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Genomics meets remote sensing in global change studies: monitoring and predicting phenology, evolution and biodiversity

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Although the monitoring and prediction of ecosystem dynamics under global change have been extensively assessed, large gaps remain in our knowledge, including a need for concepts in rapid evolution and phenotypic plasticity, and a lack of large-scale and long-term monitoring. Recent genomic studies using the model species *Arabidopsis* predict that plastic and evolutionary changes in phenology may affect plant reproduction. We propose that three genomic-scale methods would enhance global change studies. First, genome-wide RNA sequencing enables monitoring of diverse functional traits and phenology. Second, sequencing of DNA variants highlights the importance of genetic variation and evolution. Third, DNA metabarcoding provides efficient and unbiased ecosystem monitoring. Integrating these genomic-scale studies with remote sensing will promote the understanding and prediction of biodiversity change.

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Introduction

Global environmental changes resulting from human activity and climate change have considerable consequences for biodiversity and ecosystem services [1]. To achieve a sustainable Earth system, it is critical to understand and monitor current and future changes to ecosystem conditions, and to harness this information for accurate predictions or forecasting. To this end, various international platforms such as the Group on Earth Observations Biodiversity Observation Network (GEO BON) and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) have been established to monitor biodiversity and ecosystem services [2,3]. So far, scientists have developed

models to predict ecosystem changes in response to global change such as various Dynamic Global Vegetation Models [4], biogeochemical models including ecological dynamics [5] and ecological niche models to predict species distributions [6].

Gaps in previous studies: plastic traits, intraspecific genetic variation, and long-term and ecosystem-level monitoring

Although the monitoring and prediction of the effects of global change on ecosystems are ongoing and extensive [7,8], major gaps remain in the basic knowledge for creating predictive models underpinning these studies [9]. To predict ecosystem dynamics accurately, we would need to consider multiple levels of biodiversity, namely, ecosystem, species and genetic diversity [8]. However, existing studies do not focus on genetic diversity and consider that species are invariant, even though species are highly variable in their functional traits due to intraspecific genetic variants or phenotypic plasticity, which are only distinguishable by experimental investigation or genomic analysis. In addition, although traditional quantitative genetic models have been useful in predicting immediate responses to artificial selection on quantitative traits of domesticated species, they do not consider molecular mechanisms, a limitation that has been discussed previously [9–12]. In genomics, the rapid advances in high-throughput sequencing technologies now allow the within-species study of genetic and plastic responses to environmental change [13]. For example, ecological genome niche modeling was proposed to be useful to predict the distribution of genetic diversity of adaptive variants [14]. To fill this gap GEO BON included genetic composition as one of the proposed Essential Biodiversity Variable (EBV) classes [2,3]. The study of model species, such as *Arabidopsis* spp., have shown that large molecular datasets can be used for predictive modeling of plant responses to environmental factors [15], which was not previously possible. Although model species themselves may have negligible effects on mitigating or exacerbating major environmental change, genomic technologies are readily applicable to ecologically relevant species and promise fundamentally new dimensions of prediction in global change studies [16].

In addition to the lack of genomic data, the lack of widespread coverage of ecosystem-level, long-term and recurrent (e.g. monthly) data makes forecasting difficult. Although there are some efforts to monitor biodiversity at a global level [2], to date, most of the individual-level ecological data have been obtained primarily in the field, focusing on particular organisms and points in space and time [17]. Individual-level observations and measurements are therefore limited to particular organisms and sites that can be accessed by humans. High-frequency (e.g. monthly) data for a large number of traits are not available in many cases. Although there is

some global-scale monitoring such as of animal migration [18], ecosystem-level monitoring including entire organisms within ecosystems is lacking. Rapid advances in technology, namely remote sensing and data analysis, may help to overcome these gaps. Integration with recently developed genomic techniques such as DNA barcoding may make it possible to monitor large-scale biodiversity at multiple levels [17].

