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# 1 The Promise and Practice of Connecting Earth

## 2 Observation to Biodiversity and Ecosystem Services

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## 49 **Preface**

50 There is much interest in using Earth Observation (EO) satellites to track biodiversity and  
51 ecosystem services, understandable given the fast pace of biodiversity loss. However,  
52 because most biodiversity is invisible to EO, EO-based indicators could be misleading, which  
53 can unintentionally decrease conservation effort and reduce the effectiveness of nature  
54 conservation. We describe an approach that combines automated recording devices, high-  
55 throughput DNA sequencing, and ecological modelling to extract the full information content  
56 of EO data. This approach is achievable now, offering near-real-time monitoring of policy  
57 and management impacts on biodiversity and the supply of ecosystem services.

## 58 **Meeting the Aichi Biodiversity Targets**

59 From Google Earth to airborne sensors, the Copernicus Sentinels, and cube satellites, Earth  
60 Observation technology is undergoing a rapid expansion in capacity, accessibility, resolution,  
61 and signal-to-noise ratio, resulting in a recognized shift in our capability for monitoring land  
62 and water (Verrelst *et al.*, 2015; Wulder *et al.*, 2015; Toth & Jóźków, 2016). These advances  
63 are motivating calls to use Earth Observation products to manage our natural environment  
64 and to track progress toward global and national policy targets on biodiversity and  
65 ecosystem services (O'Connor *et al.*, 2015; Skidmore *et al.*, 2015; Pettorelli *et al.*, 2016b).

66 Foremost among these are the Strategic Plan for Biodiversity and the Aichi Biodiversity  
67 Targets, which were adopted in 2010 by the Parties to the Convention on Biological Diversity  
68 (CBD) to “take effective and urgent action to halt the loss of biodiversity in order to ensure  
69 that by 2020 ecosystems are resilient and continue to provide essential services...” (CBD,  
70 2010). The United Nations Sustainable Development Goals (UNGA, 2015) now include  
71 some of the Aichi Targets, and the 2015 Paris Agreement has reiterated the commitments of  
72 the UN Framework Convention on Climate Change to reducing emissions from deforestation  
73 and forest degradation (REDD+) and to secure non-carbon benefits, which include  
74 biodiversity and ecosystem services (UNFCCC, 2015).

75 However, we have struggled to track and report progress toward the Aichi Targets in a  
76 standardized and comprehensive way (Tittensor *et al.*, 2014). Although almost two-thirds of  
77 the CBD Parties have updated their National Biodiversity Strategies and Action Plans to  
78 reflect the 2010 revisions, many still do not contain measurable indicators on the state of  
79 biodiversity, let alone ecosystem services. This impedes inference on how biodiversity  
80 delivers ecosystem functions and services and conceals the impacts of policy and  
81 management interventions on them (Durance *et al.*, 2016). The difficulty of designing

82 indicators (Dawson *et al.*, 2016; IPBES, 2016; Pettorelli *et al.*, 2016a) has prompted an  
83 international consortium of biodiversity scientists called GEO BON (Group on Earth  
84 Observations' Biodiversity Observation Network) to propose a framework of Essential  
85 Biodiversity Variables (Pereira *et al.*, 2013), with the aim of setting minimum standards of  
86 coverage to ensure informativeness and to harmonize disparate local measures so that  
87 biodiversity and ecosystem data can be compared over space and time. The Essential  
88 Biodiversity Variables thus measure the 'state of biodiversity' at multiple levels: genetic  
89 composition, species populations, species traits, community composition, ecosystem  
90 structure, and ecosystem function (Pereira *et al.*, 2013).

91 Although it was originally envisioned that most of the variables (genetic to community  
92 composition) would be scaled up from "intensive *in-situ* measurements" taken on the ground,  
93 such measurements are costly and difficult because they are traditionally gathered by visual  
94 and aural detection of plants and animals in the wild (preceded by months or years of  
95 observer practice) and by mass collection of organisms (followed by months of identification  
96 from morphology), so that data collection is slowed by human-caused bottlenecks in  
97 sampling and taxonomy (Proença *et al.*, 2016).

98 As a result, attention is now being focused on designing 'Satellite Remote Sensing-Essential  
99 Biodiversity Variables' (SRS-EBVs) to enable cost-effective and global-scale monitoring  
100 (Skidmore *et al.*, 2015; Pettorelli *et al.*, 2016a; Pettorelli *et al.*, 2016b). The problem here is  
101 that only a few Earth Observation products can be mapped directly to Essential Biodiversity  
102 Variables and then to Aichi Targets, because these products primarily measure gross  
103 vegetation and landscape metrics, such as land cover and phenology (O'Connor *et al.*,  
104 2015). For example, Pettorelli *et al.* (2016a) found only two Earth Observation products (net  
105 primary productivity and fire incidence) that could serve as Essential Biodiversity Variables  
106 for the Sahara, despite this biome's suitability for remote sensing due to its visible  
107 biodiversity hotspots, remoteness, and availability of long time series. Many of the Aichi  
108 Targets require data with species-level resolution, either because some species are direct  
109 policy targets (e.g. Target 9: "invasive species controlled or eradicated") or because species  
110 compositional data define the metric (e.g. Target 11: "protected areas are ecologically  
111 representative and conserved effectively").

112 Clearly, a radically new approach (**Figure 1, Box 1**) is required if progress towards the Aichi  
113 Targets is to be accelerated, one that is robust, widely affordable, and can record stocks and  
114 changes in biodiversity and ecosystem services consistently, continuously, and at high  
115 resolution over large geographic scales. Here, we present such an approach in a framework

116 that exploits recent efficiency and capacity gains and analytical breakthroughs in sensors,  
117 computation, ecology, taxonomy, and genomics.

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### Box 1. Inferring a hidden ecosystem function from space

121 Large-bodied Amazonian monkeys are responsible for a key ecosystem function: they are  
122 the primary dispersers of large seeds, which are associated with more carbon-dense tree  
123 species. Peres *et al.* (2016) have proposed that this function boosts forest carbon storage.  
124 The idea can be tested by using Earth Observation data and public records to map human  
125 settlements and transport corridors and predict where monkey populations have declined  
126 through hunting (Levi *et al.*, 2009; Peres *et al.*, 2016). We can then use on-the-ground  
127 sampling and airborne sensors to test whether forests that are have had longer exposure to  
128 hunting lack monkey populations and have more low-carbon-density tree species dispersed  
129 by wind and birds. In short, by combining Earth-Observation-derived maps of human activity  
130 with empirical observations of the response of primate populations to that activity, it should  
131 be possible to map and track an ecosystem function (large-seed dispersal) that is invisible to  
132 satellites but contributes to an important ecosystem service (carbon storage). This would be  
133 valuable to carbon-sequestration payment programs like REDD+.

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### From Point Samples to Continuous Maps

137 Instead of trying to map Earth Observation (EO) products directly to biodiversity, as  
138 encapsulated by SRS-EBVs (O'Connor *et al.*, 2015; Skidmore *et al.*, 2015; Pettorelli *et al.*,  
139 2016a; Pettorelli *et al.*, 2016b), we propose to extract the full information content of EO data  
140 by interpolating biodiversity point samples to build continuous landscape maps of species  
141 distributions (**Figure 1**) (Ferrier, 2011). Because it is species that are mapped, it becomes  
142 possible to incorporate the vast biological knowledge that we have collectively built up over  
143 decades of research, including historical distributions, knowledge of species traits and  
144 interactions (**Box 1**), and phylogenetic relationships, to infer, map, and track the distributions  
145 of ecosystem functions and services. This approach, which we call **CEOBES** (Connecting  
146 Earth Observation to Biodiversity and Ecosystem Services), is possible because of (1) major  
147 advances in EO sensitivity and capacity, (2) more efficient techniques to record biodiversity  
148 data on the ground, and (3) modern community-analysis models from statistical ecology. We  
149 now review these advances, with additional detail in Supplementary Information.

## 150 **The New Era of Earth Observation**

151 There are now ten times as many satellites in operation as there were in the 1970s, a result  
152 of increasing sensor longevity and a six-fold increase in launches (Belward & Skøien, 2015).  
153 Spatial resolution has improved to less than 1 m in both optical and radar sensors. Data  
154 continuity is also being maintained, most directly by the launch of NASA's Landsat 8 in 2013,  
155 which technically enhances and extends the 40-year Landsat record of medium-resolution,  
156 multi-spectral surface observations (Roy *et al.*, 2014). Data continuity is a key factor in  
157 understanding changes in biodiversity, as threats to biodiversity impact at a range of scales  
158 and often across lengthy time-spans (Turner *et al.*, 2015).

159 The long-term Landsat record is being enhanced by new satellite systems and multiple  
160 sensors in a global network, a 'virtual constellation' that may help overcome problems in  
161 terrestrial monitoring from single sensors (Wulder *et al.*, 2015). As part of the Copernicus  
162 program, the ESA Sentinel satellites are the latest addition to the global network. With six  
163 missions planned and the first three launched, the Sentinels have radar, optical sensors,  
164 radiometers, and spectrometers with different goals (Butler, 2014). Sentinel-1, the radar  
165 satellite, and Sentinel-2, the superspectral high-resolution mission, are of particular interest  
166 to biodiversity monitoring, with long-term continuity of measurements, global coverage, and  
167 quick revisit times (Berger *et al.*, 2012; Malenovský *et al.*, 2012).

168 There have also been developments in hyperspectral sensors with EnMAP, HypSIRI,  
169 PRISMA, and FLEX imaging spectrometer missions planned to produce large data streams  
170 to users (Verrelst *et al.*, 2015). In addition, airborne data collection using high-resolution 3D  
171 airborne laser scanning is complementing spectral information with structure (Asner *et al.*,  
172 2017). Many of these datasets are publicly funded, allowing cheap or even open access.  
173 Swarms of commercial cube satellites and the use of drones to carry sensors are significant  
174 steps that complement these large-scale programs (**S1** "Earth Observation technology").

175 The increase in spatial resolution in the new sensors implies greater precision because  
176 smaller pixels contain less heterogeneity (Petrou *et al.*, 2015), and reference measurements  
177 taken within meter-scale plots on the ground can be matched directly to meter-scale pixels.  
178 This in turn improves the ability of EO to recognize spatial gradients and boundaries.  
179 Remote sensing is not error-free, and an ongoing challenge is to ensure that EO products  
180 are well-defined to allow accurate estimates of error (Paganini *et al.*, 2016).

