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A suite of essential biodiversity variables for detecting critical biodiversity change

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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

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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

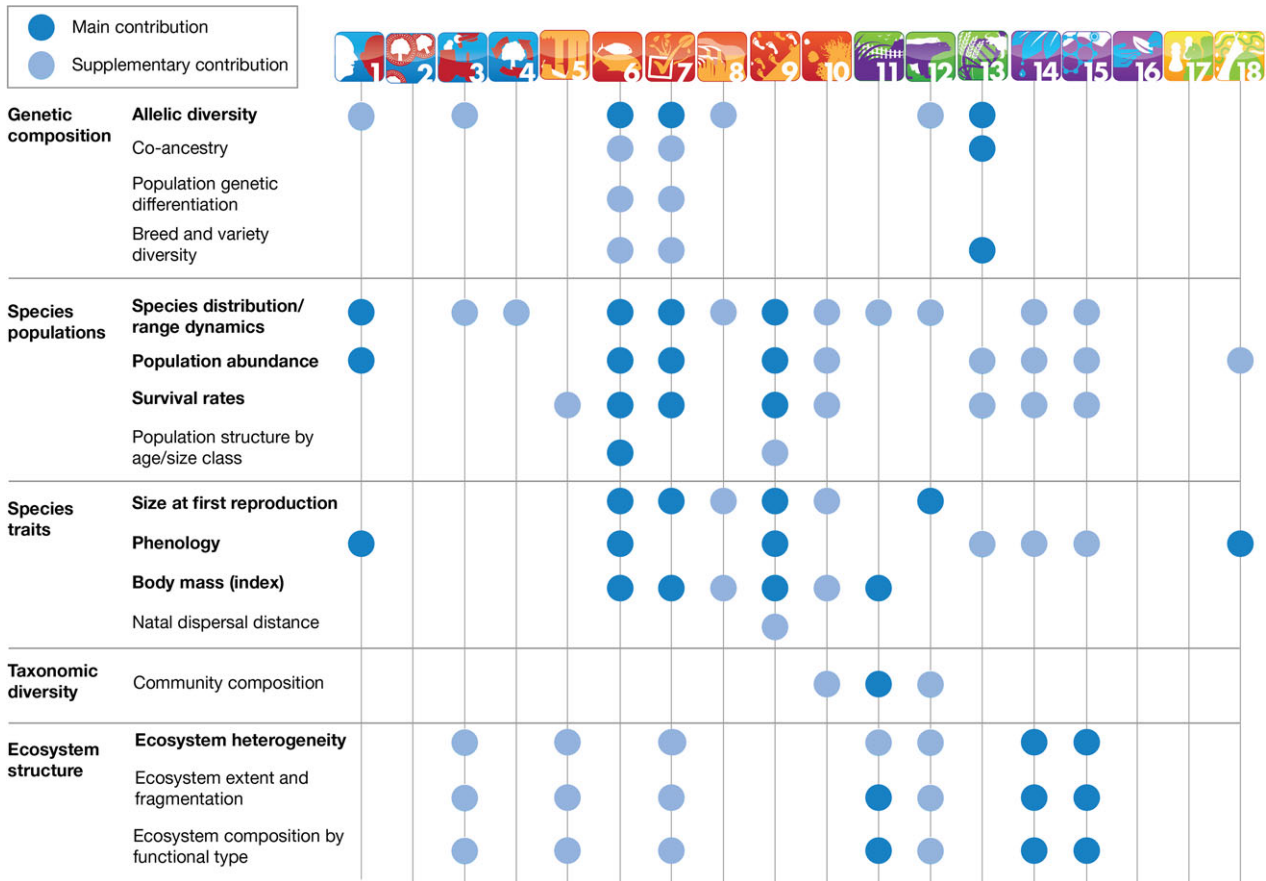


Fig. 1. Contributions of candidate essential biodiversity variables (EBVs) to the Aichi targets of the Convention on Biological Diversity (CBD), distinguishing between main contributions, i.e. direct contributions to a given target, and supplementary contributions, i.e. potential contributions to a given 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).

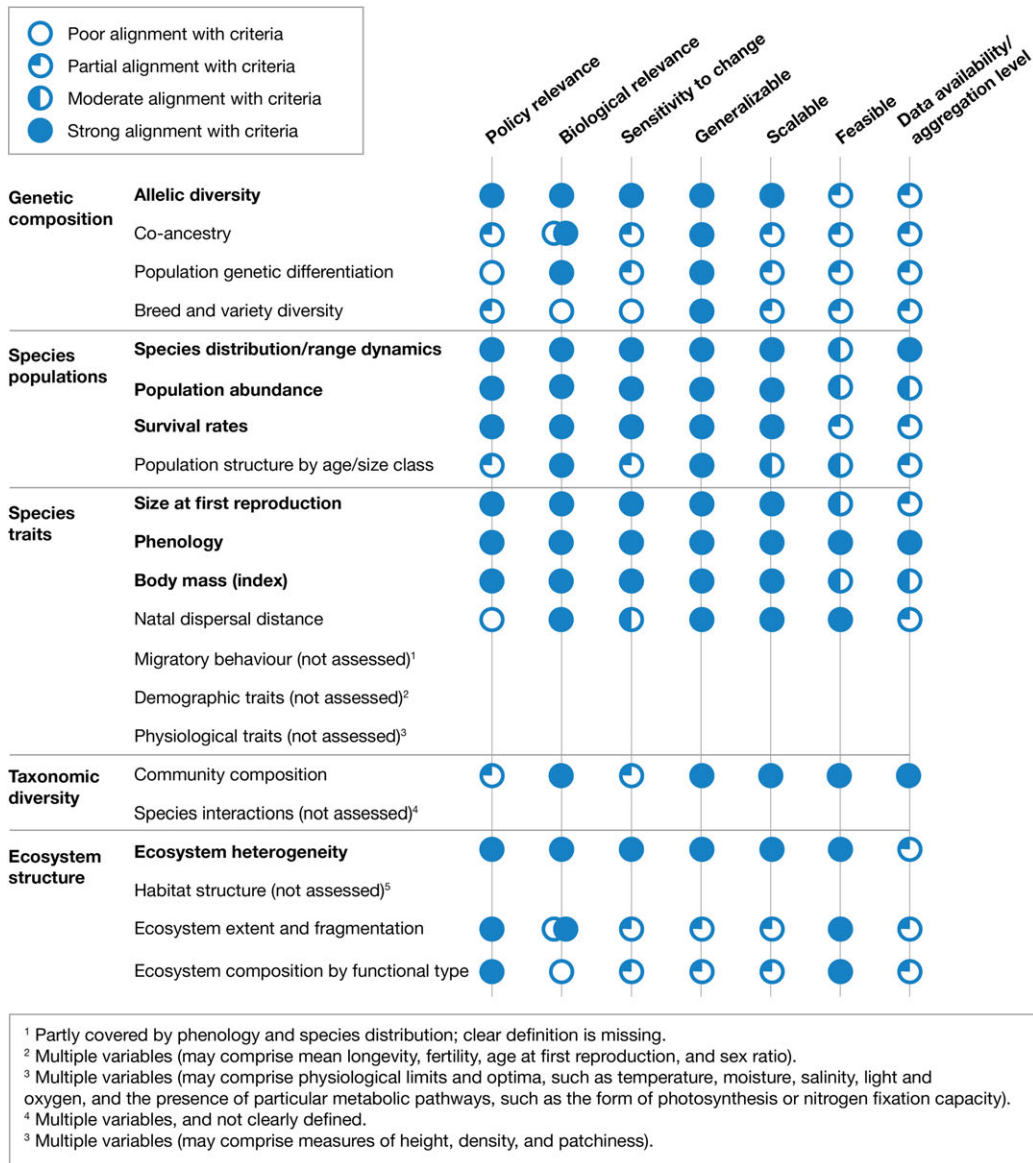
Here, we apply criteria outlined in the SBSTTA report UNEP/CBD/SBSTTA/17/INF/7 to prioritize a set of candidate EBVs for their capacity to support the development of early-warning indicators of critical ecological change. These criteria are: relevance, sensitivity to change, generalizability, scalability, 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; +++ = main relevance for three or more 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.



