Evolution as an ecosystem process: insights from genomics

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Abstract

Evolution is a fundamental ecosystem process. The study of genomic variation of organisms can not only improve our understanding of evolutionary processes, but also of contemporary and future ecosystem dynamics. We argue that integrative research between the fields of genomics and ecosystem ecology could generate new insights. Specifically, studies of biodiversity and ecosystem functioning, evolutionary rescue, and eco-evolutionary dynamics could all benefit from information about variation in genome structure and the genetic architecture of traits, whereas genomic studies could benefit from information about the ecological context of evolutionary dynamics. We propose new ways to help link research on functional genomic diversity with (reciprocal) interactions between phenotypic evolution and ecosystem change. Despite numerous challenges, we anticipate that the wealth of genomic data being collected on natural populations will improve our understanding of ecosystems.

Keywords: ecosystem function, genomics, eco-evolutionary dynamics, evolutionary rescue, hybridization, phenotypic plasticity

Introduction

Evolution both generates and maintains the biodiversity of global ecosystems, and as such is a fundamental ecosystem process (Holt 1995; Matthews et al. 2011; Hendry 2017). There is growing recognition that both ecological and evolutionary dynamics interact to shape species diversity and species interactions (Thompson 2013; Schoener 2011; Weber et al. 2017; Pennell & O'Connor 2017), and that these components of communities shape ecosystem functions such as productivity, nutrient cycling, and decomposition (Holt 1995; Matthews et al. 2011; Hendry 2017). Incorporating eco-evolutionary dynamics into predictions about ecosystems responses to environmental change is a fundamental challenge for evolutionary biology in general, and for genomics research in particular.

Research in genomics has an underappreciated potential to yield mechinistic insights into contemporary ecosystem dynamics. To date, genomics research has revealed astounding genomic diversity within natural ecosystems (both within and among species) (Seehausen et al. 2014), improved our understanding about the genetic architecture of organismal traits (for both model and non-model organisms) (Peichel & Marques 2017), and enabled us to track genetic changes in evolving populations in the laboratory (e.g. experimental evolution) and in the wild (Barrick & Lenski 2013; Charmantier et al. 2014). However, ecosystem-level processes are rarely studied through the lens of either evolution or genomics. On the one hand, the joint study of genomes and ecosystems may seem incompatible due to differences in biological scales of organization. Yet on the other hand, given the massive contribution that genomics research has made to evolutionary biology, and the growing evidence that evolutionary change can have ecosystem-level impacts (Hendry 2017), it is worth considering the potential impacts of genes and genomes on ecosystem ecology (Whitham et al. 2008; Matthews et al. 2011).

One promising way to link genomes with ecosystem processes is to study the genomic diversity of keystone and foundation species, along with the genetic basis and evolution of organismal traits that have strong, and potentially reciprocal, interactions with ecosystem processes (Genung et al. 2011). To motivate this argument, we begin by illustrating how the evolutionary history of both organisms and communities can shape our predictions about evolutionary dynamics in contemporary ecosystems. We then discuss how genomics research, particularly focussing on ecologically relevant traits, might yield new insights for studies on biodiversity and ecosystem functioning, evolutionary rescue, and eco-evolutionary dynamics and feedbacks (Kokko & López-Sepulcre 2007; Schoener 2011; Matthews et al. 2011; Thompson 2013; Hendry 2017). We specifically argue for a stronger focus on the genomics of functional effect and response traits, as a way to address some of the challenges with linking genes, traits, and ecosystems across environments, such as those arising from phenotypic plasticity and population admixture due to hybridization. In an effort to simplify the discussion of these linkages, we introduce a conceptual model and illustrate how it can be applied to a keystone species (i.e. *Sphagnum*) in peatlands - an ecosystem that harbours over a third of the terrestrial carbon on our planet (Weston et al. 2015).

Connecting ancient and recent evolutionary history with contemporary ecosystems
Throughout earth's history the emergence of life, and the processes that generate and maintain the diversity of life, have transformed the cycling of elements in the oceans, on land, and in the atmosphere (Becking 2015; Knoll 2003; Canfield 2014). Countless evolutionary events and innovations have shaped contemporary ecosystem dynamics. For example, the emergence and diversification of cyanobacteria, which was facilitated by the innovation of oxygenic photosynthesis (Dismukes et al. 2001), eventually culminated in a "Great Oxidation Event" somewhere between ~2-3 billion years ago. More than a billion years later cyanobacteria were involved in a symbiosis event that led to the evolution of chloroplasts in land plants (Margulis 1970). Such evolutionary events have dramatically altered both the genomic structure of evolving organisms and the balance of biotic and

abiotic processes governing the cycling of key elements on our planet. Eukaryotes currently harbour a mitochondrial genome originating from cyanobacteria that continues to influence adaptive evolution through interactions with the nuclear genome (Breton et al. 2014).

This historical perspective on the importance of evolution for ecosystems is undeniable, and, arguably somewhat trivial. Without major evolutionary events, there would be none of the biodiversity within or across lineages that populates contemporary ecosystems. However, we see at least three more specific reasons why an evolutionary genomics perspective could be useful for studying contemporary ecosystems. First, evolution is faster than we previously thought, and as a result, can play a significant role in shaping the contemporary dynamics of populations and species interactions (Thompson 2013; Hendry 2017). Second, genomics can help uncover how the evolutionary history of species interactions (e.g. competition, predation, mating) influences contemporary rates of phenotypic evolution and diversification (Meier et al. 2017; Dhami et al. 2016). Third, genomic studies of natural populations are already revealing staggering levels of cryptic diversity within species, which are probably functionally relevant for ecosystem dynamics (Kashtan et al. 2014), but are often hidden from common phenotyping approaches. We elaborate on each of these three reasons below.

