The distribution of genetic diversity in ecological communities: A unifying measure for monitoring biodiversity change

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Abstract

Monitoring the “health” of an ecological community is a critical component of conservation planning. We propose that aggregating intraspecific genetic variation across all species of an ecological community (Community Genetic Distribution; CGD) provides a new way to measure biodiversity that is unifying across taxa, economically scalable, and geographically transferable. Such community-scale data provides information about past dynamics that can unveil processes structuring contemporary biodiversity, and can identify communities that are resilient to perturbation. Using the CGD, high-throughput biodiversity genetic inventories (e.g. metabarcoding/eDNA) can be leveraged to identify the genetic signatures of pristine and disturbed systems. We show examples of the CGD from empirical systems, how it responds through space and time to human disturbance, and how it successfully recovers restoration and succession gradients from metabarcoding datasets with the goal of obtaining insight on community genetic health and developing indicator metrics which can identify communities that are resilient to perturbation. We outline ways in which the CGD complements and extends information in the suite of currently described essential biodiversity variables, and how it can contribute to the targets of the Kunming-Montreal Global Biodiversity Framework.

Keywords: Biodiversity, community ecology, metabarcoding, environmental DNA, essential biodiversity variables, eco-evolutionary modeling

1 Introduction

A major scientific and policy challenge in ecology and conservation is to design measures of biodiversity that are at once simple and understandable but still contain information on the many ecological, evolutionary, and taxonomic dimensions across which biodiversity varies (Humphries et al. 1995; Purvis and Hector 2000). The suite of GEOBON Essential Biodiversity Variables (EBVs) were developed to standardize the collection, sharing and use of biodiversity information, and they have been used to inform development of the headline indicators for the Kunming-Montreal Global Biodiversity Framework. However, contemporary biodiversity assessments (including the EBVs) focus on patterns at individual levels of biological organization, for example within species genetic diversity, or phylogenetic diversity or abundance distributions within communities. What is needed are measures of biodiversity state which capture information across multiple levels of organization and that may reflect important properties like ecological stability and resilience. Here, we propose such a novel measure that leverages genetic information to assess biodiversity "health" at the community level, unifying both within-species genetic composition and among-species community composition levels of organization. This approach provides a quantitative assessment of the age of a biological community, as reflected by the overall distribution of intraspecific genetic variation across taxa. Given that stability of biological communities has been linked to both diversity (Hautier et al. 2015) and co-evolved histories (May 1975; May 1981) among members of the community, we suggest that the proposed measure can provide valuable insights for research, policy, and conservation.

The genetic information contained among individuals of a given species can provide insights into underlying processes of biodiversity change (Hoban et al. 2022; Bernatchez et al. 2024). Within-population patterns of genetic variation result from a combination of neutral and adaptive processes, including mutation, drift, gene flow, and selection and reflect phenomena such as founder effects and population demography (Ellegren & Galtier, 2016) that manifest over contrasting spatial and temporal scales. Although the importance of maintaining genetic diversity at different levels of organization is largely recognized, we have yet to be successful in upscaling from individual populations or species to the community level. Recent advancements in molecular methodologies, such as DNA metabarcoding, present new opportunities for integrating genetic data into comprehensive biodiversity monitoring frameworks of entire ecological communities (Overcast et al. 2023). Specifically, the distribution of intraspecific genetic diversity across taxa in a quantitative sample of all individuals in a community can indicate the extent to which these taxa have shared a history at that site. To this end, we propose a new measure that is designed to capture this community-level genetic structure: the Community Genetic Distribution (CGD; Figure 1).

