NEWS AND VIEWS

OPINION

Phylogenetically-conserved candidate genes unify biodiversity–ecosystem function relationships and eco-evolutionary dynamics across biological scales

Simon Blanchet[1] ⓘ | **Laura Fargeot**[1] | **Allan Raffard**[2]

[1]Centre National de la Recherche Scientifique (CNRS), Station d'Écologie Théorique et Expérimentale du CNRS à Moulis, UAR2029, Moulis, France

[2]Univ. Savoie Mont Blanc, INRAE, CARRTEL, Thonon-les-Bains, France

Correspondence
Simon Blanchet, Station d'Ecologie Théorique et Expérimentale, 2 route du CNRS, 09200 Moulis, France.
Email: simon.blanchet@sete.cnrs.fr

Abstract

The intra- and interspecific facets of biodiversity have traditionally been analysed separately, limiting our understanding of how evolution has shaped biodiversity, how biodiversity (as a whole) alters ecological dynamics and hence eco-evolutionary feedbacks at the community scale. Here, we propose using candidate genes phylogenetically-conserved across species and sustaining functional traits as an inclusive biodiversity unit transcending the intra- and interspecific boundaries. This framework merges knowledge from functional genomics and functional ecology, and we first provide guidelines and a concrete example for identifying phylogenetically-conserved candidate genes (PCCGs) within communities and for measuring biodiversity from PCCGs. We then explain how biodiversity measured at PCCGs can be linked to ecosystem functions, which unifies recent observations that both intra- and interspecific biodiversity are important for ecosystem functions. We then highlight the eco-evolutionary processes shaping PCCG diversity patterns and argue that their respective role can be inferred from concepts derived from population genetics. Finally, we explain how PCCGs may shift the field of eco-evolutionary dynamics from a focal-species approach to a more realistic focal-community approach. This framework provides a novel perspective to investigate the global ecosystem consequences of diversity loss across biological scales, and how these ecological changes further alter biodiversity evolution.

KEYWORDS
biodiversity, ecology, ecosystem functioning, evolution, feedback, functional ecology, functional genomics, meta-communities, population genetics

1 | INTRODUCTION

Global change is modifying worldwide patterns of biodiversity (Newbold et al., 2015; Parmesan & Yohe, 2003). Biodiversity changes concern both species loss and the loss of the diversity within species, that is, intraspecific diversity. Genes and life-history strategies are being lost because fundamental processes impairing intraspecific diversity are altered (Hendry et al., 2008; Spielman et al., 2004). The loss of intraspecific diversity precedes (and speeds up) species loss (Spielman et al., 2004); biodiversity loss is hence an *inclusive* process occurring from genes to species (Bellard et al., 2012).

Nonetheless, in most studies, the intra- and interspecific facets of biodiversity are treated separately, whereas they form an evolutionary continuum. This limits the development of an integrative

eco-evolutionary framework linking biodiversity, the environment and ecosystem functioning (Matthews et al., 2011). This gap has historical causes: intraspecific diversity has mainly been studied by population geneticists, whereas interspecific diversity has mainly been studied by community ecologists (but see, Hubbell, 2001; Matthews et al., 2014; Vellend, 2005; Whitham et al., 2003, 2006). It also has an intrinsic cause: intra- and interspecific diversity are quantified using different units. Interspecific diversity is generally measured as the number of species, whereas intraspecific diversity is estimated through metrics of genetic (allelic richness, heterozygosity…) and phenotypic (trait variance, number of ecotypes…) diversity, impeding the *inclusive* measurement of biodiversity within communities.

Allowing for a common biodiversity measurement may change our perspective on the links between biodiversity and ecosystem functioning ('BEF'). Biodiversity sustains ecosystem functions such as primary productivity or recycling organic matter (Chapin et al., 2000; Hooper et al., 2005; Loreau et al., 2001). These links imply that increasing biodiversity promotes trait complementarity among individuals and/or may sustain highly competitive traits with dominant effects (see Box 1), both processes maximizing resource acquisition and energy conversion (Hooper et al., 2005). BEF relationships have been historically described at the *interspecific level*, and seminal experiments have demonstrated that higher plant species richness increases and stabilizes yields (Chapin et al., 1997; Tilman et al., 1996, 2006). Recently, similar observations have been reported at the *intraspecific level*; higher number of genotypes in populations increases biomass production (Crutsinger et al., 2006; Hughes & Stachowicz, 2004; Raffard et al., 2021; Reusch et al., 2005). Altogether, this suggests that both losing alleles within populations and species within communities alter ecosystem functioning. Yet, the dichotomy between intra- and interspecific diversity impedes a global assessment of the consequences of biodiversity loss on ecosystem functioning (but see, Prieto et al., 2015).

Developing a common biodiversity unit should also facilitate our understanding of how ecology affects the evolution of organisms and *vice versa*. Ecological effects generated by biodiversity described above can feedback to evolutionary processes when these ecological effects alter selective regimes and/or effective population sizes ('eco-evolutionary dynamics'; [Hendry, 2017; Schoener, 2011; Thompson, 1998]). Revealing eco-evolutionary dynamics requires tracking allele frequencies —within communities— of genes sustaining traits impacting —and reciprocally impacted by- ecological processes (Lowe et al., 2017; Skovmand et al., 2018). Although allele frequencies can 'easily' be tracked in a single focal species (Lowe et al., 2017; Rudman et al., 2018), this becomes more complicated when considering allele frequencies from genes of all species from a community (De Meester et al., 2019; Hendry, 2019). This dichotomic perception of intra- and interspecific diversity limits our capacity to predict eco-evolutionary dynamics beyond a (few) focal species, which hence minimizes the relevance of the eco-evolutionary framework for predicting the consequences of global change on biological dynamics.

Here, we propose that candidate genes that are phylogenetically-conserved across taxa and that sustain key functional traits may serve as a common biodiversity unit unifying the intra- and inter-specific diversity facets (Figure 1). Specifically, we first develop the rationales motivating our idea that 'phylogenetically-conserved candidate genes' (PCCGs) are ideal targets to unify biodiversity metrics across scales, and we present examples from functional biology having linked these genes to ecologically-important traits. We provide technical guidelines to sequence these genes and to estimate a common metric of biodiversity from PCCGs, which we illustrate with an example of freshwater Crustacean communities. We finally expand on the implications of measuring the diversity of PCCGs in communities, particularly for predicting the functioning and stability of ecosystems, for revealing the demographic and evolutionary processes shaping biodiversity patterns and for elucidating the feedback between ecological and evolutionary dynamics at the focal-community level (Figure 1).

2 | PHYLOGENETICALLY-CONSERVED CANDIDATE GENES AS A COMMON UNIT OF BIODIVERSITY

2.1 | Definition of phylogenetically-conserved candidate genes

Phylogenetically-conserved candidate genes are genes identified by functional geneticists as having major effects on traits, and whose sequences and functions are (at least partly) conserved across a broad range of species. This concerns genes coding for *ecologically-important* traits, for example, traits associated with resource acquisition or interactions with other organisms (Barbour et al., 2022; Skovmand et al., 2018; Wuest & Niklaus, 2018). Many PCCGs have been identified, but this knowledge has poorly percolated into ecological and evolutionary sciences (but see, Ducrest et al., 2008; Fitzpatrick et al., 2005).

Seminal works from the 90s have identified candidate genes sustaining traits that matter for fitness, and since then, the discovery of candidate genes has grown exponentially (Andersen & Lübberstedt, 2003; Anreiter & Sokolowski, 2019; Meinke et al., 2008; Schwander et al., 2014). In animals, some of these genes code for functional traits (e.g. foraging, metabolism, stoichiometry) that are strongly related to resource acquisition and/or biomass production (Brown et al., 2004; Wolf & Weissing, 2012). For instance, the *for* gene determines the foraging behaviour of *Drosophila melanogaster* (Anreiter & Sokolowski, 2019; de Belle et al., 1989; Sokolowski, 2001). This gene codes for a cGMP-dependent protein kinase (a signalling molecule) and encodes two behavioural strategies: the rover strategy (*Drosophila* larvae travels long distance to feed) and the sitter strategy (*Drosophila* larvae feeds in more restricted areas). This gene also impacts food intake (rover larvae have lower food intake) and preference (rover larvae absorb higher glucose quantities) of individuals (Anreiter & Sokolowski, 2019). We can expect that variation in

---

BOX 1 Biodiversity–ecosystem function relationships (BEFs) across biodiversity facets

Ecologists have long sought to understand how changes in community composition and species loss alter the fate of ecosystem functions. Theoretical works and large-scale experiments using plant communities have provided the foundation of BEFs. For instance, many studies have investigated the relationships between plant species richness and primary production, demonstrating a positive and saturating relationship between richness and primary production (Loreau, 1998; Tilman et al., 1996). The conclusions have then been extended to multiple ecosystem types (e.g. aquatic ecosystems), functional groups (e.g. consumers species) and ecosystem functions (e.g. secondary production, carbon storage or nutrient recycling; Balvanera et al., 2006; Cardinale et al., 2012; Hooper et al., 2005).

Biodiversity–ecosystem relationships are explained by several nonexclusive mechanisms, including complementarity, facilitation and sampling (or selection) effects. Complementarity among species allows species to use different resources, eventually releasing competitive interactions; facilitation occurs when species provide resources or modify habitat that benefits the others in the community; sampling effects (aka selection or dominance effects) leads to a positive effect of biodiversity on ecosystem functions because in diverse communities the probability to include a highly productive (competitive) species is higher. Interestingly, these mechanisms often led ecosystem functions to increase at low biodiversity level and then reach a plateau at higher biodiversity levels according to a saturating relationship. The probability to include species with similar functional roles is indeed higher when biodiversity is high, increasing functional redundancy among species. Contrastingly, in some cases, negative (or neutral) BEF relationships can arise (see Hagan et al., 2021 for further discussions). These particular examples suggest that in some communities, increasing diversity might actually induce negative competitive interactions among species. Finally, biodiversity has also been shown to stabilize ecosystem functions (over space and time) by buffering ecosystem variation against environmental fluctuation (the insurance hypothesis, Yachi & Loreau, 1999). Richer communities displayed higher resilience after a perturbation than poorer communities, because of the presence of species with high recovery rates.

While BEF relationships have primarily been investigated at the interspecific level, diversity within species also determines ecosystem functions. Similar mechanisms are at play—such as complementarity, redundancy and sampling effects—acting here not among species but among individuals within species. Importantly, the effects of intraspecific diversity on ecosystem functioning can be as strong as those of species diversity (Raffard et al., 2019). Therefore, recent studies plead for the existence of *intraspecific*-BEFs. This corroborates some mechanistic models that did not initially distinguish between intra- and interspecific diversity in their formulation and demonstrates that biodiversity loss *per se* alters ecosystem functions (Loreau, 1998; Norberg et al., 2001). These processes (complementarity, redundancy, sampling effect) can actually be transferred to gene functions and hence directly applied to a BEF framework in which genes phylogenetically-conserved (i.e. that can be sequenced across species from a community) and coding for important ecological traits would be the core unit of an inclusive measure of biodiversity (i.e. including both intra- and interspecific levels).

