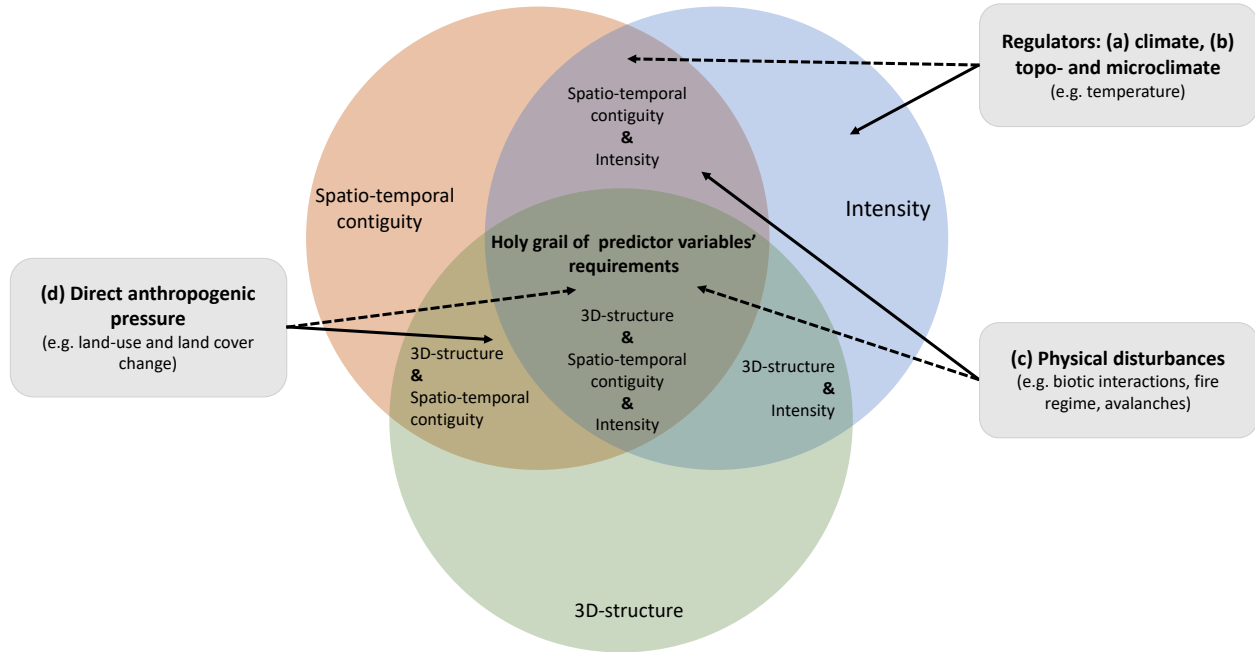
² This publication is the result of a workshop supported by the European Space Agency and Future Earth that brought together participants from the ecological modelling, biodiversity, land systems science, and remote sensing communities

Anthropocene, such as climate variability and land-cover change. As such, it is aimed at species distribution modelers and remote sensing specialists who jointly want to better support monitoring and conservation actions at different spatial and temporal scales.

2. Modeling species distribution using remote sensing data: state-of-the-art

Key processes and biophysical factors that underlie the distribution of species in the Anthropocene and are required for modeling include: climate and its variability from the global to the regional scale (Fig. 1(a), see paragraph 2 “Climate and its variability”), topo- and microclimate from the regional to the local scale (Fig. 1(b), see paragraph 3 “Topography”), physical disturbance processes modulating distribution at various scales (Fig. 1(c), see paragraph “Physical disturbances”), and anthropogenic pressures (Fig. 1(d)), such as changes in land cover and land use. Additional factors that are not explicitly discussed but merely mentioned throughout the text include resource variables (e.g., water, food resources, and nutrient availability, Austin and Van Niel, 2011). Climate and topography are often used as proxies for these types of variables. Ideally, the predictor variables in SDMs meet at least two of three requirements (holy grail, Fig. 1): spatiotemporal contiguity (i.e., full coverage of a process in space and time), intensity (i.e., the full range of variation of a continuous variable is covered, including the extremes likely to impact on an organism’s traits and ultimately on its demography), and 3D-structure.

221



222

223 **Fig. 1.** Main categories of predictor variables in SDMs and requirements they meet. Variables
 224 consist of regulators (a, b), physical disturbances (c), and direct anthropogenic pressures (d)
 225 (*sensu* Austin and Smith, 1989; Guisan and Zimmermann, 2000; Randin et al., 2009c).
 226 Requirements are contiguity, intensity, and 3D structure. Categories of predictor variables point
 227 with continuous lines to requirements they can currently meet and with dotted lines to
 228 requirements they could meet with the integration of remote sensing data.

229

230 *Climate and its variability*

231 Climate has been consistently identified as the main determinant of species ranges at the broad
 232 scale (Woodward, 1990), whereas non-climate predictors (such as topography and habitat) are
 233 more important at finer scales (e.g. Luoto et al., 2007; Normand et al., 2009). It is therefore
 234 common to build large-scale and coarse-resolution SDMs to characterize species geographic
 235 extents and spatial patterns of occurrence using only climate predictors (see e.g. Mod et al., 2016
 236 for plants; Thuiller et al., 2005). This approach is commonly referred to as bioclimatic envelope

237 modeling and climate predictor variables are defined as direct or regulator predictors (Fig. 1(a):
238 Austin and Smith, 1989; Guisan and Zimmermann, 2000), because the spatial resolution at which
239 models operate may be much greater than the processes experienced by species (Austin, 2002).
240 These variables are also routinely used without accounting for their measurement errors and
241 uncertainty, which can lead to biased estimates and erroneous inferences (Stoklosa et al., 2015).
242 In addition, temperature and precipitation interpolations from weather stations (e.g. Worldclim)
243 capture neither temperature-related processes, such as inversion, air stagnation (Vitasse et al.,
244 2017) or cold air pooling (e.g. Patsiou et al., 2017), nor precipitation-related processes, such as
245 orographic effects (Fernandez et al. 2015; but see CHELSA Karger et al., 2017). However, some
246 of these physical patterns can be captured by remote sensing products such as from the
247 Operational land Imager (OLI) on Landsat8 and the Moderate Resolution Imaging
248 Spectroradiometer (MODIS) on TERRA and AQUA for surface temperature or Tropical Rainfall
249 Measuring Mission (TRMM) and Global Precipitation Mission (GPM) for precipitation (e.g. at the
250 scale of the Andes; Bookhagen and Strecker, 2008). These products have been successfully
251 integrated in SDM studies (Cord et al., 2010; Estrada-Peña et al., 2016; Neteler et al., 2013).
252 Alongside the development of improved remote sensing data products, considerable advances
253 have also been achieved in terms of the algorithms needed to process remote sensing data. For
254 instance, algorithms for deriving land surface temperature are now sufficiently advanced that a
255 typical accuracy of 1 Kelvin is possible with data acquired at around 100 m resolution from recent
256 Landsat satellites. Such high spatial resolution surface temperature data can ultimately be used
257 to detect local features such as urban heat islands (Liu et al., 2011), which are key components
258 for the persistence or extinction of plants and animals. However, pros and cons of surface
259 temperature should be carefully listed before its integration into SDMs. On one hand, SDMs
260 mostly relate the occurrence or the abundance of species to data from standardized shaded 2-m
261 air temperature sensors, although interpolated between weather stations that can be sparse and

located in specific locations (e.g. low altitudes Hik and Williamson 2019). On the other hand, temperature derived from remote sensing might integrate, depending on the spatial resolution and the post-processing considered, a mix of surfaces such as rock, tree canopy or grassland. Although land surface temperature derived from remotely sensed datasets can substantially improve projections of SDMs (Deblauwe et al., 2016), precipitation data derived from sensors still rely on the ground projected spatial resolution of the data and the addition of ground observations (e.g. TRMM at a 0.05° native resolution versus CHIRPS at a 0.25° resolution and calibrated with 45'707 weather stations worldwide). In addition, precipitation is measured precisely but locally with water gauges, whereas currently available satellite sensors detect rainfall patterns at resolutions > 1 km. As a consequence, both satellite sensors and interpolations from direct measurements are not able to adequately capture small-scale processes (e.g. orographic processes) that influence species distribution (Deblauwe et al., 2016; Lenoir et al., 2017) (Deblauwe et al., 2016). Additionally, rainfall is usually an indirect predictor, whereas variables reflecting soil water budget or snow cover and depth are more direct predictors. Climate also enters SDM-based studies in the form of long-term averaged variables used to define range limits. However, such averages overlook information contained in the distribution of climate values, including climate extremes of increasing frequencies, whose influence on range limits remains to be fully understood (Ummenhofer and Meehl, 2017). Accordingly, Kollas and colleagues (2014) called for the use of temperature extremes during key phenological stages of focal species when attempting to explain range limits. Zimmermann and co-authors (2009) showed that the primary effect of including information on climate variability and extremes is to correct local SDMs for over- and underprediction. Such results speak in favor of the incorporation of targeted absolute climate values instead of long-term means that are only proxies of unknown relevance for the physiologically critical facets of climate that control species abundances and distributions. They also have important implications for projections of climate-change impacts on

species distributions that are based on correlative approaches only. Relevant data for deriving extremes are spectral time series. With such series approaching 20 years of records and daily time steps, it is now becoming possible, for example, to use land surface temperature from remote sensing to derive extreme climatic events. The Global Climate Observing System (GCOS) was specifically set up under the auspices of United Nations organizations and the International Council for Science to ensure the availability of so-called Essential Climate Variables (ECV, GCOS 2010), which are systematic and long-term observations of climate. An Essential Climate Variable is a physical, chemical, or biological variable or a group of linked variables that contributes to the characterization of the Earth's climate (Bojinski et al., 2014). Specific Essential Climate Variables of interests for the SDM community include land surface temperature, precipitation, snow, glaciers, permafrost, albedo, land cover, fraction of absorbed photosynthetically active radiation (FAPAR), Leaf area index (LAI), above-ground biomass, soil carbon, fire, and soil moisture. For the latter, a global ECV surface soil moisture data set has been generated within the European Space Agency (ESA) Climate Change Initiative. This soil moisture dataset covers a 38-year period from 1978 to 2016 at a daily time step and at a 0.25° spatial resolution. Snow, high-resolution land cover, surface temperature and permafrost are other ECVs currently developed by ESA (<http://cci.esa.int/>). Similar initiatives have also been developed at smaller scales. The Sentinel Alpine Observatory of Eurac Research (<http://sao.eurac.edu/sao/>) and satellite-based snow cover climatology (Hüsler et al., 2014) are two examples for the European Alps. Yet, although the temporal resolution might be appealing for the SDM community, typical spatial resolutions of 0.25° (at best 500 m) do not match the requirements for safe calibration and projections of SDMs for many organisms, calling for further data integration (Lembrechts et al., 2019).

Topography

When SDMs are calibrated only with climate data at a low spatial resolution (e.g. Worldclim; ~1-km grid cells), their fit and predictive power are often improved by incorporating additional predictors (Luoto and Heikkinen, 2008; Pradervand et al., 2014), or by enhancing them to consider finer-scale processes (e.g. topoclimate Daly, 2006; Karger et al., 2017). One important predictor is the topography, which locally controls biota, habitat structure, and growing conditions (albeit mostly indirectly, Austin and Van Niel, 2011). It does so primarily by affecting local climate (<1 km²) through elevation (adiabatic lapse rate), exposure (to solar radiation and wind), and cold air pooling (Böhner and Antonić, 2009), but also through its effect on soil development, causing spatial variability in soil depth and nutrient as well as water availability (Fisk et al., 1998). Topography-related indirect variables (*sensu* Guisan and Zimmermann, 2000), such as slope or topographic position, or more direct variables such as potential solar radiation are broadly used in SDMs and evolutionary ecology (Kozak et al., 2008; Leempoel et al., 2015). The topographic wetness index is also a commonly used proxy for soil moisture (see e.g. le Roux et al., 2013a). Including these variables improves SDMs, but interpreting the actual drivers of species distributions related to these variables can be difficult. Topographic data are indeed only surrogates for direct environmental controls of occurrence and abundance and the effects of topographic variables on plant distributions are therefore distal (*sensu* Austin, 2002, 2007; Mod et al., 2016; Moeslund et al., 2013). Improvements are also scale-dependent as topographic variables that make sense over a small geographic area can become problematic at broader scales if they are not linearly related to the environmental factors for which they serve as proxies. Regardless of scale, the problem with using indirect (i.e. distal) predictors of topography is that the identified relationships are inherently non-causal, which therefore reduces model transferability in space and time. This limitation also applies for other predictor variables based on climate or land cover, notably when SDMs are calibrated for species situated at high trophic levels.

One solution to this problem is to utilize more direct and causal predictors or resource variables (Austin, 2002; *sensu* Guisan and Zimmermann, 2000). For example, SDMs can be calibrated with nutrient status (Bertrand et al., 2012; Buri et al., 2017; Coudun et al., 2006; Dubuis et al., 2013; Vries et al., 2010), as well as fine resolution climate predictors based on topography and remote sensing-derived estimates of vegetation cover (Ashcroft and Gollan, 2011; Lenoir et al., 2017). Digital elevation models, in turn, can be used to directly estimate cold-air drainage, which can lead to improved predictions of species distributions over indirect estimates of topography (Ashcroft et al., 2014; Patsiou et al., 2017). Remote sensing offers another solution. Relevant accurate high-resolution terrain data (Jaboyedoff et al., 2012; Leempoel et al., 2015) are increasingly obtained using Light Detection and Ranging (LiDAR) technology (e.g. Mathys et al., 2004; Sørensen and Seibert, 2007; Vierling et al., 2008). The benefits of LiDAR are specifically related to its capacity to detect minor terrain features, such as hill tops, ridges, small depressions, and minor hydrological features (Engstrom et al., 2005; Kammer et al., 2013; Kemppinen et al., 2018), which are expected to play an important role in determining species distribution (Graf et al., 2009; Pradervand et al., 2014). Moreover, high point return densities (1–10 points/m) and relative ease of data collection across large areas makes LiDAR a popular option for measuring bare earth elevation and vegetation height (Hancock et al., 2017). However, the accuracy of LiDAR-derived digital elevation models can vary considerably across topographic and land-cover gradients (Leitold et al., 2015). For instance, it is common to achieve high elevation accuracies (<0.15 m root mean square error) in areas with low vegetation cover and relatively flat terrain, (Montané and Torres, 2006; Spaete et al., 2011), but elevation errors in digital elevation models tend to increase in areas covered by dense vegetation. Further work is required to determine how these errors in elevation are propagated to the direct predictors that are desirable in SDMs (cold air drainage, vegetation structure, exposure to winds and radiation, microclimate), and to the SDM itself.

Unlike high-resolution topographic information, the availability of spatial layers of soil conditions is still limited (Fang et al., 2016). Yet spaceborne multispectral and imaging spectroscopy instruments have a high potential for mapping topsoil carbon (Peón et al., 2017) and organic matter content as well as soil physical properties (Rosero-Vlasova et al., 2018). These novel possibilities should be tested in SDMs in the future.

Physical disturbances

Physical disturbances include geomorphological disturbances such as fluvial erosion, nivation, landslides, rock falls and other disturbances such as mechanical abrasion by wind or fire. Geomorphological processes in particular, create a wide range of disturbance regimes across landscapes (Aalto et al., 2017; Gooseff et al., 2003; Niittynen and Luoto, 2018) that may significantly alter local soil stability, moisture conditions, and nutrient availability (Kozłowska and Rączkowska, 2002). Due to ongoing land-use and climate change, these disturbance regimes are predicted to change rapidly as many geomorphical processes have a significant climate response (Knight and Harrison, 2013), with small changes in climate forcing triggering large changes in Earth system processes (Aalto et al., 2017). Accordingly, Earth system processes potentially represent key drivers of local habitat heterogeneity (Cannone et al., 2016), variation in ecosystem functioning (Frost et al., 2013), and species assemblages (le Roux et al., 2013b; Malanson et al., 2012).

Recent studies demonstrate that the incorporation of direct Earth system processes variables – as opposed to the indirect topographic and soil surface properties used as surrogates in plant SDMs (Dirnböck et al., 2003; Mellert et al., 2011) – can improve the explanatory and predictive power of SDMs (le Roux et al., 2013b; le Roux and Luoto, 2014; Niittynen and Luoto, 2018; Randin et al. 2009a). However, the type and necessity of including disturbance variables in models are highly environment-specific. For decades, remote sensing data have been used for

the mapping of geomorphological landforms and processes (Walsh et al., 1998). The high spatial resolution of airborne photographs provides a valuable data source in that context, particularly for detecting smaller landforms (e.g. 1-10 m). Yet, the precision (< 10 m) and increasing temporal resolution (revisit time of 1-5 days) of satellite data, such as WorldView 3 (<http://worldview3.digitalglobe.com>), the PlanetScope satellite constellation (<https://www.planet.com>), or open access ESA Sentinel-2 (<https://sentinel.esa.int>), can now compete with that of aerial photography. High-resolution satellite imagery is thereby becoming a valuable data source for the modeling of dynamic processes. Attempts to include remote sensing-based geomorphological and other non-anthropogenic physical disturbances into SDMs include Miller and Franklin (2002) with landforms derived from a DEM, and Connell et al. (2017) as well as Madani et al. (2016) for fire.

Direct anthropogenic pressure

The availability of spatially and temporally highly resolved land-cover information is central to many monitoring programs and land-cover mapping is probably one of the oldest application of remote sensing, starting with aerial photographs from hot air balloon in the 1860's and from airplane in the 1910's (Fuller et al., 1994). Assessments of changes in land systems range from local to regional and global (Stürck and Verburg, 2017; van Asselen and Verburg, 2013) and from historical (Bolliger et al., 2017; Kaim et al., 2016; Loran et al., 2017) to predictive, with scenario-based assessments of potential future changes in land use (Martinuzzi et al., 2015; Pazúr and Bolliger, 2017; Price et al., 2015).

Changes in land cover and land use affect biodiversity in different ways. In the case of urbanization, there is usually a complete replacement of (semi-)natural open land with buildings or other impervious infrastructures such as roads, which profoundly changes species distributions (Lembrechts et al., 2017). However, impacts on species distributions or abundances can also be

triggered by other forms of land-use and land management such as slash and burn cultivation or deforestation, or by modification of their intensity (e.g., agricultural practice, Randin et al., 2009b). Both the detection of changes in land cover and the differentiation between changes in land cover and land use are difficult. Yet progress has been made over recent years using change patterns in remotely sensed data as indicators of change in management and land-use intensity (Eckert et al., 2017; Franke et al., 2012; Gómez Giménez et al., 2017; Jakimow et al., 2018; Rufin et al., 2015). Examples include the mapping of grassland mowing frequencies through the identification of typical variations in greenness during the growing season (Kolecka et al., 2018), observed agricultural intensification in Kenya through the successful long-term monitoring of rainfed and irrigated agriculture using monthly satellite data composites (Eckert et al., 2017), or the occurrence of plantation forests in the southeastern United States based on high resolution spatial patterns (Fagan et al., 2018).