The CGD is defined as the distribution of nucleotide diversity values (Nei & Li, 1979) across all operational taxonomic units (OTUs) identified within a community sample. It complements the existing set of Essential Biodiversity Variables (EBVs) for community composition. Among currently accepted EBVs, genetic diversity generally refers to within-species genetic composition (diversity, heterozygosity, differentiation, REF) or adaptive potential, and as such is one of the pillars of biodiversity. However, no existing EBV captures community-wide, non-adaptive genetic diversity, which, we argue, is necessary for capturing

information on the evolutionary history contained within a community. The metric we propose captures this history by integrating information on community ecological and evolutionary processes. Important advantages of this metric are, first, that it is agnostic to taxonomy and can be used on microbial assemblages just as easily as on macro-organisms, presenting a tool for examining biodiversity across taxonomic scales. In this way the measure also captures information on poorly described or unknown taxa within the monitored community, and individuals at all developmental stages, two aspects that are particularly important in taxonomic groups that are poorly known (Callaghan et al., 2023). This problem is often compounded in tropical areas, and for cryptic or understudied taxa like fungi (Niskanen et al. 2023). Second, our proposed measure is not limited by the diversity or complexity of a given assemblage as it moves beyond simple summary statistics such as the number of OTUs or Shannon information (Hill 1973), to measure the entire distribution of genetic diversity across any number of different species in the community. In several important ways it is analogous to the Species Abundance Distribution (Borda-de-Água et al., 2012; Callaghan et al., 2023; Preston, 1948) in that it characterizes the distribution of a property across all species or OTUs in a community, but instead of characterizing species abundances, it characterizes the the distribution of both intra- and inter-specific genetic diversity.

In this perspective, we outline the conservation utility of this novel biodiversity variable with the goal of centering community genetic diversity as an emergent property of an assemblage, which provides insight into the integrity and resilience of ecological communities. In the face of growing imperatives to continuously monitor biodiversity at multiple spatial scales and its change at different levels of organization, we argue that tracking changes in the genetic distribution among species at the community level (e.g. using high-throughput metabarcoding approaches) provides a rapid, cost-effective, and information-rich means for inventorying and monitoring biodiversity.

2 Advantages of Community Genetic Distributions for Conservation

2.1 Ecological communities as units of conservation

Historically, biodiversity assessment and conservation efforts have focused on the individual species level (e.g. The Endangered Species Act in the US (16 U.S.C. § 1531) or the IUCN Red List (iucnredlist.org)), while it is well understood that species are embedded within and reliant on the complex biological matrix of their surrounding ecosystems (Smith 1983; Rohlf 1991; Díaz et al. 2019). This recognition has prompted the development of a suite of assessment metrics and tools above the species level, including several of the recently developed headline Indicators for the Kunming-Montreal Global Biodiversity Framework (Kunming-Montreal Global Biodiversity ...); e.g. Indicators A.1 IUCN Red List of Ecosystems and A.2 Extent of natural ecosystems). Focusing on conservation of communities preserves the interactions and dependencies that sustain both species of concern and those of least concern (for the moment). Conserving communities also supports continued delivery of ecosystem services and enhances resilience to environmental change and disturbance. The CGD is an

indicator of 'genetic health' of communities, providing a robust and historically focused indicator of community status.