Integration of genomics in global change studies

To date, a combination of remote sensing and ecology has been used in studies of ecosystems under global change. Here we argue that genomics should be integrated with these studies. Remote sensing and genomics have started from opposite ends of multiple axes (Figure 1a). Remote sensing began with the large-scale observation of natural environments from satellite sensors with relatively low spatial and spectral resolution (Figure 1a). Recently, the importance of measurements that can recognize individuals under natural conditions and can be linked to laboratory measurements has increased (Box 1). By contrast, molecular biology and genomics were founded on experiments under controlled laboratory conditions using both *in vitro* (in test tubes) and *in vivo* (in organisms) experiments, and focused on model species. With the advent of new sequencing technologies, genomics can now be expanded to any species of interest and ecosystem-wide phenomena in naturally fluctuating environments (*in natura*) [11,19••]. Integrative modeling using large-scale genomic data and remotely sensed data are generating a new field of research. In this review, we discuss three aspects of studies essential for prediction that are enabled by high-throughput sequencing (Figure 1b). First, we discuss RNA-Seq, or genome-wide RNA expression levels, which have the potential to serve in extensive monitoring of functional, physiological, and phenological traits. Second, we discuss the study of DNA sequences in populations which may reveal evolutionary changes. Finally, we review DNA as a metabarcoding tool that can be used to monitor changes in species composition of entire communities or ecosystems.

Methodology 1. RNA-Seq for the monitoring of diverse traits: phenology as an example

The monitoring or measurement of diverse physiological and morphological traits is critically important for ecological studies but is highly laborious. Genome-wide gene expression data as well as remote sensing can potentially provide thorough monitoring of diverse functional traits and phenology (Figure 1b). Here we will focus on phenological responses, which can be triggered by diverse environmental cues. Phenology is defined as the timing of recurring events in the life cycle of organisms [20], such as flowering, and the growth and senescence of vegetation (c.f., terminology of phenology used in different fields: de Jong R, Garonna I, Yamsaki E, Yankova Y: **Phenology,** http://www.gcb.uzh.ch/dam/jcr:

Figure 1

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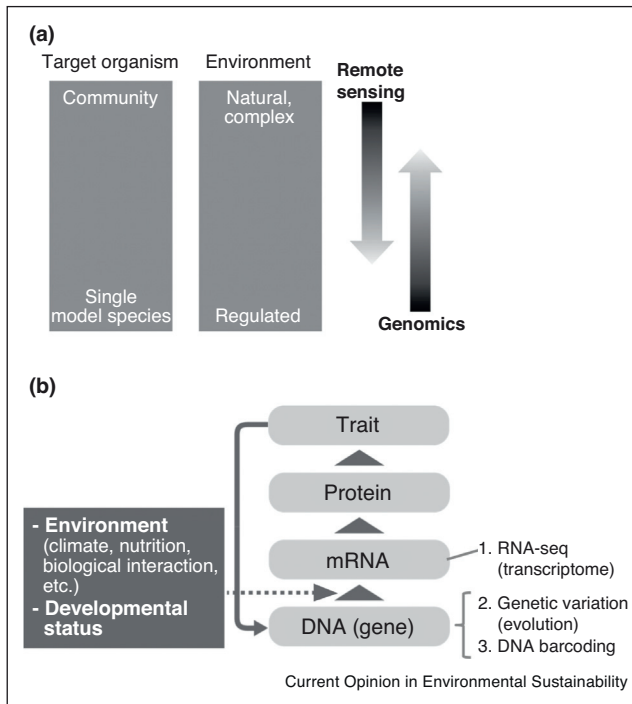
(a) While genomics started from studying single model species under highly controlled environmental conditions, remote sensing has focused on multispecies ecosystems in natural, fluctuating, and complex environments. Now is the time to integrate these two fields. **(b)** Genomic DNA encodes tens of thousands of genes and functions as the blueprint of an organism. It can be used both for the identification of species by barcoding and for the detection of evolution. The expression level of RNA (particularly messenger RNA, mRNA) of each gene is regulated by the internal developmental status of an organism and its external environments. Because the regulation of mRNA is an important mechanism of an organism's response to environmental change, many studies are conducted to find out which genes are induced or repressed by various abiotic and biotic factors such as temperature, drought, external and internal phosphate state, and pathogen load, as well as their interactions. For example, a group of drought-responsive genes has been identified in drought experiments under controlled environmental conditions in the laboratory. It follows that, in turn, physiological and environmental status may be estimated or predicted from the relative abundance of their transcripts. Modeling the integration of meteorological data with large-scale transcriptome data is generating a new field, sometimes called ecological systems biology or ecological transcriptomics [81]. For example, using time-course transcriptome data, researchers found that transcriptome dynamics are governed by environmental factors such as temperature and solar radiation together with endogenous conditions such as diurnal rhythms and plant age using the crop species rice as a model [33•].