First, evolutionary dynamics are sufficiently rapid to shape the biological, chemical, and physical dynamics of ecosystems (Hendry 2017; Thompson 2013), and influence how ecosystems respond to local and regional environmental changes (e.g. warming, pH, nutrients) (Norberg et al. 2012). A genomic perspective on the rapid evolution of trait combinations could be a major step forward in our understanding of both functional redundancy and mismatches (Arnegard et al. 2014), as well as evolutionary constraints on whether lost trait combinations might re-evolve (Alexander et al. 2017). The rapid pace of evolution is particularly evident in experimental evolution studies, and particularly relevant for understanding ecosystem dynamics when documented for keystone species. For example,

studies with algae have shown rapid evolutionary response to two important aspects of global change: elevated CO_2 (Collins & Bell 2004; Schaum et al. 2016; Lohbeck et al. 2012), and elevated temperature (Schaum et al. 2017). A key insight from such studies is that evolution in natural populations will depend not only on genetic factors, such as rates of mutation accumulation (Bell & Collins 2008), but also on ecological factors such as competitive interactions (Collins 2011), phenotypic plasticity (Schaum & Collins 2014), and population structure (Kelly et al. 2013). In the last decade, experimental evolution studies have expanded their scope to include species interactions (Hansen et al. 2007), and in these studies recent advances in genomics techniques have become instrumental for high-frequency quantification of genomic changes (Barrick & Lenski 2013; Good et al. 2017). As such studies become more common, they will not only reveal generalities about evolutionary responses of populations to environmental change, but could also help inform models about potential evolutionary responses of populations (Norberg et al. 2012).

A second reason for adopting an evolutionary genomics perspective on ecosystems is that the evolutionary history of species interactions is central to understanding both ecological and evolutionary dynamics over a broad range of time scales (Weber et al. 2017). Rapid diversification of species interaction traits is a hallmark of adaptive radiation (Schluter 2000), and particularly influential for those radiations involving the build up of species diversity across multiple trophic levels in ecosystems (Meier et al. 2017). In studies of adaptive radiation, genomics is not only essential for understanding the evolutionary relationships among extant species, but also for deciphering the evolutionary consequences of ancient interactions among species (e.g. hybridization) occurring in the early stages of, or prior to, the radiation (Seehausen et al. 2014). For example, hybridization between ancient lineages of cichlids (Meier et al. 2017) may help explain why some clades of cichlids radiate and assemble diverse communities while other clades do not (Wagner et al. 2012). Over shorter time scales, the evolution of traits governing species interactions can also dictate community dynamics in ecosystems (Dhami et al. 2016; Brunner et al. 2017). For example, a recent

genomic study of the nutrient uptake traits of a nectar yeast species (Dhami et al. 2016), revealed a genetic architecture of a nitrogen metabolism trait of an early colonizing yeast species (*Metschnikowia reukaufii*), specifically a gene cluster created by tandem duplications, that could help explain why this yeast species could sustain competitive dominance relative to later arriving species. Such examples illustrate how genomics research can uncover important insights about how ancient and recent species interactions can affect contemporary processes in ecosystems.

A third reason is the growing evidence about the enormous genomic diversity of natural populations, as revealed by recent genomic studies (Kashtan et al. 2014), and the increasing likelihood that this diversity has important consequences for the functioning of global ecosystems. The cyanobacterium *Prochlorococcus* is numerically dominant in oligotrophic tropical and subtropical oceans, where it can account for nearly half of primary productivity (Johnson et al. 2006). Populations of *Prochlorococcus* can consist of hundreds of sub-populations, some of which are estimated to have diverged millions of years ago (Kashtan et al. 2014). Genetically distinct strains can differ widely in their nutrient acquisition, thermal preference, and optimal light environment (Johnson et al. 2006), and can coexist in oligotrophic oceans (Partensky et al. 1999; Kashtan et al. 2014). Owing to its tiny size (~0.5-0.7 microns), *Prochlorococcus* was only discovered in 1988 (Chisholm et al. 1992) and recent work on single-cell genomics of *Prochlorococcus* has revealed even more surprising amounts of genomic diversity among co-occurring cells (Kashtan et al. 2014). Another ubiquitous marine cyanobacterium, *Synechococcus*, has been shown to have high genetic diversity associated with pigment diversity. Multiple gene variants, gene organisations and even polymorphic intergenic spacer regions have been shown to be associated with unique geographic, thermal and turbidity niches (Xia et al. 2017; Xia et al. 2015). Possession of these unique genomic sequences and motifs appears to result in niche differentiation that expands the geographic range of the genus beyond where individual phylotypes could persist. Further whole genome analysis could provide new insights into the genomic basis of

these pigment-related traits, constraints on their variation due to linkage or epistasis, and their associations with other traits under selection (Xia et al. 2017). Such genomic studies of natural populations of keystone primary producers reveal our staggering ignorance about the functional importance of genomic diversity in our global ecosystems. But they also offer new techniques that will allow future studies to explore the link between genomic diversity and ecosystem dynamics.

Building an evolutionary genomics perspective for ecosystem ecology

So far, we have argued that an evolutionary genomics perspective on ecosystems is useful, but we recognize that this perspective is already growing in several research fields, including: biodiversity and ecosystem functioning, evolutionary rescue, and eco-evolutionary dynamics. For each of these field, we highlight recent progress and discuss how genomics research in particular could improve our understanding about evolution as an ecosystem process.

The genomics of biodiversity and ecosystem functioning (BEF) - Classic ecological research on the relationship between biodiversity and ecosystem functioning (Hooper et al. 2005) has progressed to testing how the genetic diversity of foundation species can affect productivity at a given trophic level (e.g. plants) (Crutsinger et al. 2006), and how this might extend to broader food web interactions (Crutsinger et al. 2009; Dinnage et al. 2012; Crutsinger et al. 2014; Whitham et al. 2008; Bailey et al. 2009). By and large, this field has focussed on constant and discrete contributions of genotypes and species to ecosystem functioning (Tilman et al. 2014), and has only more recently addressed the way that evolutionary history might influence these contributions (Cadotte et al. 2008; Maherali & Klironomos 2007). For example, Maherali and Klironomos (2007) experimentally tested how phylogenetic distances among mycorrhizal species influenced the assembly and richness of fungal communities.