2.2 Cost effective and efficient to collect with metabarcoding and eDNA surveys

Observing, identifying, and quantifying the enormity of global biodiversity has been a long-standing problem in monitoring biodiversity changes. This task has become more achievable with the advent of high-throughput sequencing and metabarcoding (Taberlet et al. 2012; Ficetola and Taberlet 2023). Metabarcoding is based on the massive parallel sequencing of short and taxonomically informative DNA amplicons (DNA barcodes), to characterize diverse biological communities (Yu et al. 2012) and is well suited to explore hyperdiverse ecosystems with little or no reference data available. Within metabarcoding, (i) DNA Metabarcoding is commonly used with bulk community samples, for example all insects from a Malaise trap (Gibson et al. 2014) or marine benthic communities (Leray et al. 2015); and (ii) environmental DNA (eDNA) metabarcoding, which uses DNA traces that organisms leave behind in their environment and has gained popularity as an entirely non-invasive approach to detect species and characterize the biotic composition of ecosystems (Bohmann et al. 2014; Taberlet et al. 2018; Bodawatta et al. 2025). The approach provides insights to the different facets of biodiversity, from genes to species to entire ecosystems (Krehenwinkel et al. 2022). While metabarcoding is not free of flaws (e.g. taxonomic biases in PCR amplification efficiency, sequencing error or the co-amplification of paralogs of the barcode marker gene (see Hartig et al. 2024)), it allows rapid and straightforward assessment of the composition of an entire assemblage of species (Graham et al. 2023). Moreover, while the inherent biases during the laboratory procedures, related to the quality and quantity of the DNA extractions or the biases in PCR amplifications precludes the estimation of absolute species abundances, metabarcode datasets can provide an approximation of relative abundances of individual species in a community (Krehenwinkel et al. 2017; Luo et al. 2023). For the proposed CGD, metabarcoding data is ideal and has already been used in the recovery of community-wide patterns of genetic diversity (Weitemier et al. 2021).

2.3 Quantifying total biodiversity, including undescribed taxa

Biodiversity monitoring efforts, such as those led by the International Barcode of Life (iBOL) Consortium, use large-scale barcoding and metabarcoding to identify species through DNA sequencing. These approaches rely on reference databases to match DNA fragments (amplicons) to known taxa (Ratnasingham and Hebert 2007), but such databases face challenges related to completeness, resolution, and biases in geographic and taxonomic coverage. Creating comprehensive reference databases is time-consuming and costly, and many species remain unsequenced, limiting the effectiveness of metabarcoding for identifying cryptic or undescribed diversity. Additionally, taxonomic instability complicates database reliability, as names and classifications frequently change. Given these issues, the CGD, by design, does not require taxonomic information at all (it is 'taxonomy agnostic'), though it can be enhanced by a complete barcode sequence reference database. The ability to quantify the distribution of genetic variation within communities, without reference to taxonomy, greatly

expands the scope of its utility by applying in equal measure to well-studied and fully described communities, and those that are undescribed and understudied (i.e. those that are most in need of quantification and assessment).

2.4 Information rich

The CGD contains information at multiple levels of biological organization, including community state, and historical population size and connectivity of component species across the landscape. At the community level, in the same way as the SAD, the CGD provides an estimate of species richness as the simple count of OTUs within the focal community. Uncertainty in the estimation of species richness can be quantified using rarefaction curves (Leray and Knowlton 2015). At the species level, taking nucleotide diversity as the summary statistic of genetic diversity provides rich information about each individual species that goes beyond individual count data recorded in the SAD. Nucleotide diversity is an outcome of several processes, including historical changes in population size, connectivity with neighboring communities (migration), and the strength of selection at target loci. Because it responds to all these processes, we can obtain estimates of the strength of these from nucleotide sequences (e.g. Tajima's *D* (Tajima 1989). In this way, estimates of pi within species aggregated across the entire community gives a snapshot of the community on a population genetic timescale, averaging over short term changes in abundance (ecological drift).

2.5 Insensitive to sampling effort

The effect of sampling effort on ecological and biodiversity inference has been a focus of concern for decades (Martinez et al. 1999; Moreno and Halffter 2001; Chao et al.). Insufficient sampling can lead to biased conclusions, usually because of undersampling rare species. Ecological inventories focused on species richness may use rarefaction curves to quantify the uncertainty of species richness estimates, and similar techniques can be used to standardize sampling effort for abundance surveys. Rarefaction will necessarily underestimate biodiversity patterns and may additionally obscure true differences in ecological processes underlying such patterns. Rather than the total number of individuals in a sample, information in the CGD relies on sampling a sufficient number of haplotypes. Nucleotide diversity is classically robust to sampling, requiring only 5-10 (haploid) samples for a given species to capture a reliable estimate of within-species genetic diversity (Tajima 1983). This robustness obtains across all species within the community, so sampling effort will have less of an effect on CGD than it will on the SAD, for example. The probability of sampling a sufficient number of haplotypes for a given species is dramatically increased by the huge sample sizes of typical metabarcode/eDNA studies, with an average sample containing tens of thousands of DNA sequences or more. This benefit also accrues for so-called 'megabarcoding' studies (Chua et al. 2023; Hartop et al. 2024), large scale barcoding of individual specimens, whereby bulk samples (of arthropods for example; e.g. (Kitson et al. 2018)) can be sorted to morphospecies and then selected vouchers can be sequenced individually, rather than sequencing the entire batch, saving effort and cost while retaining information necessary for constructing a reliable CGD.

