

# ECOGRAPHY

## Research article

# Climatic stability predicts the congruence between species abundance and genetic diversity

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Unified models of biological diversity across organizational levels (genes, species, communities) provide key insight into fundamental ecological processes. Theory predicts that the strength of the correlation between species abundance and genetic diversity should be related to community age in closed communities (i.e. abundant species accumulate more genetic diversity over time than rare species). Following this rationale, we hypothesize that historical climatic events are expected to impact assembly processes, hence affecting both the species abundance distribution (SAD) and the species genetic distribution (SGD) in continental communities. Therefore, we predict that, if the congruence between SADs and SGDs depends on community age, then higher congruence would be observed in localities where climate has been more stable since the Last Glacial Maximum (LGM). We tested this prediction using relative abundance and nucleotide diversity (*cox1-5'*) data from 20 communities of leaf beetles along a latitudinal transect in the Iberian Peninsula. We observed that the congruence between SAD and SGD curves, measured as the correlation between the species' rank orders in both distributions, was significantly related to the change in mean annual temperature since the LGM, but not to current climatic conditions. Our results suggest that, despite the high connectivity of continental communities, historical climatic stability is still a relevant predictor of the congruence between species abundance and genetic diversity. Hence, the degree of congruence between SADs and SGDs could be used as a proxy of community stability, related not only to historical climatic variation but also to any other disrupting factors, including human pressure.

Keywords: biodiversity patterns, Coleoptera, community barcoding, Quaternary climate, species–genetic diversity correlation (SGDC), unified models

## Introduction

Unified macroecological models across organizational levels (genes, species, communities) provide predictive frameworks that open unique opportunities to discern the role of fundamental ecological processes shaping the variation of biological communities



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(Overcast et al. 2021, Baselga et al. 2022). These models inherently recognize the interplay between ecological and evolutionary processes as key drivers of population and community dynamics (Vellend et al. 2014). From seminal works suggesting that species and genetic diversity are under the influence of the same processes (Antonovics 1976), accumulated knowledge has shed light on the mechanisms that result in parallel patterns of diversity within and among species (Vellend 2003, 2005, Vellend et al. 2014). A crucial breakthrough was Vellend's (2016) synthetic theory of ecological communities, with the realization that the processes governing the composition and diversity of biological communities can be distilled into four high-level categories (selection, drift, speciation, and dispersal) with clear parallels in population genetics (Vellend 2010, 2016). Importantly, the recognition that the same processes govern diversity at genetic and species levels does not necessarily imply that patterns at both levels must be always correlated, but it opens the opportunity to assess the conditions under which these parallelisms arise (Vellend and Geber 2005, Baselga et al. 2013, 2015, Gómez-Rodríguez et al. 2019, Schmidt et al. 2022). Furthermore, process-based simulations can be instrumental in generating predictions about patterns emerging across hierarchical levels (genes, genealogies, and species, Baselga et al. 2015). These simulations serve as valuable tools for inferring the processes that underlie the observed patterns of variation of biological communities (Laroche et al. 2015, Overcast et al. 2021, Baselga et al. 2022).

Inferring ecological processes from observed biodiversity patterns faces a significant challenge given that most macroecological patterns might potentially arise from different mechanisms (McGill 2010, Cabral et al. 2017). An emerging field that tackles this challenge involves the use of mechanistic eco-evolutionary models to simulate large-scale biodiversity patterns at multiple hierarchical levels (Hagen 2023). These simulations are designed to generate testable benchmarks against which empirical diversity patterns can be compared, thus allowing the inference of assembly processes from whole-community genetic and species data (Baselga et al. 2022, Overcast et al. 2023b). For instance, the joint neutral model (Overcast et al. 2019) underlying the massive eco-evolutionary synthesis simulations (MESS, Overcast et al. 2021) predicts that, all other things being equal, abundant species would tend to accumulate more genetic diversity than rare species. While this aligns with previous empirical support (McCusker and Bentzen 2010, Grundler et al. 2019), it is essential to note that, in the context of island communities, this prediction leads to an additional inference: the correlation between species abundance and species genetic diversity (SGD) will vary among local communities as a function of community age (Overcast et al. 2019, 2023b). If this prediction holds, it opens an interesting avenue, as it suggests that the correlation between species abundance and genetic diversity could serve as an estimator for community age or, more broadly, community stability, as we argue below. Here we test this prediction for continental communities using a fully curated dataset of genetic barcodes and abundance data

for whole communities of leaf beetles along a latitudinal gradient in the Iberian Peninsula (Baselga et al. 2015).

The concept of community age is inherently complex, owing to the dynamic nature of biological communities. In general terms, species composition changes over time (i.e. temporal turnover) in response to environmental changes, biotic interactions, and the arrival of new species, as well as by random fluctuations in demographic processes (Magurran and Henderson 2010). Nevertheless, the age of oceanic island communities has a discernible maximum limit tied to the island's origin and subsequent colonization by different species. In contrast, determining the age of continental communities proves even more elusive due to their higher connectivity and, consequently, the larger influence of immigration processes compared to the relatively more isolated island communities. In the context of continental communities, historical climate change emerges as a key driver of community reconfiguration, inducing shifts in both the position and size of species distribution ranges (Taberlet et al. 1998, Hewitt 1999, Davis and Shaw 2001, Jansson 2003), sometimes unfolding over extended time periods (i.e. Milankovitch climatic cycles, Dynesius and Jansson 2000). These shifts in species ranges result from the interplay between niche filtering and dispersal processes (Skov and Svenning 2004, Svenning and Skov 2007) and are therefore not expected to be concerted across species (Stewart et al. 2010), thus leading to the reshuffling of communities due to climate change (Graham and Grimm 1990, Williams et al. 2001). Consequently, the more stable the climate, the higher the probability of species persistence in a given site (Fjeldsa et al. 1999, Dynesius and Jansson 2000, Jansson 2003), making it more probable that the biological community has remained unchanged over time. In other words, climatic stability could serve as a proxy for community age or, more broadly, community stability. Building on the prediction by Overcast et al. (2023a), we would expect a positive relationship between climatic stability and the correlation between species abundance and genetic diversity. We hypothesize that, if the correlation between species abundance and genetic diversity depends on community age, then higher congruence would be observed in continental localities with a more stable climate since the Last Glacial Maximum (LGM).

Our aim is to test the prediction that the congruence between relative abundance and genetic diversity within communities depends on their long-term climatic stability. To examine this, we have assessed the parallelism between the species abundance distribution (SAD) and the SGD distribution of whole communities of leaf beetles (Coleoptera: Chrysomelidae) in the Iberian Peninsula. This region offers an ideal case study, being one of the major glacial refugia in Europe. Moreover, it is also thought to have harboured multiple refugia at very small scales due to its broad topoclimatic heterogeneity (Gómez and Lunt 2007). As a consequence, late Quaternary climate changes have played an important role in structuring the spatial pattern of endemism and genetic structure in the Iberian Peninsula (Abellán and Svenning 2014). Leaf beetles are also a good biological group

to address this type of analysis because their communities are very diverse (dozens of species usually coexist locally, associated to different host plants), with marked variation in both abundance and genetic diversity across species.