One useful way to extend BEF research would be to use knowledge of gene metabolic functions and interactions to mechanistically understand the effects of genomic diversity on ecosystem level metabolic fluxes and biochemical conversion rates. For example, genomic knowledge of biochemical and metabolic pathways discretely contained within different taxa could allow a better understanding of how taxa respond to the environment and interact, and why some taxa are functionally redundant, while others are complementary (Lindemann et al. 2016). Recent research on some foundation species has used genetic modification to isolate the specific effects of particular alleles on the types of species interactions that could control ecosystem functions such as pollination and secondary production (Kessler & Baldwin 2007). Gene knock-outs, and the use of mutant libraries could also be used to understand genetic complementarity or redundancy. Some phenotypic traits may be genetically degenerate - i.e. multiple genes contribute to the trait such that a deleterious mutation results in negligible loss of function (Greenspan 2009), and others may act as "keystone" genes, being necessary for multiple, phenotypic traits e.g. via pleiotropy. Previous work has shown that resource partitioning among species may result from differential patterns of gene expression (Alexander et al. 2015). Both differences and similarities among species in gene expression across the whole genome in response to the presence of other species can highlight how species may partition the abiotic environment in order to coexist (Bowsher et al. 2017; Narwani et al. 2017), or may emphasize parallel responses among all species to the relevant species interactions (Cordero & Polz 2014).

One can also extend BEF research by studying the relationship between ecosystem functioning and genomic diversity within and among species, including variation in genome size, chromosome number, ploidy, and gene copy number. In aquatic systems, there are several useful model organisms for studying how variation in genome structure might influence nutrient dynamics. As foundation species, macrophytes determine habitat structure, nutrient cycling, and resilience to external environmental drivers (e.g. eutrophication) (Jeppesen et al. 1997). They also exhibit remarkable phenotypic variation in

their elemental ratios (e.g. of Nitrogen and Phosphorus), and this is partly governed by genomic processes such as polyploidy, interspecific hybridization, and dysploidy (Leitch et al. 2014). Variation in genome size, for example, can influence cellular demand for limiting nutrients such as N and P, and this could cause genome size to be a target of selection. In a freshwater snail (*Potamophyrgus antipdarum*) variation in ploidy within and among populations is correlated with %P and nucleic acid content, suggesting that processes affecting ploidy in natural populations could influence nutrient cycling or trophic interactions (Neiman et al. 2013). In another freshwater invertebrate (the *Hyalella azteca* species complex) multiple parallel cases of divergence in response to fish predation have produced ecomorphs that vary in both body size and genome size, with large ecomorphs having up to twice the genome size of small ectomorphs (Vergilino et al. 2012). At lower trophic levels, the small genome size of the cyanobacterium *Prochlorococcus* partly explains its low P demand and thus its dominance in oligotrophic oceans (Bertilsson et al. 2003). Substantial variation in genome size has been found both within species and among closely related species of the rotifer *Brachionus plicatilis* (Stelzer et al. 2011), and correlations between genome size and both body size and egg size (Stelzer et al. 2011) suggest an influence of variation in genome structure on life-history traits and, potentially, food web dynamics. In sticklebacks, structural variation is prevalent within populations (Feulner et al. 2013) and a subset of copy number variants displays pronounced differences between ecologically differentiated populations and genes affected are enriched with functional associations with environmental interactions (Chain et al. 2014).

Another way to extend BEF research would be to consider how the genetic architecture of adaptive traits might affect the relationship between diversity and function. Most BEF studies experimentally manipulate diversity (e.g. species, traits, genetic), and very few of them explicitly test how contemporary evolutionary change might affect ecosystems. Two notable experiments highlight how rapid trait evolution could affect the BEF relationship, although neither involved genomic analyses. In one, rapid evolution of niche differentiation among co-

occurring grasses seemed to affect both species coexistence and ecosystem productivity (e.g. community level biomass) (Zuppinger-Dingley et al. 2014). In the other, selection for resource specialization of wild isolates of marine bacteria steepened the relationship between diversity and bacterial productivity compared to isolates reared on mixed resources (Gravel et al. 2011). We are aware of no studies that have considered how variation in the genetic architecture of traits might affect BEF relationships, although fundamental questions about the genomics of adaptation could be relevant for such studies. Specifically, how many genes explain variation of adaptive traits or fitness (Schluter et al. 2010; Peichel & Marques 2017)? Are there genetic architectures that affect the rate of evolution (Kokko et al. 2017; Débarre et al. 2015)? Are the genes involved in adaptation typically regulatory, and are the same genes involved across multiple instances of adaptation (Conte et al. 2015)? Unfortunately, the genomic studies that address these questions rarely consider the implications for population or ecosystem level processes (Rodríguez-Verdugo et al. 2017). Current BEF studies are not designed with these questions in mind, and so the typical manipulations of trait diversity (within or among species) are uninformed by the genetic variation or genetic architecture of the manipulated traits.

The genomics of evolutionary rescue - Adaptive evolution can rescue species from extinction in changing environments, and this could be particularly important for ecosystems when either keystone or foundation species are threatened by global change. As such, understanding the underlying genomics of adaptation might improve predictions about when rescue may occur (or not). Previous work suggests that the probability of evolutionary rescue depends on population size, on the amount of genetic variance, and on the severity of environmental deterioration (Gomulkiewicz & Holt 1995; Lande & Shannon 1996; Willi et al. 2006; Bell & Collins 2008). Accordingly, experimental evolution with microbial organisms has found increasing probability of evolutionary rescue with increasing population size (Bell & Gonzalez 2009; Samani & Bell 2010), increasing standing genetic variation (Lachapelle & Bell 2012), and a slower rate of environmental change (Bell & Gonzalez 2009).

Studies that have combined experimental evolution with whole-genome sequencing can help detect general characteristics of adaptive mutations, quantify mutation rates and fitness effects of mutations, and explore the repeatability of evolution at both the phenotypic and the molecular level (Barrick & Lenski 2013; Bailey & Bataillon 2016). For example, experiments that test the adaptation of bacteria, yeast, and *Drosophila* to stressful or novel environments have found some degree of parallel evolution (Zhou et al. 2011; Tenaillon et al. 2012; Wong et al. 2012; Spor et al. 2014). Similarly, there is evidence for repeatability of adaptation to toxic pollution in natural populations of both amphipods (Weston et al. 2013) and killifish (Reid et al. 2016). By comparing multiple pairs of sensitive and tolerant killifish populations both experimentally and with genome sequencing, Reid et al. (2016) found that killifish from polluted sites were able to tolerate levels of pollution that were otherwise lethal to sensitive populations, and that tolerant populations shared outliers in either the same genes or pathways. Overall, this suggests that quantifying of genomic diversity might help us predict if species will be able to adapt to anthropogenic environmental change.