2.6 Responds on a timescale that is useful for conservation

Temporal stability on intermediate timescales is a useful property for biodiversity variables. If a variable changes too quickly or too slowly it is difficult to devise interventions that could be meaningfully evaluated using it. We might first consider what is meant by 'intermediate timescale.' In practical terms, we take this to mean a timescale which is relevant for measuring changes in biodiversity outcomes of conservation/remediation efforts, on the order of years to decades. Ecological drift, and in particular large-scale environmental disturbance, can cause SADs to vary substantially from one sampling time to the next. On the other hand, phylogenetic diversity (PD) does not account for short timescale processes, as it changes only in response to processes of speciation (slow), or colonization by new lineages, which can be rare occurrences, particularly in remote island systems. As a long-term average of effective population size, nucleotide diversity contains information on intermediate timescales, and so the CGD is insensitive to short term fluctuations in community state. An alternative lens on community genetic diversity could involve summarizing genetic patterns using genetic measures of historical community size change (e.g. Tajima's D; (Tajima 1989)). Shared patterns in differences between number of segregating sites and nucleotide diversity within species may indicate shared histories of population size change at the community scale, driven by recent changes in habitat or resource availability, for example.

2.7 Challenges and additional considerations of community genetic diversity

Given the focus on capturing information from the entire community, the vast majority of metabarcode studies target single-locus protein coding sequences (e.g COI for metazoa (Andújar et al. 2018)). By construction, the CGD is not limited to single locus datasets; it is only a matter of practicality and what is currently readily available. At the same time, it is important to note some limitations specific to single-locus metabarcoding that should be taken into consideration when applying the CGD to these kinds of empirical datasets. Absent a carefully curated reference database, overmerged haplotypes from distinct species would generate chimeric OTUs with inflated nucleotide diversity, potentially skewing the CGD. Additionally, there is some disagreement about the extent to which nucleotide diversity within single-locus mitochondrial protein coding genes (e.g. COI) corresponds to genome-wide nuclear diversity (Schmidt and Garroway 2021), but see (Allio et al. 2017)). Bearing this in mind, conservation implications of the CGD should be limited to considerations of how nucleotide diversity of single-locus markers fairly reflects long-term effective population size, and not genome-wide adaptive capacity (as might be tempting). Looking to the future, the limitations of single-locus metabarcode data can be overcome by leveraging multi-locus metabarcode approaches (Weitemier et al. 2021), RADSeq (Andrews et al. 2016), and/or whole genome sequencing (i.e. 'metagenomics'; (Sleator et al. 2008), which is already common for microbial communities. In principle, the CGD can be calculated using such expanded genetic datasets, providing a more robust picture of intraspecific genetic diversity across the community.