---

the expression of this gene will have consequences on trophic chains and ecosystem functioning. For plants, MADS-box genes described in *Antirrhinum majus* (Schwarz-Sommer et al., 1990) are a gene family involved in plant architecture, and fruit, seed and root development (Schilling et al., 2018). MADS-box genes are targets to improve crops' yields and are altering the short-term adaptation of plants to environmental changes (Cho et al., 2017; Theißen et al., 2018). For instance, the Flowering Loci C and T regulate flowering time in many plant species, an important trait for individual fitness and pollination (Schmidt et al., 2016).

This type of candidate genes is reinforcing the idea of 'Ecology Important Genes' (EIG; Skovmand et al., 2018), defined as genes contributing strongly to phenotypes having a large effect on communities and ecosystems. Nonetheless, we stress that our approach –contrary to Skovmand et al. (2018)– considers the impacts of a *large* number of candidate genes (a hundred or more) with differential individual contributions to traits and ecological dynamics. Our

approach acknowledges the idea that phenotypes are likely polygenic and arising from the effect of many genes (with potential epistatic interactions) with small effect sizes (Falconer, 1981). Focusing on a large number of candidate genes should also lead to identify *complementarity* and *redundancy* (i.e. in terms of trait functions, see Box 1) among genes or locus within a community, which are two important concepts for predicting the impacts of biodiversity on ecological processes (Loreau, 1998).

An important aspect is that we focus on candidate genes that are *phylogenetically-conserved* that can be sequenced across a large range of species within communities. Most candidate genes identified in model species are actually (partly) phylogenetically-conserved. For instance, the *for* gene can be retrieved from a large number of Invertebrate species (Anreiter & Sokolowski, 2019; Sokolowski, 2001). An ortholog gene—i.e. a gene whose sequence has diverged from a shared genetic ancestor—identified in vertebrates (*PRKG1*) was found associated with foraging-like behaviour (Anreiter & Sokolowski, 2019;
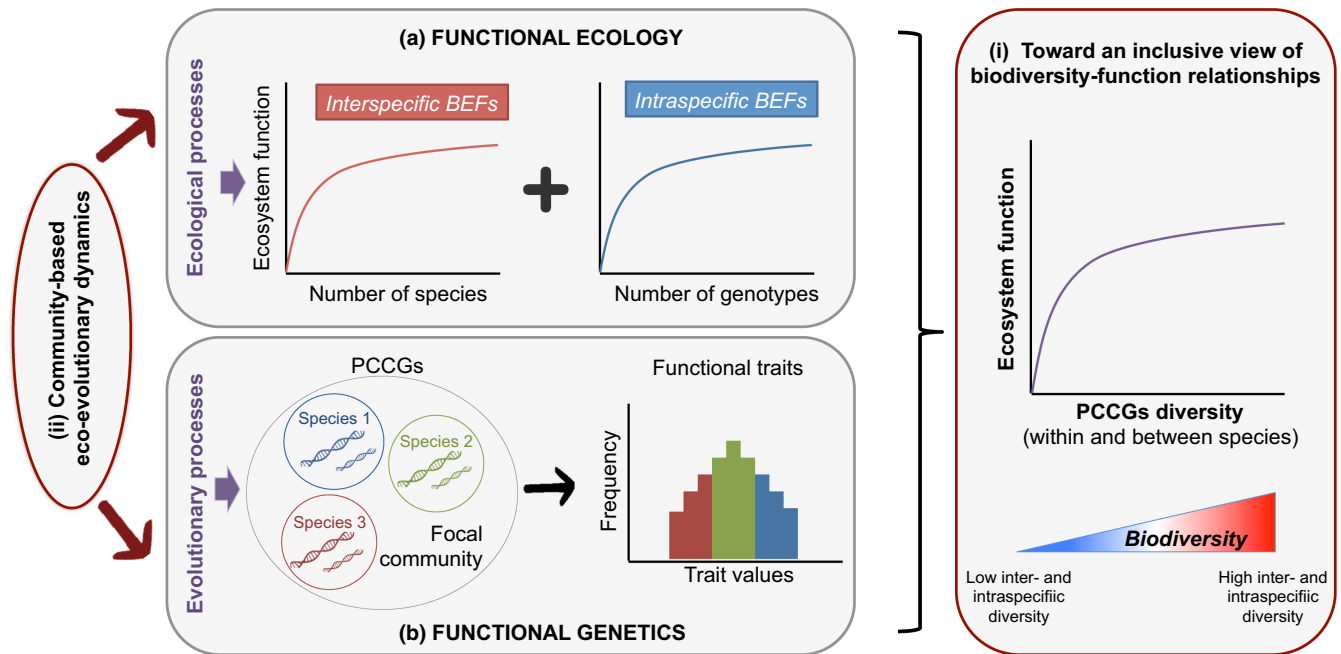
FIGURE 1 Conceptual diagram showing how a common quantification of biodiversity from phylogenetically-conserved candidate genes (PCCGs) allows to move to an integrative view of biodiversity–function (BEF) relationships (i) and to embrace a community-based perspective of eco-evolutionary dynamics (ii). Our concept is based on the idea to merge the fields of functional ecology (a) and functional biology and genetics (b) to simultaneously quantify the intra- and interspecific diversity components of focal communities through PCCGs diversity. PCCGs should be selected so as to be variables both intra- and interspecifically and to sustain ecologically-important traits.

Struk et al., 2019). Similarly, the MADS-box gene complex has been identified in mosses, gymnosperms and angiosperms (Gramzow & Theißen, 2013; Schilling et al., 2018). Conservatism of candidate genes should actually be the norm rather than the exception given their importance for biological functions (Barson et al., 2015; James et al., 2017; Marden et al., 2013; McGirr & Martin, 2017).

Using PCCGs as targets for measuring biodiversity inclusively is attractive because the dynamics of PCCGs is shaped by micro- and macro-evolutionary processes, and because PCCGs likely code for important ecological traits linked to ecological processes. PCCGs are therefore at the interface between ecological and evolutionary dynamics, which makes them good candidates to reveal mechanisms linking the environment, biodiversity and ecosystem functioning.

2.2 | Quantifying biodiversity from phylogenetically-conserved candidate genes

We hereafter describe the main steps to reveal PCCGs from focal communities (Figure 2); (i) defining and sampling the focal community, (ii) identifying PCCGs from the literature (and databases), (iii) sequencing PCCGs across species and (iv) quantifying PCCGs diversity.

2.2.1 | Defining and sampling the focal community

The PCCGs approach can be applied to all living entities (prokaryotes and eukaryotes), if (i) candidate genes have been identified in the

target taxonomic group, and (ii) they are conserved phylogenetically among species within this group. Nonetheless, phylogenetic conservatism is restrained, so that the PCCGs approach cannot be used for communities that contain highly divergent species (i.e. >20% molecular divergence, Faircloth, 2017, but see hereafter). Therefore, the focal community from which PCCGs diversity is measured must follow an 'ecological logic'. A focal community should be a 'group of trophically similar, sympatric species that actually or potentially compete in a local area for similar resources' (Hubbell, 2001). Examples of focal communities satisfying this definition nonexhaustively includes insectivorous fish, insect pollinators, desert plants, tropical trees, detritivorous insects, etc. A prerequisite for the PCCGs approach is to sample both the intra- and interspecific diversity components of the focal community. This can be done by sampling several individuals for all known species from the focal communities. An alternative approach consists of sampling as many specimens as possible to provide a representative view of the diversity of the focal community. This later approach (i) best represents the actual diversity (rare species are less represented in the final pool) and (ii) is technically feasible, as detailed later, if the DNA of specimens can be pooled across species (see below for further details on the sampling strategy).

2.2.2 | Identifying and selecting PCCGs from relevant traits

We detailed hereafter the main steps to select appropriate PCCGs, which we illustrate with a real case study (Figure 3), implying a focal
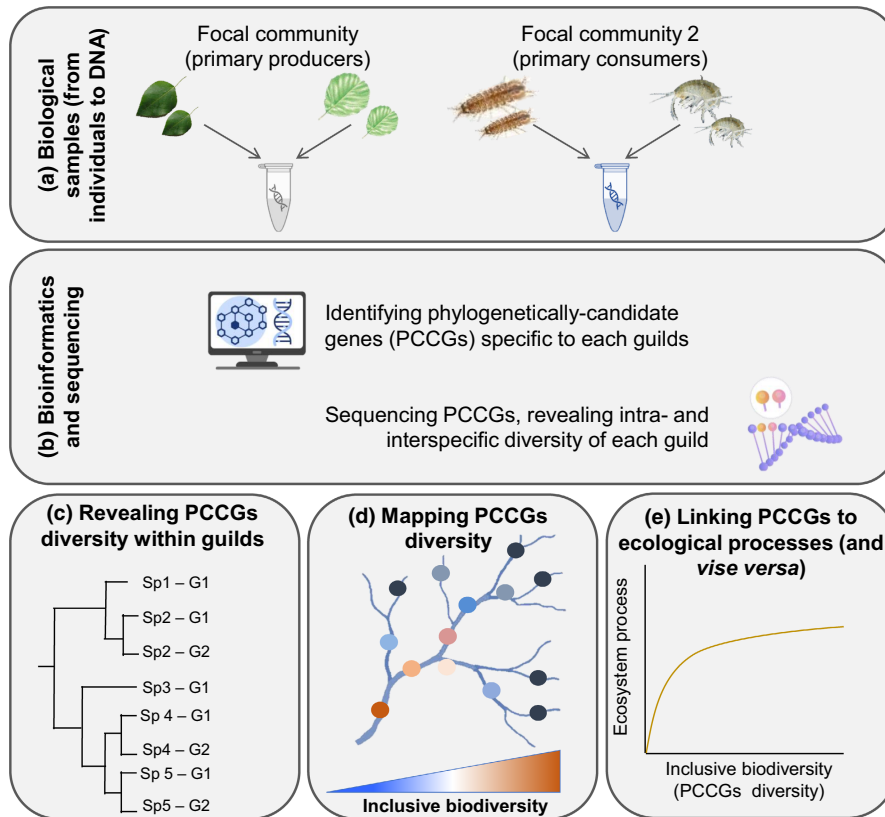
FIGURE 2 General framework describing the main steps to reveal phylogenetically-conserved candidate genes (PCCGs) diversity within focal communities. (a) This starts by defining appropriate focal communities (two examples here within a river ecosystem; leaves from riparian trees and crustaceans decomposing these leaves) and sampling the biological diversity of the focal communities, both within and between species (here two species per community and two genotypes, large and small, per species). The total DNA of this focal community is extracted so as to represent both intra- and interspecific diversity. (b) PCCGs are identified bioinformatically from existing literature (on functional genes) and available genomic resources. The selected genes (a hundred to a thousand of sequences) are sequenced for each focal community separately. (c–e) Once the raw sequence data are obtained, inclusive biodiversity can be quantified from PCCGs for each focal community, it can be analysed spatially and/or temporally to search for underlying eco-evo processes, and it can be linked (either experimentally or empirically) to ecological processes so as to reveal feedbacks between ecological and evolutionary dynamics occurring at the community level.

community of freshwater crustaceans (10 species from 4 Genera and 2 Orders, see Figure 4) involved in leaf litter decomposition and for which we uncovered 529 exons from 120 PCCGs (~338,000bp; Figure 2b).