The genomics of eco-evolutionary dynamics. - Several recent studies in the field of eco-evolutionary dynamics have shown that rapid phenotypic evolution can have large effects on populations, communities, and ecosystems (Hendry 2017). Such effects have been studied with experiments that manipulate the phenotypic distribution of traits, and/or the opportunities for trait evolution over the course of the experiment.

In laboratory experiments, previous work has nicely shown how rapid evolution of anti-predator defense traits (Fischer et al. 2014; Becks et al. 2010; Becks et al. 2012; Hiltunen et al. 2015) can affect population dynamics. Becks et al. (2010) manipulated the genetic variation in algal defenses (i.e. a clumping phenotype) and found that this changed predator-prey dynamics in line with theoretical expectations (Cortez 2016). In this same experiment, Becks et al. (2012) quantified gene expression of the algal population, and found that the

genes that were downregulated as clumping increased were upregulated as clumping decreased (Becks et al. 2012). Over multiple population cycles different subsets of genes were up- and downregulated, suggesting complex and multifarious connections between genomic and phenotypic change in these populations.

Manipulating the evolutionary process directly offers another powerful approach to link genomics with ecosystem processes. For example, one can manipulate the opportunity for evolution by resetting (or not) the genotype composition of a population after each generation. Using this approach to study range expansion, Williams et al. (2016) found the rate of dispersal of *Arabidopsis thaliana* was strongly dependent on the evolutionary responses of populations (comprised of 14 inbred recombinant lines) to habitat fragmentation (Williams et al. 2016). Populations that were allowed to disperse naturally in the experimental setup over six generations (i.e. evolving population) were compared with those that were reseeded each generation at random from the original genotype pool (i.e non-evolving population). In the treatment with the highest habitat fragmentation, the evolving population was able to spread 200% farther than the non-evolving population (Williams et al. 2016). Although range expansion might only be indirectly related to ecosystem processes, such an experimental design could help explore the ecosystem consequences of genomic change within a population that is exposed to different selection pressures. Ideally, such experiments could combine both phenotypic and genomic responses to selection, so as to compare the strength of selection acting on phenotypes and on genetic variants (Thurman & Barrett 2016)

Another approach for testing the ecosystem effects of recent phenotypic evolution is to use organisms whose phenotypic differences have been shaped by recent selection, but are fixed over the course of a experiment (Matthews et al. 2011). Such experiments, dubbed common gardening experiments (Matthews et al. 2011; Hendry & Green 2017), have documented how recent phenotypic and genomic differentiation among organisms can

influence population dynamics, community composition, and ecosystem functions (Lundsgaard-Hansen et al. 2014; Bassar et al. 2010; Harmon et al. 2009; Palkovacs & Post 2009; Best et al. 2017). In aquatic systems, studies with fish collectively suggest that rapid trait evolution can have significant ecosystem effects, and, in some cases these phenotypic effects can be large relative to other external drivers of ecosystem change, such as variation in incident light (El-Sabaawi et al. 2015) or fish density (Matthews et al. 2016). Across many fish model systems, including guppies, alewives, whitefish, and stickleback, there are putative traits (e.g. foraging traits, stoichiometric traits) that underlie the observed ecosystem effects, but very little is known about the genetic basis of these traits (Leal et al. 2017).

For all of these experimental approaches discussed above, it is crucial to identify the suite of traits that can evolve rapidly and potentially have large ecosystem effects. In stickleback research, there has been some progress toward understanding the genetic basis of a wide range of traits (Peichel & Marques 2017), some of which may be adaptive (Schluter et al. 2010), and some of which may underlie the divergent ecosystem effects of different stickleback ecotypes and species pairs (Harmon et al. 2009; Matthews et al. 2016). Stickleback are geographically widespread in the Northern Hemisphere, and common members of fish communities in water bodies ranging from ponds and streams to large temperate lakes. Rates of phenotypic evolution (Bell & Aguirre 2013) and genomic differentiation between ecotypes (Marques et al. 2016) can be rapid. Populations can also be easily reared in the laboratory, and so the ecosystem effects of genetic background and plasticity can be experimentally tested (Matthews et al. 2016). Specific crosses can also be made that alter genetic background and trait variation in an experimental population, and this can be beneficial for ecosystem experiments, quantitative designs, and QTL analyses. Furthermore, stickleback have a high-quality genome assembly and linkage map (Jones, Grabherr, et al. 2012), which has facilitated the detection of quantitative trait loci for stickleback traits (Peichel & Marques 2017) and could facilitate genomic experiments, which have been performed in other species (Egan et al. 2015; Gompert et al. 2017), that aim to

study how different putative agents of selection cause changes in allele frequency genome-wide. Such experiments could manipulate multiple agents of selection in experimental ecosystems, including productivity, habitat structure, density, and species interactions, so as to better understand the relative importance and interaction of different ecological causes of evolution (i.e. selective agents).

The genomics of eco-evolutionary feedbacks - Eco-evolutionary feedbacks are reciprocal interactions between ecological and evolutionary processes that play out over contemporary time scales (i.e. several to hundreds of generations) (Hendry 2017). Such feedbacks are one of the focal points of the broader field eco-evolutionary dynamics. Feedbacks are most likely when the traits involved in adaptation can also shape the environmental conditions that affect selection pressures (Holt 1995; Matthews et al. 2014). The presence of feedbacks has been used to explain both the stability (Kinnison et al. 2015) and potential instability (Driscoll et al. 2016) of ecosystem dynamics, both over time and in response to environmental change (Hendry 2017). New experimental evidence for feedbacks is mounting (Frickel et al. 2017; Best et al. 2017; Brunner et al. 2017), and genomic approaches are increasingly contributing to the detection and interpretation of such feedbacks (Rudman et al. In press).

