Biodiversity monitoring, earth observations and the ecology of scale

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Abstract

Human activity and land-use change are dramatically altering the sizes, geographical distributions and functioning of biological populations worldwide, with tremendous consequences for human well-being. Yet our ability to measure, monitor and forecast biodiversity change – crucial to addressing it – remains limited. Biodiversity monitoring systems are being developed to improve this capacity by deriving metrics of change from an array of *in situ* data (e.g. field plots or species occurrence records) and Earth observations (EO; e.g. satellite or airborne imagery). However, there are few ecologically based frameworks for integrating these data into meaningful metrics of biodiversity change. Here, I describe how concepts of pattern and scale in ecology could be used to design such a framework. I review three core topics: the role of scale in measuring and modelling biodiversity patterns with EO, scale-dependent challenges linking *in situ* and EO data and opportunities to apply concepts of pattern and scale to EO to improve biodiversity mapping. From this analysis emerges an actionable approach for measuring, monitoring and forecasting biodiversity change, highlighting key opportunities to establish EO as the backbone of global-scale, science-driven conservation.

Keywords

Biodiversity monitoring, biogeography, Earth observations, modelling, pattern, scale, spatial ecology.

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INTRODUCTION

Global biodiversity monitoring is a crucial but challenging task, as human activities are changing the structure and composition of biological populations at all taxonomic levels (Dirzo *et al.* 2014; Ceballos *et al.* 2017). Mitigating biodiversity loss will require understanding the rates, magnitudes and geography of these changes (Laurance *et al.* 2012; Mendenhall *et al.* 2014). However, considering the scope of action required for mitigation, our knowledge of global biodiversity change remains limited (Daily 1999; Pereira *et al.* 2012). Furthermore, what is known about biodiversity change is complicated by taxonomic, geographical and temporal scale biases (Boakes *et al.* 2010; Donaldson *et al.* 2016; Gonzalez *et al.* 2016).

Novel biodiversity monitoring systems are being developed to systematically assess change for multiple taxa over large extents (Scholes *et al.* 2008, 2012; Fernández *et al.* 2015). To support these systems, several groups have developed novel approaches to monitor species, communities and ecosystems over time using globally consistent metrics of change (Butchart *et al.* 2010; Jetz *et al.* 2012; Metzger *et al.* 2013; Pereira *et al.* 2013). These metrics are biological, sensitive to change and ecosystem agnostic, enabling consistent monitoring protocols worldwide (e.g. GEO BON 2017). These efforts have been greatly bolstered by increasing access to globally available *in situ* biodiversity observations (Geijzendorffer *et al.* 2016; Culina *et al.* 2018). However, as *in situ* data alone are often insufficient for assessing global diversity patterns (*sensu*

the Linnean and Wallacean shortfalls; Bini *et al.* 2006; Brito 2010), researchers have looked for complementary data to support monitoring efforts.

Earth observations (EO; e.g. satellite or airborne imagery) complement *in situ* data by providing repeat, thematically consistent and spatially continuous measurements of terrestrial ecosystems, characterising biodiversity patterns over large, undersampled areas. However, linking field and EO data faces many challenges. These include overcoming incomplete sampling efforts (i.e. where field measurements do not adequately characterise the extent of environmental variation; Marvin & Asner 2016) and reconciling scale mismatches (e.g. where field plots are much smaller than EO pixels). Developing EO-based biodiversity monitoring systems will require a comprehensive approach to link these data (Turner 2014; Pettorelli *et al.* 2016).

Scale plays a key role in both ecology and EO science, and identifying shared scaling dynamics could provide a basis for bridging these disciplines. Understanding the roles of spatial and temporal scales in biological communities is a central topic in ecology, and is referred to as the problem of pattern and scale (Wiens 1989; Levin 1992). The problem of pattern and scale emphasises that multiple ecological processes often drive biodiversity patterns, and that these processes can act across multiple spatial and organismal scales (Withers & Meentemeyer 1999; Waring & Running 2010; Chase & Knight 2013). Therefore, there is rarely a single measurement scale that best identifies how specific processes drive patterns (Hutchinson 1953). EO measurements are subject to similar
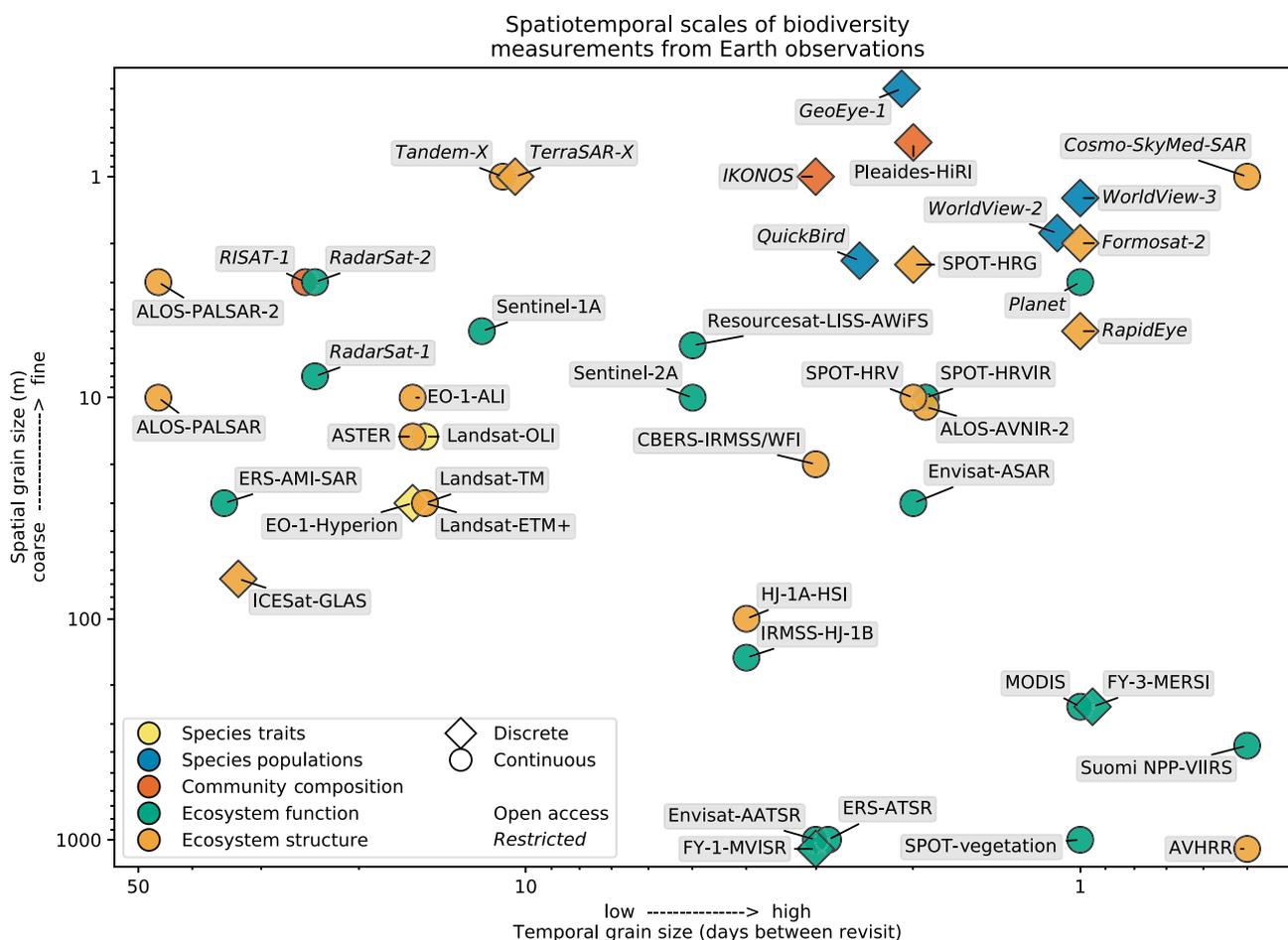
Figure 1 Log–log plot of spatial and temporal and grain sizes for 44 current and historic satellite Earth observation (EO) sensors, coloured by biodiversity pattern type. Several sensors have been used to measure multiple biodiversity patterns, and the most cited or most novel were selected in these cases. See Table S1 for references to which patterns were measured by each sensor, and for the accompanying study.