181 Two additional factors affect the utility of remote sensing data for understanding biodiversity  
182 change (**S2** "Biodiversity and ecosystem information in EO data"): affordability and access

183 (Turner *et al.*, 2015). There has been a cultural shift, with free open access on the rise. The  
184 opening of the Landsat archive in 2008 was a monumental development (Wulder *et al.*,  
185 2012), with ESA's Copernicus program following suit. Data access also refers to the ability of  
186 users to retrieve, manipulate, and extract value from EO data. Technological advances are  
187 making these processes manageable, with cloud computing allowing the hosting of large  
188 data archives, and new portals and toolboxes being rolled out.

189 The availability of copious EO data that have been shown in some studies to correlate  
190 closely with on-the-ground measures of ecosystem structure, habitat condition, and even  
191 animal communities (**S2**) might suggest that remote sensors can be used directly to define  
192 environmental indicators, but we must acknowledge that we are still in the early stages of  
193 understanding how biodiversity delivers ecosystem functions and services, and how they all  
194 respond to exogenous change. Directly observing functional diversity is a partial solution but  
195 only with 'visible' biodiversity such as vegetation (Asner *et al.*, 2017). Thus, the challenge is  
196 to find ways to exploit the high efficiency and information content of EO data while not falling  
197 prey to *reification fallacy* (**Box 2**), which can arise when convenient but incomplete indicators  
198 are made available (Lindenmayer & Likens, 2011; Mueller & Geist, 2016). Our institutions  
199 and reporting systems then retain the option to add and respond to new knowledge.

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## Box 2. The perils of convenient indicators

203 If we rely too much on EO data, we run the risk of *reification fallacy*, in which a mere  
204 indicator of a policy target itself ends up the target. Reification fallacy can reduce or narrow  
205 conservation effort (Newton, 2011) and can crowd out future discoveries (Smaldino &  
206 McElreath, 2016). For example, while remote sensing is an efficient and direct way to  
207 measure forest cover (Aichi Target 5: reducing the loss rate of natural habitats), using SRS-  
208 EBVs such as forest cover and phenology to measure ecosystem *resilience* (Target 15:  
209 contribution of biodiversity to carbon stocks) (O'Connor *et al.*, 2015) would ignore taxa  
210 invisible to satellites and could thus result in policymakers failing to exert the additional effort  
211 that is required to conserve saprotrophic fungal diversity, seed-dispersing mammals, and the  
212 seemingly inconsequential isopod, all of which have been implicated in boosting carbon  
213 storage, in dead wood, living trees, and soil, respectively (Crowther *et al.*, 2015; Peres *et al.*,  
214 2016; Yang *et al.*, 2016). More generally, land-cover class, which is a common EO-derived  
215 indicator type, is a highly error-prone way to map and assess the complex processes  
216 supporting ecosystem services (Eigenbrod *et al.*, 2010). In short, convenient EO products  
217 could lead policymakers to focus only on that portion of biodiversity and ecosystem services

218 that is measurable by satellites, ignoring the rest.

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## 220 **High-throughput biodiversity measurement**

221 Most biodiversity, whether animal, fungal, plant, or microbial, and its many functions and  
222 services, is invisible to EO and will remain so for some time. But a growing number of  
223 efficient technologies are available for detecting and identifying biodiversity on the ground  
224 (Snaddon *et al.*, 2013; Turner, 2014) (**S3** “Biodiversity technology”). Automated bioacoustic  
225 and camera-trap recording devices (ARDs), which can run continuously for weeks, can  
226 accumulate thousands of records of invertebrates, birds, fish, reptiles, amphibians, and  
227 mammals, and thus allow extended sampling of large areas at low workloads (Acevedo &  
228 Villanueva-Rivera, 2006; Lammers *et al.*, 2008; Jung & Kalko, 2011; Aide *et al.*, 2013;  
229 Sollmann *et al.*, 2017). Alternatively, high-throughput DNA sequencers can now be used in  
230 metabarcoding or metagenomic pipelines to detect and identify anywhere from one to  
231 thousands of species at a time from mass-collected, bulk samples of organisms (e.g.  
232 ‘biodiversity soups’; Yu *et al.*, 2012) or from ‘environmental DNA’, which is DNA liberated  
233 into the environment in the skin, hair, mucous, saliva, sperm, eggs, exudates, feces, urine,  
234 blood, spores, root fragments, leaves, fruit, pollen, or rotting body parts of their original  
235 owners (Taberlet *et al.*, 2012; Bohmann *et al.*, 2014) (**Figure 2, S3**). Multiple studies have  
236 now shown that metabarcode datasets reflect high-quality, morphologically identified  
237 biodiversity datasets sufficiently closely to allow correct management decisions, given best-  
238 practice protocols and controls (Ji *et al.*, 2013; Edwards *et al.*, 2014; Chariton *et al.*, 2015;  
239 Lejzerowicz *et al.*, 2015; Visco *et al.*, 2015; Aylagas *et al.*, 2016).

240 The taxonomic identities, phylogenetic affinities, functional genes (Xue *et al.*, 2016), spectral  
241 properties (of visible vegetation; Asner *et al.*, 2016; Fisher *et al.*, 2016; Asner *et al.*, 2017),  
242 and/or co-occurrence patterns (Vacher *et al.*, 2016) of the detected species can be used to  
243 parameterize process-based production functions for ecosystem services (Barnes *et al.*,  
244 2016; Brose & Hillebrand, 2016; Burley *et al.*, 2016) (**Figure 1**). For instance, the species  
245 identities and biomasses of wild bees identified metagenomically from bulk samples (Tang *et al.*  
246 *et al.*, 2015) could be combined with flower-use observation data (Wood *et al.*, 2017) and  
247 detailed vegetation classification from EO to infer the availability and nature of local  
248 pollination services. Metagenomic data matched to identified species can be particularly  
249 powerful when the impacts of species loss on ecosystem function are not random, evidence  
250 that has previously relied on intensive field sampling, e.g. in tropical freshwater (McIntyre *et al.*  
251 *et al.*, 2007) and marine benthic communities (Solan *et al.*, 2004).



## 252 **Statistical Modelling as the Bridge**

253 Earth Observation technology can produce large-scale, fine-resolution maps and dense time  
254 series of a wide range of biophysical variables (**S1**, **S2**), but it is difficult to translate the  
255 biophysical variables into biodiversity information. In contrast, ARDs and DNA sequencing  
256 are capable of generating large amounts of biodiversity information at species- or even  
257 individual-level resolution (Sunarto *et al.*, 2013; Sigsgaard *et al.*, 2016), but only from point  
258 samples (**S3**). Modern methods of statistical modelling now allow us to scale up from data-  
259 rich point samples to map the distributions of multiple species at once across large spatial  
260 extents (Ferrier, 2002; Ferrier & Guisan, 2006; Honrado *et al.*, 2016; D'Amen *et al.*, 2017),  
261 potentially also including estimates of abundance or biomass, depending on the sampling  
262 and analytical methods used (**S4** "Statistical modelling"). Statistical models also provide a  
263 rigorous framework for quantifying the most important sources of uncertainty.

264 The three approaches with immediate potential to interpolate point samples of community  
265 composition to build continuous species maps and to estimate emergent metrics such as  
266 richness and dissimilarity are: *Joint Species Distribution Models* (Warton *et al.*, 2015;  
267 Ovaskainen *et al.*, 2016a; Ovaskainen *et al.*, 2016b; Ovaskainen *et al.*, in press) (including  
268 *Latent Variable Models*), *Community Occupancy-Detection Models* (Dorazio & Royle, 2005),  
269 and *Generalized Dissimilarity Models* (Ferrier, 2002; Ferrier *et al.*, 2007) (**Figure 3**, **S4**).  
270 Each approach starts with a site-by-species matrix, from data that have been collected by  
271 ARDs or been generated via metabarcoding or metagenomics (**Figure 2**, **S3**), plus any  
272 existing species distribution data. If some species are not detected, repeat sampling can be  
273 used to infer missing occurrences (Dorazio & Royle, 2005). The site-by-species matrix is  
274 then paired with a corresponding site-by-environmental-variate matrix, generated from  
275 continuous EO data plus any relevant geographical layers, and the two datasets are  
276 combined statistically to infer the joint distributions of multiple species across entire regions  
277 (**Figure 3**, **S4**). All three statistical approaches have already been applied successfully to  
278 conventionally acquired datasets (**Box 3**).

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### 281 **Box 3. Current Practice in Community Modelling**

282 Ovaskainen *et al.* (2016b) used a joint species distribution model to predict the distributions  
283 of 55 butterfly species scored for presence/absence on a grid of 2609 10 X 10-km cells  
284 across Great Britain that had been sampled from 1995-1999 in a large citizen-science  
285 project. The model was successfully parameterized with just 300 cells and four measured

286 environmental covariates (degree-days and three types of vegetation cover), plus spatially  
287 structured latent variables. Latent variables use observed species groupings to detect  
288 the effects of unmeasured environmental filters or species interactions such as competition.  
289 The parameterized model was used to predict butterfly communities in the remaining 2309  
290 grid cells. Together, the measured and latent variables explained an average of 42% of the  
291 variance in species occurrence (with medium-prevalence species more accurately  
292 predicted), and the two most-dominant latent variables revealed a north-south gradient in  
293 species composition, with especially distinct communities in the southeast and northwest.  
294 Species richness per grid cell was accurately predicted, and the model's ability to  
295 discriminate presence and absence was high (mean AUC = 0.91).

296 Kery and Royle (2009) used community-occupancy modelling to analyze the 2001 Swiss  
297 breeding-bird survey while accounting for variation in detectability due to season, site, and  
298 species effects. The dataset consisted of 254 1-km<sup>2</sup> grid cells, each visited three times. The  
299 fitted model predicted each species' probability of occurrence as a function of site elevation  
300 and forest cover, as well as variance in the uncertainty of occurrence estimates, making it  
301 possible to estimate species distributions across the landscape and confidence in those  
302 estimates. Parameter estimates were naturally less precise for rare species, but using the  
303 nested model design, information could be 'borrowed' from data-rich species to increase the  
304 precision of predictions for rare species. These procedures were able to compensate for the  
305 fact that only 134 total bird species were recorded in the survey, less than the true total of  
306 163 species known to breed regularly in Switzerland, plus 22 occasional residents. The  
307 occupancy-corrected model estimated that between 1 and 11 species had been overlooked  
308 per grid cell and thus, that the true total in 2001 was 169 species.

