

# Relationships among taxonomic, functional, and phylogenetic ant diversity across the biogeographic regions of Europe

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Understanding how different biodiversity components are related across different environmental conditions is a major goal in macroecology and conservation biogeography. We investigated correlations among alpha and beta taxonomic (TD), phylogenetic (PD), and functional diversity (FD) in ant communities in the five biogeographic regions most representative of western Europe; we also examined the degree of niche conservatism. We combined data from 349 ant communities composed of 154 total species, which were characterized by 10 functional traits and by phylogenetic relatedness. We computed TD, PD, and FD using the Rao quadratic entropy index, which allows each biodiversity component to be partitioned into  $\alpha$  and  $\beta$  diversity within the same mathematical framework. We ran generalized least squares and multiple matrix regressions with randomization to investigate relationships among the diversity components. We used Pagel's  $\lambda$  test to explore niche conservatism in each biogeographic region. At the alpha scale, TD was consistently, positively related to PD and FD, although the strength and scatter of this relationship changed among the biogeographic regions. Meanwhile, PD and FD consistently matched up across regions. Accordingly, we found similar degrees of niche conservatism across regions. Nonetheless, these alpha-scale relationships had low coefficients of determination. At the beta scale, the three diversity components were highly correlated across all regions (especially TD and FD, as well as PD and FD). Our results imply that the different diversity components, and especially PD and FD, are consistently related across biogeographic regions and analytical scale. However, the alpha-scale relationships were quite weak, suggesting environmental factors might influence the degree of association among diversity components at the alpha level. In conclusion, conservation programs should seek to preserve functional and phylogenetic diversity in addition to species richness, and this approach should be applied universally, regardless of the biogeographic locations of the sites to be protected.

Understanding biodiversity patterns is a primary goal in community ecology and conservation biology. Much of our current understanding of biodiversity patterns comes from analyses of taxonomic diversity (TD), notably species richness and turnover. However, current measures of species diversity treat all species as functionally equivalent and evolutionarily independent (Swenson 2011), thereby ignoring the fact that the loss of certain species can have a greater impact on ecosystem functioning and evolutionary legacy (Tilman 2001). To address these limitations, new biodiversity estimates have recently been proposed that describe the functional (Petchey and Gaston 2006) and phylogenetic (Webb et al. 2002, Faith 2008) characteristics of the community. While phylogenetic diversity (PD) reflects the accumulated evolutionary history of a community (Webb et al. 2002, Lessard et al. 2012), functional diversity (FD) reflects the diversity of morphological, physiological, and ecological traits found therein (Petchey and Gaston 2006). However, compared to taxonomic diversity, these other components have faced relatively less scrutiny and their

properties are currently poorly understood (Pavoine and Bonsall 2011).

Nonetheless, it is increasingly acknowledged that examining PD and FD can shed new light on temporal and spatial changes in community structure and composition for at least three reasons (Pavoine and Bonsall 2011). First, preserving as many types of biological diversity as possible is essentially a rule of thumb in conservation biology (Devictor et al. 2010). As a result, and because it is difficult to optimally preserve all types of biodiversity simultaneously, it is important to understand how diversity components relate to each other and the dynamics associated with each (Zupan et al. 2014). For instance, species diversity hot spots do not necessarily coincide with functional or phylogenetic diversity hot spots (Mazel et al. 2014), which raises questions about using TD as the sole criterion when establishing conservation strategies. Secondly, PD and FD may better predict ecosystem productivity and stability than TD (Cadotte et al. 2009, Mouillot et al. 2013). PD may reflect a system's capacity to either generate new evolutionary solutions in the face of

environmental changes or to persist despite those changes (Forest et al. 2007, Faith 2008). Similarly, FD reveals the functional response of species assemblages to environmental filters, as well as assemblages' functional impact, or their ability to occupy functional niche space in such a way as to optimize ecosystem functioning (Díaz et al. 2007, Cadotte et al. 2009). Finally, understanding how both PD and FD are correlated with TD can provide insights into the role of deterministic or stochastic processes in community assembly (Cavender-Bares et al. 2009, Pavoine and Bonsall 2011, Purschke et al. 2013). Using TD, PD, and FD in tandem is useful since it allows us to explicitly test predictions about the differential effects of competition and environmental filtering on PD and FD. A priori, we expect a positive correlation between TD and PD or FD just by chance, since the presence of more species should mean that more lineages and functional traits are represented (Losos 2008). However, two communities with equal TD might nonetheless greatly differ in PD and FD (Safi et al. 2011, Hermant et al. 2012, Tucker and Cadotte 2013), because of different evolutionary histories and/or contrasting environmental conditions. Therefore, for a given level of TD, environmental filtering will generally tend to decrease functional and phylogenetic distances among species (PD or FD clustering), while competition will tend to increase these distances (PD or FD overdispersion) (Webb et al. 2002, Kraft et al. 2007).

The relationship between PD and FD is also complex. A strong correlation between these two diversity components is expected if the functional traits that allow species to persist in the environment are evolutionarily conserved (Webb et al. 2002). Likewise, if both PD and FD are correlated with TD, then they are also expected to be correlated with each as a side effect (Safi et al. 2011). Surprisingly, however, the few studies that have looked at the relationship between PD and FD have usually found that phylogenetic and functional patterns do not match up (Losos 2008, Devictor et al. 2010, Safi et al. 2011). In fact, different assembly processes may create the same phylogenetic patterns (Losos 2008, Mayfield and Levine 2010, Pavoine and Bonsall 2011). Blomberg et al. (2003) even suggested that situations where phylogenetic and trait variation are tightly linked may be the exception rather than the rule. Other studies have found that PD and FD may covary in different ways along geographic and environmental gradients (Devictor et al. 2010, Bernard-Verdier et al. 2013, Purschke et al. 2013), which suggests that the environment may strongly condition the relationship between different diversity components (Safi et al. 2011, Hermant et al. 2012).