Studies of rapid evolution of plant traits provide intriguing evidence for eco-evolutionary feedbacks involving soil environmental conditions. For example, experimentally reduced insect herbivory on evening primrose (*Oenothera biennis*) led to the evolution of earlier flowering times, lower phenol content, and altered competitive interactions (Fitzpatrick et al. 2015). In some contexts, this trait evolution can alter ecosystem functions (e.g. respiration, nutrient cycling) possibly through effects on soil microbial communities. As another example, the evolution of drought-resistance in *Brassica rapa* can alter both the richness and the biomass ratios of fungal and bacterial communities (Terhorst et al. 2014). Importantly, there are several mechanisms by which such trait-mediated ecosystem effects might influence selection pressures and feedback on trait evolution (terHorst & Zee 2016). During

succession in plant communities, for example, the effects of organisms on their environment can shift between having negative to positive effects on conspecifics relative to heterospecifics, implying substantial temporal variation in the strength and direction of organism-mediated selection pressures (terHorst & Zee 2016).

Evidence for feedbacks between the ecosystem effects of fish and their evolutionary responses has also been documented in three recent experimental studies of stickleback in aquatic mesocosm experiments (Matthews et al. 2016; Brunner et al. 2017; Best et al. 2017). Two of these studies tested how genomically differentiated lake and stream ecotypes of stickleback (Marques et al. 2016) can differentially modify aquatic mesocosm ecosystems (~1000L), likely via trait-mediated differences in resource depletion, or habitat modification (Matthews et al. 2016; Brunner et al. 2017). In both experiments, the recently diverged ecotypes (<150 generations) had contrasting effects on environmental conditions that differentially affected some aspect of growth, performance, or survival of juveniles in a subsequent generation. In one of the experiments, for example, stream juveniles outperformed lake juveniles in ecosystem conditions that were previously modified by adult lake fish (Brunner et al. 2017). Interestingly, in this same experiment, the patterns of gene expression for the lake juveniles depended on the effects of the adult phenotype on the rearing environment of the juveniles. These results suggest underexplored linkages between the phenotypic effects of organisms on ecosystems, and the persistence of these effects across generations. The observed transgenerational effects on both juvenile gene expression and selection pressures (Brunner et al. 2017), warrant a reconsideration of the importance of soft selection for evolution (Reznick 2016; Best et al. 2017). Specifically, soft selection might be characterized by feedbacks that are mediated by density and frequency-dependent selection. Although genomic changes associated with soft selection regimes are likely complex they might nevertheless reflect the true nature of adaptation in natural environments.

So far, we have elaborated how genomic research can contribute to a broad range of fields that study the interplay between evolutionary and ecosystem processes. We believe that even further progress can be made by developing a strong genomics perspective of organismal traits in general, and of traits that underlie the ecosystem effects of organisms in particular.

Integrating genomics with trait-based approaches: challenges and opportunities

The study of functional effect and response traits has been particularly useful in ecology for understanding how populations respond to and modify environmental conditions (Díaz & Cabido 2001; Mori et al. 2013; Violle et al. 2007), but the genetic basis and architecture of these traits are poorly understood. In ecological studies, for example, plant response traits are measured for multiple species (e.g. specific leaf area) and used to predict how communities will change along environmental gradients (Cornwell & Ackerly 2009). Functional effect traits can also be useful for determining how organisms might affect ecosystem functions. For example, the tannin concentration of litter from multiple species of *Populus* trees varies strongly among genotypes, and influences rates of decomposition in both terrestrial and aquatic environments (Schweitzer et al. 2008). It is an open question how genomics research on functional response and effect traits could improve predictions about ecological and evolutionary responses to global change. This depends on the technical challenges in identifying heritable traits and quantifying the genetic basis and architecture of these traits, as well as on our understanding about the genomic basis of adaptation and the multiple processes that affect phenotypic change in natural populations.

Heritability in natural populations - Until recently, heritability estimates providing information on the adaptive potential of traits have been limited to laboratory crosses or wild populations for which large pedigrees could be established (Charmantier et al. 2014), making such inferences hardly accessible to the many functional response and effect traits of organisms

in natural populations. However, the development of mixed linear models that use genetic relationships between individuals estimated from SNPs, offers the chance to evaluate quantitative genetic variance without a pedigree. For example, relatedness estimates from genetic markers in the dwarf shrub *Salix herbacea* have revealed heritability of phenological traits and leaf size - traits which differ among microhabitats and might underlie adaptations to changing environmental conditions (Sedlacek et al. 2016). Further, the heritability captured by SNP markers compared with pedigree based estimates reached an asymptote around 12'000 markers (Bérénos et al. 2014), suggesting that denser marker panels are not necessarily required for precise and unbiased heritability estimates. This suggests that the magnitude of genome-wide markers easily established via genotyping by sequencing approaches might suffice for estimates of heritability, provided a high enough fraction of the population can be analysed.

Quantitative trait locus analysis - Identifying the specific loci that explain variation the ecosystem-effect traits of an organism will often be be a daunting task. Quantitative trait locus (QTL) studies are increasingly defining the distribution of effect sizes of loci for a range of phenotypes (e.g. percent of phenotypic variance explained by a given locus) (Peichel & Marques 2017), but the power of this approach diminishes rapidly for highly polygenic traits. Ecosystem effect traits are likely to be highly polygenic, and the extent to which we will be able to identify the functional significance of individual loci in reference to their effects on whole ecosystems remains uncertain. Theory suggests that mutations of large phenotypic effect should be relatively rare during adaptation, particularly when in close proximity to a fitness peak (Fisher 1930). In such cases, searching (e.g. via QTL mapping) for the genes of large phenotypic effect (GLPE) might not be very informative if evolution typically proceeds via many genes of small effect (Rockman 2012). Compounding this issue, GLPE might not explain variation in how organisms either respond to changing environments (i.e. response traits) or how they modify ecosystems (i.e. effect traits). In such cases, searching for genes

of large ecosystem effect (GLEE) might be both practically challenging, and unsatisfying if we have no theoretical expectation for the distribution of ecosystem effect sizes.