## Material and methods

### Leaf beetle community data

Leaf beetle communities were sampled in 20 localities along a south–north transect (820 km, Fig. 1) in the Iberian Peninsula in April–June 2010 (for more information see Baselga et al. 2015). All localities were well-preserved areas (mostly Natural Parks or areas with some degree of protection) and cover a wide altitudinal range, from 123 m a.s.l. (ALC, see locality codes in the Supporting information and Fig. 2 caption) to 1264 m a.s.l. (OMA) as well as a wide climatic gradient, with

mean annual temperatures from 9.5°C (OMA) to 17.5°C (ALC) and mean annual precipitation from 478.7 kg/m<sup>2</sup> (HOR) to 1764.5 kg/m<sup>2</sup> (EUM, see Supporting information for more information on the sampled localities). Each locality was intensively sampled by sweeping and beating all types of vegetation, including trees, shrubs, and herbs, for 20 sampling periods of 30 min (except 18 sampling periods in UBG). All specimens were preserved in 100% ethanol for DNA extraction and amplification of a 655 base pair region from the 5' end of mitochondrial *cox1* (sequence data n = 4531, published in Baselga et al. 2015). All specimens were also identified to species level by an expert taxonomist (A. Baselga), mostly using the taxonomic monographs for the European (Warchalowski 2003) and Iberian (Petitpierre 2000) leaf beetle faunas. To assess the congruence between genetic diversity and relative species abundance at the community level, in each locality we have considered only species with an abundance of at least three individuals (Tajima 1983).

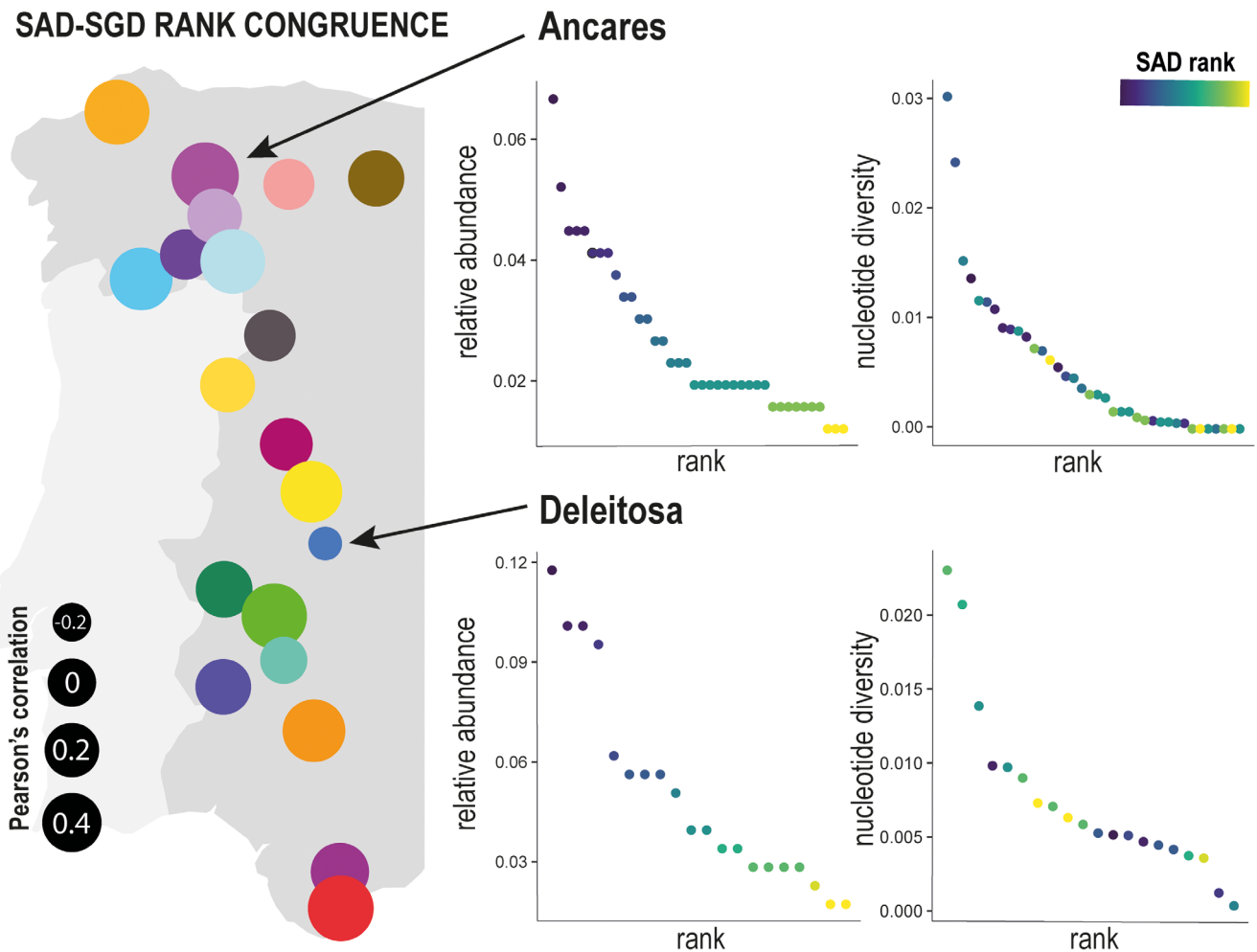


Figure 1. Spatial variation of the rank congruence between the species abundance distribution (SAD) and the species genetic diversity (SGD) curves (SAD–SGD rank congruence). On the left, Pearson's correlation values between species SAD and SGD ranks are shown for each locality, represented by the size of the circles. On the right, the SADs (left) and SGDs (right) for two example localities with the largest (Ancares, ANC) and lowest (Deleitosa, DEL) correlations. Note that the colour gradient in SAD and SGD plots always reflects the rank position in the SAD, so if SAD–SGD congruence is high, the same colours should appear in a similar order in the SGD, but not if congruence is low.

## Local species abundance distributions

We built the SAD curve in each locality, with the x-axis representing the rank of each species from most abundant to least abundant, and the y-axis representing the local relative abundance of each species. Thus, from the vector of abundances, we computed the rank order of each species within the distribution (ranked abundance distribution, RAD, [Whittaker 1965](#)), which informs about their relative commonness (low rank values) or rarity (high rank values) in the community. When two or more species had the same relative abundance within a community, they were assigned the same rank order (i.e. minimum rank).

