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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 Variables[1] (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, we[2] 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.

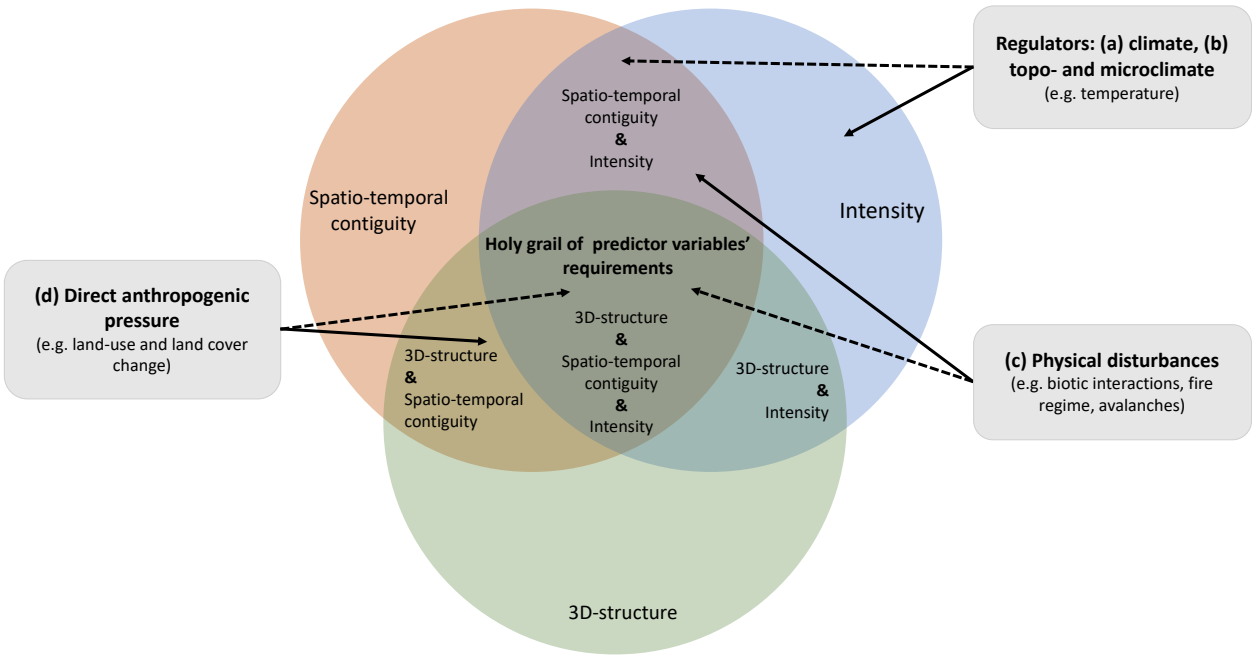

Fig. 1. Main categories of predictor variables in SDMs and requirements they meet. Variables consist of regulators (a, b), physical disturbances (c), and direct anthropogenic pressures (d) (*sensu* Austin and Smith, 1989; Guisan and Zimmermann, 2000; Randin et al., 2009c). Requirements are contiguity,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

Climate and its variability

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

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

362 Unlike high-resolution topographic information, the availability of spatial layers of soil conditions
363 is still limited (Fang et al., 2016). Yet spaceborne multispectral and imaging spectroscopy
364 instruments have a high potential for mapping topsoil carbon (Peón et al., 2017) and organic
365 matter content as well as soil physical properties (Rosero-Vlasova et al., 2018). These novel
366 possibilities should be tested in SDMs in the future.
367
368 *Physical disturbances*
369 Physical disturbances include geomorphological disturbances such as fluvial erosion, nivation,
370 landslides, rock falls and other disturbances such as mechanical abrasion by wind or fire.
371 Geomorphological processes in particular, create a wide range of disturbance regimes across
372 landscapes (Aalto et al., 2017; Gooseff et al., 2003; Niittynen and Luoto, 2018) that may
373 significantly alter local soil stability, moisture conditions, and nutrient availability (Kozłowska and
374 Rączkowska, 2002). Due to ongoing land-use and climate change, these disturbance regimes are
375 predicted to change rapidly as many geomorphical processes have a significant climate response
376 (Knight and Harrison, 2013), with small changes in climate forcing triggering large changes in
377 Earth system processes (Aalto et al., 2017). Accordingly, Earth system processes potentially
378 represent key drivers of local habitat heterogeneity (Cannone et al., 2016), variation in ecosystem
379 functioning (Frost et al., 2013), and species assemblages (le Roux et al., 2013b; Malanson et al.,
380 2012).
381 Recent studies demonstrate that the incorporation of direct Earth system processes variables –
382 as opposed to the indirect topographic and soil surface properties used as surrogates in plant
383 SDMs (Dirnböck et al., 2003; Mellert et al., 2011) – can improve the explanatory and predictive
384 power of SDMs (le Roux et al., 2013b; le Roux and Luoto, 2014; Niittynen and Luoto, 2018;
385 Randin et al. 2009a). However, the type and necessity of including disturbance variables in
386 models are highly environment-specific. For decades, remote sensing data have been used for

