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

Simon Blanchet[1], Laura Fargeot[1], and Allan Raffard[2]

[1]CNRS
[2]Université catholique de Louvain

September 20, 2022

Abstract

The intra- and interspecific facets of biodiversity have traditionally been quantified and 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 conceptual and technical guidelines for identifying phylogenetically-conserved candidate genes (PCCGs) within communities, and for measuring inclusive biodiversity from PCCGs. We then explain how biodiversity measured at PCCGs can be linked to ecosystem functions, which may unify recent observations that both intra- and interspecific biodiversity are important for ecosystem functions. We then highlight the eco-evolutionary processes shaping PCCGs 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.

Introduction

Global change is modifying worldwide patterns of biodiversity (Parmesan & Yohe 2003; Newbold *et al.* 2015). The rate of species loss is so rapid that it is actually called the 6$^{\text{th}}$ mass extinction (Barnosky *et al.* 2011). Nonetheless, biodiversity changes do not only concern species loss, but also the loss of the diversity characterising (almost) every species, *i.e.,* intraspecific diversity. Genes and life-history strategies are being lost within species, because humans are altering fundamental processes impairing intraspecific diversity (Spielman *et al.* 2004; Hendry *et al.* 2008; Leigh *et al.* 2019). The loss of intraspecific diversity always precedes (and potentially speeds up) species loss (Spielman *et al.* 2004); it is hence essential to consider biodiversity loss as an*inclusive* process occurring across genes and species (Bellard *et al.*2012).

Nonetheless, in most studies, the intra- and interspecific facets of biodiversity are treated as separate entities (but see e.g., Start & Gilbert 2019), while they actually form an evolutionary continuum. This limits our ability to provide an integrative perspective of eco-evolutionary relationships between biodiversity, the environment and ecosystem functioning (Matthews *et al.* 2011). This gap between biodiversity facets has historical causes since intraspecific diversity has mainly been studied through a population geneticist lens, whereas interspecific diversity has mainly been studied by community ecologists. This gap has progressively been conceptually concealed with the recognition of tight links between ecological and evolutionary dynamics (Hubbell 2001; Whitham*et al.* 2003; Vellend 2005; Whitham *et al.* 2008; Matthews*et al.* 2014). It also has

an intrinsic cause since intra- and interspecific diversity are quantified using different units. Interspecific diversity is generally measured as the number of species, whereas intraspecific diversity can be estimated through metrics of genetic (allelic richness, heterozygosity...) and phenotypic diversity (trait variance, number of ecotypes...), which impedes the inclusive measurement of biodiversity within communities. Some studies have proposed common statistical frameworks to jointly measure intra- and interspecific diversity within communities (e.g., Pavoine & Izsák 2014a; Gaggiotti *et al.* 2018; Carmona *et al.* 2019), demonstrating the scientific ambition to transcend the intra-/interspecific boundary. However, these attempts are rare, and they have not been developed with the initial objective of linking these*inclusive* metrics of biodiversity to both ecological and evolutionary dynamics.

Developing a biodiversity unit transcending the intra-/interspecific boundary and allowing for an inclusive measurement of biodiversity has many implications such as, changing our perspective on the links between biodiversity and ecosystem functioning. Biodiversity sustains key ecosystem functions such as primary productivity or recycling of dead organic matter (Chapin*et al.* 2000; Loreau *et al.* 2001; Hooper *et al.*2005). These links between biodiversity and ecosystem functioning ("BEF") rest on the idea that higher levels of biodiversity promote higher trait complementarity among individuals and/or increase the likelihood to sustain highly competitive traits with dominant effects (see BOX 1), both processes maximising resource acquisition and its conversion into biomass or energy (Hooper *et al.*2005). BEF relationships have been historically described at the*interspecific level,* and seminal experiments have demonstrated that higher plant species richness in communities increases and stabilises yields (Tilman *et al.*1996, 2006; Chapin *et al.* 1997). More recently, similar observations have been reported at the *intraspecific* level; plant or animal populations composed of a large number of genotypes sustain higher yields and community diversity than populations with a poor genotypic diversity (*e.g.*, Hughes & Stachowicz 2004; Reusch *et al.* 2005; Crutsinger *et al.*2006; Raffard *et al.* 2021). Altogether, this suggests that both losing alleles within populations and species within communities can alter the functioning of ecosystems. Yet, the dichotomy between intra- and interspecific diversity impedes a global assessment of biodiversity loss on ecosystem dynamics (but see, e.g., Prieto*et al.* 2015).

The use of an inclusive biodiversity unit should also ease our understanding of how ecology affects the evolution of organisms (and*vice versa*) composing communities. The ecological effects generated by trait variation described above can feedback to evolutionary processes when these ecological effects affect the selective regime and/or demographic parameters, which has been termed "eco-evolutionary dynamics" (Thompson 1998; Schoener 2011; Hendry 2017). Revealing eco-evolutionary dynamics requires tracking the allele frequencies -within communities- of genes sustaining traits that are 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 from a community (Lowe *et al.*2017; Rudman *et al.* 2018), this becomes far more complicated when it comes to allele frequencies from genes of all species from a community, which is however what reality is (De Meester *et al.* 2019; Hendry 2019). Our dichotomic perception of intra- and interspecific diversity limits our capacity to built-up and understand eco-evolutionary dynamics beyond a (few) focal species within communities, which hence minimises 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 an inclusive biodiversity unit unifying the intra- and interspecific diversity components (Figure 1). We argue that this genetic metric of inclusive biodiversity may explain ecological processes, and may allow tracing eco-evolutionary dynamics directly from genes that are found in most species of a local community and that are important for ecological processes. Phylogenetically-conserved candidate genes are here defined as genetic sequences coding for important ecological traits (e.g., resource acquisition and transformation) and that are conserved across a broad range of organisms. Thanks to the development of high-throughput sequencing approaches, the diversity of hundreds of these genes can be revealed at the intra- and interspecific levels simultaneously, providing the raw material for a genome -and community- wide measure of biodiversity. As the dynamics of candidate genes is shaped by evolutionary processes, and as they code for important traits, they constitute an ideal basis to set new perspectives on the links between the

environment, biodiversity and the functioning of natural ecosystems, as well as on biodiversity conservation.

In this Perspective, we first develop the rationales motivating our idea that phylogenetically-conserved candidate genes (PCCGs) are ideal targets to unify biodiversity metrics across scales, we present examples from functional biology having linked these genes to ecologically important traits. We further provide technical guidelines regarding the methods available to sequence these genes and to estimate an inclusive metric of biodiversity from these genes. We finally expand on the main implications of measuring the diversity of PCCGs in natural (or experimental) communities, in particular for predicting the functioning and stability of ecosystems, for revealing the demographic and evolutionary processes shaping patterns of biodiversity, and for dissecting and tracing the feedbacks between ecological and evolutionary dynamics at the focal-community level (Figure 1).

From phylogenetically-conserved candidate genes to an inclusive unit of biodiversity

Definition of phylogenetically-conserved candidate genes

PCCGs are genes identified by functional biologists as having major effects on traits, and whose sequence and function are (at least partly) conserved across a broad range of species. This concerns genes coding for *ecologically important* traits, for instance traits associated (directly or indirectly) to resource acquisition or to interactions with other organisms (Skovmand *et al.* 2018). Many PCCGs have been identified by functional biologists, but this knowledge has poorly percolated into our scientific community, but for rare exceptions such as behavioural ecology (e.g., Fitzpatrick*et al.* 2005; Ducrest *et al.* 2008). We believe that we should build on this knowledge, and that PCCGs may be fundamental to unify facets of biodiversity.

