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A suite of essential biodiversity variables for detecting critical biodiversity change

Dirk S. Schmeller^{1,2,*}, Lauren V. Weatherdon³, Adeline Loyau^{2,4}, Alberte Bondeau⁵, Lluis Brotons^{6,7,8}, Neil Brummitt⁹, Ilse R. Geijzendorffer^{5,17}, Peter Haase^{10,11}, Mathias Kuemmerlen^{10,18}, Corinne S. Martin³, Jean-Baptiste Mihoub^{1,12}, Duccio Rocchini^{13,†}, Hannu Saarenmaa¹⁴, Stefan Stoll^{10,15} and Eugenie C. Regan^{3,16}

ABSTRACT

Key global indicators of biodiversity decline, such as the IUCN Red List Index and the Living Planet Index, have relatively long assessment intervals. This means they, due to their inherent structure, function as late-warning indicators that are retrospective, rather than prospective. These indicators are unquestionably important in providing information for biodiversity conservation, but the detection of early-warning signs of critical biodiversity change is also needed so that proactive management responses can be enacted promptly where required. Generally, biodiversity conservation has dealt poorly with the scattered distribution of necessary detailed information, and needs to find a solution to assemble, harmonize and standardize the data. The prospect of monitoring essential biodiversity variables (EBVs) has been suggested in response to this challenge. The concept has generated much attention, but the EBVs themselves are still in development due to the complexity of the task, the limited resources available, and a lack of long-term commitment to maintain EBV data sets. As a first step, the scientific community and the policy sphere should agree on a set of priority candidate EBVs to be developed within the coming years to advance both large-scale ecological

¹Department of Conservation Biology, Helmholtz Center for Environmental Research – UFZ, 04318, Leipzig, Germany

²ECOLAB, Université de Toulouse, CNRS, INPT, UPS, Toulouse, France

³ United Nations Environment World Conservation Monitoring Centre, Cambridge, CB3 0DL, U.K.

⁴Department of System Ecotoxicology, Helmholtz Center for Environmental Research – UFZ, 04318, Leipzig, Germany

⁵ Institut Méditerranéen de Biodiversité et d'Ecologie marine et continentale (IMBE), Aix Marseille Université, CNRS, IRD, Avignon Université, Technopôle Arbois-Méditerranée Bât, F-13545, Aix-en-Provence cedex 04, France

⁶Forest Sciences Centre of Catalonia (CEMFOR-CTFC), Catalonia, Spain

⁷ CREAF, Centre for Ecological Research and Forestry Applications, Autonomous University of Barcelona, Catalonia, Spain

⁸CSIC, Cerdanyola del Vallés, Catalonia, Spain

⁹Department of Life Sciences, Natural History Museum, London, SW7 5BD, U.K.

¹⁰Department of River Ecology and Conservation, Senckenberg Research Institute and Natural History Museum Frankfurt, D-63571, Gelnhausen, Germany

¹¹ Faculty of Biology, University of Duisburg-Essen, 45141, Essen, Germany

¹² Sorbonne Universités, UPMC Univ Paris 06, Muséum National d'Histoire Naturelle, CNRS, CESCO, UMR 7204, 75005 Paris, France

¹³Department of Biodiversity and Molecular Ecology, Fondazione Edmund Mach, Research and Innovation Centre, 38010, S. Micehle all'Adige (TN), Italy

¹⁴Digitarium, University of Eastern Finland, Joensuu, Finland

¹⁵Ecosystem Research Facility Euβerthal, Institute of Environmental Science, University of Koblenz-Landau, Koblenz-Landau, Germany

¹⁶ The Biodiversity Consultancy, Cambridge, CB2 1S7, U.K.

¹⁷ Tour du Valat, Institut de recherche pour la conservation des zones humides méditerranéennes, Le Sambuc, Arles 13200, France

¹⁸Department of Systems Analysis, Integrated Assessment and Modelling, Swiss Federal Institute of Aquatic Science and Technology - Eawag, Überlandstrasse 133, 8600 Dübendorf, Switzerland

^{*} Address for correspondence (Tel: +49341 235 1654; E-mail: ds@die-schmellers.de).

[†] Authors present affiliation: (1) University of Trento, Center Agriculture Food Environment, 38010, S. Michele all'Adige (TN), Italy. (2) University of Trento, Centre for Integrative Biology, 38123, Povo (TN), Italy. (3) Fondazione Edmund Mach, Research and Innovation Centre, Department of Biodiversity and Molecular Ecology, 38010, S. Michele all'Adige (TN), Italy.

research as well as global and regional biodiversity conservation. Critical ecological transitions are of high importance from both a scientific as well as from a conservation policy point of view, as they can lead to long-lasting biodiversity change with a high potential for deleterious effects on whole ecosystems and therefore also on human well-being. We evaluated candidate EBVs using six criteria: relevance, sensitivity to change, generalizability, scalability, feasibility, and data availability and provide a literature-based review for eight EBVs with high sensitivity to change. The proposed suite of EBVs comprises abundance, allelic diversity, body mass index, ecosystem heterogeneity, phenology, range dynamics, size at first reproduction, and survival rates. The eight candidate EBVs provide for the early detection of critical and potentially long-lasting biodiversity change and should be operationalized as a priority. Only with such an approach can science predict the future status of global biodiversity with high certainty and set up the appropriate conservation measures early and efficiently. Importantly, the selected EBVs would address a large range of conservation issues and contribute to a total of 15 of the 20 Aichi targets and are, hence, of high biological relevance.

Key words: essential biodiversity variables, early change detection, biodiversity loss, biodiversity conservation.

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I. INTRODUCTION

The term biological diversity, or biodiversity, was introduced to conservation biology in 1980 (Soule & Wilcox, 1980), 12 years after Sears & Dasmann (1968) coined it. It took another 12 years for the term to become more widely known in the Convention on Biological Diversity (CBD), signed by 150 government leaders at the 1992 Rio Earth Summit (Balmford et al., 2005). At the 10th meeting of the Conference of the Parties to the CBD, the Strategic Plan for Biodiversity 2011-2020 was revised and updated. To make the plan more tangible, 20 clearly defined conservation targets to be met during this period, the Aichi Biodiversity Targets, were adopted. For the purposes of these targets, and for the CBD in general, biological diversity is defined as follows: 'Biological diversity means the variability among living organisms from all sources including, inter alia, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part: this includes diversity within species, between species and of ecosystems.'

Increasing conservation efforts and financial investment in protecting biodiversity have undoubtedly been made, as well as a remarkable expansion in protected areas on land and at sea. However, accumulated and increasing pressures on the natural world (Newbold *et al.*, 2016) mean it is unlikely that

many of the Aichi Biodiversity Targets will be met by 2020 if we remain on our current trajectory (Tittensor et al., 2014). One of the problems that policy makers and managers are facing is that biodiversity change is often detected or revealed when effective responses are no longer feasible and ecosystem damage is considerable or even irreversible, such as when species become extinct. Key global indicators of biodiversity decline for the Strategic Plan for Biodiversity 2011-2020 are the IUCN Red List Index (Butchart et al., 2006, 2010) and the Living Planet Index (Loh et al., 2005; McRae et al., 2012). However, there is a time lag inherent in these indicators, in particular in the IUCN Red List Index where intervals between assessments of the same species group may take up to 10 years or longer. During this period, species can go from being relatively abundant to being on the verge of extinction or at least regional extirpation, especially when new diseases emerge (Fisher et al., 2012) or when changes in climate and chemistry, proliferation of exotic species and pollution of air, water and soil cause rapid attrition of biodiversity (Clark et al., 2001). In effect, the Living Planet Index and Red List Index function as late-warning signals that are retrospective, rather than proactive, a notion that has been the subject of many studies (Graham & Grimm, 1990). It is crucial, therefore, that our capacity to detect early signs of critical biodiversity

change is improved so that effective management responses can be enacted promptly when required.

