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Community genomics: a community-wide perspective on within-species genetic diversity

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Biodiversity is a decisive factor in shaping the resilience of ecosystems and the services they can provide (Isbell et al., 2015; Buzhdygan et al., 2020). The main focus of biodiversity research and conservation effort has been on local and global species diversity referring to the number of species and their abundances. Yet, it is increasingly being recognized that diversity within species constitutes another important component of biodiversity with consequences for ecosystem functioning (Raffard et al., 2019; Stange et al., 2021). Intraspecific genetic variation provides the raw material for adaptive evolution equipping populations to track environmental change. Intraspecific genetic diversity is thus closely linked to species persistence and community-level species diversity. The awareness of such eco-evolutionary feedbacks has risen in recent years, but a mechanistic understanding of how species-diversity and within-species genetic diversity interact has yet to be achieved.

Community genetics is the field of research illuminating the interface between community ecology and population genetics. It explores the evolutionary processes shaping genetic variation within populations as a consequence of their interactions with other species in the community. A distinguishing feature setting community genetics apart from traditional population genetic studies is the focus on multiple species, rather than individual populations (Antonovics, 1992). The "reductionist approach" aims at a detailed understanding of coevolutionary dynamics and eco-evolutionary feedbacks of simple, often two species systems, with a focus on genetic variation in one of the partners. The "holistic" branch, on which we focus here, assumes a more comprehensive community perspective and is mainly concerned with understanding "species–genetic diversity correlations" (SGDC) in natural populations (Antonovics, 1992; Vellend et al., 2014). A few dozen primary studies and first reviews now show that "biodiversity begets biodiversity" across levels of integration. The SGDC are on average positive and moderately strong; that is, intraspecific genetic diversity tends to be elevated in species-rich communities (Vellend et al., 2014; Lamy et al., 2017). However, there are exceptions, and even some significantly negative SGDC have been reported, suggesting that these correlations are context-dependent (Vellend and Geber, 2005; Lamy et al., 2017). An important challenge for the future will be to gain a better mechanistic understanding of the ecological and evolutionary processes that contribute to SGDC.

There are three non-mutually exclusive hypotheses of how SGDC may arise in natural populations (Vellend and Geber, 2005). First, common site factors might influence both species diversity and genetic diversity (Figure 1). For example, community-level species diversity and intraspecific genetic diversity can both be impoverished in isolated and/or small habitat patches. Under such conditions, small viable population sizes and low colonization rates inherently contribute to high extinction risks, but also imply strong genetic drift decreasing intraspecific diversity. Second, intraspecific genetic diversity might affect species diversity

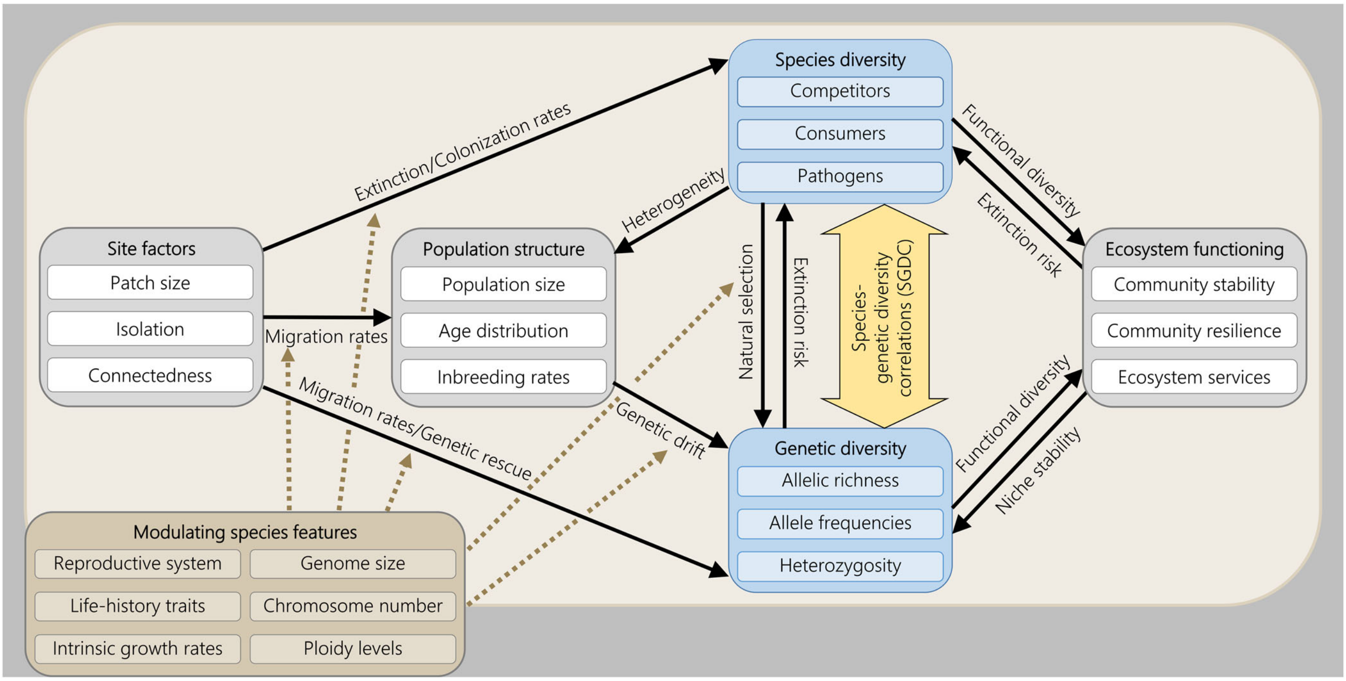

FIGURE 1 Schematic overview of causal interactions between site factors, species diversity, intraspecific genetic diversity, and ecosystem functioning. Solid arrows show possible causal relationships; dashed arrows show indirect effects with the potential to modify these relationships.