Finally, the relationship between the different diversity components might also depend on spatial scale (Emerson and Gillespie 2008, Devictor et al. 2010, Bernard-Verdier et al. 2013) because the processes that may influence biodiversity are different at different scales. At the community scale, biotic interactions, environmental filtering, and stochastic processes play major roles in determining (alpha) diversity whereas, at more regional scales, historical and evolutionary processes may largely drive (beta) diversity (Graham and Fine 2008, Cavender-Bares et al. 2009).

In this study, we examined the relationships between taxonomic, phylogenetic, and functional diversity in European ant communities in various biogeographic regions. First, we

quantified and compared alpha and beta taxonomic, phylogenetic, and functional diversity at the continental scale and then within the five different biogeographic regions (Mediterranean, Continental, Atlantic, Boreal, and Alpine) most representative of Europe. As rates of trait evolution and speciation may differ among biogeographic regions (Weir and Schluter 2007, Cooper and Purvis 2010; but see Jetz et al. 2012, Rabosky and Slater 2014), biogeographical comparisons would reveal if different diversity patterns were the product of different environmental and historical conditions. Ants are an ideal study system with which to examine large-scale, biodiversity patterns because they are among the most diverse, abundant, and dominant organisms on earth; have colonized nearly all the terrestrial habitats of the world; are taxonomically well described (at least at the genus level); have relatively well documented functional traits; and perform a great variety of critical ecosystem functions (Hölldobler and Wilson 1990, Del Toro et al. 2012, 2015, Arnan et al. 2014). We used data from 349 ant communities comprising a total of 154 ant species, and we examined 10 functional traits that are important to ant autecology and/or that relate to ecosystem functioning. Given that there are close to 600 native ant species in Europe (Czechowski et al. 2002) and that our study sites mostly covered western and central Europe, our species pool provides a good representation of overall ant diversity in the area. Our study sites spanned a range of biogeographic regions that vary in growing season length, mean annual temperature, and precipitation. We used all this information to test the following two predictions: a) since the degree of niche conservatism differs in each biogeographic region, the relationship between TD, PD, and FD may also be different in each region and deviate from the overall relationship; and b) since environmental heterogeneity differs among biogeographic regions, the relationship between the different diversity components will also differ, depending on the spatial scale considered (i.e. alpha or beta).

## Material and methods

### Ant community data

We compiled species composition data from local ground-dwelling ant communities in Europe from as many sites as possible. Our data consisted of primary data collected by the authors and data gleaned from an exhaustive search of the literature. We only took into account studies that contained species abundance or presence-absence data. We eliminated data from highly disturbed and urbanized sites and poorly sampled communities. Overall, the dataset encompassed 349 sites spanning a latitudinal gradient from approximately 36.8° to 72.0°N and from 7.1° to 24.0°W (Fig. 1). These communities comprised a total of 154 ant species (Supplementary material Appendix 1) belonging to 29 genera and 5 subfamilies. We focused our analyses on presence-absence data because they are more comparable among sites than abundance data, which can be measured in different ways (i.e. number of nests, individuals at baits, or individuals in pitfall traps) and are thus difficult to compare. Moreover, if the aim is to compare the