Recent scientific literature has explored ecological thresholds, tipping points, and critical transitions, from planetary-scale 'tipping points' (Rockström et al., 2009; Steffen et al., 2015) and drastic changes in species distributions, abundances, and diversity (Barnosky et al., 2012) to the 'critical slowing down' theory of early-warning signals that foreshadow ecological transitions (Scheffer et al., 2009; Scheffer, 2010). Early-warning signals should reflect meaningful changes in ecological status and be applicable across terrestrial, freshwater, and marine ecosystems. While theoretical assessments of early-warning signals have made significant progress (Scheffer et al., 2009; Scheffer, 2010), the remaining challenge is to identify data on real systems that provide structure to the elusive concept of 'generic' early-warning signals (Boettiger & Hastings, 2012) and, ideally, are readily available or, at the very least, continuously collected.

The challenge is to document early changes in biodiversity that have far-reaching consequences for the survival of species and persistence of ecosystems if not reversed. For example, a 'critical slowing down' of ecological systems, as determined by the statistical behaviour of variables describing the system, has been shown to provide warning of pending shifts at tipping points (Wissel, 1984), leading to three possible early-warning signals: slower recovery from perturbations (e.g. repeated coral bleaching events), increased autocorrelation (i.e. between different ecological units within a system), and increased variance (e.g. fluctuations in harvested fish populations (Scheffer et al., 2009). 'Flickering', or the shifting back and forth between two states, is also considered an early-warning signal (Scheffer et al., 2009), and has been observed in models of lake eutrophication (Pace et al., 2013), climatic shifts (Burthe et al., 2015), and trophic cascades (Kuiper et al., 2015). Likewise, species-specific traits, such as body size (Brose et al., 2006, 2008), and phenology (Barnosky et al., 2012) have been explored as potential indicators of an early but far-reaching change in biodiversity. Finally, observed (Parmesan & Yohe, 2003) and predicted (Balint et al., 2011) range shifts in species distributions are being recorded with increasing frequency, showing that range dynamics provide early-warning signs of changes at different scales.

Suggestions for early-warning systems have been numerous (Scheffer & Carpenter, 2003; Andersen et al., 2009; Burthe et al., 2015), but data on biodiversity that could be used to document change are still scattered and patchy spatially, temporally, and taxonomically. Hence, while many early-warning indicators have been developed, most may only be applicable to a narrow spatial range or a few well-documented taxa and ecosystems, and lack robustness due to spatial and/or taxonomic coverage (e.g. fluctuating asymmetry; Lens, Van Dongen & Matthysen, 2002). The current situation calls for increased efforts, as biodiversity conservation needs to improve the data coverage necessary to make informed decisions on the future

prospects of biodiversity. The Group of Earth Observations Biodiversity Observation Network (GEO BON) took up this challenge and proposed the concept of essential biodiversity variables (EBVs) (Pereira et al., 2013). The concept proposes a conceptual interface between raw observations and indicators. EBVs can be seen as a unifying or universal conceptual framework for organizing complex biodiversity data from diverse ecosystems and species in different parts of the world into a limited set of biological variables for documenting biodiversity change (Brummitt et al., in press). The conceptual EBV framework may provide a critical step towards revising strategic goals for the coordination of large-scale, integrative biodiversity monitoring by helping formalize a unified data framework across different ecological fields (Schmeller et al., 2015; Proença et al., in press). Therefore, the EBV framework may prove useful for detecting fundamental biodiversity change by providing the multidimensional data that are required for early detection of biodiversity change at both species and ecosystem levels using indicators based on the EBVs suggested here (Boettiger & Hastings, 2012).

The original EBV concept paper (Pereira et al., 2013) proposed six EBV classes: genetic composition (GC), species populations (SP), species traits (ST), community composition (CC), ecosystem structure (ES), and ecosystem function (EF). An unofficial list of 22 EBVs was proposed in the report of the 17th meeting of the Subsidiary Body on Scientific, Technical and Technological Advice (SBSTTA; UNEP/CBD/SBSTTA/17/INF/7), all of which are biological state variables forming part of the Drivers-Pressures-State-Impacts-Responses framework (European Environment Agency, 1999). However, there is currently no general agreement on candidate EBVs, which is likely to hamper their future development (Pettorelli et al., 2016). For example, it remains unclear which biodiversity change measures will be documented in the EBVs demographic traits, physiological traits, species interactions or habitat structure (SBSTTA; UNEP/CBD/SBSTTA/17/INF/7). Currently, EBVs are being developed based on the easy availability of data, such as the species distribution EBV, and remote-sensing EBVs (Skidmore et al., 2015). However, other EBVs might be equally important for documenting biodiversity change and might be even more important in detecting and anticipating critical ecological change early.

The idea behind the original EBV concept was that at least one EBV per class should be monitored. Keeping the set of EBVs limited is necessary to assure the usefulness of the EBV concept. Communication to the policy sphere will be hampered with an increasing number of EBVs and an overlap in measures of biodiversity change becomes more likely. Focusing development on EBVs necessary for documenting critical biodiversity change will be cost-effective and may improve the communication between science, policy, and the public, as well as allowing the detection of critical ecological change early. A limited set of EBVs will also overcome the technical (e.g. data formats, data

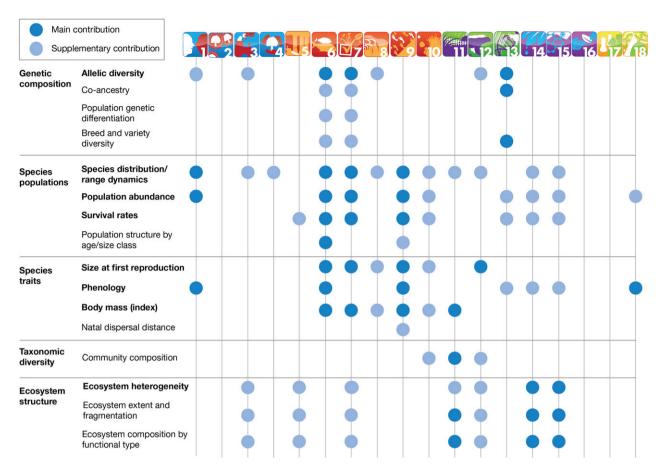


Fig. 1. Contributions of candidate essential biodiversity variables (EBVs) to the Aichi targets of the Convention on Biological Diversity (CBD), distinguishing between main contributions, i.e. direct contributions to a given target, and supplementary contributions, i.e. potential contributions to a given target, likely necessitating additional analyses. The symbols along the top represent the different Aichi targets. The bold EBVs form the suite proposed here.

processing, handling of a huge quantity of data) as well as the scientific challenges (e.g. correction of biases in data, modelling approaches to fill data gaps, harmonization of data across disparate species and ecosystems) more easily (Pettorelli *et al.*, 2016; Proença *et al.*, in press).