309 Finally, Mokany *et al.* (2011) applied Generalized Dissimilarity Modelling (GDM) to a dataset  
310 of 2330 specialist surveys of New Zealand land snails, which recorded 845 of 998 known  
311 species. The GDM used fourteen environmental variables to explain 57% of the variation in  
312 beta diversity, and a generalized additive model explained 27% of the variation in species  
313 richness (after scaling the 20 x 20-m survey quadrats to match the area of modelling units  
314 (200 x 200-m); see discussion of scaling in S4). These outputs were combined using a  
315 procedure called DynamicFOAM that used the models of richness and dissimilarity as top-  
316 down constraints to assign the most probable species of snail to communities across New  
317 Zealand. The error was assessed by predicting compositions in 50 sites, with the remaining  
318 2280 surveys used for model parameterization. On average, the model was able to predict  
319 half the species that had been observed in each cell, and the predicted total occupancy area

320 per species was highly correlated with the number of quadrat occurrences (Pearson's  $r =$   
321 0.902). When quadrats were pooled into groups of 3 to 400 to reduce sampling stochasticity,  
322 predicted species richnesses almost perfectly explained observed richnesses ( $R^2 = 0.99$ ).

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325 By mapping species distributions as the primary output, we do not lock ourselves into an  
326 arbitrary set of convenient indicators, and ongoing discoveries on the relationship between  
327 biodiversity and function (typically focused at the species level) can be added. As an  
328 illustration, the species diversity of wood-decaying fungi in natural forests is notoriously  
329 difficult to assay but can be predicted in part by the volume and species diversity of the stock  
330 of dead wood on the ground (Hottola *et al.*, 2009), and these environmental covariates are  
331 partially quantifiable via airborne LiDAR sensors (**S1**) (Mücke *et al.*, 2013), thus allowing  
332 inference of the distribution and level of wood-decaying fungal diversity via EO. Subsequent  
333 and unrelated research has suggested that dead wood pieces inhabited by a higher diversity  
334 of fungal species decompose more slowly, possibly due to more intense interference  
335 competition (Yang *et al.*, 2016). Combining the two results suggests that an EO-derived map  
336 of fungal species diversity could be used to contrast landscape management options for how  
337 well they conserve saprotrophic fungal biodiversity and thus enhance carbon storage  
338 services. Two further reasons for focusing on species maps as the primary output are that  
339 the regional species pool (*gamma diversity*) and the biological dissimilarity of sites (*beta*  
340 *diversity*) could contribute to maintaining functional stability (Pasari *et al.*, 2013; Wang &  
341 Loreau, 2014; Burley *et al.*, 2016) and that species-resolution outputs retain the option of  
342 aggregation to represent different aspects of biodiversity, including higher-taxonomic,  
343 functional, and phylogenetic groupings (Cardinale *et al.*, 2012).

344 Many methods are also available to predict *individual* species ranges, and EO can help  
345 improve their accuracy (S3 Single Species Detection; Gillespie *et al.*, 2008; Lausch *et al.*,  
346 2016). However, ecosystem functions and services are rarely delivered by a single species,  
347 and summing the outputs of multiple individual models to simulate communities is  
348 computationally inefficient, statistically flawed, and does not account for species interactions  
349 (Calabrese *et al.*, 2014). In the CEOBES framework, we focus on methods for modelling the  
350 compositions of whole communities.

351 From CEOBES to Aichi

352 In essence, our argument is that new technologies now make these statistical approaches

353 (Figure 3, Box 3) much more widely applicable, including in biodiversity hotspots where there  
354 is low capacity for generating the large conventional biodiversity datasets that have been  
355 prerequisites for the above demonstrations. Lower costs and reduced requirements for  
356 taxonomic expertise allow increased numbers of species and environmental covariates  
357 (Leitão *et al.*, 2015; Asner *et al.*, 2017) to be included, which in turn increase explanatory  
358 power by providing more predictors and by exploiting latent variables and letting rare species  
359 'borrow' information (Kery & Royle, 2009; Ovaskainen & Soininen, 2011; Sollmann *et al.*,  
360 2017). Reduced costs also allow larger numbers of training and validation samples to be  
361 taken, which improves the reliability of model parameterization, widens the range of  
362 environmental conditions under which a model is valid, and helps to justify in-situ  
363 surveillance monitoring, which is necessary for detecting threats, such as broad-spectrum  
364 insecticides, that could alter the statistical relationships between EO data and biodiversity.  
365 The maps of community composition that are the primary outputs of the CEOBES approach  
366 (Figure 1) can then be used to inform multiple Aichi Targets.

367 The first example of such a CEOBES approach is given by Sollmann *et al.* (2017), who used  
368 community-occupancy modelling to connect environmental covariates from the 5-m-  
369 resolution RapidEye satellite to point-sample data from camera traps in three tropical forest  
370 reserves managed for logging in Sabah, Malaysian Borneo. They tested whether  
371 mammalian biodiversity is being conserved more effectively in the reserve that is managed  
372 to standards set by the Forest Stewardship Council (Aichi Target 7, sustainable  
373 management under forestry). The dataset consisted of 166 camera-trap stations, each  
374 operating for a minimum of six weeks and scored for three environmental covariates:  
375 distance to water, distance to oil-palm plantation, and forest condition. Estimated  
376 relationships between species occurrence and covariates was used to interpolate species  
377 occurrences from the camera-trap stations over the three reserves. They modelled the  
378 distributions of 28 species, including estimates for the rare species that were improved by  
379 'borrowing' information from more common ones. Species richness was higher in the FSC-  
380 certified reserve, particularly for threatened species (Target 12, improved conservation  
381 status of threatened species). Percentage of area occupied, which could indicate larger  
382 population sizes, was also higher in the certified reserve for the majority of species, including  
383 for some highly endangered species like the Sunda pangolin *Manis javanica*. Finally, the  
384 species richness maps were found to correlate strongly with EO-estimated aboveground  
385 biomass at the large spatial grain of whole reserves, but not at a finer resolution (potentially  
386 due to hunting at reserve borders), further demonstrating the usefulness of ground data for  
387 linking pure-EO data to biodiversity. See also Figure S3.1 for an example combining EO

388 data and environmental DNA to successfully map an invasive diatom over a watershed  
389 (Target 9, invasive species pathway identified) (Olson *et al.*, 2014).

390 A second example is the use of Generalized Dissimilarity Modelling to assess progress  
391 against multiple Aichi Targets by connecting EO-derived metrics of habitat degradation and  
392 fragmentation (Hansen *et al.*, 2013; Newbold *et al.*, 2016) to models of spatial turnover in  
393 biodiversity composition at 1-km-resolution globally, based on over 300 million records of  
394 more than 400,000 species from the Global Biodiversity Information Facility  
395 <http://www.gbif.org/> and the Map of Life <http://mol.org/> (GEO BON, 2016). For instance, by  
396 invoking the assumption that terrestrial biodiversity declines according to the classic species-  
397 area power function, this modelling framework estimates the proportion of biodiversity  
398 associated with each grid cell that is expected to be retained based on the proportion of  
399 similar habitat remaining unimpacted within the landscape (Allnutt *et al.*, 2008). Such metrics  
400 can in turn help to track whether the rates of loss, degradation, and fragmentation of natural  
401 habitats are being reduced (Target 5). By further combining this approach with a global  
402 database of protected-area coverage <https://www.protectedplanet.net/>, it is possible to report  
403 progress against Target 11, which aims for protected areas to cover areas of particular  
404 importance to biodiversity and ecosystem services and to be ecologically representative and  
405 connected (see also Ferrier *et al.*, 2004). An important caveat is that the biodiversity data in  
406 this case are historical in nature and thus contain the taxonomic and sampling biases and  
407 constraints of the past (Box 2). Ideally, the biodiversity data will transition to up-to-date,  
408 properly sampled, and more taxonomically comprehensive point samples, and this can be  
409 implemented region by region.

## 410 **Implementation**

411 It is extremely difficult to identify all the species present in a location (*the Linnaean*  
412 *challenge*), to delimit the geographic distributions of species (*the Wallacean challenge*), and  
413 to quantify their responses to natural and anthropogenic environmental change (*the*  
414 *Hutchinsonian challenge*) (Cardoso *et al.*, 2011). A synergy of Earth Observation, automated  
415 recording devices, high-throughput DNA sequencing, and modern statistical modelling can  
416 meet these challenges by making it possible to scale up from data-rich but finite sets of point  
417 samples to spatially continuous biodiversity maps, which are more informative than a few  
418 convenient indicator species but still let us generate summary statistics to communicate  
419 trends to decision-makers and the general public. The use of formal statistical frameworks  
420 lets us quantify error, more readily identify gaps in our understanding, objectively identify the  
421 most likely pressures on biodiversity from multiple candidates, and increase the robustness

422 of change detection. Adding information on species interactions and functions helps link  
423 biodiversity to ecosystem functions and services (**Box 1, Figure 1**) in a process-based  
424 approach (Barnes *et al.*, 2016), rather than relying on crude estimates from land classes  
425 (Eigenbrod *et al.*, 2010). Finally, as DNA-based technologies mature, the same samples  
426 could track population-genetic diversity (Fitzpatrick & Keller, 2015; Crampton-Platt *et al.*,  
427 2016; Sigsgaard *et al.*, 2016).

428 A global, multi-resolution monitoring network is thus within our capacity but will still involve a  
429 number of challenges associated with technical capability, computation and data storage,  
430 and data standardization. For every biologically distinct region, there will be an initial cost to  
431 collect data for model parameterization, followed by a reduced level of continuous sampling  
432 to update models in the face of directional environmental change that could alter statistical  
433 relationships. The initial investments are probably best borne by governments, as part of  
434 their commitment to the Convention on Biological Diversity, and there is also great promise  
435 in using citizen-science networks to collect standardized, bulk biodiversity samples over  
436 large areas. A laudable example is the School Malaise Trap Program that recruited  
437 hundreds of secondary-school science classes to collect arthropods across Canada  
438 ([malaiseprogram.com](http://malaiseprogram.com)). Initial investment could also come from existing monitoring budgets  
439 with the expectation that additional information content will compensate for reduced sample  
440 numbers within existing programs (Olson *et al.*, 2014). Follow-up sampling requires steady  
441 funding streams, and the standardization of our approach meets the needs of international  
442 certification schemes, such as REDD+, Climate, Community & Biodiversity Standards,  
443 Forest Stewardship Council, and the Roundtable on Sustainable Palm Oil, which all require  
444 the continuous monitoring of biodiversity and ecosystem services. Biodiversity offset  
445 payments to mitigate the impacts of development and carbon emissions are also expected to  
446 provide funding streams, and standardized assessments are needed to ensure that  
447 offsetting results in biodiversity net gain (Maron *et al.*, 2015).

448 Our approach also depends on institutional support for the multidisciplinary collaborations  
449 needed to generate and analyze disparate datasets from multiple disciplines (EO, ARDs,  
450 genomics, functional ecology, and ecosystem services), expertise that no single individual  
451 has (Mueller & Geist, 2016; Palumbo *et al.*, 2016; Pettorelli *et al.*, 2016a). In addition,  
452 identifying causal determinants of species distributions needs a clear understanding of the  
453 phylogenetic structure and functional diversity present, what ecological processes may be  
454 involved, and what EO sensors can and cannot observe (Dafforn *et al.*, 2015). Expert  
455 knowledge will also contribute to sampling design and covariate selection so that the full

456 breadth of environmental conditions (especially those not visible to EO) is captured by the  
457 point samples.