387 the mapping of geomorphological landforms and processes (Walsh et al., 1998). The high spatial
388 resolution of airborne photographs provides a valuable data source in that context, particularly for
389 detecting smaller landforms (e.g. 1-10 m). Yet, the precision (< 10 m) and increasing temporal
390 resolution (revisit time of 1-5 days) of satellite data, such as WorldView 3
391 (http://worldview3.digitalglobe.com), the Planetscope satellite constellation
392 (https://www.planet.com), or open access ESA Sentinel-2 (https://sentinel.esa.int), can now
393 compete with that of aerial photography. High-resolution satellite imagery is thereby becoming a
394 valuable data source for the modeling of dynamic processes. Attempts to include remote sensing-
395 based geomorphological and other non-anthropogenic physical disturbances into SDMs include
396 Miller and Franklin (2002) with landforms derived from a DEM, and Connell et al. (2017) as well
397 as Madani et al. (2016) for fire.
398
399 *Direct anthropogenic pressure*
400 The availability of spatially and temporally highly resolved land-cover information is central to
401 many monitoring programs and land-cover mapping is probably one of the oldest application of
402 remote sensing, starting with aerial photographs from hot air balloon in the 1860's and from
403 airplane in the 1910's (Fuller et al., 1994). Assessments of changes in land systems range from
404 local to regional and global (Stürck and Verburg, 2017; van Asselen and Verburg, 2013) and from
405 historical (Bolliger et al., 2017; Kaim et al., 2016; Loran et al., 2017) to predictive, with scenario-
406 based assessments of potential future changes in land use (Martinuzzi et al., 2015; Pazúr and
407 Bolliger, 2017; Price et al., 2015).
408 Changes in land cover and land use affect biodiversity in different ways. In the case of
409 urbanization, there is usually a complete replacement of (semi-)natural open land with buildings
410 or other impervious infrastructures such as roads, which profoundly changes species distributions
411 (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 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

516 lag times. The Anthropocene is an era of rapid environmental changes. Under such conditions,
517 lag times in cause-effect chains may severely confound the identification of species-environment
518 relations via correlated distribution patterns. Rapid climate change, for example, is expected to
519 cause a severe disequilibrium between climate and species distribution due to both slow
520 colonization of areas that become newly suitable and delayed extinction from those sites that are
521 no longer suitable to the species (i.e., extinction debts; Dullinger et al., 2012; Svenning and
522 Sandel, 2013; Talluto et al., 2017). Land-use changes may have similar effects and many studies
523 have demonstrated that in landscapes undergoing changes in human usage, spatial biodiversity
524 patterns often represent habitat configurations of decades back rather than current ones (Auffret
525 et al., 2018; Krauss et al., 2010). Matching current species distributions and environmental
526 conditions in statistical models will hence result in flawed correlation and, as a corollary,
527 inappropriate prediction of future development. Remote sensing data products offer a way forward
528 here, because time series of many of these products now cover two decades, and several of them
529 up to five (He et al., 2015). These time series have great potential in detecting and quantifying lag
530 times, e.g. in the response of biological populations to land-cover conversions (Wearn et al.,
531 2012). Incorporating these lag times into models of species responses to past, current, and future
532 environmental change has important ramifications for the management of biodiversity because it
533 defines 'windows of opportunity' for mitigating the anticipated consequences (Kuussaari et al.,
534 2009; Wiens et al., 2015).
535 One reason for the limited transferability of purely correlative models is the generally coarse or
536 inadequate spatial and temporal resolution of the data used to calibrate models (Connor et al.,
537 2018; Manzoor et al., 2018; Potter et al., 2013). This spatial-resolution paradox (Lenoir et al.,
538 2017) is inherent to correlative models and stems from the spatial mismatch between the
539 resolution at which the predictor variables (e.g. biophysical variables, see section 2) are available,
540 the resolution that matches the response variables (e.g., species occurrence, presence-absence,