Seminal works from the 90's have identified candidate genes sustaining traits that matter for fitness (Andersen & Lübberstedt 2003; Meinke *et al.* 2008; Chu *et al.* 2011; Schwander *et al.* 2014; Hassani-Pak & Rawlings 2017; Anreiter & Sokolowski 2019). In animals, some of these genes code for functional traits, such as foraging behaviour, metabolism or stoichiometry, that are strongly related to the acquisition of resources and/or its conversion into biomass (Brown *et al.*2004; Violle *et al.* 2007; Wolf & Weissing 2012). For instance, the Sokolowski's team identified a gene (the *for* gene) strongly controlling the foraging behaviour of *Drosophila melanogaster*(de Belle *et al.* 1989; Sokolowski 2001; Anreiter & Sokolowski 2019). This gene codes for a cGMP-dependent protein kinase (a signalling molecule) and encodes two main behavioural strategies: the rover strategy describing*Drosophila* larvae travelling long distance to feed, and the sitter strategy describing *Drosophila* larvae feeding in more restricted areas. This gene also impacts the food intake of individuals (rover larvae have lower food intake) and the food preference (rover larvae absorb higher glucose quantities) (Anreiter & Sokolowski 2019). We can reasonably expect that variation in 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 family of genes encoding transcription factors involved in flowering time, plant and floral architecture, and fruit, seed and root development (Schilling *et al.* 2018). MADS-box genes are key 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 for the function of pollination by insects (Schmidt*et al.* 2016).

This type of candidate genes is similar to (and is therefore 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 the purpose of our approach –contrary to Skovmand *et al* . (2018)– is not to search for rare EIGs with disproportionately large effects (what they called Keystone Genes, KGs), but rather to consider the impacts of a large number of these candidate genes (a hundred or more) with small to large individual contributions to traits and to ecological dynamics. Our approach acknowledges the idea that phenotypes likely arise from the collective effect of many genes with small effect sizes (Falconer 1981). Focusing on a large number of candidate genes should also offer the opportunity to identify *complementarity* and *redundancy* (in term 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 of our framework is that we focus on candidate genes that are *phylogenetically conserved* , meaning that they can be sequenced across a large range of species within communities. The fact that genes are ecologically important is not sufficient to warrant their integration across the intra-/interspecific biodiversity facets; they must also be phylogenetically conserved. Noteworthily, most candidate genes identified in model species are actually conserved (at least partly) across species. For instance, the *for* gene is extremely conserved, and its sequence can be retrieved from a large number of Invertebrate species (Sokolowski 2001; Anreiter & Sokolowski 2019). An ortholog -i.e., a gene whose the sequence has diverged over the course of evolution from a shared genetic ancestor- gene (*PRKG1*) identified in Vertebrates was found associated with foraging-like behaviour in humans, amphibians and small mammals (Anreiter & Sokolowski 2019; Struk *et al.* 2019). Similarly, the MADS-box gene complex has been identified in many taxonomic groups including mosses, gymnosperms and angiosperms (Gramzow & Theißen 2013; Schilling *et al.* 2018). Conservatism of candidate traits should actually be the norm rather than the exception given their importance for essential biological functions (Marden *et al.*2013; Barson *et al.* 2015; McGirr & Martin 2016; James *et al.* 2017).

Using PCCGs as target for measuring biodiversity inclusively is particularly attractive because the dynamics of PCCGs is shaped by demographic and (micro- and macro-) evolutionary processes, and because PCCGs likely code for important ecological traits and functions linked to ecological processes. PCCGs are therefore at the intersection of ecological and evolutionary dynamics, which makes them an ideal basis to identify new mechanisms linking the environment, biodiversity and the functioning of ecosystems. Hereafter, we provide insights into the concepts and tools currently available to inform PCCG diversity across species, and we provide a technical framework that forms the basis of future research (Figure 2).

Quantifying inclusive biodiversity from phylogenetically-conserved candidate genes

We hereafter describe the main steps to reveal PCCGs from focal communities (Figure 2). They mainly consist in (i) sampling specimens of a focal community and extracting the DNA, (ii) identifying from the literature (and databases) the genes and sequencing them, and (iii) quantifying PCCGs diversity and performing analyses.

Defining and sampling the focal community . A key step is to define the term "focal community". First, 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 can not be used to estimate the diversity of communities that contain species that are highly divergent (i.e., $>$20% molecular divergence, see hereafter). We further propose that the focal community from which PCCGs diversity is measured must follow an "ecological logic". Here, we therefore use the Hubbel's definition (2001): a focal community "is a group of trophically similar, sympatric species that actually or potentially compete in a local area for the same or similar resources". This definition (i) roots our approach into clearly-defined theoretical and conceptual grounds, and (ii) intrinsically satisfies our phylogenetic premise as a sympatric species sharing a similar resource are likely to be close phylogenetically. Of course, exceptions to this second premise exist, which means in these cases that the focal community would be split into "phylogenetic clusters". Examples of focal communities satisfying this definition are numerous: insectivorous fish, insect pollinators, desert plants, tropical trees, detritivorous insects, etc.

A second important step is to sample this focal community. The goal here is to sample all (or most) species of the focal community *and* the diversity within each species to estimate the entire diversity of the focal community. A first *a priori* approach would consist 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. An alternative "blinded" approach would consist in 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). This approach is technically feasible as -as explained later- the DNA of specimens can actually be pooled across species to investigate PCCGs diversity. Both approaches are valuable since both intra- and interspecific diversity are captured; the choice of one or the other will depend on the local context and objectives.

Identifying and selecting relevant PCCGs . The second crucial step concerns the selection of appropriate PCCGs (Figure 2b). We first draw the attention to a trade-off between intraspecific polymorphism and the conservatism of PCCGs. Then, we describe how to identify the most relevant traits associated with the targeted ecological process. Third, we describe how to use available literature to identify putative PCCGs coding for these traits. Finally, we describe some bioinformatic tools useful to recover *in silico* the sequences that best fit the species from the focal community (see Figure 3).

An important prerequisite is that PCCGs must be polymorphic both among and within species from the focal community. This condition is nonetheless complicated to meet for all PCCGs from a panel (assuming panels of 200-1000 genes or sequences per focal community), since genes that are highly polymorphic intraspecifically are generally not conserved among many species, and *vice versa* . For instance, developmental genes are generally extremely conserved among species, but are unlikely to be intraspecifically variable in most species from the focal community (Cardoso-Moreira*et al.* 2019). A compromise must therefore be reached to optimise the final choice of PCCGs, and a potential solution is to mix genes with various levels of conservatism in the PCCGs panel. This compromise 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 variables), and/or that some PCCGs from the panel will not display intraspecific polymorphism in most species from the focal community (i.e., genes that are expected to be conserved in all species).

The choice of relevant traits will mostly depend upon the targeted ecological process(es). For instance, for pollination, traits targeted in the plant community could be accessibility of floral reward, floral shape or colour and floral scent production (Klahre *et al.*2011; Naghiloo *et al.* 2020). For leaf litter decomposition in freshwaters, potential traits of a decomposer crustacean community associated with this function could be locomotion activity, body size or food assimilation (Rota *et al.*2018) (Figure 3a). As the PCCGs approach assumes that hundreds of genes with small effect sizes will be sequenced, it is mandatory to be inclusive rather than reductionist in trait selection. This list of traits will be the basis for searching associated candidate genes in the literature. Noteworthily, pleiotropic genes (i.e., genes that affect multiple traits) are excellent putative PCCGs as they are particularly relevant for linking traits to ecological processes and functions (Ducrest *et al.*2008; Watanabe *et al.* 2019). In the same vein, neutral genes (or sequences) randomly taken from the genome (or known to be neutral) can be added to the panel of genes to test for instance the role of selection *vs* . drift.

