RESEARCH PAPER

Community level niche overlap and broad scale biogeographic patterns of bee communities are driven by phylogenetic history

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Abstract

Aim: Because the ecological similarity between species is expected to increase with relatedness and that speciation is a local process, phylogeny may provide a common measure for the influence of ecological and biogeographic processes on community assembly. We tested if similarities in floral visitation patterns within communities and the phylogenetic beta-diversity among communities were related to the position of bees within the bee phylogeny.

Location: Global.

Methods: We combined a genus level phylogeny with within-genera phylogenies for the bee species occurring within 18 globally distributed bee-flower networks. Networks consisted of a matrix of bee and plant species and information on whether or not a bee species had been observed visiting flowers of a given plant species. For each network, we used Abouheif's C_{mean} to test if the similarity in floral associations (niche similarity) between bees and the number of plant species visited displayed a significant phylogenetic signal. To test if biogeography influenced the relatedness among species within networks we tested if the phylogenetic beta-diversity increased with geographical distance and dissimilarity in climatic conditions among networks.

Results: We found a phylogenetic signal for niche similarity in only 50% of the bee-flower networks. However, network size influenced the likelihood of observing a phylogenetic signal and for seven of the eight bee-flower networks with >20 species it was statistically significant. On a global scale, the phylogenetic beta-diversity increased with geographical distances and with climatic dissimilarity between sites.

Main conclusions: Bee communities are structured by processes of speciation and migration so that regional species pools are dominated by a subset of the global phylogenetic clades, resulting in increasing phylogenetic beta-diversity with geographical distance. Moreover, ecological filtering processes operating at both local (floral resource use) and continental (climatic constraints) scale determine the distribution of species among resources and geographical regions. The assembly of bee communities should therefore be understood as a product of both biogeographic and community ecological processes.

1 | INTRODUCTION

By focusing on how functional traits determine if species can establish populations within an area, community ecologists have become increasingly reductionist in their search for general species assembly rules (Keddy, 1992; McGill et al., 2006; Williams et al., 2010). Hypotheses about the ecological processes that influence the dispersion of functional traits (de Bello et al., 2013; Weiher & Keddy, 1995) and the phylogenetic relatedness among community members (Hoiss et al., 2012; Webb, 2000; Webb et al., 2002), have resulted in several important conceptual syntheses to community ecology (Cavender-Bares et al., 2009; Vamosi et al., 2009; Weiher et al., 2011), leading to a new mechanistic theoretical framework. The suggested theory of community ecology states that the species composition of local communities is the product of speciation, migration, ecological filtering and ecological drift (Vellend, 2010). As speciation is a local process, the species richness within taxonomic clades are highest near the origin of the taxa (e.g. *Bombus* diversity on the Tibetan plateau (Hines, 2008)) and decreases as the distance to the area of origin increases. Regional species pools are thus shaped by the biogeographic history of their members (Cornell & Harrison, 2014). Environmental heterogeneity within a region produces gradients in habitat quality that determine which species from the regional pool are able to establish viable populations within a given area (Keddy, 1992). If species that possess similar evolutionarily inherited traits are more likely to establish within an area than species that do not possess such traits, the community will be dominated by closely related species (Webb et al., 2002). The phylogenetic composition of communities is therefore a product of both environmental filtering and the biogeography of the regional species pool. By focusing on the phylogenetic composition of communities, it may therefore be possible to use phylogenetic distance as an analytical basis for measuring how both biogeographic processes (i.e. speciation, migration and broad scaled ecological filtering) and ecological filtering within communities influence community assembly.

The use of phylogenetic relatedness in community ecology has a long history (Elton, 1946) and can be traced back to Darwin (1859), who stated that because closely related species generally are more functionally similar than distantly related species, they should compete more intensively. Competition should therefore result in communities in which species are less closely related than expected by chance (Webb, 2000). However, interpreting the phylogenetic dispersion observed within communities solely as a product of community level processes such as competition or environmental filtering is problematic as these patterns may also arise due to regional speciation and dispersal processes (Warren et al., 2014). Moreover, in

contrast to sessile organisms that rely on spatially fixed resources, the observed patterns of co-occurrence of mobile organisms within an area need not be inherently linked to shared resources (Weiher et al., 2011). These issues may be overcome by sampling species on a resource scale, thereby linking the phylogenetic signal to actual resource use, or on a biogeographic scale, thereby linking the phylogenetic signal to migration.

Wild bees are well-suited model organisms for community ecology studies as they form a monophyletic group and belong to the same trophic level (i.e. visit flowers for nectar and females often also for pollen: Michener, 2007). Moreover, as bees are central place foragers, with typical foraging ranges within a 1 km radius from the nest (Darvill et al., 2004; Gathmann & Tscharntke, 2002), their presence within an area suggests that suitable nest locations occur nearby. The ecology of wild bees has received increasing attention during the past two decades due to documented declines in population sizes and diversity (Biesmeijer et al., 2006; Potts et al., 2010; Winfree et al., 2011). It is well documented that filtering processes operating at the habitat level, through gradients in floral (Potts et al., 2003) and nest site (Murray et al., 2012; Potts et al., 2005) availability and diversity, are important determinants of the diversity of local bee species assemblages. The availability of these resources at the landscape scale is also an important driver of local bee diversity (Steffan-Dewenter et al., 2002; Williams et al., 2010). Finally, differences in climatic conditions within a region, for example along gradients in elevation or latitude (Hoiss et al., 2012; Sydenham et al., 2015), act as important environmental filters on local bee diversity. To our knowledge, less is known about the drivers of resource partitioning within bee species assemblages and thereby the relationship between bee and floral diversity (but see Potts et al., 2003). The importance of migration history or environmental filtering at larger spatial scales and their roles in shaping local bee species assemblages have also received limited attention (but see Hedtke et al., 2013), although these processes are important precursors for the regional and local species diversity (Vellend, 2010). We addressed these questions by hypothesizing that (1) the similarity in the floral associations of bee species is determined by their place in the phylogeny. We therefore expected to find that the relative position of species in a multidimensional niche space should reveal a phylogenetic signal. Secondly, that (2) the phylogenetic beta-diversity among bee species assemblages is driven by speciation and migration history as well as environmental filtering at a continental scales. We therefore expected that the degree of phylogenetic beta-diversity among bee species assemblages would increase with geographical distance because speciation events and subsequent range expansions should lead to a spatial autocorrelation in the mean pairwise phylogenetic