A prerequisite of our approach is that PCCGs must be polymorphic both among and within species from the focal community. This condition is complicated to meet for all PCCGs from a panel (assuming 100–1000 genes), since genes that are highly polymorphic intraspecifically are generally not conserved among many species and *vice versa*. For instance, developmental genes are extremely conserved interspecifically but should be less variable intraspecifically (Cardoso-Moreira et al., 2019). A compromise must therefore be reached, and a solution is to mix genes with various levels of conservatism in the PCCGs panel. This implies that some PCCGs from the panel will not necessarily be sequenced in all species from the focal community (i.e. genes that are expected to be intraspecifically variable), and/or that some PCCGs will not display intraspecific polymorphism in some species from the focal community (i.e. genes that are expected to be highly conserved).

Then, PCCGs must be chosen according to relevant functional traits that will depend upon the targeted ecological process(es). For instance, for leaf litter decomposition in freshwaters, relevant traits of crustaceans are locomotion activity, metabolism, body size, aggregation behaviour and food assimilation (Rota et al., 2018; Figure 3a). As the PCCGs approach assumes that the expression of trait is polygenic and that this list of traits will be the basis to search candidate genes in the literature, we must consider a large set of potential traits, rather than a restricted set. Noteworthily, pleiotropic genes (i.e. affecting multiple traits) are excellent putative PCCGs as they are particularly relevant for linking traits to ecological dynamics (Ducrest et al., 2008; Watanabe et al., 2019). Similarly, neutral genes (or sequences) randomly taken from the genome (or known to be neutral) can be added to the PCCGs panel to test for instance the role of selection *versus* drift.

Potential PCCGs are then identified from the literature establishing a link between a gene and its phenotypic function (Figure 3b). Most of these studies are focusing on models (e.g. *Arabidopsis thaliana, Zea mays, Mus musculus, Drosophila melanogaster, Danio rerio*...)
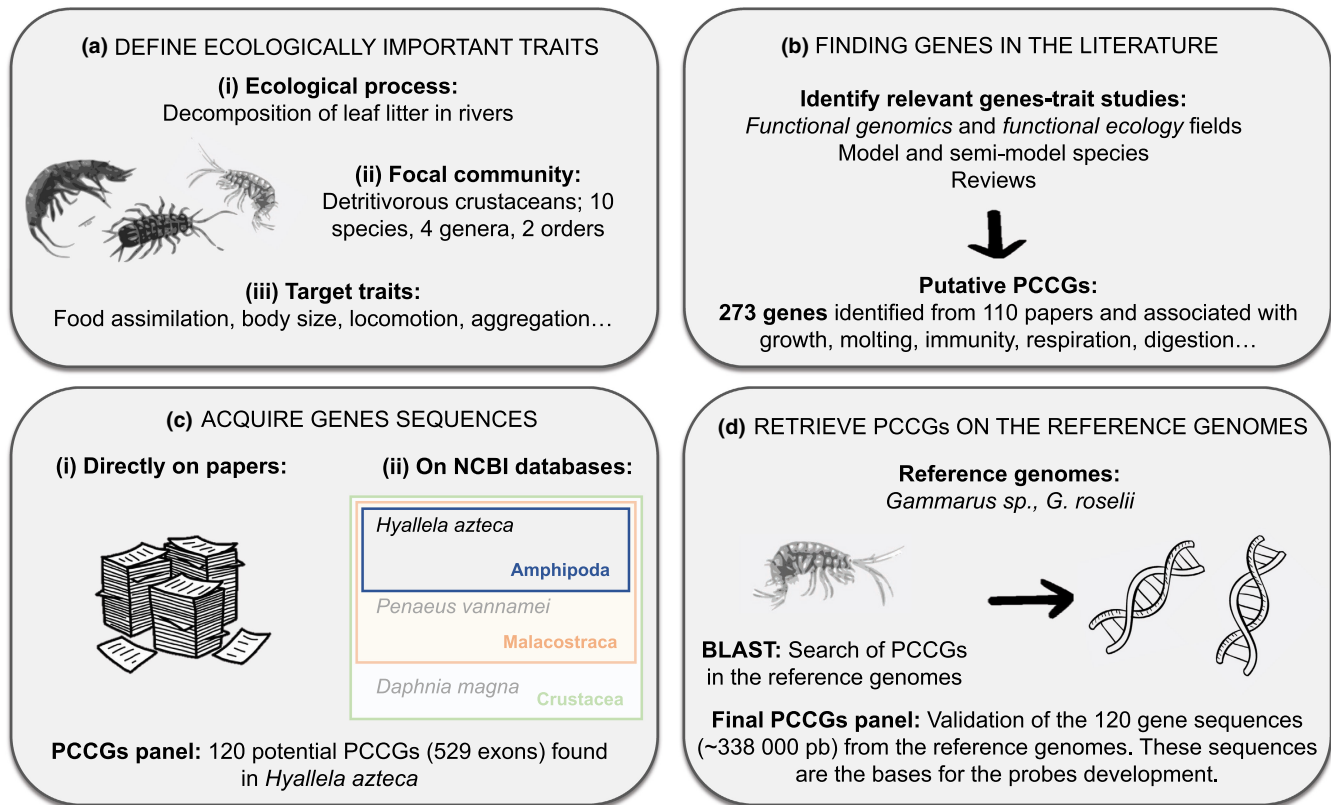
FIGURE 3 Diagram illustrating the four main steps to select phylogenetically-conserved candidate genes (PCCGs) from a focal community. The diagram builds on a concrete example involving the search of PCCGs for a community of detritivorous freshwater Crustaceans (10 species, 4 Genera, 2 Orders). (a) A first step consists in defining the ecological process and the focal community to target, as well as the traits associated with the ecological process and focal community. (b) A second step aims at finding the appropriate genes associated with the selected traits from the available literature. (c) In a third step, the sequences associated with these genes are acquired directly from articles or from the National Center for Biotechnology Information (NCBI) database. Here, the gene sequences were identified from NCBI by focusing on annotated genomes of Amphipoda (*Hyalella azteca*), the closest annotated genome to the focal community. (d) A final step uses a local base alignment search tool (BLAST) to retrieve the PCCG sequences on the reference genome of some focal species of the focal community. For Crustaceans, we used a published reference genome (*Gammarus roselii*) and a reference genome that we assembled (*Gammarus* sp., see Figure 4). As genes cannot be targeted over their entire sequences, exons and/or promoter regions are generally selected for the final panel of PCCGs. This final PCCGs panel will serve as the basis for the design of the probes and for the hybridization-based capture sequencing. DNA strand vector comes from www.svgrepo.com.

and 'semimodel' species (*Macrobrachium rosenbergii*, *Populus nigra*, *Cyprinus carpio*…). Although natural communities often lack one of these species, our favourite biological models generally have phylogenetic cousins from one of these species, making them relevant to identify putative PCCGs. It is noteworthy that because the genetic architecture of ecologically-important traits likely varies among species, it is important to be taxonomically exhaustive in the search and selection of potential PCCGs, so as to take into account (and potentially reveal) these different genetic architectures. For the focal community of freshwater crustaceans, we screened ~110 papers that focused on gammarids, amphipods and crustaceans in general from which we preselected 273 genes coding for traits associated with (among others) fatty acid digestion, respiration, circadian rhythm, growth, locomotion activity, moulting, etc. (Figure 3b).

Once identified, the sequences of putative PCCGs are retrieved from databases such as NCBI (Figure 3c). An annotated genome from a phylogenetically close species must be available to efficiently retrieve the sequences of PCCGs. Our Crustacean genes have been found in various crustaceans' species (*Hyalella azteca*, *Penaeus vannamei*, *Daphnia magna*, etc.), but we kept sequences that were most likely to be retrieved in our target community and we discarded more distant matches. Consequently, we mainly relied on *Hyalella azteca* (the most closely related annotated genome from our focal community) and on gammarids, from which we retrieved the sequences of 120 out of the 273 preselected genes (we kept the most commonly reported genes in the literature). Genes are often constituted of several exons that can all be potentially informative and gene promoters are also essential, and we therefore recommend retrieving all exons from the genes and conserving ~100–200 bp of the flanking regions of each exon to possibly simultaneously retrieve the promoters.

The final step (Figure 3d) is to obtain the homologous sequences of these PCCGs on species that are phylogenetically close to the focal community or that belong to the focal community but for which an annotated genome is not available. For Crustaceans, we
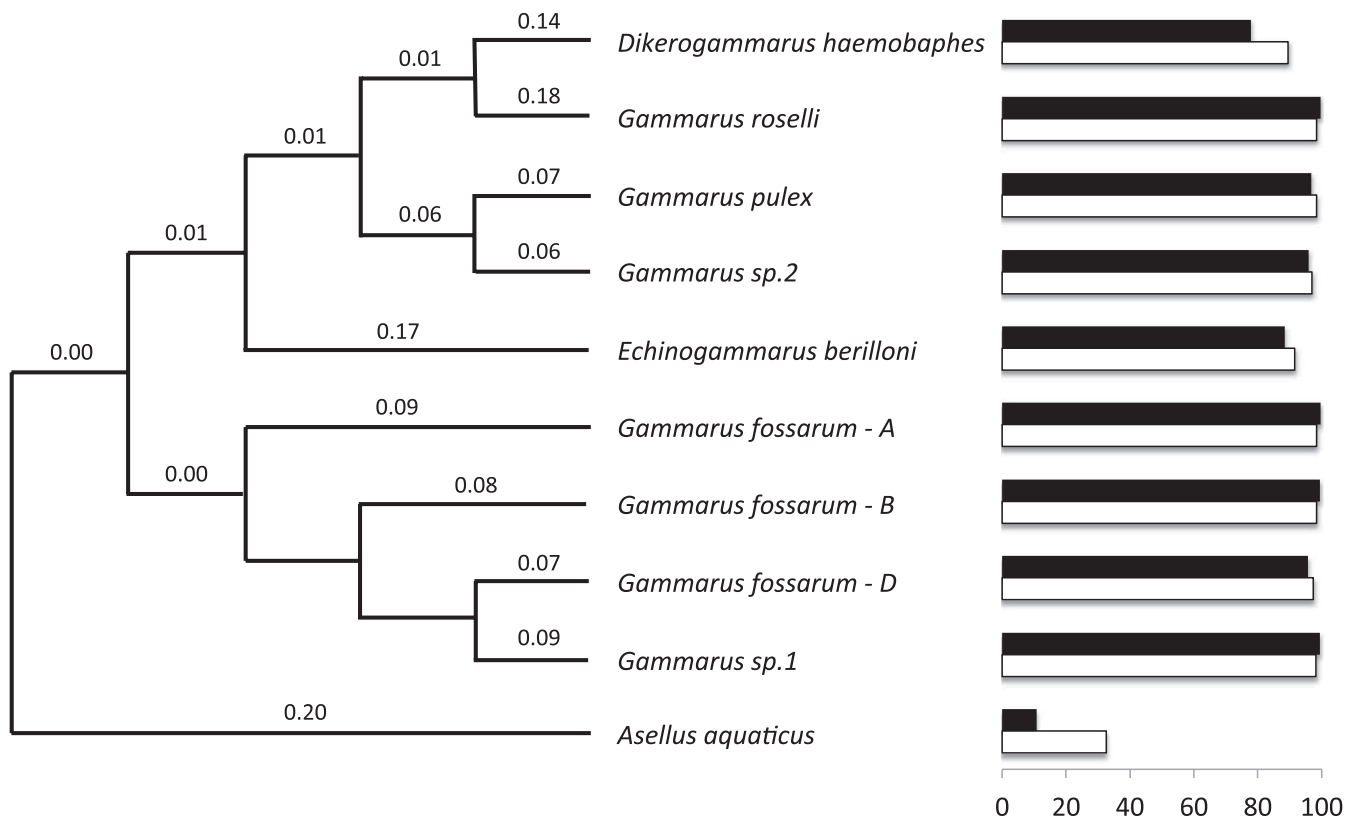
FIGURE 4 The left panel depicts the phylogenetic relationships among the 10 Crustacean species from the focal community using COI mitochondrial sequences gathered from GeneBank. Evolutionary distances were computed using the Tajima-Nei method; the overall mean distance among pairs of species was 0.29 ± 0.02 and varied from 0.13 to 0.42, which is within the range observed in this group (Hou et al., 2007) *Gammarus fossarum* A, B and D represents potentially cryptic species (Wattier et al., 2020), whereas *Gammarus* spp. *1 & 2* are two new species from Southern France being described. The right panel depicts the percentage of genes (white bars) and exons (black bars) retrieved out of the 120 genes and 529 exons of the PCCGs panel.