The existing literature relevant to identifying PCCGs is extensive, and merely relies on functional genomics (links between genes and traits) and functional ecology (links between traits and ecosystem processes) studies (Figure 3b). Candidate genes are directly identified from the profuse literature establishing a link between a gene and its phenotypic function at the individual level. Most of these studies are focusing on plant or animal models (*e.g.* , *Arabidopsis thaliana* ,*Zea mays* , *Mus musculus* , *Drosophila melanogaster* ,*Danio rerio* ...) and "semi-model" species (*Macrobrachium rosenbergii* , *Populus nigra* , *Cyprinus carpio* ...). Although natural communities often lack one of these species, our favourite biological models generally have a phylogenetic cousin from one of these models, making them relevant to identify putative PCCGs. Specific reviews focusing on candidate genes sustaining a particular trait (*e.g.* , 47 genes associated with crustacean growth, Jung *et al.* 2014; 98 genes associated with plant disease resistance, Sekhwal *et al.*2015) and study cases that have identified a specific gene polymorphism responsible for an individual trait variation are also valuable. For instance, for floral scent production (associated to pollination), existing studies identifies allelic variation at tree locus encoding the MYB transcription factor ODORANT1 (Klahre *et al.*2011), the LIMONENE-MYRCENE SYNTHASE (LM) and the OCIMENE SYNTHASE (OS) (Byers *et al.*2014). For food assimilation in crustaceans, GLUCOSE TRANSPORTER PROTEIN (Wang *et al.* 2016),

and CATHEPSIN L SYNTHESIS (Jung *et al.*2013) genes are two potential PCCGs. To summarise: basic information is already there, one just needs to dig into the literature linking genes to important traits to create a panel of hundreds putative PCCGs for a given trait or function (Figure 3b).

Usually, initial sequences of putative PCCGs can be retrieved directly from papers, or databases such as NCBI using appropriate keywords (Figure 3c). To continue on the example of floral scent production, gene sequences of LMS and OS are available both in the initial paper (Byers et al. 2014) and on NCBI ("ocimene synthase arabidopsis" ended-up with 9 hits in September 2022). The next step is to obtain the homologous sequences of these PCCGs on a species that is phylogenetically as close as possible from those of the focal community, or even better that belongs to the focal community. This step consists in blasting the sequences (Figure 3d) found on model species in appropriate search engines (or in the home-made reference genome(s) of your favourite species) to search for their homology in the reference genome(s) that is(are) the closest from the focal community. These final PCCG sequences will best match the phylogenetic composition of the focal community (see Faircloth 2017 for further details).

Sequencing hundreds of PCCGs across species . PCCGs sequencing benefits from the recent development of target enrichment methods (capture of specific regions of the genome, Mertes *et al.* 2011; Jones & Good 2016; Jiménez-Mena *et al.* 2022). Here, we focus on the hybridization-based capture sequencing (HBCS) method which is classically used in phylogenomic studies and efficient to retrieve sequences from species that display up to 20% of molecular divergence (Hawkins *et al.*2016). The general principle of HBCS is to design oligonucleotides (called "probes" or "baits") that are complementary to the target (PCCG) sequences. These oligos enrich complementary sequences from an Next-Generation-Sequencing (NGS) library. The classical NGS library preparation workflow is completed by the capture of targeted sequences before the sequencing step, which reduces the size of the library and hence the sequencing cost. This method has been described in 2007 and has been used in many taxa (Albert *et al.*2007; Mamanova *et al.* 2010); some studies are thoroughly describing its use and potential for evolution (Faircloth 2017; Jimenez-Mena *et al.* 2022). A main advantage -compared to traditional approach based on PCR enrichment- is that HBCS allows for large mismatches between probes and the target sequences, allowing to sequence species that diverge by 15-20%; this threshold is the one that should (ideally) be used to define the appropriate focal species. As said above, if the focal community contains species with a higher level of divergence, it is possible to develop several probe sets according to "phylogenetic clusters" (species from the focal species that are below the 20% divergence threshold).

HBCS can be performed (i) at the individual level in which case all individuals from all species are sequenced independently, or (ii) at the focal community level in which case the DNA of all individuals from all species of the community are pooled (from 50-100 individuals per pool, Schlotterer *et al.* 2014; Abrams *et al.* 2021) and this DNA pool is then sequenced. Individual-based sequencing is more costly but provides more precise information that can be used to relate specific gene polymorphism to individual traits or to ecological processes for instance. In contrast, pool-seq approaches are extremely affordable given the current power of sequencers. For instance, for 48 focal communities, each composed of 10 species (from which we sampled 5 individuals per species), the cost for DNA extraction, library preparation, capture and sequencing would be ~240000 euros if performed at the individual level, whereas it would be ~10000 euros if performed using a pooled-seq approach. Information acquired with pool-seq approaches does not provide individual data, but it is actually sufficient to get allele frequencies for each marker (Sham *et al.*2002; Gautier *et al.* 2022), and hence to estimate inclusive biodiversity from PCCGs (see hereafter). Moreover, pool-seq approaches are increasingly being used with astonishing successes, and many tools have been developed for improving evolutionary inferences from these data (Schlotterer*et al.* 2014; Gautier *et al.* 2022). Pool-seq approaches are hence in our opinion the best option for developing the PCCGs approach in a wide range of contexts.

Defining metrics for estimating PCCGs diversity of focal communities . Given that raw data obtained from HBCS are DNA sequences, all metrics used by population geneticists and community phylogeneticists can be used to describe biodiversity patterns. Overall, biodiversity metrics must follow the classical diversity partitioning proposed by ecologists in the 1960's (Whittaker 1960), including: a and γ components as the

local and regional diversity components, and the ß component quantifies the diversity differentiation among local sites. This framework was initially applied to communities and variation in species diversity within and between local sites, and was extended to trait and phylogenetic measures of (meta-)community diversity (Pavoine & Bonsall 2011; Mouquet *et al.* 2012; Pavoine & Izsák 2014b; Tucker*et al.* 2017; Carmona *et al.* 2019b). Population geneticists (and ecologists) recognized that the metrics traditionally used to describe genetic diversity patterns in (meta-)populations (such as the allelic richness or Fst) actually conform to the Whittaker's framework, that tight (statistical) connections exist between the "population" and "community" approaches, and that developing a unified framework to analyse diversity patterns across populations and communities would be beneficial (Vellend 2005; Jost 2008; Gaggiotti *et al.* 2018). Many papers discussed the specific metrics that should be used to unify disciplines (e.g., Gaggiotti*et al.* 2018), but we do not intend to orient readers to a specific type of metrics, as they all have their advantages and disadvantages, and the choice of a metric should be dictated by the scientific goals (Mouquet *et al.*2012; Tucker *et al.* 2017). For instance, the Fst provides estimates and information on drift (Holsinger & Weir 2009), whereas some dissimilarity metrics can provide precise cues about the relative role of nestedness and turnover for explaining regional patterns of ß-diversity (Baselga 2010). Nonetheless, we underline that the choice of inclusive biodiversity metrics derived from PCCGs must follow the principle that intra- and interspecific diversity are actually 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.