## Local species genetic diversity distributions

Analogously to SADs, we computed local SGD distributions based on the species nucleotide diversity ( $\pi$ , [Nei and Li 1979](#)) in each locality (i.e. nucleotide diversity of each population). To calculate the nucleotide diversity of each population we used the *nuc.div()* function in the 'pegas' package ([Paradis et al. 2023](#)) in R ([www.r-project.org](http://www.r-project.org)). Sorting species based on their nucleotide diversity provides their rank order within the community according to their genetic variability. This SGD rank order was compared to the rank order in the SAD to assess the congruence between both levels (section 'Congruence between SADs and SGDs and climatic predictors').

For each community, we also summarized genetic diversity across species using the SGD mean (genetic diversity mean, GDM) and its evenness (genetic diversity evenness, GDE). GDM is the average nucleotide diversity across species. GDE is based on Shannon entropy and corresponds to the first-order Hill number of nucleotide diversity (measured as exponential Shannon's diversity or  ${}^1D$ ) standardized by species richness (i.e.  ${}^1D / S$ ) ([French et al. 2023](#)). GDE informs about the variability in genetic diversity among species within a community (i.e. high values of GDE indicate similar genetic diversity among species in a locality). Analogous measures of diversity were computed at the species level: species richness (S) and abundance distribution evenness measured as exponential Shannon's diversity standardized by species richness (i.e.  ${}^1D / S$ ).

## Congruence between SADs and SGDs and climatic predictors

To assess the congruence between species abundance and SGD in each locality, we computed the Pearson's correlation between the species rank order in the SAD and in the SGD. This SAD–SGD rank congruence informs about species rank shifts between the two levels, so high positive congruence values would indicate that the most abundant species are also the ones with higher genetic diversity, as expected for older communities according to [Overcast et al. \(2023a\)](#).

We also assessed the relationship between SAD–SGD rank congruence and both current and past climatic conditions,

as well as the long-term climatic stability in each locality, using linear regression models. We obtained current climate data from the CHELSA 2.1. database ([Karger et al. 2017](#)) and past climate data from the CHELSA database (PMIP3, CCSM4 model) for the LGM ([Karger et al. 2021](#)). We selected the following climatic variables as major descriptors of local climatic conditions: mean annual temperature (bio1), mean maximum temperature of the warmest month (bio5), mean minimum temperature of the coldest month (bio6), annual precipitation (bio12), mean precipitation of the wettest quarter (bio16), and mean precipitation of the driest quarter (bio17). We measured long-term climatic stability as the difference between the current and the LGM mean annual temperature ( $\text{temp\_diff} = \text{bio1.present} - \text{bio1.LGM}$ ) and, independently, as the difference between the current and the LGM annual precipitation ( $\text{prec\_diff} = \text{bio12.present} - \text{bio12.LGM}$ ). We also included altitude, spatial coordinates (latitude and longitude), and species richness as potential predictors to control for alternative spatially structured factors as well as potential biases due to the diversity of communities. The best regression model was identified following a forward stepwise process based on AIC. Additionally, we built equivalent regression models using standard diversity measures as response variables: species richness (S) and abundance distribution evenness ( ${}^1D / S$ ) for the species level and GDM and GDE for the genetic level. See Supporting information for complementary regression models.

## Results

### Leaf beetle community data

A total of 5100 specimens and 209 species were collected for this study, with local species richness ranging from 27 (HOR) to 67 (ANC). The most abundant species in the dataset were *Longitarsus juncicola*, *Gonioctena olivacea*, and *Calomicrus circumfusus*, present in 7, 18, and 13 localities, respectively. The barcode region (*cox1-5'*) of the mitochondrial genome was successfully amplified for 4531 specimens (88.8% of the total). Once the less frequent species ( $n < 3$ ) were removed from each locality, the total number of specimens for further analyses was 4091, corresponding to 140 species. Leaf beetle communities showed a wide range of variation in both genetic diversity and species abundances ([Fig. 2](#)).

### Local species abundance distributions and species genetic diversity curves

Mean relative abundance ranged from  $0.026 \pm 0.013$  (SD) in ANC to  $0.067 \pm 0.064$  (SD) in ALC and  $0.067 \pm 0.033$  (SD) in HOR ([Table 1](#)), with the most locally dominant species being *L. juncicola* (53 specimens) and *L. dorsalis* (34 specimens), both in ALC. The locality with the most even abundance distribution was ANC ( ${}^1D / S = 0.745$ ) while ALC showed the most unbalanced abundance distribution ( ${}^1D / S = 0.509$ , see [Table 1](#)). Contrasting results were observed