CRITERIA	○	○	○	●
Policy relevance	No relevance	Main relevance (1 target)	Main relevance (2 targets)	Main relevance (3+ targets)
Biological relevance	Anthropogenic	–	–	Natural
Sensitivity to change	No sensitivity	Low sensitivity	Medium sensitivity	High sensitivity
Generalizable	Not generalizable	One realm	Two realms	All realms
Scalable	Not scalable	Low scalability	Medium scalability	High scalability
Feasibility	Unfeasible	Feasible with high costs	Feasible with high effort and high cost	Feasible with normal effort and cost-effective
Data availability	Not available	Highly scattered and patchy	Scattered and/or patchy	Aggregated data available

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 deltoideus*) 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; Morissette *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-, temperature- and 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

Definition: 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 time- and 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-collinearity 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.

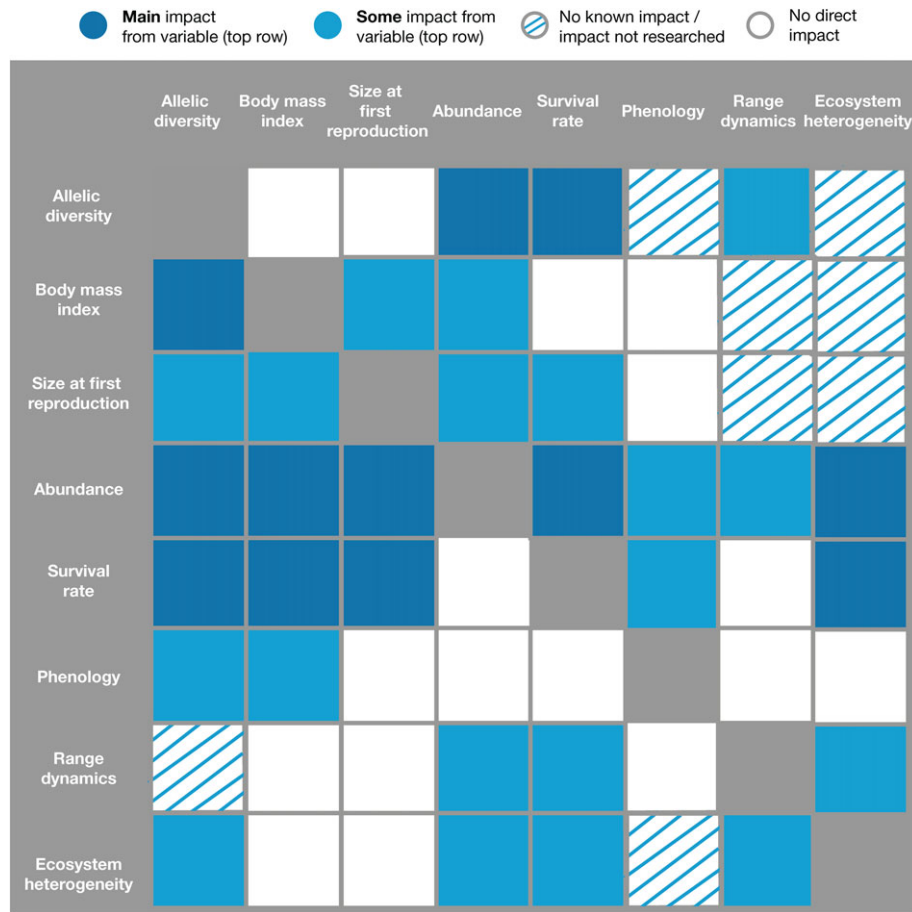


Fig. 3. The direct interconnectivity of the essential biodiversity variable (EBV) suite proposed here. The relationship is always given in regard to the upper EBV, the upper and lower squares are therefore not equal, as e.g. allelic diversity can influence body mass index, but not the reverse. The colour 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 microendemics (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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VI. REFERENCES