3 Empirical conservation utility of CGDs

The CGD offers a sensitive metric for the ecological impacts of disturbances (e.g., habitat destruction, fires, droughts), as well as the effectiveness of conservation measures (e.g., protected areas, translocations) (Reynolds et al., 2012). We illustrate the sensitivity of CGDs to changes in community assembly dynamics and conservation-relevant ecological/environmental drivers using reanalysed data from four different case studies for which whole-community quantitative metabarcoding data had been previously generated (Figure 2). In each case we downloaded the published data from publicly available repositories, reproduced the bioinformatic analysis, and calculated and plotted the CGD, which is a pattern that was not investigated in any of the case studies. We tested different aspects of the CGD, first whether it can reflect co-evolved history, using Hawaiian spider communities (Graham et al. 2023). Here we demonstrate a pattern of increasing CGD with increasing age of the community, as reflected by the geological age of the different islands, and reflecting the expected increase in co-evolutionary history of these communities over time. Second, we examined whether habitat type and fragmentation can be measured using the CGD (Noguerales et al. 2021), and found a strong effect, with arthropod communities from broadly distributed habitats showing increased CGD, potentially as an effect of reduced environmental constraint and increased connectivity. Finally, we tested the extent to which the CGD might detect anthropogenic disturbance In both arthropod communities (Kennedy et al. 2023) and marine eukaryotic communities (Holman et al. 2021), environmental disturbance shows a strong and predictable effect in reducing CGD at disturbed sites. Jupyter notebooks for reproducing all analyses are provided in the GitHub repository (https://github.com/isaacovercast/IMEMEBA-BCI).

4 Connecting CGD to global conservation efforts

4.1 Connecting community genetic diversity to policy frameworks

Community genetic diversity captures information that is relevant across a range of domains: Scientists care about 'healthy' ecosystems, resilience/resistance, intactness; Local, regional, and national governments care about ecosystem services and human health and wellbeing; Businesses care about reducing overhead, increasing revenue, and managing their public image. Community genetic diversity offers a means for designing rapid, cost-effective, and information-rich biodiversity indicators suitable for implementation within the corporate sustainability reporting directive (CSRD European Commission 2022), global reporting initiative (GRI n.d.), Science-Based Targets Network (SBTN 2020). We propose that this allows it to be potentially informative to many existing regulatory frameworks that require the continuous monitoring of biodiversity over time. While EBVs have been proposed for these frameworks, community genetic diversity captures an element of biodiversity that has not been captured within existing EBVs, namely the co-evolutionary history of the community. While traditional community composition metrics have yielded mixed results in distinguishing disturbed from undisturbed sites, incorporating genetic diversity may enhance their effectiveness, offering a more precise tool for ecological monitoring and conservation.

4.2 Biodiversity Credit Markets

Because the CGD provides operationalization of 'biodiversity health', one application would be to quantify biodiversity so that it can be purchased in biodiversity credit markets (Ducros & Steele, 2022; Wunder et al., 2024). The purpose of such markets is to use private finance to compensate landowners for the direct and opportunity costs of carrying out restoration and conservation projects. Companies purchase biodiversity credits in order to offset negative impacts or to effect positive impacts on biodiversity. The potential benefits of such reporting include improved access to finance, reduced physical, litigation and regulatory risks, and enhanced corporate reputation. However, making biocredit markets work requires a difficult transformation: reducing the high-dimensional complexity of biodiversity to one-dimensional credits representing units of biodiversity status or change (Wauchope et al. 2024). It is also necessary to verify biodiversity improvements, because the value of the credits to buyers is reputational. The problem is that verification involves high transaction costs that reduce the funds available for conservation action. For example, in the Wallacea Trust (2023) scheme, one credit per hectare is earned for each 1% step towards convergence with a counterfactual reference site. Convergence is measured as the median percentage change in a suite of five or more metrics with a determined set of properties that may be chosen on a per project basis, one of which must measure habitat structural complexity and the rest the abundances of functionally important taxa (e.g. pollinators), with higher weights given to threatened species. All the taxon metrics require costly repeated measurements in the field. Similar basket-of-metrics approaches are used for other biodiversity credits, with different trade-offs between cost, comprehensibility, and credibility (Maczik et al., 2024; Wunder et al., 2024). The potential advantage of a future CGD-derived metric is that it could reduce transaction costs by providing a single, direct, and efficient measure of the underlying goal of all biocredit projects, which is to conserve or restore ecosystems.