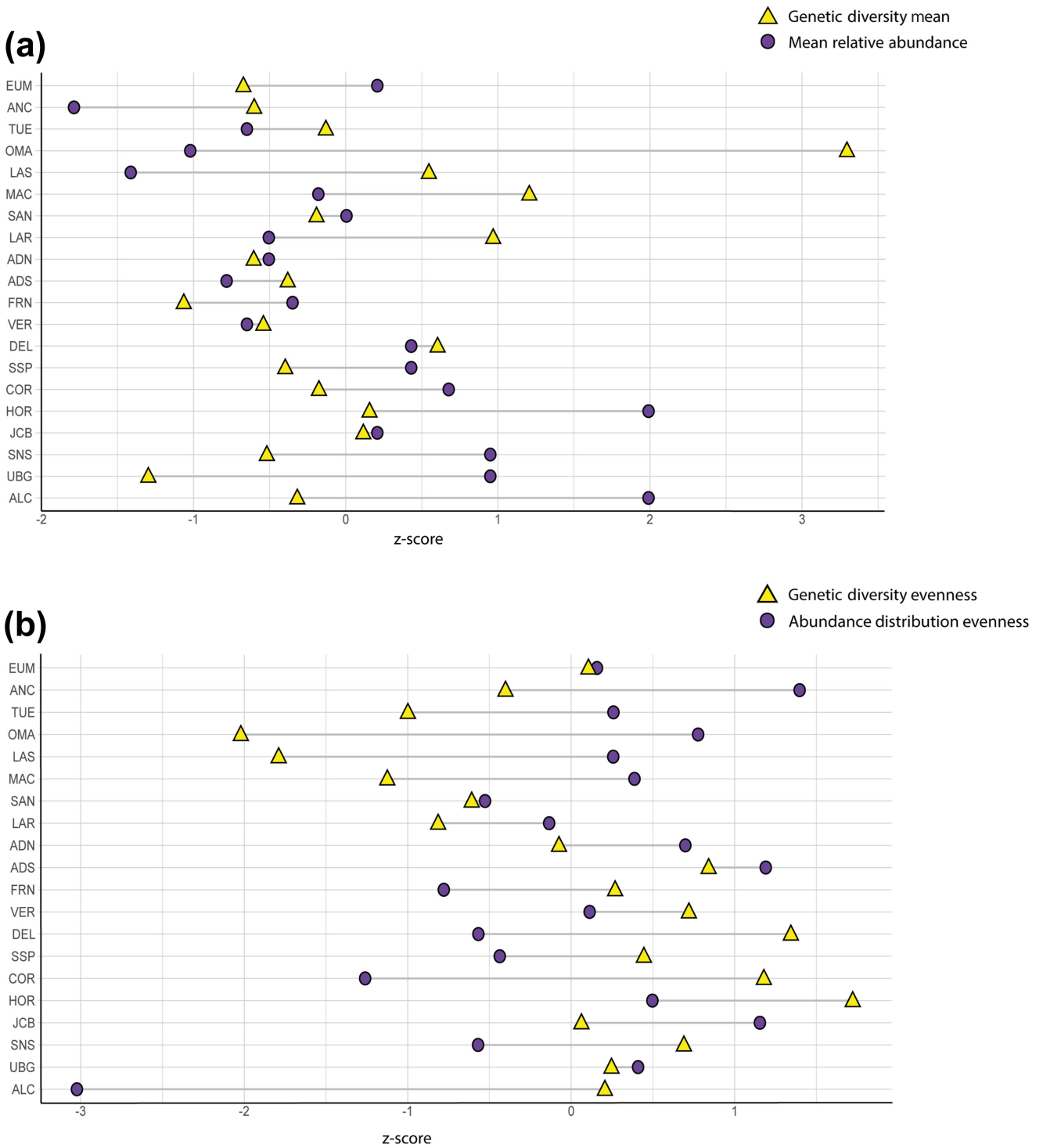


Figure 2. Spatial variation in relative abundance and genetic diversity among the studied communities. (a) Genetic diversity mean (GDM) and mean relative abundance for each locality. (b) Genetic diversity evenness (GDE) and abundance distribution evenness, measured as exponential Shannon's diversity standardized by species richness ( $1^D / S$ ) for each locality. The values of all variables were standardised (z-scores) to allow a visual comparison of the genetic diversity and abundance attributes of communities. Locality codes: Arribes del Duero-Norte (ADN), Arribes del Duero-Sur (ADS), Alcornocales (ALC), Ancares (ANC), Cornalvo (COR), Deleitosa (DEL), Fragas do Eume (EUM), Sierra de Francia (FRN), Hornachos (HOR), Jerez de los Caballeros (JCB), Larouco (LAR), Lastra (LAS), Macizo Central (MAC), Omaña (OMA), Sanabria (SAN), Sierra Norte de Sevilla (SNS), Sierra de San Pedro (SSP), Valle del Tuéjar (TUE), Ubrique-Grazalema (UBG), La Vera (VER).

Table 1. Diversity measures and rank congruence between the species abundance distribution (SAD) and the species genetic diversity (SGD) curves (SAD–SGD rank congruence) for each locality. See Fig. 2 caption for explanation of Locality codes.

Locality	Richness	Evenness ( <sup>1</sup> D/S)	Relative abundance (Mean ± SD)	GDM <sup>1</sup> (Mean ± SD)	GDE <sup>2</sup>	Congruence <sup>3</sup>
ADN	42	0.707	0.040 ± 0.020	0.005 ± 0.008	0.568	−0.048
ADS	41	0.733	0.037 ± 0.021	0.006 ± 0.005	0.690	0.039
ALC	30	0.509	0.067 ± 0.064	0.006 ± 0.006	0.606	0.412
ANC	67	0.745	0.026 ± 0.013	0.005 ± 0.007	0.525	<b>0.476</b>
COR	34	0.603	0.053 ± 0.029	0.006 ± 0.005	0.735	0.402
DEL	41	0.640	0.050 ± 0.030	0.007 ± 0.006	0.757	−0.252
EUM	41	0.678	0.048 ± 0.025	0.005 ± 0.006	0.592	0.375
FRN	43	0.628	0.042 ± 0.026	0.005 ± 0.005	0.614	−0.013
HOR	27	0.696	0.067 ± 0.033	0.007 ± 0.005	0.807	−0.134
JCB	36	0.732	0.048 ± 0.018	0.007 ± 0.000	0.587	0.060
LAR	40	0.663	0.040 ± 0.028	0.008 ± 0.012	0.470	0.292
LAS	56	0.684	0.030 ± 0.017	0.007 ± 0.015	0.340	0.035
MAC	49	0.691	0.043 ± 0.023	0.008 ± 0.013	0.429	−0.072
OMA	45	0.711	0.034 ± 0.023	0.012 ± 0.022	0.310	−0.055
SAN	47	0.642	0.045 ± 0.023	0.006 ± 0.008	0.497	0.367
SNS	35	0.640	0.056 ± 0.041	0.006 ± 0.005	0.670	0.291
SSP	35	0.647	0.050 ± 0.034	0.006 ± 0.006	0.637	0.090
TUE	48	0.684	0.038 ± 0.018	0.006 ± 0.011	0.445	0.075
UBG	34	0.692	0.056 ± 0.026	0.004 ± 0.005	0.611	0.138
VER	41	0.676	0.038 ± 0.026	0.006 ± 0.005	0.674	0.253

<sup>1</sup>GDM: genetic diversity mean. <sup>2</sup>GDE: genetic diversity evenness. <sup>3</sup>Congruence: Pearson's correlation between the species rank order in the SAD and the SGD distribution. The only significant correlation value is highlighted in bold ( $p=0.002$ ).

for nucleotide diversity, with UBG being the locality with the lowest GDM ( $0.004 \pm 0.005$  [SD]) and OMA with the largest GDM ( $0.012 \pm 0.022$  [SD]). The locality with the most even genetic diversity was HOR (GDE = 0.807), while OMA (GDE = 0.310) showed the most unbalanced genetic diversity distribution.

For each locality, we represented SADs and SGDs by sorting species according to their relative abundance and nucleotide diversity, respectively. These plots graphically represent the rank shift between the genetic and species level and hence the congruence between SADs and SGDs (see Fig. 1 for illustrative purposes, and Supporting information for the SAD and SGD plots of all sites). SAD–SGD rank congruence ranged from Pearson's  $r = -0.25$  (DEL) to Pearson's  $r = 0.48$  (ANC) (Fig. 1 and Table 1). The average Pearson's correlation across localities was  $r = 0.14 \pm 0.21$  (SD), with only one correlation being significant (ANC).

### SAD–SGD rank congruence and climatic stability

The best multiple regression model for explaining SAD–SGD rank congruence included both temperature stability (the difference between current and LGM mean annual temperature) and current mean temperature (bio1) ( $R^2 = 0.32$ ,  $F_{2,17} = 4.01$ ,  $p = 0.037$ ), although only temperature stability was significant (Fig. 3; see Supporting information for parameter details). Climatic stability varied among localities, from relatively low temperature change in ALC ( $\Delta T = 2.7^\circ\text{C}$ ) to the largest variation in DEL ( $\Delta T = 6.4^\circ\text{C}$ ). See Supporting information for results for models of species richness, abundance distribution evenness, GDM, and GDE.