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

543 Here, we argue that remote sensing could be used to better calibrate SDMs, by integrating
544 spatially and temporally (through multiple years) more proximal environmental data to derive more
545 comprehensive quantifications of species' response curves along environmental gradients (see
546 Austin and Gaywood, 1994). An improved calibration process may in turn increase the spatial and
547 temporal transferability of both correlative and process-based models. This can be illustrated by
548 focusing on environmentally-specific species response curves, such as temperature response
549 curves (sensu Austin, 2002; Fig. 2(a)) and thermal performance curves (*sensu* Schulte et al.,
550 2011; Fig. 2(a)-(b)) are at the foundation of both correlative (Guisan and Zimmermann, 2000) and
551 certain types of process-based (Kearney and Porter, 2009) models, respectively. Temperature
552 response curves generated by SDMs are usually parameterized through the statistical
553 relationship between field observations and spatial layers of temperature. Temperature
554 performance curves used in process-based models on the other hand are best parameterized
555 from experimental data depicting metabolic requirements, usually in the absence of competition
556 (e.g., Chuine and Beaubien, 2001). Because they explicitly rely on a physiological basis,
557 temperature performance curves are expected to better identify species thermal tolerance limits
558 that set range boundaries and to be thus more robust when extrapolating species redistributions
559 under future climate change (Eckert et al., 2017). However, physiologically-based species
560 performance curves represent the fundamental rather than post-interactive realized niches of
561 species (Hutchinson, 1978; Pulliam, 2000). Such performance curves are not as time- and cost-
562 efficient as statistically-based species response curves. For some species, the quantifications of
563 statistically-based performance curves by the integration of remote sensing data (Fig. 2(c)) might
564 better inform on the real microhabitat conditions experienced by living organisms, and thus might
565 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 (Chuine 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.