Until recently, small or heterogeneous areas important to landscape structure and land-use management were not detected due to low spatial, spectral, and temporal resolution. These limitations are partially addressed with spatially, spectrally, and temporally highly resolved instruments such as on the Sentinel-2 constellation (ESA, 2018). Every five days, these sensors provide global coverage of the land surface at a spatial resolution of 10, 20, and 60 m (depending on spectral band setting and product definition).

However, in spite of the novel developments and achievements of remote sensing, limitations will persist in observing land management practices relevant to biodiversity. Proper characterization of land-cover and land-use change faces the difficulty of the 'curse of dimensionality'. By improving any of the spatial, spectral or temporal resolutions of an Earth observation instrument, exponential increase of the other two remaining dimensions is needed to properly describe the dimensionality of the signal per se. Currently, data integration, fusion or multi-modality seems to hold most promise. Examples of such approaches are provided by Van Asselen and Verburg (2013), Price et al. (2015), See et al. (2015), and Estel et al. (2018).

Land cover and land use have traditionally relied on two-dimensional (2D) representations of the environment. Yet, 3D vegetation structure not only allows for more continuous landscape representations but is also a crucial determinant of species habitat (Fawcett et al., 2018; Gastón et al., 2017; Huber et al., 2016; Milanesi et al., 2017; Torabzadeh et al., 2014; Zellweger et al., 2016) and functional connectivity (Marrotte et al., 2017; Milanesi et al., 2017). Such evidence stresses the need for more detailed landscape-content information, and for 3D structure information to supplement habitat assessments. These structures are captured using digital aerial photogrammetry (Ginzler and Hobi, 2015) or active remote sensors, e.g., LiDAR (Bergen et al., 2009; Merrick and Koprowski, 2017). 3D structure represented as morphological traits are increasingly combined with physiological traits allowing to model and predict substantial detail on functional diversity (Asner et al., 2017; Schneider et al., 2017) as well as light interaction within the 3D canopy (Schneider et al., 2019).

Moving from simple land-cover representations to more species-relevant representations of land use requires advances in remote sensing and integration with other data (Wulder et al., 2018). Yet, following Franklin et al. (2014) and others (Boulangeat et al., 2014; Martin et al., 2013; Newbold, 2018), adaptations are also needed for SDMs to properly account for such novel landscape representations and address not only climate change (Titeux et al., 2016) but also land-use change. Increasing the detail in landscape characterization not only requires SDMs to be capable of addressing the represented diversity, but it also requires understanding of the temporal dynamics and climate responses of land use at a higher level of detail. To avoid overwhelming and, sometimes unnecessary, complexity, the sensitivity of the SDMs to the refined detail should be continuously tested and simplifications made as part of the modeling process.

Besides land-use composition, land-use configuration can in some cases represent a good proxy for those species requiring corridors and landscape borders to survive (e.g., Neilan et al., 2019; Vinter et al., 2016). Accordingly, the heterogeneity of land use or of satellite reflectance data has been widely assessed in the past, using various algorithms and metrics such as multivariate

statistical analysis (Feilhauer and Schmidtlein, 2009), the spectral species concept (Féret and Asner, 2014), self-organizing feature maps (Foody, 1999), multidimensional distance metrics (Rocchini et al., 2016), and Rao's Q diversity (Rocchini et al., 2017). Each of them addresses one or several issues related to heterogeneity measurements. These can then be incorporated as metrics of land-cover heterogeneity and land-cover change into SDMs to drive future predictions, such as in Coops et al. (2016).

3. Modeling species distribution using remote sensing data: closing gaps and moving forward

We are coming to an era of cost-efficient mass processing of high-resolution remote sensing data products over extensive geographical areas and long periods of time (Hansen et al., 2013). This coincides with the increasing demand for reliable, spatially comprehensive and time-sensitive information on the status of and trends in biodiversity (Navarro et al., 2017) and the urgent need to achieve significant progress towards sustainability. Remote sensing data are increasingly recommended for and applied to biodiversity monitoring and conservation (e.g. see Alleaume et al., 2018; Lausch et al., 2016; Rocchini et al., 2016; Schneider et al., 2017; Schulte to Bühne and Pettorelli, 2018; Vihervaara et al., 2017). In this context, such data are used notably in the monitoring of EBVs (e.g., see Alleaume et al., 2018; Fernandez et al., 2019; Pettorelli et al., 2016) and the adoption of systematic observation requirements is steadily improving (Navarro et al., 2017; Pettorelli et al., 2016; Skidmore et al., 2015). However, the use of remote sensing data in the reporting on individual sustainable development goal indicators is not systematic. For instance, whereas the methodologies to assess progress on “forest area as a proportion of total land” (SDG 15.1.1), “sustainable forest management” (SDG 15.2.1), “proportion of land that is degraded over total land area” (SDG 15.3.1), or “mountain green cover index” (SDG 15.4.2) are largely or fully based on remote sensing data, this is not the case for reporting on the “coverage by protected areas of important sites for mountain biodiversity” (SDG 15.4.1). Here we discuss

joint ventures between the ecological modeling and remote sensing communities that could ultimately contribute to improving as well as accelerating the modeling and prediction of species' distributions across large spatial scales and the delivery of reliable information for reporting on progress towards specific sustainable developments goals such as SDG 15.4.1. The joint ventures we propose pertain to time series and temporal stacking (see paragraph 2 below, Fig. 2), the direct detection and sampling of species and their traits (see paragraph 3), the improvement of integrated and dynamic range models (see paragraph 4, Fig. 3), and the prediction of belowground processes, disease and biotic interactions (see paragraph 5).

Time series and temporal stacking

Most SDM studies that have included remote sensing data products so far have used static and temporally aggregated remote sensing-derived layers as predictors (e.g. land surface temperature, water availability, topography, land cover and 3D structure, section 2). Fewer attempts have been made to take advantage of the existing time series data and the dynamic information contained in remote sensing data products (Fernández et al., 2016; Pinto-Ledezma and Cavender-Bares, 2020), despite the pivotal role that such temporally explicit data play. For instance, long-term time series of remote sensing data are key to test the temporal transferability of SDMs (Yates et al., 2018), a basic requirement to formally guide and inform monitoring strategies in changing environments and make sure that model projections follow the observed trajectories of species. Likewise, long-term observations of response variables, such as occurrences or abundances of focal organisms, are essential to understand and project the impact of global change with SDMs. Andrew and Ustin (2009), Bradley and Mustard (2006), or Malavasi et al. (2019) provide examples of the integration of occurrence data derived from remote sensing into SDMs. The availability of long time series from satellites or cost-effective tools such as Unmanned Aerial Vehicles (UAVs, e.g. Kellenberger et al., 2018) will undoubtedly lead to a rapid increase in such applications. Finally, long-term time series are also critical for estimating

lag times. The Anthropocene is an era of rapid environmental changes. Under such conditions, lag times in cause-effect chains may severely confound the identification of species-environment relations via correlated distribution patterns. Rapid climate change, for example, is expected to cause a severe disequilibrium between climate and species distribution due to both slow colonization of areas that become newly suitable and delayed extinction from those sites that are no longer suitable to the species (i.e., extinction debts; Dullinger et al., 2012; Svenning and Sandel, 2013; Talluto et al., 2017). Land-use changes may have similar effects and many studies have demonstrated that in landscapes undergoing changes in human usage, spatial biodiversity patterns often represent habitat configurations of decades back rather than current ones (Auffret et al., 2018; Krauss et al., 2010). Matching current species distributions and environmental conditions in statistical models will hence result in flawed correlation and, as a corollary, inappropriate prediction of future development. Remote sensing data products offer a way forward here, because time series of many of these products now cover two decades, and several of them up to five (He et al., 2015). These time series have great potential in detecting and quantifying lag times, e.g. in the response of biological populations to land-cover conversions (Wearn et al., 2012). Incorporating these lag times into models of species responses to past, current, and future environmental change has important ramifications for the management of biodiversity because it defines ‘windows of opportunity’ for mitigating the anticipated consequences (Kuussaari et al., 2009; Wiens et al., 2015).

One reason for the limited transferability of purely correlative models is the generally coarse or inadequate spatial and temporal resolution of the data used to calibrate models (Connor et al., 2018; Manzoor et al., 2018; Potter et al., 2013). This spatial-resolution paradox (Lenoir et al., 2017) is inherent to correlative models and stems from the spatial mismatch between the resolution at which the predictor variables (e.g. biophysical variables, see section 2) are available, the resolution that matches the response variables (e.g., species occurrence, presence-absence,

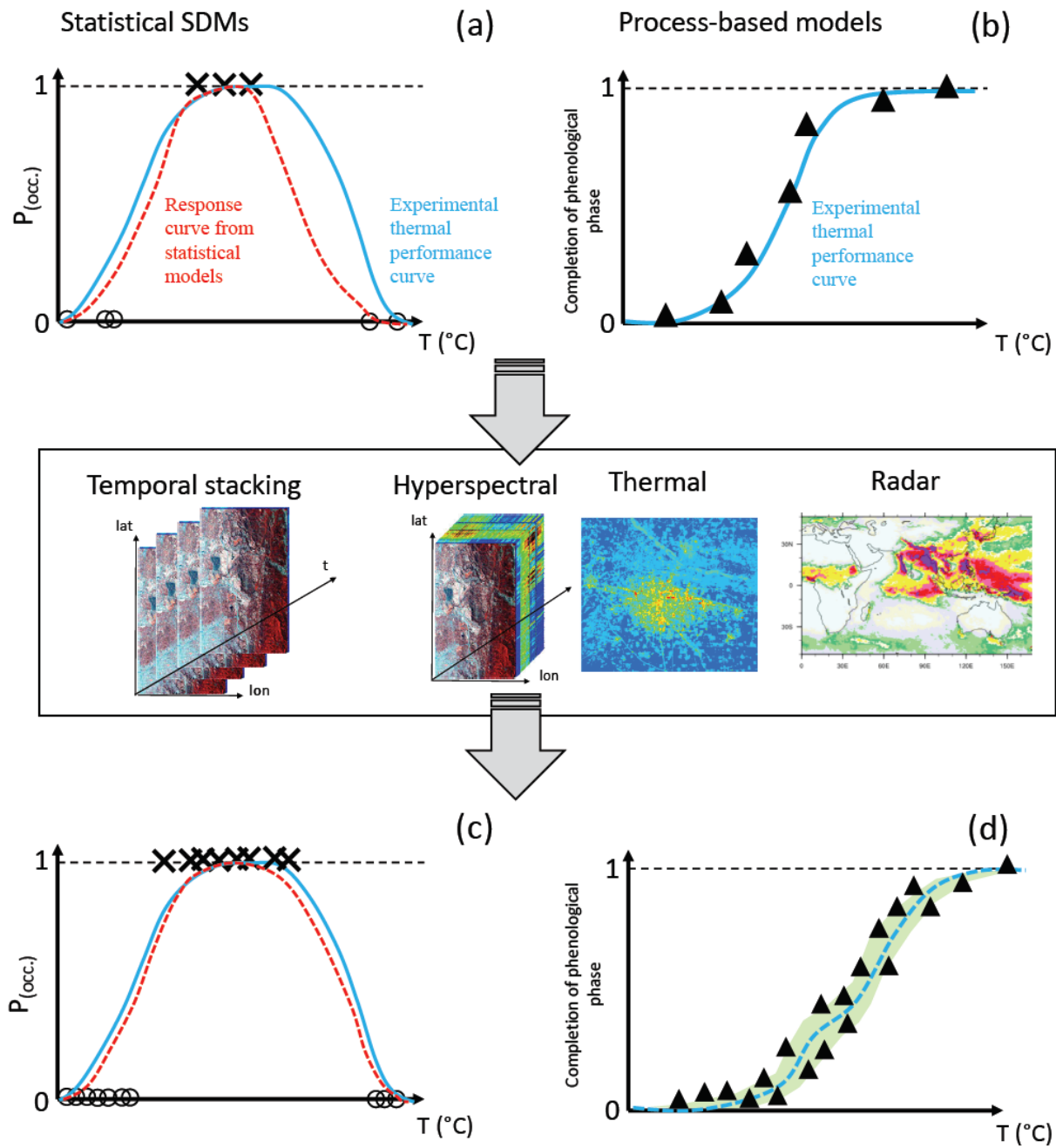
abundance or trait data; Guisan and Thuiller, 2005), and the size of the studied organism (Potter et al., 2013).

Here, we argue that remote sensing could be used to better calibrate SDMs, by integrating spatially and temporally (through multiple years) more proximal environmental data to derive more comprehensive quantifications of species' response curves along environmental gradients (see Austin and Gaywood, 1994). An improved calibration process may in turn increase the spatial and temporal transferability of both correlative and process-based models. This can be illustrated by focusing on environmentally-specific species response curves, such as temperature response curves (*sensu* Austin, 2002; Fig. 2(a)) and thermal performance curves (*sensu* Schulte et al., 2011; Fig. 2(a)-(b)) are at the foundation of both correlative (Guisan and Zimmermann, 2000) and certain types of process-based (Kearney and Porter, 2009) models, respectively. Temperature response curves generated by SDMs are usually parameterized through the statistical relationship between field observations and spatial layers of temperature. Temperature performance curves used in process-based models on the other hand are best parameterized from experimental data depicting metabolic requirements, usually in the absence of competition (e.g., Chuine and Beaubien, 2001). Because they explicitly rely on a physiological basis, temperature performance curves are expected to better identify species thermal tolerance limits that set range boundaries and to be thus more robust when extrapolating species redistributions under future climate change (Eckert et al., 2017). However, physiologically-based species performance curves represent the fundamental rather than post-interactive realized niches of species (Hutchinson, 1978; Pulliam, 2000). Such performance curves are not as time- and cost-efficient as statistically-based species response curves. For some species, the quantifications of statistically-based performance curves by the integration of remote sensing data (Fig. 2(c)) might better inform on the real microhabitat conditions experienced by living organisms, and thus might help to capture species' response curves that are closer to the fundamental responses (response

niche; Maiorano et al., 2013 ; e.g. for dominant late-successional species; Pearman et al., 2008) obtained from experiments. Hence, the integration of remote sensing data into SDMs has the potential to generate more transferable SDMs (Maiorano et al., 2013). Similarly, the combination of experimental and remote sensing data (i.e. the combination of fundamental and realized niches) through e.g. the direct use of land surface temperature to derive thermal performance curves could better capture the geographic variability caused by local adaptations (Fig. 2(d)).

Temporal stacking of remote sensing images (e.g. spectroscopy, thermal or radar images; Fig. 2) allows more observations of both response and predictor variables to be obtained and can be used to reduce the temporal mismatch between these variables (e.g. George et al., 2015). This in turn allows the generation of more comprehensive representations of the realized response curves. Images from imaging spectroscopy in particular can be used to gather a large amount of occurrence, abundance, and trait data (Lausch et al., 2019; e.g. van Ewijk et al., 2014). Conversely, remote sensing data can also be used to develop more accurate estimates of elevation, microclimate and other direct environmental predictors (see section 2, paragraph 3 “Topography”), which will improve estimates based on coarse-scale climate grids or indirect predictors alone.

Similarly, process-based distribution models such as Phenofit that integrate phenology and frost resistance for instance (Chaine and Beaubien, 2001) also strongly rely on experimental response curves (Fig. 2(b)). As a consequence, responses such as the completion of a phenological phase as a function of temperature are usually limited to a restricted set of plant species for which data are available. When remote sensing data cover large geographic extents, the same combination of temporally-stacked remote sensing images could potentially help extend such models to more species and take into account the variability due to local adaptation.



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591 **Fig. 2.** Temporal stacking of imaging spectroscopy, thermal or radar images for improving
 592 response curves of statistical (a and c) and process-based (b and d) models. Thermal response
 593 curves derived from statistical models (a) describe the realized thermal niche of species whereas
 594 experimental thermal performance curves are closer to the thermal fundamental niche, thus

potentially increasing the transferability of such relationship in space and time. The response curve from statistical models in (a) is calibrated with presence (black crosses) and absence (black circles). Thermal performance curve of a phenological phase in (b) derived from phenological observations (black triangle). Time series of remote sensing images potentially allows to increase the number of observations for both calibrating thermal response curves of statistical SDMs (c) and thermal performance curves used in process-based models (d). In (c), presences and absences are extracted from remote sensing data, thus allowing to derive a high number of observations and to calibrate a response curve closer to the thermal performance curve. Similarly, in (d), phenological observations are derived from remote sensing data, allowing to estimate the spatiotemporal variability of the performance curve caused by e.g. local adaptation (green surface on d). It is also important to note that the spatiotemporal accuracy of species' occurrence, presence-absence or abundance data collected from field observations need to be at least as high as the spatiotemporal resolution of the predictors used to fit the model to ensure robust model transferability (Manzoor et al., 2018). Optimizing environmental and biological monitoring for better data availability is hence key for the usefulness of remote sensing in SDMs (Bush et al., 2017). A promising development is the European research infrastructure for Long-Term Ecological Research (<http://www.lter-europe.net/elter-esfri>), which is being rolled out during the coming years to provide the combined *in situ* data needed for future SDM improvements (Haase et al., 2018; Mirtl et al., 2018).

Direct detection and sampling of species and their traits

The direct detection of species using full-range (400-2500 nm) spectroscopic data (Féret and Asner, 2014) is becoming increasingly accurate, notably for trees but also for smaller organisms such as bryophytes (Skowronek et al., 2017). However, the spatial resolution of data collection remains critical and successful detection will likely remain limited to certain lifeforms and groups

of species in the near future. Beyond the detection of species, new possibilities are also emerging for capturing plant functional types using spectroscopy (Ustin and Gamon, 2010). Accurately mapping of some functional traits such as canopy traits (Asner and Martin, 2009; Singh et al., 2015) and changes in other plant traits (Jetz et al., 2016; Schneider et al., 2017) is now also possible. Direct species detection and the link of spectra to the tree of life (Cavender-Bares et al., 2017) can equally be achieved by using a combination of high spatial and high spectral resolution. Spectra from leaves (Cavender-Bares et al., 2016; Deacon et al., 2017) can be used with high accuracy to differentiate populations within a species and to separate hybrids from parental species. Partial Least Squares Regression methods applied to spectral profiles differentiate species with higher accuracy than genotypes and clades with higher accuracy than species (Cavender-Bares et al., 2016). In some cases, with 1 m² spatial resolution remote sensing allows differentiation of different genotypes of poplar clones (Madritch et al., 2014). Tree canopies are likely to be well distinguished if functional information on morphology and physiology at species level are available (Torabzadeh et al., 2019). In recent years, the use of remote sensing has enabled great advances in both functional as well as scaling-based approaches (Gamon et al., 2019; Malenovský et al., 2019). In forests where species groups are well characterized and occur in clumps, species distributions can be fairly readily mapped using satellite derived data (Chastain and Townsend, 2007). Many living resources exist that contain geolocated and botanically identified trees for developing spectral libraries for tree canopies.