Concretely, one needs to consider the type of data that can be gathered either from individual or pooled sequencing approaches. In the first case, the data consist of a series of aligned DNA sequences, each attributed to a single specimen and to a given gene. SNP loci (including both intra- and interspecific SNPs) and haplotypes that groups all loci from a given sequence (or gene) can be derived from these data. SNPs are classical bi-allelic loci from which many types of metrics can be derived; the number of polymorphic SNPs estimated from PCCGS can be compared among communities (a community composed of a few species will likely have a lower number of polymorphic SNPs than a community composed of many species, even if the former is rich intraspecifically), the evenness can be derived from allele frequencies, as well as the differentiation (dissimilarity) among local communities (e.g., Gaggiotti*et al.* 2018), etc. Haplotypes can be used to draw phylogenetic trees (including both intraspecific and interspecific tips) from which all types of phylogenetic metrics of community can be derived (Tucker *et al.*2017). Possibilities are more restricted for the pool-seq approach. In that case, a series of SNPs are therefore retrieved, together with their relative frequency within the community; alleles can not be attributed to a particular species or a particular individual within a species, which impedes the reconstruction of haplotypes. For pool-seq approaches, the metrics derived from SNP data (including information on allele frequencies) are therefore favoured (Schlötterer *et al.* 2014).

Implications for BEFs: BEFs across biodiversity and spatial scales

BEF relationships have historically used species richness to quantify the diversity of communities (Hooper *et al.*2005). However, alternative approaches have emerged and improved our understanding of BEFs. In particular, phylogenetic diversity and/or functional traits diversity have been used as alternative measures of community diversity (*e.g.*, Cadotte*et al.* 2012; Le Bagousse-Pinguet *et al.* 2019). Functional (trait) diversity has improved mechanistic inferences and revealed the causal mechanisms underlying BEFs (Norberg *et al.*2001; Cadotte *et al.* 2011). The use of phylogenetic diversity metrics 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 to estimate community diversity has the potential to encompass most aspects of the phylogenetic and functional approaches because PCCGs are intrinsically related to functional traits, and they are directly influenced by evolutionary processes. By aggregating both the functional and evolutionary components of diversity, we anticipate using PCCGs for studying BEF relationships 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 approach we propose here intrinsically includes both the intra- and interspecific facets of biodiversity, which is -in our opinion- an important step forward 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 revealed relevant insights (*e.g.*, Fridley & Grime 2010; Hargrave *et al.* 2011). In particular, they demonstrated that the relative effect of intra- *vs* . interspecific diversity was dependent upon the considered function. 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 an ecological complementarity between intra- and interspecific diversity that can not be revealed if only one of them is considered. While valuable, these studies failed to reproduce the continuum naturally occuring in nature, which would be overcome using the PCCGs approach that quantifies the two facets of biodiversity. This is an essential step for better understanding this potential complementarity along the intra-interspecific biodiversity continuum.

In addition, more specific -yet unresolved- 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 specific function (Huston 1997). The performance of a species in monoculture is likely determined -amongst others- by its intraspecific diversity that can be revealed using PCCGs (Figure 4b). Species with higher performance should be more diversified, as expected if genetic complementarity (or the presence of particular genetic variants in that species) is linked to species performance (Hughes*et al.* 2008). Moreover, as a consequence of these differences in monocultures' productions, species-rich communities might show high performances solely 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 -rather than diversity metrics at the species level- 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* , or because containing this species increases substantially PCCGs diversity (Figure 4c). By accounting for intra- and inter-specific diversity, PCCGs quantifies the "true" diversity present in the community, and allows forecasting ecosystem functions based on biodiversity with finer precision.

More generally, PCCGs diversity can reveal different patterns of biodiversity, and for instance communities with the same species richness might actually encompass different levels of PCCGs diversity (Figure 4c), and an apparently poor community might be as diverse as a community with many species 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 as a continuous and realistic metric. This is particularly interesting when comparing, for example, the ecological efficiency (in terms of functions) of communities from different biomes. For instance, 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 (although not necessarily true, De Kort *et al.* 2021), and *vice versa* . We can hypothesise that communities at higher latitudes mainly rely on intraspecific diversity and 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 universal metric. This is essential for scaling-up BEF relationships to local from global scales (Gonzalez*et al.* 2020).

To sum up, PCCGs have the potential to be an inclusive measure of biodiversity tackling pending questions on BEF relationships. Assessing the ecological effects of diversity of communities through genes underlying ecologically-important traits, also permits rooting BEF relationships into an (eco-)evolutionary framework, which we discuss in the next section.

PCCGs implications for eco-evolutionary dynamics: toward focal-community eco-evolutionary dynamics

Evolutionary processes acting over micro- and macro-evolutionary scales are shaping the diversity of PCCGs. The PCCG diversity of a focal community is governed by its past demographic and evolutionary history, which encompasses geological processes (*e.g.* , isolation from a glacial refugee) and contemporary processes (*e.g.* , recent bottlenecks). If we assume that PCCGs are governing ecological dynamics, it appears that quantifying biodiversity from PCCGs is particularly relevant for predicting reciprocal feedbacks between ecological and evolutionary dynamics (Schoener 2011).

Considering PCCGs for measuring inclusive biodiversity and 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 feedbacks have considered feedbacks between evolutionary processes acting within a single species and ecosystem processes (Schoener 2011; De Meester *et al.* 2019; Hendry 2019); evolution alters gene frequencies and trait distribution within a species, which alters ecological dynamics, the laters potentially altering further the evolutionary dynamics of the focal species (Matthews *et al.* 2014, 2016). 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, that themselves feedback to the gene pool of the focal community (but see, Norberg*et al.* 2012; Aubree *et al.* 2019; Moorsel *et al.*2019). Thus, with PCCGs measured inclusively in a community, the "focal-species approach" traditionally used in most eco-evolutionary dynamics studies will naturally shift toward a "focal-community" perspective (De Meester *et al.* 2019; Hendry 2019; Govaert *et al.* 2021), making more realistic empirical eco-evolutionary studies. Here after, we detail three perspectives for exploring the implications of PCCGs for eco-evolutionary dynamics.

First, our basic premise is that spatial and temporal patterns of PCCG diversity must be uncovered in various communities to reveal the underlying evolutionary and demographic processes. While studies on patterns of intra- and interspecific diversity have often been partitioned, there is growing calls for merging knowledge from ecology and evolutionary biology into a single integrative framework (Hubbell 2001; Vellend 2005; Bolnick *et al.* 2011; Gaggiotti *et al.* 2018). In particular, Hubbell (2001) and Vellend (2005) proposed that spatial patterns of intraspecific (gene) diversity and interspecific (species) diversity can be understood through similar processes (natural selection/environmental filtering, gene flow/dispersal, genetic drift/ecological drift, mutation/speciation) acting over time in populations and communities. This was an important step toward the unification of empirical patterns of biodiversity (e.g., Taberlet*et al.* 2012; Vellend *et al.* 2014; Laroche *et al.*2015; Fourtune *et al.* 2016; Manel *et al.* 2020). Nonetheless, in all these studies the two facets of diversity are still dichotomized (see also, Govaert *et al.* 2021). Here, by quantifying diversity of genes that transcend this dichotomic boundary, we take the 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 (meta-)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 homogenise the gene frequencies among local communities; and drift acts on genes, which eventually differentiate local communities. Population geneticists have developed a surge of theories and tools to infer processes over various time scales, which eases inferences (from patterns) of local and regional processes shaping biodiversity (Lowe *et al.*2017). In our opinion, a first important perspective would therefore be to reveal these patterns of PCCGs at different spatial and temporal scales, in different environmental contexts and taxonomic groups. Understanding patterns of PCCGs diversity allow for a thorough evaluation of the evolutionary processes governing gene frequencies in focal communities, and hence to relate the potential for eco-evolutionary dynamics to *both* adaptive (selection) and non-adaptive processes (gene flow, drift, mutation), since both can contribute to the evolution of traits in communities (Lowe *et al.*2017). This is in our opinion an important starting point as this contributes to embrace a more realistic perspective of empirical eco-evolutionary dynamics (Norberg *et al.*2012; De Meester *et al.* 2019).