scale dependencies: the grain size of an EO sensor often determines which patterns can be measured (Fig. 1; Lechner *et al.*, 2012; Anderson 2012; Nagendra *et al.* 2013), and multi-scale EO analyses can reveal the influences of multiple processes driving biodiversity patterns (Keil *et al.* 2012; Taylor *et al.* 2015). Applying concepts of pattern and scale in ecology to EO could provide a means to better link these fields, paving the way for improved biodiversity monitoring.

Here, I review the scales at which EO have been used to measure and model metrics of biodiversity change, and the role of scale in linking field data with EO. This is not strictly a review of which biodiversity patterns EO can measure (*sensu* Roughgarden *et al.* 1991; Turner *et al.* 2003; Wang *et al.* 2010; Pettorelli *et al.* 2014b; Lausch *et al.* 2016). Instead, this review addresses three questions: (1) At what scales have current and historical EO been used to measure or model spatial biodiversity patterns? (2) What are the major challenges linking field-based and EO-based biodiversity measurements, and how does scale impact these challenges? and (3) How can concepts of pattern and scale, applied to EO, facilitate the translation of biodiversity patterns across scales? This work aims to further integrate EO into biodiversity monitoring systems, and to support science-driven conservation efforts.

COMPONENTS OF PATTERN AND SCALE IN ECOLOGY

Explorations of pattern and scale in ecology focus on two distinct but related measurement scales: grain size and extent (Box 1). In this review, I refer to these scales in a spatial sense, though temporal grain size could describe the frequency of observations (e.g. one diurnal cycle for net primary productivity) and temporal extent could describe the total time over which an ecological process occurs (e.g. phenological variation throughout a year). Furthermore, I adopt the classes and metrics of biodiversity change from the Essential Biodiversity Variables framework (Pereira *et al.* 2013), and refer to these metrics as biodiversity patterns. This framework captures the multiple biological scales of diversity (i.e. variation in genes, species, communities and ecosystems) as opposed to a more narrow interpretation that refers to biodiversity as variations in species richness, abundance and evenness. I believe these disaggregated classes and metrics more comprehensively address the patterns that can be measured and modelled using EO. In this section I discuss how concepts of pattern and scale in ecology apply in biodiversity and EO contexts, then I review domains of scale, which constrain efforts to generalise patterns across scales.

Box 1 Terminology

- *Extent*: the range over which a pattern or process occurs or is expected to occur (Nekola & White 1999), such as a species fundamental niche, or the total area measured by an EO sensor.
- *Grain size*: the size of the smallest individual unit of measurement (Jensen & Lulla 1987), such as a plot or transect in ecology, or the ground sampling distance of an EO sensor.
- *Biodiversity pattern*: recurring and structured variation in the distributions of genes, species, communities and ecosystems.
- *Ecological processes*: Activities that result from interactions among organisms and between organisms and their environment (Martinez 1996).
- *EO sensor*: spaceborne or airborne instruments (e.g. a camera or radar) that record the electromagnetic radiation emitted or reflected by the landscape (Campbell & Wynne 2011).
- *Sensor type*: general classifications of EO sensors based on the range of electromagnetic radiation measured, and how it was measured. Sensors are typically classified as active (i.e. sensors that emit their own energy, then record the reflection of that energy by the surface) or passive (i.e. sensors that measure energy emitted by the surface, not generated by the sensor). Radar sensors (e.g. Sentinel-1) are an example of active microwave (1 mm to 1 m) sensors. Multispectral sensors (e.g. Landsat) are an example of passive optical sensors that measure a range of typically visible (0.38–0.78 µm) to near-infrared (0.78–1.3 µm) or shortwave-infrared (1.3–3 µm) wavelengths (Campbell & Wynne 2011).
- *Sensor fidelity*: the ability of a sensor to discriminate between land surface properties, and to discriminate signal from noise across the dynamic range of the sensor (Campbell & Wynne 2011).
- *Continuous measurements*: EO measurements mapping the full geographical extent of a region without gaps.
- *Discrete measurements*: EO measurements mapping specific areas that do not cover the full geographical extent of a region.
- *Multi-sensor fusion*: integrating measurements from multiple sensors with complementary spatial and temporal characteristics to characterise a single pattern (Hilker *et al*. 2009).
- *Radiometric calibration*: the conversion of raw image data (e.g. in digital number format) to units of absolute radiance (e.g. in $W\ m^{-2}\ sr^{-1}\ \mu m^{-1}$) to standardise data from multiple sensors into a common scale (Chander *et al*. 2009).
- *Data dimensionality*: the minimum number of free variables needed to represent data without information loss (Camastra 2003).

Changing measurement scales

Measurement scales are often selected to understand biodiversity patterns or ecological processes at a specific scale or set of scales. A key scaling dynamic is that when the scale of measurement changes, the variation within that measurement is also subject to change (Wiens 1989; Levin 1992). For example early biodiversity/ecosystem function research suggested the relationship between species richness and productivity to be "hump-shaped", predicting peak biomass accumulation at intermediate diversity for both primary and secondary productivity (Rosenzweig & Abramsky 1993). However, this functional form was shown to be an artefact of plot size as opposed to any ecological process (Oksanen 1996), and a global synthesis found mixed evidence for a generalised relationship (Adler *et al*. 2011). Recently, long-term studies addressing scale directly have demonstrated a positive diversity-productivity relationship in multiple ecosystems (Liang *et al*. 2016; Hungate *et al*. 2017).