- ALLENDORF, F. W. (1986). Genetic drift and the loss of alleles versus heterozygosity. *Zoo Biology* **5**, 181–190.
- ANDERSEN, T., CARSTENSEN, J., HERNANDEZ-GARCIA, E. & DUARTE, C. M. (2009). Ecological thresholds and regime shifts: approaches to identification. *Trends in Ecology & Evolution* **24**, 49–57.
- BALINT, M., DOMISCH, S., ENGELHARDT, C., HAASE, P., LEHRIAN, S., SAUER, J., THEISSINGER, K., PAULS, S. & NOWAK, C. (2011). Cryptic biodiversity loss linked to global climate change. *Nature Climate Change* **1**, 313–318.
- BALL, A. D., STAPLEY, J., DAWSON, D. A., BIRKHEAD, T. R., BURKE, T. & SLATE, J. (2010). A comparison of SNPs and microsatellites as linkage mapping markers: lessons from the zebra finch (*Taeniopygia guttata*). *BMC Genomics* **11**, 1.
- BALMFORD, A., BENNUN, L., TEN BRINK, B., COOPER, D., CÔTÉ, I. M., CRANE, P., DOBSON, A. P., DUDLEY, N., DUTTON, I., GREEN, R. E., GREGORY, R. D., HARRISON, J., KENNEDY, E. T., KREMEN, C., LEADER WILLIAMS, N., et al. (2005). The convention on biological diversity's 2010 target. *Science* **307**, 212–213.
- BANCILA, R. I., HARTEL, T., PLAIASU, R., SMETS, J. & COGALNICEANU, D. (2010). Comparing three body condition indices in amphibians: a case study of yellow-bellied toad *Bombina variegata*. *Amphibia-Reptilia* **31**, 558–562.
- BARNOSKY, A. D., HADLY, E. A., BASCOMPTE, J., BERLOW, E. L., BROWN, J. H., FORTELIUS, M., GETZ, W. M., HARTE, J., HASTINGS, A. & MARQUET, P. A. (2012). Approaching a state shift in Earth's biosphere. *Nature* **486**, 52–58.
- BATTIN, J. (2004). When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology* **18**, 1482–1491.
- BEAUGRAND, G. G., REID, P. C., IBANEZ, F. D. R., LINDLEY, J. A. & EDWARDS, M. (2002). Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* **296**, 1692–1694.
- BEISSINGER, S. R. & McCULLOUGH, D. R. (2002). *Population Viability Analysis*. University of Chicago Press, Chicago and London.
- BENNETT, A. M. & MURRAY, D. L. (2014). Maternal body condition influences magnitude of anti-predator response in offspring. *Proceedings of the Royal Society of London Series B: Biological Sciences* **281**, 20141806.
- BERGMAN, E. J., DOHERTY, P. F. JR., BISHOP, C. J., WOLFE, L. L. & BANULIS, B. A. (2014). Herbivore body condition response in altered environments: mule deer and habitat management. *PLoS ONE* **9**, e106374.
- BOETTIGER, C. & HASTINGS, A. (2012). Quantifying limits to detection of early warning for critical transitions. *Journal of the Royal Society Interface* **9**, 2527–2539.
- BOOY, G., HENDRIKS, R. J. J., SMULDERS, M. J. M., VAN GROENENDAEL, J. M. & VOSMAN, B. (2000). Genetic diversity and the survival of populations. *Plant Biology (Stuttgart, Germany)* **2**, 379–395.
- BRAWN, J. D. & ROBINSON, S. K. (1996). Source-sink population dynamics may complicate the interpretation of long-term census data. *Ecology* **77**, 3–12.
- BROSE, U., EHNS, R. B., RALL, B. C., VUCIC-PESTIC, O., BERLOW, E. L. & SCHEU, S. (2008). Foraging theory predicts predator–prey energy fluxes. *Journal of Animal Ecology* **77**, 1072–1078.
- BROSE, U., JONSSON, T., BERLOW, E. L., WARREN, P., BANASEK-RICHTER, C., BERSIER, L.-F., BLANCHARD, J. L., BREY, T., CARPENTER, S. R., BLANDENIER, M.-F., CUSHING, L., DAWAH, H. A., DELL, T., EDWARDS, F., HARPER-SMITH, S., JACOB, U., LEDGER, M. E., MARTINEZ, N. D., MEMMOTT, J., MINTENBECK, K., PINNEGAR, J. K., RALL, B. C., RAYNER, T. S., REUMAN, D. C., RUESS, L., ULRICH, W., WILLIAMS, R. J., WOODWARD, G. & COHEN, J. E. (2006). Consumer-resource body-size relationships in natural food webs. *Ecology* **87**, 2411–2417.
- BRUMMITT, N., REGAN, E. C., WEATHERDON, L. V., MARTIN, C., GEIJZENDORFFER, I. R., ROCCHINI, D., GAVISH, Y., HAASE, P., MARSH, C. J. & SCHMELLER, D. S. (in press). Taking stock of nature: essential biodiversity variables explained. *Biological Conservation* <http://dx.doi.org/10.1016/j.biocon.2016.09.006>.
- BRUNS, E., CHMIELEWSKI, F.-M. & ARNOLD, J. (2003). The global phenological monitoring concept. In *Phenology: An Integrative Environmental Science* (ed. SCHWARTZ M.D.), pp. 93–104. Springer, Dordrecht.
- BUERKI, S. & BAKER, W. J. (2016). Collections-based research in the genomic era. *Biological Journal of the Linnean Society* **117**, 5–10.
- BUITENWERF, R., ROSE, L. & HIGGINS, S. I. (2015). Three decades of multi-dimensional change in global leaf phenology. *Nature Climate Change* **5**, 364–368.
- BURNHAM, K. P., WHITE, G. C. & ANDERSON, D. R. (1995). Model selection strategy in the analysis of capture-recapture data. *Biometrics* **51**, 888–898.
- BURTHE, S. J., HENRYS, P. A., MACKAY, E. B., SPEARS, B. M., CAMPBELL, R., CARVALHO, L., DUDLEY, B., GUNN, I. D. M., JOHNS, D. G., MABERLY, S. C., MAY, L., NEWELL, M. A., WANLESS, S., WINFIELD, I. J., THACKERAY, S. J. & DAUNT, F. (2015). Do early warning indicators consistently predict nonlinear change in long-term ecological data? *Journal of Applied Ecology* **53**, 666–676.
- BUTCHART, S. H. M., AKCAKAYA, H. R., KENNEDY, E. & HILTON-TAYLOR, C. (2006). Biodiversity indicators based on trends in conservation state: strengths of the IUCN red list index. *Conservation Biology* **20**, 579–581.
- BUTCHART, S. H., WALPOLE, M., COLLEN, B., VAN STRIEN, A., SCHARLEMANN, J. R. P., ALMOND, R. E., BAILLIE, J. E., BOMHARD, B., BROWN, C. & BRUNO, J. (2010). Global biodiversity: indicators of recent declines. *Science* **328**, 1164–1168.
- CABALLERO, A. & GARCÍA-DORADO, A. (2013). Allelic diversity and its implications for the rate of adaptation. *Genetics* **195**, 1373–1384.
- CARDILLO, M., MACE, G. M., JONES, K. E., BIELBY, J., BININDA-EMONDS, O. R., SEGREST, W., ORME, C. D. L. & PURVIS, A. (2005). Multiple causes of high extinction risk in large mammal species. *Science* **309**, 1239–1241.
- CASWELL, H. 2001. *Matrix population models: Construction, analysis and interpretation, 2nd Edition*. Sinauer Associates, Sunderland, Massachusetts.
- CATTANEO, A., ASIOLI, A., COMOLI, P. & MANCA, M. (1998). Organisms' response in a chronically polluted lake supports hypothesized link between stress and size. *Limnology and Oceanography* **43**, 1938–1943.
- CÉZILLY, F., QUINARD, A., MOTREUIL, S. & PRADEL, R. (2016). Adult survival selection in relation to multilocus heterozygosity and body size in a tropical bird species, the Zenaïda dove, *Zenaidura aurita*. *Oecologia* **180**, 127–136.
- CHAPIN, F. S. III, ZAVALA, E. S., EVINER, V. T., NAYLOR, R. L., VITOUSEK, P. M., REYNOLDS, H. L., HOOPER, D. U., LAVOREL, S., SALA, O. E. & HOBBS, S. E. (2000). Consequences of changing biodiversity. *Nature* **405**, 234–242.
- CHASTEL, O., WEIMERSKIRCH, H. & JOUVENTIN, P. (1995). Body condition and seabird reproductive performance: a study of three petrel species. *Ecology* **76**, 2240–2246.
- CHEN, S. L., WU, M., HENDERSON, J. P., HOOTON, T. M., HIBBING, M. E., HULTGREN, S. J. & GORDON, J. I. (2013). Genomic diversity and fitness of *E. coli* strains recovered from the intestinal and urinary tracts of women with recurrent urinary tract infection. *Science Translational Medicine* **5**, 184ra60.
- CHEUNG, W. W., SARMIENTO, J. L., DUNNE, J., FRÖLICHER, T. L., LAM, V. W., PALOMARES, M. D., WATSON, R. & PAULY, D. (2013). Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. *Nature Climate Change* **3**, 254–258.
- CLANCEY, E. & BYERS, J. A. (2014). The definition and measurement of individual condition in evolutionary studies. *Ethology* **120**, 845–854.
- CLARE, F. C., DANIEL, O., HALDER, J. B., BIELBY, J., SEMENOV, M. A., JOMBART, T., LOYAU, A., SCHMELLER, D. S., CUNNINGHAM, A. A., ROWCLIFFE, M. J., GARNER, T. W. J., BOSCH, J. & FISHER, M. C. (2016). Climate change will force fungal pathogen infection across a multi-species community. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **371**(1709), 20150454.
- CLARK, J. S., CARPENTER, S. R., BARBER, M., COLLINS, S., DOBSON, A., FOLEY, J. A., LODGE, D. M., PASCUAL, M., PIELKE, R. & PIZER, W. (2001). Ecological forecasts: an emerging imperative. *Science* **293**, 657–660.