Here, we apply criteria outlined in the SBSTTA report UNEP/CBD/SBSTTA/17/INF/7 to prioritize a set of candidate EBVs for their capacity to support the development of early-warning indicators of critical ecological change. These criteria are: relevance, sensitivity to change, generalizability, scalability, feasibility and data availability. Further, we describe the proposed candidate EBVs in terms of their capacity to support the development of early-warning indicators of critical ecological change. We show their limitations but also their relevance to international policy targets, providing a set of EBVs that deserves urgent attention.

II. EBVS OF CRITICAL BIODIVERSITY CHANGE

We here provide definitions of the candidate EBVs, ordered by the organizational level they cover. We prioritize candidate EBVs using the criteria relevance, sensitivity to change, generalizability, scalability, feasibility and data availability (UNEP/CBD/SBSTTA/17/INF/7; Figs 1 and 2). As EBVs are an intermediate level between raw observation data and indicators, the wide range of possible criteria to evaluate and develop indicators (Brummitt *et al.*, in press) were not considered here: These criteria for indicators we consider of importance only for the next steps when indicators are developed or refined based on the candidate EBVs proposed here.

We here define relevance as the contribution an EBV can make to advancing global biodiversity conservation policy by providing data for assessing progress in reaching the Aichi targets. For scoring each EBV, we determined whether the EBV has the potential to provide relevant data for the assessment of one or more Aichi targets (0 = no relevance for Aichi targets; += main relevance for one Aichi target; ++= main relevance for two Aichi targets). In addition, we assessed whether or not the EBV is anthropocentric (0), meaning it has little relevance for biological/ecological conservation aims, or natural (+), meaning that it is relevant for biological/ecological conservation aims.

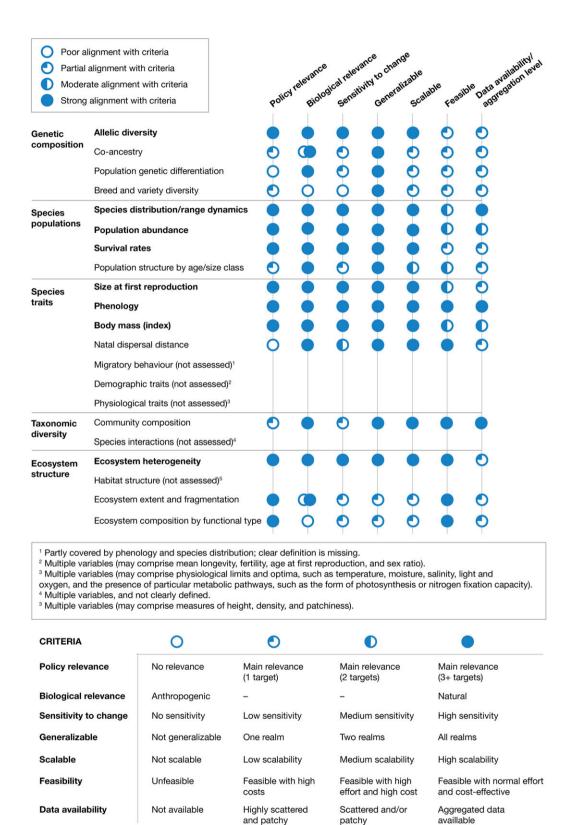


Fig. 2. Summary of assessment of candidate essential biodiversity variables (EBVs), with the EBVs prioritized here shown in bold. We did not assess any EBVs of the ecosystem functioning class, as we do not consider them essential with regard to critical ecological transitions. See main text for details of the scoring exercise.

The sensitivity of an EBV to change should also be over policy-relevant timescales, which in the case of the Aichi targets is a decade. Annual and seasonal variation in biodiversity variables has been considered to be noise (UNEP/CBD/SBSTTA/17/INF/7). We oppose this view, as we think it important to document biodiversity change early and because not all short-term variations are simply noise. The faster that data for an EBV can show change, the higher we consider its sensitivity to detecting change. We considered variables that take 10 or more years to show change as having low sensitivity (+); variables revealing change within 2–9 years as medium sensitivity (++); a variable detecting change in less than 2 years as high sensitivity (+++); and as no sensitivity when no changes can be detected.

We assessed the generalizability of EBVs across terrestrial, freshwater and marine realms. We scored generalizability according to how many realms an EBV can cover (0 = not generalizable; += one realm; ++= two realms; +++= all realms).

The scalability criterion refers to the potential to aggregate and disaggregate an EBV to answer questions at local, regional and global scales. Where an EBV has a fixed scale (local, regional or global) we considered it not scalable (0); if data can only be aggregated or disaggregated with loss of information (e.g. due to conversions) on a local to regional or regional to global scale we considered it of low scalability (+); medium scalability was achieved if data can be aggregated or disaggregated without loss of information on a local to regional or regional to global scale (++); and when data can be scaled to any scale up to global without loss of information, scalability was high (+++).

Measuring an EBV globally should be technically feasible, meaning methods should be established, cost-effective, scientifically proven and applicable at large scales. If that is not the case, we considered an EBV not feasible (0); if costs for measuring an EBV are high we scored it feasible with high costs (+); in cases where high efforts (e.g. through unpaid citizen science involvement or similar) are needed to measure an EBV and high costs must be expected we scored it feasible, but not cost-effective (++); finally, if measurement of an EBV is cost-effective, incurring normal resource use (human and financial), we scored an EBV as feasible and cost-effective with normal effort (+++).

We also assessed data availability for aggregating into an EBV, and their potential to be harmonized and standardized. We scored the absence of data as 0; scored data as highly scattered and patchy when only a few data sets covering only a few localities, species and time periods are available (+); where data sets are available that cover a large number of species across larger scales and time periods (e.g. the majority of species across a continent over more than 20 years), we scored it as scattered and/or patchy (++); and where aggregated data are readily available (e.g. availability of large databases) we scored it as +++.

The results of this scoring exercise are summarized in Figs 1 and 2.

Below we describe each candidate EBV and their relevance to indicating critical ecological transitions based on current knowledge, and consider their relevance for international conservation policy, including where potential pitfalls (e.g. data availability) need to be considered during their development.

(1) Allelic diversity

Definition: allelic diversity is the average number of alleles per locus in a population of a given species (Allendorf, 1986).