458 On the other hand, collaborations need not be global. Political and social interests will vary  
459 by region, and agencies should be encouraged to trial CEOBES within their jurisdictions  
460 where there are clear opportunities to improve management, while also enforcing the  
461 publication of primary data, sampling design, and analytical pipelines (Petrou *et al.*, 2015;  
462 Schmeller *et al.*, 2015). The Intergovernmental Platform on Biodiversity and Ecosystem  
463 Services (IPBES) could play an important role as a coordinating institution.

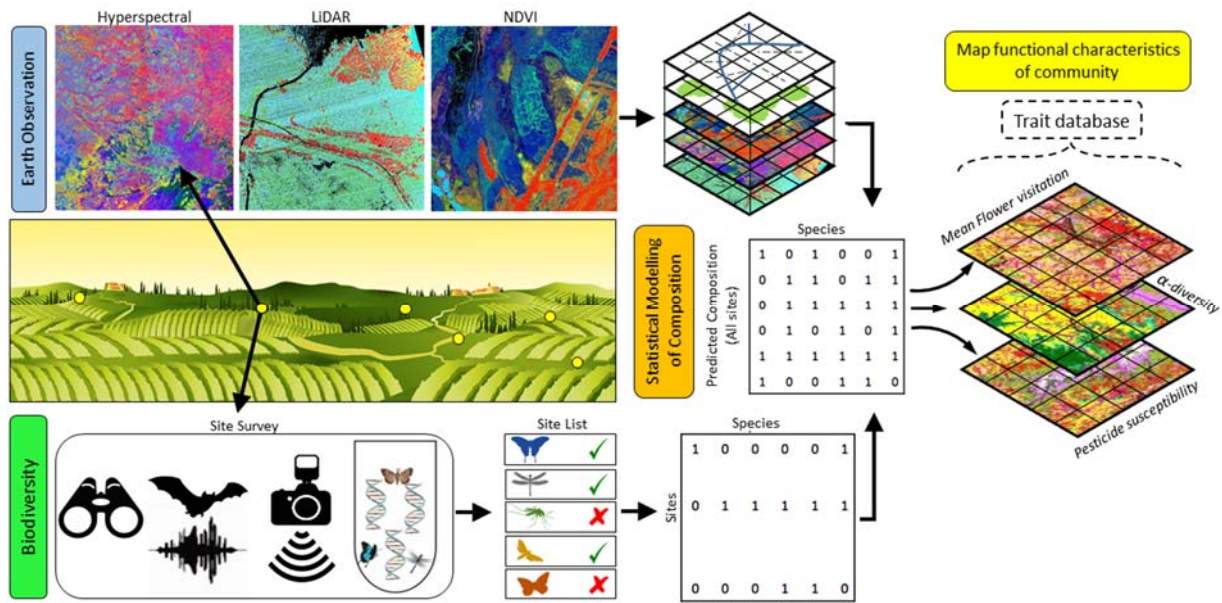
464 Resources for environmental management are always likely to be limited, but by doing more  
465 with our expensively gained field data, we can take action more efficiently and effectively.  
466 What is required now is leadership by governments and international organizations to  
467 stimulate integrated research and to endorse the use of comprehensive biodiversity  
468 information (Pettorelli *et al.*, 2016b).

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473

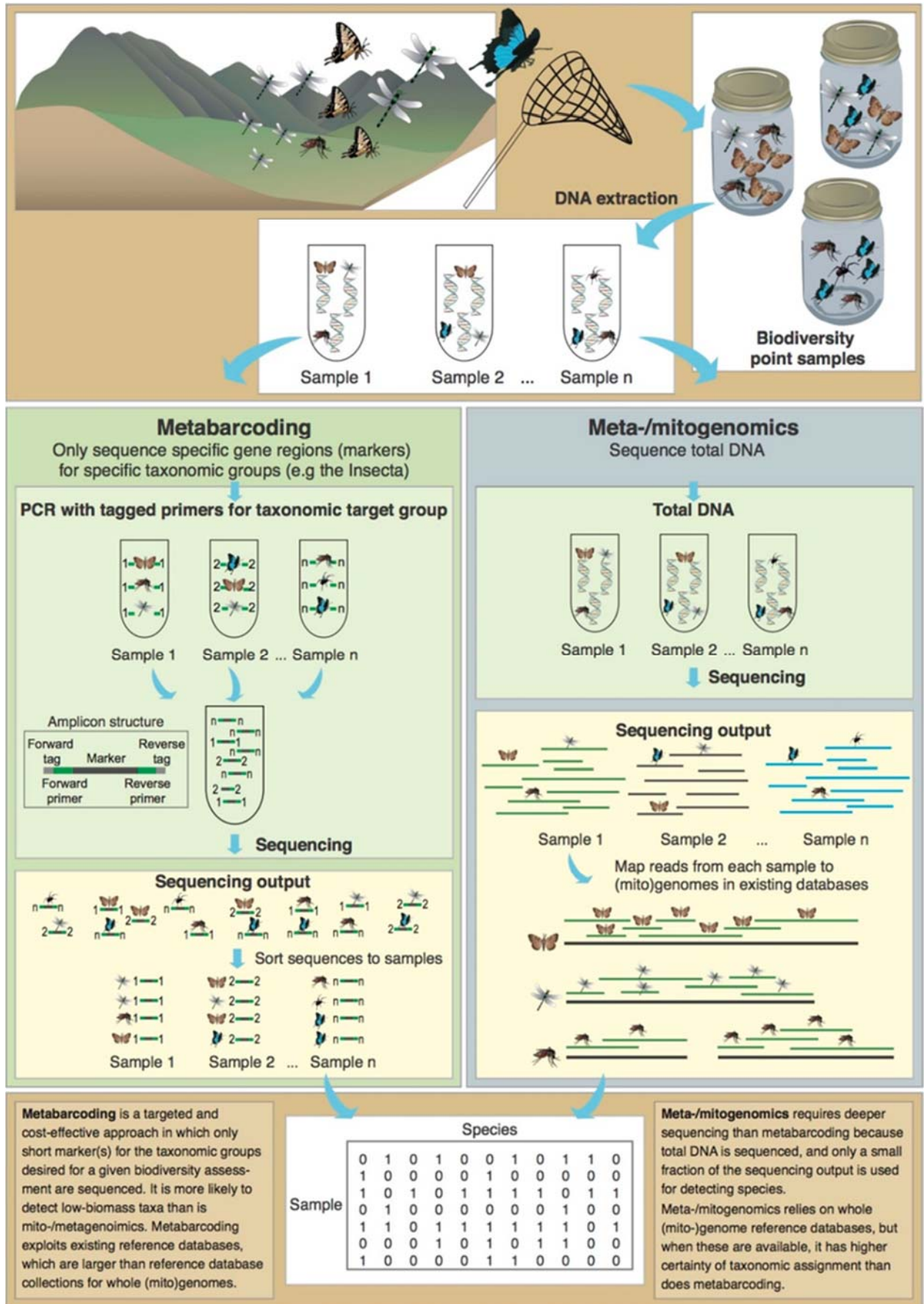
474 **Figures**



475

476 **Figure 1.** CEOBES: Connecting Earth Observation data to Biodiversity and Ecosystem  
 477 Services. **Top row left:** EO data and other geographical datasets are used to generate  
 478 spatially continuous maps of biophysical data (**S1**, **S2**). **Middle row left:** A real landscape  
 479 with sampling locations indicated by yellow dots. **Bottom row left:** Biodiversity is recorded  
 480 manually using traditional methods, automated audio or image recording devices, or  
 481 metabarcoding or metagenomic pipelines to generate a site X species table (**Figure 2**, **S3**).  
 482 However, most of the landscape is not sampled (empty rows in the table). **Right side:** The  
 483 point biodiversity samples are combined statistically with continuous biophysical maps to  
 484 predict biodiversity composition over the whole landscape (**S4**). In combination with ancillary  
 485 data like trait databases, process-based models can then identify the functional composition  
 486 of any location and map the expected distributions of ecosystem functions and services.