UAVs or drones are mainly used to capture data with limited spectral resolution, to acquire thermal data, or to produce very high-resolution digital elevation models by means of stereophotogrammetry (Coops et al., 2019). UAVs can notably serve to overcome the issue of partially missing spectral resolution with high-density time series (Böhler et al., 2019). Multi-View Stereo analysis (Furukawa and Ponce, 2010) and Structure-from-Motion (Westoby et al., 2012) algorithms are increasingly used as they make it possible to estimate three-dimensional structures from partly overlapping image sequences. These approaches are very useful to analyze forest

and vegetation structures (Webster et al., 2018) and also to model marine environments including the complex structure of coral reefs (Ferrari et al., 2016), a domain of particular interest in the current period of intense coral bleaching (Walsworth et al., 2019).

Another function is the collection of animal occurrences to calibrate SDMs with presence only or presence/absence data. Van Gemert et al. (2015) evaluated how animal detection and animal counting could be implemented on the basis of a combination of images acquired by drones and state-of-the-art object recognition methods. Most of the time, such images are used to carry out surveys and to count animals in a management or conservation projects (Hodgson et al., 2018; Koh and Wich, 2012). However, as all UAVs are equipped with a GPS device, the exact location of investigated individuals can also be retrieved from precisely georeferenced image data. The main challenge is related to the detection and recognition of the correct species by means of machine learning algorithms (Kellenberger et al., 2018; Ofli et al., 2016; Rey et al., 2017). Beyond this step, the generation of presence/absence of a single taxon is straightforward. This is a component included in the concept of Next Generation Species Distribution Models proposed by He et al. (2015).

Improving integrated and dynamic range models

Demographic processes and demographic data are increasingly integrated into models of the spatiotemporal dynamics of species' ranges. This results from the realization that considering dynamic aspects is important and potentially markedly improves the quantification of ecological niches, the process-based understanding of range dynamics, and the forecasting of species responses to environmental change (Pagel and Schurr, 2012). This is because commonly-used static SDMs ignore spatial population dynamics, which can cause mismatches between species niches and species distributions (Holt, 2009; Pellissier et al., 2013). The data needed to parameterize dynamic range models can be obtained from demographic field measurements and small-scale experiments. However, small-scale environmental responses are not necessarily

transferable to the spatial and temporal scales of dynamic range models. In this context, time series of multi-spectral, imaging spectroscopy, and LiDAR data (Fig. 3(a)) can help to quantify changes in the environment of the focal and modeled species such as changes of suitable vegetation (Strecha et al., 2012; Fig. 3(b)) or 3D structures such as buildings or tree canopy height (e.g. Droz et al., 2019; Fig. 3(b)). Knowledge of suitable areas for, and population size of, animals in large wildlife reserves helps park rangers and managers in their efforts to protect endangered species (Guisan et al., 2013). However, correlative SDMs rely on the assumptions that species location data used for modeling are representative of a species' true distribution and that observed species distributions are in equilibrium with environmental factors that limit those distributions. To better support conservation practice, conservation biogeography should thus favor dynamic range models and metapopulation dynamics rather than correlative SDMs. However, the more detailed information needed for dynamic range models (e.g. manual animal censuses) is expensive and sometimes potentially dangerous to collect. Hence, UAVs with consumer level digital cameras are becoming a popular alternative tool to estimate populations of large mammals (Fig. 3(a); Kellenberger et al., 2018). Furthermore, such data allow the modeling of metapopulation dynamics (Fernández et al., 2016) and species migration in order to understand the ability of a species to occupy suitable habitat in new locations. At the same time, movements of species can be linked to landscape disturbance and succession also obtained by remote sensing and models of habitat suitability (Fig. 3(b); Franklin, 2010).

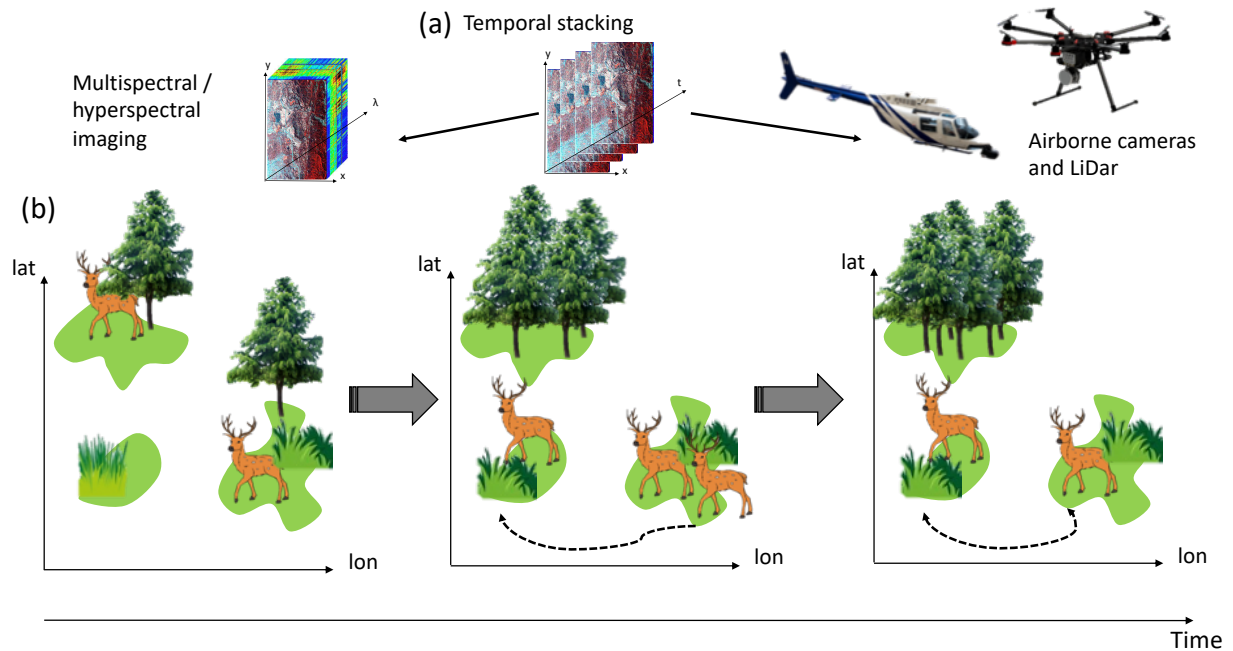


Fig. 3. Acquisition of demographic parameters for dynamic range models with time series of multispectral and / or imaging spectroscopy and airborne laser scanning data (a). The combination of such data allows to track movements of animals in suitable habitats.

Predicting belowground processes, disease and biotic interactions

Valuable information on belowground processes, disease, and biotic interactions can be obtained from imaging spectroscopy data. Carbon-based defense traits can be retrieved from spectral information (Couture et al., 2016), facilitating integration of information on host-specific herbivores and pathogens with leaf chemical composition. Variation in biomass and leaf chemistry, including condensed tannins, lignin, and nitrogen should be linked to the chemistry of below-ground root exudation and to litter chemistry and litter abundance (Cavender-Bares et al., 2017). These inputs from aboveground vegetation to soil influence substrates available as food for soil organisms, the activity of enzymes secreted by soil microorganisms, and thus decomposition and nutrient cycling (Madritch et al., 2014), which are all important for species distribution. An example of the use of imaging spectroscopy in the context of biotic interactions is that of the detection of declines in

hemlock (*Tsuga canadensis*) stands in the eastern United States due to invasion of the exotic woolly adelgid (*Adelges tsugae*) (Hanavan et al., 2015). Recent work has also shown that a combination of imaging spectroscopy and thermal data can be used to diagnose *Xylella fastidiosa* plants that are visually asymptomatic (Zarco-Tejada et al., 2018), and that airborne imaging spectroscopy can be used to track the spread of invasive submerged aquatic vegetation at high spatial resolution (Santos et al., 2016). These examples, and others from the early detection of moss species (Skowronek et al., 2017) and the assessment of ecosystem processes in forests (Ewald et al., 2018) illustrate the high potential of leveraging the rich information content of imaging spectroscopy data, for the description of biotic environments in SDMs.

4. Conclusions

In their review, He et al. (2015) discussed the importance of remote sensing data for the development of new predictor variables and the next generation of SDMs, which will include spatially explicit values of uncertainty. Here we argue that an additional value of remote sensing data lies in their temporal coverage (see section 3, paragraph and Fig. 2), which could overcome the inability of current temporally-aggregated variables to reflect the intensity or the frequency of biophysical processes and contribute to fulfilling all requirements across variables (Fig. 1). Taking advantage of long-term time series of remote sensing data to extract (absolute) extremes as well as frequencies and improve both these variables and the models in which they are used would be an avenue to explore through formal evaluation and model improvement (e.g. Zimmermann et al., 2009).

Temporal stacking of available time series (see section 3, paragraph and Fig. 2) can also be performed to better capture the realized niche of species, their actual rather than potential distributions, and increase the transferability of SDMs. In this context, evidence exists that building the niche as an ensemble through time allows a better understanding and forecasting of species' ranges under changing environmental conditions (Maiorano et al., 2013). To support this, airborne

or satellite sensors can deliver a large amount of observations pertaining to the response variable at a very high spatiotemporal resolution for both animal and plant organisms (e.g. drone multispectral images, LiDAR or high-resolution satellite data). Temporal stacking thus further allows tracking population dynamics and dispersal, which are both key variables to build hybrid and process-based models such as dynamic range models. Such observations can then be transformed from occurrences to abundance. Ultimately, gathering a large amount of data to build models should allow correlative SDMs to better estimate the true response curves along environmental gradients.

Over the last decade, several studies have questioned the ability of SDMs to predict the persistence of species when these models are projected into warming conditions. Indeed, some species may be able to escape the negative effects of climate warming by moving into or persisting in microrefugia with unusual and stable climates conditions (Ashcroft and Gollan, 2013), or by adapting to new conditions. In all these cases, remotely sensed data of high spatial resolution could be used in SDMs to better capture microclimatic conditions (e.g., soil humidity, surface and air temperature). However, important challenges remain in determining to which extent microclimate detected by remote sensing can be scaled and coupled to climate change projections from broader scale Earth system models. Indeed, models such as regional climate models provide values and anomalies of e.g. 2 m air temperature, precipitations and cloudiness and it remains to be tested whether relationships between microclimate detected by remote sensing and climate from e.g. regional climate models can be described statistically and later projected into a future climate. However, remote sensing products could be used to bias-correct Regional Climate Modes and Global Climate Models outputs (e.g. as done in Lange, 2019).

Land cover has been identified as one of the thirteen terrestrial ECVs because of its feedbacks on climate through the modification of water and energy exchanges with the atmosphere. Land use and land-use change, assessed from the local to the global scale, are typically more difficult to map and in many cases cannot be remotely sensed. As a consequence, spatially-explicit data

of land use are less available and land-use changes, variability, and intensity are often neglected in SDMs, despite their potentially critical importance for species distributions. Despite recent progress to develop indicators of changes in management and land-use intensity obtained from remote sensing, online access to spatially explicit data of land use can be improved.

This is particularly critical to identify the contribution of land use in SDMs applied as explanatory tools or to improve the accuracy of projections of SDMs integrated in monitoring programs.

In situ monitoring, modeling, and remote sensing

Although developments of remote sensing and SDM techniques have occasionally intersected over the last 30 years, combining these two fields better has great potential for future scientific progress. In line with Franklin and colleagues (Franklin et al., 2016) and others, we advocate a closer integration of remote sensing in the monitoring and modeling of species and ecosystems to better understand and predict current and future impacts of global change drivers on biodiversity (Fernandez et al., 2019). We stress that models should serve the same fundamental role in ecological monitoring as in any other scientific activity; that is, both the *a priori* guiding of monitoring designs, and the *a posteriori* guiding of data analyses. Essential elements of the monitoring design are management actions, replicated spatial climatic gradients, as well as temporal resolution and extents that capture both fast and slow processes. Ecosystem-based monitoring should be dynamic and adaptive in the sense that models and monitoring designs are iteratively improved by new empirical results, new technologies and the evolving needs of stakeholders (Ims and Yoccoz, 2017; Fig. 4). Once conceptual models (Fig. 4(a)) and appropriate monitoring designs (Fig. 4(b)) have been built, field data can be collected (Fig. 4(c)) for tracking the trajectories of individual species or the entire ecosystems. In this context, SDMs can serve as tools to identify the main drivers of changes or to project the fate of species or ecosystems (by e.g. stacked SDMs; Calabrese et al., 2014; Guisan and Rahbek, 2011; Fig. 4(d)). Finally, new field monitoring can later validate projections of SDMs and the robustness of conceptual models

(Fig. 4(e)). Here, remote sensing data can strongly contribute to adaptive monitoring programs by providing simultaneously additional data that complement field monitoring and observations for the validation of SDM projections in-between two field campaigns that are often expensive in terms of time and money.

A better integration of *in situ* and remote sensing observations through SDMs will also contribute to devise monitoring systems capable to provide consistent biodiversity data for addressing conservation targets in multi-scale policy contexts ranging from subnational to national and global. A major area of application is the production of data informing on EBVs for species populations, which typically require interpolation and extrapolation models with the view of obtaining continuous and temporally consistent probabilistic species occurrence data from sparsely-distributed observations. These model-derived data are critical for deriving consistent and scalable biodiversity change indicators that can accommodate the reporting needs of multiple management programs and policy targets (Jetz et al., 2019; Navarro et al., 2017).

The SDGs are one of the key global frameworks for addressing the environmental challenges of the Anthropocene. From a biodiversity perspective, to safeguard life below water (SDG 14) and life on land (SDG 15) it is crucial to characterize and understand current species distributions and how these may change under future land use and climate scenarios. SDMs make an essential contribution to providing this information but have several important limitations that can compromise their accuracy and hence the effectiveness of resulting conservation interventions and environmental policy. We suggest that, together with novel methodological applications such as the temporal image stacking, currently available and upcoming remote sensing data can alleviate or resolve many of the data gaps that constrain SDMs. However, there is the risk that non-specialists may unintentionally misinterpret remote sensing data, and that key data requirements for SDMs are not fully appreciated. We argue that greater collaboration between the two communities by developing jointly data platforms with standardized metadata and documentation will be a key step in achieving the full potential of remote sensing data and

products for SDMs, thereby supporting more effective conservation monitoring, management, and policy decisions for a sustainable future.

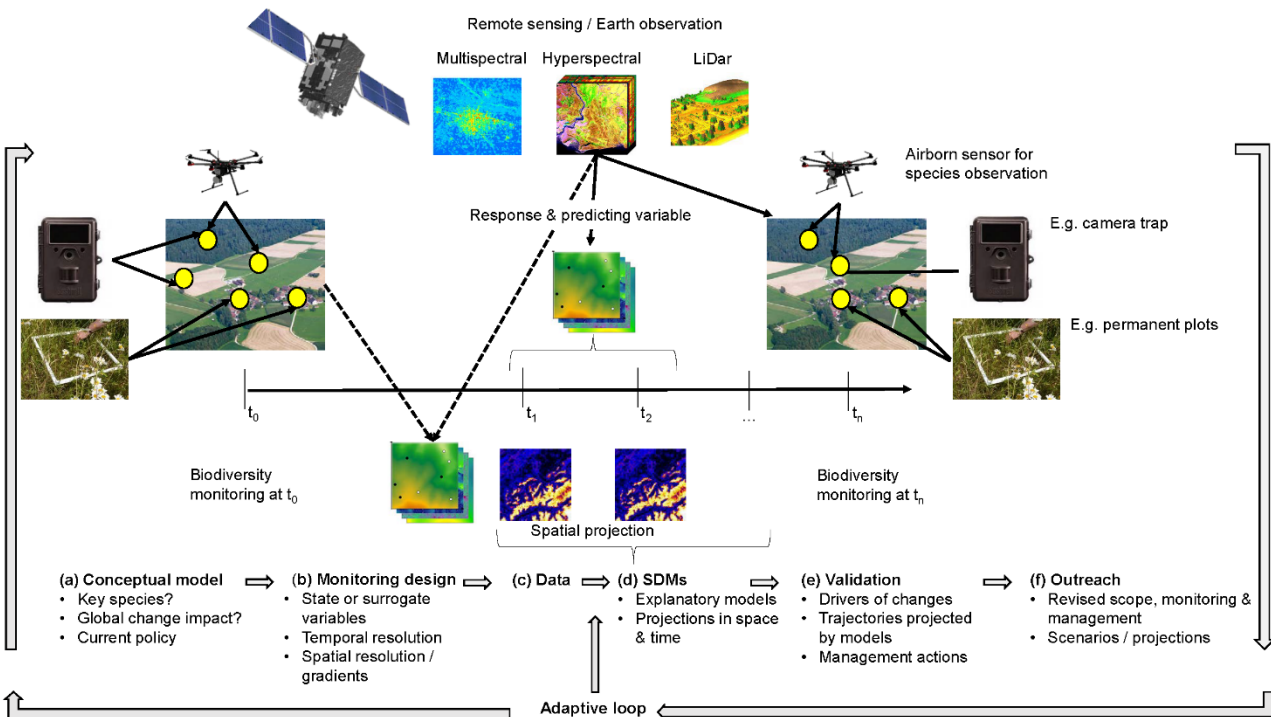


Fig. 4. An ideal loop of adaptive monitoring in which remote sensing data and SDMs are combined (adapted from Ims and Yoccoz, 2017).

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BOX 1 | Species Distribution Models

Two categories of SDMs can be distinguished: statistical (or statistical learning *sensu* Drake 2014) and process-based models. Statistical SDMs (*sensu* Franklin 2010 also called habitat suitability

models *sensu* Guisan et al. 2017) are methods that relate field observations or museum specimens (e.g. occurrences, abundances, or species' traits) to environmental predictor variables. In such models, processes are empirically inferred from a combination of statistically or theoretically derived response curves (Guisan et al. 2017). In contrast, process-based models build upon explicit causal relationships determined experimentally. In these models, processes such as phenology and distribution are explicitly described (see Chuine and Régnière, 2017), which increases the confidence in extrapolating beyond the known spatiotemporal extent (Zurell et al., 2016). The continuum between these two modeling approaches includes hybrid (e.g. Dullinger et al., 2012), dynamic range (e.g. Cotto et al., 2017; Engler et al., 2012; Pagel and Schurr, 2012), and integrated models (Pagel and Schurr, 2012).