Measurements of community-scale patterns, like species richness and turnover (i.e. alpha and beta diversity), have also been shown to vary directly with scale (Rosenzweig 1995). Coarse grains are expected to contain higher species richness per grain, and thus lower species turnover between grains (Nekola & White 1999; Whittaker *et al*. 2001). This is because larger grains are expected to contain more rare species and more environmental variation (e.g. more variation in niche space; Keil *et al*. 2015). Indeed, Hurlbert & Jetz (2007) showed systematic increases in species richness at coarser grain sizes for birds in South Africa and Australia. Similarly, species turnover has been shown to decrease at coarser grains for birds in Britain and North America (Mac Nally *et al*. 2004; Gaston *et al*. 2007), and for mammals in Mexico (Arita & Rodriguez 2002).

Measurement scales likewise determine which biodiversity patterns can be measured by EO (Fig. 1). Generally, fine-grain sensors measure species- and community-scale patterns like species occurrences (Immitzer *et al*. 2012) and taxonomic diversity (Khare *et al*. 2018). Measuring species traits has proven challenging due in part to difficulties distinguishing individual organisms in EO imagery (Nagendra *et al*. 2013; Jetz *et al*. 2016). But some plant traits, like canopy nitrogen content and photosynthetic rates, can be measured at moderate grain sizes (Martin *et al*. 2008; Serbin *et al*. 2014). High frequency measurements can map temporally sensitive processes like vegetation phenology (Bradley *et al*. 2007), but high frequency, continuous measurements often come at the expense of coarser grain sizes. Coarse grain EO sensors measure ecosystem-scale patterns, like disturbance regime (Wang *et al*. 2012; Kogan *et al*. 2015) and ecosystem extent (Maillard *et al*. 2008; Bartsch *et al*. 2009). Satellite EO have historically focused on measuring ecosystem-scale patterns, due to the grain sizes of historic sensors, but the increasing number of fine-grain EO sensors in orbit could shift EO biodiversity mapping to focus on more species- and community-scale patterns (Fig. 2; Butler 2014b).
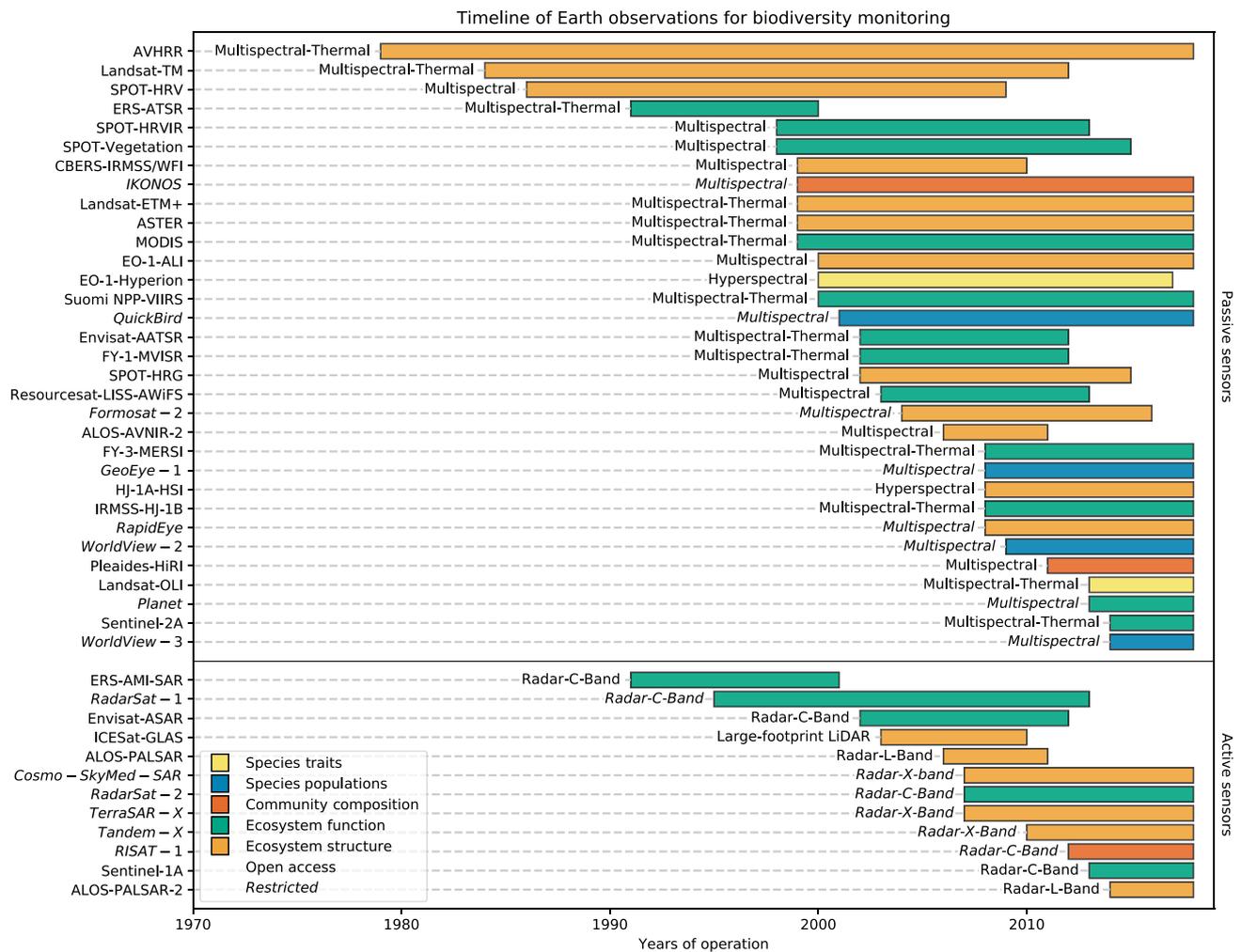
Figure 2 Temporal extents of current and historic satellite sensors, coloured by biodiversity pattern type. Temporally coincident measurements can be leveraged for analysis in a multi-sensor fusion framework to increase data dimensionality (Box 1).