Population genomics - Population genomic approaches may be able to provide further insights into identifying functionally important genes. Yeaman et al (2016) made use of the convergent climate adaptation of two conifer taxa (lodgepole pine and interior spruce) to identify a small set of key genes important for climate adaptation. This is one example of how reverse genomic approaches can be utilised for ecologically important but long-lived organisms such as conifer trees and how cases of convergent or parallel adaptation can be utilised to strengthen statistical inferences about polygenic signatures of adaptation (Yeaman et al. 2016). Those approaches rely on substantial genomic resources, which are increasingly being established for more and more taxa. After the establishment of genomic resources for the Silver birch (*Betula pendula*), population scale resequencing revealed signatures of selective sweeps in some genomic regions, some of which could be associated with climate variables such as temperature and precipitation (Salojärvi et al. 2017). Population genomic approaches can also help reveal general patterns of adaptation, such as whether it is associated with regulatory or structural changes of proteins (Jones, Chan, et al. 2012). However, genome scans only provide us with a list of candidate genes and potential gene functions inferred via orthology of genes with functional annotations in model organisms. Those candidate gene lists may not provide fully satisfying answers, but can be a valuable resource to direct further research, either by pointing towards previously not considered genes and their associated phenotypic traits (e.g. metabolic or biochemical traits), or by directing a concerted effort to understand the functional relevance of some of the identified gene variants in an ecosystem context. The recent developments in crispr/cas9 technology and its ability to systematically analyze gene functions (Doudna & Charpentier 2014) could also help functionally test the ecosystem effects of individual genes or mutations.

In addition to the technical challenges of identifying the heritability of traits in natural populations and quantifying the genetic basis and architecture of these traits, there is the formidable challenge of understanding which processes are governing phenotypic change in natural ecosystems. Here we focus on challenges inherent to phenotypic plasticity, which can decouple genomic from phenotypic variation, and hybridization, which can decouple the current effect of a gene from its historical genomic background.

Phenotypic plasticity - A key challenge for studying evolution in a natural ecosystem context, is that adaptive alleles discovered in a highly controlled and isolated environment (i.e. the lab) might have limited significance in another environment (Barrett & Hoekstra 2011). Predicting phenotypic variation produced by the same genotype across a range of environmental conditions (i.e. phenotypic plasticity) is complicated by questions about whether genotype-specific levels of plasticity are an evolved response to past environmental variability, whether plastic responses in novel environments will be adaptive or non-adaptive (Ghalambor et al. 2007), and whether adaptive responses across environments will lead to different phenotypes or enable phenotypic similarity via metabolic buffering (Reusch 2014).

In the context of global change, plasticity in both the response and effect traits of key species will determine both their ability to withstand new stressors and their contribution to ecosystem function (Kanaga et al. 2009; Wang et al. 2010; Best et al. 2015). Currently, however, we have virtually no information about how the complex relationships between genomic variation, phenotypes, and ecosystems are affected by phenotypic plasticity (Crutsinger 2016). Whereas most research investigating the community consequences of phenotypic plasticity has focused on pairwise interactions, usually in the context of coevolution (Miner et al. 2005; Scheiner et al. 2015), or on competitors (Callaway et al. 2003; Berg & Ellers 2010), very few have investigated impacts on whole ecosystems (but see (Lundsgaard-Hansen et al. 2014; Johnson & Agrawal 2005). Making progress in this area will require studies that investigate the genomic determinants of both the mean and the

variance in important functional traits, and aim to link this to environment-dependent ecosystem outcomes.

Hybridization - Whereas studies of the genomic basis of phenotypic plasticity provide insight about the impacts of the same genome in novel environments, studies of hybrid phenotypes might be useful for unravelling the impacts of the same gene operating in a different genetic background. Genomic variation among individuals and populations in hybrid zones may be a particularly promising focus for studies aiming to link genetic variation at the scale of the genome with variation in ecological impact (Best et al. 2017). Hybridization in both plants and animals can recombine genetic variation much more quickly than the accumulation of mutations, exposing novel genotypes and phenotypes to selection within and between environments (Barton & Hewitt 1985; Abbott et al. 2013). So far, studies of genetic variation in hybrid zones have focused on identifying mechanisms of speciation or radiation (Seehausen 2004; Abbott et al. 2013). Artificial hybrid crosses have also long been used for mapping phenotypes and fitness under relatively controlled conditions (Barrett & Hoekstra 2011). However, hybrid zones may also be an especially useful tool for linking multivariate genomic variation to multivariate phenotypic variation and its effects on ecosystems. By recombining genome components that have evolved under very different selection pressures, hybridization decouples past evolution from current and future phenotypic change. Because of their separate evolutionary history, different sections of the genome (e.g., with different amounts of polymorphism and linkage) may interact with novel environments in different ways, impacting response to selection, hybrid viability (Lee et al. 2014), and ecological impact. Essentially, hybridization provides an opportunity to identify phenotypic variation arising from selection on standing variation evolved under very different conditions (Barrett & Schluter 2008; Jones, Grabherr, et al. 2012), but with multiple cases of this process recombined in the same genome. In addition, there is increasing recognition of the need to better understand evolutionary origins of trait correlations (Saltz et al. 2017), and to explicitly model those correlations as constraints on the flexibility of species distributions

under global change (Laughlin & Messier 2015). Hybrid zones provide a direct opportunity to test existing and changing correlations or interactions (e.g. epistasis) between multiple genes and multiple traits.

Studies of hybridization have documented critical links between genomic structure and phenotypic variation (e.g., complementary gene action of loci with dominance, (Stelkens & Seehausen 2009)). However, work in this field has also highlighted ongoing uncertainty about the way that morphological vs. immune traits in hybrids interact with abiotic stress or competition intensity to predict hybrid fitness (Domínguez & Albornoz 1987; Brock et al. 2015; Shcherbakov et al. 2013). Work that connects the novel genomic combinations generated by hybridization, the expression of novel phenotype combinations that allow hybrids to expand into new habitats and niches (Rieseberg et al. 2007; Lucek et al. 2010; Bailey et al. 2012; Lamichhaney et al. 2015), and their subsequent effects on those ecosystems has the potential to make large contributions to our understanding of genomic and phenotypic control on ecosystem processes at the landscape scale. This is especially important as many aspects of anthropogenic global change, including climate change, habitat modification, and species introductions continue to facilitate hybridization by inducing rapid range shifts and expansions (Brennan et al. 2015; Todesco et al. 2016).