References

- Aalto, J., Harrison, S., Luoto, M., 2017. Statistical modelling predicts almost complete loss of major periglacial processes in Northern Europe by 2100. *Nat. Commun.* 8, 515. <https://doi.org/10.1038/s41467-017-00669-3>
- Alleaume, S., Dusseux, P., Thierion, V., Commagnac, L., Laventure, S., Lang, M., Féret, J.-B., Hubert-Moy, L., Luque, S., 2018. A generic remote sensing approach to derive operational essential biodiversity variables (EBVs) for conservation planning. *Methods Ecol. Evol.* 9, 1822–1836. <https://doi.org/10.1111/2041-210X.13033>
- Araujo, M.B., Cabeza, M., Thuiller, W., Hannah, L., Williams, P.H., 2004. Would climate change drive species out of reserves? An assessment of existing reserve-selection methods. *Glob. Chang. Biol.* 10, 1618–1626. <https://doi.org/10.1111/j.1365-2486.2004.00828.x>
- Ashcroft, M.B., Cavanagh, M., Eldridge, M.D.B., Gollan, J.R., 2014. Testing the ability of topoclimatic grids of extreme temperatures to explain the distribution of the endangered brush-tailed rock-wallaby (*Petrogale penicillata*). *J. Biogeogr.* 41, 1402–1413. <https://doi.org/10.1111/jbi.12298>
- Ashcroft, M.B., Gollan, J.R., 2013. Moisture, thermal inertia, and the spatial distributions of near-surface soil and air temperatures: understanding factors that promote microrefugia. *Agric. For. Meteorol.* 176, 77–89. <https://doi.org/10.1016/J.AGRFORMET.2013.03.008>
- Ashcroft, M.B., Gollan, J.R., 2011. Fine-resolution (25 m) topoclimatic grids of near-surface (5 cm) extreme temperatures and humidities across various habitats in a large (200 × 300 km) and diverse region. *Int. J. Climatol.* 32, n/a-n/a. <https://doi.org/10.1002/joc.2428>
- Asner, G.P., Martin, R.E., 2009. Airborne spectranomics: mapping canopy chemical and taxonomic diversity in tropical forests. *Front. Ecol. Environ.* 7, 269–276. <https://doi.org/10.1890/070152>
- Asner, G.P., Martin, R.E., Knapp, D.E., Tupayachi, R., Anderson, C.B., Sinca, F., Vaughn, N.R., Llactayo, W., 2017. Airborne laser-guided imaging spectroscopy to map forest trait diversity and guide conservation. *Science* (80-.). 355, 385–389. <https://doi.org/10.1126/science.aaj1987>
- Auffret, A.G., Kimberley, A., Plue, J., Waldén, E., 2018. Super-regional land-use change and effects on the grassland specialist flora. *Nat. Commun.* 9, 3464. <https://doi.org/10.1038/s41467-018-05991-y>
- Austin, M., 2002. Spatial prediction of species distribution: an interface between ecological

theory and statistical modelling. *Ecol. Modell.* 157, 101–118. [https://doi.org/10.1016/S0304-3800\(02\)00205-3](https://doi.org/10.1016/S0304-3800(02)00205-3)

Austin, M., 2007. Species distribution models and ecological theory: a critical assessment and some possible new approaches. *Ecol. Modell.* 200, 1–19. <https://doi.org/10.1016/J.ECOLMODEL.2006.07.005>

Austin, M.P., Gaywood, M.J., 1994. Current problems of environmental gradients and species response curves in relation to continuum theory. *J. Veg. Sci.* 5, 473–482. <https://doi.org/10.2307/3235973>

Austin, M.P., Smith, T.M., 1989. A new model for the continuum concept. *Vegetatio* 83, 35–47. <https://doi.org/10.1007/BF00031679>

Austin, M.P., Van Niel, K.P., 2011. Improving species distribution models for climate change studies: variable selection and scale. *J. Biogeogr.* 38, 1–8. <https://doi.org/10.1111/j.1365-2699.2010.02416.x>

Benítez-López, A., Santini, L., Schipper, A.M., Busana, M., Huijbregts, M.A.J., 2019. Intact but empty forests? Patterns of hunting-induced mammal defaunation in the tropics. *PLOS Biol.* 17, e3000247. <https://doi.org/10.1371/journal.pbio.3000247>

Bergen, K.M., Goetz, S.J., Dubayah, R.O., Henebry, G.M., Hunsaker, C.T., Imhoff, M.L., Nelson, R.F., Parker, G.G., Radeloff, V.C., 2009. Remote sensing of vegetation 3-D structure for biodiversity and habitat: review and implications for lidar and radar spaceborne missions. *J. Geophys. Res. Biogeosciences* 114, n/a–n/a. <https://doi.org/10.1029/2008JG000883>

Bertrand, R., Perez, V., Gégout, J.-C., 2012. Disregarding the edaphic dimension in species distribution models leads to the omission of crucial spatial information under climate change: the case of *Quercus pubescens* in France. *Glob. Chang. Biol.* 18, 2648–2660. <https://doi.org/10.1111/j.1365-2486.2012.02679.x>

Böhler, J.E., Schaepman, M.E., Kneubühler, M., 2019. Optimal timing assessment for crop separation using multispectral Unmanned Aerial Vehicle (UAV) data and textural features. *Remote Sens.* 11, 1780. <https://doi.org/10.3390/rs11151780>

Böhner, J., AntoniĆ, O., 2009. Land-surface parameters specific to topo-climatology. *Dev. Soil Sci.* 33, 195–226. [https://doi.org/10.1016/S0166-2481\(08\)00008-1](https://doi.org/10.1016/S0166-2481(08)00008-1)

Bojinski, S., Verstraete, M., Peterson, T.C., Richter, C., Simmons, A., Zemp, M., Bojinski, S., Verstraete, M., Peterson, T.C., Richter, C., Simmons, A., Zemp, M., 2014. The concept of

901 Essential Climate Variables in support of climate research, applications, and policy. *Bull.*
902 *Am. Meteorol. Soc.* 95, 1431–1443. <https://doi.org/10.1175/BAMS-D-13-00047.1>

903 Bolliger, J., Kienast, F., Soliva, R., Rutherford, G., 2007. Spatial sensitivity of species habitat
904 patterns to scenarios of land use change (Switzerland). *Landsc. Ecol.* 22, 773–789.
905 <https://doi.org/10.1007/s10980-007-9077-7>

906 Bolliger, J., Schmatz, D., Pazúr, R., Ostapowicz, K., Psomas, A., 2017. Reconstructing forest-
907 cover change in the Swiss Alps between 1880 and 2010 using ensemble modelling. *Reg.*
908 *Environ. Chang.* 17, 2265–2277. <https://doi.org/10.1007/s10113-016-1090-4>

909 Bookhagen, B., Strecker, M.R., 2008. Orographic barriers, high-resolution TRMM rainfall, and
910 relief variations along the eastern Andes. *Geophys. Res. Lett.* 35, L06403.
911 <https://doi.org/10.1029/2007GL032011>

912 Boulangeat, I., Georges, D., Dentant, C., Bonet, R., Es, J. Van, Abdulhak, S., Zimmermann,
913 N.E., Thuiller, W., 2014. Anticipating the spatio-temporal response of plant diversity and
914 vegetation structure to climate and land use change in a protected area 1230–1239.
915 <https://doi.org/10.1111/ecog.00694>

916 Buri, A., Cianfrani, C., Pinto-Figueroa, E., Yashiro, E., Spangenberg, J.E., Adate, T.,
917 Verrecchia, E., Guisan, A., Pradervand, J.-N., 2017. Soil factors improve predictions of
918 plant species distribution in a mountain environment. *Prog. Phys. Geogr. Earth Environ.* 41,
919 703–722. <https://doi.org/10.1177/0309133317738162>

920 Bush, A., Sollmann, R., Wilting, A., Bohmann, K., Cole, B., Balzter, H., Martius, C., Zlinszky, A.,
921 Calvignac-Spencer, S., Cobbold, C.A., Dawson, T.P., Emerson, B.C., Ferrier, S., Gilbert,
922 M.T.P., Herold, M., Jones, L., Leendertz, F.H., Matthews, L., Millington, J.D.A., Olson, J.R.,
923 Ovaskainen, O., Raffaelli, D., Reeve, R., Rödel, M.-O., Rodgers, T.W., Snape, S.,
924 Visseren-Hamakers, I., Vogler, A.P., White, P.C.L., Wooster, M.J., Yu, D.W., 2017.
925 Connecting Earth observation to high-throughput biodiversity data. *Nat. Ecol. Evol.* 1, 0176.
926 <https://doi.org/10.1038/s41559-017-0176>

927 Calabrese, J.M., Certain, G., Kraan, C., Dormann, C.F., 2014. Stacking species distribution
928 models and adjusting bias by linking them to macroecological models. *Glob. Ecol.*
929 *Biogeogr.* 23, 99–112. <https://doi.org/10.1111/geb.12102>

930 Cannone, N., Guglielmin, M., Convey, P., Worland, M.R., Favero Longo, S.E., 2016. Vascular
931 plant changes in extreme environments: effects of multiple drivers. *Clim. Change* 134,
932 651–665. <https://doi.org/10.1007/s10584-015-1551-7>

933 Cavender-Bares, J., Gamon, J.A., Hobbie, S.E., Madritch, M.D., Meireles, J.E., Schweiger, A.K.,

934 Townsend, P.A., 2017. Harnessing plant spectra to integrate the biodiversity sciences
 935 across biological and spatial scales. *Am. J. Bot.* 104, 966–969.
 936 <https://doi.org/10.3732/ajb.1700061>

937 Cavender-Bares, J., Meireles, J., Couture, J., Kaproth, M., Kingdon, C., Singh, A., Serbin, S.,
 938 Center, A., Zuniga, E., Pilz, G., Townsend, P., Cavender-Bares, J., Meireles, J.E., Couture,
 939 J.J., Kaproth, M.A., Kingdon, C.C., Singh, A., Serbin, S.P., Center, A., Zuniga, E., Pilz, G.,
 940 Townsend, P.A., 2016. Associations of leaf spectra with genetic and phylogenetic variation
 941 in oaks: prospects for remote detection of biodiversity. *Remote Sens.* 8, 221.
 942 <https://doi.org/10.3390/rs8030221>

943 Ceballos, G., Ehrlich, P.R., Dirzo, R., 2017. Biological annihilation via the ongoing sixth mass
 944 extinction signaled by vertebrate population losses and declines. *Proc. Natl. Acad. Sci. U.*
 945 *S. A.* 114, E6089–E6096. <https://doi.org/10.1073/pnas.1704949114>

946 Chastain, R. a., Townsend, P. a., 2007. Use of Landsat ETM and topographic data to
 947 characterize evergreen understory communities in appalachian deciduous forests.
 948 *Photogramm. Eng. Remote Sens.* 73, 563–575. <https://doi.org/10.14358/PERS.73.5.563>

949 Chaudhary, A., Kastner, T., 2016. Land use biodiversity impacts embodied in international food
 950 trade. *Glob. Environ. Chang.* 38, 195–204. <https://doi.org/10.1016/j.gloenvcha.2016.03.013>

951 Chaudhary, S., McGregor, A., Houston, D., Chettri, N., 2015. The evolution of ecosystem
 952 services: A time series and discourse-centered analysis. *Environ. Sci. Policy* 54, 25–34.
 953 <https://doi.org/10.1016/j.envsci.2015.04.025>

954 Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B., Thomas, C.D., 2011. Rapid range shifts of
 955 species associated with high levels of climate warming. *Science* 333, 1024–6.
 956 <https://doi.org/10.1126/science.1206432>

957 Chuine, I., Beaubien, E.G., 2001. Phenology is a major determinant of tree species range. *Ecol.*
 958 *Lett.* 4, 500–510. <https://doi.org/10.1046/j.1461-0248.2001.00261.x>

959 Chuine, I., Régnière, J., 2017. Process-based models of phenology for plants and animals.
 960 *Annu. Rev. Ecol. Evol. Syst.* 48, 159–182. [https://doi.org/10.1146/annurev-ecolsys-110316-](https://doi.org/10.1146/annurev-ecolsys-110316-022706)
 961 [022706](https://doi.org/10.1146/annurev-ecolsys-110316-022706)

962 Cianfrani, C., Broennimann, O., Loy, A., Guisan, A., 2018. More than range exposure: global
 963 otter vulnerability to climate change. *Biol. Conserv.* 221, 103–113.
 964 <https://doi.org/10.1016/J.BIOCON.2018.02.031>

965 Cianfrani, C., Satizábal, H.F., Randin, C., 2015. A spatial modelling framework for assessing

966 climate change impacts on freshwater ecosystems: response of brown trout (*Salmo trutta*
 967 L.) biomass to warming water temperature. *Ecol. Modell.* 313, 1–12.
 968 <https://doi.org/10.1016/J.ECOLMODEL.2015.06.023>

969 Connell, J., Watson, S.J., Taylor, R.S., Avitabile, S.C., Clarke, R.H., Bennett, A.F., Clarke, M.F.,
 970 Manorina, M., 2017. Testing the effects of a century of fires : Requirements for fire
 971 succession predict the distribution of threatened bird species 1078–1089.
 972 <https://doi.org/10.1111/ddi.12597>

973 Connor, T., Hull, V., Viña, A., Shortridge, A., Tang, Y., Zhang, J., Wang, F., Liu, J., 2018. Effects
 974 of grain size and niche breadth on species distribution modeling. *Ecography (Cop.)*. 41,
 975 1270–1282. <https://doi.org/10.1111/ecog.03416>

976 Coops, N.C., Goodbody, T.R.H., Cao, L., 2019. Four steps to extend drone use in research.
 977 *Nature* 572, 433–435. <https://doi.org/10.1038/d41586-019-02474-y>

978 Coops, N.C., Waring, R.H., Plowright, A., Lee, J., Dilts, T.E., 2016. Using remotely-sensed land
 979 cover and distribution modeling to estimate tree species migration in the Pacific Northwest
 980 region of North America. *Remote Sens.* 8. <https://doi.org/10.14288/1.0378973>

981 Cord, A.F., Dech, S., Klein, D., Dech, S., 2010. Remote sensing time series for modeling
 982 invasive species distribution: a case study of *Tamarix* spp. in the US and Mexico. *Proc. Int.*
 983 *Congr. Environ. Model. Softw. Model. Environ. Sake 5th Bienni.*

984 Cotto, O., Wessely, J., Georges, D., Klonner, G., Schmid, M., Dullinger, S., Thuiller, W.,
 985 Guillaume, F., 2017. A dynamic eco-evolutionary model predicts slow response of alpine
 986 plants to climate warming. *Nat. Commun.* 8, 15399. <https://doi.org/10.1038/ncomms15399>

987 Coudun, C., Gégout, J.-C., Piedallu, C., Rameau, J.-C., 2006. Soil nutritional factors improve
 988 models of plant species distribution: an illustration with *Acer campestre* (L.) in France. *J.*
 989 *Biogeogr.* 33, 1750–1763. <https://doi.org/10.1111/j.1365-2699.2005.01443.x>

990 Couture, J.J., Singh, A., Rubert-Nason, K.F., Serbin, S.P., Lindroth, R.L., Townsend, P.A.,
 991 2016. Spectroscopic determination of ecologically relevant plant secondary metabolites.
 992 *Methods Ecol. Evol.* 7, 1402–1412. <https://doi.org/10.1111/2041-210X.12596>

993 Daly, C., 2006. Guidelines for assessing the suitability of spatial climate data sets. *Int. J.*
 994 *Climatol.* 26, 707–721. <https://doi.org/10.1002/joc.1322>

995 de Jong, R., Verbesselt, J., Zeileis, A., Schaepman, M., de Jong, R., Verbesselt, J., Zeileis, A.,
 996 Schaepman, M.E., 2013. Shifts in global vegetation activity trends. *Remote Sens.* 5, 1117–
 997 1133. <https://doi.org/10.3390/rs5031117>

998 Deacon, N.J., Grossman, J.J., Schweiger, A.K., Armour, I., Cavender-Bares, J., 2017. Genetic,
 999 morphological, and spectral characterization of relictual Niobrara River hybrid aspens (
 1000 *Populus × smithii*). Am. J. Bot. 104, 1878–1890. <https://doi.org/10.3732/ajb.1700268>

1001 Deblauwe, V., Droissart, V., Bose, R., Sonké, B., Blach-Overgaard, A., Svenning, J.-C.,
 1002 Wieringa, J.J., Ramesh, B.R., Stévant, T., Couvreur, T.L.P., 2016. Remotely sensed
 1003 temperature and precipitation data improve species distribution modelling in the tropics.
 1004 Glob. Ecol. Biogeogr. 25, 443–454. <https://doi.org/10.1111/geb.12426>

1005 Dirnböck, T., Dullinger, S., Grabherr, G., 2003. A regional impact assessment of climate and
 1006 land-use change on alpine vegetation. J. Biogeogr. 30, 401–417.
 1007 <https://doi.org/10.1046/j.1365-2699.2003.00839.x>

1008 Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in
 1009 the Anthropocene. Science (80-.). 345, 401–6. <https://doi.org/10.1126/science.1251817>

1010 Dormann, C.F., Schymanski, S.J., Cabral, J., Chuine, I., Graham, C., Hartig, F., Kearney, M.,
 1011 Morin, X., Römermann, C., Schröder, B., Singer, A., 2012. Correlation and process in
 1012 species distribution models: bridging a dichotomy. J. Biogeogr. 39, 2119–2131.
 1013 <https://doi.org/10.1111/j.1365-2699.2011.02659.x>

1014 Droz, B., Arnoux, R., Bohnenstengel, T., Laesser, J., Spaar, R., Ayé, R., Randin, C.F., 2019.
 1015 Moderately urbanized areas as a conservation opportunity for an endangered songbird.
 1016 Landsc. Urban Plan. 181, 1–9. <https://doi.org/10.1016/J.LANDURBPLAN.2018.09.011>

1017 Dubuis, A., Giovanettina, S., Pellissier, L., Pottier, J., Vittoz, P., Guisan, A., 2013. Improving the
 1018 prediction of plant species distribution and community composition by adding edaphic to
 1019 topo-climatic variables. J. Veg. Sci. 24, 593–606. <https://doi.org/10.1111/jvs.12002>