There are key similarities in scaling dynamics between field and EO data; grain size and extent both constrain within and between-grain measurement variation. Large field plots tend to contain more species per plot, and lower turnover between plots. Likewise, large EO pixels tend to contain more organisms per grain, and lower turnover between grains, constraining measurement specificity. However, the grain size of an EO sensor places a constraint only on the smallest unit of measurement; these data can be spatially aggregated to larger scales (Fisher 1997). For example contiguous pixels measuring the same tree could be aggregated to delineate a single crown, or clusters of forested pixels could be aggregated to delineate forest fragments (Yu *et al.* 2006). This enables comparisons between crowns or across fragments, instead of pixels, helping bridge the gap between spatial and biological scales. This is known as object-based image analysis (Hay & Castilla 2008), which is likely to become more common in biodiversity monitoring as novel segmentation algorithms are tuned for EO (Krizhevsky *et al.* 2012; Basu *et al.* 2015). And though this approach facilitates ecological interpretations of EO data, there are key scaling dynamics associated with aggregating data across scales.

Domains of scale

One tenet of the problem of pattern and scale in ecology suggests that, since multiple ecological processes often drive spatial biodiversity patterns, there is rarely a single scale at which any pattern must be examined (Hutchinson 1953; Levin 1992). These patterns are often examined at multiple points along biological, spatial or temporal scale spectrums in order to understand how multiple processes drive patterns. For example the drivers of net primary productivity in plants could be examined at leaf, whole plant and landscape scales. The leaf, plant and landscape, here, represent domains of scale: the scales over which patterns either do not change, or change monotonically with changes in scale (Wiens 1989). In this example, fine-scale processes, like intracrown shading, may drive the majority of variation in leaf-scale productivity, but may be less important at landscape scales, where ecosystem processes like resource availability drive the majority of variation (Field *et al.* 1995). Partitioning biodiversity patterns into genetic, species, community and ecosystem-scale patterns organises them as domains of scale; the processes that drive variation in species-scale patterns are expected to drive

variation in ecosystem-scale patterns through separate but potentially nested pathways (Pereira *et al.* 2012, 2013).

Constraining measurements and models to discrete domains of scale is key for simplifying predictions of how species respond to change (Field 1991). Multi-scale analyses have been used to identify domains of scale, revealing where transitions across scales has nonlinear effects on observed patterns (Palmer & White 1994). In community ecology, hierarchical regression models have been employed to this end (Legendre *et al.* 2005). For example Keil *et al.* (2012) tested how beta diversity patterns for birds, butterflies, plants, amphibians and reptiles across Europe varied with distance, climate and land cover. They found beta diversity (here, dissimilarity) decreased systematically at coarser grain sizes for each taxon. Their hierarchical analysis found climate was important for predicting beta diversity patterns at coarse grain sizes, and land cover was important at fine-grain sizes, though these effects varied by taxon. Their results suggest that predicting changes in turnover should assess multiple domains of change simultaneously, and that these scale dependencies are taxon-specific.

The domains of scale where processes drive patterns may not always be known *a priori*, however. These are often identified using multi-scale sensitivity analysis. For example Mendenhall *et al.* (2011) developed a multi-scale model to predict how bird community composition changed with land cover change in Costa Rica. They assessed species turnover along tree cover gradients, finding turnover varied nonlinearly with cover at both fine and coarse grain sizes. Their results suggested there are two domains of scale over which tree cover patterns determine turnover patterns for birds (perhaps tracking habitat and resource availability; Morrison *et al.* 2012). Furthermore, their results suggested tree cover change could serve as a proxy to predict turnover in other communities. Indeed, Mendenhall *et al.* (2016) found tree cover change predicted changes in composition for understory plants, non-flying mammals, bats, reptiles and amphibians. Furthermore, they found the grain size of tree cover which best predicted turnover varied by taxon. Their work highlights one approach to mapping biodiversity change with EO – identifying domains of scale through multi-scale sensitivity analysis, then modelling turnover via regression with EO-derived environmental features.

MEASURING AND MODELLING PATTERNS WITH EO

There are currently two principal paradigms for mapping biodiversity patterns with EO (Turner *et al.* 2003). First is to directly measure species, community or ecosystem-scale patterns. Examples of this paradigm include identifying individual organisms within a species (Gairola *et al.* 2013) or mapping the extent of an ecosystem (Henderson & Lewis 2008). Second is to model biodiversity patterns indirectly using EO as predictive environmental features. Examples of this paradigm include modelling species richness from measurements of habitat structure (Saatchi *et al.* 2008), or modelling species distributions and turnover using land cover maps (Guisan & Thuiller 2005; Keil *et al.* 2012). Here I review the roles of measurement type and measurement scales in these paradigms, focusing on biodiversity patterns mapped

by current and historic spaceborne sensors that can be accessed by biodiversity monitoring systems (Table S1).

Measuring biodiversity patterns

EO measurements of biodiversity patterns are characterised by three key properties: sensor type, sensor fidelity and measurement scales (Pettorelli *et al.* 2014a; O'Connor *et al.* 2015). Sensor type determines which patterns can be measured, sensor fidelity constrains the variation in those measurements, and measurement scales determine the amount of variation within and between measurements (Box 1; Jensen & Lulla 1987). Passive sensors, such as multispectral sensors and imaging spectrometers, often measure patterns of ecosystem function, like leaf area index (Fensholt *et al.* 2004), vegetation phenology (Fan *et al.* 2015) or disturbance regime (Feng *et al.* 2008). Active sensors, such as radio or light detection and ranging sensors (i.e. radar and lidar), often measure patterns of ecosystem structure, like tree height (Lefsky *et al.* 2005) and ecosystem extent (Bartsch *et al.* 2009). These distinctions are not axiomatic; multiple sensor types have been used to measure the same pattern (Pohl & Van Genderen 1998). For example both radar and multispectral sensors have been used to measure tree cover. Radar sensors map tree cover by measuring woody structural and hydrological characteristics (Walker *et al.* 2010; Shimada *et al.* 2014), and multispectral sensors map tree cover by measuring leaf optical properties like pigment concentrations (Sims & Gamon 2002; Sexton *et al.* 2013).

Using multiple sensors to map a single biodiversity pattern can improve model accuracy and reduce sensor-specific uncertainties, and is known as multi-sensor fusion (Box 1; Hall & Llinas 1997). One application of this approach has been in tree cover mapping. Though multispectral sensors are sensitive to pigment concentrations, measuring tree cover in leaf-off conditions remains a challenge; exposed branches are optically similar to dried grass or other non-photosynthetic vegetation (Asner 1998). To obviate this issue, Naidoo *et al.* (2016) mapped cover in a South African savannah by combining multispectral and radar measurements. Radar is sensitive to woody biomass regardless of phenology. but can itself be noisy due to speckling (Lee *et al.* 1994). Combining these two sensor types, they mapped tree cover with 90% accuracy, which was 12% higher than using either sensor independently. Multi-sensor fusion approaches to biodiversity mapping hold great promise for reducing sensor-specific uncertainties, and are poised to become more valuable as access to novel sensor types increases (Fig. 2; Butler 2014a; Schulte to Bühne & Pettorelli 2018).