Scaling from genomes to ecosystem-effect traits
Understanding the importance of genomic variation in our global ecosystem is a long-standing and difficult challenge, and is fundamentally an issue of resolving (reciprocal) interactions among the hierarchical levels of ecosystems. Decades before the genomics era, O'Neil et al. (1986) formulated a theory dubbed "A Hierarchical Concept of Ecosystems", which posited that ecosystems are best viewed as complex hierarchical systems with subsystems that interact to greater and lesser degrees (O'Neill 1986). In this context, does choosing genomics as our scale of analysis help us test hypotheses at the scale of ecosystems? O'Neil et al. (1986) argued that studying subsystems (e.g. genomics, nutrient

fluxes) in isolation neglects potential effects of processes that can influence subsystems from distant hierarchical levels.

One approach to this issue is to elucidate how processes influencing genomes can also change how organisms interact with and modify their environment (Figure 1). Nearly a century ago, Bass Becking pioneered a framework for thinking about how organisms can be reciprocally connected to elemental cycling in the environment (Becking 2015). He placed organisms at the center of a circle, which defined the environment that it directly interacts with (Figure 1: intrinsic environment), and drew arrows for different elements (or compounds) originating from outside the circle (i.e. extrinsic environment) toward the organism. This simple approach has been enormously useful for understanding how organisms interact with elemental cycling. For example, when applied to *Sphagnum* living in bog water, which was one of Bass Becking's primary research interests (Becking 2015), one can track how *Sphagnum* absorbs cations from the water and expels hydrogen ions, which lowers the pH of the water. One can also see how this process is partially mediated by both free-living and host-associated bacteria (e.g. Diazotrophs). In Figure 1, we have extended Bass Becking's idea about how organisms interact with their environment by including a hierarchical perspective, which has been a useful approach for thinking about interactions between ecological and evolutionary dynamics (Hendry 2017). Figure 1 emphasizes that interactions between organisms and their environment can depend on heritable phenotypes that can evolve rapidly, potentially involving feedbacks with ecosystem components. For example, key interactions with abiotic and biotic environments (double headed solid arrows to illustrate reciprocal interactions) can evolve in response to multiple environmental sources of natural selection, originating from both extrinsic or intrinsic environmental conditions. In addition, these environmental conditions can influence phenotype distributions of the population, partly through their effect on the expression of genes, both within and across generations.

Our approach can also be used to help target genomics research on key interactions between a particular organism and its environment, as we illustrate using *Sphagnum* as a model (Figure 2). In figure 1 (see legend), we identify seven research themes where genomics can be particularly useful to study linkages between genes, evolution, and ecosystems. While these are relevant for all organisms, we summarize four of them in the context of *Sphagnum* research. First, metagenomics of bacterial communities is a rapidly growing field that is transforming our understanding of a wide range of ecosystem processes (Treseder & Lennon 2015), and is yielding new insights about the functional diversity of free-living, host-associated, and endo-symbiotic bacteria (Yu. Rusin 2016). This is particularly the case for the interaction between diazotrophs (nitrogen fixing cyanobacteria) and *Sphagnum*, which can strongly influence carbon and nitrogen cycling in peatland ecosystems (Lindo et al. 2013). Second, some genes associated with glycolysis (e.g. GapC) in *Sphagnum* have interesting spatial patterns of polymorphism that might reflect adaptation to latitudinal environmental gradients (Szövényi et al. 2009). Given the importance of traits associated with N-use efficiency and symbiont recruitment for *Sphagnum*, it would be particularly interesting to extend this work to identify the genetic architecture and basis of these resource use related traits. Third, sequencing of the genome of *Sphagnum fallax* is currently underway (Shaw et al. 2016), and this holds great promise for linkages between genomic variation of a species that makes a substantial contribution to global carbon cycling. Fourth, as the genomic resources for *Sphagnum* improve, we anticipate that studies will be able to explore population genomics response to environmental change. More generally, as genomics becomes more accessible to studies of non-model organisms, such as S*phagnum*, there will be more opportunities to study the genomics of adaptation along naturally occurring environmental gradients (Westram et al. 2014).

Conclusion

Over the past few decades we have rapidly advanced our understanding of the genomics of adaptation and our ability to track the temporal and spatial variation of genotypes and allele

frequencies in natural populations. We can now study the dynamics of genomes in natural populations at timescales that are relevant for understanding ecosystem dynamics. It is conceivable that much of the resilience and stability of natural ecosystems in the face of environmental change results from rapid genomic changes that have been previously undetectable (Kinnison et al. 2015). While testing such ideas is challenging, we can begin by understanding the linkages between genes, traits, species interactions, and ecosystem processes (Figure 1). In sum, we are optimistic that rapid developments in the field of genomics will make an important contribution to our understanding of ecosystems in an era of unprecedented human influence on the Earth system.