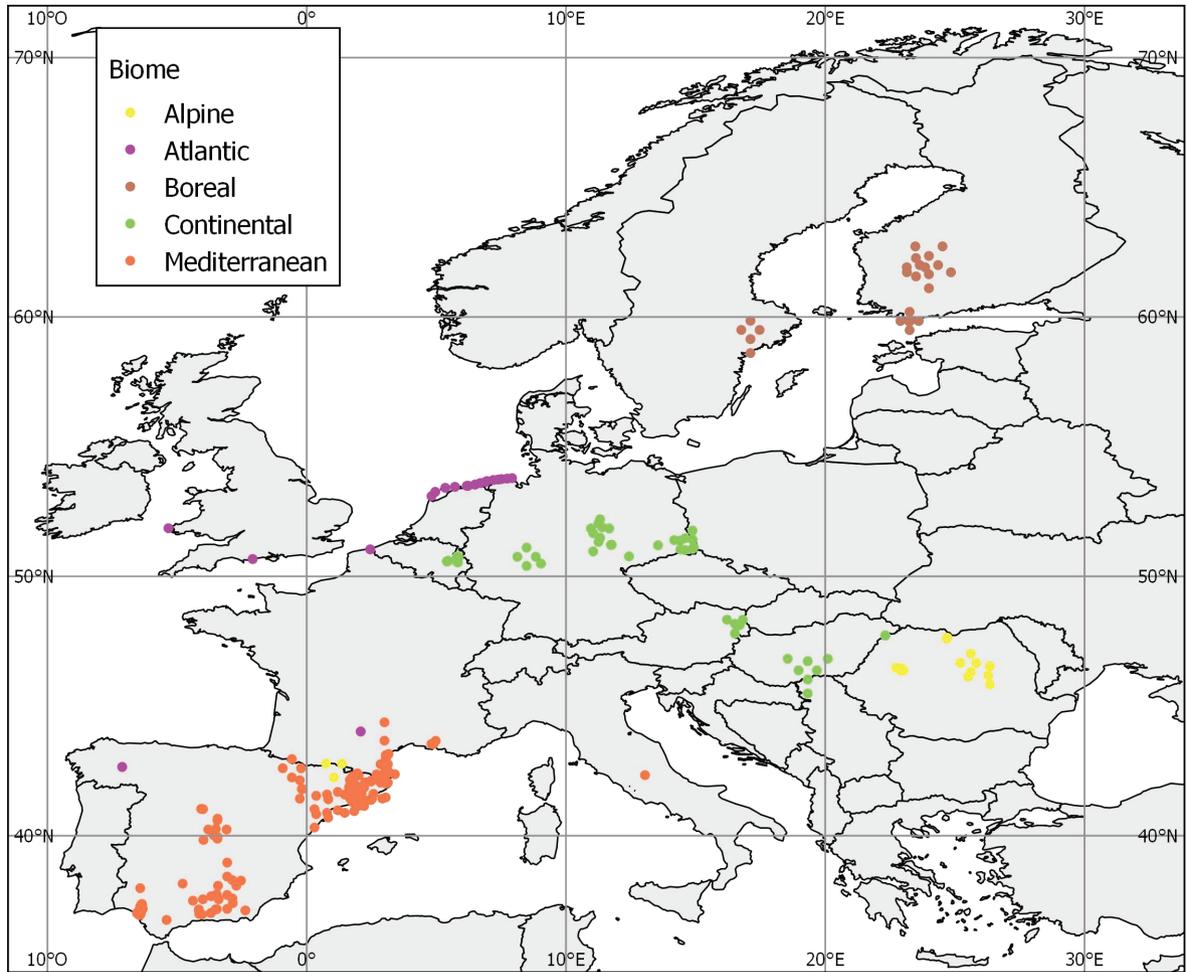


Figure 1. Map of the study area showing the distribution of sites.

relative contribution of several diversity components, then including abundance is not necessarily helpful (Devictor et al. 2010).

### Ant trait data

The 154 ant species were scored for 10 traits that reflect different dimensions of the functional niche (i.e. morphology, life history and behavior). Because ants are social insects, functional traits may be quantified at the level of both the individual worker and that of the colony. The following traits were used: worker size, worker polymorphism, colony size, food resource type exploited (i.e. relative consumption of seeds, insects, or liquid food), daily period of activity, position in the behavioral dominance hierarchy, foraging strategy (how a species searches for and exploits food resources), number of queens per colony, number of nests per colony, and colony foundation type. Note that these traits may be continuous, ordinal, or binary (Supplementary material Appendix 2). They are also traits considered to be important in ants because they help define ant autecology and influence ecosystem functioning (Hölldobler and Wilson 1990, Arnan et al. 2014). Trait data are provided in Supplementary material Appendix 1.

### Ant phylogeny

We built a complete phylogeny for the 154 ant species considered (Supplementary material Appendix 3). This tree was the product of a super tree derived from a genus-level phylogeny created using a molecular dataset (Moreau and Bell 2013). We then added species to this basal tree using both molecular and morphological data. While we recognize that, ideally, a phylogeny should be reconstructed solely from molecular data, such data were not universally available. We gathered information from 38 references (Supplementary material Appendix 3); 23 (60.5%) of them provided molecular data. For the 154 taxa considered, we found molecular data for 74 species (48%); however, this information was unavailable for the other 80 species (52%). The tree was reconstructed with Mesquite ver. 3.0 (Maddison and Maddison 2014) by manually combining the Moreau and Bell (2013) genus-level phylogeny with information about different species-specific phylogenetic relationships taken from those 38 references (see the phylogenetic tree in Supplementary material Appendix 3). For this phylogeny, reliable estimates of branch length and node ages were unavailable. First, to solve the polytomies, we used ‘multi2di’ from R package ‘phytools’. Second, the tree was ultrametrized applying Grafen’s Rho transformation to

branch lengths (Carneiro et al. 2014), we used the function ‘compute.brln’ from R package ‘ape’. Although it would have been preferable to have consistent branch length estimates, these relationships remain unresolved for most insect groups, as well as for most animal and plant groups. It is likely that our community phylogeny captures most of the phylogenetic structure of the community, even if there is noise within genera. Although our tree is clearly not without its flaws, it is the most complete species-level phylogeny for European ants to date.

## Delineation of biogeographic regions

Sites were assigned to different biogeographic regions using a map provided by the European Environment Agency (<www.eea.europa.eu/>). Our communities were found in one of five regions: Mediterranean (199 sites), Continental (71, including 10 sites from the Pannonian region, with similar climatic conditions), Atlantic (27), Boreal (29), and Alpine (23). These biogeographic regions differ in temperature and precipitation (Fig. 2; see also Supplementary material Appendix 4 for the main characteristics of these regions and how they differ in mean annual temperature and precipitation).

## Partitioning taxonomic, functional, and phylogenetic ant diversity

We used the Rao quadratic entropy index, which allows each biodiversity component (TD, FD, and PD) to be partitioned into  $\alpha$ ,  $\beta$ , and  $\gamma$  diversity; it is also a standardized method that can be used to compare these components within the same mathematical framework (Pavoine et al. 2004, de Bello et al. 2010, Devictor et al. 2010, Meynard et al. 2011). Overall gamma diversity was additively partitioned into within (alpha) and among (beta) community diversity.