Secondly, we suggest that considering 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-(meta-)community" approach (De Meester *et al.* 2019; Hendry 2019). We know from long-term BEF experiments in plants that (i) evolutionary dynamics are different among plant species having been seeded in plots with different

levels of interspecific diversity (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 alters plant productivity under some conditions (evolution-to-ecology, *e.g.* , van Moorsel *et al.* 2018). This really looks like an eco-evolutionary dynamics occurring at the community level, and theoretical models of BEFs are now integrating the potential for community evolution as a driver/modulator of ecological functions and their stability (*e.g.*, Loeuille 2010; Aubree *et al.* 2020). Eco-evolutionary dynamics involving the evolution of communities have been further suggested in experiments manipulating microorganisms (*e.g.*, Gravel *et al.* 2010; Lawrence *et al.* 2012; Faillace & Morin 2017), 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 a tracking and therefore breaks down a major wall (to quote Loreau *et al.* 2022). This genetic tracking can be done in the wild, and alternatively it becomes possible to assemble focal (meta-)communities -in common gardens, Matthews *et al.*2011- varying according to their PCCGs diversity, and then to track over time the consequences of this diversity on ecological processes, and reciprocally the consequences of the later on PCCGs diversity.

Finally, a PCCGs approach allows identifying the genetic sequences that matter for ecology (Skovmand *et al.* 2018) and their distribution in (meta-)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 (non-heritable) and a genetic component, the latter being central for 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 non-heritable components into the eco-evolutionary equation, and allows to focus more tightly on the "genes that matter". Classical genome-wide-association approaches (GWAs) can be used to relate genomic (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 for ecological processes may be concentrated in a single species or multiple species, and may be spread (or not) over multiple genes. In the same way, gene complementarity may 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. These questions remain -up to our knowledge- largely unexplored even theoretically, although they 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 is possible. For instance, it has recently been shown that epigenetic marks play a pivotal role for controlling the sitter/rover behaviour associated to 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.

Concluding remarks

The framework we propose here provides a novel perspective to quantify biodiversity, which may allow breaking the historical boundary between the intra- and interspecific facets of diversity. We hope that we have been convincing enough in demonstrating that using this novel framework has the potential to substantially change our ability to understand the reciprocal links between environmental changes, biodiversity and ecosystem dynamics. There has been previous attempts to break this boundary (*e.g.*, Vellend 2005; Gaggiotti *et al.* 2018; Start & Gilbert 2019), but our approach differs from previous ones in that it is rooted on the idea of a single biodiversity unit that goes beyond the species concept, that is directly affected by demographic and evolutionary processes and that putatively affects ecological processes. This approach is somewhat similar to that used by microbiologists (*e.g.*, Konopka 2009; Burke *et al.* 2011; Morris *et al.* 2019) that uses molecular markers to characterise bacterial communities, mainly because specifically naming bacteria is an unresolvable and irrelevant issue. Our approach is also "agnostic" (*sensu* Morris *et al.* 2019) 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 in a certain sense join the neutral perspective developed by Hubbell (2001).

The PCCGs approach is based on the sum of data and knowledge acquired in the last decades from functional

biologists and geneticists. Contrary to recent perspectives (Rudman *et al.*2018; Skovmand *et al.* 2018), we do not aim to search for "new" candidate genes with extremely strong ecological effects (Skovmand et al. 2018). Although this quest for keystone genes is valuable and necessary, we rather believe that novel insights can emerge by merging previous findings from research fields that are yet poorly connected. Moreover (and more pragmatically), we are in an Era in which all of us must be aware about our energy consumption. Looking for novel candidate genes in a few species is costly energetically given that this requires sequencing entire genomes, archiving these data, and long bioinformatic runs. The PCCGs approach is based on sequences that already exist and that represents relatively short sequence lengths to reveal (portions of 500 hundreds PCCGs represents ˜200000 bp, which is a tiny portion of entire genomes that are often billions bp each, Figure 4), and hence much less energy consumption overall. This is even more evident when pool-seq approaches are used (see above) as tens of communities can be sequenced on a single lane. Of course, our *a priori* approach is not without limitations, and it is evident that important genes will be missed, whereas they would have been revealed from a keystone gene approach. Both approaches are therefore valuable and should be pursued. But we underline that controlling the energy we consume for Science should also be our collective responsibility.

Another limit of the PCCGs approach is that it only focuses on genes that code for important ecological traits, while ignoring functional trait variability observed in the wild. The main implication is that the environmental component of trait variability is missed. There has been some attempts to link traits measured at the community level (including or not intraspecific variability) and ecological processes and functions (*e.g.*, Le Bagousse-Pinguet *et al.* 2019; Start & Gilbert 2019), and we fully acknowledge that this is certainly an excellent way to illuminate mechanistic pathways (Norberg *et al.*2001). Nonetheless, traits can be tricky to estimate, especially for animals when trait measurements need to be done under laboratory conditions (*e.g.* , behavioural traits), which can bias estimations. Moreover, some important traits may be missed while being captured by genetic diversity of populations of communities ("ghost" traits); for instance, Raffard *et al* . (2021) found that both traits diversity and genetic diversity in fish populations were complementary for explaining a series of ecological processes. Because the PCCGs approach is based on a large number of genes, this "missing" information may be limited. Finally, for eco-evolutionary dynamics, what matters is the information that is transmitted across generations (De Meester *et al.* 2019), and the environment is rarely (but see Danchin*et al.* 2011) transmitted across generations. Focusing directly on the genes that potentially sustain trait variation therefore allows for a better integration of biodiversity into the framework of eco-evolutionary dynamics.

To conclude, we suspect that the approach we described here has many implications that actually goes 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 begins by simplifying premises (Loreau 1998; Norberg *et al.* 2001; Govaert *et al.* 2019). We now hope that empiricists and theoreticians will be convinced enough that future works integrating PCCGs will soon emerge.

References

Abrams, A.N., McDaneld, T.G., Keele, J.W., Chitko-McKown, C.G., Kuehn, L.A. & Gonda, M.G. (2021). Evaluating Accuracy of DNA Pool Construction Based on White Blood Cell Counts. *Front. Genet.*, 12, 635846.

Albert, T.J., Molla, M.N., Muzny, D.M., Nazareth, L., Wheeler, D., Song, X., *et al.*(2007). Direct selection of human genomic loci by microarray hybridization. *Nat. Methods*, 4, 903–905.

Andersen, J.R. & Lübberstedt, T. (2003). Functional markers in plants. *Trends Plant Sci.*, 8, 554–560.

Anreiter, I., Kramer, J.M. & Sokolowski, M.B. (2017). Epigenetic mechanisms modulate differences in *Drosophila* foraging behavior. *Proc. Natl. Acad. Sci.*, 114, 12518–12523.

Anreiter, I. & Sokolowski, M.B. (2019). The *foraging* Gene and Its Behavioral Effects: Pleiotropy and Pla-

sticity. *Annu. Rev. Genet.*, 53, 373–392.

Aubree, F., David, P., Jarne, P., Loreau, M., Mouquet, N. & Calcagno, V. (2020). How community adaptation affects biodiversity-ecosystem functioning relationships.*Ecol. Lett.*, 23, 1263-1275.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D., *et al.* (2006). Quantifying the evidence for biodiversity effects on ecosystem functioning and services: Biodiversity and ecosystem functioning/services. *Ecol. Lett.*, 9, 1146–1156.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B.,*et al.* (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, 471, 51–57.