## Discussion

Our results show that the impact of long-term climatic stability on biological communities can be detected when evaluating diversity patterns simultaneously at both the species and genetic level. Long-term climatic stability serves as an indicator of abiotic conditions experienced by the biological community but, more importantly, it also functions as a proxy for community age. This association is grounded in the fact that narrower climatic oscillations result in smaller changes in

### SAD–SGD RANK CONGRUENCE VERSUS CLIMATIC STABILITY

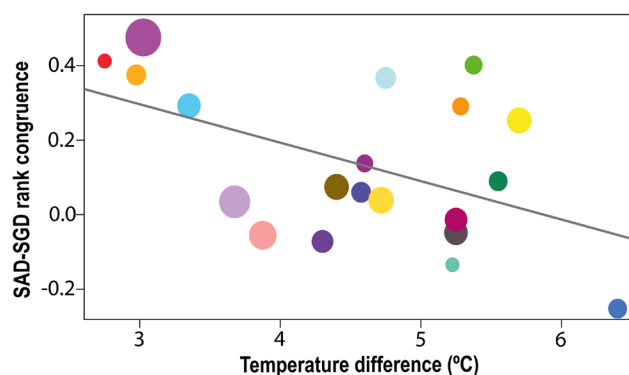


Figure 3. Relationship between the rank congruence of the species abundance distribution (SAD) and the species genetic diversity (SGD) (SAD–SGD rank congruence) and climatic stability since the Last Glacial Maximum (LGM; difference between current mean annual temperature and mean annual temperature at the LGM). Colours correspond to the localities in the map of Fig. 1. Dot size is proportional to species richness.

species' range positions and sizes (Dynesius and Jansson 2000, Brown et al. 2020), thus resulting in increased stability of biological communities over time. Therefore, our study supports the prediction of a positive relationship between community age and the correlation between species abundance and genetic diversity (Overcast et al. 2023a). While this prediction was made in the context of island biogeography, our results extend this expectation to any biological community, as the legacy of climatic stability is observed in the degree of correlation between species abundance and genetic diversity of continental communities. Consequently, our study underscores the relevance of unified models of biological diversity across organizational levels (genes, species, communities) to understand fundamental ecological processes (Vellend et al. 2014, Vellend 2016). In particular, here we show that the impact of historical climatic events in assembly processes conditions our ability to predict community structure at the genetic level (i.e. the distribution of genetic diversity among species in the community) based on observations at the species level (i.e. the distribution of abundance among species in the community).

We observe higher congruence between abundance and genetic diversity distributions in localities that have experienced greater climatic stability, measured as temperature difference since the LGM. In these localities (e.g. ALC, ANC, COR, or EUM), the most abundant species tend to be the ones with higher nucleotide diversity as well, as would be expected for communities that have remained stable over an extended period of time (Overcast et al. 2019, 2023b). Conversely, the correlation between species abundance and genetic diversity decreases in localities that have undergone larger temperature changes since the LGM. This aligns with expectations for communities that have recently reassembled, so abundant species may have not accumulated genetic diversity, although other factors such as competition may also be at play. Our comparison of community structure at two organizational levels complements previous studies evidencing the imprint of past climatic events on contemporary diversity patterns at either the species (Araújo et al. 2008, Ordonez and Svenning 2015, Svenning et al. 2015) or the genetic (Taberlet et al. 1998, Hewitt 2000) level. Furthermore, it contributes new evidence supporting the significant impact of long-term climatic stability on biological communities (Petit et al. 2003, Carnaval et al. 2009, Brown et al. 2020). From a theoretical standpoint, current ecological theory, as proposed by Vellend (2016), asserts that the same fundamental processes shape ecological communities at both the species and molecular levels: selection, drift, dispersal (gene flow), and speciation (mutation). However, it is important to note that the existence of analogous processes does not necessarily imply the existence of identical patterns at both levels (Laroche et al. 2015), as our study also demonstrates. In fact, we highlight that community stability is key to explaining the correlation (or lack thereof) between species abundance and genetic diversity distributions. In other words, climatic stability is a major driver of a macroecological property emerging across organizational levels: the degree of congruence

between community structures at the genetic and species levels.

Our results support the notion that climatic stability serves as a predictor for the correlation between abundance and genetic diversity. This emerges even in the face of generally low correlation values between abundance and genetic diversity, along with substantial variations observed across different localities. Notably, low SAD–SGD rank correlations are expected in continental communities given their higher connectivity, which increases the likelihood of species immigration. Despite this inherent ecological dynamism, both the variability in local SAD–SGD rank correlation values and its relationship with climatic stability underscore the potential of assessing diversity patterns across hierarchical levels, from genetic variants to clades and to species (Vellend 2003, Vellend and Geber 2005, Baselga et al. 2013, Vellend et al. 2014, Baselga et al. 2015). For instance, a spatio-temporal continuum of biodiversity becomes apparent when the same processes operate with equal strength at both the species and genetic levels (Baselga et al. 2013). Given that haplotypes and intraspecific lineages are delimited using neutral molecular markers, which are not subject to selection processes (Diniz-Filho and Bini 2011), the existence of such a spatio-temporal continuum has allowed the inference of dispersal processes playing a major role in shaping diversity patterns at the species level (Baselga et al. 2015, Gómez-Rodríguez et al. 2019, Arribas et al. 2020). Other studies have also contrasted patterns at both levels to detect a dominant effect of environmental constraints (Múrria et al. 2017) or historical factors (Robuchon et al. 2019), as well as to argue about their important implications in biodiversity conservation (Kahilainen et al. 2014). Recent advances in the field, such as metabarcoding of whole communities (Arribas et al. 2020, Noguerales et al. 2021) or community-scale eco-evolutionary simulations (Overcast et al. 2019, 2021, Baselga et al. 2022), hold promise for expediting the inference of ecological and evolutionary processes from the simultaneous assessment of species and genetic diversity patterns (Gillespie et al. 2023, Overcast et al. 2023b). However, here we have benefited from the availability of a fully curated DNA barcoding dataset of whole communities along a latitudinal gradient (Baselga et al. 2015). While taxonomic identification and DNA barcoding of all specimens of complete assemblages may be costly compared to metabarcoding approaches, it also offers two main advantages to test the prediction of Overcast et al. (2019, 2023a): 1) it provides direct measures of relative abundance of each species, and 2) in this particular study, species identification is based on morphological characteristics and hence is independent of the molecular data used to estimate nucleotide diversity.