ffffffff-8f53-4fa0-ffff-ffffdc9c2cc0/Terminology BriefPhenology.pdf). For example, recorded observations showed that many plant organisms are active earlier in spring than previously observed (as reviewed in Primack *et al.* [21]). Numerous modeling studies use observational data to predict phenology in response to global change [22]. However, it is emphasized that these data may be inadequate for constructing realistic models [8].

Box 1 Remote sensing: from distant to proximal sensing

The research community is eager to fill in the gaps related to our knowledge about the spatial distribution of species traits [39•]; therefore, it is of the highest importance to add clarity about the concept of species and more specifically on how traits vary within species among genotypes, and among and within individuals over time and in space. Pixel values derived from satellites or airborne sensors rarely represent species or individuals, because light-matter interaction within a pixel is confined to its columnar scattering behavior over a given area. Methods have been developed to outline boundaries of individuals (e.g. single trees) and assign pixels within these boundaries as signals of individuals [60•,79]. However, most remote sensing information integrates several individuals, including signals originating from different species and background (e.g. soil, rocks, understorey) in one pixel. Separation of the contributing signals is key to both the fully trait-based approach using remote sensing and deriving genetic information from remote sensing.

For crops and some larger species, new methods derived from remote sensing allow for efficient field-based phenotyping of a large number of individuals using quantitative traits. All traits of an individual are referred to as a phenome in analogy to all genetic material of an individual being called the genome. Phenotyping systems using remote-sensing methods have already been successfully implemented from close range on tractors [80] to airborne platforms [56]. A large set of physiological and morphological traits can be derived from imaging spectroscopy, thermal imaging and laser scanning, including leaf pigments, sun-induced fluorescence, canopy temperature and height [57].

Remote sensing for monitoring phenology

Remote sensing is rapidly advancing the understanding of the seasonal dynamics of vegetated land surfaces, a field of study referred to as *land–surface phenology* [23]. Long-term and global satellite records are analyzed to map large-scale changes in the timing of the start, end, and duration of vegetation growing seasons in many areas of the world [24••,25,26•], as well as analyzing the respective constraints [27]. As an example, Garonna *et al.* [24••] detected start and end of seasons from satellite images and reported a global lengthening of the growing season that averaged 0.22–0.34 days/year during the period 1982–2012, but with strong spatial variation. Oehri *et al.* [26•] studied relationships between this lengthening of growing seasons and biodiversity, land cover, climate and topography data and found that the extent of this lengthening was increased in landscapes with high species richness, which indicates that ecosystem responses to global change may be modified by extent of biodiversity within communities and ecosystems.

Modeling of phenology using time-course gene expression data of the model species *Arabidopsis* and rice

Morphological observation of flowering can only provide discrete phenological transitions (i.e. flowering or not), which significantly limits predictive power. In contrast, time-course molecular expression data can monitor internal states that quantitatively integrate diverse environmental conditions over days and weeks, which is referred

to as 'molecular phenology' [19••]. Aikawa *et al.* [28] focused on the perennial *Arabidopsis halleri in natura* and quantified the mRNA level of a key flowering gene for vernalization, *FLC* (*FLOWERING LOCUS C*), every week for 2 years. Because *FLC* is a key gene for vernalization and directly regulates expression of *FT* (*FLOWERING LOCUS T*, coding floral inducing protein called florigen), studying the relationship between *FLC* expression and temperature reveals requirements for temperature and duration of vernalization. Models show that a temperature of below 10.5°C for 42 days before flowering explained as much as 83% of the expression level of *FLC*. The model accurately predicted the response when plants were transplanted into laboratory conditions, providing experimental verification of the model [28]. Further study created models based on laboratory experiments and predicted that *A. halleri* may experience local extinction due to the failure of flowering if temperatures rise 4.5°C above current levels [29], which is not an unrealistic assumption for the next 100 years. It should be noted that these models did not incorporate other environmental factors or evolutionary rescue by rapid evolution, which will be discussed in Methodology 2. In addition, transplantation data is also valuable to predict flowering times of *Arabidopsis thaliana* under various global warming scenarios [30].