Allelic diversity is a measure of genetic diversity that is indicative of a population's long-term potential for adaptability and persistence. A decrease in allelic diversity is linked directly to a reduction in the potential of a population to adapt to future changes, since alleles are the raw material for evolution through natural selection (Allendorf, 1986; Caballero & García-Dorado, 2013). High allelic diversity is thought to increase a species' capacity to evolve by making a larger fraction of the genotypic space accessible through fewer mutation events (Wagner, 2008), and therefore indicates the evolutionary potential of a population and its survival chances under changing environments (Greenbaum et al., 2014). The only source of new alleles is mutations, which usually occur at very low frequencies. By contrast, genetic drift (Masel, 2011) can very quickly deplete a population of alleles, depending on the effective population size (Schmeller & Merilä, 2007). Once an allele becomes fixed, genetic drift comes to a halt, and allelic diversity cannot change unless a new allele is introduced into the population via mutation or gene flow. Thus, although genetic drift is a random, directionless process, it can eliminate genetic variation over time and is deleterious from a conservation point of view (Frankham et al., 1999). Effects of bottlenecks can be traced back through time (Piry, Luikart & Cornuet, 1999) and thereby provide information on the recovery process of a population or species, facilitating observation of change in allelic diversity over longer timescales as well as retrospectively. Therefore, allelic diversity determines the capacity of long-term responses to selection and the survival of populations and species (Allendorf, 1986; Reed & Frankham, 2003). In contrast to heterozygosity, which might not be significantly reduced by short-term (~1 generation) population bottlenecks (increasing genetic drift), allelic diversity will be more severely reduced. The longer the bottleneck lasts, the stronger the impact from inbreeding, leading to inbreeding depression. Thus, it has been suggested that a measure of allelic diversity is of key importance in population conservation and management (Frankham et al., 1999). The relationship between population fitness and allelic diversity has been shown in a variety of species groups, including plants (Booy et al., 2000), amphibians (Schmeller, 2004; Schmeller et al., 2005), insects (Mattila & Seeley, 2007) and microbes (Thompson et al., 2005; Chen et al., 2013). However, the detection of the loss of allelic diversity largely depends on the frequency of sampling and

the sampling effort, as the variance of the number of alleles should be low in an undisturbed and healthy population (Ruzzante, 1998).

The limitations to developing an allelic diversity EBV are mainly technical. Population genetics is a relatively young research field and the first large-scale genetic studies were conducted using allozyme electrophoresis (Tigerstedt, 1973). Since then, methods to determine alleles in populations have expanded and data comparisons across these methods are challenging (Ball et al., 2010). Furthermore, due to costs, sampling is often restricted to populations and areas at small spatial and temporal scales and for a restricted number of loci. Although the development of an allelic diversity EBV appears to be feasible in certain regions of the world, it would be challenging to retrieve data across large geographic and temporal scales and for a large number of populations and species. Moreover, there is no common database reporting allelic diversity values for multiple species, with information scattered across many publications and sources. An important concerted effort would be needed to assemble this information to produce a robust allelic diversity EBV with significant potential for predicting critical biodiversity change at a genetic level.

(2) Body mass

Definition: body mass scaled by body size, or the body mass index (BMI), indicates the condition and energy reserves of animals (Krebs & Singleton, 1993).

The BMI provides an estimation of energy reserves and is a direct consequence of the individual's ability to acquire and metabolize food. Therefore, BMI is linked to resource availability, foraging success, suitability of habitat, ability to cope with environmental pressures, and an individual's health status and vigour (Peig & Green, 2010; Labocha & Hayes, 2012; Clancey & Byers, 2014). BMI may vary at fine spatial and temporal scales depending on the species (Cheung et al., 2013) and decreases rapidly during food shortage and impaired health, or when the environment deteriorates or is contaminated by pollutants (Chastel, Weimerskirch & Jouventin, 1995; Sheppard, Pitt & Schlacher, 2009; Bergman et al., 2014; Macedá-Veiga, Green & De Sostoa, 2014). Variations in BMI at the individual level may translate into long-lasting impacts at the population level (Mousseau & Fox, 1998; Ozgul et al., 2010; Rode, Amstrup & Regehr, 2010). For example, declines in body condition have provided early indicators of population decline in polar bears (Ursus maritimus) due to changing ice conditions (Rode et al., 2010), and the BMI of the beach clam (Donax deltoids) was shown to be lower on beaches subjected to vehicle traffic (Sheppard et al., 2009). Indeed, when BMI is low, individuals usually have reduced immune capacity and survival prospects. The most extreme example is the strong and direct link between survival and BMI measured just before individuals enter hibernation. Individuals can also respond by not breeding or by reducing their energy expenditure through reduced offspring numbers, offspring size and parental care, which leads to reduced offspring survival (Mousseau & Fox, 1998; Karell et al., 2008; Rode et al., 2010; Johnson et al., 2014). Maternal condition can also influence offspring survival through the transfer of maternal hormones, antibodies or other substances (Karell et al., 2008; Bennett & Murray, 2014; Bergman et al., 2014) and therefore shows carry-over effects to future generations (Van Allen et al., 2010). However, individuals sometimes increase their reproductive effort as a terminal investment to maintain their breeding output, but may die of exhaustion after reproduction is complete (Clutton-Brock, 1984). Following from the above, a change in the BMI at a population or even species level can indicate a change in the condition of that population or species, allowing an early assessment of future survival prospects under given conditions.

The BMI is restricted to animals and therefore does not directly cover all biodiversity. However, as it reflects the health status of animals, it also indicates the occurrence of microbial pathogens and parasites as well as plant food sources and is therefore more comprehensive than implied. BMI is used widely across all animal groups [invertebrates (Sheppard et al., 2009; Tomiyama et al., 2010; Johnson et al., 2014); fish (Kolm, 2002; Macedá-Veiga et al., 2014); amphibians (Bancila et al., 2010); birds (Chastel et al., 1995; Karell et al., 2008; Labocha & Hayes, 2012); mammals (Ozgul et al., 2010; Peig & Green, 2010; Rode et al., 2010)]. However, the ecological literature contains a substantial number of alternative indices for BMI (Peig & Green, 2010; Labocha & Hayes, 2012; Macedá-Veiga et al., 2014). These indices can be calculated with various formulae from the same measures, and size/length can even be measured in various ways, such as in birds (Labocha & Hayes, 2012); ecologists usually follow traditions within their discipline independently of other disciplines. In addition, as BMI is linked to food shortage, it can show natural seasonal variation (= noise), depending on the species. BMI can further show important variations by sex, age class, social status or subspecies (Peig & Green, 2010). Finally, the reproductive stage of an individual can bias the calculated BMI, given that gestating females or females with eggs will have a higher BMI despite not having higher energy reserves.

(3) Size at first reproduction

Definition: size at first reproduction is the individual body size (length) reached by an organism at the time when its first reproduction occurs.