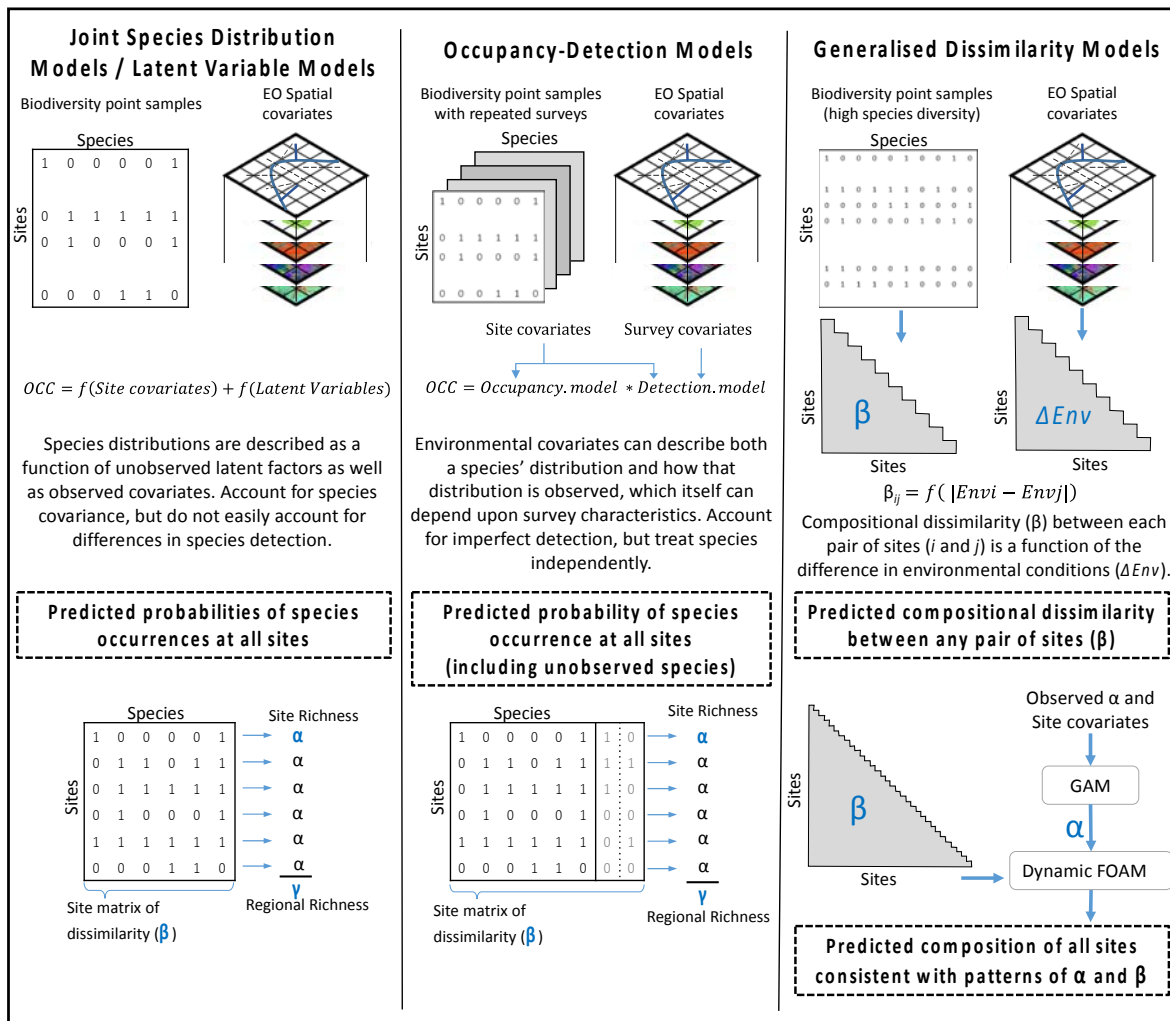


488

489 **Figure 2.** Metabarcoding and metagenomic processing pipelines for high-throughput  
490 biodiversity surveys. **Top row:** Point locations across a landscape are sampled for  
491 biodiversity, and DNA is separately extracted from each sample. Three common sample  
492 types are (i) bulk samples of arthropods (depicted here), (ii) environmental DNA from soil,  
493 water, and air, and (iii) invertebrate collectors of vertebrate DNA (iDNA), such as  
494 mosquitoes, leeches, flies, dung beetles, and ticks. **Left column:** Metabarcoding – Each  
495 sample’s DNA is amplified via PCR (polymerase chain reaction) for a particular marker gene  
496 that is taxonomically informative, the samples are pooled and sequenced on a high-  
497 throughput sequencer, and then sorted back to sample by the sample-specific tags added  
498 during PCR. The sequences are then clustered into Operational Taxonomic Units (OTUs),  
499 which are species hypotheses, and assigned taxonomies by matching against online  
500 databases. **Right column:** Meta/mitogenomics – Each sample’s total DNA is sequenced,  
501 and the output DNA reads are matched to reference genomes, which are often mitochondrial  
502 genomes. **Bottom row:** The output of both processing pipelines is a ‘sample X species’  
503 table. Metabarcoding pipelines are useful for general biodiversity discovery and surveys  
504 because online barcode databases are more taxonomically complete, and even without  
505 taxonomic assignment, it is possible to calculate community metrics from OTUs only.  
506 Metagenomic pipelines are more costly, but advantageous when it is important to reliably  
507 identify particular sets of species and to a greater extent preserve relative biomass  
508 information. See **S3** for further details.

509

510



511

512 **Figure 3.** Three statistical pathways to map community composition and summary metrics  
 513 (local diversity –  $\alpha$ , species turnover –  $\beta$ , and regional diversity –  $\gamma$ ) from the combination of  
 514 biodiversity point samples and continuous Earth Observation (EO) maps. For clarity, the  
 515 figure only considers models for species occurrence (OCC), not abundance. GAM:  
 516 Generalized Additive Model. DynamicFOAM is described in Mokany *et al.* (2011). See **S4** for  
 517 further details.

518

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# 1 The Promise and Practice of Connecting Earth 2 Observation to Biodiversity and Ecosystem 3 Services: Supplementary Information

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## 47 **S1. Earth Observation Technology**

48 Earth Observation (EO) sensors can be differentiated into active and passive types. Active  
49 sensors direct their own source of electromagnetic radiation at the Earth and receive the  
50 signal reflected back from the target (e.g. Synthetic Aperture Radar, SAR, transmits  
51 microwave pulses). Passive sensors rely on external radiation sources such as the Sun  
52 (optical and thermal sensors fall into this category). Different sensors record electromagnetic  
53 radiation in specific ranges of the electromagnetic spectrum, with wavelengths from 400-700  
54 nm (visible light) to 700-2400 nm (near to shortwave infrared), 3000-14000 nm (thermally  
55 emitted radiation), and 1 cm-1 m (microwave radar wavelengths). Passive EO instruments  
56 record radiances at sensor, which generally have to be corrected for atmospheric aerosol  
57 and water vapour impacts in order to estimate the land surface reflectances from which EO-  
58 derived metrics are usually extracted. Active radar sensors record the transmitted energy  
59 that is scattered back from the surface, and since microwaves penetrate clouds, they provide  
60 an all-weather observing capability. However longer wavelengths such as L-band (15-30 cm)  
61 and P-band (30-100 cm) can be affected by fluctuations in the total electron content of the  
62 ionosphere and the Faraday rotation. Optical and radar sensors are available from both  
63 airborne platforms (drones, aircraft) and spaceborne platforms (polar orbiting and  
64 geostationary satellites, international space station). Important characteristics of an EO  
65 sensor are its spectral coverage and spectral resolution (which bands of the electromagnetic  
66 spectrum it measures and at what wavelength detail), its spatial resolution (pixel size), and  
67 temporal repeat-frequency (number of days between two acquisitions at the same location).  
68 Many applications do not require frequent acquisitions, but multiple images can for instance  
69 help account for artefacts and error due to cloud cover (Wilson & Jetz, 2016).

70 Light Detection and Ranging (LiDAR) is an active remote-sensing technique that transmits  
71 infrared or visible polarised light and records the intensity and temporal delay of the received  
72 signal. Because of the constant speed of light in air, airborne LiDAR can measure the  
73 vertical height of objects with very high accuracy (Bradbury *et al.*, 2005). Radar  
74 interferometry from tandem satellite constellations can also measure vertical height but is not  
75 as accurate as LiDAR and has a coarser spatial resolution than airborne LiDAR (Balzter *et*  
76 *al.*, 2016). LiDAR systems can be imaging LiDARs or profiling LiDARs, and some systems  
77 record the full waveform of the received radiation, allowing the study of vegetation canopies  
78 in great detail, while others only record the first and last return of the waveform. LiDAR  
79 instruments are usually mounted on airborne platforms (aircraft, drones) or used as  
80 terrestrial instruments (mounted on a tripod or used as a handheld device), with the  
81 exception of the spaceborne ICESAT-GLAS profiling LiDAR and the planned GEDI mission  
82 to be mounted on the International Space Station.

## 83 **S2. Biodiversity and ecosystem information in EO data**

84 The spatial and temporal coverage of EO cannot be matched by *in-situ* surveys, and  
85 mapping of habitat extent and land cover types has therefore been incorporated into national  
86 monitoring programs for many years (Firbank *et al.*, 2003; Duro *et al.*, 2007).

87 *Aboveground biomass and carbon storage* – Forest ecosystems play a crucial role in global  
88 biogeochemical cycles, and deforestation has been a major contributing factor to increasing  
89 anthropogenic carbon emissions. Global initiatives such as REDD+ (Reducing emissions  
90 from deforestation and forest degradation, and the role of conservation, sustainable  
91 management of forests and enhancement of forest carbon stocks in developing countries)  
92 has been negotiated by the UNFCCC for years and was reiterated in the Paris Agreement  
93 (UNFCCC, 2015). While the main aim is to mitigate climate change by reducing carbon  
94 emissions, for which developing countries receive results-based payments, safeguards and  
95 non-carbon benefits (NCBs) are recognized, including consistency with the conservation of  
96 natural forests and biodiversity (UNFCCC, 2010; Turnhout *et al.*, 2016). The success of  
97 REDD+ therefore depends on our ability to accurately quantify the global distribution of  
98 carbon sources and sinks, for which EO such as SAR or LiDAR are now being developed  
99 (Lynch *et al.*, 2013).

100 Airborne LiDAR can quantify forest canopy height and complexity, and understory density  
101 over large areas, and has been particularly useful in forestry (Vierling *et al.*, 2008). Although  
102 individual trees can be mapped by very high pulse densities (Maltamo *et al.*, 2004), forest  
103 structure is more commonly described by the heights of a lower density point-cloud  
104 aggregated over a forest plot. The average parameters for that forest can then be used to  
105 estimate aboveground biomass, which can be translated to ecosystem services like carbon  
106 sequestration and storage (McKinley *et al.*, 2011). Hollaus *et al.* (2009) demonstrated that  
107 even simple models could make accurate predictions of timber stock in alpine forests after  
108 being calibrated with inventory plot data ( $r^2 > 0.80$ ). The study also showed model accuracy  
109 was not sensitive to LiDAR point density or the season of acquisition.

110 Although performance is likely to vary among habitat types, with accuracy usually greater in  
111 low diversity systems, and dependent on the number and size of calibration plots, a meta-  
112 analysis of more than 70 studies by Zolkos *et al.* (2013) found airborne LiDAR to be more  
113 accurate than radar or passive optical data. Yet more accurate estimates of carbon stocks  
114 may be possible using hyperspectral to discriminate tree species (Dalponte & Coomes,  
115 2016). LiDAR can also be used in ecosystems other than forests. For example, Zlinszky *et al.*  
116 *al.* (2015) demonstrated that LiDAR can replicate ground-based multi-parameter

117 assessments of habitat conservation status in a Natura 2000 grassland reserve in Hungary  
118 (Overall Accuracy=0.8); and using EO, the entire reserve could be surveyed.

119 *Biodiversity* – While the main focus of REDD+ is to reduce carbon emissions, there is also  
120 great potential to improve predictions of spatial patterns of biodiversity from vegetation  
121 structure. As argued elsewhere in this paper, these relationships could prove critical to  
122 achieving the ambitions of initiatives like REDD+ without compromising the benefits for  
123 biodiversity conservation (Beaudrot *et al.*, 2016a).