Molecular expression studies *in natura* can be conducted in two approaches: (1) hypothesis-driven approaches focusing on flowering or relevant genes as described above and (2) data mining of entire physiological processes using genome-wide data [31,32] (Figure 1b). To analyze genome-wide gene expression pattern of 500 or thousands of samples of multiple genotypes is realistic due to decreasing cost of RNA-seq or microarray to obtain data for both approaches [32], while small-scale experiments such as real-time PCR would be enough for the first approach. In the first approach (1), measuring the expression level of genes responsible for flowering time allows the monitoring of the flowering status of a plant long before there are visible morphological changes in flowering. Although many genes would affect quantitative phenotypes such as flowering time, key genes connecting flowering and a particular environmental cue are known and thus researchers can focus on a single or several genes. In the second approach (2), it is notable that the time-course genome-wide gene expression data encompass an enormous potential, although researchers still can decipher only a tip of the iceberg. For example, Matsuzaki *et al.* succeeded in estimating (and predicting) the sampling time of the day within an accuracy of 22 min from the mRNA levels of only 16 out of >27 000 genes in the model crop rice [33•]. As a data-mining tool to study model and other species, functions of genes which change expression patterns (differentially expressed genes, DEGs) can be examined using Gene Ontology categories or publicly available transcriptome datasets. While generating accurate predictions would be challenging in the second approach because the sizes of the effects and sometimes the functions themselves may differ between the plants used to generate the initial data set, and the plants under study, we contend that this approach is useful to examine the contribution of environmental factors in complex natural environments.

Monitoring community-wide flowering in tropical forests: RNA-seq and remote sensing

Using genomic and remote sensing approaches, we describe general flowering (GF) in Southeast Asian forests. During GF, hundreds of dipterocarp and other tree species flower synchronously at irregular time intervals from several months to several years [34]. Whereas previous studies based on observation by human eyes have suggested many possible environmental triggers for GF, such as maximum or minimum temperature, sunshine hours, drought, and soil nutrients, these studies have been disputed due to a lack of empirical evidence. Kobayashi *et al.* [31] conducted a RNA-Seq study of an individual of the non-model dipterocarp species *Shorea beccariana*. During a GF episode in 2009, about 1000 DEGs were detected. The expression level of many flowering genes changed two weeks before the morphologically visible flowering which coincided with a prolonged drought. In the data mining approach, many genes that are responsive to prolonged drought changed expression patterns two weeks before flowering. Both RNA-Seq approaches supported that drought is a trigger of GF, although the synergistic contribution of other triggers is possible. Yeoh *et al.* [35] studied the expression of a few key flowering genes and suggested that both cool temperature and drought are important triggers for flowering in *Shorea curtisii* and *Shorea leprosula*. A rapidly dropping genomic cost would allow further studies using a larger sample number.

In parallel, remote sensing methods have recently been introduced to study GF. Azmy *et al.* [36] examined relationships between the intensity of GF observed by human-eyes and satellite-based large-scale meteorological data. They demonstrated that drought is highly related to the intensity of GF, and that photosynthetically active radiation and low temperature are also relevant. Nagai *et al.* [37] analyzed images obtained from interval cameras installed on a canopy observation crane and found that the ratio of the reflectance in the red, green and blue wavelength range can detect characteristics of phenology of individual trees.

Future climate scenarios for the tropics suggest that the frequency of extreme events such as severe droughts will increase [38]. This raises concerns regarding disturbed plant reproduction in tropical forests in addition to direct dieback due to drought. The combination of quantitative datasets of transcriptomic and remote

sensing analyses for monitoring and prediction is now feasible.