5 Concluding Remarks

The distribution of genetic variation in ecological communities is an informative yet largely unstudied biodiversity pattern with significant conservation relevance. It could be particularly useful for improving the functioning and oversight of the biodiversity finance and impact-disclosure policy instruments that have been proposed in Target 19 of the Kunming-Montreal Global Biodiversity Framework (REF), as well as being generally useful as research variables in ecology and conservation. Beyond the advantages of studying the CGD that we have enumerated, the data necessary to construct the CGD already exists in thousands of published metabarcoding and eDNA studies and simply awaits to be unlocked.

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Figures

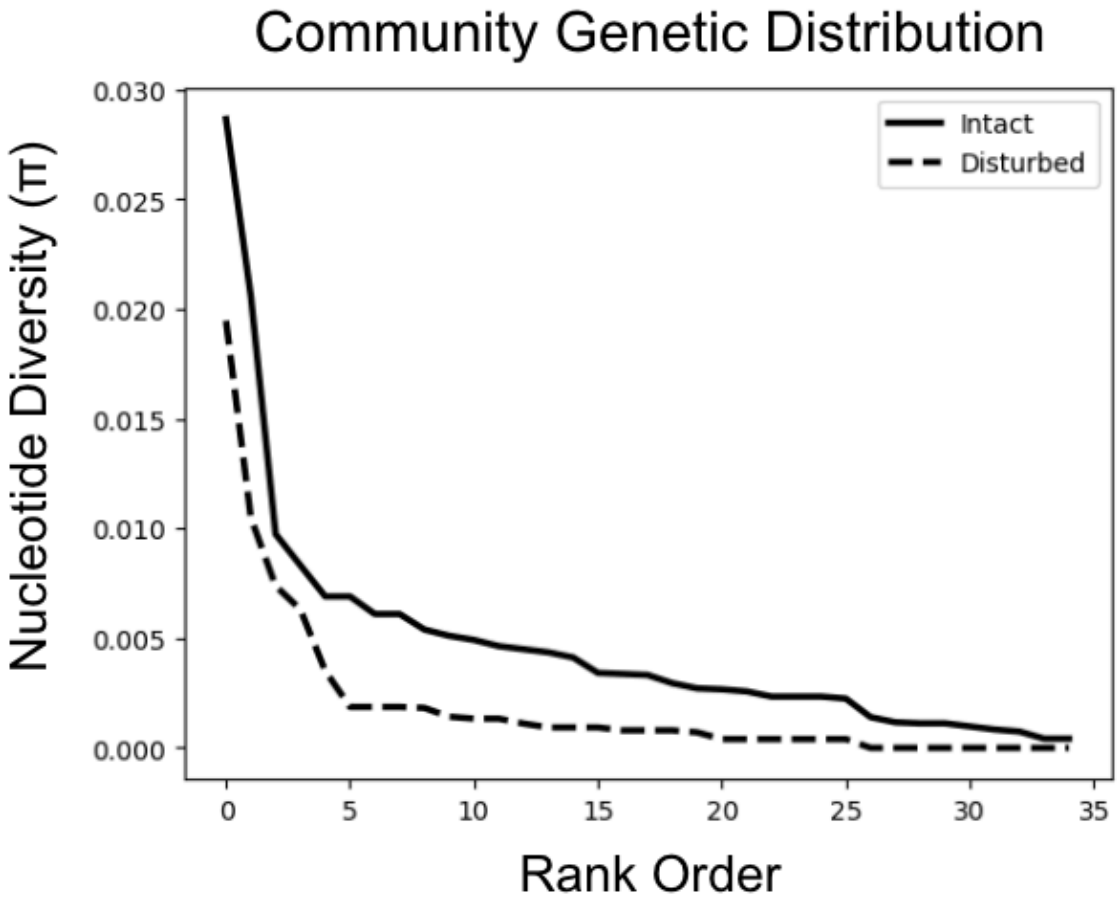

Figure 1 - The form of the CGD for two hypothetical communities
Two hypothetical communities illustrate different potential distributions of genetic diversity including an intact (solid line) and a disturbed site (dashed line). Aggregating values of genetic diversity across all species in each community and ordering them by rank produces unique distributions which can be used to diagnose community state, and infer historical ecological and evolutionary processes that have shaped the community.