- CLAVEL, J., JULLIARD, R. & DEVICTOR, V. (2011). Worldwide decline of specialist species: toward a global functional homogenization? *Frontiers in Ecology and the Environment* **9**, 222–228.
- CLAY, C. A., LEHMER, E. M., ST JEOR, S. & DEARING, M. D. (2009). Testing mechanisms of the dilution effect: deer mice encounter rates, Sin Nombre virus prevalence and species diversity. *EcoHealth* **6**, 250–259.
- CLELAND, E. E., CHUINE, I., MENZEL, A., MOONEY, H. A. & SCHWARTZ, M. D. (2007). Shifting plant phenology in response to global change. *Trends in Ecology & Evolution* **22**, 357–365.
- CLUTTON-BROCK, T. H. (1984). Reproductive effort and terminal investment in iteroparous animals. *American Naturalist* **123**, 212–229.
- COLLINSON, N. & SPARKS, T. (2008). Phenology—nature’s calendar: an overview of results from the UK phenology network. *Arbicultural Journal* **30**, 271–278.
- CONOVER, D. O. & MUNCH, S. B. (2002). Sustaining fisheries yields over evolutionary time scales. *Science* **297**, 94–96.
- COURCHAMP, F., CLUTTON-BROCK, T. & GRENFELL, B. (1999). Inverse density dependence and the Allee effect. *Trends in Ecology & Evolution* **14**, 405–410.
- CURTISINGER, J. W. & MING, R. (1997). Non-linear selection responses in *Drosophila*: a strategy for testing the rare-alleles model of quantitative genetic variability. *Genetica* **99**, 59–66.
- DE BEURS, K. M. & HENEERY, G. M. (2004). Land surface phenology, climatic variation, and institutional change: analyzing agricultural land cover change in Kazakhstan. *Remote Sensing of Environment* **89**, 497–509.
- DEMPSTER, J. P. & POLLARD, E. (1986). Spatial heterogeneity, stochasticity and the detection of density dependence in animal populations. *Oikos* **46**, 413–416.
- DEVICTOR, V., JULLIARD, R., COUVET, D. & JIGUET, F. (2008). Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **275**, 2743–2748.
- DEVICTOR, V., VAN SWAAY, C., BRERETON, T., BROTONS, L., CHAMBERLAIN, D., HELIOLA, J., HERRANDO, S., JULLIARD, R., KUUSAAARI, M., LINDSTROM, A., REIF, J., ROY, D. B., SCHWEIGER, O., SETTELE, J., STEFANESCU, C., et al. (2012). Differences in the climatic debts of birds and butterflies at a continental scale. *Nature Climate Change* **2**, 121–124.
- DEVICTOR, V., WHITTAKER, R. J. & BELTRAME, C. (2010). Beyond scarcity: citizen science programmes as useful tools for conservation biogeography. *Diversity and Distributions* **16**, 354–362.
- DOMISCH, S., ARAÚJO, M. B., BONADA, N., PAULS, S. U., JÄHNIG, S. C. & HAASE, P. (2013). Modelling distribution in European stream macroinvertebrates under future climates. *Global Change Biology* **19**, 752–762.
- DONALD, P., GREEN, R. & HEATH, M. (2001). Agricultural intensification and the collapse of Europe’s farmland bird populations. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **268**, 25–29.
- EARL, J. E. & SEMLITSCH, R. D. (2013). Carryover effects in amphibians: are characteristics of the larval habitat needed to predict juvenile survival? *Ecological Applications* **23**, 1429–1442.
- EDWARDS, M. & RICHARDSON, A. J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature* **430**, 881–884.
- EINZMANN, H. J., BEYSLAG, J., HOFHANSL, F., WANEK, W. & ZOTZ, G. (2015). Host tree phenology affects vascular epiphytes at the physiological, demographic and community level. *Arb Plants* **7**, plu073.
- ELITH, J. & LEATHWICK, J. R. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution, and Systematics* **40**, 677.
- ELMQUIST, T., FOLKE, C., NYSTRÖM, M., PETERSON, G., BENGTTSSON, J., WALKER, B. & NORBERG, J. (2003). Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment* **1**, 488–494.
- European Environment Agency (1999). Environmental indicators: typology and overview. In Technical Report No. 25. European Environment Agency, Copenhagen, pp. 19.
- FATTORINI, L., PISANI, C. & SPORZI, A. (2004). The estimation of wildlife ungulate abundance using sample area surveys: an application to Maremma Regional Park. *Statistical Methods and Applications* **13**, 197–212.
- FISHER, M. C., HENK, D. A., BRIGGS, C. J., BROWNSTEIN, J. S., MADOFF, L. C., MCCRAW, S. L. & GURR, S. J. (2012). Emerging fungal threats to animal, plant and ecosystem health. *Nature* **484**, 186–194.
- FLYNN, D. F., GOGOL-PROKURAT, M., NOGEIRE, T., MOLINARI, N., RICHERS, B. T., LIN, B. B., SIMPSON, N., MAYFIELD, M. M. & DECLERCK, F. (2009). Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters* **12**, 22–33.
- FOLEY, J. A., DEFRIES, R., ASNER, G. P., BARFORD, C., BONAN, G., CARPENTER, S. R., CHAPIN, F. S., COE, M. T., DAILY, G. C. & GIBBS, H. K. (2005). Global consequences of land use. *Science* **309**, 570–574.
- FORREST, J. & MILLER-RUSHING, A. J. (2010). Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **365**, 3101–3112.
- FRANKHAM, R., LEES, K., MONTGOMERY, M. E., ENGLAND, P. R., LOWE, E. H. & BRISCOE, D. A. (1999). Do population size bottlenecks reduce evolutionary potential? *Animal Conservation* **2**, 255–260.
- GARNER, T. W. J., ROWCLIFFE, J. M. & FISHER, M. C. (2011). Climate change, chytridiomycosis or condition: an experimental test of amphibian survival. *Global Change Biology* **17**, 667–675.