Comparing measurements from similar sensor types with different grain sizes has been used to assess the importance of scale in measuring biodiversity patterns. For example Brown *et al.* (2006) compared NDVI measurements from four spaceborne multispectral sensors and found that up to 20% of the measurement variance between sensors was driven by differences in grain size. Furthermore, Garrigues *et al.* (2006) found that changes in grain size explained to up to 50% of the variance in comparisons of multi-scale leaf area index measurements, which increased at coarser grains and in spatially
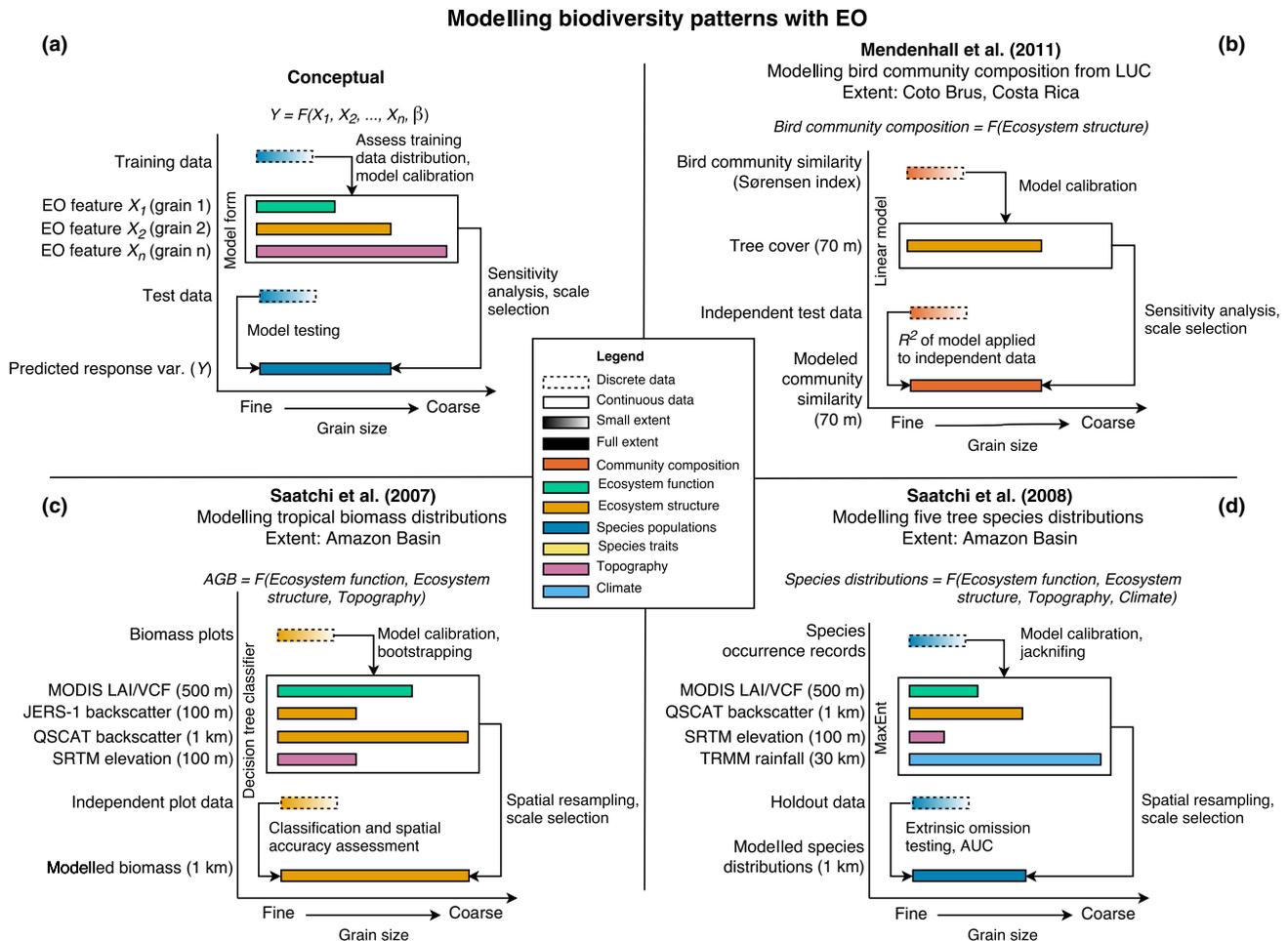
Modelling biodiversity patterns with EO

Figure 3 Summary of how biodiversity patterns have been modelled using EO data. (a) Conceptual model of how EO have been used to predict biodiversity patterns using supervised modelling approaches. (b) An example from Mendenhall et al. (2011) modelling bird community similarity as a function of tree cover across Coto Brus, Costa Rica. (c) An example from Saatchi et al. (2007) modelling aboveground biomass distributions across Amazonia. (d) An example from Saatchi et al. (2008) modelling tree species distributions across Amazonia.

heterogeneous landscapes. Comparing these spatial uncertainties to the radiometric calibration uncertainties of EO sensors (i.e. sensor fidelity), which are often between ±5 and 10% absolute radiance (Chander et al. 2009), suggests that differences in measurement scales can be similarly important as differences in sensor fidelity for mapping biodiversity patterns. The physical drivers of this scale dependence have been explored with radiative transfer models, particularly for patterns of ecosystem function (Asner et al. 1998; Jacquemoud et al. 2009), but should be further quantified for other biodiversity patterns.

Modelling biodiversity patterns

Biodiversity patterns that are difficult to measure directly with EO are often modelled as a function of environmental features (Fig. 3). There are many approaches to modelling biodiversity patterns with EO, including models of species-scale (Fig. 3d; Saatchi et al. 2008), community-scale (Fig. 3b; Mendenhall et al. 2011) and ecosystem-scale biodiversity patterns (Fig. 3c; Saatchi et al. 2007). These approaches typically resample all data layers to a uniform grain size and extent,

occasionally after multi-scale sensitivity analysis (McGarigal et al. 2016). Here I briefly discuss models of individual species distributions (Guisan & Thuiller 2005) and models of community-scale patterns like alpha and beta diversity (Rocchini 2007). These modelling methods have been reviewed elsewhere (Gillespie et al. 2008; Rocchini et al. 2010; Pettorelli et al. 2014a), but this section reviews role of scale in these approaches.