1020 Dullinger, S., Gatttringer, A., Thuiller, W., Moser, D., Zimmermann, N.E., Guisan, A., Willner, W.,
 1021 Plutzar, C., Leitner, M., Mang, T., Caccianiga, M., Dirnböck, T., Ertl, S., Fischer, A., Lenoir,
 1022 J., Svenning, J.-C., Psomas, A., Schmatz, D.R., Silc, U., Vittoz, P., Hülber, K., 2012.
 1023 Extinction debt of high-mountain plants under twenty-first-century climate change. Nat.
 1024 Clim. Chang. 2, 619–622. <https://doi.org/10.1038/nclimate1514>

1025 Eckert, S., Kiteme, B., Njuguna, E., Zaehring, J., Eckert, S., Kiteme, B., Njuguna, E.,
 1026 Zaehring, J.G., 2017. Agricultural expansion and intensification in the foothills of Mount
 1027 Kenya: a landscape perspective. Remote Sens. 9, 784. <https://doi.org/10.3390/rs9080784>

1028 Ellis, E.C., 2015. Ecology in an anthropogenic biosphere. Ecol. Monogr. 85, 287–331.
 1029 <https://doi.org/10.1890/14-2274.1>

1030 Ellis, E.C., 2011. Anthropogenic transformation of the terrestrial biosphere. *Philos. Trans. R.*
1031 *Soc. A Math. Phys. Eng. Sci.* 369, 1010–1035. <https://doi.org/10.1098/rsta.2010.0331>

1032 Engler, R., Hordijk, W., Guisan, A., 2012. The MIGCLIM R package - seamless integration of
1033 dispersal constraints into projections of species distribution models. *Ecography (Cop.)*. 35,
1034 872–878. <https://doi.org/10.1111/j.1600-0587.2012.07608.x>

1035 Engstrom, R., Hope, A., Kwon, H., Stow, D., Zamolodchikov, D., 2005. Spatial distribution of
1036 near surface soil moisture and its relationship to microtopography in the Alaskan Arctic
1037 coastal plain. *Hydrol. Res.* 36, 219–234. <https://doi.org/10.2166/nh.2005.0016>

1038 Esselman, P.C., Allan, J.D., 2011. Application of species distribution models and conservation
1039 planning software to the design of a reserve network for the riverine fishes of northeastern
1040 Mesoamerica. *Freshw. Biol.* 56, 71–88. <https://doi.org/10.1111/j.1365-2427.2010.02417.x>

1041 Estel, S., Mader, S., Levers, C., Verburg, P.H., Baumann, M., Kuemmerle, T., 2018. Combining
1042 satellite data and agricultural statistics to map grassland management intensity in Europe.
1043 *Environ. Res. Lett.* 13, 074020. <https://doi.org/10.1088/1748-9326/aacc7a>

1044 Estrada-Peña, A., Alexander, N., Wint, G.R.W., 2016. Perspectives on modelling the distribution
1045 of ticks for large areas: so far so good? *Parasit. Vectors* 9, 179.
1046 <https://doi.org/10.1186/s13071-016-1474-9>

1047 Ewald, M., Aerts, R., Lenoir, J., Fassnacht, F.E., Nicolas, M., Skowronek, S., Piat, J., Honnay,
1048 O., Garzón-López, C.X., Feilhauer, H., Van De Kerchove, R., Somers, B., Hattab, T.,
1049 Rocchini, D., Schmidtlein, S., 2018. LiDAR derived forest structure data improves
1050 predictions of canopy N and P concentrations from imaging spectroscopy. *Remote Sens.*
1051 *Environ.* 211, 13–25. <https://doi.org/10.1016/J.RSE.2018.03.038>

1052 Fagan, M.E., Morton, D.C., Cook, B.D., Masek, J., Zhao, F., Nelson, R.F., Huang, C., 2018.
1053 Mapping pine plantations in the southeastern U.S. using structural, spectral, and temporal
1054 remote sensing data. *Remote Sens. Environ.* 216, 415–426.
1055 <https://doi.org/10.1016/J.RSE.2018.07.007>

1056 Fang, L., Hain, C.R., Zhan, X., Anderson, M.C., 2016. An inter-comparison of soil moisture data
1057 products from satellite remote sensing and a land surface model. *Int. J. Appl. Earth Obs.*
1058 *Geoinf.* 48, 37–50. <https://doi.org/10.1016/J.JAG.2015.10.006>

1059 Fawcett, D., Verhoef, W., Schläpfer, D., Schneider, F.D., Schaepman, M.E., Damm, A., 2018.
1060 Advancing retrievals of surface reflectance and vegetation indices over forest ecosystems
1061 by combining imaging spectroscopy, digital object models, and 3D canopy modelling.
1062 *Remote Sens. Environ.* 204, 583–595. <https://doi.org/10.1016/J.RSE.2017.09.040>

1063 Feilhauer, H., Schmidtlein, S., 2009. Mapping continuous fields of forest alpha and beta
 1064 diversity. *Appl. Veg. Sci.* 12, 429–439. <https://doi.org/10.1111/j.1654-109X.2009.01037.x>

1065 Féret, J.-B., Asner, G.P., 2014. Mapping tropical forest canopy diversity using high-fidelity
 1066 imaging spectroscopy. *Ecol. Appl.* 24, 1289–1296. <https://doi.org/10.1890/13-1824.1>

1067 Fernandez, N., Ferrier, S., Navarro, L.M., Pereira, H.M., 2019. Essential Biodiversity Variables:
 1068 integrating in-situ observations and remote sensing through modelling, in: Cavender-Bares,
 1069 J., Gamon, J.A., Towsend, P.A. (Eds.), *Remote Sensing of Vegetation*. Springer.

1070 Fernández, N., Román, J., Delibes, M., 2016. Variability in primary productivity determines
 1071 metapopulation dynamics. *Proc. R. Soc. B Biol. Sci.* 283, 20152998.
 1072 <https://doi.org/10.1098/rspb.2015.2998>

1073 Ferrari, R., McKinnon, D., He, H., Smith, R., Corke, P., González-Rivero, M., Mumby, P.,
 1074 Upcroft, B., 2016. Quantifying multiscale habitat structural complexity: a cost-effective
 1075 framework for underwater 3D modelling. *Remote Sens.* 8, 113.
 1076 <https://doi.org/10.3390/rs8020113>

1077 Fisk, M.C., Schmidt, S.K., Seastedt, T.R., 1998. Topographic patterns of above- and
 1078 belowground production and nitrogen cycling in alpine tundra. *Ecology* 79, 2253–2266.
 1079 [https://doi.org/10.1890/0012-9658\(1998\)079\[2253:TPOAAB\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[2253:TPOAAB]2.0.CO;2)

1080 Foody, G.M., 1999. Applications of the self-organising feature map neural network in community
 1081 data analysis. *Ecol. Modell.* 120, 97–107. [https://doi.org/10.1016/S0304-3800\(99\)00094-0](https://doi.org/10.1016/S0304-3800(99)00094-0)

1082 Franke, J., Keuck, V., Siegert, F., 2012. Assessment of grassland use intensity by remote
 1083 sensing to support conservation schemes. *J. Nat. Conserv.* 20, 125–134.
 1084 <https://doi.org/10.1016/J.JNC.2012.02.001>

1085 Franklin, J., 2010. Moving beyond static species distribution models in support of conservation
 1086 biogeography. *Divers. Distrib.* 16, 321–330. [https://doi.org/10.1111/j.1472-](https://doi.org/10.1111/j.1472-4642.2010.00641.x)
 1087 [4642.2010.00641.x](https://doi.org/10.1111/j.1472-4642.2010.00641.x)

1088 Franklin, J., 1995. Predictive vegetation mapping: Geographic modelling of biospatial patterns in
 1089 relation to environmental gradients. *Prog. Phys. Geogr.* 19, 474–499.
 1090 <https://doi.org/10.1177/030913339501900403>

1091 Franklin, J., Regan, H.M., Syphard, A.D., 2014. Linking spatially explicit species distribution and
 1092 population models to plan for the persistence of plant. *Environ. Conserv.* 41, 97–109.
 1093 <https://doi.org/10.1017/S0376892913000453>

1094 Franklin, J., Serra-Diaz, J.M., Syphard, A.D., Regan, H.M., 2016. Global change and terrestrial

1095 plant community dynamics. *Proc. Natl. Acad. Sci. U. S. A.* 113, 3725–3734.
 1096 <https://doi.org/10.1073/pnas.1519911113>
 1097 Frost, G. V, Epstein, H.E., Walker, D.A., Matyshak, G., Ermokhina, K., 2013. Patterned-ground
 1098 facilitates shrub expansion in Low Arctic tundra. *Environ. Res. Lett.* 8, 015035.
 1099 <https://doi.org/10.1088/1748-9326/8/1/015035>
 1100 Fuller, R.M., Groom, G.B., Jones, A.R., 1994. The Land Cover Map of Great Britain: An
 1101 Automated Classification of Landsat Thematic Mapper Data. *Photogramm. Eng. Remote*
 1102 *Sens.* 60, 553–562. <https://doi.org/10.1016/j.jmarsys.2011.11.027>
 1103 Furukawa, Y., Ponce, J., 2010. Accurate, dense, and robust multiview stereopsis. *IEEE Trans.*
 1104 *Pattern Anal. Mach. Intell.* 32, 1362–1376. <https://doi.org/10.1109/TPAMI.2009.161>
 1105 Gamon, J.A., Somers, B., Malenovský, Z., Middleton, E.M., Rascher, U., Schaepman, M.E.,
 1106 2019. Assessing vegetation function with imaging spectroscopy. *Surv. Geophys.* 40, 489–
 1107 513. <https://doi.org/10.1007/s10712-019-09511-5>
 1108 Garonna, I., de Jong, R., Stöckli, R., Schmid, B., Schenkel, D., Schimel, D., Schaepman, M.E.,
 1109 2018. Shifting relative importance of climatic constraints on land surface phenology.
 1110 *Environ. Res. Lett.* 13, 024025. <https://doi.org/10.1088/1748-9326/aaa17b>
 1111 Gastón, A., Ciudad, C., Mateo-Sánchez, M.C., García-Viñas, J.I., López-Leiva, C., Fernández-
 1112 Landa, A., Marchamalo, M., Cuevas, J., de la Fuente, B., Fortin, M.-J., Saura, S., 2017.
 1113 Species' habitat use inferred from environmental variables at multiple scales: How much
 1114 we gain from high-resolution vegetation data? *Int. J. Appl. Earth Obs. Geoinf.* 55, 1–8.
 1115 <https://doi.org/10.1016/J.JAG.2016.10.007>
 1116 George, A.D., Thompson, F.R., Faaborg, J., 2015. Using LiDAR and remote microclimate
 1117 loggers to downscale near-surface air temperatures for site-level studies. *Remote Sens.*
 1118 *Lett.* 6, 924–932. <https://doi.org/10.1080/2150704X.2015.1088671>
 1119 Ginzler, C., Hobi, M., 2015. Countrywide stereo-image matching for updating digital surface
 1120 models in the framework of the Swiss national forest inventory. *Remote Sens.* 7, 4343–
 1121 4370. <https://doi.org/10.3390/rs70404343>
 1122 Gómez Giménez, M., de Jong, R., Della Peruta, R., Keller, A., Schaepman, M.E., 2017.
 1123 Determination of grassland use intensity based on multi-temporal remote sensing data and
 1124 ecological indicators. *Remote Sens. Environ.* 198, 126–139.
 1125 <https://doi.org/10.1016/J.RSE.2017.06.003>
 1126 Gooseff, M.N., Barrett, J.E., Doran, P.T., Fountain, A.G., Lyons, W.B., Parsons, A.N.,

1127 Porazinska, D.L., Virginia, R.A., Wall, D.H., 2003. Snow-patch influence on soil
 1128 biogeochemical processes and invertebrate distribution in the McMurdo Dry Valleys,
 1129 Antarctica. *Arctic, Antarct. Alp. Res.* 35, 91–99. [https://doi.org/10.1657/1523-](https://doi.org/10.1657/1523-0430(2003)035[0091:SPIOSB]2.0.CO;2)
 1130 [0430\(2003\)035\[0091:SPIOSB\]2.0.CO;2](https://doi.org/10.1657/1523-0430(2003)035[0091:SPIOSB]2.0.CO;2)

1131 Graf, R.F., Mathys, L., Bollmann, K., 2009. Habitat assessment for forest dwelling species using
 1132 LiDAR remote sensing: Capercaillie in the Alps. *For. Ecol. Manage.* 257, 160–167.
 1133 <https://doi.org/10.1016/J.FORECO.2008.08.021>

1134 Guisan, A., Rahbek, C., 2011. SESAM - a new framework integrating macroecological and
 1135 species distribution models for predicting spatio-temporal patterns of species assemblages.
 1136 *J. Biogeogr.* 38, 1433–1444. <https://doi.org/10.1111/j.1365-2699.2011.02550.x>

1137 Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat
 1138 models. *Ecol. Lett.* 8, 993–1009. <https://doi.org/10.1111/j.1461-0248.2005.00792.x>

1139 Guisan, A., Tingley, R., Baumgartner, J.B., Naujokaitis-Lewis, I., Sutcliffe, P.R., Tulloch, A.I.T.,
 1140 Regan, T.J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T.G.,
 1141 Rhodes, J.R., Maggini, R., Setterfield, S.A., Elith, J., Schwartz, M.W., Wintle, B.A.,
 1142 Broennimann, O., Austin, M., Ferrier, S., Kearney, M.R., Possingham, H.P., Buckley, Y.M.,
 1143 2013. Predicting species distributions for conservation decisions. *Ecol. Lett.* 16, 1424–
 1144 1435. <https://doi.org/10.1111/ele.12189>

1145 Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. *Ecol.*
 1146 *Modell.* 135, 147–186. [https://doi.org/10.1016/S0304-3800\(00\)00354-9](https://doi.org/10.1016/S0304-3800(00)00354-9)

1147 Haase, P., Tonkin, J.D., Stoll, S., Burkhard, B., Frenzel, M., Geijzendorffer, I.R., Häuser, C.,
 1148 Klotz, S., Kühn, I., McDowell, W.H., Mirtl, M., Müller, F., Musche, M., Penner, J., Zacharias,
 1149 S., Schmeller, D.S., 2018. The next generation of site-based long-term ecological
 1150 monitoring: linking essential biodiversity variables and ecosystem integrity. *Sci. Total*
 1151 *Environ.* 613–614, 1376–1384. <https://doi.org/10.1016/J.SCITOTENV.2017.08.111>

1152 Hanavan, R.P., Pontius, J., Hallett, R., 2015. A 10-year assessment of Hemlock decline in the
 1153 Catskill mountain region of New York State using hyperspectral remote sensing
 1154 techniques. *J. Econ. Entomol.* 108, 339–349. <https://doi.org/10.1093/jee/tou015>

1155 Hancock, S., Anderson, K., Disney, M., Gaston, K.J., 2017. Measurement of fine-spatial-
 1156 resolution 3D vegetation structure with airborne waveform lidar: calibration and validation
 1157 with voxelised terrestrial lidar. *Remote Sens. Environ.* 188, 37–50.
 1158 <https://doi.org/10.1016/J.RSE.2016.10.041>

1159 Hansen, M.C., Potapov, P. V, Moore, R., Hancher, M., Turubanova, S. a, Tyukavina, A., Thau,

1160 D., Stehman, S. V, Goetz, S.J., Loveland, T.R., Kommareddy, A., Egorov, A., Chini, L.,
 1161 Justice, C.O., Townshend, J.R.G., 2013. High-resolution global maps of 21st-century forest
 1162 cover change. *Science* (80-.). 850, 2011–2014. <https://doi.org/10.1126/science.1244693>
 1163 Hansen, M.C., Roy, D.P., Lindquist, E., Adusei, B., Justice, C.O., Altstatt, A., 2008. A method
 1164 for integrating MODIS and Landsat data for systematic monitoring of forest cover and
 1165 change in the Congo Basin. *Remote Sens. Environ.* 112, 2495–2513.
 1166 <https://doi.org/10.1016/J.RSE.2007.11.012>
 1167 He, K.S., Bradley, B.A., Cord, A.F., Rocchini, D., Tuanmu, M., Schmidtlein, S., Turner, W.,
 1168 Wegmann, M., Pettorelli, N., 2015. Will remote sensing shape the next generation of
 1169 species distribution models ? *Remote Sens. Ecol. Conserv.* 4–18.
 1170 <https://doi.org/10.1002/rse2.7>
 1171 Hodgson, J.C., Mott, R., Baylis, S.M., Pham, T.T., Wotherspoon, S., Kilpatrick, A.D., Raja
 1172 Segaran, R., Reid, I., Terauds, A., Koh, L.P., 2018. Drones count wildlife more accurately
 1173 and precisely than humans. *Methods Ecol. Evol.* 9, 1160–1167.
 1174 <https://doi.org/10.1111/2041-210X.12974>
 1175 Holt, R.D., 2009. Bringing the Hutchinsonian niche into the 21st century: ecological and
 1176 evolutionary perspectives. *Proc. Natl. Acad. Sci. U. S. A.* 106 Suppl 2, 19659–65.
 1177 <https://doi.org/10.1073/pnas.0905137106>
 1178 Huber, N., Kienast, F., Ginzler, C., Pasinelli, G., 2016. Using remote-sensing data to assess
 1179 habitat selection of a declining passerine at two spatial scales. *Landsc. Ecol.* 31, 1919–
 1180 1937. <https://doi.org/10.1007/s10980-016-0370-1>
 1181 Hüsler, F., Jonas, T., Riffler, M., Musial, J.P., Wunderle, S., 2014. A satellite-based snow cover
 1182 climatology (1985–2011) for the European Alps derived from AVHRR data. *Cryosph.* 8, 73–
 1183 90. <https://doi.org/10.5194/tc-8-73-2014>
 1184 Hutchinson, G.E. (George E., 1978. *An introduction to population ecology*. Yale University
 1185 Press.
 1186 Ibrahim, S., Balzter, H., Tansey, K., Tsutsumida, N., Mathieu, R., 2018. Estimating fractional
 1187 cover of plant functional types in African savannah from harmonic analysis of MODIS time-
 1188 series data. *Int. J. Remote Sens.* 39, 2718–2745.
 1189 <https://doi.org/10.1080/01431161.2018.1430914>
 1190 Ims, R.A., Yoccoz, N.G., 2017. Ecosystem-based monitoring in the age of rapid climate change
 1191 and new technologies. *Curr. Opin. Environ. Sustain.* 29, 170–176.
 1192 <https://doi.org/10.1016/J.COSUST.2018.01.003>

1193 IPCC, 2014. Summary for policymakers, in: Field, C.B., Barros, V.R., Dokken, D.J., Mach, K.J.,
 1194 Mastrandrea, M.D., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrad, a Y.O., Genova, R.C.,
 1195 Girms, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R., White, L.L. (Eds.),
 1196 Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral
 1197 Aspects. Contribution of Working Group II to the Fifth Assessment Report of the
 1198 Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK
 1199 and New York, USA, pp. 1–32.