used the published reference genome from *Gammarus rosaeli* and the partial genome that we assembled for another *Gammarus* species (not named yet; Figures 3d and 4). This step consists in blasting the sequences found on model species to search for their homology in the reference genome(s), which improves the design of capture probes (see hereafter and Faircloth, 2017 for further details). In Crustaceans, we generate homologous sequences for the 120 genes, which corresponds to 529 exons for a total of ~338,000 bp.

2.2.3 | Sequencing hundreds of PCCGs across species

Phylogenetically-conserved candidate genes sequencing benefits from the recent development of target enrichment methods (capture of specific regions of the genome, Jiménez-Mena et al., 2022; Jones & Good, 2016; Mertes et al., 2011) such as the hybridization-based capture sequencing (HBCS; Hawkins et al., 2016). In HBCS, we design oligonucleotides (called 'probes' or 'baits') that are complementary to the target (PCCG) sequences. These oligos capture and enrich complementary target sequences from a next-generation sequencing (NGS) library. This method has been used in many taxa

(Albert et al., 2007; Mamanova et al., 2010); its use and potential for evolution are well described (Faircloth, 2017; Jiménez-Mena et al., 2022). HBCS allows for mismatches between probes and the target sequences, allowing 15%–20% of divergence (Faircloth, 2017); this threshold should (ideally) be used to define the appropriate focal species. In crustaceans, we successfully sequenced 89.92% of the PCCGs on average across the 10 species (Figure 4). The success rate was always higher than 89%, but for one species (*Aselus aquaticus*, 32.54%) that was the most phylogenetically distant species (~42% molecular divergence, Figure 4). In this case (highly divergent species), it is possible to develop several probe sets according to 'phylogenetic clusters' and/or to fine-tune the library preparation to allow for a relaxed capture ability (Faircloth, 2017).

The sampling of focal communities in the wild can be performed according to two approaches. The first approach consists in sampling all known species from the focal communities and, for each of them, sampling several individuals (5–30 individuals per species depending on their rarity) to reveal intraspecific diversity. This approach is appropriate when the focal community is already well-described taxonomically. The second approach consists of sampling as many specimens as possible in the focal community to provide a holistic and representative view of the diversity of the focal

community. This approach does not require *a priori* knowledge on the focal community, and it best represents the actual diversity (rare species may be less represented in the final pool, but they are also inherently less represented in the actual community). Then, HBCS can be performed either (i) at the individual level: all individuals from all species are sequenced or (ii) at the focal community level: the DNA of all individuals from all species are pooled (from 50 to 100 individuals per pool, Schlötterer et al., 2014) and this DNA pool is sequenced. Individual-based sequencing is more costly but can be used to relate specific gene polymorphism to individual traits or ecological processes for instance. In contrast, pool-seq approaches are extremely affordable (Schlötterer et al., 2014). An intermediate approach consists in pooling individuals per species, which allows conserving both the intra- and interspecific information. Pool-seq approaches allow estimating allele frequencies for each marker (Gautier et al., 2022; Sham et al., 2002) and hence estimating inclusive biodiversity from PCCGs.

2.2.4 | Defining metrics for estimating PCCGs diversity of focal communities

All metrics used by population geneticists and community phylogeneticists are valid to describe PCCG biodiversity patterns. Biodiversity metrics should follow the diversity partitioning proposed by community ecologists in the 1960s (Whittaker, 1960): α and γ components as the local and regional diversity components, and the ß component quantifies the differentiation among local sites. Population geneticists (and ecologists) acknowledged that (i) the metrics traditionally used to describe genetic diversity patterns in populations (such as the allelic richness or Fst) actually conform to Whittaker's framework, (ii) that tight (statistical) connections exist between the 'population' and 'community' approaches and (iii) that developing a unified framework to analyse diversity patterns across populations and communities would be beneficial (Gaggiotti et al., 2018; Jost, 2008; Vellend, 2005). Many papers discussed the metrics that can be used to unify disciplines (Gaggiotti et al., 2018), and the choice of a metric should be dictated by scientific objectives (Mouquet et al., 2012; Tucker et al., 2017). For instance, the Fst measures drift (Holsinger & Weir, 2009), whereas dissimilarity metrics inform about the relative role of nestedness and turnover for explaining ß-diversity patterns (Baselga, 2010). Nonetheless, the choice of metrics derived from PCCGs must take into account that intra- and interspecific diversity are shaped by similar processes (drift, selection, mutation/speciation, dispersal) acting over a continuum from ecological to evolutionary scales (Hubbell, 2001; Vellend & Geber, 2005). The description of biodiversity using PCCGS inherently helps following this principle.

For individual-based sequencing, SNP loci (including both intra- and interspecific SNPs) and haplotypes that group all loci from a given gene can be derived. In the Crustacean focal community, we detected 51,012 SNPs at the interspecific level (nucleotidic variation observed among species) and on average 2480 SNPs per species

(range, 141–4307) at the intraspecific level (nucleotidic variation observed within species). Many types of metrics can be derived from SNPs; the number of polymorphic SNPs can be compared among communities, and the evenness can be derived from allele frequencies, as well as the dissimilarity among local communities (Gaggiotti et al., 2018). Haplotypes can be used to build phylogenetic trees (including both intraspecific and interspecific tips) from which all phylogenetic metrics of community can be derived (Tucker et al., 2017). For the pool-seq approach, SNPs can be retrieved together with their relative frequency within the community; alleles cannot be attributed to a particular species (except when pools are built at the species level) or a particular individual within a species, which impedes the reconstruction of haplotypes. For this approach, metrics derived from SNP data (including information on allele frequencies) are therefore favoured (Schlötterer et al., 2014). As a proof of example, we built artificial communities of freshwater Crustaceans by mixing the DNA of various species (1, 3 or 5 species per pool) and several individuals per species (15, 5 or 3 individuals per species); we found that the Shannon diversity index estimated from SNP frequencies was in average $S=14{,}723$, $S=16{,}840$ and $S=17{,}964$ for pools with 1, 3 and 5 species, respectively.

3 | IMPLICATIONS FOR BEFS: BEFS ACROSS BIODIVERSITY AND SPATIAL SCALES

Biodiversity and ecosystem functioning relationships have historically used species richness to quantify the diversity of communities (Hooper et al., 2005). Alternative approaches have emerged and improved our understanding of BEFs; in particular, phylogenetic diversity and/or functional traits diversity have recently been used as measures of community diversity (Cadotte et al., 2012; Le Bagousse-Pinguet et al., 2019). Functional (trait) diversity has revealed the causal mechanisms underlying BEFs (Cadotte et al., 2011; Norberg et al., 2001). The use of phylogenetic diversity (based on one or a few supposedly neutral genes) has permitted capturing macro-evolutionary processes shaping community assemblages and therefore the evolution of niche complementarity among species (Cadotte et al., 2012; Mouquet et al., 2012). The use of PCCGs has the potential to encompass most aspects of the phylogenetic and functional approaches because PCCGs are related to functional traits and directly influenced by evolutionary processes. In addition, and contrary to the classic phylogenetic approach, the PCCGs considered the possibility of interactions (e.g. epistatic interactions) both among and within species as drivers of ecological dynamics. By aggregating both the functional and evolutionary components of diversity, PCCGs may reveal novel causal processes and may improve the general fit of BEF relationships.

Most studies having used functional and phylogenetic diversity failed to integrate the intraspecific component of diversity (Mouquet et al., 2012). The PCCGs approach intrinsically includes both the intra- and interspecific facets of biodiversity, which is

important given that intraspecific diversity can affect ecosystem functions as much as interspecific diversity (Raffard et al., 2019, Box 1). The few experimental works having simultaneously manipulated the two facets of diversity demonstrated that the relative effect of intra- *versus* interspecific diversity was dependent upon the considered function (Fridley & Grime, 2010; Hargrave et al., 2011). For instance, intraspecific diversity improved the temporal stability of biomass production in plant populations, whereas species richness improved the mean biomass production of the same community (Prieto et al., 2015). This suggests a complementarity between intra- and interspecific diversity that cannot be revealed if only one of them is considered. While valuable, these studies are still rare and do not reflect the observation that genetic diversity within a species can vary according to the number of species in the community. The PCCGs approach opens novel perspectives to grasp the relative contribution of intra- and interspecific diversity for ecosystem functioning. For instance, the PCCGs approach would permit testing whether the effects of intra- and interspecific diversity facets on ecosystem functions are additive or not and if the potential additivity of their effects is context-dependent. This would also allow testing the hypothesis that intraspecific diversity may 'compensate' for the loss of interspecific diversity under some circumstances.