Reproduction is the process by which offspring are produced, encompassing several successive events that can be used to define its timing: for example, calling/singing, mating, ovulation, egg laying/spawning, flowering, pollination, parturition, egg hatching, and seed dispersal. Body size is strongly correlated with many physiological and fitness parameters in a wide range of taxa, with larger individuals being more dominant, living longer, and having better immune capacity (Lee, 2006). Larger individuals are usually more fertile, produce more propagules, and propagules of better quality with higher survival prospects (Loyau, Sorci & Jalme, 2005). A smaller size at reproduction

can result from (i) genetic inheritance (i.e. smaller parents have smaller offspring), (ii) non-genetic parental effects (e.g. parents invested lower resources in offspring production (Roach & Wulff, 1987; Mousseau & Fox, 1998; Kolm, 2002; Loyau & Lacroix, 2010); and (iii) environmental effects (e.g. limited resources for growth, or stressors hampering growth. (Cattaneo et al., 1998; Conover & Munch, 2002; Rohr et al., 2004; Rode et al., 2010). In a given individual, the energy spent dealing with environmental stress is substantial and allocated at the expense of other functions such as growth and reproduction. Therefore, body size in general, and size at first reproduction in particular, is sensitive to environmental changes. The impact of environmental deterioration on size at first reproduction is well known among diverse taxa. For example, plants growing in a high-quality environment can be larger at reproduction and reach maturity earlier, while larger plants in a population frequently flower earlier (Roach & Wulff, 1987; Forrest & Miller-Rushing, 2010). Plankton species have reduced size due to metal and acid pollution (Cattaneo et al., 1998). Food constraints, low precipitation, and chemical pollutants have been shown to reduce the size of amphibians such as the streamside salamander Ambystoma barbouri (Rohr et al., 2004). A decrease in size at first reproduction is a common response to exploitation of fish stocks (Conover & Munch, 2002). Lower temperatures and food availability have also been shown to lead to reduced size at first reproduction for many plants and insects (Forrest & Miller-Rushing, 2010). As with BMI, size at first reproduction is an important determinant of lifetime fitness, and has direct consequences on the strength of recruitment to the population and therefore population persistence. Size at first reproduction is also a ubiquitous indicator of lifetime fitness across very different taxonomic groups.

Size at first reproduction can be measured for both plants and animals. Contrary to BMI, there is no dispute regarding the methodology and formulae that should be applied. However, because reproduction is not limited to a single point in time, it might be challenging to record size at first reproduction for a given population and between populations. Depending on the species monitored, males and females may ideally need to be measured at different points in time (e.g. when there is a delay between mating and gestation due to embryonic diapause). Size at first reproduction can also show variation by sex or population. The main drawback of this parameter is the disturbance caused by catching and measuring individuals at the time of first reproduction. Contrary to the measurement of BMI, which can take place at less critical times (outside the reproductive season), measurement of size at first reproduction may cause excessive stress in some species and even interrupt mating events and therefore reproduction.

(4) Phenology

Definition: phenology is defined as annually recurring life-cycle events, such as the timing of migration or flowering.

Changes in phenology can be the first indicators of important ecological changes in terrestrial, freshwater, and

marine environments, including changing predator-prey or pathogen-host and phenological relationships (Walther et al., 2002; De Beurs & Henebry, 2004; Edwards & Richardson, 2004; Cleland et al., 2007; Morisette et al., 2008; Liang & Schwartz, 2009; Devictor et al., 2012; Clare et al., 2016). For instance, earlier salmon migrations in response to warmer temperatures can provide an early warning of cascading impacts on predator-prey dynamics and the availability of ecosystem services, such as the marine-derived nutrients that salmon bring to freshwater systems (Kovach et al., 2013). Changes in phenology can also result in decoupling of temporally matched biotic interactions; co-evolved processes with different triggers (e.g. light-, temperatureand precipitation-triggered processes) are prone to such decoupling. This has important ramifications for trophic interactions, altering food-web structures and leading eventually to ecosystem-level changes. In the Arctic, for example, the advance in plant phenology is attributable to the accelerating decline in Arctic sea ice, and contributes to declining reproductive performance of large herbivores via trophic mismatches (Kerby & Post, 2013). In the marine environment, there are different degrees of climate change responses throughout the community and the seasonal cycle, leading to a mismatch between trophic levels and functional groups (Edwards & Richardson, 2004). In many species, successful reproduction depends on the temporally matched availability of suitable reproductive habitat in good condition (Probst et al., 2009; Stoll et al., 2010) and the availability of certain food types during critical periods for the offspring (Stenseth & Mysterud, 2002). These changes can have far-reaching impacts on biodiversity, including species extinctions.

There is a large body of available phenological data for the terrestrial, freshwater, and marine realms and numerous techniques to measure it, including species-level observations (Menzel et al., 2006; Devictor et al., 2012), satellite remote-sensing (Zhang et al., 2003), and atmospheric monitoring of carbon dioxide concentrations (Keeling, Chin & Whorf, 1996). In addition, there are many networks around the world monitoring phenology for a diverse range of species, including the USA National Phenology Network, the European Phenology Network, Canada's PlantWatch, and India's SeasonWatch. The monitoring of phenology is popular with citizen science initiatives and the media frequently picks up the results from these networks. Therefore, phenological variables are also an important awareness-raising tool for biodiversity change amongst the general public.

Substantial seasonal and inter-annual variation in phenology may make it difficult to discern and compare long-term trends (Liang & Schwartz, 2009). In addition, geographical variation in data availability can make it difficult to monitor global patterns in phenological change. While there is a large number of ground-based phenology studies and resulting data, it can be difficult to detect ecological change at a global scale because of the difficulty of unifying data records over species and different phenological events (Schwartz, Ahas & Aasa, 2006). Remotely sensed data has the

advantage of global coverage but also presents drawbacks, such as the influence of the atmosphere, its inherent temporal frequency of data acquisition making it unsuitable for detecting certain changes in phenology, or a lack of species-level resolution. However, recent studies (Buitenwerf, Rose & Higgins, 2015) show that comprehensive global assessments are possible and that previously detected changes in the northern hemisphere have now been confirmed for the southern hemisphere.

(5) Abundance

Defintion: abundance is the number of individuals of a species within a local population.

Abundance can be measured using a variety of often taxon-specific methods. Different parameters of abundance (e.g. absolute abundance, relative abundance, effective population size) are used in different scientific contexts. Species abundance data in form of counts is probably one of the most readily available types of data for biodiversity monitoring (Marsh & Trenham, 2008; Schmeller et al., 2009, 2012; Geijzendorffer et al., 2016). Further, the analysis of temporal trends in species abundances is already an established macroecological approach to identify environmental changes at local, regional, and global scales (Butchart et al., 2010) and can also be inferred using genetic as well as demographic methods (Schmeller & Merilä, 2007). Species populations are sensitive sentinels of environmental status since organisms integrate the effects of environmental pressures over their lifetime (Guisan & Thuiller, 2007; Devictor et al., 2012). This is particularly true towards the edges of a species' distribution range, where changes in local species abundance may be sensitive to climatic changes and typically precede species range expansion or contraction (Devictor et al., 2008). Furthermore, local abundance is critical for assessing population extinction risk (Lande, 1993), and small populations often incur genetic drift, which can very rapidly reduce genetic diversity (Masel, 2011). For example, declines of farmland birds (Donald, Green & Heath, 2001) and plants (Flynn et al., 2009) were underpinned by the detrimental effects of agricultural land-use intensification. Changes in the abundance of species with certain traits are also directly linked to ecosystem functioning (Winfree et al., 2015). For example, the decline of predatory species can lead to regime shifts in ecosystems through trophic cascades (Pace et al., 1999).