RNA-Seq and remote sensing can monitor diverse traits such as pigment and nutrient levels [39•]. From the monitoring of the expression of some flowering genes, nutrient concentration under natural condition and resource manipulation experiments, Miyazaki *et al.* [40] found that mRNA levels of a few flowering genes such as *FT*, *LEAFY* and *APETALA1*, known as key regulators of flower development, were related to nitrogen availability in the Japanese beech *Fagus crenata* and proposed this as a mechanism for maintaining synchronized flowering. As remote sensing can now monitor nitrogen concentration in leaves or canopies [39•], this may provide a way forward in the integration of genomics and remote sensing.

Methodology 2. Genetic variation and rapid evolution within species
It has long been pointed out that genetic variation is an important factor in the adaptation of populations to new environments, and that evolution, namely changes in allele frequencies in populations over time by mutation, gene flow, selection or genetic drift, can occur on ecological time scales and have a measurable impact on responses to global change [8,9,41,42]. These evolutionary responses encompass a variety of traits and mechanisms including shifting responses to temperature, self-fertilization due to habitat fragmentation [43], and the emergence of new hybrid species [44], as just a few examples. However, due to the lack of a large-scale monitoring that would need interdisciplinary collaboration, it is not clear how prevalent or rapid such changes are, or whether variation and evolution have large effects on the responses of organisms and ecosystems to global change [9]. Even more difficult would be the prediction of evolution, which has been a major challenge in evolutionary biology. Here we discuss that: firstly, rapid experimental evolution is common in plants as well as in microorganisms; secondly, evolutionary prediction models by identifying genes responsible for adaptive traits are established using large datasets of genomes and phenotypes of the model plant *Arabidopsis*; and finally, remote sensing may provide large-scale phenotype data for ecologically relevant species.

Plant rapid evolution in experimental settings simulating environmental changes
Experimental evolution under regulated laboratory conditions has shown that evolution can occur rapidly, particularly in microorganisms with short generation times [45,46]. Large-scale plant growth experiments have emphasized that rapid evolution also occurs in plant communities, and reduced genetic diversity may result in local extinctions [47•,48]. Growth experiments with grassland plant species have indicated that when plants are grown in communities with higher plant species diversity, genotypes within plant species (which increase niche differentiation between species) may be selected from existing intraspecific genetic variation, which is evidence of evolutionary changes during a single experiment. This can lead to increased resource use as plants adapt to the experimental community [48]. Within a single species, plants grown in monocultures or mixed species assemblages were clearly differentiated by their metabolic fingerprints, which suggests changes in biochemical pathways that may be linked to genetic alterations and differential selection of genotypes [49]. Furthermore, primary productivity has been shown to increase with genetic diversity both in wild plants such as *Solidago altissima* and in crops such as wheat (*Triticum aestivum*) [50,51]. In experimental evolution using *Brassica rapa*, the difference of pollinators induced changes in plant architecture, flower fragrance and mating systems within several generations [52]. These experiments showed that rapid evolution can occur not only in microorganisms but in plants in diverse experimental settings, and raises the possibility that a large-scale monitoring may detect prevalent rapid evolution in natural environments.

Predictive models of evolution using DNA sequences of the model species *Arabidopsis*
Because it was difficult to identify genes responsible for adaptive traits until recently, traditional quantitative genetic models were designed to predict evolution with simplified assumptions about the genetic basis. However, the limitation of quantitative genetic models are often pointed out [9–12]. The challenge of incorporating genomic data to predict plant evolutionary trajectories under global climate change began with *A. thaliana*. In these studies, rapid evolution was predicted in which variations in many genes are responsible for adaptation to local climates. Two large datasets are necessary for such studies: the genome-wide genotyping of a large number of natural accessions, and fitness-related traits in growth experiments under various conditions. Banta *et al.* [53] extended niche modeling (more specifically climate-envelope modeling) to study the change of the spatial distribution of a specific genotype. They showed that two alleles of the *FLC* gene affected the ecological niche. Hancock *et al.* [54] identified a large number of genome-wide loci responsible for local adaptation, and these loci predicted the relative fitness of genotypes in a common garden experiment. Fournier-Level *et al.* [55•] developed evolutionary prediction models for three potential future climates, and suggested that *FRI* (an upstream gene of *FLC*) would become frequently fixed by the year 2100. They also suggested that evolutionary rescue by rapid evolution is limited compared with the phenotypic plasticity to seasonal climate change. Although the methodologies are still under development, a next challenge would be to extend these to agriculturally and ecologically relevant species.