Species distribution models (SDMs) predict species geographical distributions across an extent as a function of environmental features that constrain habitat availability and use (Soberon & Peterson 2005). There have been many discussions on feature selection in SDM (Booth et al. 2014; Brandt et al. 2017; Fourcade et al. 2018), but some key reviews have emphasised that scale selection can play a similarly important role (Mayor et al. 2009; McGarigal et al. 2016). Even so, studies addressing scale directly have found equivocal results. For example Guisan et al. (2007) modelled bird and plant distributions at multiple grain sizes, finding only small decreases in model accuracy at coarser grain sizes on average. Disaggregating these results by taxon, however, revealed significant decreases in accuracy at coarser grains for all plants, but only

some birds. In addition, species with the least training data saw the largest decreases in accuracy. Seo *et al.* (2009) further explored these patterns in nine plant species, comparing both model accuracy and the spatial patterns of distributions. They found model accuracy decreased consistently at coarser grains, and that these decreases were species-specific. They also found significant spatial disagreement between models of varying grain size for each species, which could have major consequences for spatial conservation planning (Faleiro *et al.* 2013).

There are two principal approaches to modelling community-scale patterns with EO. First is to predict the distributions of all species in a community, then overlay these outputs to estimate community composition (i.e. stacked SDMs; Thuiller *et al.* 2009; Calabrese *et al.* 2014). Second is to model community diversity metrics via regression (Gillespie *et al.* 2008; Saatchi *et al.* 2008). As above, the role of scale in these approaches has been equivocal. For example Thuiller *et al.* (2015) modelled multiple plant community diversity metrics in the French Alps using a stacked-SDM approach at varying grain sizes. They found that estimates of functional diversity, phylogenetic diversity and species richness all varied independently with changes in grain size. Functional diversity was best predicted at the finest grain size (250 m), whereas phylogenetic diversity and species richness were best predicted at coarser grain sizes (1000 m), suggesting scale dependence at the community scale is often process specific.

Assessing scale dependence in regression approaches has been done by comparing species richness predictions across multiple sensors. Nagendra *et al.* (2010) modelled plant species richness using features from a fine grain, low fidelity sensor (IKONOS) and a moderate grain, high fidelity sensor (Landsat). Since community diversity metrics assess within- and between-grain variation, one may expect that fine-grain EO better predict these patterns. On the other hand, high fidelity measurements may better discriminate the between-grain variation in environmental features that predict spatial turnover in communities. They found that, despite the coarser grain size, Landsat-based models better predicted plot-level species richness. Though the IKONOS data matched the grain size of the field plots, they failed to meaningfully discriminate the spatial variation in environmental features that predicted spatial richness patterns. Further disentangling the effects of sensor fidelity from varying measurement scales will help discriminate sensor dependence from scale dependence in modelling other biodiversity patterns.

Linking measurements and models

EO measurements and models of biodiversity patterns are tightly connected. They are both subject to pattern-specific scale dependencies, and multi-scale comparisons or sensitivity analyses are essential for quantifying and understanding these dependencies. Furthermore, when EO measurements are the features used to model biodiversity patterns, scale-dependent measurement variation becomes embedded within the models. This might obfuscate process-driven scale dependence for variation driven by changing measurement scales. Constraining scale-dependent variation in EO measurements of biodiversity

patterns, and disentangling this variation from variation driven by sensor fidelity, will be key for reducing uncertainties in multi-scale modelling efforts. In the following section I review some other challenges linking measurements and models of biodiversity patterns, and opportunities for multi-scale analyses to address these challenges.

TRANSLATING BIODIVERSITY PATTERNS ACROSS SCALES

One central challenge linking field and EO data is overcoming scale mismatches. These mismatches occur where response and feature data were sampled at disparate and irreconcilable scales. The size of field plots (i.e. the response data) are often much smaller than the grain size of EO sensors (i.e. the feature data), which can obscure key patterns and processes operating between these scales. For example Cleveland *et al.* (2015) modelled spatial patterns of net primary productivity across the Amazon basin using three models at three scales: from plot data upscaled to the study extent (0.1 ha grain size), from MODIS data collected across the full extent (1 km^2 grain size) and from a community land model (12 500 km^2 grain size). These methods calculated the same average net primary productivity across the Amazon, indicating a potential convergence of processes driving forest productivity. However, results from the finer-scale methods were shown to be spatially independent from the others, suggesting they converged on the same average for different reasons. In this case, comparing multiple models at mismatched scales that calculated the same result can make it difficult to disaggregate the role of process from the role of scale in understanding spatial patterns of productivity.

One key challenge in translating patterns across mismatched scales is capturing the dynamics of intermediate-scale biodiversity patterns that are poorly characterised by field data. These patterns are too rare to be characterise with field plots alone, and are often difficult to reliably measure with coarse grain EO. For example Fisher *et al.* (2008) and Chambers *et al.* (2009) identified that tree falls patterns, which tend to be both rare and spatially clustered, are underrepresented in field plots in the Amazon. Their analyses demonstrated that efforts to model related patterns using just field data (e.g. carbon sequestration) would necessarily underestimate feedbacks from these intermediate-scale disturbances. Marvin *et al.* (2014) quantified these mismatches using airborne lidar data, finding between 44 and 85 field plots per forest type would be required to characterise mean, community-scale carbon and disturbance dynamics. These results suggest that, to translate patterns across scales, field measurements should be greatly expanded, or novel data should be used to characterise intermediate-scale patterns.