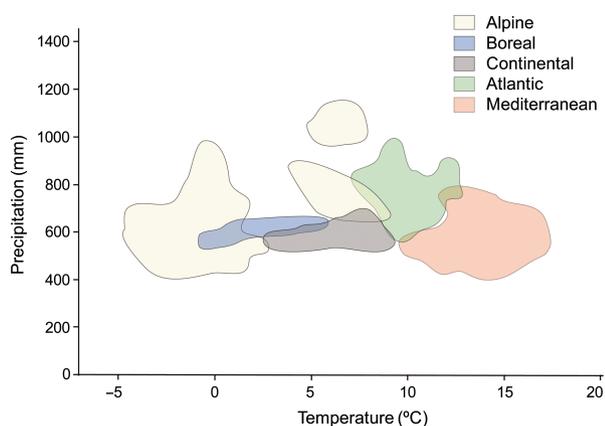


Figure 2. Distribution of Europe’s broadly defined biogeographic regions, which differ in temperature and precipitation. To draw this plot, we used the mean annual temperature and mean annual precipitation for each 1-km cell within each biogeographic region. The area of each biogeographic region on the plot is delimited by smooth curves and encompasses the temperature and precipitation values associated with a high density of cells (60% of values) in this region.

Within each community  $k$ , alpha diversity was calculated using Rao’s coefficient of diversity (Rao 1982, Pavoine et al. 2004) modified for presence–absence data:

$$\alpha Rao(k) = \sum_{i=1}^n \sum_{j=1}^n dij$$

where  $d_{ij}$  is the distance between species  $i$  and  $j$ , which can be taxonomic, functional, or phylogenetic. This index represents the expected dissimilarity between two individuals of different species chosen at random from the community. Between communities  $k$  and  $l$ , beta diversity was computed using the Rao’s dissimilarity index (Rao 1982, Pavoine et al. 2004):

$$\beta Rao_{pairwise}(k, l) = \frac{\gamma_{(k+l)} - \bar{\alpha}_{(k,l)}}{\gamma_{(k+l)}}$$

where  $\gamma_{k+l}$  is the gamma diversity of the pair of communities (calculated using the same equation as for alpha diversity, except that all the species in the two communities are included) and  $\bar{\alpha}_{(k,l)}$  is the mean alpha diversity of the two communities. This index is the expected distance between two individuals of different species chosen at random from two distinct communities. To properly quantify beta diversity independently of alpha diversity, we applied Jost’s correction (Jost 2007) to  $\gamma$  and  $\alpha$  values prior to determining the Rao indices (de Bello et al. 2010). Calculations were performed using the ‘rao’ function (de Bello et al. 2010) in R (R Development Core Team).

Several distance measures can be used to calculate the Rao quadratic entropy index, depending on the diversity component of interest. Taxonomic distances between species were measured as  $d_{ij} = 1$ , where  $i \neq j$  and  $d_{ij} = 0$  when  $i = j$ . To determine functional distances between species, we first conducted principal component analysis (PCA) on the standardized (mean = 0, SD = 1) trait data to correct for the effect of highly correlated traits on the distance matrix (Devictor et al. 2010, Purschke et al. 2013). The resulting PCA axes were used to calculate Euclidean distances. Phylogenetic distances between species were measured using the cophenetic distances from the phylogeny. To make the taxonomic, functional, and phylogenetic distances comparable, we transformed all the distances by dividing each type of distance by its maximum value, which resulted in values ranging between 0 and 1 (de Bello et al. 2010).

## Statistical analyses

To investigate the relationships among the alpha diversity components in ant assemblages across Europe and in different biogeographic regions, we used generalized least squares (GLS) regressions implemented in R. We used GLS models because there was likely to be a substantial amount of spatial autocorrelation in the values of the diversity indices across sites. These models can account for correlated errors, and therefore spatial autocorrelation. We used AIC-based model comparison to determine the optimal spatial correlation structure, and upon inspecting the residuals, we found that spatial effects had been almost entirely removed from all our models. GLS models use simultaneous autoregression to estimate means. When appropriate, we used multiple contrasts to test whether the slopes of the relationships between

the different biodiversity components were significantly different for different biogeographic regions. Since the relationship between TD and PD or FD might be better described by a quadratic function, we also included the quadratic term in our models. Although we obtained a better fit with the quadratic term, the coefficient of determination was only slightly improved (by less than 7% in both cases), and we decided to proceed using only linear terms to make all the analyses more comparable. We analyzed the relationships among the ant beta diversity components while controlling for the influence of geographic distance on beta dissimilarity using multiple matrix regression with randomization (MMRR) analyses (999 permutations); we employed the ‘MMRR’ function (Wang 2013) in R. This function takes a set of distance matrices, calculates the regression coefficients and coefficient of determination, performs the randomized permutation, and estimates significance values for all the parameters. Since only distance matrices can be included in these models, we ran one model for each biogeographic region; the slopes were then qualitatively compared among regions. Since taxonomic diversity intrinsically influences functional and phylogenetic diversity and their turnover (see Results), taxonomic diversity was a covariate in all our analyses of the relationship between FD and PD (Devictor et al. 2010, Pavoine et al. 2013).

To characterize the degree of niche conservatism in ant species functional traits at the continental scale and the biogeographical scale, we tested for the presence of a phylogenetic signal in each trait, first using all the species and then using the subset of species found in each biogeographic region. We used Pagel’s  $\lambda$  test (Pagel 1999), which assumes a Brownian motion (BM) model of trait evolution. Pagel’s  $\lambda$  was calculated using the ‘fitContinuous’ and ‘fitDiscrete’ functions (depending on whether the trait was continuous or discrete) in the Geiger package in R. To test for the presence

of a significant phylogenetic signal, we used a likelihood ratio test approximated by a chi-squared distribution to compare the negative log likelihood obtained when there is no signal (i.e. using the tree transformed  $\lambda = 0$ ) to that estimated from the original topology.

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.c763m>> (Arnan et al. 2016).