Remote sensing to measure genetic variation via functional traits

In studying variations and rapid evolution, it is necessary to obtain genotypic and phenotypic data of a large number of individuals as explained above. To extend the scope to crop species, a large-scale phenotyping using remote sensing turns out to be a key [56,57] (Box 1) because the cost of genome-wide genotyping is rapidly reducing. Here we summarize a few recent studies on ecologically relevant species to document genetic variation using remote sensing. Madritch *et al.* [58•] used imaging spectroscopy data to map genetic variation of trembling aspen *Populus tremuloides* in two ecoregions of the USA. Whereas this study may not be easily applicable to other species because a single genotype (genet) of this species provides a large surface for monitoring, the approach has a high potential for detecting intraspecific variation with sufficient spatial resolution. The potential for detecting within-species variation (or population differentiation) of *Quercus oleoides* under randomized common garden conditions using imaging spectroscopy fingerprints at the leaf level has also been demonstrated [59•]. The oak study indicated that spectral data follows evolutionary models and suggests it has the potential to accurately place spectra of unidentified taxa in the tree of life. Within-species and even within-individual phenotypic variation in tree functional traits in a temperate forest in Switzerland have recently been mapped in continuous space using a combination of airborne laser scanning and imaging spectroscopy [60•].

A major method to identify a large number of loci responsible for phenotypic variations in model species including *A. thaliana* and *Homo sapiens* is the genome-wide association study (GWAS). Remote sensing technology described above may be valuable to conduct GWAS of ecologically relevant species, although there remain challenges. The number of individuals should be at least one hundred, and the power and resolution would be increased using millions of individuals. To reduce the rate of false positives, various methods have been developed including redundancy analysis (RDA) [61], least absolute shrinkage and selection operator (LASSO) [62].

Methodology 3. Monitoring and predicting using barcoding of environmental DNA

Traditionally, biodiversity monitoring is based on direct records of indicator taxa such as birds, vascular plants, or macroinvertebrates [26•]. Developments in high-throughput sequencing technologies enable the assessment of many organisms, ranging from microbes to plants and animals, by eDNA metabarcoding. In this technique, DNA is extracted from environmental samples such as soil or water [63]. eDNA metabarcoding can track biodiversity across ecosystems, such as across the land–water interface, and across major taxonomic groups in a unifying way [64••]. It enables the measurement of not only biodiversity but also associated ecosystem processes [65] and the assessment of intrataxa abundance and population structure [66].

eDNA metabarcoding for effective ecosystem monitoring

The monitoring of biodiversity using eDNA metabarcoding can replace existing biodiversity indicators [67] due to three main advantages. First, it can be done in a taxonomy-free manner [60•]. Second, the method is nondestructive and thus especially useful in detecting rare or endangered species [68]. Third, this method has the potential to be easily scalable, for example, by using automated sampling and DNA extraction, such that a high spatiotemporal resolution of biodiversity data is foreseeable [17,65] although its implementation is still in its infancy. The most strongly debated next steps are in improving the ability of the methods to give not only qualitative but also quantitative data about the presence of organisms, that is, population density or abundance estimates [67]. However, less has been done to enable the use of eDNA-based data with multicellular organisms and in population genetics and demography [66]. eRNA may also provide monitoring of functional traits [69].