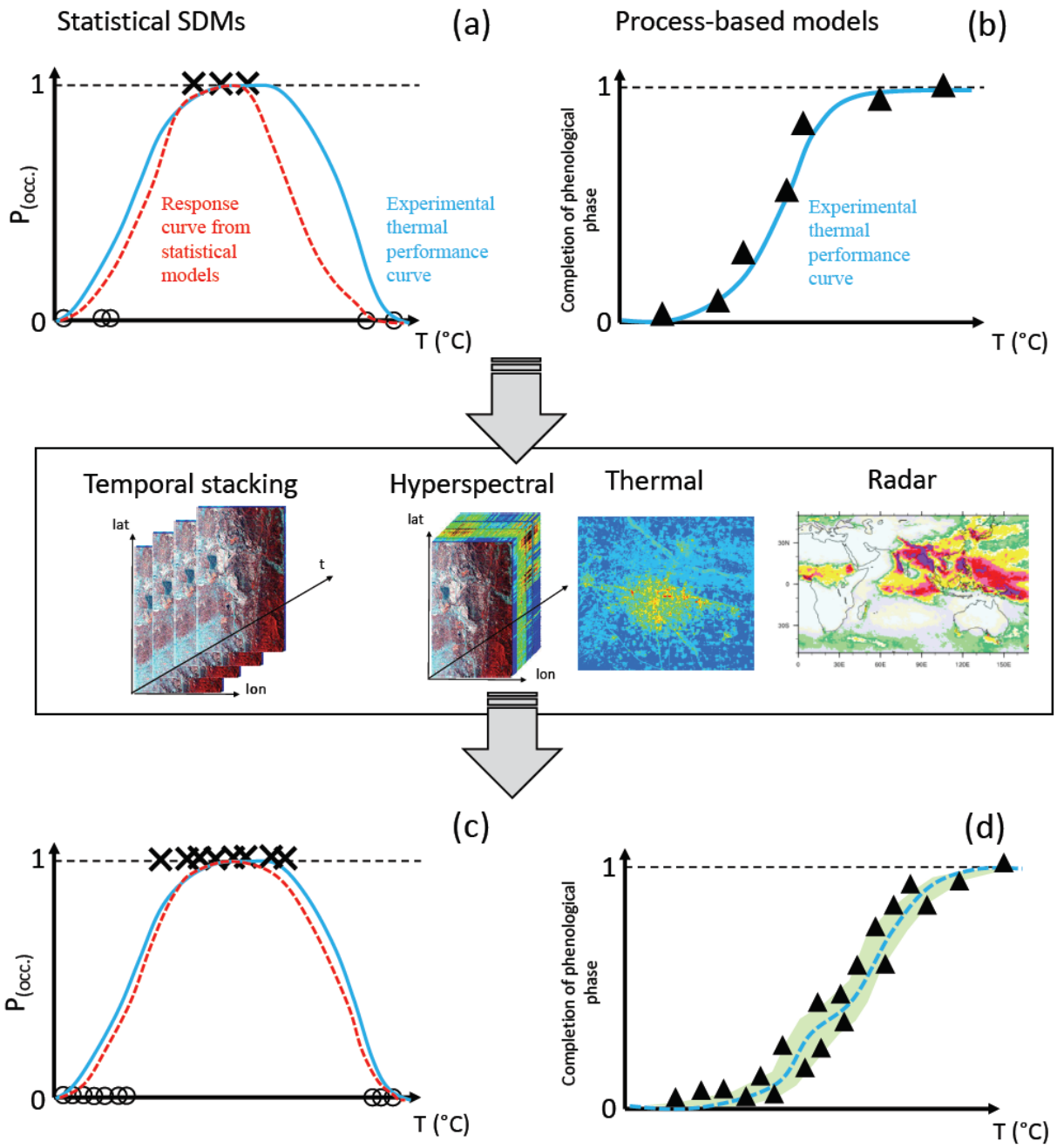

Fig. 2. Temporal stacking of imaging spectroscopy, thermal or radar images for improving response curves of statistical (a and c) and process-based (b and d) models. Thermal response curves derived from statistical models (a) describe the realized thermal niche of species whereas experimental thermal 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

620 of species in the near future. Beyond the detection of species, new possibilities are also emerging
621 for capturing plant functional types using spectroscopy (Ustin and Gamon, 2010). Accurately
622 mapping of some functional traits such as canopy traits (Asner and Martin, 2009; Singh et al.,
623 2015) and changes in other plant traits (Jetz et al., 2016; Schneider et al., 2017) is now also
624 possible. Direct species detection and the link of spectra to the tree of life (Cavender-Bares et al.,
625 2017) can equally be achieved by using a combination of high spatial and high spectral resolution.
626 Spectra from leaves (Cavender-Bares et al., 2016; Deacon et al., 2017) can be used with high
627 accuracy to differentiate populations within a species and to separate hybrids from parental
628 species. Partial Least Squares Regression methods applied to spectral profiles differentiate
629 species with higher accuracy than genotypes and clades with higher accuracy than species
630 (Cavender-Bares et al., 2016). In some cases, with 1 m^2 spatial resolution remote sensing allows
631 differentiation of different genotypes of poplar clones (Madritch et al., 2014). Tree canopies are
632 likely to be well distinguished if functional information on morphology and physiology at species
633 level are available (Torabzadeh et al., 2019). In recent years, the use of remote sensing has
634 enabled great advances in both functional as well as scaling-based approaches (Gamon et al.,
635 2019; Malenovský et al., 2019). In forests where species groups are well characterized and occur
636 in clumps, species distributions can be fairly readily mapped using satellite derived data (Chastain
637 and Townsend, 2007). Many living resources exist that contain geolocated and botanically
638 identified trees for developing spectral libraries for tree canopies.
639 UAVs or drones are mainly used to capture data with limited spectral resolution, to acquire thermal
640 data, or to produce very high-resolution digital elevation models by means of
641 stereophotogrammetry (Coops et al., 2019). UAVs can notably serve to overcome the issue of
642 partially missing spectral resolution with high-density time series (Böhler et al., 2019). Multi-View
643 Stereo analysis (Furukawa and Ponce, 2010) and Structure-from-Motion (Westoby et al., 2012)
644 algorithms are increasingly used as they make it possible to estimate three-dimensional structures
645 from partly overlapping image sequences. These approaches are very useful to analyze forest