## Results

### Continental patterns of ant diversity

Both PD and FD were positively correlated with TD (Fig. 3a, b; Table 1), although the relationship was not very strong ( $R^2 = 0.20$  and  $0.32$  in PD and FD, respectively). The relationship between FD and PD was positive ( $R^2 = 0.34$ ), even when TD was added as a covariate ( $R^2 = 0.46$ ) (Fig. 3c). With regards to beta diversity, phylogenetic and functional turnover were both positively correlated with taxonomic turnover (Fig. 3d, e; Table 2). Functional and phylogenetic turnover were also positively correlated and remained so even after taxonomic turnover was controlled for (Fig. 3f). For these continental patterns, the coefficient of determination was much higher for beta- than for alpha-level relationships (Table 1).

### Biogeographic patterns of ant diversity

The different components of alpha biodiversity differed significantly among biogeographic regions (GLS model; TD:  $F_{1,4} = 20.6$ ,  $p < 0.0001$ ; PD:  $F_{1,4} = 27.3$ ,  $p < 0.0001$ ; and FD:  $F_{1,4} = 38.8$ ,  $p < 0.0001$ ), and followed similar patterns. Ant TD and FD were highest in the Mediterranean region,

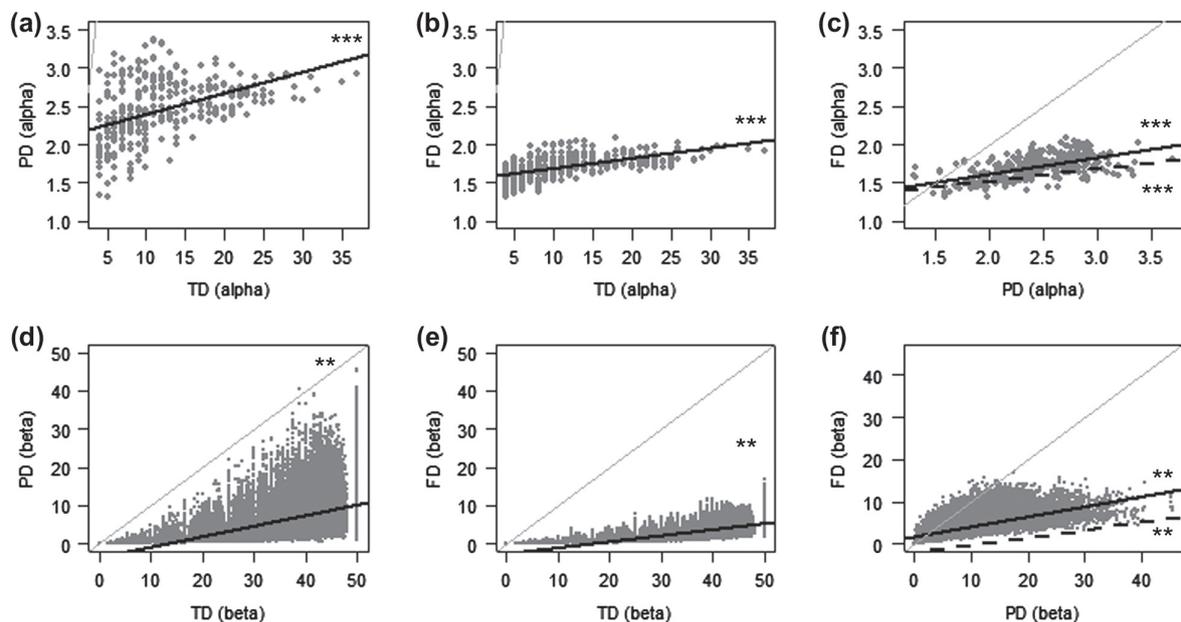


Figure 3. Relationships between the components of alpha and beta diversity at the continental scale (solid line, without controlling for TD; broken line, controlling for TD). The gray diagonal line depicts a hypothetical relationship with slope( $\beta$ ) = 1. Abbreviations: TD, taxonomic diversity; PD, phylogenetic diversity; FD, functional diversity; NS, non-significant; \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$ .

Table 1. Summary of the outputs from the GLS models for alpha diversity used to analyze the relationship between the different diversity components, i.e. taxonomic diversity (TD), functional diversity (FD), and phylogenetic diversity (PD). The pseudo  $R^2$  ( $pR^2$ ) for the entire model is provided. Different superscript letters indicate significant differences among biogeographic regions in the slopes of the relationships between the different components of diversity (multiple contrasts;  $p < 0.05$ ).

	PD				FD				
	Estimate $\pm$ SE	t/F	p	$pR^2$	Estimate $\pm$ SE	t/F	p	$pR^2$	DF
Europe									
TD	0.028 $\pm$ 0.003	9.3	< 0.0001	0.20	0.013 $\pm$ 0.001	12.9	< 0.0001	0.32	349,347
PD					0.22 $\pm$ 0.02	13.5	< 0.0001	0.34	349,347
PD (+TD)					0.16 $\pm$ 0.017	8.7	< 0.0001	0.46	349,346
Biogeographic regions									
TD $\times$ Biome		17.0	< 0.0001	0.44		6.8	< 0.0001	0.48	349,339
Mediterranean	0.012 $\pm$ 0.003 <sup>ab</sup>	3.9	< 0.0001	0.08	0.008 $\pm$ 0.001 <sup>a</sup>	6.3	< 0.0001	0.17	199,197
Continental	0.102 $\pm$ 0.014 <sup>c</sup>	7.5	< 0.0001	0.46	0.025 $\pm$ 0.004 <sup>bc</sup>	6.9	< 0.0001	0.36	71,69
Atlantic	0.042 $\pm$ 0.014 <sup>bd</sup>	3.1	0.005	0.31	0.027 $\pm$ 0.004 <sup>bc</sup>	6.2	< 0.0001	0.64	27,25
Alpine	0.136 $\pm$ 0.000 <sup>d</sup>	2.8	< 0.0001	0.33	0.035 $\pm$ 0.009 <sup>b</sup>	3.9	0.0008	0.29	23,21
Boreal	0.034 $\pm$ 0.008 <sup>a</sup>	4.4	< 0.0001	0.40	0.012 $\pm$ 0.003 <sup>ac</sup>	4.1	0.0004	0.31	29,27
PD $\times$ Biome						0.5	0.738	0.47	349,339
PD $\times$ Biome (+TD)						0.7	0.580	0.53	349,338