The challenges presented by scale mismatches can be framed by two tenets of the problem of pattern and scale: that multiple ecological processes can drive biodiversity patterns, and that there is rarely a single scale that best identifies how specific processes drive patterns (Wiens 1989; Levin 1992). These tenets suggest that multi-scale analyses, which capture the intermediate-scale patterns obscured between fine and coarse grain patterns, could improve empirical approaches to
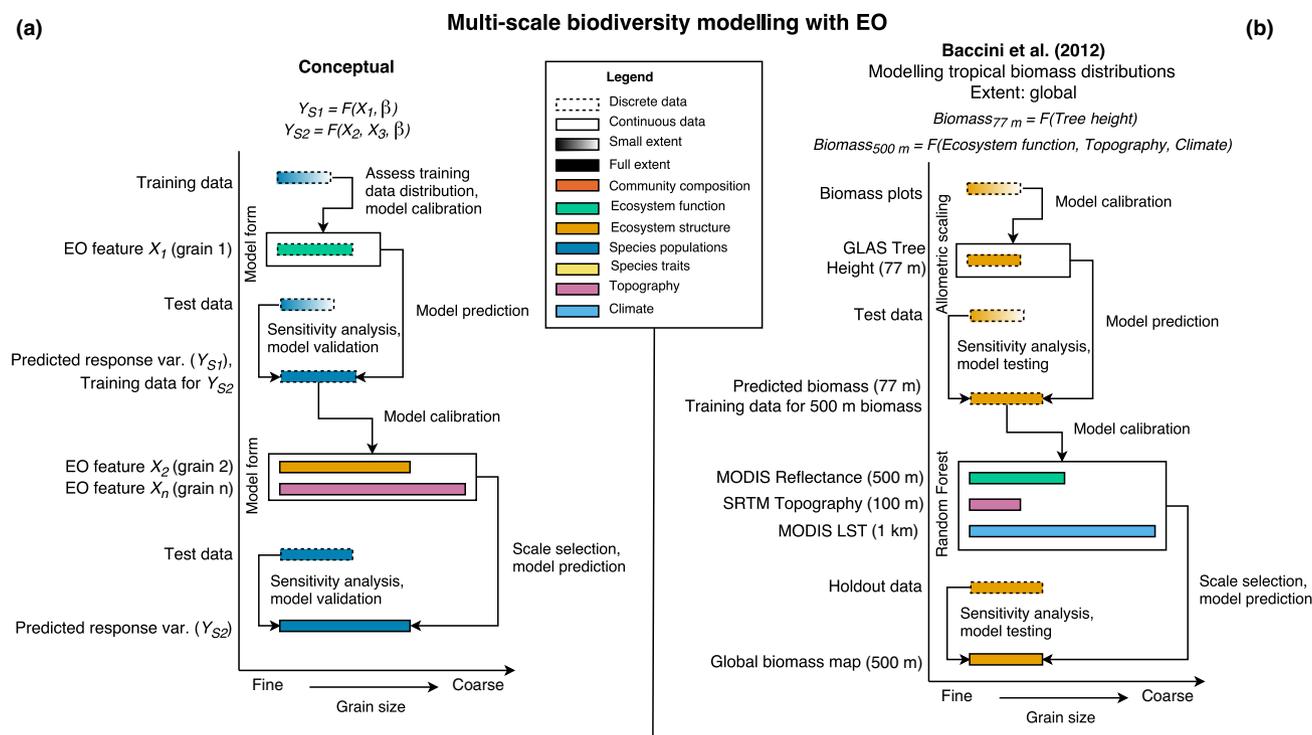
Figure 4 Summary of how biodiversity patterns have been modelled using EO data in a multi-scale modelling framework. (a) Conceptual model of how EO data have been used to predict biodiversity patterns using a multi-scale modelling approach. (b) An example from Baccini et al. (2012) demonstrating the multi-scale modelling approach for predicting tropical biomass globally. Leveraging coincident data from multiple sensors in this framework provide opportunities to translate biodiversity patterns across scales.

mapping biodiversity patterns with EO. Iteratively modelling patterns with multi-scale EO has been used to map a range of biodiversity patterns at moderate grain sizes across large extents, and presents an actionable approach to overcoming some of the challenges presented by scale mismatches.

Multi-scale modelling

Multi-scale models attempt to obviate scale mismatches through iteratively modelling patterns at varying grain sizes (Fig. 4a). One key innovation of the multi-scale modelling approach was to leverage intermediate-scale data sources that capture the extent-wide variation in EO features, which is difficult to cover with field plots alone. For example Baccini et al. (2012) developed a benchmark map of pantropical aboveground biomass using a multi-scale model, a network of field plots, discrete spaceborne lidar data (70 m) and continuous, coarse grain EO (500 m; Fig. 4b). First, they calibrated an allometric model (e.g. Chave et al. 2005) using biomass plots coincident with lidar-derived tree height data. Next, they applied this model to all tree height measurements, creating a discrete, global biomass map. Finally, they modelled biomass continuously using a regression tree model, with lidar-derived biomass as the response and EO data on climate, topography and ecosystem function as the environmental features. Their final map of aboveground biomass served as a benchmark for global carbon monitoring (Ciais et al. 2014).

Multi-scale models have also been used to monitor temporal changes using intermediate-scale EO, overcoming some of the

challenges highlighted by Fisher *et al.* (2008) and Marvin *et al.* (2014). For example Baccini *et al.* (2017) assessed temporal patterns of change in aboveground biomass using EO measurements of forest growth, disturbance and deforestation. Intermediate-scale disturbance measurements were essential for capturing the magnitude of change: their results revealed that disturbance accounts for nearly 70% of forest emissions, and that the Earth's tropical forests are now a net source of carbon to the atmosphere. Considering how little is known about the rate, magnitude and direction of global biodiversity change (Pereira *et al.* 2012; McGill *et al.* 2015), I expect these multi-scale analyses will prove essential for settling debates over other key knowledge gaps (e.g. Vellend *et al.* 2013; Gonzalez *et al.* 2016). These analyses have also proven essential for mapping patterns that have been difficult to directly measure with EO: species traits.

Multi-scale trait mapping

Measuring species traits as a complement to species counts has become a priority for biodiversity science. Traits have been touted as a link between applied and theoretical biodiversity research and as a means to better represent ecosystem function in Earth systems models (Shipley *et al.* 2006; Jetz *et al.* 2016; Funk *et al.* 2017). Plant functional traits (PFTs) are one subset of species traits that can be mapped using EO, specifically by imaging spectroscopy (Kokaly *et al.* 2009). One key benefit of measuring PFTs with EO is that they can be mapped without having to identify and characterise every

species *a priori*; capturing the range and variation in traits is often more important. The prospective launches of spaceborne imaging spectrometers, such as EnMAP, PRISMA and HISUI, are currently touted as the best bet for mapping PFTs globally (Stuffler *et al.* 2007; Galeazzi *et al.* 2008; Matsunaga *et al.* 2011). Simulations from preparatory campaigns have found mixed results, however. Bachmann *et al.* (2015) demonstrated that the moderate fidelity of these sensors should lead to high variation in surface reflectance measurements (the basis for measuring PFTs). Furthermore, the moderate grain size of these sensors (30 m) has been shown to significantly reduce classification accuracies compared to fine-grain measurements in other contexts (Kruse *et al.* 2011). This decrease in accuracy is expected to be exacerbated for PFTs since canopy structure, not trait variation, drives the majority of reflectance signal at moderate grains (Yao *et al.* 2015).

These results suggest spaceborne trait measurements may not yet provide a panacea. Fortunately, airborne imaging spectrometers can measure these traits at the scales of individual organisms, and these measurements can be combined with other EO to model PFT distributions over large extents (*sensu* Fig. 4a). For example Asner *et al.* (2016) used a multi-scale modelling approach to map PFTs across the Peruvian Amazon. First they measured PFTs for all canopy trees in a network of field plots, capturing the physiological range of each trait. Next they trained regression models using each trait as the response variable, and the imaging spectroscopy data as features. These trait models were then applied to all airborne data, which were collected across gradients of elevation, geology and forest type. Finally, they modelled these traits continuously using the airborne-scale trait maps as the responses, and satellite measurements of ecosystem structure, ecosystem function, climate and topography as features. Since these traits vary widely within plots, and more so across the full study extent, the airborne-scale trait maps were essential for capturing local-scale trait variation across the region. The intermediate-scale maps provided more data to train the satellite-based models and, aggregated to the grain size of the satellite data, obviated problems of sampling effort and scale mismatch.