124 For instance, early EO products like NDVI (normalized difference vegetation index) have  
125 been shown to approximate changes in vegetation structure and hence turnover of the  
126 invertebrate ground fauna (Lassau *et al.*, 2005; Lassau & Hochuli, 2008), and more recently  
127 high spatial resolution airborne imagery has been shown to identify canopy gaps that are  
128 associated with the diversity of understorey vegetation (Getzin *et al.*, 2012). Spectral traits of  
129 plants are determined by their physiological and morphological traits, and there are  
130 demonstrated applications using EO to reveal the distribution of vegetation types (Gillespie  
131 *et al.*, 2008; Asner *et al.*, 2017), functional types (Ustin & Gamon, 2010), richness (Fricker *et al.*  
132 *et al.*, 2015), and temporal changes (Hansen *et al.*, 2013) to name but a few (Lausch *et al.*,  
133 2016). Nonetheless, the success of habitat mapping varies with habitat type, and research  
134 into the right combination of sensors and algorithms is ongoing (Pfeifer *et al.*, 2012; Petrou  
135 *et al.*, 2015; Rocchini *et al.*, 2016). Finally, the combination of hyperspectral sensors and  
136 LiDAR provides an extremely detailed picture of Earth's surface, potentially capable of  
137 identifying the composition of individual trees in some landscapes (Colgan *et al.*, 2012) and  
138 reproducing patterns of tree richness and turnover in highly diverse rainforests at landscape  
139 scales (Féret & Asner, 2014a, b; Asner *et al.*, 2017). Eventually, similar measurements that  
140 directly observe or predict the distribution of biodiversity could be extended globally as  
141 satellite-based LiDAR and hyperspectral imaging systems become operational (**S1**).

142 LiDAR-derived structural metrics have also proven useful as predictors in many *animal*  
143 groups (Davies & Asner, 2014; Simonson *et al.*, 2014), and LiDAR could be more cost-  
144 effective than traditional methods for censusing invertebrate communities (Müller & Brandl,  
145 2009) and is likely to perform even better once taxonomic uncertainties are reduced with  
146 DNA-based identification (Vierling *et al.*, 2011).

### 147 **S3. Biodiversity technology**

#### 148 **Automated Recording Devices (ARDs)**

149 The first set of technologies encompass ARDs, such as camera traps and bioacoustic  
150 recorders that can be left in even remote field locations for weeks to months, continuously  
151 capturing records of birds, amphibians, and mammals, and thus allow continuous sampling  
152 of tens of thousands of hectares at a time, with only occasional fieldwork to maintain sensors  
153 and retrieve data.

154 *Camera traps.* - Camera traps are powerful tools for detecting medium to larger-sized  
155 mammal species, particularly in forests (e.g. Sunarto *et al.*, 2013), and they have also been  
156 used to study ground-dwelling bird species (O'Brien & Kinnaird, 2008; Suwanrat *et al.*, 2015)  
157 and lizards (Broeckhoven & le Fras Nortier Mouton, 2015). Camera traps readily detect rare  
158 and cryptic or nocturnal species, and once set up, operate independently of an observer until  
159 battery life or memory capacity is exhausted. Early models used film roll cameras and active  
160 sensors, where an infrared beam was established across a potential animal path, and the  
161 unit was triggered when that beam was broken. Set-up of the infrared beam (height,  
162 positioning) had to be tailored specifically to the target species, and early studies often  
163 focused on the demography of single charismatic species such as tigers (e.g. Karanth &  
164 Nichols, 1998; Karanth *et al.*, 2006). Even with passive heat-in-motion sensors, which made  
165 for a more flexible set-up because of the increased area over which animals can be  
166 detected, the low number of exposures on film rolls was a severely limiting factor to the time  
167 that camera traps could be left in the field without revisiting.

168 The development of a wide range of digital models in the last 10 years greatly expanded the  
169 applications of camera traps. With increasingly powerful memory cards and batteries,  
170 cameras can now routinely be left unattended for weeks up to several months (depending on  
171 the expected amount of animal traffic). Options for infrared flash make the equipment nearly  
172 invisible, even at night, preventing theft. Modern camera traps capture images of sufficient  
173 quality to allow identification to species in 80-90% of photos. Rapid sequential triggers of  
174 video options further increase the likelihood of obtaining the footage needed to identify  
175 species and individuals. Whereas the up-front investment in the equipment can be high  
176 (depending on manufacturer and specifications, a single trap can cost anywhere between  
177 \$80 and \$800), camera traps have repeatedly been shown to beat other methods (e.g.  
178 transects, track plates) in their efficiency to document medium to large terrestrial mammal  
179 species (Silveira *et al.*, 2003; Lyra-Jorge *et al.*, 2008; Balme *et al.*, 2009), and they become  
180 more cost effective for longer surveys (Lyra-Jorge *et al.*, 2008).

181 Although the method is still used to study the demography of individual species, particularly  
182 those with natural coat patterns allowing individual identification (Gardner *et al.*, 2010;  
183 Sollmann *et al.*, 2011; Wilting *et al.*, 2012), camera traps are now also used in behavioural  
184 studies (Armenteros *et al.*, 2015) and to study species interactions in space and time (e.g.  
185 Linkie & Ridout, 2011; Sollmann *et al.*, 2012). Moreover, camera traps have increasingly  
186 become a tool to survey mammal biodiversity. Several studies have employed camera  
187 trapping to characterize terrestrial (Brodie *et al.*, 2015; Beaudrot *et al.*, 2016b; Sollmann *et*  
188 *al.*, 2017) and even arboreal mammal communities (Gregory *et al.*, 2014; Bowler *et al.*,  
189 2016; Whitworth *et al.*, 2016). Camera traps have been proposed as a tool in systematic  
190 biodiversity assessments in the context of biodiversity co-benefits of forest management  
191 certification and REDD+ payments (Waldon *et al.*, 2011). As an example application, a  
192 recent study on mammalian communities in Bornean forest reserves revealed that  
193 particularly threatened species benefit from sustainable forest management practices,  
194 applied in the context of certification by the Forest Stewardship Council (FSC) (Sollmann *et*  
195 *al.*, 2017). Similarly, such standardized camera-trapping surveys, if repeated over time, can  
196 be used to monitor population and biodiversity trends, which would be impossible using  
197 traditional, observer-based fieldwork techniques.

198 How readily camera traps detect certain species is a function of many factors, including the  
199 species' behaviour and abundance, and the specific location and setup of the camera traps  
200 (Harmsen *et al.*, 2010; Sollmann *et al.*, 2013). For example, arboreal species are harder to  
201 detect with ground-based cameras than terrestrial species; and if cameras are set up  
202 preferably along roads and trails, those species that use these trails will be detected sooner  
203 and more frequently than species that prefer to move through vegetation. Comparing  
204 biodiversity inventory data across sites and/or years therefore requires a standardized study  
205 design, and application of analytical methods that account for these differences in  
206 detectability (see Occupancy Modelling, below).

207 *Bioacoustic sensors.* - Species that produce acoustic signals can further be surveyed with  
208 standalone bioacoustic sensors (Blumstein *et al.*, 2011). Taxonomic groups most frequently  
209 studied with bioacoustic methods include birds (Hobson *et al.*, 2002; Acevedo & Villanueva-  
210 Rivera, 2006), bats (e.g. O'Farrell & Gannon, 1999; Russo & Voigt, 2016), anurans  
211 (Acevedo & Villanueva-Rivera, 2006), certain insects (Diwakar & Balakrishnan, 2007;  
212 Lehmann *et al.*, 2014), and cetaceans (Sousa-Lima *et al.*, 2013). Bioacoustic recordings  
213 have also been used to study fish (Rountree *et al.*, 2006), and non-flying mammals such as  
214 forest elephants (Thompson *et al.*, 2010) and primates (Heinicke *et al.*, 2015; Kalan *et al.*,  
215 2015).

216 Using calls to detect and identify species has a long standing history in bird studies (e.g.



217 Graber & Cochran, 1959). Handheld sound recorders are a useful tool in such surveys to  
218 create permanent records of species audio-detections and to allow for later identification (or  
219 verification) of records by specialists. In contrast to these handheld devices, Automatic  
220 Recording Systems (Peterson & Dorcas, 1994) are standalone bioacoustic sensors that,  
221 similar to camera traps, can be set up in the field to collect audio information without an  
222 observer's presence. Also similar to camera traps, they are primarily limited by battery and  
223 storage capacity, but particularly storage capacity has increased dramatically with the switch  
224 from analogue to digital equipment (Acevedo & Villanueva-Rivera, 2006). Automatic Digital  
225 Recording Systems can be programmed to record 24 hours, or at certain times of the day, or,  
226 alternatively, more advanced equipment can be triggered by calls above a certain amplitude  
227 or of a certain frequency spectrum (Obrist *et al.*, 2010; Stahlschmidt & Brühl, 2012).

228 Once recorded, calls/songs can be identified 'by ear' by a trained human observer  
229 (obviously, only if the species produces a sound that is audible to humans) and/or by  
230 visualization. The latter depicts species-specific acoustic parameters such as the temporal  
231 structure and frequency composition of a call/song. Most frequently, visualization takes the  
232 form of a spectrogram, which shows the evolution of the frequency structure of a call over  
233 time, using color-coding for changes in amplitude (Obrist *et al.*, 2010). Such visualization can  
234 reveal call characteristics that the human ear might not perceive. Call-matching to species  
235 based on these characteristics can be performed manually, or using automated computer  
236 algorithms. Obrist *et al.* (2010) indicate that most automated identification software packages  
237 achieve a 90% recognition rate but can rarely be expected to cover all species present in a  
238 sample. Conversely, Russo and Voigt (2016) have voiced concern over the accuracy of  
239 automated species identification of bat calls.

240 Criticism notwithstanding, advances in the development of audio-recorders and call-  
241 matching software make automated devices a promising tool for biodiversity inventory and  
242 monitoring (Waldon *et al.*, 2011). Such surveys, however, require extensive preliminary  
243 studies to compile reference call data bases. Similar to genetic reference libraries, there are  
244 now multiple available sound libraries (e.g. <http://www.ibac.info/links.html#libs>, accessed 8  
245 Dec 2016), but especially for species-rich tropical communities, bioacoustic databases are  
246 currently limited (Walters *et al.*, 2013). Circumventing the need for species identification,  
247 some studies have suggested the use of bioacoustic diversity as a measure in and of itself.  
248 Rather than identifying individual calls and species, this approach is based on measuring the  
249 acoustic entropy (i.e. temporal and frequency heterogeneity) of the entire soundscape, and,  
250 on the assumption that there is competition for sound niches in time and frequency, a more  
251 complex soundscape is taken as an index for a more diverse community (Sueur *et al.*,  
252 2009). Such bioacoustics diversity indices have been shown to correlate with taxonomic and

253 functional diversity in birds (Gasc *et al.*, 2013) and are a promising emergent field of study,  
254 albeit in need of further development and testing (Sueur *et al.*, 2014).