intermediate in the Continental, Atlantic, and Boreal regions, and lowest in the Alpine region (Fig. 4). Ant PD followed the same pattern, with the only difference being that the Boreal region also showed the lowest values (together with the Alpine region). The interaction between the alpha diversity components and biogeographic region was significant for the relationships between PD and TD as well as between FD and TD, but not for the relationship between FD and PD, even after controlling for TD (Table 1). These results highlight that the relationships between PD and FD with TD vary across biogeographic regions, while the relationship between FD and PD remain constant across biogeographic regions.

Within each of the five biogeographic regions, both ant PD and FD were positively correlated with TD (Table 1), which was consistent with the overall pattern. However, there was a significant interaction between TD and biogeographic

region, which suggests that the slopes of the relationships differed between regions (Table 1, Supplementary material Appendix 5). TD explained more variation in PD in the Continental (46%) and Boreal (40%) regions than in the Mediterranean region (8%), and TD accounted for more variation in FD in the Atlantic (64%) than in the Mediterranean (17%) (Table 1).

With regards to beta diversity, the values of the ant biodiversity components also differed among biogeographic regions (one-way ANOVA; TD:  $F_{4,46736} = 846.5$ ,  $p < 0.0001$ ; PD:  $F_{4,46736} = 468.2$ ,  $p < 0.0001$ ; and FD:  $F_{4,46736} = 330.2$ ,  $p < 0.0001$ ). Furthermore, the patterns for beta diversity differed from those for alpha diversity. Taxonomic turnover was highest in the Mediterranean, Continental, and Alpine regions and lowest in the Atlantic and Boreal regions. Phylogenetic turnover was highest in the Continental and Alpine regions, intermediate in the Mediterranean and

Table 2. Summary of the outputs from the multiple matrix regression with randomization (MMRR) models for beta diversity used to analyze the relationship between the different diversity components, i.e. taxonomic diversity (TD), functional diversity (FD), and phylogenetic diversity (PD). The coefficient of determination ( $R^2$ ) for the entire model is provided.

	PD					FD					n
	Intercept	Estimate	t	p	$R^2$	Intercept	Estimate	t	p	$R^2$	
TD	-3.81	0.283	112.4	0.001	0.25	-2.66	0.164	200.0	0.001	0.51	349
Mediterranean	-4.16	0.288	85.1	0.001	0.29	-2.39	0.154	140.2	0.001	0.53	199
Continental	-4.27	0.321	27.6	0.001	0.33	-0.71	0.119	45.9	0.001	0.51	71
Atlantic	-0.13	0.115	9.0	0.001	0.39	0.20	0.080	29.2	0.001	0.73	27
Alpine	0.23	0.282	8.8	0.001	0.25	-0.45	0.169	22.0	0.001	0.67	23
Boreal	-4.07	0.527	29.0	0.001	0.68	-1.32	0.175	32.7	0.001	0.73	29
PD						1.61	0.243	203.9	0.001	0.52	349
Mediterranean						1.18	0.273	136.6	0.001	0.52	199
Continental						1.86	0.197	55.2	0.001	0.59	71
Atlantic						1.19	0.205	13.1	0.001	0.39	27
Alpine						2.63	0.251	15.6	0.001	0.50	23
Boreal						0.38	0.269	30.8	0.001	0.71	29
PD (+TD)						-2.00	0.173	154.9	0.001	0.65	349
Mediterranean						-1.65	0.178	91.8	0.001	0.67	199
Continental						-0.098	0.143	41.9	0.001	0.71	71
Atlantic						0.210	0.092	8.9	0.001	0.78	27
Alpine						-0.488	0.144	11.9	0.001	0.79	23
Boreal						-0.77	0.135	10.3	0.001	0.79	29