- GASTON, K. J. (2011). Common ecology. *BioScience* **61**, 354–362.
- GEIJZENDORFFER, I. R., REGAN, E., PEREIRA, H. M., BROTONS, L., BRUMMITT, N., GAVISH, Y., HAASE, P., MARTIN, C. S., MIHOUB, J.-B., SECADES, C., SCHMELLER, D. S., STOLL, S., WETZEL, F. T. & WALTERS, M. (2016). Bridging the gap between biodiversity data and policy reporting needs: an essential biodiversity variables perspective. *Journal of Applied Ecology* **53**, 1341–1350.
- GILLESPIE, T. W., FOODY, G. M., ROCCHINI, D., GIORGI, A. P. & SAATCHI, S. (2008). Measuring and modelling biodiversity from space. *Progress in Physical Geography* **32**, 203–221.
- GRAHAM, R. W. & GRIMM, E. C. (1990). Effects of global climate change on the patterns of terrestrial biological communities. *Trends in Ecology & Evolution* **5**, 289–292.
- GREENBAUM, G., TEMPLETON, A. R., ZARMI, Y. & BAR-DAVID, S. (2014). Allelic richness following population founding events – a stochastic modeling framework incorporating gene flow and genetic drift. *PLoS ONE* **9**, e115203.
- GROSBOIS, V., GIMENEZ, O., GAILLARD, J. M., PRADEL, R., BARBRAUD, C., CLOBERT, J., MOLLER, A. & WEIMERSKIRCH, H. (2008). Assessing the impact of climate variation on survival in vertebrate populations. *Biological Reviews* **83**, 357–399.
- GUISAN, A. & THUILLER, W. (2007). Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **10**, 435.
- HAMPE, A. & PETTIT, R. J. (2005). Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters* **8**, 461–467.
- HANSKI, I., ALHO, J. & MOILANEN, A. (2000). Estimating the parameters of survival and migration of individuals in metapopulations. *Ecology* **81**, 239–251.
- HEINO, J., VIRKKALA, R. & TOIVONEN, H. (2009). Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. *Biological Reviews* **84**, 39–54.
- HENLE, K., DAVIES, K. F., KLEYER, M., MARGULES, C. & SETTELE, J. (2004). Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation* **13**, 207–251.
- HENLE, K., POTTS, S., KUNIN, W., MATSINOS, Y., SIMILA, J., PANTIS, J., GROBELNIK, V., PENEV, L. & SETTELE, J. (2014). *Scaling in Ecology and Biodiversity Conservation, Advanced Books* (Volume 1), p. e1169 Pensoft, Sofia, Bulgaria.
- HOPP, R. J. (1974). Plant phenology observation networks. In *Phenology and Seasonality Modeling* (ed. H. LIETH), pp. 25–43. Springer, Dordrecht.
- HUDSON, L. N., NEWBOLD, T., CONTU, S., HILL, S. L., LYSSENKO, I., DE PALMA, A., PHILLIPS, H. R., SENIOR, R. A., BENNETT, D. J. & BOOTH, H. (2014). The PREDICTS database: a global database of how local terrestrial biodiversity responds to human impacts. *Ecology and Evolution* **4**, 4701–4735.
- HUGHES, A. R. & STACHOWICZ, J. J. (2004). Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 8998–9002.
- JETZ, W., MCPHERSON, J. M. & GURALNICK, R. P. (2012). Integrating biodiversity distribution knowledge: toward a global map of life. *Trends in Ecology & Evolution* **27**, 151–159.
- JOHNSON, J. C., MILES, L. S., TRUBL, P. J. & HAGENMAIER, A. (2014). Maternal effects on egg investment and offspring performance in black widow spiders. *Animal Behaviour* **91**, 67–73.
- JOUQUET, P., DAUBER, J., LAGERLÖF, J., LAVELLE, P. & LEPAGE, M. (2006). Soil invertebrates as ecosystem engineers: intended and accidental effects on soil and feedback loops. *Applied Soil Ecology* **32**, 153–164.
- KARELL, P., KONTIAINEN, P., PIETIÄINEN, H., SITARI, H. & BROMMER, J. (2008). Maternal effects on offspring Igs and egg size in relation to natural and experimentally improved food supply. *Functional Ecology* **22**, 682–690.
- KEELING, C. D., CHIN, J. F. S. & WHORF, T. P. (1996). Increased activity of northern vegetation inferred from atmospheric CO₂ measurements. *Nature* **382**, 146–149.
- KELLER, L. F. & WALLER, D. M. (2002). Inbreeding effects in wild populations. *Trends in Ecology & Evolution* **17**, 230–241.
- KERBY, J. T. & POST, E. (2013). Advancing plant phenology and reduced herbivore production in a terrestrial system associated with sea ice decline. *Nature Communications* **4**, 2514.
- KOCH, E. W., BARBIER, E. B., SILLIMAN, B. R., REED, D. J., PERILLO, G. M., HACKER, S. D., GRANEK, E. F., PRIMAVERA, J. H., MUTHIGA, N., POLASKY, S., HALPERN, B. S., KENNEDY, C. J., KAPPEL, C. V. & WOLANSKI, E. (2009). Non-linearity in ecosystem services: temporal and spatial variability in coastal protection. *Frontiers in Ecology and the Environment* **7**, 29–37.
- KOKKO, H. & RUXTON, G. D. (2000). Breeding suppression and predator–prey dynamics. *Ecology* **81**, 252–260.
- KOLM, N. (2002). Male size determines reproductive output in a paternal mouthbrooding fish. *Animal Behaviour* **63**, 727–733.
- KOVACH, R. P., JOYCE, J. E., ECHAVE, J. D., LINDBERG, M. S. & TALLMON, D. A. (2013). Earlier migration timing, decreasing phenotypic variation, and biocomplexity in multiple salmonid species. *PLoS ONE* **8**, e53807.
- KREBS, C. J. & SINGLETON, G. R. (1993). Indexes of condition for small mammals. *Australian Journal of Zoology* **41**, 317–323.