1200 Jaboyedoff, M., Oppikofer, T., Abellán, A., Derron, M.-H., Loye, A., Metzger, R., Pedrazzini, A.,
 1201 2012. Use of LIDAR in landslide investigations: a review. *Nat. Hazards* 61, 5–28.
 1202 <https://doi.org/10.1007/s11069-010-9634-2>

1203 Jakimow, B., Griffiths, P., van der Linden, S., Hostert, P., 2018. Mapping pasture management
 1204 in the Brazilian Amazon from dense Landsat time series. *Remote Sens. Environ.* 205, 453–
 1205 468. <https://doi.org/10.1016/J.RSE.2017.10.009>

1206 Jetz, W., Cavender-Bares, J., Pavlick, R., Schimel, D., Davis, F.W., Asner, G.P., Guralnick, R.,
 1207 Kattge, J., Latimer, A.M., Moorcroft, P., Schaepman, M.E., Schildhauer, M.P., Schneider,
 1208 F.D., Schrod, F., Stahl, U., Ustin, S.L., 2016. Monitoring plant functional diversity from
 1209 space. *Nat. Plants* 2, 16024. <https://doi.org/10.1038/nplants.2016.24>

1210 Jetz, W., McGeoch, M.A., Guralnick, R., Ferrier, S., Beck, J., Costello, M.J., Fernandez, M.,
 1211 Geller, G.N., Keil, P., Merow, C., Meyer, C., Muller-Karger, F.E., Pereira, H.M., Regan,
 1212 E.C., Schmeller, D.S., Turak, E., 2019. Essential biodiversity variables for mapping and
 1213 monitoring species populations. *Nat. Ecol. Evol.* 3, 539–551.
 1214 <https://doi.org/10.1038/s41559-019-0826-1>

1215 Jolly, W.M., Nemani, R., Running, S.W., 2005. A generalized, bioclimatic index to predict foliar
 1216 phenology in response to climate. *Glob. Chang. Biol.* 11, 619–632.
 1217 <https://doi.org/10.1111/j.1365-2486.2005.00930.x>

1218 Kaim, D., Kozak, J., Kolečka, N., Ziółkowska, E., Ostafin, K., Ostapowicz, K., Gimmi, U.,
 1219 Munteanu, C., Radeloff, V.C., 2016. Broad scale forest cover reconstruction from historical
 1220 topographic maps. *Appl. Geogr.* 67, 39–48.
 1221 <https://doi.org/10.1016/J.APGEOG.2015.12.003>

1222 Kammer, P.M., Schöb, C., Eberhard, G., Gallina, R., Meyer, R., Tschanz, C., 2013. The
 1223 relationship between soil water storage capacity and plant species diversity in high alpine
 1224 vegetation. *Plant Ecol. Divers.* 6, 457–466. <https://doi.org/10.1080/17550874.2013.783142>

1225 Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann,

1226 N.E., Linder, H.P., Kessler, M., 2017. Climatologies at high resolution for the earth's land
 1227 surface areas. *Sci. Data* 4, 170122. <https://doi.org/10.1038/sdata.2017.122>

1228 Kearney, M., Porter, W., 2009. Mechanistic niche modelling: combining physiological and spatial
 1229 data to predict species' ranges. *Ecol. Lett.* 12, 334–350. [https://doi.org/10.1111/j.1461-](https://doi.org/10.1111/j.1461-0248.2008.01277.x)
 1230 [0248.2008.01277.x](https://doi.org/10.1111/j.1461-0248.2008.01277.x)

1231 Kellenberger, B., Marcos, D., Tuia, D., 2018. Detecting mammals in UAV images: Best practices
 1232 to address a substantially imbalanced dataset with deep learning. *Remote Sens. Environ.*
 1233 216, 139–153. <https://doi.org/10.1016/J.RSE.2018.06.028>

1234 Kemppinen, J., Niittynen, P., Riihimäki, H., Luoto, M., 2018. Modelling soil moisture in a high-
 1235 latitude landscape using LiDAR and soil data. *Earth Surf. Process. Landforms* 43, 1019–
 1236 1031. <https://doi.org/10.1002/esp.4301>

1237 Kim, H., Rosa, I.M.D., Alkemade, R., Leadley, P., Hurtt, G., Popp, A., van Vuuren, D.P.,
 1238 Anthoni, P., Arneth, A., Baisero, D., Caton, E., Chaplin-Kramer, R., Chini, L., De Palma, A.,
 1239 Di Fulvio, F., Di Marco, M., Espinoza, F., Ferrier, S., Fujimori, S., Gonzalez, R.E.,
 1240 Gueguen, M., Guerra, C., Harfoot, M., Harwood, T.D., Hasegawa, T., Haverd, V., Havlík,
 1241 P., Hellweg, S., Hill, S.L.L., Hirata, A., Hoskins, A.J., Janse, J.H., Jetz, W., Johnson, J.A.,
 1242 Krause, A., Leclère, D., Martins, I.S., Matsui, T., Merow, C., Obersteiner, M., Ohashi, H.,
 1243 Poulter, B., Purvis, A., Quesada, B., Rondinini, C., Schipper, A.M., Sharp, R., Takahashi,
 1244 K., Thuiller, W., Titeux, N., Visconti, P., Ware, C., Wolf, F., Pereira, H.M., 2018. A protocol
 1245 for an intercomparison of biodiversity and ecosystem services models using harmonized
 1246 land-use and climate scenarios. *Geosci. Model Dev.* 11, 4537–4562.
 1247 <https://doi.org/10.5194/gmd-11-4537-2018>

1248 Klein, T., Randin, C., Körner, C., 2015. Water availability predicts forest canopy height at the
 1249 global scale. *Ecol. Lett.* 18, 1311–1320. <https://doi.org/10.1111/ele.12525>

1250 Knight, J., Harrison, S., 2013. The impacts of climate change on terrestrial Earth surface
 1251 systems. *Nat. Clim. Chang.* 3, 24–29. <https://doi.org/10.1038/nclimate1660>

1252 Koh, L.P., Wich, S.A., 2012. Dawn of drone ecology: low-cost autonomous aerial vehicles for
 1253 conservation. *Trop. Conserv. Sci.* 5, 121–132.
 1254 <https://doi.org/10.1177/194008291200500202>

1255 Kolečka, N., Ginzler, C., Pazur, R., Price, B., Verburg, P., Kolečka, N., Ginzler, C., Pazur, R.,
 1256 Price, B., Verburg, P.H., 2018. Regional scale mapping of grassland mowing frequency
 1257 with Sentinel-2 time series. *Remote Sens.* 10, 1221. <https://doi.org/10.3390/rs10081221>

1258 Kollas, C., Körner, C., Randin, C.F., 2014. Spring frost and growing season length co-control

1259 the cold range limits of broad-leaved trees. *J. Biogeogr.* 41, 773–783.
1260 <https://doi.org/10.1111/jbi.12238>

1261 Kozak, K.H., Graham, C.H., Wiens, J.J., 2008. Integrating GIS-based environmental data into
1262 evolutionary biology. *Trends Ecol. Evol.* 23, 141–148.
1263 <https://doi.org/10.1016/J.TREE.2008.02.001>

1264 Kozłowska, A., Rączkowska, Z., 2002. Vegetation as a tool in the characterisation of
1265 geomorphological forms and processes: an example from the abisko mountains. *Geogr.*
1266 *Ann. Ser. A, Phys. Geogr.* 84, 233–244. <https://doi.org/10.1111/j.0435-3676.2002.00178.x>

1267 Krauss, J., Bommarco, R., Guardiola, M., Heikkinen, R.K., Helm, A., Kuussaari, M., Lindborg,
1268 R., Öckinger, E., Pärtel, M., Pino, J., Pöyry, J., Raatikainen, K.M., Sang, A., Stefanescu,
1269 C., Teder, T., Zobel, M., Steffan-Dewenter, I., 2010. Habitat fragmentation causes
1270 immediate and time-delayed biodiversity loss at different trophic levels. *Ecol. Lett.* 13, 597–
1271 605. <https://doi.org/10.1111/j.1461-0248.2010.01457.x>

1272 Kuussaari, M., Bommarco, R., Heikkinen, R.K., Helm, A., Krauss, J., Lindborg, R., Ockinger, E.,
1273 Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M., Steffan-Dewenter, I.,
1274 2009. Extinction debt: a challenge for biodiversity conservation. *Trends Ecol. Evol.* 24,
1275 564–71. <https://doi.org/10.1016/j.tree.2009.04.011>

1276 Lange, S., 2019. Trend-preserving bias adjustment and statistical downscaling with
1277 ISIMIP3BASD (v1.0). *Geosci. Model Dev.* 12, 3055–3070. [https://doi.org/10.5194/gmd-12-](https://doi.org/10.5194/gmd-12-3055-2019)
1278 3055-2019

1279 Lausch, A., Baade, J., Bannehr, L., Borg, E., Bumberger, J., Chabrilliat, S., Dietrich, P.,
1280 Gerighausen, H., Glässer, C., Hacker, J.M., Haase, D., Jagdhuber, T., Jany, S., Jung, A.,
1281 Karnieli, A., Kraemer, R., Makki, M., Mielke, C., Möller, M., Mollenhauer, H., Montzka, C.,
1282 Pause, M., Rogass, C., Rozenstein, O., Schmullius, C., Schrod, F., Schrön, M., Schulz, K.,
1283 Schütze, C., Schweitzer, C., Selsam, P., Skidmore, A.K., Spengler, D., Thiel, C.,
1284 Truckenbrodt, S.C., Vohland, M., Wagner, R., Weber, U., Werban, U., Wollschläger, U.,
1285 Zacharias, S., Schaepman, M.E., 2019. Linking remote sensing and geodiversity and their
1286 traits relevant to biodiversity—Part I: soil characteristics. *Remote Sens.* 11, 2356.
1287 <https://doi.org/10.3390/rs11202356>

1288 le Roux, P.C., Aalto, J., Luoto, M., 2013a. Soil moisture's underestimated role in climate change
1289 impact modelling in low-energy systems. *Glob. Chang. Biol.* 19, 2965–2975.
1290 <https://doi.org/10.1111/gcb.12286>

1291 le Roux, P.C., Luoto, M., 2014. Earth surface processes drive the richness, composition and

1292 occurrence of plant species in an arctic-alpine environment. *J. Veg. Sci.* 25, 45–54.
1293 <https://doi.org/10.1111/jvs.12059>

1294 le Roux, P.C., Virtanen, R., Luoto, M., 2013b. Geomorphological disturbance is necessary for
1295 predicting fine-scale species distributions. *Ecography (Cop.)*. 36, 800–808.
1296 <https://doi.org/10.1111/j.1600-0587.2012.07922.x>

1297 Leempoel, K., Parisod, C., Geiser, C., Daprà, L., Vittoz, P., Joost, S., 2015. Very high-resolution
1298 digital elevation models: are multi-scale derived variables ecologically relevant? *Methods*
1299 *Ecol. Evol.* 6, 1373–1383. <https://doi.org/10.1111/2041-210X.12427>

1300 Leitold, V., Keller, M., Morton, D.C., Cook, B.D., Shimabukuro, Y.E., 2015. Airborne lidar-based
1301 estimates of tropical forest structure in complex terrain: opportunities and trade-offs for
1302 REDD+. *Carbon Balance Manag.* 10, 3. <https://doi.org/10.1186/s13021-015-0013-x>

1303 Lembrechts, J.J., Alexander, J.M., Cavieres, L.A., Haider, S., Lenoir, J., Kueffer, C., McDougall,
1304 K., Naylor, B.J., Nuñez, M.A., Pauchard, A., Rew, L.J., Nijs, I., Milbau, A., 2017. Mountain
1305 roads shift native and non-native plant species' ranges. *Ecography (Cop.)*. 40, 353–364.
1306 <https://doi.org/10.1111/ecog.02200>

1307 Lembrechts, J.J., Lenoir, J., Roth, N., Hattab, T., Milbau, A., Haider, S., Pellissier, L., Pauchard,
1308 A., Ratier Backes, A., Dimarco, R.D., Nuñez, M.A., Aalto, J., Nijs, I., 2019. Comparing
1309 temperature data sources for use in species distribution models: From in-situ logging to
1310 remote sensing. *Glob. Ecol. Biogeogr.* 28, 1578–1596. <https://doi.org/10.1111/geb.12974>

1311 Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., Grenouillet, G.,
1312 2019. Species better track the shifting isotherms in the oceans than on lands. *bioRxiv*
1313 765776. <https://doi.org/10.1101/765776>

1314 Lenoir, J., Hattab, T., Pierre, G., 2017. Climatic microrefugia under anthropogenic climate
1315 change: implications for species redistribution. *Ecography (Cop.)*. 40, 253–266.
1316 <https://doi.org/10.1111/ecog.02788>

1317 Lenoir, J., Svenning, J.-C., 2015. Climate-related range shifts - a global multidimensional
1318 synthesis and new research directions. *Ecography (Cop.)*. 38, 15–28.
1319 <https://doi.org/10.1111/ecog.00967>

1320 Lenzen, M., LANE, A., Widmer-Cooper, A., Williams, M., 2009. Effects of land use on
1321 threatened species. *Conserv. Biol.* 23, 294–306. [https://doi.org/10.1111/j.1523-](https://doi.org/10.1111/j.1523-1739.2008.01126.x)
1322 [1739.2008.01126.x](https://doi.org/10.1111/j.1523-1739.2008.01126.x)

1323 Liu, L., Zhang, Y., Liu, L., Zhang, Y., 2011. Urban heat island analysis using the Landsat TM

1324 data and ASTER data: a case study in Hong Kong. *Remote Sens.* 3, 1535–1552.
1325 <https://doi.org/10.3390/rs3071535>

1326 Loran, C., Munteanu, C., Verburg, P.H., Schmatz, D.R., Bürgi, M., Zimmermann, N.E., 2017.
1327 Long-term change in drivers of forest cover expansion: an analysis for Switzerland (1850-
1328 2000). *Reg. Environ. Chang.* 17, 2223–2235. <https://doi.org/10.1007/s10113-017-1148-y>

1329 Luoto, M., Heikkinen, R.K., 2008. Disregarding topographical heterogeneity biases species
1330 turnover assessments based on bioclimatic models. *Glob. Chang. Biol.* 14, 483–494.
1331 <https://doi.org/10.1111/j.1365-2486.2007.01527.x>

1332 Luoto, M., Virkkala, R., Heikkinen, R.K., 2007. The role of land cover in bioclimatic models
1333 depends on spatial resolution. *Glob. Ecol. Biogeogr.* 16, 34–42.
1334 <https://doi.org/10.1111/j.1466-8238.2006.00262.x>

1335 Mackey, B.G., Lindenmayer, D.B., 2001. Towards a hierarchical framework for modelling the
1336 spatial distribution of animals. *J. Biogeogr.* 28, 1147–1166. <https://doi.org/10.1046/j.1365-2699.2001.00626.x>

1338 Madani, N., Kimball, J.S., Nazeri, M., Kumar, L., Affleck, D.L.R., 2016. Remote sensing derived
1339 fire frequency, soil moisture and ecosystem productivity explain regional movements in emu
1340 over Australia. *PLoS One* 11, e0147285. <https://doi.org/10.1371/journal.pone.0147285>

1341 Madritch, M.D., Kingdon, C.C., Singh, A., Mock, K.E., Lindroth, R.L., Townsend, P.A., 2014.
1342 Imaging spectroscopy links aspen genotype with below-ground processes at landscape
1343 scales. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 369, 20130194.
1344 <https://doi.org/10.1098/rstb.2013.0194>

1345 Mahecha, M.D., Gans, F., Sippel, S., Donges, J.F., Kaminski, T., Metzger, S., Migliavacca, M.,
1346 Papale, D., Rammig, A., Zscheischler, J., 2017. Detecting impacts of extreme events with
1347 ecological in situ monitoring networks. *Biogeosciences* 1–33. <https://doi.org/10.5194/bg-2017-130>

1349 Maiorano, L., Cheddadi, R., Zimmermann, N.E., Pellissier, L., Petitpierre, B., Pottier, J.,
1350 Laborde, H., Hurdu, B.I., Pearman, P.B., Psomas, A., Singarayer, J.S., Broennimann, O.,
1351 Vittoz, P., Dubuis, A., Edwards, M.E., Binney, H.A., Guisan, A., 2013. Building the niche
1352 through time: using 13,000 years of data to predict the effects of climate change on three
1353 tree species in Europe. *Glob. Ecol. Biogeogr.* 22, 302–317. <https://doi.org/10.1111/j.1466-8238.2012.00767.x>

1355 Malanson, G.P., Bengtson, L.E., Fagre, D.B., 2012. Geomorphic determinants of species
1356 composition of alpine tundra, Glacier National Park, U.S.A. *Arctic, Antarct. Alp. Res.* 44,

1357 197–209. <https://doi.org/10.1657/1938-4246-44.2.197>

1358 Malavasi, M., Barták, V., Jucker, T., Acosta, A.T.R., Carranza, M.L., Bazzichetto, M., 2019.

1359 Strength in Numbers: Combining Multi-Source Remotely Sensed Data to Model Plant

1360 Invasions in Coastal Dune Ecosystems. *Remote Sens.* 11, 275.

1361 <https://doi.org/10.3390/rs11030275>

1362 Malenovský, Z., Homolová, L., Lukeš, P., Buddenbaum, H., Verrelst, J., Alonso, L., Schaepman,

1363 M.E., Lauret, N., Gastellu-Etchegorry, J.-P., 2019. Variability and uncertainty challenges in

1364 scaling imaging spectroscopy retrievals and validations from leaves up to vegetation

1365 canopies. *Surv. Geophys.* 40, 631–656. <https://doi.org/10.1007/s10712-019-09534-y>

1366 Manzoor, S.A., Griffiths, G., Lukac, M., 2018. Species distribution model transferability and

1367 model grain size – finer may not always be better. *Sci. Rep.* 8, 7168.

1368 <https://doi.org/10.1038/s41598-018-25437-1>

1369 Marques, A., Martins, I.S., Kastner, T., Plutzer, C., Theurl, M.C., Eisenmenger, N., Huijbregts,

1370 M.A.J., Wood, R., Stadler, K., Bruckner, M., Canelas, J., Hilbers, J.P., Tukker, A., Erb, K.,

1371 Pereira, H.M., 2019. Increasing impacts of land use on biodiversity and carbon

1372 sequestration driven by population and economic growth. *Nat. Ecol. Evol.* 3, 628–637.