Barson, N.J., Aykanat, T., Hindar, K., Baranski, M., Bolstad, G.H., Fiske, P., *et al.*(2015). Sex-dependent dominance at a single locus maintains variation in age at maturity in salmon. *Nature*, 528, 405–408.

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity: Partitioning beta diversity. *Glob. Ecol. Biogeogr.*, 19, 134–143.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012). Impacts of climate change on the future of biodiversity: Biodiversity and climate change. *Ecol. Lett.*, 15, 365–377.

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, 157–163.

Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M.,*et al.* (2011). Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.*, 26, 183–192.

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

Burke, C., Steinberg, P., Rusch, D., Kjelleberg, S. & Thomas, T. (2011). Bacterial community assembly based on functional genes rather than species. *Proc. Natl. Acad. Sci.*, 108, 14288–14293.

Byers, K.J.R.P., Vela, J.P., Peng, F., Riffell, J.A. & Bradshaw, H.D. (2014). Floral volatile alleles can contribute to pollinator-mediated reproductive isolation in monkeyflowers (*Mimulus*). *Plant J.*, 80, 1031–1042.

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. *J. Appl. Ecol.*, 48, 1079–1087.

Cadotte, M.W., Dinnage, R. & Tilman, D. (2012). Phylogenetic diversity promotes ecosystem stability. *Ecology*, 93, S223–S233.

Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P.,*et al.* (2012). Biodiversity loss and its impact on humanity.*Nature*, 486, 59–67.

Cardoso-Moreira, M., Halbert, J., Valloton, D., Velten, B., Chen, C., Shao, Y., *et al.*(2019). Gene expression across mammalian organ development.*Nature*, 571, 505–509.

Carmona, C.P., Bello, F., Mason, N.W.H. & Lepš, J. (2019). Trait probability density (TPD): measuring functional diversity across scales based on TPD with R.*Ecology*, 100, e02816.

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

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., *et al.* (2000). Consequences of changing biodiversity.*Nature*, 405, 234–242.

Cho, L.-H., Yoon, J. & An, G. (2017). The control of flowering time by environmental factors. *Plant J.*, 90, 708–719.

Chu, H.Y., Wegel, E. & Osbourn, A. (2011). From hormones to secondary metabolism: the emergence of metabolic gene clusters in plants: The emergence of metabolic gene clusters in plants. *Plant J.*, 66, 66–79.

Crutsinger, G.M., Collins, MD, Fordyce, J.A., Gompert, Z., Nice, C. & Sanders, N.J. (2006). Plant Genotypic Diversity Predicts Community Structure and Governs an Ecosystem Process. *Science*, 313, 966–968.

Danchin, É., Charmantier, A., Champagne, F.A., Mesoudi, A., Pujol, B. & Blanchet, S. (2011). Beyond DNA: integrating inclusive inheritance into an extended theory of evolution. *Nat. Rev. Genet.*, 12, 475–486.

De Kort, H., Prunier, J.G., Ducatez, S., Honnay, O., Baguette, M., Stevens, V.M., *et al.* (2021). Life history, climate and biogeography interactively affect worldwide genetic diversity of plant and animal populations. *Nat. Commun.*, 12, 516.

De Meester, L., Brans, K.I., Govaert, L., Souffreau, C., Mukherjee, S., Vanvelk, H., *et al.* (2019). Analysing eco-evolutionary dynamics—The challenging complexity of the real world. *Funct. Ecol.*, 33, 43–59.

Ducrest, A., Keller, L. & Roulin, A. (2008). Pleiotropy in the melanocortin system, coloration and behavioural syndromes. *Trends Ecol. Evol.*, 23, 502–510.

Faillace, C.A. & Morin, P.J. (2017). Evolution alters the consequences of invasions in experimental communities. *Nat. Ecol. Evol.*, 1, 0013.

Faircloth, B.C. (2017). Identifying conserved genomic elements and designing universal bait sets to enrich them. *Methods Ecol. Evol.*, 8, 1103–1112.

Falconer, D. (1981).*Introduction to Quantitative Genetics*. Longman Group Limited, New York.

Fitzpatrick, M.J., Ben-Shahar, Y., Smid, H.M., Vet, L.E., Robinson, G.E. & Sokolowski, M.B. (2005). Candidate genes for behavioural ecology. *Trends Ecol. Evol.*, 20, 96–104.

Fourtune, L., Paz-Vinas, I., Loot, G., Prunier, J.G. & Blanchet, S. (2016). Lessons from the fish: a multispecies analysis reveals common processes underlying similar species-genetic diversity correlations. *Freshw. Biol.*, 61, 1830–1845.

Fridley, J.D. & Grime, J.P. (2010). Community and ecosystem effects of intraspecific genetic diversity in grassland microcosms of varying species diversity.*Ecology*, 91, 2272–2283.

Gaggiotti, O.E., Chao, A., Peres-Neto, P., Chiu, C.-H., Edwards, C., Fortin, M.-J., *et al.* (2018). Diversity from genes to ecosystems: A unifying framework to study variation across biological metrics and scales. *Evol. Appl.*, 11, 1176–1193.

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*. *Mol. Ecol. Resour.*, 22, 1394–1416.

Gonzalez, A., Germain, R.M., Srivastava, D.S., Filotas, E., Dee, L.E., Gravel, D., *et al.* (2020). Scaling-up biodiversity-ecosystem functioning research.*Ecol. Lett.*, 23, 757–776.

Govaert, L., Altermatt, F., De Meester, L., Leibold, M.A., McPeek, M.A., Pantel, J.H., *et al.* (2021). Integrating fundamental processes to understand eco-evolutionary community dynamics and patterns.*Funct. Ecol.*, 35, 2138–2155.

Govaert, L., Fronhofer, E.A., Lion, S., Eizaguirre, C., Bonte, D., Egas, M., *et al.* (2019). Eco-evolutionary feedbacks—Theoretical models and perspectives. *Funct. Ecol.*, 33, 13–30.

Gramzow, L. & Theissen, G. (2013). Phylogenomics of MADS-Box Genes in Plants — Two Opposing Life Styles in One Gene Family. *Biology*, 2, 1150–1164.

Gravel, D., Bell, T., Barbera, C., Bouvier, T., Pommier, T., Venail, P., *et al.* (2010). Experimental niche evolution alters the strength of the diversity–productivity relationship. *Nature*, 469, 89–92.

Hagan, J.G., Vanschoenwinkel, B. & Gamfeldt, L. (2021). We should not necessarily expect positive relationships between biodiversity and ecosystem functioning in observational field data. *Ecol. Lett.*, 24, 2537–2548.

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, 1226–1235.

Hassani-Pak, K. & Rawlings, C. (2017). Knowledge Discovery in Biological Databases for Revealing Candidate Genes Linked to Complex Phenotypes. *J. Integr. Bioinforma.*, 14.

Hawkins, M.T.R., Hofman, C.A., Callicrate, T., McDonough, M.M., Tsuchiya, M.T.N., Gutierrez, E.E., *et al.* (2016). In-solution hybridization for mammalian mitogenome enrichment: pros, cons and challenges associated with multiplexing degraded DNA. *Mol. Ecol. Resour.*, 16, 1173–1188.

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

Hendry, A.P. (2019). A critique for eco-evolutionary dynamics. *Funct. Ecol.*, 33, 84–94.

Hendry, A.P., Farrugia, T.J. & Kinnison, M.T. (2008). Human influences on rates of phenotypic change in wild animal populations. *Mol. Ecol.*, 17, 20-29. doi:10.1111/j.1365.