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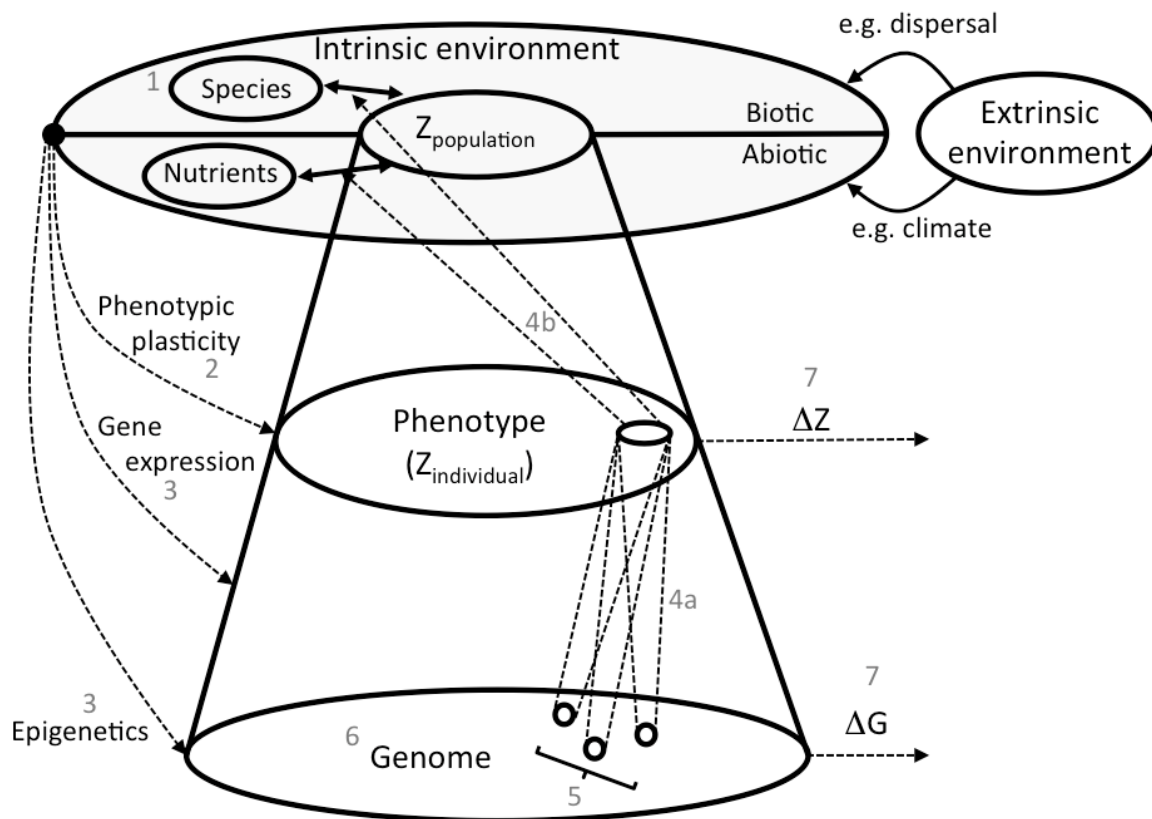
Figure 1: A conceptual model to help link genomics research with interactions between organisms and their environment, which is split into extrinsic and intrinsic components. The intrinsic environment is further divided into biotic and abiotic components, which consist of components that the organism (reciprocally) interacts with (e.g. nutrients or species). The phenotype (Z) of the target organism is determined by the collection of individual traits (smaller circle in the Phenotype ellipse), and the genes (small circles in the Genome ellipse) that make up the genome (G) of individuals. Seven processes are highlighted (dashed arrows with grey numbers) that are relevant for genomics research: (1) Identifying species, interactions, and functional diversity (e.g. microbiome). Studying the environmental dependence of (2) genotype to phenotype mapping and (3) expression and inheritance. Identifying genes of large phenotypic (4a) or ecosystem (4b) effect, and determining the genetic architecture of adaptive traits (5). Quantifying (6) standing levels of genomic variation in populations, and (7) evolutionary responses to environmental change.
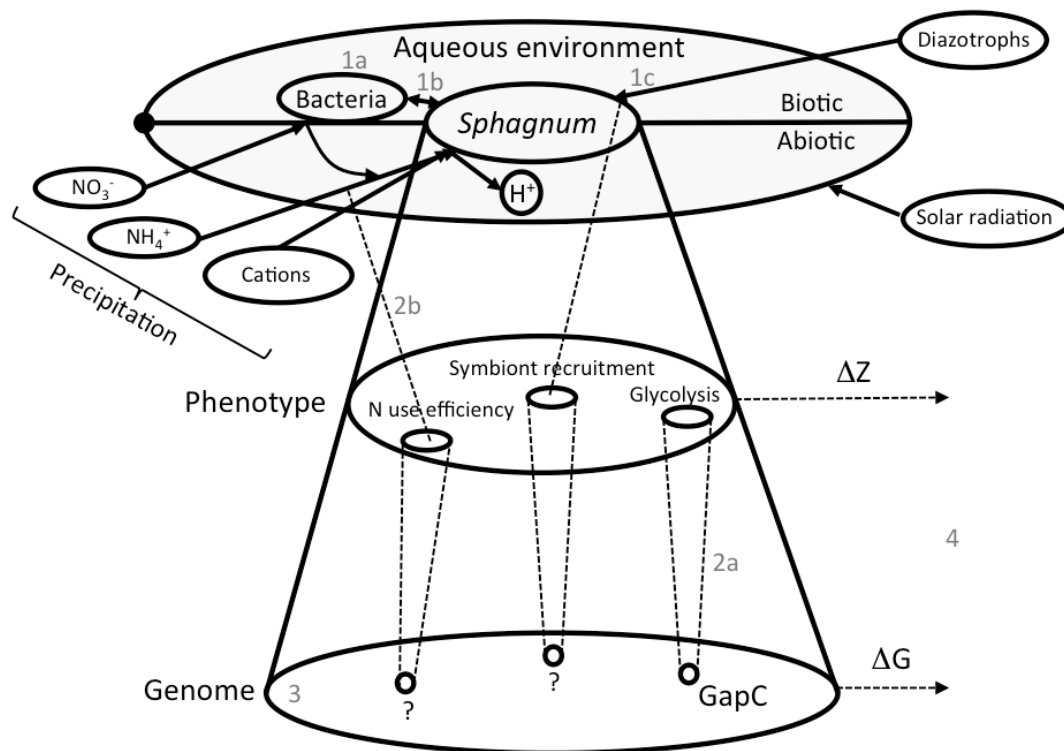
Figure 2: A conceptual model for identifying research priorities for the genomics of interactions between *Sphagnum* and its aqueous environment. The four key areas are: (1) Using metagenomics to identify free-living (1a), host-associated (1b), and symbiotic (1c) bacteria. (2) Identifying genes of large phenotypic (2a) or ecosystem (2b) effects. Sequencing the genome to facilitate population genomic studies (3) and the understanding of evolutionary responses to selection by biotic and abiotic environmental change (4).