646 and vegetation structures (Webster et al., 2018) and also to model marine environments including
647 the complex structure of coral reefs (Ferrari et al., 2016), a domain of particular interest in the
648 current period of intense coral bleaching (Walsworth et al., 2019).
649 Another function is the collection of animal occurrences to calibrate SDMs with presence only or
650 presence/absence data. Van Gemert et al. (2015) evaluated how animal detection and animal
651 counting could be implemented on the basis of a combination of images acquired by drones and
652 state-of-the-art object recognition methods. Most of the time, such images are used to carry out
653 surveys and to count animals in a management or conservation projects (Hodgson et al., 2018;
654 Koh and Wich, 2012). However, as all UAVs are equipped with a GPS device, the exact location
655 of investigated individuals can also be retrieved from precisely georeferenced image data. The
656 main challenge is related to the detection and recognition of the correct species by means of
657 machine learning algorithms (Kellenberger et al., 2018; Ofli et al., 2016; Rey et al., 2017). Beyond
658 this step, the generation of presence/absence of a single taxon is straightforward. This is a
659 component included in the concept of Next Generation Species Distribution Models proposed by
660 He et al. (2015).
661
662 *Improving integrated and dynamic range models*
663 Demographic processes and demographic data are increasingly integrated into models of the
664 spatiotemporal dynamics of species' ranges. This results from the realization that considering
665 dynamic aspects is important and potentially markedly improves the quantification of ecological
666 niches, the process-based understanding of range dynamics, and the forecasting of species
667 responses to environmental change (Pagel and Schurr, 2012). This is because commonly-used
668 static SDMs ignore spatial population dynamics, which can cause mismatches between species
669 niches and species distributions (Holt, 2009; Pellissier et al., 2013). The data needed to
670 parameterize dynamic range models can be obtained from demographic field measurements and
671 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).

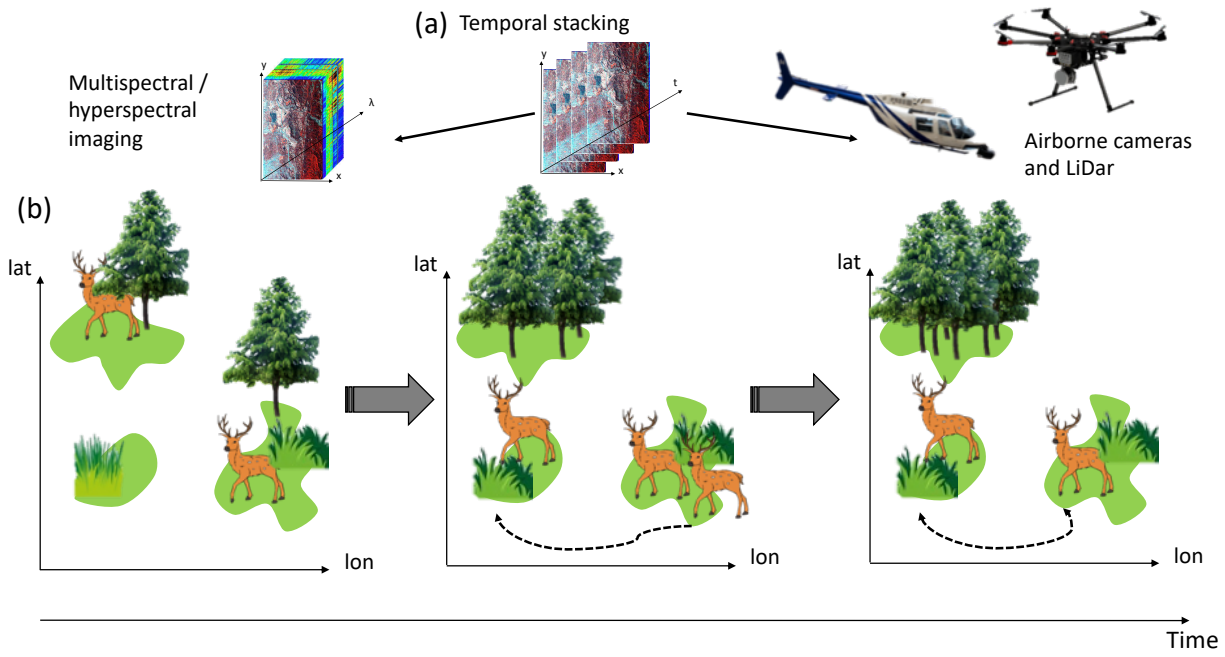

Fig. 3. Acquisition of demographic parameters for dynamic range models with time series of multispectral and / or imaging spectroscopy and airborne laser scanning data (a). The combination of such data allows to track movements of animals in suitable habitats.