Holsinger, K.E. & Weir, B.S. (2009). Genetics in geographically structured populations: defining, estimating and interpreting FST. *Nat. Rev. Genet.*, 10, 639–650.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., *et al.*(2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecol. Monogr.*, 75, 3–35.

Hubbell, S. (2001).*The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, New Jersey.

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. *Ecol. Lett.*, 11, 609–623.

Hughes, A.R. & Stachowicz, J.J. (2004). Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proc. Natl. Acad. Sci.*, 101, 8998–9002.

Huston, M.A. (1997). Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, 110, 449–460.

James, A.M., Ma, D., Mellway, R., Gesell, A., Yoshida, K., Walker, V., *et al.* (2017). Poplar MYB115 and MYB134 Transcription Factors Regulate Proanthocyanidin Synthesis and Structure. *Plant Physiol.*, 174, 154–171.

Jimenez-Mena, B., Flavio, H., Henriques, R., Manuzzi, A., Ramos, M., Meldrup, D., *et al.* (2022). Fishing for DNA? Designing baits for population genetics in target enrichment experiments: Guidelines, considerations and the new tool supeRbaits. *Mol. Ecol. Resour.*, 22, 2105–2119.

Jones, M.R. & Good, J.M. (2016). Targeted capture in evolutionary and ecological genomics.*Mol. Ecol.*, 25, 185–202.

Jost, L. (2008).G_{ST} and its relatives do not measure differentiation. *Mol. Ecol.*, 17, 4015–4026.

Jung, H., Lyons, R.E., Hurwood, D.A. & Mather, P.B. (2013). Genes and growth performance in crustacean species: a review of relevant genomic studies in crustaceans and other taxa. *Rev. Aquac.*, 5, 77–110.

Jung, H., Lyons, R.E., Li, Y., Thanh, N.M., Dinh, H., Hurwood, D.A., *et al.* (2014). A Candidate Gene Association Study for Growth Performance in an Improved Giant Freshwater Prawn (*Macrobrachium rosenbergii*) Culture Line.*Mar. Biotechnol.*, 16, 161–180.

Klahre, U., Gurba, A., Hermann, K., Saxenhofer, M., Bossolini, E., Guerin, P.M., *et al.*(2011). Pollinator Choice in Petunia Depends on Two Major Genetic Loci for Floral Scent Production. *Curr. Biol.*, 21, 730–739.

Konopka, A. (2009). What is microbial community ecology? *ISME J.*, 3, 1223–1230.

Laroche, F., Jarne, P., Lamy, T., David, P. & Massol, F. (2015). A Neutral Theory for Interpreting Correlations between Species and Genetic Diversity in Communities. *Am. Nat.*, 185, 59–59.

Lawrence, D., Fiegna, F., Behrends, V., Bundy, J.G., Phillimore, A.B., Bell, T., *et al.*(2012). Species Interactions Alter Evolutionary Responses to a Novel Environment. *PLoS Biol.*, 10, e1001330.

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.*Proc. Natl. Acad. Sci.*, 116, 8419–8424.

Leigh, D.M., Hendry, A.P., Vazquez-Dominguez, E. & Friesen, V.L. (2019). Estimated six per cent loss of genetic variation in wild populations since the industrial revolution. *Evol. Appl.*, 12, 1505–1512.

Loeuille, N. (2010). Influence of evolution on the stability of ecological communities: Evolution and stability of communities. *Ecol. Lett.*, 13, 1536–1545.

Loreau, M. (1998). Biodiversity and ecosystem functioning: A mechanistic model. *Proc. Natl. Acad. Sci.*, 95, 5632–5636.

Loreau, M., Jarne, P. & Martiny, J. (2022). *Breaking down the wall between ecology and evolution* (preprint). Preprints.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., *et al.*(2001). Biodiversity and ecosystem functioning: Current knowledge and future challenges. *Science*, 294, 804–808.

Lowe, W.H., Kovach, R.P. & Allendorf, F.W. (2017). Population Genetics and Demography Unite Ecology and Evolution. *Trends Ecol. Evol.*, 32, 141–152.

Mamanova, L., Coffey, A.J., Scott, C.E., Kozarewa, I., Turner, E.H., Kumar, A., *et al.*(2010). Target-enrichment strategies for next-generation sequencing.*Nat. Methods*, 7, 111–118.

Manel, S., Guerin, P.-E., Mouillot, D., Blanchet, S., Velez, L., Albouy, C., *et al.*(2020). Global determinants of freshwater and marine fish genetic diversity. *Nat. Commun.*, 11, 692.

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, 1105–1115.

Matthews, B., Aebischer, T., Sullam, K.E., Lundsgaard-Hansen, B. & Seehausen, O. (2016). Experimental Evidence of an Eco-evolutionary Feedback during Adaptive Divergence. *Curr. Biol.*, 26, 483–489.

Matthews, B., De Meester, L., Jones, C.G., Ibelings, B.W., Bouma, T.J., Nuutinen, V.,*et al.* (2014). Under niche construction: an operational bridge between ecology, evolution, and ecosystem science. *Ecol. Monogr.*, 84, 245–263.

Matthews, B., Narwani, A., Hausch, S., Nonaka, E., Peter, H., Yamamichi, M., *et al.*(2011). Toward an integration of evolutionary biology and ecosystem science. *Ecol. Lett.*, 14, 690–701.

McGirr, J.A. & Martin, C.H. (2016). Novel candidate genes underlying extreme trophic specialization in Caribbean pupfishes. *Mol. Biol. Evol.*, msw286.

Meinke, D., Muralla, R., Sweeney, C. & Dickerman, A. (2008). Identifying essential genes in Arabidopsis thaliana. *Trends Plant Sci.*, 13, 483–491.

Mertes, F., ElSharawy, A., Sauer, S., van Helvoort, J.M.L.M., van der Zaag, P.J., Franke, A., *et al.* (2011). Targeted enrichment of genomic DNA regions for next-generation sequencing. *Brief. Funct. Genomics*, 10, 374–386.

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. *Mol. Ecol.*, 28, 4097–4117.

van Moorsel, S.J., Hahl, T., Wagg, C., De Deyn, G.B., Flynn, D.F.B., Zuppinger-Dingley, D., *et al.* (2018). Community evolution increases plant productivity at low diversity. *Ecol. Lett.*, 21, 128–137.

Morris, A.H., Meyer, K.M. & Bohannan, B.J.M. (2019). *Linking microbial communities to ecosystem functions: what we can learn from genotype-phenotype mapping in organisms* (preprint). Ecology.

Mouquet, N., Devictor, V., Meynard, C.N., Munoz, F., Bersier, L.-F., Chave, J., *et al.*(2012). Ecophylogenetics: advances and perspectives. *Biol. Rev.*, 87, 769–785.

Naghiloo, S., Bellstedt, D.U. & Classen-Bockhoff, R. (2020). Pollination biology in *Roepera* (Zygophyllaceae): How flower structure and shape influence foraging activity. *Plant Species Biol.*, 35, 72–80.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., *et al.*(2015). Global effects of land use on local terrestrial biodiversity. *Nature*, 520, 45–50.

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. *Proc. Natl. Acad. Sci.*, 98, 11376–11381.

Norberg, J., Urban, M.C., Vellend, M., Klausmeier, C.A. & Loeuille, N. (2012). Eco-evolutionary responses of biodiversity to climate change. *Nat. Clim. Change*, 2, 747–751.

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

Pavoine, S. & Bonsall, M.B. (2011). Measuring biodiversity to explain community assembly: a unified approach. *Biol. Rev.*, 86, 792–812.