(Figure 1). If species within a community show low genetic diversity, they are more likely to face an increased risk of extinction. On the population level, low diversity can reduce adaptive potential reducing the probability of population persistence during periods of environmental change. On the level of the individual, consanguineous matings will reduce genetic variability and can accelerate declines due to inbreeding depression (Frankham, 2005). Inbreeding rates will thus affect species diversity and concomitant ecosystem functioning.

Third, species diversity might affect intraspecific diversity directly via so called community factors (Lamy et al., 2017). Different processes might act in different directions, and we currently neither know how relevant they are, nor how they interact (Vellend and Geber, 2005). Positive SGDC might arise when high species diversity leads to the development of a wide range of microniches due to variable interactions with competitors, facilitators, above- and belowground pathogens or herbivores (Scherber et al., 2010). Differences between microniches will impose heterogeneous selection pressures that, on average, will maintain greater intraspecific diversity in polycultures than in mono- and oligocultures with more homogenous selection. Negative SGDC might arise when species-rich communities cause niche separation leading to narrowing niche width within species and correspondingly reduce genetic variation in loci relevant to resource use. These two selective processes thus make opposite predictions. Both processes primarily concern non-neutral genetic variation, but neutral genetic variation within the genome will also be affected via linked selection.

Besides effects of selection, nonselective processes can also affect within-species diversity (Figure 1). Genetic variation is strongly affected by genetic drift, the magnitude of which is reflected by the effective size of a population (Charlesworth, 2009). The effective population size depends on census population size, but also on population structure, generation time, the frequency of consanguineous mating, and more generally on variance in reproductive success (Peart et al., 2020). Although population size of individual species will be reduced on average in plots of high species diversity (due to space constraints), effective population sizes might be unaffected or may even be increased. Any environmental factors that promote outbreeding, equalize reproductive success, increase turnover and/or promote metapopulation structure may elevate effective population sizes and thus facilitate the maintenance of intraspecific diversity.

Two methodological challenges have so far hindered a hypothesis-specific understanding of SGDC. First, there are few large-scale and long-term biodiversity research programs that allow an experimental separation of the role of selective and demographic effects of species diversity on intraspecific genetic diversity. Eco-evolutionary feedbacks require multiple generations to be detectable as changes in the allelic composition of populations. There is thus a need for long-term experimental manipulations of plant diversity within communities and/or genetic diversity within plant populations under natural conditions. Long-term field experiments such as the Cedar Creek experiment or the Jena Experiment (Tilman et al., 2014; Weisser et al., 2017) are particularly valuable in this respect. Complemented by surveys of within-species diversity, long-term experimental biodiversity experiments hold promise to isolate the mechanistic underpinnings of SGDC.

The second challenge has been the labor and costs associated with the quantification of genetic diversity within populations. Studies on SGDC have so far been largely limited in scope both in the number genetic markers and species within a community (Lamy et al., 2017). In the fledgling stage of community genetics, Antonovics (1992) identified the lack of suitable "DNAometers" as one of the major hurdles in the recognition of genetic variants. The challenge of estimating genetic diversity with high precision for genetic nonmodel organisms has been mitigated within the past decade by decreasing costs of high-throughput sequencing technologies (Ekblom and Galindo, 2011; da Fonseca et al., 2016). With the availability of genome-wide data, community genetics is transitioning to community genomics. Reduced-representation sequencing allows for rapid and cost-efficient quantification of genetic variation genome-wide in a large number of individuals in nonmodel species (Narum et al., 2013; Andrews et al., 2016). Long-read sequencing and improved scaffolding methods facilitate genome assemblies of nonmodel species and allow localizing genetic variation (Sedlazeck et al., 2018). Access to transcriptome data further provides the basis for functional annotation establishing the functional genomic context of genetic variation (Ekblom and Wolf, 2014). State-of-the-art sequencing technologies therefore open opportunities for separating effects of neutral genetic variation and genetic variation putatively shaped by selection, a major step in getting at the mechanistic basis of SGDC.

The field can capitalize on over a century of population genetic theory examining the eco-evolutionary processes shaping genetic variation among and along genomes. The merger of manipulative biodiversity experiments and population genomics holds great promise for understanding the relationship between species-, population- and individual-level biodiversity and to solve a number of key questions (see box below). To leverage this potential, it will be vital to appreciate insights of longstanding theoretical work from both community ecology and population genetics and address the knowledge gaps arising from their integration. By lifting the question of SGDC to a full representation of species in a community, we can address how species' features relating to their life-history traits (e.g., generation time, dispersal mode) and genomic constitution (e.g., genome size, ploidy level) influence the interaction between species and intraspecific diversity. This research is interdisciplinary at heart, involving community ecologists, theoreticians, geneticists, and population geneticists. If impediments resulting from deviant paradigms and terminology can be overcome, there is much progress to be made in this field, potentially also with relevant implications for the agricultural sciences, conservation and management practice.

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