Our study relies on assessing the distribution of relative abundance and, independently, of nucleotide diversity within biological communities. The distribution of abundance within a community (SAD) stands as one of the most studied patterns in ecology (Magurran and Henderson 2011, McGill 2011). It has proven mostly useful to assess changes in biodiversity structure across communities, space or time

(Antão et al. 2017, Matthews et al. 2019). For instance, temporal changes in biological communities can be assessed by tracking the shifts of species in SADs from one time period to another (Dornelas 2010, Tsai et al. 2014). Here we assess analogous shifts but, instead of comparing the temporal shifts in communities' SADs (SAD in time 1 versus SAD in time 2), we compare organizational levels within communities (SAD versus SGD) in a wide spatial context. The geographic variation of SADs has recently garnered attention, with studies showing how their shape depends on spatial scale (Antão et al. 2017) or varies along latitudinal gradients (Qiao et al. 2015, Ulrich et al. 2016). In contrast, SGDs have not received comparable attention in a biogeographical context (Griffiths and Tavaré 1994). Alternatively, the burgeoning field of 'macrogenetics' is providing interesting insight into how intraspecific genetic diversity varies across multiple communities at larger spatial scales, as well as the evolutionary processes that generate, maintain, and erode biodiversity (Miraldo et al. 2016, Leigh et al. 2021, Schmidt et al. 2023). Previous contributions to macrogenetics have predominantly focused on average measures of genetic diversity, rather than the complete distribution of nucleotide diversity across species within communities. However, a particularly noteworthy study on insect macrogenetics demonstrates that nucleotide diversity is more uneven across species in areas that were glaciated during the LGM (French et al. 2023). Hence, using a summary metric, this study points to historical climatic events shaping the current distribution of genetic diversity within a community. Our study takes a step further, analyzing Iberian leaf beetles to investigate whether the distribution of genetic diversity is correlated with the distribution of abundance and how this may be mediated by historical climatic events.

In conclusion, continental leaf beetle communities exhibit low correlation values between species abundance and genetic diversity, as expected from the higher connectivity of continental communities compared to insular ones. The continental setting is expected to raise the likelihood of novel species arriving to local communities, thereby increasing the variability of species abundances over time. However, despite the relatively modest SGD–SAD correlations, their variation across localities is linked to the magnitude of climate change since the LGM. This evidences the key role of historical climatic stability in shaping biological communities from the molecular to the species level. These results carry two important implications. First, the degree of congruence between SADs and SGDs could be used as a proxy for community stability, not only related to historical climatic change but also to other disrupting factors, including human pressure. Second, in climatically stable localities, species abundance could be used as a proxy for genetic diversity, which is a key facet of biological diversity and should therefore be contemplated in conservation planning (Carvalho et al. 2017, Hanson et al. 2021, Schmidt et al. 2023). If genetic diversity data were available, deviations from SAD–SGD congruence could also be leveraged to infer recent colonizations, thus providing valuable insights into historical biodiversity dynamics and conservation efforts.

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## Author contributions

**Victoria Formoso-Freire:** Formal analysis (lead); Writing – original draft (equal); Writing – review and editing (equal). **Andrés Baselga:** Data curation (equal); Formal analysis (supporting); Funding acquisition (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Carola Gómez-Rodríguez:** Conceptualization (lead); Data curation (equal); Formal analysis (supporting); Funding acquisition (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal).

## Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.dbrv15f8d> (Formoso-Freire et al. 2024). See Supporting information for the R code.

## Supporting information

The Supporting information associated with this article is available with the online version.

## References

- Abellán, P. and Svenning, J. 2014. Refugia within refugia – patterns in endemism and genetic divergence are linked to Late Quaternary climate stability in the Iberian Peninsula. – *Biol. J. Linn. Soc.* 113: 13–28.
- Antão, L. H., Connolly, S. R., Magurran, A. E., Soares, A. and Dornelas, M. 2017. Prevalence of multimodal species abundance distributions is linked to spatial and taxonomic breadth. – *Global Ecol. Biogeogr.* 26: 203–215.
- Antonovics, J. 1976. The input from population genetics: 'The new ecological genetics'. – *Syst. Bot.* 1: 233.
- Araújo, M. B., Nogués-Bravo, D., Diniz-Filho, J. A. F., Haywood, A. M., Valdes, P. J. and Rahbek, C. 2008. Quaternary climate changes explain diversity among reptiles and amphibians. – *Ecography* 31: 8–15.
- Arribas, P., Andújar, C., Salces-Castellano, A., Emerson, B. C. and Vogler, A. P. 2020. The limited spatial scale of dispersal in soil arthropods revealed with whole-community haplotype-level metabarcoding. – *Mol. Ecol.* 30: 48–61.
- Baselga, A., Fujisawa, T., Crampton-Platt, A., Bergsten, J., Foster, P. G., Monaghan, M. T. and Vogler, A. P. 2013. Whole-community DNA barcoding reveals a spatio-temporal continuum of biodiversity at species and genetic levels. – *Nat. Commun.* 4: 1892.
- Baselga, A., Gómez-Rodríguez, C. and Vogler, A. P. 2015. Multi-hierarchical macroecology at species and genetic levels to dis-