Applying these multi-scale modelling approaches could enable monitoring similar biodiversity patterns that have otherwise proven difficult to map over large extents. Though access to intermediate-scale data has been historically limited, it should increase with the launch of novel fine-grain sensors (Fig. 2; Malenovský *et al.* 2012). Monitoring intermediate-scale patterns could be further bolstered by expanding the scope of airborne mapping by groups like NEON's Airborne Operations Platform (Keller *et al.* 2008), DLR's Optical Airborne Remote Sensing platform (OpAiRS; Baumgartner *et al.* 2012; Leutner *et al.* 2012), or the Carnegie Airborne Observatory (CAO; Asner *et al.* 2012). Linking field, airborne and spaceborne measurements could be used to map fine-scale patterns like species traits across large extents, generate intermediate-scale data to train and test satellite measurements, and link the distributions of community and ecosystem-scale patterns to species identities (Clark *et al.* 2005; Baldeck *et al.* 2015). Furthermore, implementing large-scale airborne mapping efforts could be done at a fraction of the price of building and launching a satellite (Mascaro *et al.* 2014).

PATTERN, SCALE AND BIODIVERSITY MONITORING

Global biodiversity monitoring systems hold great promise for biodiversity science and conservation. These systems could help forecast the rate, magnitude and geography of biodiversity change, identifying opportunities to mitigate human impacts on biological communities. EO can support biodiversity monitoring with consistent and repeat assessments of biodiversity change, providing a unique global perspective on our changing biosphere. Applying concepts of pattern and scale in ecology to EO could link these fields in support of this vision. However, Estes *et al.* (2018) found little overlap in the ecology literature between studies analysing field data and studies analysing EO data, highlighting the gap between these communities. Furthermore, problems presented by scaling dynamics (e.g. scale mismatches) have helped frame EO science as distinct from ecology, subject to different rules and standards. Developing an ecologically based framework for monitoring biodiversity change with EO will require overcoming this distinction.

There are several key similarities between field and EO data: changing their grain size or extent fundamentally alters within and between-grain variation, there is rarely a single scale at which any pattern should be examined, and aggregating measurements to discrete domains of scale can constrain nonlinear responses to change. These similarities frame EO as an extension of field data; their differences are more in scale than they are in kind. Multi-scale analyses linking field and EO data support this, emphasising that targeted field collections are essential for mapping biodiversity patterns that are difficult to measure independently with EO. In the context of biodiversity monitoring with EO, field data play three key roles: training EO to map novel biodiversity patterns; developing and testing forecasts of biodiversity change, and constraining the extents to which we can generalise patterns of change.

One key challenge in measuring biodiversity patterns with EO is converting at-sensor measurements into biologically meaningful metrics of change (e.g. from at-sensor radiance to percent tree cover). This is often done empirically via calibration with field measurements. These calibrations require a lot of data; EO data dimensionality is often very high (Box 1) and the variation in biological communities that drives measurement variance is similarly high. However, it is difficult for any one research group to independently collect the field data necessary to capture this variation. One way to overcome this challenge is to leverage open data. Access to open biodiversity data has increased dramatically over the past decade (Kattge *et al.* 2011; Jetz *et al.* 2012; Metzger *et al.* 2013; Culina *et al.* 2018), as has access to open EO (Nemani *et al.* 2011; Irons *et al.* 2012; Gorelick *et al.* 2017). And though there are known spatial, temporal and taxonomic gaps in open biodiversity data (Beck *et al.* 2014; Geijzendorffer *et al.* 2016), extrapolating from incomplete measurements to fill these gaps is a key role for EO. Training global, multi-scale EO models using centralised and curated field data could provide baseline estimates of spatial biodiversity patterns that have been otherwise difficult to characterise. These baselines could be tested independently by researchers with improved local data and local knowledge, identifying opportunities to improve regional

and global models. These analyses could spur modelling and data collection efforts to fill gaps, and to develop better forecasting tools. These are urgently needed in ecology (Dietze *et al.* 2018).

Another key role for field data is to develop and test predictive, process-based models of temporal change. EO are uniquely suited for empirically monitoring change, especially for directly measurable patterns (e.g. disturbance; Zhu *et al.* 2012; Cohen *et al.* 2016). Yet forecasting change under conditions outside the range of historic variation (e.g. under novel climate and land-use scenarios) remains a challenge for EO. Furthermore, temporal lags between local environmental change and other scales of change (e.g. for species or community-scale patterns) can obfuscate efforts to identify the impacts of change (Essl *et al.* 2015). Developing process-based models that couple temporal changes in EO to changes in other biodiversity patterns could address these issues (Korzukhin *et al.* 1996; Adams *et al.* 2013). And while there are many process-based EO models, and many process-based biodiversity models, we now have the technical capacity to link and test them using open data at multiple scales, identifying consensus models and key data gaps. Coupling process-based models with long-term, regularly updated and globally consistent measurements of change from EO could be used to develop early warning systems for identifying where species, communities and ecosystems will respond to change in novel ways, and may identify opportunities for science-driven mitigation (Daily 1999; Scholes *et al.* 2008).

Finally, field data are key for constraining how we generalise EO measurements and models of biodiversity change. One advantage of monitoring change with EO is that measurements are globally consistent; tree cover change can be mapped continuously across tropical, temperate and boreal forests (Hansen *et al.* 2013). This enables other models of change that use tree cover data as features to be applied globally, such as the models of community composition in Mendenhall *et al.* (2016). This would be imprecise, however; the relationships between tree cover and community composition in tropical countrysides may not apply to timber plantations. In other words, this model is not stationary; the relationships between feature and response variables can change across the extent of the data (Hawkins 2012). The regions over which these relationships are stationary can be considered domains of scale, constraining the extents to which a model can generalise. It is currently difficult to identify these domains of scale with EO alone. Several algorithms can be employed to automate this task for EO (e.g. segmentation, clustering), but field data are key for interpreting and constraining these extents to biologically meaningful domains, and for testing their accuracy. Linking field and EO data to identify these domains of scale will be central to ecologically translating knowledge of local biodiversity patterns to regional and global scales.

After decades of work from biodiversity scientists, EO scientists and conservation groups, the stage is now set to establish ambitious, science-driven biodiversity monitoring systems and consistent, repeat and globally available EO will play a key role in these systems. Scale is a central and unifying concept for biodiversity and EO sciences, and monitoring change with EO should be based on the principles and ecology of

scale. Global biodiversity monitoring promises to expand our understanding of Earth's species, communities and ecosystems and, with luck, could help us discover the wisdom necessary to conserve them.

AUTHORSHIP

CBA designed research, performed research and wrote the final manuscript.

DATA ACCESSIBILITY STATEMENT

The data and figures in this manuscript have been uploaded to Dryad under the following https://doi.org/10.5061/dryad.26q7j45.

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SUPPORTING INFORMATION

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