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

707 hemlock (*Tsuga canadensis*) stands in the eastern United States due to invasion of the exotic
708 woolly adelgid (*Adelges tsugae*) (Hanavan et al., 2015). Recent work has also shown that a
709 combination of imaging sepctroscopy and thermal data can be used to diagnose *Xylella fastidiosa*
710 plants that are visually asymptomatic (Zarco-Tejada et al., 2018), and that airborne imaging
711 spectroscopy can be used to track the spread of invasive submerged aquatic vegetation at high
712 spatial resolution (Santos et al., 2016). These examples, and others from the early detection of
713 moss species (Skowronek et al., 2017) and the assessment of ecosystem processes in forests
714 (Ewald et al., 2018) illustrate the high potential of leveraging the rich information content of
715 imaging spectroscopy data, for the description of biotic environments in SDMs.
716

717 **4. Conclusions**

718 In their review, He et al. (2015) discussed the importance of remote sensing data for the
719 development of new predictor variables and the next generation of SDMs, which will include
720 spatially explicit values of uncertainty. Here we argue that an additional value of remote sensing
721 data lies in their temporal coverage (see section 3, paragraph and Fig. 2), which could overcome
722 the inability of current temporally-aggregated variables to reflect the intensity or the frequency of
723 biophysical processes and contribute to fulfilling all requirements across variables (Fig. 1). Taking
724 advantage of long-term time series of remote sensing data to extract (absolute) extremes as well
725 as frequencies and improve both these variables and the models in which they are used would
726 be an avenue to explore through formal evaluation and model improvement (e.g. Zimmermann et
727 al., 2009).
728 Temporal stacking of available time series (see section 3, paragraph and Fig. 2) can also be
729 performed to better capture the realized niche of species, their actual rather than potential
730 distributions, and increase the transferability of SDMs. In this context, evidence exists that building
731 the niche as an ensemble through time allows a better understanding and forecasting of species'
732 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

759 of land use are less available and land-use changes, variability, and intensity are often neglected
760 in SDMs, despite their potentially critical importance for species distributions. Despite recent
761 progress to develop indicators of changes in management and land-use intensity obtained from
762 remote sensing, online access to spatially explicit data of land use can be improved.
763 This is particularly critical to identify the contribution of land use in SDMs applied as explanatory
764 tools or to improve the accuracy of projections of SDMs integrated in monitoring programs.
765
766 *In situ monitoring, modeling, and remote sensing*
767 Although developments of remote sensing and SDM techniques have occasionally intersected
768 over the last 30 years, combining these two fields better has great potential for future scientific
769 progress. In line with Franklin and colleagues (Franklin et al., 2016) and others, we advocate a
770 closer integration of remote sensing in the monitoring and modeling of species and ecosystems
771 to better understand and predict current and future impacts of global change drivers on
772 biodiversity (Fernandez et al., 2019). We stress that models should serve the same fundamental
773 role in ecological monitoring as in any other scientific activity; that is, both the *a priori* guiding of
774 monitoring designs, and the *a posteriori* guiding of data analyses. Essential elements of the
775 monitoring design are management actions, replicated spatial climatic gradients, as well as
776 temporal resolution and extents that capture both fast and slow processes. Ecosystem-based
777 monitoring should be dynamic and adaptive in the sense that models and monitoring designs are
778 iteratively improved by new empirical results, new technologies and the evolving needs of
779 stakeholders (Ims and Yoccoz, 2017; Fig. 4). Once conceptual models (Fig. 4(a)) and appropriate
780 monitoring designs (Fig. 4(b)) have been built, field data can be collected (Fig. 4(c)) for tracking
781 the trajectories of individual species or the entire ecosystems. In this context, SDMs can serve as
782 tools to identify the main drivers of changes or to project the fate of species or ecosystems (by
783 e.g. stacked SDMs; Calabrese et al., 2014; Guisan and Rahbek, 2011; Fig. 4(d)). Finally, new
784 field monitoring can later validate projections of SDMs and the robustness of conceptual models

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

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

798 The SDGs are one of the key global frameworks for addressing the environmental challenges of
799 the Anthropocene. From a biodiversity perspective, to safeguard life below water (SDG 14) and
800 life on land (SDG 15) it is crucial to characterize and understand current species distributions and
801 how these may change under future land use and climate scenarios. SDMs make an essential
802 contribution to providing this information but have several important limitations that can
803 compromise their accuracy and hence the effectiveness of resulting conservation interventions
804 and environmental policy. We suggest that, together with novel methodological applications such
805 as the temporal image stacking, currently available and upcoming remote sensing data can
806 alleviate or resolve many of the data gaps that constrain SDMs. However, there is the risk that
807 non-specialists may unintentionally misinterpret remote sensing data, and that key data
808 requirements for SDMs are not fully appreciated. We argue that greater collaboration between
809 the two communities by developing jointly data platforms with standardized metadata and
810 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.