As species are patchily distributed, finding for each species the appropriate spatial scale at which to determine its abundance is essential. Determining the spatial context of abundance is particularly difficult in group-living animals, e.g. large-distance migrating herds of ungulates or colonies of bats that roost in caves but use large areas for foraging (Fattorini, Pisani & Sforzi, 2004). In groups that are able to reproduce asexually, determining abundance in clonal populations is an issue as ecological properties and resilience to environmental change differs with the genetic diversity of a local population (Hughes & Stachowicz, 2004; Massa *et al.*, 2013). Generally, linking

genetic processes in populations to present-day abundances is challenging, as these processes are determined by effective population sizes of reproducing individuals only, and often requires an understanding of previous population sizes (Schmeller & Merilä, 2007). Also, in a conservation context, the uncritical use of abundance data can produce undesired effects, with relative processes of source and sink populations (Brawn & Robinson, 1996) as well as the possibility of ecological traps (Battin, 2004) requiring consideration.

(6) Survival rates

Definition: survival rate is the average probability that an organism will stay alive between two time points.

Among demographic traits, survival is a critical variable for assessing and forecasting biodiversity changes and trends. Survival rates are sensitive to environmental changes and vary both in time (over consecutive time steps; Lebreton et al., 1992; Ozgul et al., 2006) and space (between populations, countries, regions; Hanski, Alho & Moilanen, 2000) and between individuals (Nichols et al., 2004; Péron et al., 2010; Earl & Semlitsch, 2013). Consequently, survival estimates offer robust evidence for measuring spatio-temporal changes in population trends and conservation status (Nichols & Williams, 2006; Kupferberg et al., 2012), as well as to test a very large set of ecological hypotheses (Lebreton et al., 1992). In the context of global changes, monitoring survival over large spatio-temporal scales can help to evaluate the impact of multiple drivers such as climate change (Grosbois et al., 2008) or the spread of invasive species and disease (Garner, Rowcliffe & Fisher, 2011). Survival is a fundamental parameter supporting population dynamics and ultimately, species persistence (Caswell, 2001; Morris & Doak, 2002). Population growth rate, viability and extinction probabilities are particularly sensitive to survival (Caswell, 2001), so that estimating survival rates becomes of primary interest for quantitative ecology, conservation biology and wildlife management (Morris & Doak, 2002). For example, survival is a keystone parameter in population viability analysis (PVA; Beissinger & McCullough, 2002; Morris & Doak, 2002). Lastly, monitoring demographic parameters such as survival allows much earlier signals of biodiversity change or the impact of drivers to be detected than do abundance counts or occurrence records. In this regard, changes in abundance and occupancy can be seen as delayed and consecutive by-products of changes in survival rates (Lamb et al., 2009).

Relatively few data are available for measuring survival over large scales and taxonomic groups because monitoring individual species usually requires substantial and intense efforts, for example through capture—mark—recapture studies (Lebreton *et al.*, 1992; Nichols, 1992; Burnham, White & Anderson, 1995). In addition, estimating survival rates requires specific statistical analyses that can be challenging to deal with (Nichols & Kendall, 1995; Pradel *et al.*, 1997; Pradel, 2005) and which can restrict widespread survival assessment. Few species have been the focus of such monitoring and, even for the most-studied species, both survival and fecundity data

are usually scattered, geographically localized (usually one or very few populations) and limited in time (from a few years up to a decade in duration), which prevents reliable and comprehensive large-scale assessments even within a single species.

(7) Range dynamics

Definition: range dynamics are changes in species distributions through time, space and shape. This EBV is derived from the species distribution EBV for detecting critical ecological change early.

Range dynamics, as induced by anthropogenic environmental changes, have been associated with reduced resilience and species declines (Moritz & Agudo, 2013). Range contractions are the most frequently observed range dynamic. We generally see range contractions for species associated with particular environmental conditions and/or those that are vulnerable to anthropogenic degradation (Lesica, McCune & Ezcurra, 2004). Conversely, highly tolerant species tend to expand their ranges as the landscape is modified and as the climate changes. While species constantly modify their distributions, particularly fast, sudden and concerted changes may be important indicators of ongoing biodiversity change. Species ranges can shift in space, either upwards (altitudinal) or along the surface (latitudinal & longitudinal); they can also be transformed in their size (expansion or contraction) and/or shape (e.g. fragmentation). Many such range shifts have been observed in the marine, freshwater and terrestrial realms (Beaugrand et al., 2002; Parmesan & Yohe, 2003; Heino, Virkkala & Toivonen, 2009). However, most shifts are related to transformations in the size of the ranges, indicating range expansions or contractions. These two phenomena are also of great interest as ranges could be transformed, but not shift in space. If such a change remains undetected, it might mean that extinctions or invasions remain unnoticed or that species reach a physical limit of distribution leading to an increased risk of extinction (e.g. hill topping; Sauer et al., 2011; Domisch et al., 2013). Further possible changes include modification of range shapes, eventually leading to range fragmentation. In this case, isolated populations are subject to similar conditions as range contractions.

Changes in species' ranges can be accurate early-warning indicators of critical changes to biodiversity. Pereira et al. (2013) propose an EBV class 'species populations' that includes species' distributions, extinctions and invasions. Beyond the mere distribution of biodiversity, however, changes in distributions serve as a critical indicator of a species' current status. For example, the area occupied by a species is far less informative from the EBV perspective than whether the same species is losing range at a specific velocity, or is undergoing an accelerated altitudinal shift (Moritz & Agudo, 2013). Such rates of change raise significantly more awareness of the status of a species, allowing those under the most critical circumstances to be flagged up. Further, modifications in species distribution patterns have the potential to affect associated ecosystems significantly (Record et al., 2013).

To understand the range dynamics of individual species or communities, replicated measurements are necessary with an absolute minimum of two events: an original distribution and a subsequent distribution (Sheldon, 2012). Current data-collection frameworks aim at recording sufficient species occurrences to monitor trends in biodiversity associated with global environmental change. However, the detailed and standardized analysis of changes to individual distribution patterns is still missing. The density of monitoring sites may not deliver sufficient information to monitor the range dynamics for many species. Species with very restricted distributions and of high vulnerability may not be covered at all by current monitoring efforts. Resorting to species distribution model (SDM)-assisted monitoring of range dynamics has been put forward as an important tool with which to predict future range dynamics (Pereira et al., 2013), and will have to deal with additional uncertainties related to input data and collecting intensity, as well as those arising from the modelling procedure (Elith & Leathwick, 2009).

(8) Ecosystem heterogeneity

Definition: ecosystem heterogeneity describes the amount of variability in space and time of ecosystems.

High ecosystem heterogeneity has been considered important for increasing species diversity in some species groups (Murdoch, Evans & Peterson, 1972; Roth, 1976; Tews et al., 2004). The processes by which ecosystem heterogeneity may provide a wider range of habitats supporting higher species diversity are manifold, including greater surface area, more physical refugia, higher or more varied supplies of limiting resources, and therefore a larger number of ecological niches (Tews et al., 2004). This is due to the fact that the realized niche of a species is ultimately a function of environmental conditions and their variability (Palmer et al., 2002). Human activity leads to the homogenization of environmental conditions (Vitousek et al., 1997; McKinney, 2006), and hence to the attrition of biodiversity (Foley et al., 2005). A decrease in ecosystem heterogeneity can therefore be an early-warning indicator of a decrease in species richness, followed by a reduction in ecosystem resilience (Elmqvist et al., 2003) and finally a decrease of the diversity of functional types and ecosystem functions (Clavel, Julliard & Devictor, 2011).