- KUIPER, J. J., VAN ALTENA, C., DE RUITER, P. C., VAN GERVEN, L. P., JANSE, J. H. & MOOIJ, W. M. (2015). Food-web stability signals critical transitions in temperate shallow lakes. *Nature Communications* **6**, 7727.
- KUPFERBERG, S. J., PALEN, W. J., LIND, A. J., BOBZIEN, S., CATENAZZI, A., DRENNAN, J. & POWER, M. E. (2012). Effects of flow regimes altered by dams on survival, population declines, and range-wide losses of California river-breeding frogs. *Conservation Biology* **26**, 513–524.
- KUTIEL, P. (1994). Fire and ecosystem heterogeneity: a Mediterranean case study. *Earth Surface Processes and Landforms* **19**, 187–194.
- LABOCHA, M. K. & HAYES, J. P. (2012). Morphometric indices of body condition in birds: a review. *Journal of Ornithology* **153**, 1–22.
- LAMB, E. G., BAYNE, E., HOLLOWAY, G., SCHIECK, J., BOUTIN, S., HERBERS, J. & HAUGHLAND, D. L. (2009). Indices for monitoring biodiversity change: are some more effective than others? *Ecological Indicators* **9**, 432–444.
- LANDE, R. (1993). Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* **142**, 911–927.
- LEBRETON, J. D., BURNHAM, K. P., CLOBERT, J. & ANDERSON, D. R. (1992). Modeling survival and testing biological hypothesis using marked animals: a unified approach with case studies. *Ecological Monographs* **62**, 67–118.
- LEE, K. A. (2006). Linking immune defenses and life history at the levels of the individual and the species. *Integrative and Comparative Biology* **46**, 1000–1015.
- LENS, L., VAN DONGEN, S. & MATTHYSEN, E. (2002). Fluctuating asymmetry as an early warning system in the critically endangered Taita thrush. *Conservation Biology* **16**, 479–487.
- LESICA, P., McCUNE, B. & EZZURRA, E. (2004). Decline of Arctic-alpine plants at the southern margin of their range following a decade of climatic warming. *Journal of Vegetation Science* **15**, 679–690.
- LEVINE, N. M., ZHANG, K., LONGO, M., BACCINI, A., PHILLIPS, O. L., LEWIS, S. L., ALVAREZ-DÁVILA, E., DE ANDRADE, A. C. S., BRIENEN, R. J. & ERWIN, T. L. (2016). Ecosystem heterogeneity determines the ecological resilience of the Amazon to climate change. *Proceedings of the National Academy of Sciences of the United States of America* **113**, 793–797.
- LIANG, L. & SCHWARTZ, M. D. (2009). Landscape phenology: an integrative approach to seasonal vegetation dynamics. *Landscape Ecology* **24**, 465–472.
- LOH, J., GREEN, R. E., RICKETTS, T., LAMOREUX, J., JENKINS, M., KAPOS, V. & RANDERS, J. (2005). The living planet index: using species population time series to track trends in biodiversity. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* **360**, 289–295.
- LOYAU, A. & LACROIX, F. D. R. (2010). Watching sexy displays improves hatching success and offspring growth through maternal allocation. *Proceedings of the Royal Society of London Series B: Biological Sciences* **277**, 3453–3460.
- LOYAU, A., SORCI, G. & JALME, M. S. (2005). Intra- and intersexual selection for multiple traits in the peacock (*Pavo cristatus*). *Ethology* **111**, 810–820.
- MACEDÁ-VEIGA, A., GREEN, A. J. & DE SOSTOA, A. (2014). Scaled body-mass index shows how habitat quality influences the condition of four fish taxa in north-eastern Spain and provides a novel indicator of ecosystem health. *Freshwater Biology* **59**, 1145–1160.
- MAGNUSSON, W. E. (2014). Uncertainty and the design of in-situ biodiversity-monitoring programs. *Nature Conservation* **8**, 77–94.
- MARSH, D. M. & TRENHAM, P. C. (2008). Current trends in plant and animal population monitoring. *Conservation Biology* **22**, 647–655.
- MASEL, J. (2011). Genetic drift. *Current Biology* **21**, R837–R838.
- MASSA, S. N. I., PAULINO, C. M., SERRÃO, E. A., DUARTE, C. M. & ARNAUD-HAOND, S. (2013). Entangled effects of allelic and clonal (genotypic) richness in the resistance and resilience of experimental populations of the seagrass *Zostera noltii* to diatom invasion. *BMC Ecology* **13**, 1.
- MATTILA, H. R. & SEELEY, T. D. (2007). Genetic diversity in honey bee colonies enhances productivity and fitness. *Science* **317**, 362–364.
- McKINNEY, M. L. (2006). Urbanization as a major cause of biotic homogenization. *Biological Conservation* **127**, 247–260.
- MCRAE, L., COLLEN, B., DEINET, S., HILL, P., LOH, J., BAILLIE, J. & PRICE, V. (2012). The living planet index. In *Living Planet Report 2012*. WWF International, Gland.
- MENZEL, A., SPARKS, T. H., ESTRELLA, N., KOCH, E., AASA, A., AHA, R., ALM-KUBLER, K., BISSOLLI, P., BRASLAVSKA, O., BRIEDE, A., CHMIELEWSKI, F. M., CREPINSEK, Z., CURNEL, Y., DAHL, A., DEFILA, C., et al. (2006). European phenological response to climate change matches the warming pattern. *Global Change Biology* **12**, 1969–1976.
- MIHOUB, J. B., HENLE, K., TITEUX, N., BROTONS, L., BRUMMITT, N. & SCHMELLER, D. S. (2017). Setting temporal baselines for biodiversity: the limits of available monitoring data for capturing the full impact of anthropogenic pressures. *Scientific Reports* **7**, 41591.
- MORISSETTE, J. T., RICHARDSON, A. D., KNAPP, A. K., FISHER, J. I., GRAHAM, E. A., ABATZOGLOU, J., WILSON, B. E., BRESHEARS, D. D., HENEERY, G. M. & HANES, J. M. (2008). Tracking the rhythm of the seasons in the face of global change: phenological research in the 21st century. *Frontiers in Ecology and the Environment* **7**, 253–260.