In addition, more specific questions might be addressed using the PCCGs approach. For instance, ecosystem functions generally display high variability among monocultures, which has often been explained by the intrinsic efficiency of a species to perform a function (Huston, 1997). The performance of a species in monoculture is likely determined—among others—by its intraspecific diversity that can be revealed using PCCGs (Figure 5b). Species with higher performance should be more diversified, as expected if genetic complementarity is linked to species performance (Hughes et al., 2008). Alternatively, highly performing species might arise because of the selection of certain genotypes (or variants) that increase the performance of these species (selection effect, Box 1, see also, Wuest & Niklaus, 2018). Both alternatives can be tested using the PCCGs approach by using appropriate statistical methods (e.g. GWAs, GEAs). As a consequence of these differences in monocultures' productions, species-rich communities might show high performances because of the presence of the most performant species (sampling effect, see Box 1). Although this sampling effect has long been debated (Loreau, 1998), assessing BEF relationships using PCCGs diversity might reveal underlying mechanisms. For instance, understanding whether communities containing a high-performance species increase the rate of the target function because they contain the species per se (i.e. because this species contains a specific genomic variant that increases performance, Barbour et al., 2022; Wuest & Niklaus, 2018) or because this species increases substantially PCCGs diversity (Figure 5c). By accounting for intra- and interspecific diversity, PCCGs quantify the 'true' diversity present in the community and allow forecasting ecosystem functions based on biodiversity with finer precision.
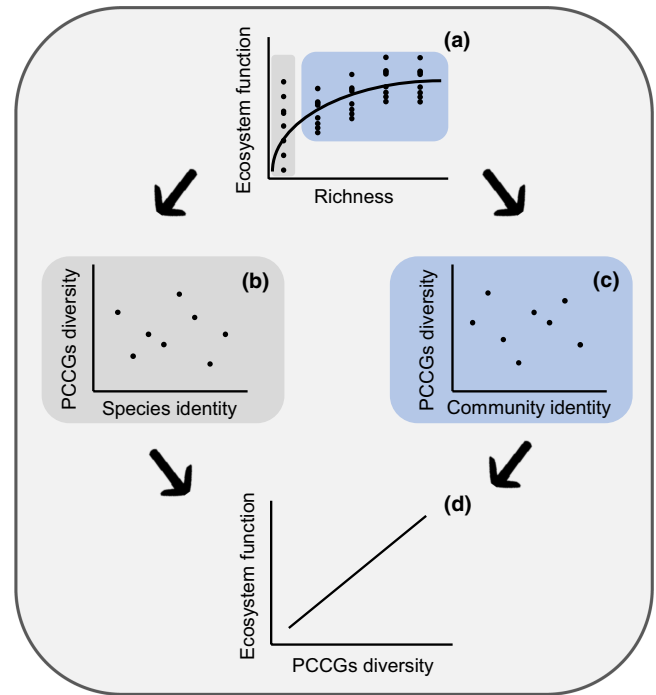

FIGURE 5 The relationships between biodiversity (measured as the number of species per local community) and ecosystem functioning classically follows a saturating shape (a). The high variability observed among monocultures (grey area in [a]) may be attributed to variation in (intraspecific) PCCGs diversity within species (b). A PCCGs approach may allow illuminating variation that is generally overlooked in classical BEF relationships. Similarly, pluricultures (blue area in [a]) may differ in their PCCGs diversity regardless of the number of species (c). Eventually, this might allow forecasting ecosystem functions more accurately, for instance by changing the shape of BEF relationships and/or increasing the predictive power (d).

More generally, PCCGs diversity can reveal different patterns of biodiversity. For instance, communities with the same species richness might actually encompass different levels of PCCGs diversity (Figure 5c), and a species-poor community might be as diverse as a species-rich community if the former has a high intraspecific diversity for each species (compensation effect). Therefore, important questions regarding the spatial and the temporal heterogeneity of biodiversity can be addressed using PCCGs diversity. This is particularly interesting when comparing, for example, the efficiency of functions in communities from different biomes. Communities in tropical areas exhibit higher species diversity than communities at higher latitude, whereas they may exhibit lower intraspecific diversity than communities at higher latitude (De Kort et al., 2021). We can hypothesize that communities at higher latitudes mainly rely on complementarity among individuals within populations—rather than on complementarity among species—to use and transform energy efficiently (Hughes et al., 2008). Comparing the strength and form of BEFs among contrasted biomes of this type is complicated using traditional approaches, whereas it becomes possible using the PCCGs approach because it relies on a single metric. This is essential for scaling-up BEF relationships from local to global scales (Gonzalez et al., 2020).

4 | PCCGS IMPLICATIONS FOR ECO-EVOLUTIONARY DYNAMICS: TOWARD FOCAL-COMMUNITY ECO-EVOLUTIONARY DYNAMICS

The PCCG diversity of a focal community is governed by its past demographic and evolutionary history (macro-evolution), which encompasses geological processes (e.g. isolation from a glacial refugee) and contemporary processes (micro-evolution such as recent bottlenecks). Assuming that PCCGs are governing ecological dynamics, quantifying biodiversity from PCCGs is particularly relevant for predicting eco-evolutionary feedbacks (Schoener, 2011).

Considering PCCGs for understanding eco-evolutionary dynamics constitutes a major conceptual shift, as this permits moving from a focal-species approach to a focal-community approach. Most studies investigating empirical eco-evolutionary feedback have considered reciprocal effects between evolutionary processes acting within a single species and ecosystem processes (De Meester et al., 2019; Hendry, 2019; Schoener, 2011). Contrastingly, very few studies have considered the possibility that evolution affects the genotypic (and trait) distribution of an entire focal community, with consequences for the dynamics of the community itself and the ecosystem, which themselves feedback to the gene pool of the focal community (but see, Aubree et al., 2020; Moorsel et al., 2019; Norberg et al., 2012). Thus, with PCCGs measured inclusively in a community, the 'focal-species approach' used in most eco-evolutionary dynamics studies will naturally shift toward a 'focal-community' perspective (De Meester et al., 2019; Govaert et al., 2021; Hendry, 2019), making more realistic empirical eco-evolutionary studies. Hereafter, we detail three perspectives for exploring the implications of PCCGs for eco-evolutionary dynamics.

First, spatial and temporal patterns of PCCG diversity must be uncovered in various communities to reveal the underlying processes. Hubbell (2001) and Vellend (2005) proposed that spatial patterns of intraspecific (gene) diversity and interspecific (species) diversity are driven by similar processes (natural selection/environmental filtering, gene flow/dispersal, genetic drift/ecological drift, mutation/speciation). Nonetheless, in all associated empirical studies (Fourtune et al., 2016; Manel et al., 2020; Taberlet et al., 2012; Vellend et al., 2014), the two facets of diversity are still dichotomized (see also, Govaert et al., 2021). Here, we offer an alternative view that they actually form a continuum that must be analysed as a single entity; *biodiversity*. Spatial patterns of biodiversity can then be understood through processes derived from population genetics: mutation acts on genes, which eventually leads to speciation; natural selection (indirectly) acts on genes, which eventually leads to different gene frequencies; gene flow acts on genes, which eventually homogenize the gene frequencies among local communities; and drift acts on genes, which eventually differentiate local communities. By using appropriate tools (Lowe et al., 2017), patterns of PCCGs diversity and underlying processes can be revealed at different spatial and temporal scales, in different environmental contexts and taxonomic groups. Revealing the evolutionary processes governing

gene frequencies in focal communities allows relating the potential for eco-evolutionary dynamics to *both* adaptive (selection) and non-adaptive processes (gene flow, drift, mutation; Lowe et al., 2017). This contributes to embracing a more realistic perspective of empirical eco-evolutionary dynamics (De Meester et al., 2019; Norberg et al., 2012).

Secondly, PCCGs as a unit of biodiversity will provide a relevant substratum to move research on eco-evolutionary dynamics from a 'focal-species' approach to a 'focal-community' approach (De Meester et al., 2019; Hendry, 2019). Long-term experiments have shown that (i) interspecific diversity alters the evolutionary dynamics of plant species (ecology-to-evolution, e.g. Moorsel et al., 2019) and (ii) that the evolution of some plants within plots with different levels of interspecific diversity may alter plant productivity (evolution-to-ecology, e.g. van Moorsel et al., 2018). This suggests eco-evolutionary dynamics occurring at the community level, and theoretical models are now integrating the potential for community evolution as a driver/modulator of ecological dynamics (Aubree et al., 2020; Loeuille, 2010). Eco-evolutionary dynamics involving the evolution of communities have been suggested in experiments manipulating microorganisms (Faillace & Morin, 2017; Gravel et al., 2010; Lawrence et al., 2012), but these studies remain limited by the difficulty to simultaneously track gene frequencies for a substantial number of species. Quantifying diversity from PCCGs inherently allows for such tracking and therefore breaks down a major wall. This genetic tracking can be done in the wild over large spatial and/or temporal scales, especially using pool-seq approaches (Czech et al., 2022). Alternatively, it becomes possible to experimentally assemble focal communities varying according to their PCCGs diversity and track the consequences of this diversity on ecological processes, and reciprocally the consequences of the later on PCCGs diversity.

Finally, a PCCGs approach allows identifying ecologically-important genetic sequences (Barbour et al., 2022; Skovmand et al., 2018) and their distribution in communities. It has long been argued that phenotype is pivotal for linking ecological and evolutionary dynamics. While we agree with that statement, phenotypic diversity includes both an environmental (nonheritable) and a genetic component, the latter being central to eco-evolutionary dynamics. By assuming that functional genes are sustaining (at least partly) phenotypic variation among individuals and species, the PCCGs approach overcomes the shortcoming of including nonheritable components and allows focusing more tightly on the 'genes that matter'. Genome-wide-association approaches (GWAs) can be used to relate SNP diversity at the community level and any ecological process to identify the gene(s) that is/are the most tightly linked to the process (Rudman et al., 2018). Important variants may be concentrated in a single species or multiple species and may be spread (or not) over multiple genes. Gene complementarity may also arise when two or more variants are beneficial to each other for ecological processes, which would underlie the importance of (synergistic or antagonistic) 'genomic interactions' for ecological processes. In the same way, by building PCCGs panels in interacting guilds (e.g. tree leaves and crustaceans, Figure 2), this provides

the possibility to reveal complementarity, gene–gene interactions and co-evolution among trophic levels, which has yet poorly been explored. Nonetheless, we anticipate that comparing the relative influence of PCCGs and functional trait diversity (measured at the community scale) on ecological dynamics would greatly help in understanding the heritable and environmental components of eco-evolutionary dynamics. Interestingly, by screening a panel of PCCGs, this approach might also allow to investigate particular traits and combinations of traits. Using adequate statistics, assessing the linkage between PCCGs diversity on a sub-sample of traits (for instance with random permutations) and ecosystem functions would indeed permit uncovering whether some specific trait combinations are ecologically-important. These questions may reveal whether genes in a community are complementary or whether a few of them are driving ecological processes. Because we propose an approach using genes extremely well known by functional biologists, a deeper understanding of the molecular mechanisms sustaining these gene–function relationships are further possible. For instance, it has recently been shown that epigenetic marks play a pivotal role in controlling the sitter/rover behaviour associated with the *for* gene in *D. melanogaster* (Anreiter et al., 2017). The toolbox of functional biologists may be transferred to functional ecologists for improving the mechanistic linkage that exists between genes and ecological dynamics.

5 | CONCLUDING REMARKS

We provide a novel framework to quantify biodiversity that breaks the historical boundary between the intra- and interspecific facets of diversity. This framework may substantially improve our ability to understand the reciprocal links between environmental changes, biodiversity and ecosystem dynamics. There have been previous attempts to break this boundary (Gaggiotti et al., 2018; Start & Gilbert, 2019; Vellend, 2005), but our approach differs from previous ones in that it relies on the idea of a biodiversity unit going beyond the species concept, that is driven by demographic and evolutionary processes and that putatively affects ecological processes. This approach is similar to that used by microbiologists (Burke et al., 2011; Konopka, 2009; Morris et al., 2020) that use molecular markers to characterize bacterial communities, mainly because specifically naming bacteria is tricky. Our approach is also 'agnostic' (sensu Morris et al., 2020) in that this is not species that matters anymore, but candidate gene frequencies at the community level (whatever the species that carry the genes), which, from a theoretical point of view, is similar to the neutral perspective developed by Hubbell (2001).