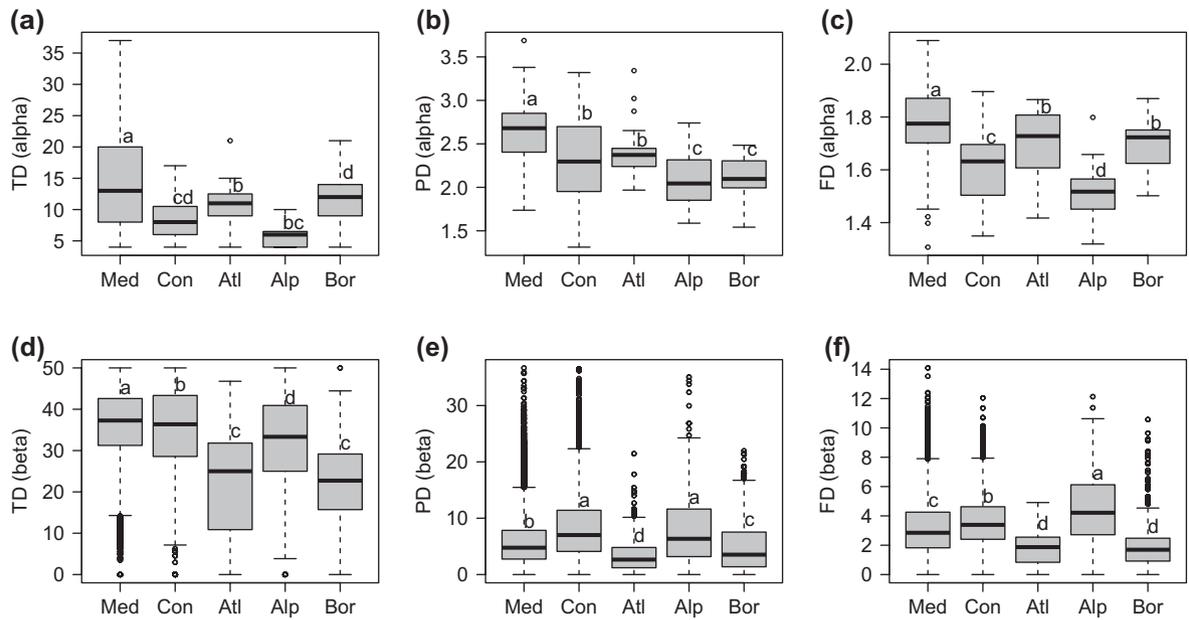


Figure 4. Boxplots of alpha and beta taxonomic, phylogenetic, and functional diversity values for the five biogeographic regions. Letters indicate significant differences ( $p < 0.05$ ) according to the Tukey post-hoc test.

Boreal regions, and lowest in the Atlantic region. Finally, functional turnover was highest in the Alpine region, intermediate in the Mediterranean and Continental regions, and lowest in the Atlantic and Boreal regions (Fig. 4). In all five biogeographic regions, the different ant diversity components were always positively correlated, and there were no substantial deviations from the continental patterns (Table 2, Supplementary material Appendix 6). It is worth noting that the results for alpha and beta diversity are quite similar to how FD related to PD across biogeographic regions.

### Phylogenetic signals in ant functional traits

Strong, significant phylogenetic signals were present in most of the ant functional traits at the continental scale and the biogeographical scale (Supplementary material Appendix 3), which is evidence (albeit not definitive) for niche conservatism at the two scales of study. Ant colony size in the Alpine regions was the only trait that did not show phylogenetic signal.

### Discussion

Our results confirm that TD, PD, and FD do somewhat covary in European ant communities. With regards to alpha biodiversity, TD seems to predict both PD and FD (albeit weakly); however, the strength of this relationship is dependent on biogeography. PD and FD are also positively correlated across ant communities. Contrary to our expectations, the strength of this relationship is constant across the main European biogeographic regions, which is consistent with the strong phylogenetic signal found in the functional traits used in this study across the different biogeographic regions. With regards to beta diversity, the three diversity components demonstrated a high degree of congruence:

very similar patterns emerged at continental and biogeographical scales and were associated with relatively large coefficients of determination. Interestingly, the highest levels of alpha diversity, regardless of component, occurred in the Mediterranean region (Fig. 3), which suggests that the Mediterranean Basin is a hot spot not only for taxonomic diversity (Médail and Quézel 1999), but also for phylogenetic diversity and functional diversity, at least in the case of ants. Another study examining bird communities across France found similar results (Devictor et al. 2010). The Mediterranean Basin is an exceptional ecoregion containing a fine and complex mosaic of habitats because of its paleogeography and historical disturbance regime (mainly land-use changes and fire) (Médail and Quézel 1999), which probably explain these high diversity levels. Nonetheless, although the highest levels of taxonomic turnover are also in the Mediterranean region, the highest levels of phylogenetic and functional turnover are in the Continental and Alpine regions (Fig. 3). All this together suggests that biogeographic (gamma) diversity is highest in the Mediterranean region when considering taxonomy, but this might not be the case for functions and lineages.

Paying special attention to the alpha diversity patterns, positive relationships between TD and both PD and FD have been reported in other organisms, including mammals across the globe (Safi et al. 2011), bird communities in France (Devictor et al. 2010), and pteridophyte communities in Costa Rica (Kluge and Kessler 2011) (but see Forest et al. 2007, Tucker et al. 2012). Such positive correlations are to be expected (Pavoine et al. 2013) since, due to random sampling only, increased ant species richness will be associated with increased PD and FD. However, TD does not account for all the variation in PD and FD, which means that a given level of TD may be associated with higher or lower levels of PD and FD than expected. This finding suggests that at least partial congruence exists between TD and PD and between

TD and FD; it also implies that ecological factors other than TD explain patterns of both PD and FD across the different biogeographic regions of Europe. However, identifying these factors is beyond the scope of this paper. The positive relationship of TD with PD and FD at the continental scale reflected the relationship observed within each of the biogeographic regions, although the slope and the scatter of these relationships differed (Supplementary material Appendix 5). On the one hand, coefficients of determination varied among regions, which suggests that one or more environmental factors related to biogeography influenced the degree of congruence between TD and PD and between TD and FD. On the other hand, the slope of the relationship between TD and FD was comparatively steeper in the Continental, Atlantic, and Alpine regions than in the Mediterranean and Boreal regions, while PD increased more rapidly with TD in the Continental and Boreal regions than elsewhere (Supplementary material Appendix 5). Interestingly, if all these indices were measuring the same thing, they would demonstrate a one-to-one correlation (slope of one, which assumes the relationship is linear). However, this was never the case; all the slopes were less than 1. This implies that, regardless of biogeographic region, European ant communities are phylogenetically and functionally clustered (Zupan et al. 2014), which might be the result of recent massive diversification events (Slingsby and Verboom 2006).