255 As with other survey methods, detectability and identifiability of individuals and species can  
256 be influenced by their vocalization and other behaviour, habitat, weather, time of day, or the  
257 sensitivity of the recording equipment. For example, wind and concurrent vocalization by  
258 other species were found to have a negative impact on the ability to identify frog calls (Aide  
259 *et al.*, 2013), and different equipment has been shown to result in different numbers of bird  
260 species detected (Rempel *et al.*, 2013). In addition to false negatives (i.e. failing to record a  
261 species even though it is present), misidentification of calls can also result in false positives  
262 (Towsey *et al.*, 2012). As such, standardized surveys and appropriate analytical methods are  
263 required to ensure comparability of results across space and time. Occupancy models, for  
264 example (discussed below) were developed to account for false negatives, and can be  
265 adjusted to account for false positives as well (Miller *et al.*, 2011; Miller *et al.*, 2012). They  
266 have been successfully used in combination with automated acoustic monitoring (Campos-  
267 Cerqueira & Aide, 2016).

#### 268 **DNA-based methods**

269 Almost all DNA-based techniques exploit the stylised fact that some DNA regions exhibit  
270 higher levels of sequence difference between species and low levels of difference within  
271 species, which can be used to tell species apart. For animals, the best known of these so-  
272 called 'DNA barcodes' is a 658-nucleotide portion of the mitochondrial cytochrome oxidase  
273 subunit I gene, or COI, which taxonomists have used to build an online reference database  
274 that links sequences to species ([boldsystems.org](http://boldsystems.org), accessed 11 Oct 2016) (Ratnasingham &  
275 Hebert, 2007). Other mitochondrial markers can also be used for taxonomic assignment, and  
276 these are available in online databases such as GenBank ([blast.ncbi.nlm.nih.gov](http://blast.ncbi.nlm.nih.gov), accessed  
277 11 Oct 2016). An organism can thus be assigned a taxonomic identification by extracting its  
278 DNA, amplifying it with a primer set for the chosen marker(s), sequencing these, and  
279 comparing them to a DNA reference database. Even if a species is not represented in a  
280 database, its congeners or confamilials usually are, allowing at least higher-level taxonomic  
281 identification.

282 When going from DNA barcoding of single specimens, as described above, to using DNA in  
283 synoptic biodiversity surveys, the major challenge is the need to assign taxonomic names to  
284 mixed samples containing DNA from multiple taxa, such as occurs in soil, water, faeces, and  
285 bulk insect samples. The rise of high-throughput sequencing platforms now makes this  
286 routine, and three major approaches are now being used: metabarcoding, high-throughput  
287 individual barcoding, and meta/mitogenomics.

288 *Metabarcoding*. – DNA is extracted from bulk or environmental samples containing DNA  
289 from a mix of different taxa, and a taxonomically informative marker like COI is PCR  
290 amplified using a universal primer set targeting the taxonomic group of interest (**Fig. 2** Main  
291 Text). In this way, only DNA markers of interest are sequenced, making this a cost-effective  
292 approach. The resulting sequences are then clustered into self-similar sets of sequences,  
293 each known as an Operational Taxonomic Unit (OTU), which is a species hypothesis. A  
294 representative sequence is taken from each OTU and assigned a taxonomy using an online  
295 database. The main output of metabarcoding is the classic ecological table of sample by  
296 species (OTU), but now achieved for at least hundreds of species across hundreds of  
297 samples, plus, to a lesser extent, their phylogenetic relationships. Metabarcoding data thus  
298 carry information on species co-occurrence at an unprecedented scale for joint-species-  
299 distribution modelling.

300 Metabarcoding relieves the taxonomic bottleneck, and it also helps relieve the sampling  
301 bottleneck. Firstly, metabarcoding can be applied to taxa such as meiofauna and dipterans  
302 that are easy to collect and ecologically informative but are so difficult to identify  
303 morphologically that they have been ignored in conventional surveys. Secondly,  
304 metabarcoding allows difficult-to-find species, such as fungi, fish, and terrestrial vertebrates,  
305 to be detected directly from microscopic bits of tissue that can be filtered out of soil, water,  
306 air, and parasites, known as ‘environmental DNA’ or eDNA (Bohmann *et al.*, 2014; Thomsen  
307 & Willerslev, 2015). For instance, leeches, flies, mosquitoes, dung beetles, and ticks retain  
308 trace amounts of DNA from their previous meals on animal hosts or faeces, so mass  
309 invertebrate trapping could be used to survey other wildlife (Calvignac-Spencer *et al.*, 2013).

310 However, metabarcoding unavoidably introduces error, including *inter alia* taxonomic  
311 uncertainty due to e.g. PCR and sequencing error and incomplete reference databases,  
312 sample cross-contamination, and loss of species, biomass, and abundance information.  
313 Judicious sampling and primer design, lab practice, and bioinformatic and statistical  
314 pipelines are able to correct or compensate for these errors, and studies have shown that  
315 metabarcoding datasets reflect on-the-ground reality sufficiently closely to allow correct  
316 management decisions (Ji *et al.*, 2013; Edwards *et al.*, 2014; Gibson *et al.*, 2015;  
317 Lejzerowicz *et al.*, 2015; Hänfling *et al.*, 2016; Madden *et al.*, 2016). It is worth noting that  
318 errors are explicit and quantifiable in DNA-based pipelines, whereas conventional surveys  
319 contain important error sources, such as visual misidentifications (Austen *et al.*, 2016), that  
320 are essentially impossible to quantify or correct retrospectively.

321 *High-throughput individual barcoding* – In this method (Meier *et al.*, 2016), large numbers of  
322 organisms, typically insects, are *individually* extracted, amplified, and tagged during

323 amplification. Hundreds of individual amplicons are then pooled and sequenced, producing a  
324 separate barcode for each organism. Throughput is lower and workload is higher than in  
325 metabarcoding, but abundance information is preserved, and individual organisms can be  
326 revisited for further taxonomic study.

327 *Meta/mitogenomics* – Like metabarcoding, metagenomics can be used on bulk or  
328 environmental samples, but instead of targeting a specific gene, all DNA is sequenced, and  
329 the output datasets are interrogated *in silico* for taxonomically and functionally informative  
330 gene sequences (**Fig. 2** Main Text). Compared to metabarcoding, the advantage of this  
331 genomic approach is that it does not require a PCR amplification step to enrich for target  
332 taxa, which should reduce bias. If samples are sequenced deeply enough, even low-  
333 biomass species can be detected in the mix (although sequencer library construction still  
334 imposes some biases). Metagenomics also preserves more information on species relative  
335 biomasses (a proxy for ecosystem-function importance), can reduce the risk of sample  
336 contamination, and depending on the number of samples, can reduce workload. Lastly, it  
337 increases the certainty of taxonomic assignment for species that are present in reference  
338 database. Currently, metagenomics is routinely applied to microbial communities but is not  
339 yet applied to Eukaryotes, due to their much larger genomes and thus higher costs.  
340 However, bioinformatic approaches that allow rapid pairwise comparisons of genomic  
341 datasets (Ondov *et al.*, 2016) and continued decreases in sequencing costs will make this  
342 approach feasible for Eukaryotes. That said, because orders-of-magnitude fewer species  
343 have been genome-sequenced, relative to barcode databases, metagenomics applied to  
344 Eukaryotes is best suited for studies that focus on hundreds of target species or fewer, for  
345 which it is possible to build custom reference databases.

346 In mitogenomics, the focus is on mitochondrial genomes, which can be individually  
347 assembled out of even low-coverage sequencing of bulk samples ('genome skims'), even  
348 though mitochondrial reads typically make up <1% of a sequencer's output (Crampton-Platt  
349 *et al.*, 2016). This greatly reduces the cost of building reference databases. Mitogenomics  
350 has been used to reconstruct the phylogenetic community structure of soil-dwelling beetle  
351 communities (Andújar *et al.*, 2015) and to reliably assign bee species to samples, even after  
352 the samples had been DNA-cross-contaminated by handling (Tang *et al.*, 2015).

353 *Single-species detection* – Finally, in situations where it is imperative to detect particular  
354 species of concern (e.g. early detection of invasive species or monitoring threatened  
355 species) with high probability, older molecular techniques can be used and/or added to the  
356 above methods. Species-specific primers can be used in addition to generic primers during  
357 metabarcoding to increase detection probability (Schubert *et al.*, 2015), or species-specific

358 quantitative PCR (qPCR) can be conducted on eDNA samples. Although low throughput,  
 359 this application of targeted qPCR reduces false negatives, provided that proper lab  
 360 procedure, including negatives controls, is followed (Wilcox *et al.*, 2016). Improved detection  
 361 rates lead to improvements in model performance, thus increasing the reliability of the  
 362 predicted distributions of these species of concern, and greater cost efficiency (Lahoz-  
 363 Monfort *et al.*, 2016). Single-species detections using qPCR have been combined with  
 364 MODIS satellite observations to build maximum-entropy species distribution models that  
 365 predicted the distribution of an invasive diatom (*Didymosphenia geminata*) across the Rocky  
 366 Mountains (Fig S3.1; Olson *et al.*, 2014). Models based on occurrence data from both eDNA  
 367 and traditional methods correctly predicted occurrence of *D. geminata* at external validation  
 368 sites with a 93 – 100% correct classification rate (area under the receiver operating  
 369 characteristic curve, a combined measure of sensitivity and specificity, ranged from 0.94 to  
 370 1.00). Temporally concurrent environmental predictors, including evapotranspiration or land  
 371 surface temperature data from MODIS, allow these models to account for spatial and  
 372 temporal variation and produce robust predictions (Fig S3.1a). This provides natural  
 373 resource managers spatially explicit and extensive predictions on where this invasive  
 374 species is likely to occur. The same approach is also being applied to mapping distributions  
 375 of six native fish on the north-slope of Alaska to aid in their conservation (Olson *et al.*, 2014).

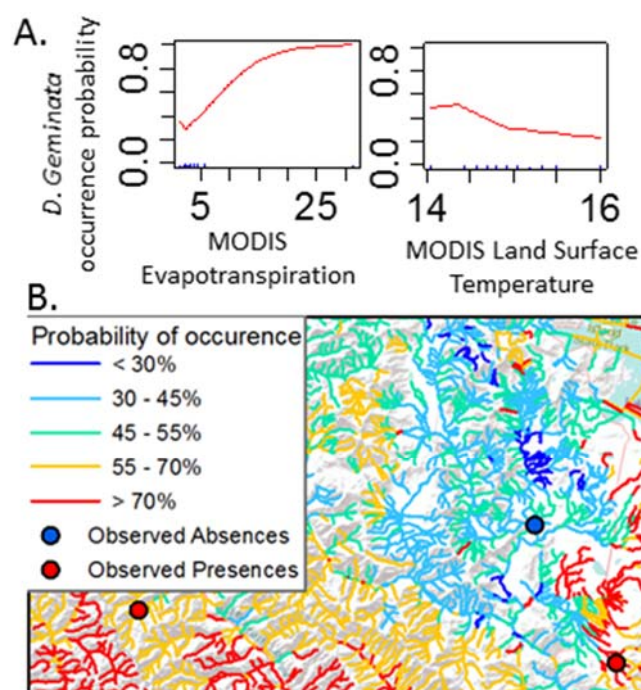


Fig. S3.1 A: Relationship between MODIS measurements of evapotranspiration and land surface temperature and the occurrence of the invasive diatom *D. geminata*. B: Resulting maps of probability of *D. geminata* occurrence from applying model to individual stream segments.