The PCCGs approach is based on knowledge accumulated by functional geneticists. Contrary to recent perspectives (Rudman et al., 2018; Skovmand et al., 2018), we do not aim to search for 'new' candidate genes with strong ecological effects (Skovmand et al., 2018). Although this quest for keystone genes is valuable and necessary (Barbour et al., 2022), we argue that novel insights can also

emerge by merging previous findings from research fields that are poorly connected. Of course, our *a priori* approach is not without limitations, and it is obvious that important genes (as well as interactions among genes or gene regulatory sequences) may be missed, whereas they would have been revealed using alternative approaches. Both approaches are therefore valuable and should be pursued. Moreover, by focusing on phylogenetically-conserved genes, we might underestimate intraspecific diversity that matters for ecological and evolutionary dynamics. Although technical solutions can be set to solve this issue (see above Section 2.2.2), a failure to do so would still be highly relevant to reveal patterns and consequences of functional genomic diversity at the community level, which would open relevant research opportunities (Mouquet et al., 2012).

Another limit of the PCCGs approach is that it focuses on genes coding for important traits, while 'ignoring' functional trait variability observed in the wild. The main implication is that the environmental component (i.e. plasticity) of trait variability is missed. There have been some attempts to link traits measured at the community level and ecological processes and functions (Le Bagousse-Pinguet et al., 2019; Start & Gilbert, 2019), and we fully acknowledge that this is relevant to illuminate mechanistic pathways (Norberg et al., 2001). Although traits can be tricky to estimate (especially for animals), revealing the causal links between PCCGs, trait diversity (measured at the community scale) and ecological dynamics would be extremely valuable to test for redundancy/complementarity among the genetic and phenotypic diversity of communities. For instance, some important traits may be missed while being captured by the genetic diversity of populations of communities ('ghost' traits) and *vice versa*; trait diversity and genetic diversity can be complementary for explaining ecological processes (Raffard et al., 2021). Combining both PCCGs and traits will likely generate unexpected mechanistic insights into the links between biodiversity, ecological dynamics and the environment. Yet, for eco-evolutionary dynamics, what matters is information transmitted across generations (De Meester et al., 2019). Focusing directly on genes that sustain trait variation therefore allows for better integration of biodiversity into the framework of eco-evolutionary dynamics.

To conclude, the PCCGs approach has many implications that actually go beyond BEF relationships and eco-evolutionary dynamics (e.g. conservation biology), and that could be discussed elsewhere and after some proof of concepts have emerged. Reducing the complexity of natural communities to candidate gene frequencies will likely ease the links between theories and empirical observations, as the theory generally simplifies premises (Govaert et al., 2019; Hubbell, 2011; Loreau, 1998; Norberg et al., 2001). We now hope that empiricists and theoreticians will be convinced enough and that future works integrating PCCGs will soon emerge.

AUTHOR CONTRIBUTION

SB proposed the basic idea; SB, LF and AR developed the framework and ideas; SB, LF and AR wrote the first draft of the manuscript and contributed substantially to revisions.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Not applicable.

ORCID

Simon Blanchet https://orcid.org/0000-0002-3843-589X

REFERENCES

Albert, T. J., Molla, M. N., Muzny, D. M., Nazareth, L., Wheeler, D., Song, X., Richmond, T. A., Middle, C. M., Rodesch, M. J., Packard, C. J., Weinstock, G. M., & Gibbs, R. A. (2007). Direct selection of human genomic loci by microarray hybridization. *Nature Methods*, 11, 903–905. https://doi.org/10.1038/nmeth1111

Andersen, J. R., & Lübberstedt, T. (2003). Functional markers in plants. *Trends in Plant Science*, 11, 554–560. https://doi.org/10.1016/j.tplants.2003.09.010

Anreiter, I., Kramer, J. M., & Sokolowski, M. B. (2017). Epigenetic mechanisms modulate differences in *Drosophila* foraging behavior. *Proceedings of the National Academy of Sciences*, 114(47), 12518–12523. https://doi.org/10.1073/pnas.1710770114

Anreiter, I., & Sokolowski, M. B. (2019). The *foraging* gene and its behavioral effects: Pleiotropy and plasticity. *Annual Review of Genetics*, 53(1), 373–392. https://doi.org/10.1146/annurev-genet-112618-043536

Aubree, F., David, P., Jarne, P., Loreau, M., Mouquet, N., & Calcagno, V. (2020). How community adaptation affects biodiversity–ecosystem functioning relationships. *Ecology Letters*, 23(8), 1263–1275. https://doi.org/10.1111/ele.13530

Balvanera, P., Pfisterer, A. B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D., & Schmid, B. (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services: Biodiversity and ecosystem functioning/services. *Ecology Letters*, 9(10), 1146–1156. https://doi.org/10.1111/j.1461-0248.2006.00963.x

Barbour, M. A., Kliebenstein, D. J., & Bascompte, J. (2022). A keystone gene underlies the persistence of an experimental food web. *Science*, 376(6588), 70–73. https://doi.org/10.1126/science.abf2232

Barson, N. J., Aykanat, T., Hindar, K., Baranski, M., Bolstad, G. H., Fiske, P., Jacq, C., Jensen, A. J., Johnston, S. E., Karlsson, S., Kent, M., Moen, T., Niemelä, E., Nome, T., Næsje, T. F., Orell, P., Romakkaniemi, A., Sægrov, H., Urdal, K., ... Primmer, C. R. (2015). Sex-dependent dominance at a single locus maintains variation in age at maturity in salmon. *Nature*, 528(7582), 405–408. https://doi.org/10.1038/nature16062

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity: Partitioning beta diversity. *Global Ecology and Biogeography*, 19(1), 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W., & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity: Biodiversity and climate change. *Ecology Letters*, 15(4), 365–377. https://doi.org/10.1111/j.1461-0248.2011.01736.x

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85(7), 1771–1789.

Burke, C., Steinberg, P., Rusch, D., Kjelleberg, S., & Thomas, T. (2011). Bacterial community assembly based on functional genes rather than species. *Proceedings of the National Academy of Sciences of the United States of America*, 108(34), 14288–14293. https://doi.org/10.1073/pnas.1101591108

Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services: Functional diversity in ecology and conservation. *Journal of Applied Ecology*, 48(5), 1079–1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x

Cadotte, M. W., Dinnage, R., & Tilman, D. (2012). Phylogenetic diversity promotes ecosystem stability. *Ecology*, 93(sp8), S223–S233. https://doi.org/10.1890/11-0426.1

Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., Narwani, A., Mace, G. M., Tilman, D., Wardle, D. A., Kinzig, A. P., Daily, G. C., Loreau, M., Grace, J. B., Larigauderie, A., Srivastava, D. S., & Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, 486(7401), 59–67. https://doi.org/10.1038/nature11148

Cardoso-Moreira, M., Halbert, J., Valloton, D., Velten, B., Chen, C., Shao, Y., Liechti, A., Ascenção, K., Rummel, C., Ovchinnikova, S., Mazin, P. V., Xenarios, I., Harshman, K., Mort, M., Cooper, D. N., Sandi, C., Soares, M. J., Ferreira, P. G., Afonso, S., ... Kaessmann, H. (2019). Gene expression across mammalian organ development. *Nature*, 571(7766), 505–509. https://doi.org/10.1038/s41586-019-1338-5

Chapin, F. S., Walker, B. H., Hobbs, R. J., Hooper, D. U., Lawton, J. H., Sala, O. E., & Tilman, D. (1997). Biotic control over the functioning of ecosystems. *Science*, 277(5325), 500–504.

Chapin, F. S., Zavaleta, E. S., Eviner, V. T., Naylor, R. L., Vitousek, P. M., Reynolds, H. L., Hooper, D. U., Lavorel, S., Sala, O. E., Hobbie, S. E., Mack, M. C., & Diaz, S. (2000). Consequences of changing biodiversity. *Nature*, 405(6783), 234–242.

Cho, L.-H., Yoon, J., & An, G. (2017). The control of flowering time by environmental factors. *The Plant Journal*, 90(4), 708–719. https://doi.org/10.1111/tpj.13461

Crutsinger, G. M., Collins, M. D., Fordyce, J. A., Gompert, Z., Nice, C., & Sanders, N. J. (2006). Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science*, 313(5789), 966–968. https://doi.org/10.1126/science.1128326

Czech, L., Peng, Y., Spence, J. P., Lang, P. L. M., Bellagio, T., Hildebrandt, J., Fritschi, K., Schwab, R., Rowan, B. A., GrENE-net consortium, Weigel, D., Scheepens, J. F., Vasseur, F., & Exposito-Alonso, M. (2022). *Monitoring rapid evolution of plant populations at scale with Pool-Sequencing* [Preprint]. Evolutionary Biology. https://doi.org/10.1101/2022.02.02.477408

de Belle, J. S., Hilliker, A. J., & Sokolowski, M. B. (1989). Genetic localization of foraging (for): A major gene for larval behavior in *Drosophila melanogaster*. *Genetics*, 123(1), 157–163.

De Kort, H., Prunier, J. G., Ducatez, S., Honnay, O., Baguette, M., Stevens, V. M., & Blanchet, S. (2021). Life history, climate and biogeography interactively affect worldwide genetic diversity of plant and animal populations. *Nature Communications*, 12(1), 516. https://doi.org/10.1038/s41467-021-20958-2

De Meester, L., Brans, K. I., Govaert, L., Souffreau, C., Mukherjee, S., Vanvelk, H., Korzeniowski, K., Kilsdonk, L., Decaestecker, E., Stoks, R., & Urban, M. C. (2019). Analyzing eco-evolutionary dynamics – The challenging complexity of the real world. *Functional Ecology*, 33, 43–59.

Ducrest, A., Keller, L., & Roulin, A. (2008). Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends in Ecology & Evolution*, 23(9), 502–510. https://doi.org/10.1016/j.tree.2008.06.001

Faillace, C. A., & Morin, P. J. (2017). Evolution alters the consequences of invasions in experimental communities. *Nature Ecology and Evolution*, 1(1), 0013. https://doi.org/10.1038/s41559-016-0013

Faircloth, B. C. (2017). Identifying conserved genomic elements and designing universal bait sets to enrich them. *Methods in Ecology and Evolution*, 8(9), 1103–1112. https://doi.org/10.1111/2041-210X.12754

Falconer, D. (1981). *Introduction to quantitative genetics*. Longman Group Limited.