1373 <https://doi.org/10.1038/s41559-019-0824-3>

1374 Marrotte, R.R., Bowman, J., Brown, M.G.C., Cordes, C., Morris, K.Y., Prentice, M.B., Wilson,

1375 P.J., 2017. Multi-species genetic connectivity in a terrestrial habitat network. *Mov. Ecol.* 5,

1376 21. <https://doi.org/10.1186/s40462-017-0112-2>

1377 Martin, Y., Dyck, H. Van, Dendoncker, N., Titeux, N., 2013. Testing instead of assuming the

1378 importance of land use change scenarios to model species distributions under climate

1379 change. *Glob. Ecol. Biogeogr.* 22, 1204–1216. <https://doi.org/10.1111/geb.12087>

1380 Martinuzzi, S., Radeloff, V.C., Joppa, L.N., Hamilton, C.M., Helmers, D.P., Plantinga, A.J.,

1381 Lewis, D.J., 2015. Scenarios of future land use change around United States' protected

1382 areas. *Biol. Conserv.* 184, 446–455. <https://doi.org/10.1016/J.BIOCON.2015.02.015>

1383 Mathys, L., Zimmermann, N.E., Guisan, A., 2004. Spatial pattern of forest resources in a

1384 multifunctional landscape . *Int. Arch. Photogramm. Remote Sens. Spat. Inf. Sci.* 36, 340–

1385 342.

1386 McShea, W.J., 2014. What are the roles of species distribution models in conservation

1387 planning? *Environ. Conserv.* 41, 93–96. <https://doi.org/10.1017/S0376892913000581>

1388 Mellert, K.H., Fensterer, V., Küchenhoff, H., Reger, B., Kölling, C., Klemmt, H.J., Ewald, J.,

1389 2011. Hypothesis-driven species distribution models for tree species in the Bavarian Alps.
1390 J. Veg. Sci. 22, 635–646. <https://doi.org/10.1111/j.1654-1103.2011.01274.x>

1391 Merrick, M.J., Koprowski, J.L., 2017. Circuit theory to estimate natal dispersal routes and
1392 functional landscape connectivity for an endangered small mammal. Landsc. Ecol. 32,
1393 1163–1179. <https://doi.org/10.1007/s10980-017-0521-z>

1394 Meyfroidt, P., Lambin, E.F., Hertel, T.W., 2013. Globalization of land use: distant drivers of land
1395 change and geographic displacement of land use. Curr. Opin. Environ. Sustain. 5, 438–
1396 444. <https://doi.org/10.1016/J.COSUST.2013.04.003>

1397 Milanesi, P., Holderegger, R., Bollmann, K., Gugerli, F., Zellweger, F., 2017. Three-dimensional
1398 habitat structure and landscape genetics: a step forward in estimating functional
1399 connectivity. Ecology 98, 393–402. <https://doi.org/10.1002/ecy.1645>

1400 Miller, J., Franklin, J., 2002. Modeling the distribution of four v egetation alliances using
1401 generalized linear models and classification trees with spatial dependence 157.

1402 Mirtl, M., T. Borer, E., Djukic, I., Forsius, M., Haubold, H., Hugo, W., Jourdan, J., Lindenmayer,
1403 D., McDowell, W.H., Muraoka, H., Orenstein, D.E., Pauw, J.C., Peterseil, J., Shibata, H.,
1404 Wohner, C., Yu, X., Haase, P., 2018. Genesis, goals and achievements of Long-Term
1405 Ecological Research at the global scale: a critical review of ILTER and future directions.
1406 Sci. Total Environ. 626, 1439–1462. <https://doi.org/10.1016/J.SCITOTENV.2017.12.001>

1407 Mod, H.K., Scherrer, D., Luoto, M., Guisan, A., 2016. What we use is not what we know:
1408 environmental predictors in plant distribution models. J. Veg. Sci. 27, 1308–1322.
1409 <https://doi.org/10.1111/jvs.12444>

1410 Moeslund, J.E., Arge, L., Bøcher, P.K., Dalgaard, T., Odgaard, M. V, Nygaard, B., Svenning, J.-
1411 C., 2013. Topographically controlled soil moisture is the primary driver of local vegetation
1412 patterns across a lowland region. Ecosphere 4, art91. [https://doi.org/10.1890/ES13-](https://doi.org/10.1890/ES13-00134.1)
1413 00134.1

1414 Montané, J.M., Torres, R., 2006. Accuracy assessment of Lidar saltmarsh topographic data
1415 using RTK GPS. Photogramm. Eng. Remote Sensing 72, 961–967.

1416 Naumann, G., Barbosa, P., Carrao, H., Singleton, A., Vogt, J., Naumann, G., Barbosa, P.,
1417 Carrao, H., Singleton, A., Vogt, J., 2012. Monitoring drought conditions and their
1418 uncertainties in Africa using TRMM data. J. Appl. Meteorol. Climatol. 51, 1867–1874.
1419 <https://doi.org/10.1175/JAMC-D-12-0113.1>

1420 Navarro, L.M., Fernández, N., Guerra, C., Guralnick, R., Kissling, W.D., Londoño, M.C., Muller-

1421 Karger, F., Turak, E., Balvanera, P., Costello, M.J., Delavaud, A., El Serafy, G., Ferrier, S.,
 1422 Geijzendorffer, I., Geller, G.N., Jetz, W., Kim, E.-S., Kim, H., Martin, C.S., McGeoch, M.A.,
 1423 Mwampamba, T.H., Nel, J.L., Nicholson, E., Pettorelli, N., Schaepman, M.E., Skidmore, A.,
 1424 Sousa Pinto, I., Vergara, S., Vihervaara, P., Xu, H., Yahara, T., Gill, M., Pereira, H.M.,
 1425 2017. Monitoring biodiversity change through effective global coordination. *Curr. Opin.*
 1426 *Environ. Sustain.* 29, 158–169. <https://doi.org/10.1016/J.COSUST.2018.02.005>
 1427 Neilan, W.L., Barton, P.S., McAlpine, C.A., Wood, J.T., Lindenmayer, D.B., 2019. Contrasting
 1428 effects of mosaic structure on alpha and beta diversity of bird assemblages in a human-
 1429 modified landscape. *Ecography (Cop.)*. 42, 173–186. <https://doi.org/10.1111/ecog.02981>
 1430 Neteler, M., Metz, M., Rocchini, D., Rizzoli, A., Flacio, E., Engeler, L., Guidi, V., Lüthy, P.,
 1431 Tonolla, M., 2013. Is Switzerland suitable for the invasion of *Aedes albopictus*? *PLoS One*
 1432 8, e82090. <https://doi.org/10.1371/journal.pone.0082090>
 1433 Newbold, T., 2018. Future effects of climate and land-use change on terrestrial vertebrate
 1434 community diversity under different scenarios. *Proc. R. Soc. B Biol. Sci.* 285, 20180792.
 1435 <https://doi.org/10.1098/rspb.2018.0792>
 1436 Newbold, T., Hudson, L., Hill, S., Contu, S., Lysenko, I., Senior, R., Boerger, L., Bennett, D.J.,
 1437 Choimes, A., Collen, B., Day, J., De Palma, A., Diaz, S., Echeverria-Londono, S., Edgar,
 1438 M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y.,
 1439 Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Pinto Correia, D., Martin, C.D., Meiri, S.,
 1440 Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck,
 1441 S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W., Purvis, A.,
 1442 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520, 45–50.
 1443 <https://doi.org/10.1038/nature14324>
 1444 Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Gray, C.L., Scharlemann, J.P.W., Börger, L.,
 1445 Phillips, H.R.P., Sheil, D., Lysenko, I., Purvis, A., 2016. Global patterns of terrestrial
 1446 assemblage turnover within and among land uses. *Ecography (Cop.)*. 39, 1151–1163.
 1447 <https://doi.org/10.1111/ecog.01932>
 1448 Niittynen, P., Luoto, M., 2018. The importance of snow in species distribution models of arctic
 1449 vegetation. *Ecography (Cop.)*. 41, 1024–1037. <https://doi.org/10.1111/ecog.03348>
 1450 Normand, S., Treier, U.A., Randin, C., Vittoz, P., Guisan, A., Svenning, J.-C., 2009. Importance
 1451 of abiotic stress as a range-limit determinant for European plants: insights from species
 1452 responses to climatic gradients. *Glob. Ecol. Biogeogr.* 18, 437–449.
 1453 <https://doi.org/10.1111/j.1466-8238.2009.00451.x>

1454 Ofli, F., Meier, P., Imran, M., Castillo, C., Tuia, D., Rey, N., Briant, J., Millet, P., Reinhard, F.,
 1455 Parkan, M., Joost, S., 2016. Combining human computing and machine learning to make
 1456 sense of big (aerial) data for disaster response. *Big Data* 4, 47–59.
 1457 <https://doi.org/10.1089/big.2014.0064>

1458 Pagel, J., Schurr, F.M., 2012. Forecasting species ranges by statistical estimation of ecological
 1459 niches and spatial population dynamics. *Glob. Ecol. Biogeogr.* 21, 293–304.
 1460 <https://doi.org/10.1111/j.1466-8238.2011.00663.x>

1461 Patsiou, T.S., Conti, E., Theodoridis, S., Randin, C.F., 2017. The contribution of cold air pooling
 1462 to the distribution of a rare and endemic plant of the Alps. *Plant Ecol. Divers.* 10, 29–42.
 1463 <https://doi.org/10.1080/17550874.2017.1302997>

1464 Pazúr, R., Bolliger, J., 2017. Land changes in Slovakia: Past processes and future directions.
 1465 *Appl. Geogr.* 85, 163–175. <https://doi.org/10.1016/J.APGEOG.2017.05.009>

1466 Pearman, P.B., Randin, C.F., Broennimann, O., Vittoz, P., Knaap, W.O. van der, Engler, R.,
 1467 Lay, G. Le, Zimmermann, N.E., Guisan, A., 2008. Prediction of plant species distributions
 1468 across six millennia. *Ecol. Lett.* 11, 357–369. [https://doi.org/10.1111/j.1461-](https://doi.org/10.1111/j.1461-0248.2007.01150.x)
 1469 [0248.2007.01150.x](https://doi.org/10.1111/j.1461-0248.2007.01150.x)

1470 Pearson, R.G., Dawson, T.P., 2003. Predicting the impacts of climate change on the distribution
 1471 of species: are bioclimate envelope models useful? *Glob. Ecol. Biogeogr.* 12, 361–371.
 1472 <https://doi.org/10.1046/j.1466-822X.2003.00042.x>

1473 Pekin, B.K., Pijanowski, B.C., 2012. Global land use intensity and the endangerment status of
 1474 mammal species. *Divers. Distrib.* 18, 909–918. [https://doi.org/10.1111/j.1472-](https://doi.org/10.1111/j.1472-4642.2012.00928.x)
 1475 [4642.2012.00928.x](https://doi.org/10.1111/j.1472-4642.2012.00928.x)

1476 Pellissier, L., Meltofte, H., Hansen, J., Schmidt, N.M., Tamstorf, M.P., Maiorano, L., Aastrup, P.,
 1477 Olsen, J., Guisan, A., Wisz, M.S., 2013. Suitability, success and sinks: how do predictions
 1478 of nesting distributions relate to fitness parameters in high arctic waders? *Divers. Distrib.*
 1479 19, 1496–1505. <https://doi.org/10.1111/ddi.12109>

1480 Peón, J., Recondo, C., Fernández, S., F. Calleja, J., De Miguel, E., Carretero, L., Peón, J.,
 1481 Recondo, C., Fernández, S., F. Calleja, J., De Miguel, E., Carretero, L., 2017. Prediction of
 1482 topsoil organic carbon using airborne and satellite hyperspectral imagery. *Remote Sens.* 9,
 1483 1211. <https://doi.org/10.3390/rs9121211>

1484 Pereira, H.M., Ferrier, S., Walters, M., Geller, G.N., Jongman, R.H.G., Scholes, R.J., Bruford,
 1485 M.W., Brummitt, N., Butchart, S.H.M., Cardoso, A.C., Coops, N.C., Dulloo, E., Faith, D.P.,
 1486 Freyhof, J., Gregory, R.D., Heip, C., Hoft, R., Hurtt, G., Jetz, W., Karp, D.S., McGeoch,

1487 M.A., Obura, D., Onoda, Y., Pettorelli, N., Reyers, B., Sayre, R., Scharlemann, J.P.W.,
 1488 Stuart, S.N., Turak, E., Walpole, M., Wegmann, M., 2013. Essential Biodiversity Variables.
 1489 Science (80-.). 339, 277–278. <https://doi.org/10.1126/science.1229931>
 1490 Pereira, H.M., Navarro, L.M., Martins, I.S., 2012. Global Biodiversity Change: The Bad, the
 1491 Good, and the Unknown. *Annu. Rev. Environ. Resour.* 37, 25–50.
 1492 <https://doi.org/10.1146/annurev-environ-042911-093511>
 1493 Pettorelli, N., Wegmann, M., Skidmore, A., Mücher, S., Dawson, T.P., Fernandez, M., Lucas, R.,
 1494 Schaepman, M.E., Wang, T., O'Connor, B., Jongman, R.H.G., Kempeneers, P.,
 1495 Sonnenschein, R., Leidner, A.K., Böhm, M., He, K.S., Nagendra, H., Dubois, G., Fatoyinbo,
 1496 T., Hansen, M.C., Paganini, M., de Klerk, H.M., Asner, G.P., Kerr, J.T., Estes, A.B.,
 1497 Schmeller, D.S., Heiden, U., Rocchini, D., Pereira, H.M., Turak, E., Fernandez, N., Lausch,
 1498 A., Cho, M.A., Alcaraz-Segura, D., McGeoch, M.A., Turner, W., Mueller, A., St-Louis, V.,
 1499 Penner, J., Vihervaara, P., Belward, A., Reyers, B., Geller, G.N., 2016. Framing the
 1500 concept of satellite remote sensing essential biodiversity variables: challenges and future
 1501 directions. *Remote Sens. Ecol. Conserv.* 2, 122–131. <https://doi.org/10.1002/rse2.15>
 1502 Pinto-Ledezma, J., Cavender-Bares, Jeannine, 2020. Using remote sensing for modeling and
 1503 monitoring species distributions, in: Cavender-Bares, J, Gamon, J., Townsend, P. (Eds.),
 1504 Remote Sensing of Plant Biodiverist. Springer.
 1505 Potter, K.A., Arthur Woods, H., Pincebourde, S., 2013. Microclimatic challenges in global
 1506 change biology. *Glob. Chang. Biol.* 19, 2932–2939. <https://doi.org/10.1111/gcb.12257>
 1507 Pradervand, J.-N., Dubuis, A., Pellissier, L., Guisan, A., Randin, C., 2014. Very high resolution
 1508 environmental predictors in species distribution models. *Prog. Phys. Geogr.* 38, 79–96.
 1509 <https://doi.org/10.1177/0309133313512667>
 1510 Price, B., Kienast, F., Seidl, I., Ginzler, C., Verburg, P.H., Bolliger, J., 2015. Future landscapes
 1511 of Switzerland: risk areas for urbanisation and land abandonment. *Appl. Geogr.* 57, 32–41.
 1512 <https://doi.org/10.1016/J.APGEOG.2014.12.009>
 1513 Pulliam, H.R., 2000. On the relationship between niche and distribution. *Ecol. Lett.* 3, 349–361.
 1514 <https://doi.org/10.1046/j.1461-0248.2000.00143.x>
 1515 Randin, C.F., Engler, R., Normand, S., Zappa, M., Zimmermann, N.E., Pearman, P.B., Vittoz,
 1516 P., Thuiller, W., Guisan, A., 2009a. Climate change and plant distribution: local models
 1517 predict high-elevation persistence. *Glob. Chang. Biol.* 15, 1557–1569.
 1518 <https://doi.org/10.1111/j.1365-2486.2008.01766.x>
 1519 Randin, C.F., Jaccard, H., Vittoz, P., Yoccoz, N.G., Guisan, A., 2009b. Land use improves

1520 spatial predictions of mountain plant abundance but not presence-absence. *J. Veg. Sci.* 20,
1521 996–1008. <https://doi.org/10.1111/j.1654-1103.2009.01098.x>

1522 Randin, C.F., Vuissoz, G., Liston, G.E., Vittoz, P., Guisan, A., 2009c. Introduction of snow and
1523 geomorphic disturbance variables into predictive models of alpine plant distribution in the
1524 Western Swiss Alps. *Arctic, Antarct. Alp. Res.* 41, 347–361. [https://doi.org/10.1657/1938-](https://doi.org/10.1657/1938-4246-41.3.347)
1525 4246-41.3.347

1526 Rey, N., Volpi, M., Joost, S., Tuia, D., 2017. Detecting animals in African Savanna with UAVs
1527 and the crowds. <https://doi.org/10.1016/j.rse.2017.08.026>

1528 Rocchini, D., Boyd, D.S., Féret, J.-B., Foody, G.M., He, K.S., Lausch, A., Nagendra, H.,
1529 Wegmann, M., Pettorelli, N., 2016. Satellite remote sensing to monitor species diversity:
1530 potential and pitfalls. *Remote Sens. Ecol. Conserv.* 2, 25–36. <https://doi.org/10.1002/rse2.9>

1531 Rocchini, D., Marcantonio, M., Ricotta, C., 2017. Measuring Rao's Q diversity index from remote
1532 sensing: a n open source solution. *Ecol. Indic.* 72, 234–238.
1533 <https://doi.org/10.1016/J.ECOLIND.2016.07.039>

1534 Rosero-Vlasova, O.A., Vlassova, L., Pérez-Cabello, F., Montorio, R., Nadal-Romero, E., 2018.
1535 Modeling soil organic matter and texture from satellite data in areas affected by wildfires
1536 and cropland abandonment in Aragón, Northern Spain. *J. Appl. Remote Sens.* 12, 1.
1537 <https://doi.org/10.1117/1.JRS.12.042803>

1538 Rudel, T.K., 2007. Changing agents of deforestation: from state-initiated to enterprise driven
1539 processes, 1970–2000. *Land use policy* 24, 35–41.
1540 <https://doi.org/10.1016/J.LANDUSEPOL.2005.11.004>

1541 Rufin, P., Müller, H., Pflugmacher, D., Hostert, P., 2015. Land use intensity trajectories on
1542 Amazonian pastures derived from Landsat time series. *Int. J. Appl. Earth Obs. Geoinf.* 41,
1543 1–10. <https://doi.org/10.1016/J.JAG.2015.04.010>