Spatial heterogeneity might be measured in a timeand cost-effective manner with spatial statistics based on information theory applied to remotely sensed imagery. Such an approach might allow a high spatial extent to be covered in a short time period. Such high temporal resolution is needed as an early warning against these homogenizing effects if effective management decisions are to be taken. Moreover, ecosystem heterogeneity can be used to map species diversity and detect species hotspots directly (Rocchini *et al.*, 2016).

Remotely sensed information shows high multi-colinearity and might carry redundant information (Gillespie *et al.*, 2008). Therefore, care must be taken in using only remotely sensed variables without considering additional multi-scale drivers like climate, soil types, topographic variables and

biotic interactions (Clark et al., 2001; Levine et al., 2016). Moreover, a potential drawback in the use of remotely sensed data for estimating ecosystem heterogeneity is related to spatial scale. Finding a perfect match between remotely sensed imagery and sampling units is difficult. Obviously, pixels should ideally be smaller than the sampling units, at least when calculating local spectral heterogeneity. Nonetheless, when pixels with a high granularity (e.g. a spatial distance of 1-5 m on the ground) are used (high spatial resolution), shadows may create higher spatial heterogeneity among spectra leading to higher noise rather than information content (Nagendra & Rocchini, 2008). On the other hand, lower spatial resolution may hamper estimates of heterogeneity due to information-smoothing processes which can hinder the detection of fine-grained patterns (Turner et al., 2003). An inappropriate match of satellite spatial resolution and the grain size of field data can hide actual spatial heterogeneity with sub-pixel variability remaining undetected (Rocchini & Ricotta, 2007). This is especially important as the relationship between ecosystem heterogeneity and biodiversity change depends on the grain size used in the analysis, alongside technical and scientific pitfalls (Rocchini et al., 2016). For instance, it has been demonstrated that water stress operates at the scale of individual plants within the Amazon rainforest, but only when the information is combined with spatial variation in soil texture can the observed patterns of variation in ecosystem heterogeneity be explained across the Amazonian region as a whole (Levine et al., 2016).

III. DISCUSSION

Biodiversity is many times more complex than climate due to considerable diversity in genetic, species and ecosystem components, manifold ecological interactions and numerous pressures interacting synergistically to impact multiple aspects of biodiversity. This complexity also asks for an enormous amount of biodiversity data of various types if an integrative monitoring framework is to be developed that will allow conservation goals to be tracked and achieved (Noss, 1990). The EBV concept was developed to assemble, harmonize, and standardize biodiversity data, thereby ensuring that existing data are available for conservation decision-making. With rapid and increasing biodiversity loss, the scientific community needs promptly to operationalize the EBV concept and prioritize the effective measurement of EBVs. Here, we provide a suite of candidate EBVs with clear definitions and explanations of their potential for detecting critical biodiversity change early. This suite is an important step towards prioritizing an agreed list of EBVs for developing global headline indicators of critical biodiversity change. The proposed suite of EBVs comprises abundance, allelic diversity, body mass index, ecosystem heterogeneity, phenology, range dynamics, size at first reproduction, and survival rates. Importantly, the selected EBVs would address a large range of conservation issues and contribute to a total of 15 of the 20 Aichi targets and are by definition of high biological relevance (Figs 1 and 2).

As a trade-off between data availability, challenges in data standardization and harmonization, and biological relevance as a descriptor of critical change (Mihoub et al., 2017), we consider the abundance EBV to be one of the most important. This EBV can document detrimental biodiversity change relatively rapidly, largely dependent on sampling effort, and may be based on large data sets currently brought together from scattered and patchy sources (Hudson et al., 2014). The challenge will be either to agree a common measure of abundance or to harmonize measures as disparate as effective population size, effective breeding population size and absolute and relative abundance - to mention only the most important. Further, a measure of abundance is a major contributor to four Aichi targets and can also be used to inform or at least complement any EBV linked to species distribution, depending on the spatial representation of data collection.

The ecosystem heterogeneity EBV provides a straightforward method for documenting change globally through remote sensing. We believe it has huge potential to document past change given the long history of studies on ecosystem heterogeneity (Kutiel, 1994). Depending on the sampling frequency, assessments of changes in ecosystem heterogeneity could be carried out annually across the globe and could detect critical change as early as after 1 year. It complements the population-level EBVs with an ecosystem and community level (Fig. 3).

The EBVs BMI and size at first reproduction may also be developed rapidly due to a large amount of available data, especially in well-monitored species groups, such as marine fishes, mammals and birds (Marsh & Trenham, 2008; Schmeller *et al.*, 2009, 2012). However, missing data from less-well studied species groups may introduce an important bias, both spatially and temporally. This will need to be taken into consideration when developing these two EBVs further. The major advantage of these EBVs is their capacity to respond quickly to environmental drivers and pressures – in the case of the BMI even over a few weeks depending on the organism – complementing well the other candidate EBVs.

The range dynamics and phenology EBVs may also be developed relatively quickly due to the large amount of available data. The range dynamics EBV, as an EBV derived from the species distribution EBV, mainly relies on observed and modelled species-occurrence data, which is now increasingly available through portals such as GBIF and Map of Life (Jetz, McPherson & Guralnick, 2012). Phenological data are also organized into larger databases worldwide and due to the high sampling effort, yearly changes can be detected with high reliability (Hopp, 1974; Bruns, Chmielewski & Arnold, 2003; Collinson & Sparks, 2008). The allelic diversity EBV is a fundamental and important EBV for documenting critical biodiversity change at the genetic level, but the scattered local-scale data, compiled with different methods and markers, and the large temporal data gaps make it challenging to operationalize as an EBV.

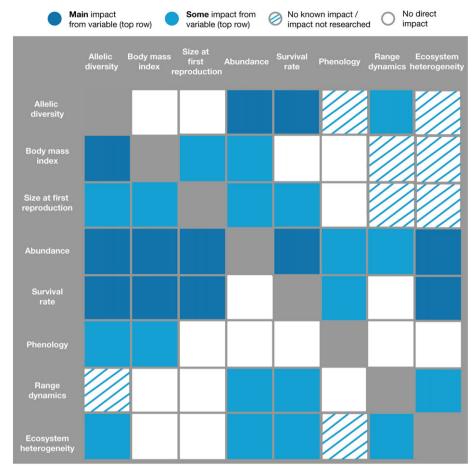


Fig. 3. The direct interconnectivity of the essential biodiversity variable (EBV) suite proposed here. The relationship is always given in regard to the upper EBV, the upper and lower squares are therefore not equal, as e.g. allelic diversity can influence body mass index, but not the reverse. The colour does not indicate a positive or negative relationship between the two variables, as both relations are potentially possible.

However, with the future development of high-throughput analysis of genotypes across large geographic scales and analyses of museum samples, those current drawbacks should be slowly overcome (Buerki & Baker, 2016).

