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, 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
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 & LüBerstedt, 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 forest 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;
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
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 (~338,000 bp; 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...).
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 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 (Hyallela 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 Hyallela azteca (the closest annotated genome to 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...
BLANCHET et al. used the published reference genome from *Gammarus rosaei* 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.

**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.
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 β 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 β-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 of 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.

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).
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 refuge) 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 genetic 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 environment 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.

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REFERENCES


BLANCHET ET AL.