1544 Santos, M.J., Khanna, S., Hestir, E.L., Greenberg, J.A., Ustin, S.L., 2016. Measuring landscape-
1545 scale spread and persistence of an invaded submerged plant community from airborne
1546 remote sensing. *Ecol. Appl.* 26, 1733–1744. <https://doi.org/10.1890/15-0615>

1547 Schneider, F.D., Kükenbrink, D., Schaepman, M.E., Schimel, D.S., Morsdorf, F., 2019.
1548 Quantifying 3D structure and occlusion in dense tropical and temperate forests using close-
1549 range LiDAR. *Agric. For. Meteorol.* 268, 249–257.
1550 <https://doi.org/10.1016/J.AGRFORMET.2019.01.033>

1551 Schneider, F.D., Leiterer, R., Morsdorf, F., Gastellu-Etchegorry, J.-P., Lauret, N., Pfeifer, N.,

1552 Schaepman, M.E., 2014. Simulating imaging spectrometer data: 3D forest modeling based
 1553 on LiDAR and in situ data. *Remote Sens. Environ.* 152, 235–250.
 1554 <https://doi.org/10.1016/j.rse.2014.06.015>
 1555 Schneider, F.D., Morsdorf, F., Schmid, B., Petchey, O.L., Hueni, A., Schimel, D.S., Schaepman,
 1556 M.E., 2017. Mapping functional diversity from remotely sensed morphological and
 1557 physiological forest traits. *Nat. Commun.* 8, 1441. [https://doi.org/10.1038/s41467-017-](https://doi.org/10.1038/s41467-017-01530-3)
 1558 [01530-3](https://doi.org/10.1038/s41467-017-01530-3)
 1559 Schulte, P.M., Healy, T.M., Fanguie, N.A., 2011. Thermal performance curves, phenotypic
 1560 plasticity, and the time scales of temperature exposure. *Integr. Comp. Biol.* 51, 691–702.
 1561 <https://doi.org/10.1093/icb/icr097>
 1562 See, L., Schepaschenko, D., Lesiv, M., McCallum, I., Fritz, S., Comber, A., Perger, C., Schill,
 1563 C., Zhao, Y., Maus, V., Siraj, M.A., Albrecht, F., Cipriani, A., Vakolyuk, M., Garcia, A.,
 1564 Rabia, A.H., Singha, K., Marcarini, A.A., Kattenborn, T., Hazarika, R., Schepaschenko, M.,
 1565 van der Velde, M., Kraxner, F., Obersteiner, M., 2015. Building a hybrid land cover map
 1566 with crowdsourcing and geographically weighted regression. *ISPRS J. Photogramm.*
 1567 *Remote Sens.* 103, 48–56. <https://doi.org/10.1016/J.ISPRSJPRS.2014.06.016>
 1568 Shmueli, G., 2009. To explain or to predict? *Stat. Sci.* 25, 289–310.
 1569 <https://doi.org/10.2139/ssrn.1351252>
 1570 Singh, A., Serbin, S.P., McNeil, B.E., Kingdon, C.C., Townsend, P.A., 2015. Imaging
 1571 spectroscopy algorithms for mapping canopy foliar chemical and morphological traits and
 1572 their uncertainties. *Ecol. Appl.* 25, 2180–2197. <https://doi.org/10.1890/14-2098.1>
 1573 Skidmore, A., Pettorelli, N., Coops, N.C., Geller, G.N., Hansen, M., Lucas, R., Muecher, C.,
 1574 O'Connor, B., Paganini, M., Pereira, H.M., Schaepman, M.E., Turner, W., Wang, T.,
 1575 Wegmann, M., 2015. Agree on biodiversity metrics to track from space. *Nature* 523, 5–7.
 1576 Skowronek, S., Ewald, M., Isermann, M., Kerchove, R. Van De, Lenoir, J., Aerts, R., Warrie, J.,
 1577 Hattab, T., Honnay, O., Schmidtlein, S., Rocchini, D., Somers, B., Feilhauer, H., 2017.
 1578 Mapping an invasive bryophyte species using hyperspectral remote sensing data. *Biol.*
 1579 *Invasions* 19, 239–254. <https://doi.org/10.1007/S10530-016-1276-1>
 1580 Sørensen, R., Seibert, J., 2007. Effects of DEM resolution on the calculation of topographical
 1581 indices: TWI and its components. *J. Hydrol.* 347, 79–89.
 1582 <https://doi.org/10.1016/J.JHYDROL.2007.09.001>
 1583 Spaete, L.P., Glenn, N.F., Derryberry, D.R., Sankey, T.T., Mitchell, J.J., Hardegree, S.P., 2011.
 1584 Vegetation and slope effects on accuracy of a LiDAR-derived DEM in the sagebrush

1585 steppe. *Remote Sens. Lett.* 2, 317–326. <https://doi.org/10.1080/01431161.2010.515267>

1586 Stoklosa, J., Daly, C., Foster, S.D., Ashcroft, M.B., Warton, D.I., 2015. A climate of uncertainty:
1587 accounting for error in climate variables for species distribution models. *Methods Ecol.*
1588 *Evol.* 6, 412–423. <https://doi.org/10.1111/2041-210X.12217>

1589 Strecha, C., Fletcher, A., Lechner, A., Erskine, P., Fua, P., 2012. Developing species specific
1590 vegetation maps using multi-spectral hyperspatial imagery from unmanned aerial vehicles.
1591 *ISPRS Ann. Photogramm. Remote Sens. Spat. Inf. Sci.* 1, 311–316.
1592 <https://doi.org/10.5194/isprsannals-I-3-311-2012>

1593 Stürck, J., Verburg, P.H., 2017. Multifunctionality at what scale? A landscape multifunctionality
1594 assessment for the European Union under conditions of land use change. *Landsc. Ecol.*
1595 32, 481–500. <https://doi.org/10.1007/s10980-016-0459-6>

1596 Svenning, J.-C., Sandel, B., 2013. Disequilibrium vegetation dynamics under future climate
1597 change. *Am. J. Bot.* 100, 1266–1286. <https://doi.org/10.3732/ajb.1200469>

1598 Talluto, M. V., Boulangeat, I., Vissault, S., Thuiller, W., Gravel, D., 2017. Extinction debt and
1599 colonization credit delay range shifts of eastern North American trees. *Nat. Ecol. Evol.* 1,
1600 0182. <https://doi.org/10.1038/s41559-017-0182>

1601 Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats
1602 to plant diversity in Europe. *Proc. Natl. Acad. Sci. U. S. A.* 102, 8245–50.
1603 <https://doi.org/10.1073/pnas.0409902102>

1604 Titeux, N., Henle, K., Mihoub, J.-B., Regos, A., Geijzenborffer, I.R., Cramer, W., Verburg, P.H.,
1605 Brotons, L., 2016. Biodiversity scenarios neglect future land-use changes. *Glob. Chang.*
1606 *Biol.* 22, 2505–2515. <https://doi.org/10.1111/gcb.13272>

1607 Torabzadeh, H., Leiterer, R., Hueni, A., Schaepman, M.E., Morsdorf, F., 2019. Tree species
1608 classification in a temperate mixed forest using a combination of imaging spectroscopy and
1609 airborne laser scanning. *Agric. For. Meteorol.* 279, 107744.
1610 <https://doi.org/10.1016/J.AGRFORMET.2019.107744>

1611 Torabzadeh, H., Morsdorf, F., Schaepman, M.E., 2014. Fusion of imaging spectroscopy and
1612 airborne laser scanning data for characterization of forest ecosystems – A review. *ISPRS*
1613 *J. Photogramm. Remote Sens.* 97, 25–35.
1614 <https://doi.org/10.1016/J.ISPRSJPRS.2014.08.001>

1615 Ummenhofer, C.C., Meehl, G.A., 2017. Extreme weather and climate events with ecological
1616 relevance : a review. *Philos. Trans. R. Soc. B.* <https://doi.org/10.1098/rstb.2016.0135>

1617 Ustin, S.L., Gamon, J.A., 2010. Remote sensing of plant functional types. *New Phytol.* 186,
 1618 795–816. <https://doi.org/10.1111/j.1469-8137.2010.03284.x>
 1619 van Asselen, S., Verburg, P.H., 2013. Land cover change or land-use intensification: simulating
 1620 land system change with a global-scale land change model. *Glob. Chang. Biol.* 19, 3648–
 1621 3667. <https://doi.org/10.1111/gcb.12331>
 1622 van Ewijk, K.Y., Randin, C.F., Treitz, P.M., Scott, N.A., 2014. Predicting fine-scale tree species
 1623 abundance patterns using biotic variables derived from LiDAR and high spatial resolution
 1624 imagery. *Remote Sens. Environ.* 150, 120–131. <https://doi.org/10.1016/J.RSE.2014.04.026>
 1625 van Gemert, J.C., Verschoor, C.R., Mettes, P., Epema, K., Koh, L.P., Wich, S., 2015. Nature
 1626 conservation drones for automatic localization and counting of animals, in: *European*
 1627 *Conference on Computer Vision*. Springer, Cham, pp. 255–270.
 1628 https://doi.org/10.1007/978-3-319-16178-5_17
 1629 Verburg, P.H., Crossman, N., Ellis, E.C., Heinimann, A., Hostert, P., Mertz, O., Nagendra, H.,
 1630 Sikor, T., Erb, K.-H., Golubiewski, N., Grau, R., Grove, M., Konaté, S., Meyfroidt, P.,
 1631 Parker, D.C., Chowdhury, R.R., Shibata, H., Thomson, A., Zhen, L., 2015. Land system
 1632 science and sustainable development of the earth system: a global land project
 1633 perspective. *Anthropocene* 12, 29–41. <https://doi.org/10.1016/J.ANCENE.2015.09.004>
 1634 Verburg, P.H., Neumann, K., Nol, L., 2011. Challenges in using land use and land cover data for
 1635 global change studies. *Glob. Chang. Biol.* 17, 974–989. <https://doi.org/10.1111/j.1365-2486.2010.02307.x>
 1636
 1637 Vierling, K.T., Vierling, L.A., Gould, W.A., Martinuzzi, S., Clawges, R.M., 2008. Lidar: shedding
 1638 new light on habitat characterization and modeling. *Front. Ecol. Environ.* 6, 90–98.
 1639 <https://doi.org/10.1890/070001>
 1640 Vinter, T., Dinnétz, P., Danzer, U., Lehtilä, K., 2016. The relationship between landscape
 1641 configuration and plant species richness in forests is dependent on habitat preferences of
 1642 species. *Eur. J. For. Res.* 135, 1071–1082. <https://doi.org/10.1007/s10342-016-0994-3>
 1643 Vitasse, Y., Klein, G., Kirchner, J.W., Rebetez, M., 2017. Intensity, frequency and spatial
 1644 configuration of winter temperature inversions in the closed La Brevine valley, Switzerland.
 1645 *Theor. Appl. Climatol.* 130, 1073–1083. <https://doi.org/10.1007/s00704-016-1944-1>
 1646 Vries, W. De, Wamelink, G.W.W., Dobben, H. van, Kros, J., Reinds, G.J., Mol-Dijkstra, J.P.,
 1647 Smart, S.M., Evans, C.D., Rowe, E.C., Belyazid, S., Sverdrup, H.U., Hinsberg, A. van,
 1648 Posch, M., Hettelingh, J.-P., Spranger, T., Bobbink, R., 2010. Use of dynamic soil–
 1649 vegetation models to assess impacts of nitrogen deposition on plant species composition:

1650 an overview. *Ecol. Appl.* 20, 60–79. <https://doi.org/10.1890/08-1019.1>
 1651 Walsh, S.J., Butler, D.R., Malanson, G.P., 1998. An overview of scale, pattern, process
 1652 relationships in geomorphology: a remote sensing and GIS perspective. *Geomorphology*
 1653 21, 183–205. [https://doi.org/10.1016/S0169-555X\(97\)00057-3](https://doi.org/10.1016/S0169-555X(97)00057-3)
 1654 Walsworth, T.E., Schindler, D.E., Colton, M.A., Webster, M.S., Palumbi, S.R., Mumby, P.J.,
 1655 Essington, T.E., Pinsky, M.L., 2019. Management for network diversity speeds evolutionary
 1656 adaptation to climate change. *Nat. Clim. Chang.* 9, 632–636.
 1657 <https://doi.org/10.1038/s41558-019-0518-5>
 1658 Waters, C.N., Zalasiewicz, J., Summerhayes, C., Barnosky, A.D., Poirier, C., Gałuszka, A.,
 1659 Cearreta, A., Edgeworth, M., Ellis, E.C., Ellis, M., Jeandel, C., Leinfelder, R., McNeill, J.R.,
 1660 Richter, D. deB, Steffen, W., Syvitski, J., Vidas, D., Wagreich, M., Williams, M., Zhisheng,
 1661 A., Grinevald, J., Odada, E., Oreskes, N., Wolfe, A.P., 2016. The Anthropocene is
 1662 functionally and stratigraphically distinct from the Holocene. *Science* 351, aad2622.
 1663 <https://doi.org/10.1126/science.aad2622>
 1664 Wearn, O.R., Reuman, D.C., Ewers, R.M., 2012. Extinction debt and windows of conservation
 1665 opportunity in the Brazilian Amazon. *Science* 337, 228–32.
 1666 <https://doi.org/10.1126/science.1219013>
 1667 Webster, C., Westoby, M., Rutter, N., Jonas, T., 2018. Three-dimensional thermal
 1668 characterization of forest canopies using UAV photogrammetry. *Remote Sens. Environ.*
 1669 209, 835–847. <https://doi.org/10.1016/J.RSE.2017.09.033>
 1670 Werkowska, W., Márquez, A.L., Real, R., Acevedo, P., 2017. A practical overview of
 1671 transferability in species distribution modeling. *Environ. Rev.* 25, 127–133.
 1672 <https://doi.org/10.1139/er-2016-0045>
 1673 Westoby, M.J., Brasington, J., Glasser, N.F., Hambrey, M.J., Reynolds, J.M., 2012. ‘Structure-
 1674 from-Motion’ photogrammetry: A low-cost, effective tool for geoscience applications.
 1675 *Geomorphology* 179, 300–314. <https://doi.org/10.1016/J.GEOMORPH.2012.08.021>
 1676 Wiens, J.J., Lapoint, R.T., Whiteman, N.K., 2015. Herbivory increases diversification across
 1677 insect clades. *Nat. Commun.* 6, 8370. <https://doi.org/10.1038/ncomms9370>
 1678 Woodward, F.I., 1990. The impact of low temperatures in controlling the geographical
 1679 distribution of plants. *Philos. Trans. R. Soc. B Biol. Sci.* 326, 585–593.
 1680 <https://doi.org/10.1098/rstb.1990.0033>
 1681 Wulder, M.A., Coops, N.C., Roy, D.P., White, J.C., Hermosilla, T., 2018. Land cover 2.0. *Int. J.*

1682 Remote Sens. 39, 4254–4284. <https://doi.org/10.1080/01431161.2018.1452075>
 1683 Xie, J., Kneubühler, M., Garonna, I., Notarnicola, C., De Gregorio, L., De Jong, R., Chimani, B.,
 1684 Schaepman, M.E., 2017. Altitude-dependent influence of snow cover on alpine land
 1685 surface phenology. *J. Geophys. Res. Biogeosciences* 122, 1107–1122.
 1686 <https://doi.org/10.1002/2016JG003728>
 1687 Yates, K.L., Bouchet, P.J., Caley, M.J., Mengersen, K., Randin, C.F., Parnell, S., Fielding, A.H.,
 1688 Bamford, A.J., Ban, S., Barbosa, A.M., Dormann, C.F., Elith, J., Embling, C.B., Ervin, G.N.,
 1689 Fisher, R., Gould, S., Graf, R.F., Gregr, E.J., Halpin, P.N., Heikkinen, R.K., Heinänen, S.,
 1690 Jones, A.R., Krishnakumar, P.K., Lauria, V., Lozano-Montes, H., Mannocci, L., Mellin, C.,
 1691 Mesgaran, M.B., Moreno-Amat, E., Mormede, S., Novaczek, E., Oppel, S., Ortuño Crespo,
 1692 G., Peterson, A.T., Rapacciuolo, G., Roberts, J.J., Ross, R.E., Scales, K.L., Schoeman, D.,
 1693 Snelgrove, P., Sundblad, G., Thuiller, W., Torres, L.G., Verbruggen, H., Wang, L., Wenger,
 1694 S., Whittingham, M.J., Zharikov, Y., Zurell, D., Sequeira, A.M.M., 2018. Outstanding
 1695 challenges in the transferability of ecological models. *Trends Ecol. Evol.* 33, 790–802.
 1696 <https://doi.org/10.1016/j.tree.2018.08.001>
 1697 Zarco-Tejada, P.J., Camino, C., Beck, P.S.A., Calderon, R., Hornero, A., Hernández-Clemente,
 1698 R., Kattenborn, T., Montes-Borrego, M., Susca, L., Morelli, M., Gonzalez-Dugo, V., North,
 1699 P.R.J., Landa, B.B., Boscia, D., Saponari, M., Navas-Cortes, J.A., 2018. Previsual
 1700 symptoms of *Xylella fastidiosa* infection revealed in spectral plant-trait alterations. *Nat.*
 1701 *Plants* 4, 432–439. <https://doi.org/10.1038/s41477-018-0189-7>
 1702 Zellweger, F., Baltensweiler, A., Ginzler, C., Roth, T., Braunisch, V., Bugmann, H., Bollmann,
 1703 K., 2016. Environmental predictors of species richness in forest landscapes: abiotic factors
 1704 versus vegetation structure. *J. Biogeogr.* 43, 1080–1090. <https://doi.org/10.1111/jbi.12696>
 1705 Zimmermann, N.E., Yoccoz, N.G., Edwards, T.C., Meier, E.S., Thuiller, W., Guisan, A.,
 1706 Schmatz, D.R., Pearman, P.B., 2009. Climatic extremes improve predictions of spatial
 1707 patterns of tree species. *Proc. Natl. Acad. Sci. U. S. A.* 106 Suppl, 19723–8.
 1708 <https://doi.org/10.1073/pnas.0901643106>
 1709 Zurell, D., Thuiller, W., Pagel, J., Cabral, J.S., Münkemüller, T., Gravel, D., Dullinger, S.,
 1710 Normand, S., Schiffers, K.H., Moore, K.A., Zimmermann, N.E., 2016. Benchmarking novel
 1711 approaches for modelling species range dynamics. *Glob. Chang. Biol.* 22, 2651–2664.
 1712 <https://doi.org/10.1111/gcb.13251>

1713
 1714