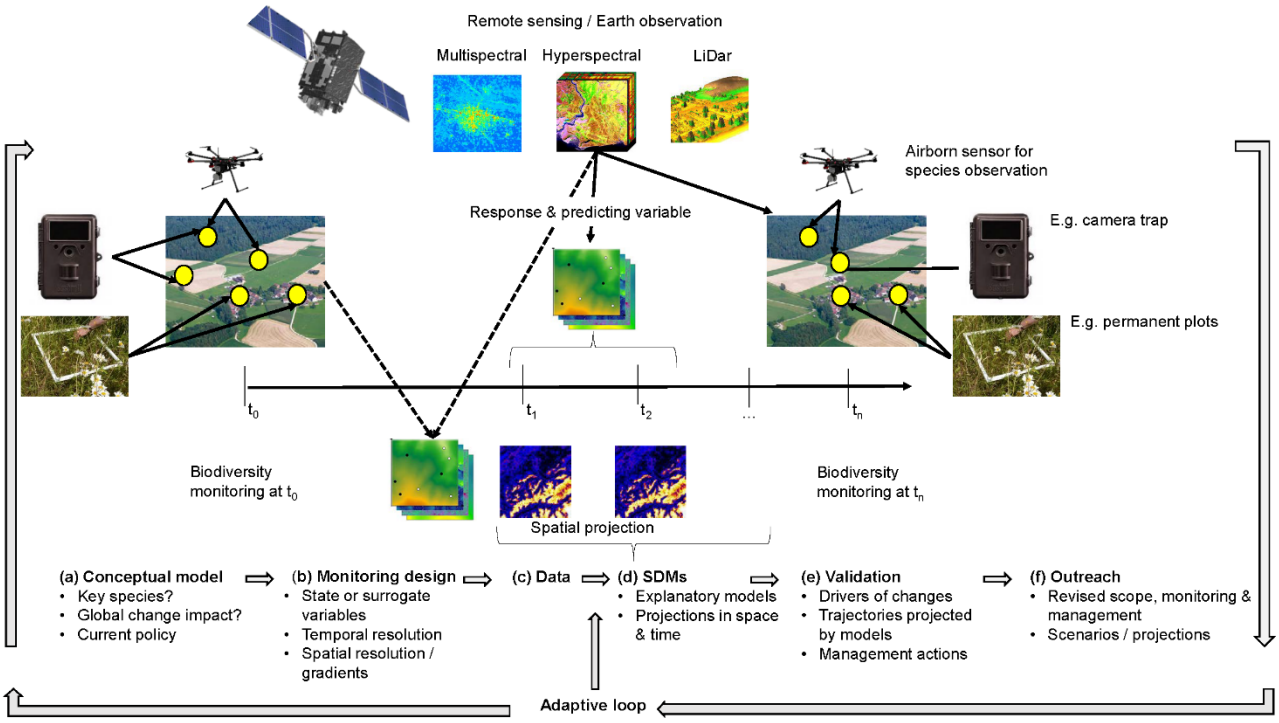

Fig. 4. An ideal loop of adaptive monitoring in which remote sensing data and SDMs are combined (adapted from Ims and Yoccoz, 2017).

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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

826 models *sensu* Guisan et al. 2017) are methods that relate field observations or museum
827 specimens (e.g. occurrences, abundances, or species' traits) to environmental predictor
828 variables. In such models, processes are empirically inferred from a combination of statistically
829 or theoretically derived response curves (Guisan et al. 2017). In contrast, process-based models
830 build upon explicit causal relationships determined experimentally. In these models, processes
831 such as phenology and distribution are explicitly described (see Chuine and Régnière, 2017),
832 which increases the confidence in extrapolating beyond the known spatiotemporal extent (Zurell
833 et al., 2016). The continuum between these two modeling approaches includes hybrid (e.g.
834 Dullinger et al., 2012), dynamic range (e.g. Cotto et al., 2017; Engler et al., 2012; Pagel and
835 Schurr, 2012), and integrated models (Pagel and Schurr, 2012).
836

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