Fitzpatrick, M., Benshahar, Y., Smid, H., Vet, L., Robinson, G., & Sokolowski, M. (2005). Candidate genes for behavioural ecology. *Trends in Ecology & Evolution*, 20(2), 96–104. https://doi.org/10.1016/j.tree.2004.11.017

Fourtune, L., Paz-Vinas, I., Loot, G., Prunier, J. G., & Blanchet, S. (2016). Lessons from the fish: A multi-species analysis reveals common processes underlying similar species-genetic diversity correlations. *Freshwater Biology*, 61(11), 1830–1845. https://doi.org/10.1111/fwb.12826

Fridley, J. D., & Grime, J. P. (2010). Community and ecosystem effects of intraspecific genetic diversity in grassland microcosms of varying species diversity. *Ecology*, 91(8), 2272–2283. https://doi.org/10.1890/09-1240.1

Gaggiotti, O. E., Chao, A., Peres-Neto, P., Chiu, C.-H., Edwards, C., Fortin, M.-J., Jost, L., Richards, C. M., & Selkoe, K. A. (2018). Diversity from genes to ecosystems: A unifying framework to study variation across biological metrics and scales. *Evolutionary Applications*, 11(7), 1176–1193. https://doi.org/10.1111/eva.12593

Gautier, M., Vitalis, R., Flori, L., & Estoup, A. (2022). F -statistics estimation and admixture graph construction with Pool-Seq or allele count data using the R package *poolfstat*. *Molecular Ecology Resources*, 22(4), 1394–1416. https://doi.org/10.1111/1755-0998.13557

Gonzalez, A., Germain, R. M., Srivastava, D. S., Filotas, E., Dee, L. E., Gravel, D., Thompson, P. L., Isbell, F., Wang, S., Kéfi, S., Montoya, J., Zelnik, Y. R., & Loreau, M. (2020). Scaling-up biodiversity-ecosystem functioning research. *Ecology Letters*, 23(4), 757–776. https://doi.org/10.1111/ele.13456

Govaert, L., Altermatt, F., De Meester, L., Leibold, M. A., McPeek, M. A., Pantel, J. H., & Urban, M. C. (2021). Integrating fundamental processes to understand eco-evolutionary community dynamics and patterns. *Functional Ecology*, 8(10), 2138–2155. https://doi.org/10.1111/1365-2435.13880

Govaert, L., Fronhofer, E. A., Lion, S., Eizaguirre, C., Bonte, D., Egas, M., Hendry, A. P., De Brito Martins, A., Melián, C. J., Raeymaekers, J. A. M., Ratikainen, I. I., Saether, B., Schweitzer, J. A., & Matthews, B. (2019). Eco-evolutionary feedbacks—Theoretical models and perspectives. *Functional Ecology*, 33(1), 13–30. https://doi.org/10.1111/1365-2435.13241

Gramzow, L., & Theißen, G. (2013). Phylogenomics of MADS-box genes in plants—Two opposing life styles in one gene family. *Biology*, 2(3), 1150–1164. https://doi.org/10.3390/biology2031150

Gravel, D., Bell, T., Barbera, C., Bouvier, T., Pommier, T., Venail, P., & Mouquet, N. (2010). Experimental niche evolution alters the strength of the diversity–productivity relationship. *Nature*, 469(7328), 89–92. https://doi.org/10.1038/nature09592

Hagan, J. G., Vanschoenwinkel, B., & Gamfeldt, L. (2021). We should not necessarily expect positive relationships between biodiversity and ecosystem functioning in observational field data. *Ecology Letters*, 24(12), 2537–2548. https://doi.org/10.1111/ele.13874

Hargrave, C. W., Hambright, K. D., & Weider, L. J. (2011). Variation in resource consumption across a gradient of increasing intra- and interspecific richness. *Ecology*, 92(6), 1226–1235. https://doi.org/10.1890/09-1948.1

Hawkins, M. T. R., Hofman, C. A., Callicrate, T., McDonough, M. M., Tsuchiya, M. T. N., Gutiérrez, E. E., Helgen, K. M., & Maldonado, J. E. (2016). In-solution hybridization for mammalian mitogenome enrichment: Pros, cons and challenges associated with multiplexing degraded DNA. *Molecular Ecology Resources*, 16(5), 1173–1188. https://doi.org/10.1111/1755-0998.12448

Hendry, A. P. (2017). *Eco-evolutionary dynamics*. Princeton University Press.

Hendry, A. P. (2019). A critique for eco-evolutionary dynamics. *Functional Ecology*, 33(1), 84–94. https://doi.org/10.1111/1365-2435.13244

Hendry, A. P., Farrugia, T. J., & Kinnison, M. T. (2008). Human influences on rates of phenotypic change in wild animal populations. *Molecular Ecology*, 17(1), 20–29. https://doi.org/10.1111/j.1365

Holsinger, K. E., & Weir, B. S. (2009). Genetics in geographically structured populations: Defining, estimating and interpreting FST. *Nature Reviews Genetics*, 10(9), 639–650. https://doi.org/10.1038/nrg2611

Hou, Z., Fu, J., & Li, S. (2007). A molecular phylogeny of the genus Gammarus (Crustacea: Amphipoda) based on mitochondrial and nuclear gene sequences. *Molecular Phylogenetics and Evolution*, 10, 596–611.

Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A. J., Vandermeer, J., & Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, 75(1), 3–35.

Hubbell, S. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton University Press.

Hughes, A. R., Inouye, B. D., Johnson, M. T. J., Underwood, N., & Vellend, M. (2008). Ecological consequences of genetic diversity: Ecological effects of genetic diversity. *Ecology Letters*, 11(6), 609–623. https://doi.org/10.1111/j.1461-0248.2008.01179.x

Hughes, A. R., & Stachowicz, J. J. (2004). Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proceedings of the National Academy of Sciences*, 101(24), 8998–9002. https://doi.org/10.1073/pnas.0402642101

Huston, M. A. (1997). Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. *Oecologia*, 110(4), 449–460. https://doi.org/10.1007/s004420050180

James, A. M., Ma, D., Mellway, R., Gesell, A., Yoshida, K., Walker, V., Tran, L., Stewart, D., Reichelt, M., Suvanto, J., Salminen, J.-P., Gershenzon, J., Séguin, A., & Constabel, C. P. (2017). Poplar MYB115 and MYB134 transcription factors regulate Proanthocyanidin synthesis and structure. *Plant Physiology*, 174(1), 154–171. https://doi.org/10.1104/pp.16.01962

Jiménez-Mena, B., Flávio, H., Henriques, R., Manuzzi, A., Ramos, M., Meldrup, D., Edson, J., Pálsson, S., Ásta Ólafsdóttir, G., Ovenden, J. R., Nielsen, E. E., & Alexander, A. (2022). Fishing for DNA? Designing baits for population genetics in target enrichment experiments: Guidelines, considerations and the new tool supeRbaits. *Molecular Ecology Resources*, 22(5), 2105–2119. https://doi.org/10.1111/1755-0998.13598

Jones, M. R., & Good, J. M. (2016). Targeted capture in evolutionary and ecological genomics. *Molecular Ecology*, 25(1), 185–202. https://doi.org/10.1111/mec.13304

Jost, L. (2008). G_{ST} and its relatives do not measure differentiation. *Molecular Ecology*, 17(18), 4015–4026. https://doi.org/10.1111/j.1365-294X.2008.03887.x

Konopka, A. (2009). What is microbial community ecology? *The ISME Journal*, 3(11), 1223–1230. https://doi.org/10.1038/ismej.2009.88

Lawrence, D., Fiegna, F., Behrends, V., Bundy, J. G., Phillimore, A. B., Bell, T., & Barraclough, T. G. (2012). Species interactions Alter evolutionary responses to a novel environment. *PLoS Biology*, 10(5), e1001330. https://doi.org/10.1371/journal.pbio.1001330

Le Bagousse-Pinguet, Y., Soliveres, S., Gross, N., Torices, R., Berdugo, M., & Maestre, F. T. (2019). Phylogenetic, functional, and taxonomic richness have both positive and negative effects on ecosystem multifunctionality. *Proceedings of the National Academy of Sciences*, 116(17), 8419–8424. https://doi.org/10.1073/pnas.1815727116

Loeuille, N. (2010). Influence of evolution on the stability of ecological communities: Evolution and stability of communities. *Ecology Letters*, *13*(12), 1536–1545. https://doi.org/10.1111/j.1461-0248.2010.01545.x

Loreau, M. (1998). Biodiversity and ecosystem functioning: A mechanistic model. *Proceedings of the National Academy of Sciences*, *95*(10), 5632–5636. https://doi.org/10.1073/pnas.95.10.5632

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., Hooper, D. U., Huston, M. A., Raffaelli, D., Schmid, B., Tilman, D., & Wardle, D. A. (2001). Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science*, *294*(5543), 804–808.

Lowe, W. H., Kovach, R. P., & Allendorf, F. W. (2017). Population genetics and demography unite ecology and evolution. *Trends in Ecology & Evolution*, *32*(2), 141–152. https://doi.org/10.1016/j.tree.2016.12.002

Mamanova, L., Coffey, A. J., Scott, C. E., Kozarewa, I., Turner, E. H., Kumar, A., Howard, E., Shendure, J., & Turner, D. J. (2010). Target-enrichment strategies for next-generation sequencing. *Nature Methods*, *7*(2), 111–118. https://doi.org/10.1038/nmeth.1419

Manel, S., Guerin, P.-E., Mouillot, D., Blanchet, S., Velez, L., Albouy, C., & Pellissier, L. (2020). Global determinants of freshwater and marine fish genetic diversity. *Nature Communications*, *11*(1), 692. https://doi.org/10.1038/s41467-020-14409-7

Marden, J. H., Fescemyer, H. W., Schilder, R. J., Doerfler, W. R., Vera, J. C., & Wheat, C. W. (2013). Genetic variation in HIF signaling underlies quantitative variation in physiological and life-history traits within lowland butterfly populations. *Evolution*, *67*(4), 1105–1115. https://doi.org/10.1111/evo.12004

Matthews, B., De Meester, L., Jones, C. G., Ibelings, B. W., Bouma, T. J., Nuutinen, V., van de Koppel, J., & Odling-Smee, J. (2014). Under niche construction: An operational bridge between ecology, evolution, and ecosystem science. *Ecological Monographs*, *84*(2), 245–263. https://doi.org/10.1890/13-0953.1

Matthews, B., Narwani, A., Hausch, S., Nonaka, E., Peter, H., Yamamichi, M., Sullam, K. E., Bird, K. C., Thomas, M. K., Hanley, T. C., & Turner, C. B. (2011). Toward an integration of evolutionary biology and ecosystem science. *Ecology Letters*, *14*(7), 690–701. https://doi.org/10.1111/j.1461-0248.2011.01627.x

McGirr, J. A., & Martin, C. H. (2017). Novel candidate genes underlying extreme trophic specialization in Caribbean pupfishes. *Molecular Biology and Evolution*, *34*, 873–888.

Meinke, D., Muralla, R., Sweeney, C., & Dickerman, A. (2008). Identifying essential genes in *Arabidopsis thaliana*. *Trends in Plant Science*, *13*(9), 483–491. https://doi.org/10.1016/j.tplants.2008.06.003

Mertes, F., ElSharawy, A., Sauer, S., van Helvoort, J. M. L. M., van der Zaag, P. J., Franke, A., Nilsson, M., Lehrach, H., & Brookes, A. J. (2011). Targeted enrichment of genomic DNA regions for next-generation sequencing. *Briefings in Functional Genomics*, *10*(6), 374–386. https://doi.org/10.1093/bfgp/elr033

Moorsel, S. J., Schmid, M. W., Wagemaker, N. C. A. M., Gurp, T., Schmid, B., & Vergeer, P. (2019). Evidence for rapid evolution in a grassland biodiversity experiment. *Molecular Ecology*, *28*(17), 4097–4117. https://doi.org/10.1111/mec.15191

Morris, A., Meyer, K., & Bohannan, B. (2020). Linking microbial communities to ecosystem functions: What we can learn from genotype–phenotype mapping in organisms. *Philosophical Transactions of the Royal Society, B: Biological Sciences*, *375*(1798), 20190244. https://doi.org/10.1098/rstb.2019.0244

Mouquet, N., Devictor, V., Meynard, C. N., Munoz, F., Bersier, L.-F., Chave, J., Couteron, P., Dalecky, A., Fontaine, C., Gravel, D., Hardy, O. J., Jabot, F., Lavergne, S., Leibold, M., Mouillot, D., Münkemüller, T., Pavoine, S., Prinzing, A., Rodrigues, A. S. L., … Thuiller, W. (2012). Ecophylogenetics: Advances and perspectives. *Biological Reviews*, *87*(4), 769–785. https://doi.org/10.1111/j.1469-185X.2012.00224.x

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., … Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, *520*(7545), 45–50. https://doi.org/10.1038/nature14324

Norberg, J., Swaney, D. P., Dushoff, J., Lin, J., Casagrandi, R., & Levin, S. A. (2001). Phenotypic diversity and ecosystem functioning in changing environments: A theoretical framework. *Proceedings of the National Academy of Sciences*, *98*(20), 11376–11381. https://doi.org/10.1073/pnas.171315998

Norberg, J., Urban, M. C., Vellend, M., Klausmeier, C. A., & Loeuille, N. (2012). Eco-evolutionary responses of biodiversity to climate change. *Nature Climate Change*, *2*(10), 747–751. https://doi.org/10.1038/nclimate1588

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*(6918), 37–42.