Integration of ecosystem monitoring by eDNA techniques and remote sensing

The most speculative integration is the use of eDNA with remote sensing, where opinions, but so far no data have been published [17,70]. Importantly, the two methods may complement each other: eDNA metabarcoding can assess the diversity of organisms for which remote sensing is 'blind' (such as microbes or small invertebrates), whereas remote sensing can deliver data on ecosystem variables such as productivity and phenology, for which eDNA metabarcoding is not suitable. Together, they may give an integrated measure of both the state (e.g. diversity) and the function of ecosystems, especially if eRNA is included. Given that the two approaches can deliver comparable quality, both the current state but also potential changes in biodiversity would be much better monitored with respect to the spatial, temporal, and taxonomic scales covered. The resulting data will fill large gaps and may thus increase our ability to predict the dynamics of ecological systems and biodiversity. Challenges to be addressed are that eDNA metabarcoding is well-suited for aquatic ecosystems but is less developed for terrestrial systems. To tackle these challenges, the focus of eDNA barcoding advances should move beyond aquatic systems, whereas remote sensing should focus on aquatic (freshwater) systems.

Perspectives and conclusions

Given the rapid loss of biodiversity, it is both necessary and urgent to monitor changes in ecosystems and to create reliable predictions. However, the monitoring and prediction in biota are falling behind those in abiotic

components such as the atmosphere and ocean [8]. This is because the biota are highly heterogeneous and complex at every level of ecological hierarchy, from individuals to landscapes.

Novel technologies enabling integration of genomics and remote sensing

In this review, we argue that integrating genomics and remote sensing into an ecosystem science will increase our ability to predict ecosystem-level responses to global change. With the advent of high-throughput sequencing technologies in genomics and high-dimensional airborne observations at larger scales in remote sensing, the integration of these two fields is at hand. Although it is still not negligible, the cost of high-throughput sequencing is dropping dramatically. Thanks to the development of commercial kits, devices and analysis methods, handling of samples and their analysis is much easier than a few years ago. Portable sequencing devices, which are under development [71], would enable transcriptomic monitoring and metabarcoding without bringing samples back to the laboratory. These new technologies allow us to increase the number of samples and time points in a study and therefore enable experiments with an increased ecological value. We also observe remote sensing striving toward becoming a commodity. For example, imaging phenomics allows imaging of phenotypic traits from cell to canopy levels [72]. In addition, new advances in imaging spectroscopy and LiDAR have contributed to retrieving physiological and morphological plant traits [60•] and the linkage to plant strategies, growth and life forms [73].

How to integrate genomics and remote sensing

Genomics and remote sensing are expected to provide cost-efficient monitoring and may complement or substitute more traditional monitoring approaches in the near future. To this end, we emphasize the importance of ecological monitoring data in two ways. First, to examine the relationships between environment and ecosystem responses, collecting diverse ecological traits together with meteorological, genomic, and remote sensing data in time-course series is essential. This will allow researchers to find appropriate indicators of functional traits, for example, marker genes derived from genomic analysis or spectroscopic indices derived from the analysis of remote sensing data. Various international biodiversity monitoring organizations are working to integrate a variety of biodiversity variables in a unified manner [74]. These data would be helpful to generate accurate predictive models [2,3]. The indicators can then be used in predictive modeling of ecosystem responses to global change. For the analysis, novel algorithms have become available. For example, conversion cross mapping (CCM) [75] helps to discover causal relationships in time-series data. Although it may still be necessary to focus on a few species to begin with, it could be important in evaluating

differences among species. Second, verification by controlling environmental conditions in experimental settings is still essential to disentangle complex interacting environmental factors. For example, throughfall-exclusion, nitrogen-addition, warming and CO_2-addition experiments have been conducted in various ecosystems [40,76,77]. Integrating these experiments with the monitoring of genomic and remote sensing variables may help to extract the effects of a particular environmental factor.

Interdisciplinary collaboration to enhance global change studies

Interdisciplinary collaboration will be the key for the studies discussed here. We propose that communication should be enhanced by a mutual understanding of terminology with different definitions and emphasis [78]. Studies that integrated genomics and remote sensing data for monitoring and predicting ecosystem responses to global change have been successful for model species. It is now time to apply the integration of the new tools to non-model species and ecologically and environmentally relevant situations. Finally, a better understanding of ecosystem responses to global change will also improve our ability to study effects in the other direction, that is, the feedback of the ecosystems on global change, where biodiversity becomes the driver and physical environment the response.

Conflict of interest
The authors declare that there is no conflict of interests.

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Papers of particular interest, published within the period of review, have been highlighted as:

• of special interest
•• of outstanding interest

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