Finally, the survival rates EBV has the largest data limitations due to the very high monitoring effort needed, but has the highest potential to document critical ecological change early. Different avenues for developing this EBV exist. New devices, such as satellite transmitters, allow automatic acquisition of data through the global system for mobile (GSM) network or satellite transmission with great spatio-temporal accuracy. The rapid development of the survival rates EBV, although very important, is unlikely, but should be advanced due to its high policy and biological relevance and our understanding of biological processes (Henle *et al.*, 2004).

The different early-warning EBVs proposed here have important uni- and bidirectional relationships with each other and act at different levels of biological organization (Fig. 3). The abundance EBV in particular has many important relationships with the other EBVs (Fig. 3).

Abundance itself is an ecological feature that maintains species and ecosystems (Gaston, 2011) as well as ecosystem services (Chapin et al., 2000; Zu Ermgassen et al., 2013). Abundance impacts directly on allelic diversity, for example, as with lower abundance allelic loss due to gene drift becomes more important (Allendorf, 1986). Due to density-dependent processes, both BMI and size at first reproduction are related to abundance, for example the lower the abundance the higher might be the food resources available and thereby a higher BMI and size at first reproduction (Dempster & Pollard, 1986). Above a certain abundance threshold, several density-dependent processes can lead to a reduction in BMI and size at first reproduction, such as lower food resources, but also increased pressure due to pathogens spreading more easily in a population (Clay et al., 2009) or due to predators finding more prey (Kokko & Ruxton, 2000). The latter process could cause an increase in BMI and size at first reproduction of the predator species, while the reverse would be true for the prey species. Therefore, survival rates are also density-dependent and interact with species' abundance (Courchamp, Clutton-Brock & Grenfell,

1999). These interactions at a population level then also impact range dynamics and ecosystem heterogeneity at larger organizational levels. Abundance may also impact phenology, for example fruiting times (Peres, 1994) and vice-versa with migration or breeding timing impacting on individuals' survival (or reproduction), and then, on abundance. Allelic diversity may impact on other EBVs, but its main impact will be on BMI through heterosis effects or through inbreeding effects (Keller & Waller, 2002), leading to a higher BMI of more heterozygotic individuals (Cézilly et al., 2016; but also see Whitlock, 1993). BMI may not affect the allelic diversity directly, but it impacts the survival rate, with a low population-wide BMI leading to a low survival rate in that population (Wells et al., 2016). Survival rate would then lead to a reduced population size, lower abundance and increased genetic drift leading to a loss of alleles. Phenology itself can impact on the abundance and survival of a species, depending on the degree to which a phenological change would hamper reproduction, for example (Einzmann et al., 2015). Range dynamics link the three levels of organization: ecosystems, species and individual populations. How species are distributed is a consequence of which habitats are favoured in an ecosystem and this, in turn, determines whether any variation within populations can be assumed (Balint et al., 2011). Further, widespread and highly dynamic species are more likely to be resilient towards ecosystem change, unlike more static and restricted species such as microendemites (Hampe & Petit, 2005). Range dynamics are therefore directly impacted by survival rates, but may indirectly also depend on e.g. allelic diversity, BMI, and abundance. Any impact (both positive and negative) occurring at any of the lower organization levels will propagate to the remaining levels and leave a trace that should be detectable by monitoring the species' range dynamics. Similarly, ecosystem heterogeneity acts at an ecosystem and community level and may influence all lower-level EBVs. Abundance, survival of species and ecosystem heterogeneity impact in a bidirectional manner (Jouquet et al., 2006), and ecosystem heterogeneity determines the resilience of biodiversity to climate change (Levine et al., 2016). An ecosystem heterogeneity EBV would be an important step to investigate the relationships with the other EBVs proposed here. However, all these relationships are scale-dependent (Henle et al., 2014) and non-linear (Curtsinger & Ming, 1997; Nicoll, Jones & Norris, 2003; Koch et al., 2009).

Three of the EBVs proposed here [abundance, range dynamics (species distribution), and phenology] are also interesting due to their potential for citizen-science-based biodiversity monitoring (Schmeller *et al.*, 2009, 2012; Devictor, Whittaker & Beltrame, 2010). This would have several important implications; it would help to raise awareness about the importance of harmonizing biodiversity monitoring protocols; it would allow citizen science monitoring to be placed in a global context, which will be likely to have a motivating element for volunteers contributing to monitoring; and it may motivate

local and regional authorities to invest in establishing new monitoring programs to fill current spatial gaps. As we cannot monitor all of biodiversity, these three EBVs in particular and all suggested EBVs in general, will also help biodiversity monitoring to be tailored to specific questions about ecosystem conditions, allowing rigorous assessment of biodiversity data within the context of prevailing scientific theory to evaluate ecological responses to management decisions (Schindler & Hilborn, 2015). With increasing and rapid biodiversity loss, the scientific community needs to operationalize the EBV concept promptly and prioritize those EBVs that can document critical biodiversity change early. We propose a suite of eight EBVs to this end; it will still be challenging to operationalize these at a global scale.

Our assessment has also shed new light on potential issues with the current structure of the EBV concept (UNEP/CBD/SBSTTA/17/INF/7). Currently, six classes have been proposed, genetic composition (GC), species populations (SP), species traits (ST), community composition (CC), ecosystem structure (ES), and ecosystem function (EF); EBVs are placed directly below this class level. However, in the SBSTTA report (UNEP/CBD/SBSTTA/17/INF/7) the proposed EBVs do not always represent a single biological variable, for example the demographic traits, physiological traits, and habitat structure EBVs. Furthermore, species distribution data may be used for several derived EBVs, such as range dynamics, taxonomic diversity, migratory behaviour, and ecosystem composition. Such inconsistencies may cause problems in communicating the potential of the EBV concept and its operationalization, and will not help in producing a consistent and robust image of biodiversity change. We consider it important to revise the current structure for clarity and communication purposes.

IV. CONCLUSIONS

- (1) The set of EBVs proposed here has the advantage that the different EBVs are all clearly interlinked, overlapping, and act at different timescales and with different magnitudes of variance. Furthermore, the relationships between the different early-warning EBVs allow predictions of other EBVs to be made based on changes documented in only one EBV (Cardillo *et al.*, 2005; Fig. 3).
- (2) With only six EBVs allelic diversity and survival rates may not become operational quickly the scientific community should be able to document current critical biodiversity change rapidly and robustly. The suggested EBVs show clear signs of change with a maximum delay of 1 year and will allow solid predictions of the future state of biodiversity to be made, if the current negative trend is not to be reversed. The predictions would largely depend on the available data and the scientific knowledge of the relationships among EBVs and may come with associated uncertainties (Magnusson, 2014).
- (3) The relationships among the different EBVs may be used to inform decision makers about where more data

are needed in order to develop a robust image of critical ecological transitions. For example, in regions with high range dynamics and lower ecosystem heterogeneity, data on other EBVs, such as abundance, allelic diversity, body mass index or size at first reproduction should be collected with high priority. Such regions have been termed leading- and rear-edge distributions, and represent areas where important changes are either happening, or could happen in the near future (Hampe & Petit, 2005).

(4) Projections based on the six EBVs could serve to prepare specifically targeted management plans to either facilitate or prevent shifts and fragmentation of species ranges. Only with such an approach can science predict the future status of global biodiversity with high certainty and set up the appropriate conservation measures early and efficiently.

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