Prieto, I., Violle, C., Barre, P., Durand, J.-L., Ghesquiere, M., & Litrico, I. (2015). Complementary effects of species and genetic diversity on productivity and stability of sown grasslands. *Nature Plants*, *1*(4), 15033. https://doi.org/10.1038/nplants.2015.33

Raffard, A., Cucherousset, J., Montoya, J. M., Richard, M., Acoca-Pidolle, S., Poésy, C., Garreau, A., Santoul, F., & Blanchet, S. (2021). Intraspecific diversity loss in a predator species alters prey community structure and ecosystem functions. *PLoS Biology*, *19*(3), e3001145. https://doi.org/10.1371/journal.pbio.3001145

Raffard, A., Santoul, F., Cucherousset, J., & Blanchet, S. (2019). The community and ecosystem consequences of intraspecific diversity: A meta-analysis: The ecological effects of intraspecific diversity. *Biological Reviews*, *94*(2), 648–661. https://doi.org/10.1111/brv.12472

Reusch, T. B. H., Ehlers, A., Hämmerli, A., & Worm, B. (2005). Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proceedings of the National Academy of Sciences*, *102*(8), 2826–2831. https://doi.org/10.1073/pnas.0500008102

Rota, T., Jabiol, J., Chauvet, E., & Lecerf, A. (2018). Phenotypic determinants of inter-individual variability of litter consumption rate in a detritivore population. *Oikos*, *127*(11), 1670–1678. https://doi.org/10.1111/oik.05228

Rudman, S. M., Barbour, M. A., Csilléry, K., Gienapp, P., Guillaume, F., Hairston, N. G., Jr., Hendry, A. P., Lasky, J. R., Rafajlović, M., Räsänen, K., Schmidt, P. S., Seehausen, O., Therkildsen, N. O., Turcotte, M. M., & Levine, J. M. (2018). What genomic data can reveal about eco-evolutionary dynamics. *Nature Ecology and Evolution*, *2*(1), 9–15. https://doi.org/10.1038/s41559-017-0385-2

Schilling, S., Pan, S., Kennedy, A., & Melzer, R. (2018). MADS-box genes and crop domestication: The jack of all traits. *Journal of Experimental Botany*, *69*(7), 1447–1469. https://doi.org/10.1093/jxb/erx479

Schlötterer, C., Tobler, R., Kofler, R., & Nolte, V. (2014). Sequencing pools of individuals—Mining genome-wide polymorphism data without big funding. *Nature Reviews Genetics*, *15*(11), 749–763. https://doi.org/10.1038/nrg3803

Schmidt, N. M., Mosbacher, J. B., Nielsen, P. S., Rasmussen, C., Høye, T. T., & Roslin, T. (2016). An ecological function in crisis? The temporal overlap between plant flowering and pollinator function shrinks as the Arctic warms. *Ecography*, *39*(12), 1250–1252. https://doi.org/10.1111/ecog.02261

Schoener, T. W. (2011). The newest synthesis: Understanding the interplay of evolutionary and ecological dynamics. *Science*, *331*(6016), 426–429. https://doi.org/10.1126/science.1193954

Schwander, T., Libbrecht, R., & Keller, L. (2014). Supergenes and complex phenotypes. *Current Biology*, *24*(7), R288–R294. https://doi.org/10.1016/j.cub.2014.01.056

Schwarz-Sommer, Z., Huijser, P., Nacken, W., Saedler, H., & Sommer, H. (1990). Genetic control of flower development by homeotic genes

in *Antirrhinum majus*. *Science*, *250*(4983), 931–936. https://doi.org/10.1126/science.250.4983.931

Sham, P., Bader, J. S., Craig, I., O'Donovan, M., & Owen, M. (2002). DNA pooling: A tool for large-scale association studies. *Nature Reviews Genetics*, *3*(11), 862–871. https://doi.org/10.1038/nrg930

Skovmand, L. H., Xu, C. C. Y., Servedio, M. R., Nosil, P., Barrett, R. D. H., & Hendry, A. P. (2018). Keystone genes. *Trends in Ecology & Evolution*, *33*(9), 689–700. https://doi.org/10.1016/j.tree.2018.07.002

Sokolowski, M. B. (2001). Drosophila: Genetics meets behaviour. *Nature Reviews Genetics*, *2*(11), 879–890.

Spielman, D., Brook, B. W., & Frankham, R. (2004). Most species are not driven to extinction before genetic factors impact them. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(42), 15261–15264.

Start, D., & Gilbert, B. (2019). Trait variation across biological scales shapes community structure and ecosystem function. *Ecology*, *100*(9), e02769. https://doi.org/10.1002/ecy.2769

Struk, A. A., Mugon, J., Huston, A., Scholer, A. A., Stadler, G., Higgins, E. T., Sokolowski, M. B., & Danckert, J. (2019). Self-regulation and the *foraging* gene (*PRKG1*) in humans. *Proceedings of the National Academy of Sciences*, *116*(10), 4434–4439. https://doi.org/10.1073/pnas.1809924116

Taberlet, P., Zimmermann, N. E., Englisch, T., Tribsch, A., Holderegger, R., Alvarez, N., Niklfeld, H., Coldea, G., Mirek, Z., Moilanen, A., Ahlmer, W., Marsan, P. A., Bona, E., Bovio, M., Choler, P., Cieślak, E., Colli, L., Cristea, V., Dalmas, J.-P., … IntraBioDiv Consortium. (2012). Genetic diversity in widespread species is not congruent with species richness in alpine plant communities. *Ecology Letters*, *15*(12), 1439–1448. https://doi.org/10.1111/ele.12004

Theißen, G., Rümpler, F., & Gramzow, L. (2018). Array of MADS-box genes: Facilitator for rapid adaptation? *Trends in Plant Science*, *23*(7), 563–576. https://doi.org/10.1016/j.tplants.2018.04.008

Thompson, J. (1998). Rapid evolution as an ecological process. *Trends in Ecology & Evolution*, *13*(8), 329–332.

Tilman, D., Reich, P. B., & Knops, J. M. H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, *441*(7093), 629–632. https://doi.org/10.1038/nature04742

Tilman, D., Wedin, D., & Knops, J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, *379*(6567), 718–720. https://doi.org/10.1038/379718a0

Tucker, C. M., Cadotte, M. W., Carvalho, S. B., Davies, T. J., Ferrier, S., Fritz, S. A., Grenyer, R., Helmus, M. R., Jin, L. S., Mooers, A. O., Pavoine, S., Purschke, O., Redding, D. W., Rosauer, D. F., Winter, M., & Mazel, F. (2017). A guide to phylogenetic metrics for conservation, community ecology and macroecology: A guide to phylogenetic metrics for ecology. *Biological Reviews*, *92*(2), 698–715. https://doi.org/10.1111/brv.12252

van Moorsel, S. J., Hahl, T., Wagg, C., De Deyn, G. B., Flynn, D. F. B., Zuppinger-Dingley, D., & Schmid, B. (2018). Community evolution increases plant productivity at low diversity. *Ecology Letters*, *21*(1), 128–137. https://doi.org/10.1111/ele.12879

Vellend, M. (2005). Species diversity and genetic diversity: Parallel processes and correlated patterns. *The American Naturalist*, *166*(2), 199–215. https://doi.org/10.1086/431318

Vellend, M., & Geber, M. A. (2005). Connections between species diversity and genetic diversity. *Ecology Letters*, *8*(7), 767–781. https://doi.org/10.1111/j.1461-0248.2005.00775.x

Vellend, M., Lajoie, G., Bourret, A., Múrria, C., Kembel, S. W., & Garant, D. (2014). Drawing ecological inferences from coincident patterns of population- and community-level biodiversity. *Molecular Ecology*, *23*(12), 2890–2901. doi:10.1111/mec.12756

Wattier, R., Mamos, T., Copilas-Ciocianu, D., Jelic, M., Ollivier, A., Chaumot, A., Danger, M., Felten, V., Piscart, C., Žganec, K., & Rewicz, T. (2020). Continental-scale patterns of hyper-cryptic diversity within the freshwater model taxon *Gammarus fossarum* (Crustacea, Amphipoda). *Scientific Reports*, *10*, 16536.

Watanabe, K., Stringer, S., Frei, O., Umićević Mirkov, M., de Leeuw, C., Polderman, T. J. C., van der Sluis, S., Andreassen, O. A., Neale, B. M., & Posthuma, D. (2019). A global overview of pleiotropy and genetic architecture in complex traits. *Nature Genetics*, *51*(9), 1339–1348. https://doi.org/10.1038/s41588-019-0481-0

Whitham, T. G., Bailey, J. K., Schweitzer, J. A., Shuster, S. M., Bangert, R. K., LeRoy, C. J., Lonsdorf, E. V., Allan, G. J., DiFazio, S. P., Potts, B. M., Fischer, D. G., Gehring, C. A., Lindroth, R. L., Marks, J. C., Hart, S. C., Wimp, G. M., & Wooley, S. C. (2006). A framework for community and ecosystem genetics: From genes to ecosystems. *Nature Reviews Genetics*, *7*(7), 510–523. https://doi.org/10.1038/nrg1877

Whitham, T. G., Young, W. P., Martinsen, G. D., Gehring, C. A., Schweitzer, J. A., Shuster, S. M., Wimp, G. M., Fischer, D. G., Bailey, J. K., Lindroth, R. L., Woolbright, S., & Kuske, C. R. (2003). Community and ecosystem genetics: A consequence of the extended phenotype. *Ecology*, *84*(3), 559–573.

Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, *30*(3), 279–338. https://doi.org/10.2307/1943563

Wolf, M., & Weissing, F. J. (2012). Animal personalities: Consequences for ecology and evolution. *Trends in Ecology & Evolution*, *27*(8), 452–461. https://doi.org/10.1016/j.tree.2012.05.001

Wuest, S., & Niklaus, P. A. (2018). A plant biodiversity effect resolved to a single chromosomal region. *Nature Ecology and Evolution*, *2*(12), 1933–1939.

Yachi, S., & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences*, *96*(4), 1463–1468. https://doi.org/10.1073/pnas.96.4.1463