Meanwhile, alpha PD and FD were also positively correlated at the continental scale, and this pattern does not seem to be only indirectly driven by TD: the relationship between PD and FD was still significant when we controlled for TD. Surprisingly, the relationship between PD and FD was always positive and depicting similar slopes across the different biogeographic regions. This is striking because the few studies that have analyzed the relationship between PD and FD have usually found that phylogenetic and functional patterns do not match up (Losos 2008, Devictor et al. 2010, Safi et al. 2011). However, this is in agreement with the phylogenetic signal results, which contrary to our predictions, displayed similar degrees of niche conservatism among the different biogeographic regions. In spite of contrasted environmental and historical conditions among biogeographic regions that promoted different rates of trait evolution and speciation (Weir and Schluter 2007, Cooper and Purvis 2010), our results show similar and high levels of niche conservatism across European ant communities. Consequently, a strong correlation between PD and FD is expected (Webb et al. 2002). However, this was not the case in our study area – the relationship was weak, meaning that PD and FD are congruent at some sites but not at many others. Such spatial mismatches might be attributable to environmental factors (Safi et al. 2011).

However, the mechanism that drives the consistent relationship between PD and FD across the biogeographic regions is not clear. On the one hand, this pattern may have more plausible explanations than niche conservatism, or at least other factors could also account for it. It is possible that the same result could manifest in different regions in spite of the mechanism. For instance, the stress-gradient hypothesis (Weiher and Keddy 1995) states that regional phylogenetic or functional diversity is filtered to a greater degree in local communities located in abiotically harsher habitats than in

benign habitats. If harsh conditions are filtering these two diversity components at the same rates, that would explain the relationship between PD and FD. On the other hand, and considering that we might start from different pools of species, it has been reported that different assembly processes may create the same phylogenetic patterns (Losos 2008, Mayfield and Levine 2010, Pavoine and Bonsall 2011), so we might be caused to think that completely different mechanisms might be acting in the different regions to account for the same pattern. Such mechanisms might be, for instance, the phylogenetic conservation hypothesis (Wiens and Graham 2005, Losos 2008), the abovementioned stress-gradient hypothesis (Weiher and Keddy 1995) and colonization processes (Emerson and Gillespie 2008). Whatever the case, and in spite of theoretical (Losos 2008, Swenson and Enquist 2009) and empirical (Devictor et al. 2010, Safi et al. 2011, Hermant et al. 2012, Bernard-Verdier et al. 2013, Purschke et al. 2013) criticism of the relationship between PD and FD, we found a consistent positive (albeit weak) relationship between PD and FD in European ant communities in this study.

If we analyze the beta diversity patterns in detail, TD, PD, and FD exhibited a relatively high degree of spatial congruence at global and biogeographical scales, especially as compared to the alpha diversity patterns. Our finding of stronger correlations among beta diversity components than among alpha diversity components is consistent with some past work (Devictor et al. 2010, Bernard-Verdier et al. 2013). It also supports our second hypothesis because the diversity components demonstrated some biogeographical differences in their relationships at the alpha, but not at the beta, scale; this raises the question as to why these differences show a seemingly universal scale-dependence. We do not have a conclusive explanation, but what seems clear is that differences in phylogenetic composition among communities are closely related to differences in functional composition. This finding underscores that similar heterogeneity exists in both phylogenetic and functional composition in European ant communities, even within biogeographic regions. Interestingly, the slope of the relationship between PD and FD was less than 1 at the continental scale and in all biogeographic regions, both for alpha and beta diversity. This result suggests that local communities had an FD ‘deficit’ (s. str. Safi et al. 2011), where species in a community share more functional traits than expected for a given PD. The presence of such an FD ‘deficit’ in our communities is supported by the phylogenetic signal results, which suggest that a high degree of niche conservatism exists in European ant communities.

Similar to the other studies, our conclusions are obviously contingent on the reliability of the estimated relationships between phylogenetic and functional diversity (Petchey and Gaston 2002). However, even though our analyses might be somewhat flawed because we lacked molecular data for some species, we did use the most complete phylogeny available thus far for extant European ants and exploited a wide array of functional traits, which were explored within the same mathematical framework – the Rao quadratic entropy index (de Bello et al. 2010). Although some issues warrant further analyses (e.g. which kind of morphological, physiological, behavioral, and life-history traits are most appropriate

for calculating PD), our results clearly imply that PD is related to FD across the different European biogeographic regions. However, at the alpha diversity level, the relationship between PD and FD as well as the relationships of both PD and FD with TD are quite weak. This fact suggests that different environmental factors that do not necessarily differ among the biogeographic regions might be better predictors of change for the different components of diversity rather than only changes in other diversity-related components. In fact, the few studies on this topic demonstrated that the different components of diversity respond to environmental gradients, but in different ways (Devictor et al. 2010, Bernard-Verdier et al. 2013, Purschke et al. 2013). This is a relevant point that needs to be addressed in future studies. At any rate, using patterns of phylogenetic composition to infer ant community assembly rules is possible although actual ecological data are not available for the constituent species found in most of Europe's broad biogeographic regions. Also, it has been stated that developing a clearer understanding of how different biodiversity components relate to each other within regions will greatly improve conservation programs and diversity research (Devictor et al. 2010, Tucker and Cadotte 2013), which until recently only focused on taxonomy. Our results draw attention to the 'conservation dilemma' (Devictor et al. 2010). Although preserving TD per se might also indirectly preserve PD and FD, the scatter in TD's relationship with PD and FD strongly suggests that further studies are needed to uncover the factors responsible for such variability, with a view to clarifying when and where ant phylogenetic and functional biodiversity need to be expressly considered when establishing conservation policies.

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Supplementary material (Appendix ECOG-01938 at <[www.ecography.org/appendix/ecog-01938](http://www.ecography.org/appendix/ecog-01938)>). Appendix 1–6.