- cern neutral and non-neutral processes. – *Global Ecol. Biogeogr.* 24: 873–882.
- Baselga, A., Gómez-Rodríguez, C., Araújo, M. B., Castro-Insua, A., Arenas, M., Posada, D. and Vogler, A. P. 2022. Joint analysis of species and genetic variation to quantify the role of dispersal and environmental constraints in community turnover. – *Ecography* 2022: e05808.
- Brown, S. C., Wigley, T. M. L., Otto-Bliesner, B. L., Rahbek, C. and Fordham, D. A. 2020. Persistent Quaternary climate refugia are hospices for biodiversity in the Anthropocene. – *Nat. Clim. Change* 10: 244–248.
- Cabral, J. S., Valente, L. and Hartig, F. 2017. Mechanistic simulation models in macroecology and biogeography: state-of-art and prospects. – *Ecography* 40: 267–280.
- Carnaval, A. C., Hickerson, M. J., Haddad, C. F. B., Rodrigues, M. T. and Moritz, C. 2009. Stability predicts genetic diversity in the Brazilian Atlantic forest hotspot. – *Science* 323: 785–789.
- Carvalho, S. B., Velo-Antón, G., Tarroso, P., Portela, A. P., Barata, M., Carranza, S., Moritz, C. and Possingham, H. P. 2017. Spatial conservation prioritization of biodiversity spanning the evolutionary continuum. – *Nat. Ecol. Evol.* 1: 1–8.
- Davis, M. B. and Shaw, R. G. 2001. Range shifts and adaptive responses to Quaternary climate change. – *Science* 292: 673–679.
- Diniz-Filho, J. A. F. and Bini, L. M. 2011. Geographical patterns in biodiversity: towards an integration of concepts and methods from genes to species diversity. – *Nat. Conserv.* 9: 179–187.
- Dornelas, M. 2010. Disturbance and change in biodiversity. – *Phil. Trans. R. Soc. B* 365: 3719–3727.
- Dynesius, M. and Jansson, R. 2000. Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. – *Proc. Natl Acad. Sci. USA* 97: 9115–9120.
- Fjeldsa, J., Lambin, E. and Mertens, B. 1999. Correlation between endemism and local ecoclimatic stability documented by comparing Andean bird distributions and remotely sensed land surface data. – *Ecography* 22: 63–78.
- Formoso-Freire, V., Baselga, A. and Gómez-Rodríguez, C. 2024. Data from: Climatic stability predicts the congruence between species abundance and genetic diversity. – *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.dbrv15f8d>.
- French, C. M., Bertola, L. D., Carnaval, A. C., Economo, E. P., Kass, J. M., Lohman, D. J., Marske, K. A., Meier, R., Overcast, I., Rominger, A. J., Staniczenko, P. P. A. and Hickerson, M. J. 2023. Global determinants of insect mitochondrial genetic diversity. – *Nat. Commun.* 14: 5276.
- Gillespie, R., Bik, H., Hickerson, M., Krehenwinkel, H., Overcast, I. and Rominger, A. 2023. Insights into ecological & evolutionary processes via community metabarcoding. – *Mol. Ecol.* 32: 6083–6092.
- Gómez, A. and Lunt, D. H. 2007. Refugia within refugia: patterns of phylogeographic concordance in the Iberian Peninsula. – In: Weiss, S. and Ferrand, N. (eds), *Phylogeography of southern European refugia*. Springer, pp. 155–188.
- Gómez-Rodríguez, C., Miller, K. E., Castillejo, J., Iglesias-Piñeiro, J. and Baselga, A. 2019. Understanding dispersal limitation through the assessment of diversity patterns across phylogenetic scales below the species level. – *Global Ecol. Biogeogr.* 28: 353–364.
- Graham, R. W. and Grimm, E. C. 1990. Effects of global climate change on the patterns of terrestrial biological communities. – *Trends Ecol. Evol.* 5: 289–292.
- Griffiths, R. C. and Tavaré, S. 1994. Sampling theory for neutral alleles in a varying environment. – *Philos. Trans. R. Soc. B* 344: 403–410.
- Grundler, M. R., Singhal, S., Cowan, M. A. and Rabosky, D. L. 2019. Is genomic diversity a useful proxy for census population size? Evidence from a species-rich community of desert lizards. – *Mol. Ecol.* 28: 1664–1674.
- Hagen, O. 2023. Coupling eco-evolutionary mechanisms with deep-time environmental dynamics to understand biodiversity patterns. – *Ecography* 2023: e06132.
- Hanson, J. O., Veríssimo, A., Velo-Antón, G., Marques, A., Camacho-Sanchez, M., Martínez-Solano, Í., Gonçalves, H., Sequeira, F., Possingham, H. P. and Carvalho, S. B. 2021. Evaluating surrogates of genetic diversity for conservation planning. – *Conserv. Biol.* 35: 634–642.
- Hewitt, G. M. 1999. Post-glacial re-colonization of European biota. – *Biol. J. Linn. Soc.* 68: 87–112.
- Hewitt, G. M. 2000. The genetic legacy of the Quaternary ice ages. – *Nature* 405: 907–913.
- Jansson, R. 2003. Global patterns in endemism explained by past climatic change. – *Proc. R. Soc. B* 270: 583–590.
- Kahilainen, A., Puurtinen, M. and Kotiaho, J. S. 2014. Conservation implications of species–genetic diversity correlations. – *Global Ecol. Conserv.* 2: 315–323.
- Karger, D. N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R. W., Zimmermann, N. E., Linder, H. P. and Kessler, M. 2017. Climatologies at high resolution for the earth's land surface areas. – *Sci. Data* 4: 170122.
- Karger, D. N., Nobis, M. P., Normand, S., Graham, C. H. and Zimmermann, N. E. 2021. CHELSA-TraCE21k v1.0. Downscaled transient temperature and precipitation data since the last glacial maximum. – *Clim. Past Discuss.* 20: 1–27.
- Laroche, F., Jarne, P., Lamy, T., David, P. and Massol, F. 2015. A neutral theory for interpreting correlations between species and genetic diversity in communities. – *Am. Nat.* 185: 59–69.
- Leigh, D. M., Van Rees, C. B., Millette, K. L., Breed, M. F., Schmidt, C., Bertola, L. D., Hand, B. K., Hunter, M. E., Jensen, E. L., Kershaw, F., Liggins, L., Luikart, G., Manel, S., Mergeay, J., Miller, J. M., Segelbacher, G., Hoban, S. and Paz-Vinas, I. 2021. Opportunities and challenges of macrogenetic studies. – *Nat. Rev. Genet.* 22: 791–807.
- Magurran, A. E. and Henderson, P. A. 2010. Temporal turnover and the maintenance of diversity in ecological assemblages. – *Phil. Trans. R. Soc. B* 365: 3611–3620.
- Magurran, A. E. and Henderson, P. 2011. Commonness and rarity. – In: Magurran, A. E. and McGill, B. (eds), *Biological diversity*. Oxford Univ. Press, pp. 97–104.
- Matthews, T. J., Sadler, J. P., Kubota, Y., Woodall, C. W. and Pugh, T. A. M. 2019. Systematic variation in North American tree species abundance distributions along macroecological climatic gradients. – *Global Ecol. Biogeogr.* 28: 601–611.
- McCusker, M. R. and Bentzen, P. 2010. Positive relationships between genetic diversity and abundance in fishes. – *Mol. Ecol.* 19: 4852–4862.
- McGill, B. J. 2010. Towards a unification of unified theories of biodiversity. *Ecol. Lett.* 13: 627–642.
- McGill, B. J. 2011. Species abundance distributions. – In: Magurran, A. E. and McGill, B. (eds), *Biological diversity*. Oxford Univ. Press, pp. 105–122.
- Miraldó, A., Li, S., Borregaard, M. K., Flórez-Rodríguez, A., Gopalakrishnan, S., Rizvanovic, M., Wang, Z., Rahbek, C., Marske, K. A. and Nogués-Bravo, D. 2016. An Anthropocene map of genetic diversity. – *Science* 353: 1532–1535.