- MORITZ, C. & AGUDO, R. (2013). The future of species under climate change: resilience or decline? *Science* **341**, 504–508.
- MORRIS, W. F. & DOAK, D. F. (2002). *Quantitative Conservation Biology*. Sinauer, Sunderland.
- MOUSSEAU, T. A. & FOX, C. W. (1998). The adaptive significance of maternal effects. *Trends in Ecology & Evolution* **13**, 403–407.
- MURDOCH, W. W., EVANS, F. C. & PETERSON, C. H. (1972). Diversity and pattern in plants and insects. *Ecology* **53**, 819–829.
- NAGENDRA, H. & ROCCHINI, D. (2008). High resolution satellite imagery for tropical biodiversity studies: the devil is in the detail. *Biodiversity and Conservation* **17**, 3431–3442.
- NEWBOLD, T., HUDSON, L. N., ARNELL, A. P., CONTU, S., DE PALMA, A., FERRIER, S., HILL, S. L., HOSKINS, A. J., LYSENKO, I. & PHILLIPS, H. R. (2016). Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. *Science* **353**, 288–291.
- NICHOLS, J. D. (1992). Capture-recapture models. *BioScience* **42**, 94–102.
- NICHOLS, J. D. & KENDALL, W. L. (1995). The use of multi-state capture-recapture models to address questions in evolutionary ecology. *Journal of Applied Statistics* **22**, 835–846.
- NICHOLS, J. D., KENDALL, W. L., HINES, J. E. & SPENDELOW, J. A. (2004). Estimation of sex-specific survival from capture-recapture data when sex is not always known. *Ecology* **85**, 3192–3201.
- NICHOLS, J. D. & WILLIAMS, B. K. (2006). Monitoring for conservation. *Trends in Ecology & Evolution* **21**, 668–673.
- NICOLL, M. A. C., JONES, C. G. & NORRIS, K. (2003). Declining survival rates in a reintroduced population of the Mauritius kestrel: evidence for non-linear density dependence and environmental stochasticity. *Journal of Animal Ecology* **72**, 917–926.
- NOSS, R. F. (1990). Indicators for monitoring biodiversity: a hierarchical approach. *Conservation Biology* **4**, 355–364.
- OZGUL, A., ARMITAGE, K. B., BLUMSTEIN, D. T. & OLI, M. K. (2006). Spatiotemporal variation in survival rates: implications for population dynamics of yellow-bellied marmots. *Ecology* **87**, 1027–1037.
- OZGUL, A., CHILDS, D. Z., OLI, M. K., ARMITAGE, K. B., BLUMSTEIN, D. T., OLSON, L. E., TULJAPURKAR, S. & COULSON, T. (2010). Coupled dynamics of body mass and population growth in response to environmental change. *Nature* **466**, 482–485.
- PACE, M. L., CARPENTER, S. R., JOHNSON, R. A. & KURTZWEL, J. T. (2013). Zooplankton provide early warnings of a regime shift in a whole lake manipulation. *Limnology and Oceanography* **58**, 525–532.
- PACE, M. L., COLE, J. J., CARPENTER, S. R. & KITCHELL, J. F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends in Ecology & Evolution* **14**, 483–488.
- PALMER, M. W., EARLS, P. G., HOAGLAND, B. W., WHITE, P. S. & WOHLGEMUTH, T. (2002). Quantitative tools for perfecting species lists. *Environmetrics* **13**, 121–137.
- PARMESAN, C. & YOHE, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**, 37–42.
- PEIG, J. & GREEN, A. J. (2010). The paradigm of body condition: a critical reappraisal of current methods based on mass and length. *Functional Ecology* **24**, 1323–1332.
- PEREIRA, H. M., FERRIER, S., WALTERS, M., GELLER, G., JONGMAN, R., SCHOLE, R., BRUFORD, M., BRUMMITT, N., BUTCHART, S. & CARDOSO, A. (2013). Essential biodiversity variables. *Science* **339**, 277–278.
- PERES, C. A. (1994). Composition, density, and fruiting phenology of arboreous palms in an Amazonian terra firme forest. *Biotropica* **26**, 285–294.
- PÉRON, G., CROCHET, P.-A., CHOQUET, R., PRADEL, R., LEBRETON, J.-D. & GIMENEZ, O. (2010). Capture-recapture models with heterogeneity to study survival senescence in the wild. *Oikos* **119**, 524–532.
- PETTORRELLI, N., WEGMANN, M., SKIDMORE, A., MÜCHER, S., DAWSON, T. P., FERNANDEZ, M., LUCAS, R., SCHAEPMAN, M. E., WANG, T., O'CONNOR, B., JONGMAN, R. H. G., KEMPENEERS, P., SONNENSCHNEIN, R., LEIDNER, A. K., BÖHM, M., et al. (2016). Framing the concept of satellite remote sensing essential biodiversity variables: challenges and future directions. *Remote Sensing in Ecology and Conservation* **2**, 122–131.
- PIRY, S., LUIKART, G. & CORNUET, J.-M. (1999). Computer note. BOTTLENECK: a computer program for detecting recent reductions in the effective size using allele frequency data. *Journal of Heredity* **90**, 502–503.
- PRADEL, R. (2005). Multievent: an extension of multistate capture-recapture models to uncertain states. *Biometrics* **61**, 442–447.
- PRADEL, R., HINES, J. E., LEBRETON, J. D. & NICHOLS, J. D. (1997). Capture-recapture survival models taking account of transients. *Biometrics* **53**, 60–72.
- PROBST, W. N., STOLL, S., PETERS, L., FISCHER, P. & ECKMANN, R. (2009). Lake water level increase during spring affects the breeding success of bream *Abramis brama* (L.). *Hydrobiologia* **632**, 211–224.
- PROENÇA, V., MARTIN, L. J., PEREIRA, H. M., FERNANDEZ, M., MCRAE, L., BELNAP, J., BÖHM, M., BRUMMITT, N., GARCÍA-MORENO, J., GREGORY, R. D., HONRADO, J. P., JÜRGENS, N., OPIGE, M., PENG, C., SCHMELLER, D. S., TIAGO, P. & VAN SWAAY, C. A. M. (yyy). Global biodiversity monitoring: from data sources to essential biodiversity variables. *Biological Conservation*, in press.