## 377 **S4. Statistical modelling**

378 *Occupancy Detection Models* – Logistical constraints dictate that a site-by-species matrix  
379 can only ever comprise a finite set of point samples, leaving most of the environment  
380 unsampled. Moreover, even within sampled sites, an unavoidable problem is false  
381 negatives: species that are indeed present but not detected (Chen *et al.*, 2013; Tingley &  
382 Beissinger, 2013), and in some cases false positives (species detected are in fact absent).  
383 To correct for imperfect detection, occupancy-detection models are used to disentangle the  
384 factors that determine the occurrence of a species from those that affect the probability of  
385 detection, given occurrence (Guillera-Arroita, 2016). To estimate the probability of detection,  
386 a location is repeatedly sampled, either by spatially sub-sampling a site, or by re-visiting the  
387 same location multiple times within a short time period. A hierarchical generalised linear  
388 mixed model (GLMM) – technically a zero-inflated logistic regression of species  
389 detection/non-detection data – is then used to predict the probability that a species occurs at  
390 a site, based on the site’s environmental covariates and the empirically estimated probability  
391 of detection, which can also itself be a function of site- and time-specific covariates.

392 *Community Occupancy Detection Models* – In the simplest application of occupancy  
393 detection, each species is considered independent, so a multi-species model simply  
394 combines the species’ environmental responses and their different detectabilities, and  
395 calculates metrics of diversity either from occupancy probabilities (in a likelihood framework,  
396 richness is the sum of all occupancy probabilities at a site), or from realized occupancy  
397 states (in a Bayesian framework, richness is the number of species estimated to occur at  
398 that site) (Dorazio & Royle, 2005; Mihaljevic *et al.*, 2015). However, if the environmental  
399 responses of multiple species follow a common distribution, community occupancy detection  
400 models allow individual coefficients to be modelled as a random effect, whereby the data-  
401 poor species borrow information from data-rich species (Gelman & Hill, 2006; Ovaskainen &  
402 Soininen, 2011), which allows information on species traits to be included as predictors  
403 (Pollock *et al.*, 2012). Furthermore, based on differences in species detection probabilities,  
404 occupancy models can also estimate the number of species that were never detected, by  
405 introducing zero-inflation within the inputs (“data augmentation”; Royle *et al.*, 2007; Royle &  
406 Dorazio, 2012), recently extended for multi-region comparison (Sutherland *et al.*, 2016).  
407 More complex models can include the effect of community dynamics on spatial and temporal  
408 variation in occurrence (Dorazio *et al.*, 2010).

409 *Joint Species Distribution Models / Latent Variable Models* – An extension of the single-  
410 species approach is to consider all pairwise co-occurrences among species (Pollock *et al.*,  
411 2014). These so-called joint species distribution models (J-SDMs) predict multi-species

412 responses by not only modelling species-specific responses to environmental covariates as  
413 random effects but also accounting for residual patterns of co-occurrence not explained by  
414 environmental factors (Warton *et al.*, 2015). In the past, the number of taxa that J-SDMs  
415 could consider was limited because the number of parameters in unstructured variance-  
416 covariance matrices rises rapidly (Ovaskainen *et al.*, 2010). However, J-SDMs can now  
417 analyse high numbers of species by inducing correlation among taxa using ‘latent’  
418 unobserved factors (Warton *et al.*, 2015). Residual correlation might indicate species  
419 interactions, like competition or predation, unmeasured predictors, spatial autocorrelation, or  
420 misspecification of the model, all of which warrant further investigation (Ovaskainen *et al.*,  
421 2016a). Spatially explicit latent variables allow one to predict a species community for a focal  
422 site using as predictors not only the environmental variables measured at the focal site, but  
423 also the occurrences and co-occurrences of the species in nearby sites (Ovaskainen *et al.*,  
424 2016b), thus providing a statistically efficient tool for producing interpolated species  
425 distribution maps from sparse data on species rich communities. In principle, the detection  
426 probability itself could also be included as a layer describing the observation process  
427 (Dorazio *et al.*, 2015; Beissinger *et al.*, 2016; Warton *et al.*, 2016). LVMs are currently an  
428 area of active research, and there has been rapid progress to expand computational limits  
429 and integrate with the breadth of previous development using hierarchical mixed models  
430 (Warton *et al.*, 2015). Of particular interest is the opportunity to cluster species responses to  
431 environmental covariates according to species traits (i.e. “the fourth-corner problem”: Jamil  
432 *et al.*, 2013) making it easier to translate compositional turnover to functional shifts (Abrego  
433 *et al.*, 2017).

434 *Generalised Dissimilarity Models* – Finally, in very diverse communities with hundreds or  
435 thousands of taxa (e.g. soil fauna), it might not be meaningful to model the responses of  
436 individual species. Instead, generalised dissimilarity models (GDM) use a pairwise matrix of  
437 compositional dissimilarity to predict the nonlinear response of compositional turnover to  
438 environmental changes; weighting and transforming environmental variables so that  
439 conversion of multidimensional environmental space best describes the scaled turnover of  
440 biological composition (Ferrier *et al.*, 2007). GDM can help identify new sampling sites for  
441 more reliable prediction (Rose *et al.*, 2015), and uncertainty in variable selection can be  
442 further evaluated using Bayesian bootstrapping (Woolley *et al.*, 2017). The dissimilarity  
443 matrix can also be derived from other biological distance metrics like sequence reads, allelic  
444 turnover, functional differences, or phylogenetic diversity (Rosauer *et al.*, 2014; Fitzpatrick &  
445 Keller, 2015; Ondov *et al.*, 2016). The link between turnover of composition or function can  
446 then be tested using scaled environmental variables as predictors of spatial or temporal  
447 changes in service provision (Mokany *et al.*, 2016).

448 GDM has already been incorporated into EO-based applications to estimate ecological  
449 values at landscape scales (Willis *et al.*, 2012; Willis *et al.*, 2015), and model performance  
450 improves when combined with multispectral EO sensors (Leitão *et al.*, 2015). By predicting  
451 the dissimilarity of sites alongside an expected species-area relationship, GDM can also be  
452 used to estimate the proportion of biodiversity retained regionally (**Box 3** in main text). This  
453 has numerous conservation applications (e.g. protected areas effectiveness – Aichi Target  
454 11: Reside *et al.*, 2013), as well as quantifying the biodiversity left regionally (gamma  
455 diversity) to support ecosystem services (Allnutt *et al.*, 2008). If the identity of species  
456 composition is still desired, GDM can be combined with a model of alpha diversity to  
457 estimate the probable species composition of every cell in a landscape (Mokany *et al.*,  
458 2011). Furthermore, ecological processes like dispersal, growth rates, and metacommunity  
459 dynamics have been incorporated to predict ecosystem function and to rank management  
460 actions (Mokany *et al.*, 2015; Mokany *et al.*, 2016).

461 *Sampling design.* – Proper sampling design is fundamental to proper model inference and  
462 should consider environmental representativeness, sampling adequacy, and spatial grain.  
463 Sampling should capture the full range of environmental conditions within the region of  
464 interest so that model extrapolation is minimised (Stevens & Olsen, 2004). If possible,  
465 sampling design should also consider the relative rate of change between environmental  
466 gradients and biological turnover, helping to identify when the former are more likely to be  
467 influencing the latter (e.g. Rose *et al.*, 2015). Implicit in this process are decisions regarding  
468 the spatial grain of analysis, again ideally informed by an understanding of the heterogeneity  
469 of the target community. Importantly, the signal for some ecological processes can be  
470 dependent on scale, and multiple resolutions may need to be tested to demonstrate reliable  
471 conclusions (Münkemüller *et al.*, 2014; Yuan *et al.*, 2016). The advances in EO resolution  
472 offer more opportunities for our assumptions about the scales of community assembly to be  
473 tested (Leibold *et al.*, 2004; Pavoine & Bonsall, 2011; D'Amen *et al.*, 2017).

474 A given survey design must also sample diversity adequately at the spatial grain of interest.  
475 For example, if quadrats are used to sample a large grid cell, the species-area relationship  
476 can predict how many species we would expect to find if we could survey the whole grid cell;  
477 and the slope of this function will depend on the average dissimilarity among samples (i.e.  
478 beta diversity; Tjørve & Tjørve, 2008). If the point samples collectively underestimate the  
479 diversity of the target spatial unit, the model will be biased toward common species, and  
480 typically overestimate turnover between separate sites. Using simulations and tropical forest  
481 inventories, Mokany *et al.* (2013) showed that while a power function could help scale  
482 species richness and dissimilarity estimates, these performed poorly when a sample covered  
483 less than 10% of the 'local unit'. Another limitation is that scaling based on the species-area



484 relationship is also inherently limited to holistic measures of diversity like richness and  
485 dissimilarity. However, the accumulation of species as the sampled area increases could  
486 also be considered as an increase in sampling effort. Diversity is therefore underestimated  
487 as a result of imperfect detection (see the example of community occupancy-detection  
488 modelling by Kery and Royle (2009) in main text). Where multiple samples are available  
489 from sites, it is possible to explicitly correct for sampling sufficiency, retain species identity,  
490 and predict the true diversity at any scale required (Dorazio *et al.*, 2006). If occupancy  
491 models are impractical (e.g. in highly diverse communities), other scaling methods are  
492 available but require parameterisation (e.g. Guilhaumon *et al.*, 2010). Therefore, when not  
493 explicitly accounting for imperfect detection, model performance could be improved by  
494 testing for sampling sufficiency and calibrating scaling relationships (Schuldt *et al.*, 2015).

495 In addition to the pathways that we have described above and in the Main Text (Figure 3),  
496 there of course exist other methods to model communities, which take into explicit account  
497 biological mechanisms such as demography, dispersal, evolution, and specialist interactions  
498 (Wisz *et al.*, 2013; D'Amen *et al.*, 2017). We have not covered these methods because they  
499 require much more input data (Urban *et al.*, 2016) and thus are limited in their applicability,  
500 although when possible, of course all information should be exploited. We note that the  
501 species co-occurrence matrices, latent variables, phylogenetic structure, and ecological  
502 functions that can be extracted from the three statistical pathways in Figure 3 do provide an  
503 efficient way to generate causal hypotheses from large datasets for further, targeted  
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