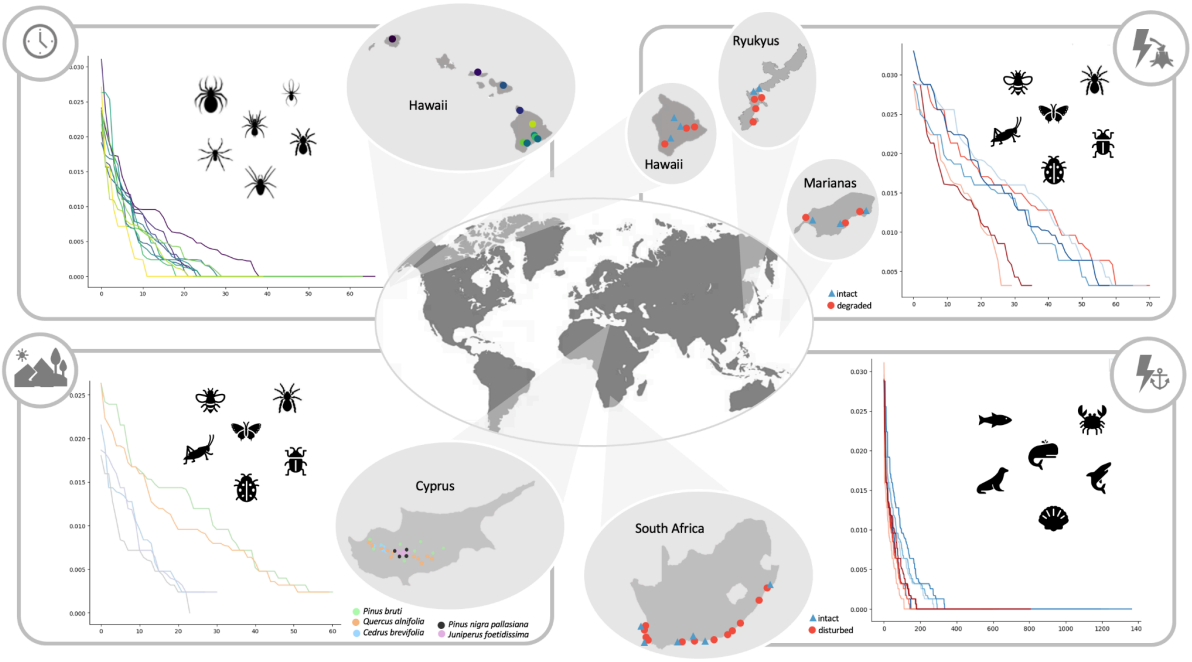

Figure 2 - Empirical examples of CGD across disparate spatial and taxonomic scales
Empirical examples from four different systems across the globe illustrate the effects of community age and co-evolution (top left), habitat type (bottom left), and disturbance regimes (top and bottom right) on community genetic diversity composition. Top-left: The CGD for spider communities from Hawaii show an increasing pattern of CGD magnitude with increasing community age. The color of each CGD curve indicates substrate age from which the community was sampled, with age increasing from yellow (youngest) to dark purple (oldest). Bottom-left: Soil microarthropod communities from montane forests on Cyprus sampled from five different habitat types show a pattern of increased CGD for more widely distributed pine (green) and oak (orange) forests, with reduced CGD in narrowly restricted cedar (blue) and high-elevation pine/juniper (purple and black, respectively) forests. Both panels on the right show the effect of different disturbance regimes, with forest dwelling arthropod communities at top and marine eukaryotic communities at bottom. In both cases blue curves show stable and intact community CGDs and red curves show disturbed sites.