- RECORD, S., CHARNEY, N., ZAKARIA, R. & ELLISON, A. M. (2013). Projecting global mangrove species and community distributions under climate change. *Ecosphere* **4**, art34.
- REED, D. H. & FRANKHAM, R. (2003). Correlation between fitness and genetic diversity. *Conservation Biology* **17**, 230–237.
- ROACH, D. A. & WULF, R. D. (1987). Maternal effects in plants. *Annual Review of Ecology and Systematics* **18**, 209–235.
- ROCCHINI, D., BOYD, D. S., FÉRET, J.-B., FOODY, G. M., HE, K. S., LAUSCH, A., NAGENDRA, H., WEGMANN, M. & PETTORELLI, N. (2016). Satellite remote sensing to monitor species diversity: potential and pitfalls. *Remote Sensing in Ecology and Conservation* **2**, 25–36.
- ROCCHINI, D. & RICOTTA, C. (2007). Are landscapes as crisp as we may think? *Ecological Modelling* **204**, 535–539.
- ROCKSTRÖM, J., STEFFEN, W., NOONE, K., PERSSON, A., CHAPIN, F. S., LAMBIN, E. F., LENTON, T. M., SCHEFFER, M., FOLKE, C., SCHELLNHUBER, H. J., NYKVIST, B., DE WIT, C. A., HUGHES, T., VAN DER LEEUW, S., RODHE, H., et al. (2009). A safe operating space for humanity. *Nature* **461**, 472–475.
- RODE, K. D., AMSTRUP, S. C. & REGEHR, E. V. (2010). Reduced body size and cub recruitment in polar bears associated with sea ice decline. *Ecological Applications* **20**, 768–782.
- ROHR, J. R., ELSKOV, A. A., SHEPHERD, B. S., CROWLEY, P. H., MCCARTHY, T. M., NIEDZWIECKI, J. H., SAGER, T., SHI, A. & PALMER, B. D. (2004). Multiple stressors and salamanders: effects of an herbicide, food limitation, and hydroperiod. *Ecological Applications* **14**, 1028–1040.
- ROTH, R. R. (1976). Spatial heterogeneity and bird species diversity. *Ecology* **57**, 773–782.
- RUZZANTE, D. E. (1998). A comparison of several measures of genetic distance and population structure with microsatellite data: bias and sampling variance. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 1–14.
- SAUER, J., DOMISCH, S., NOWAK, C. & HAASE, P. (2011). Low mountain ranges: summit traps for montane freshwater species under climate change. *Biodiversity and Conservation* **20**, 3133–3146.
- SCHEFFER, M. (2010). Complex systems: foreseeing tipping points. *Nature* **467**, 411–412.
- SCHEFFER, M., BASCOMPTE, J., BROCK, W. A., BROVKIN, V., CARPENTER, S. R., DAKOS, V., HELD, H., VAN NES, E. H., RIETKERK, M. & SUGIHARA, G. (2009). Early-warning signals for critical transitions. *Nature* **461**, 53–59.
- SCHEFFER, M. & CARPENTER, S. R. (2003). Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends in Ecology & Evolution* **18**, 648–656.
- SCHINDLER, D. E. & HILBORN, R. (2015). Prediction, precaution, and policy under global change. *Science* **347**, 953–954.
- SCHMELLER, D. S. (2004). Tying ecology and genetics of hemiclinaly reproducing waterfrogs (*Rana*, Anura). *Annales Zoologici Fennici* **41**, 681–687.
- SCHMELLER, D. S., HENLE, K., LOYAU, A., BESNARD, A. & HENRY, P.-Y. (2012). Bird-monitoring in Europe – a first overview of practices, motivations and aims. *Nature Conservation* **2**, 41–57.
- SCHMELLER, D. S., HENRY, P.-Y., JULLIARD, R., CLOBERT, J., GRUBER, B., DZIOCK, F., LENGYEL, S., NOWICKI, P., DÉRI, E., BUDRYS, E., KULL, T., TALI, K., BAUCH, B., SETTELE, J., SWAAY, C. V., KOBLER, A., BABJ, V., PAPASTERGIADOU, E. & HENLE, K. (2009). Advantages of volunteer-based biodiversity monitoring in Europe. *Conservation Biology* **23**, 307–316.
- SCHMELLER, D. S., JULLIARD, R., BELLINGHAM, P. J., BÖHM, M., BRUMMITT, N., CHIARUCCI, A., COUVET, D., ELMENDORF, S., FORSYTH, D. M., GARCIA-MORENO, J., GREGORY, R. D., MAGNUSSON, W. E., MARTIN, L. J., MCGEOCH, M. A., MIHOUB, J.-B., et al. (2015). Towards a global terrestrial species monitoring program. *Journal for Nature Conservation* **25**, 51–57.
- SCHMELLER, D. S. & MERILÄ, J. (2007). Demographic and genetic estimates of effective population size in the amphibian *Rana temporaria*. *Conservation Biology* **21**, 142–151.
- SCHMELLER, D. S., SEITZ, A., CRIVELLI, A. & VEITH, M. (2005). Crossing species' range borders: interspecies gene exchange mediated by hybridogenesis. *Proceedings of the Royal Society of London. Series B: Biological Sciences* **272**, 1625–1631.
- SCHWARTZ, M. D., AHAS, R. & AASA, A. (2006). Onset of spring starting earlier across the Northern Hemisphere. *Global Change Biology* **12**, 343–351.
- SEARS, P. B. & DASMANN, R. (1968). *A Different Kind of Country*. MacMillan Company, New York.
- SHELDON, A. L. (2012). Possible climate-induced shift of stoneflies in a southern Appalachian catchment. *Freshwater Science* **31**, 765–774.
- SHEPPARD, N., PITT, K. A. & SCHLACHER, T. A. (2009). Sub-lethal effects of off-road vehicles (ORVs) on surf clams on sandy beaches. *Journal of Experimental Marine Biology and Ecology* **380**, 113–118.
- SKIDMORE, A., PETTORELLI, N., COOPS, N., GELLER, G., HANSEN, M., LUCAS, R., MÜCHER, C., O'CONNOR, B., PAGANINI, M. & PEREIRA, H. (2015). Environmental science: agree on biodiversity metrics to track from space. *Nature* **523**, 403.
- SOULE, M. E. & WILCOX, B. A. (1980). *Conservation Biology. An Evolutionary-Ecological Perspective*. Sinauer Associates, Inc., Sunderland, Massachusetts.
- STEFFEN, W., RICHARDSON, K., ROCKSTRÖM, J., CORNELL, S. E., FETZER, I., BENNETT, E. M., BIGGS, R., CARPENTER, S. R., DE VRIES, W., DE WIT, C. A., FOLKE, C., GERTEN, D., HEINKE, J., MACE, G. M., PERSSON, L. M., et al. (2015). Planetary boundaries: guiding human development on a changing planet. *Science* **347**, 1259855.
- STENSETH, N. C. & MYSTERUD, A. (2002). Climate, changing phenology, and other life history traits: nonlinearity and match–mismatch to the environment. *Proceedings of the National Academy of Sciences of the United States of America* **99**, 13379–13381.
- STOLL, S., PROBST, W. N., ECKMANN, R. & FISCHER, P. (2010). A mesocosm experiment investigating the effects of substratum quality and wave exposure on the survival of fish eggs. *Aquatic Sciences* **72**, 509–517.
- TEWS, J., BROSE, U., GRIMM, V., TIELBÖRGER, K., WICHMANN, M., SCHWAGER, M. & JELTSCH, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography* **31**, 79–92.
- THOMPSON, J. R., PACOCHA, S., PHARINO, C., KLEPAC-CERAJ, V., HUNT, D. E., BENOIT, J., SARMA-RUPAVTARM, R., DISTEL, D. L. & POLZ, M. F. (2005). Genotypic diversity within a natural coastal bacterioplankton population. *Science* **307**, 1311–1313.
- TIGERSTEDT, P. (1973). Studies on isozyme variation in marginal and central populations of *Picea abies*. *Hereditas* **75**, 47–60.
- TITENSOR, D. P., WALPOLE, M., HILL, S. L. L., BOYCE, D. G., BRITTEN, G. L., BURGESS, N. D., BUTCHART, S. H. M., LEADLEY, P. W., REGAN, E. C., ALKAMADE, R., BAUMUNG, R., BELLARD, C., BOUWMAN, L., BOWLES-NEWARK, N. J., CHENERY, A. M., et al. (2014). A mid-term analysis of progress towards international biodiversity targets. *Science* **14**, 241–244.
- TOMIYAMA, T., KOMIZUNAI, N., ITO, K. & OMORI, M. (2010). Spatial variation in the abundance and condition of the bivalve *Nuttallia olivacea* in relation to environmental factors and sublethal predation. *Marine Ecology Progress Series* **406**, 185–196.
- TURNER, W., SPECTOR, S., GARDINER, N., FLADELAND, M., STERLING, E. & STEININGER, M. (2003). Remote sensing for biodiversity science and conservation. *Trends in Ecology & Evolution* **18**, 306–314.
- VAN ALLEN, B. G., BRIGGS, V. S., MCCOY, M. W. & VONESH, J. R. (2010). Carry-over effects of the larval environment on post-metamorphic performance in two hylid frogs. *Oecologia* **164**, 891–898.
- VITOUSEK, P. M., MOONEY, H. A., LUBCHENCO, J. & MELILLO, J. M. (1997). Human domination of Earth's ecosystems. *Science* **277**, 494–499.
- WAGNER, A. (2008). Robustness and evolvability: a paradox resolved. *Proceedings of the Royal Society of London Series B: Biological Sciences* **275**, 91–100.
- WALTHER, G.-R., POST, E., CONVEY, P., MENZEL, A., PARMESAN, C., BEEBEE, T. J. C., FROMENTIN, J.-M., HOEGH-GULDBERG, O. & BAIRLEIN, F. (2002). Ecological responses to recent climate change. *Nature* **416**, 389–395.
- WELLS, K., O'HARA, R. B., COOKE, B. D., MUTZE, G. J., PROWSE, T. A. & FORDHAM, D. A. (2016). Environmental effects and individual body condition drive seasonal fecundity of rabbits: identifying acute and lagged processes. *Oecologia* **181**, 853–864.
- WHITLOCK, M. (1993). Lack of correlation between heterozygosity and fitness in forked fungus beetles. *Heredity* **70**, 574–581.
- WINFREE, R. W., FOX, J., WILLIAMS, N. M., REILLY, J. R. & CARIVEAU, D. P. (2015). Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters* **18**, 626–635.
- WISSEL, C. (1984). A universal law of the characteristic return time near thresholds. *Oecologia* **65**, 101–107.
- ZHANG, X., FRIEDL, M. A., SCHAAF, C. B., STRAHLER, A. H., HODGES, J. C., GAO, F., REED, B. C. & HUETE, A. (2003). Monitoring vegetation phenology using MODIS. *Remote Sensing of Environment* **84**, 471–475.
- ZU ERMGASSEN, P. S., SPALDING, M. D., GRIZZLE, R. E. & BRUMBAUGH, R. D. (2013). Quantifying the loss of a marine ecosystem service: filtration by the eastern oyster in US estuaries. *Estuaries and Coasts* **36**, 36–43.

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