Pavoine, S. & Izsak, J. (2014). New biodiversity measure that includes consistent interspecific and intraspecific components. *Methods Ecol. Evol.*, 5, 165–172.

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. *Nat. Plants*, 1, 15033.

Raffard, A., Cucherousset, J., Montoya, J.M., Richard, M., Acoca-Pidolle, S., Poesy, C., *et al.* (2021). Intraspecific diversity loss in a predator species alters prey community structure and ecosystem functions. *PLOS Biol.*, 19, e3001145.

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. *Biol. Rev.*, 94, 648–661.

Reusch, T.B.H., Ehlers, A., Hammerli, A. & Worm, B. (2005). Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proc. Natl. Acad. Sci.*, 102, 2826–2831.

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, 1670–1678.

Rudman, S.M., Barbour, M.A., Csillery, K., Gienapp, P., Guillaume, F., Hairston Jr, N.G., *et al.* (2018). What genomic data can reveal about eco-evolutionary dynamics. *Nat. Ecol. Evol.*, 2, 9–15.

Schilling, S., Pan, S., Kennedy, A. & Melzer, R. (2018). MADS-box genes and crop domestication: the jack of all traits. *J. Exp. Bot.*, 69, 1447–1469.

Schlotterer, C., Tobler, R., Kofler, R. & Nolte, V. (2014). Sequencing pools of individuals — mining genome-wide polymorphism data without big funding. *Nat. Rev. Genet.*, 15, 749–763.

Schmidt, N.M., Mosbacher, J.B., Nielsen, P.S., Rasmussen, C., Hoye, 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, 1250–1252.

Schoener, T.W. (2011). The Newest Synthesis: Understanding the Interplay of Evolutionary and Ecological Dynamics. *Science*, 331, 426–429.

Schwander, T., Libbrecht, R. & Keller, L. (2014). Supergenes and Complex Phenotypes.*Curr. Biol.*, 24, R288–R294.

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, 931–936.

Sekhwal, M., Li, P., Lam, I., Wang, X., Cloutier, S. & You, F. (2015). Disease Resistance Gene Analogs (RGAs) in Plants. *Int. J. Mol. Sci.*, 16, 19248–19290.

Sham, P., Bader, J.S., Craig, I., O'Donovan, M. & Owen, M. (2002). DNA Pooling: a tool for large-scale association studies. *Nat. Rev. Genet.*, 3, 862–871.

Skovmand, L.H., Xu, C.C.Y., Servedio, M.R., Nosil, P., Barrett, R.D.H. & Hendry, A.P. (2018). Keystone Genes. *Trends Ecol. Evol.*, 33, 689–700.

Sokolowski, M.B. (2001). Drosophila: Genetics meets behaviour. *Nat. Rev. Genet.*, 2, 879–890.

Spielman, D., Brook, B.W. & Frankham, R. (2004). Most species are not driven to extinction before genetic factors impact them. *Proc. Natl. Acad. Sci. U. S. A.*, 101, 15261–15264.

Start, D. & Gilbert, B. (2019). Trait variation across biological scales shapes community structure and ecosystem function. *Ecology*, 100.

Struk, A.A., Mugon, J., Huston, A., Scholer, A.A., Stadler, G., Higgins, E.T., *et al.*(2019). Self-regulation and the *foraging* gene (*PRKG1*) in humans. *Proc. Natl. Acad. Sci.*, 116, 4434–4439.

Taberlet, P., Zimmermann, N.E., Englisch, T., Tribsch, A., Holderegger, R., Alvarez, N., *et al.* (2012). Genetic diversity in widespread species is not congruent with species richness in alpine plant communities. *Ecol. Lett.*, 15, 1439–1448.

Theissen, G., Rumpler, F. & Gramzow, L. (2018). Array of MADS-Box Genes: Facilitator for Rapid Adaptation? *Trends Plant Sci.*, 23, 563–576.

Thompson, J. (1998). Rapid evolution as an ecological process. *Trends Ecol. Evol.*, 13, 329–332.

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

Tilman, D., Wedin, D. & Knops, J. (1996). Productivity and sustainability influenced by biodiversity in grassland ecosystems. *Nature*, 379, 718–720.

Tucker, C.M., Cadotte, M.W., Carvalho, S.B., Davies, T.J., Ferrier, S., Fritz, S.A., *et al.* (2017). A guide to phylogenetic metrics for conservation, community ecology and macroecology: A guide to phylogenetic metrics for ecology.*Biol. Rev.*, 92, 698–715.

Vellend, M. (2005). Species Diversity and Genetic Diversity: Parallel Processes and Correlated Patterns. *Am. Nat.*, 166, 199–215.

Vellend, M. & Geber, M.A. (2005). Connections between species diversity and genetic diversity. *Ecol. Lett.*, 8, 767–781.

Vellend, M., Lajoie, G., Bourret, A., Murria, C., Kembel, S.W. & Garant, D. (2014). Drawing ecological inferences from coincident patterns of population- and community-level biodiversity. *Mol. Ecol.*, 23, 2890–2901.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., *et al.*(2007). Let the concept of trait be functional! *Oikos*, 116, 882–892.

Wang, M.-S., Huo, Y.-X., Li, Y., Otecko, N.O., Su, L.-Y., Xu, H.-B., *et al.* (2016). Comparative population genomics reveals genetic basis underlying body size of domestic chickens. *J. Mol. Cell Biol.*, 8, 542–552.

Watanabe, K., Stringer, S., Frei, O., Umićević Mirkov, M., de Leeuw, C., Polderman, T.J.C., *et al.* (2019). A global overview of pleiotropy and genetic architecture in complex traits. *Nat. Genet.*, 51, 1339–1348.

Whitham, T.G., DiFazio, S.P., Schweitzer, J.A., Shuster, S.M., Allan, G.J., Bailey, J.K., *et al.* (2008). Extending Genomics to Natural Communities and Ecosystems. *Science*, 320, 492–495.

Whitham, T.G., Young, W.P., Martinsen, G.D., Gehring, C.A., Schweitzer, J.A., Shuster, S.M.,*et al.* (2003). Community and ecosystem genetics: A consequence of the extended phenotype. *Ecology*, 84, 559–573.

Whittaker, R.H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California.*Ecol. Monogr.*, 30, 279–338.

Wolf, M. & Weissing, F.J. (2012). Animal personalities: consequences for ecology and evolution. *Trends Ecol. Evol.*, 27, 452–461.

Yachi, S. & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proc. Natl. Acad. Sci.*, 96, 1463–1468.

Figure captions

Figure 1 . Conceptual diagram showing how an inclusive 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 for ecologically important traits.

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 specie 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.

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. (a) A first step consists in defining the ecological process and the focal community to target, as well as identifying the closest reference genome to the focal community, and the traits associated to 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. (d) A final step uses a local base alignment search tool (BLAST) to retrieve the sequence on the genome of reference(s) species. As genes can not 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 come from*www.svgrepo.com*.

Figure 4. The relationship 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 monoculture (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, which might for instance change in the shape of the BEF relationship and/or a higher predictive power (d).

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

Ecologists have long sought to understand how changes in community composition and species loss of species 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 (e.g., Tilman *et al.* 1996; Loreau 1998). 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) (Hooper *et al.*2005; Balvanera *et al.* 2006; Cardinale *et al.* 2012).

Biodiversity-ecosystem relationships are explained by several non-exclusive 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 benefit the others in the community; sampling effects (aka selection or dominance effect) 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 stabilise 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 rate.

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, 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 PCCGs would be the inclusive measure of biodiversity.