- Múrria, C., Bonada, N., Vellend, M., Zamora-Muñoz, C., Alba-Tercedor, J., Sainz-Cantero, C. E., Garrido, J., Acosta, R., El Alami, M., Barquín, J., Derka, T., Álvarez-Cabria, M., Sáinz-Bariain, M., Filipe, A. F. and Vogler, A. P. 2017. Local environment rather than past climate determines community composition of mountain stream macroinvertebrates across Europe. – *Mol. Ecol.* 26: 6085–6099.
- Nei, M. and Li, W. H. 1979. Mathematical model for studying genetic variation in terms of restriction endonucleases. – *Proc. Natl Acad. Sci. USA* 76: 5269–5273.
- Noguerales, V., Meramveliotakis, E., Castro-Insua, A., Andújar, C., Arribas, P., Creedy, T. J., Overcast, I., Morlon, H., Emerson, B. C., Vogler, A. P. and Papadopoulou, A. 2021. Community metabarcoding reveals the relative role of environmental filtering and spatial processes in metacommunity dynamics of soil microarthropods across a mosaic of montane forests. – *Mol. Ecol.* 32: 6110–6128.
- Ordóñez, A. and Svenning, J. 2015. Geographic patterns in functional diversity deficits are linked to glacial-interglacial climate stability and accessibility. – *Global Ecol. Biogeogr.* 24: 826–837.
- Overcast, I., Emerson, B. C. and Hickerson, M. J. 2019. An integrated model of population genetics and community ecology. – *J. Biogeogr.* 46: 816–829.
- Overcast, I., Ruffley, M., Rosindell, J., Harmon, L., Borges, P. A. V., Emerson, B. C., Etienne, R. S., Gillespie, R., Krehenwinkel, H., Mahler, D. L., Massol, F., Parent, C. E., Patiño, J., Peter, B., Week, B., Wagner, C., Hickerson, M. J. and Rominger, A. 2021. A unified model of species abundance, genetic diversity, and functional diversity reveals the mechanisms structuring ecological communities. – *Mol. Ecol. Resour.* 21: 2782–2800.
- Overcast, I. et al. 2023a. Towards a genetic theory of island biogeography: inferring processes from multidimensional community-scale data. – *Global Ecol. Biogeogr.* 32: 4–23.
- Overcast, I., Noguerales, V., Meramveliotakis, E., Andújar, C., Arribas, P., Creedy, T. J., Emerson, B. C., Vogler, A. P., Papadopoulou, A. and Morlon, H. 2023b. Inferring the ecological and evolutionary determinants of community genetic diversity. – *Mol. Ecol.* 32: 6093–9109.
- Paradis, E., Jombart, T., Kamvar, Z. N., Knaus, B., Schliep, K., Potts, A. and Winter, D. 2023. *pegas*: population and evolutionary genetics analysis system. – <https://CRAN.R-project.org/package=pegas>.
- Petit, R. J., Aguinalde, I., De Beaulieu, J. L., Bittkau, C., Brewer, S., Cheddadi, R., Ennos, R., Fineschi, S., Grivet, D., Lascoux, M., Mohanty, A., Müller-Starck, G., Demesure-Musch, B., Palmé, A., Martín, J. P., Rendell, S. and Vendramin, G. G. 2003. Glacial refugia: hotspots but not melting pots of genetic diversity. – *Science* 300: 1563–1565.
- Petitpierre, E. 2000. *Fauna Ibérica 13: Coleoptera: Chrysomelidae I*. – Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas.
- Qiao, X., Jabot, F., Tang, Z., Jiang, M. and Fang, J. 2015. A latitudinal gradient in tree community assembly processes evidenced in Chinese forests. – *Global Ecol. Biogeogr.* 24: 314–323.
- Robuchon, M., Leroy, B., Jézéquel, C. and Huguény, B. 2019. Correlations between broad-scale taxonomic and genetic differentiations suggest a dominant imprint of historical processes on beta diversities. – *J. Biogeogr.* 46: 1083–1095.
- Schmidt, C., Dray, S. and Garroway, C. J. 2022. Genetic and species-level biodiversity patterns are linked by demography and ecological opportunity. – *Evolution* 76: 86–100.
- Schmidt, C., Hoban, S. and Jetz, W. 2023. Conservation macrogenetics: harnessing genetic data to meet conservation commitments. – *Trends Genet.* 39: 816–829.
- Skov, F. and Svenning, J. 2004. Potential impact of climatic change on the distribution of forest herbs in Europe. – *Ecography* 27: 366–380.
- Stewart, J. R., Lister, A. M., Barnes, I. and Dalén, L. 2010. Refugia revisited: individualistic responses of species in space and time. – *Proc. R. Soc. B* 277: 661–671.
- Svenning, J. and Skov, F. 2007. Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? – *Ecol. Lett.* 10: 453–460.
- Svenning, J., Eiserhardt, W. L., Normand, S., Ordóñez, A. and Sandel, B. 2015. The influence of paleoclimate on present-day patterns in biodiversity and ecosystems. – *Annu. Rev. Ecol. Evol. Syst.* 46: 551–572.
- Taberlet, P., Fumagalli, L., Wust-Saucy, A. and Cosson, J. 1998. Comparative phylogeography and postglacial colonization routes in Europe. – *Mol. Ecol.* 7: 453–464.
- Tajima, F. 1983. Evolutionary relationship of DNA sequences in finite populations. – *Genetics* 105: 437–460.
- Tsai, C.-H., Miki, T., Chang, C.-W., Ishikawa, K., Ichise, S., Kumagai, M. and Hsieh, C. 2014. Phytoplankton functional group dynamics explain species abundance distribution in a directionally changing environment. – *Ecology* 95: 3335–3343.
- Ulrich, W., Kusumoto, B., Shiono, T. and Kubota, Y. 2016. Climatic and geographic correlates of global forest tree species-abundance distributions and community evenness. – *J. Veg. Sci.* 27: 295–305.
- Vellend, M. 2003. Island biogeography of genes and species. – *Am. Nat.* 162: 358–365.
- Vellend, M. 2005. Species diversity and genetic diversity: parallel processes and correlated patterns. – *Am. Nat.* 166: 199–215.
- Vellend, M. 2010. Conceptual synthesis in community ecology. – *Q. Rev. Biol.* 85: 183–206.
- Vellend, M. 2016. *The theory of ecological communities*. – Princeton Univ. Press.
- Vellend, M. and Geber, M. A. 2005. Connections between species diversity and genetic diversity. – *Ecol. Lett.* 8: 767–781.
- Vellend, M., Lajoie, G., Bourret, A., Múrria, C., Kembel, S. W. and Garant, D. 2014. Drawing ecological inferences from coincident patterns of population- and community-level biodiversity. – *Mol. Ecol.* 23: 2890–2901.
- Warchalowski, A. 2003. *Chrysomelidae: the leaf-beetles of Europe and the Mediterranean area*. – Natura optima dux Foundation.
- Whittaker, R. H. 1965. Dominance and diversity in land plant communities: numerical relations of species express the importance of competition in community function and evolution. – *Science* 147: 250–260.
- Williams, J. W., Shuman, B. N. and Webb, T. 2021. Dissimilarity analyses of late quaternary vegetation and climate in eastern North America. – *Ecology* 82: 2246–3362.