distance between species (Warren et al., 2014). Because range expansions—and later range contractions—may be restricted by climatic conditions, we expected that the phylogenetic beta-diversity would increase with increasing dissimilarities in present day climatic conditions, indicative of ecological filters operating at the continental scale. Moreover, as climatic gradients may select for a subset of closely related species from the regional species pool (Hoiss et al., 2012; Sydenham et al., 2015) we expected that bee species assemblages situated at high absolute latitudes would be phylogenetically under-dispersed.

2 | METHODS

We downloaded data on bee species and their floral associations from 26 previously published plant–pollinator networks (Appendix S1). Bees that had not been designated species epithets were removed from the datasets. Thereafter, we updated the nomenclature of the species within each network according to the Integrated Taxonomic Information System (ITIS, 2014) and Ascher and Pickering (2015). Following the update, networks with fewer than 10 bee species were included for the construction of the phylogeny, but otherwise excluded from the analyses. We added one unpublished bee-flower network from Norway (Appendix S2) to the collection, resulting in 18 bee-flower networks with at least 10 bee species, covering climatic zones from the tropics to the boreal zone (Figure 1). The networks consisted of binary information on the plant species each bee species visited (i.e. Qualitative networks).

To quantify the relatedness among the 592 bee species included in the bee flower networks, we assembled a polytomous, phylogenetic tree. We used a published species level phylogeny based on 20 genes (Hedtke et al., 2013) and collapsed all tips at their respective genera thus retaining branch length information to the genus level.

The tree was rooted at the Sphecidae genus *Sceliphron*. The genera *Anthophora*, *Bombus* and *Ceratina* appeared to be paraphyletic. In these cases we retained the node containing the largest number of species, so that all genera were monophyletic and the topology of the tree matched that in the review of Danforth et al. (2013). We added the *Bombus* phylogeny published by Hines (2008) which contained all 54 *Bombus* species found within the bee flower networks, to the *Bombus* tip in the genus level phylogeny. For the remaining genera, comprehensive phylogenies have not been published. We therefore constructed separate species level phylogenies for each genus based on mitochondrial cytochrome oxidase I (COI). We downloaded all COI sequences available for each bee family present in our dataset (Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, Melittidae) from the "Barcode of life Data Systems" (http://www.boldsystems.org/-accessed July 2016) and selected the longest sequence available for each bee species, resulting in sequences for 20 of the 76 bee genera. If more than one sequence of the same length was available for a species we randomly selected one of them, resulting in a total of 221 species with COI sequences. Sequences were aligned using ClustalW (Larkin et al., 2007) followed by manual adjustments of the resulting alignments. We used the program MEGA 6.06 (Koichiro et al., 2013) to construct a maximum likelihood phylogeny for each genus using the Kimura 2-parameter model, with gamma distributed transition rates, five gamma categories, and invariant sites. Gaps were treated as missing values. The statistical significance of each phylogeny (with ≥3 species) was tested using a bootstrap test with 999 permutations. The species-level phylogenies were then grafted onto the genus level phylogeny at their respective genera. We manually placed the remaining 317 species at the nodes of their respective genera, so their positions in the phylogeny were resolved to the genus level, without branch length information at the intra-genus level. This was also done for 31 species that were the only representatives for their genera. The
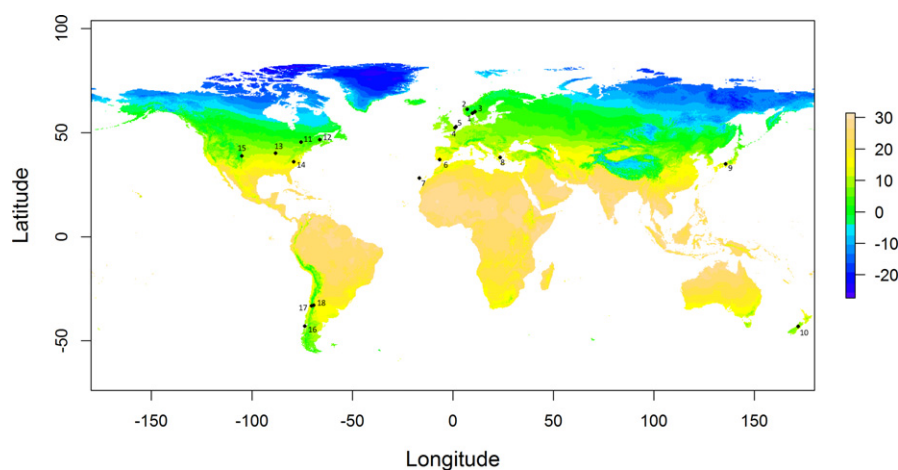
FIGURE 1 World map coloured according to the mean annual temperature (BioClim model 1) and the geographical locations of the 18 bee-flower networks included in this study. Numbers correspond to the location of networks: (1) Norway1; (2) Norway2; (3) Norway3; (4) England4; (5) England5; (6) Spain; (7) Canary Islands; (8) Greece; (9) Japan; (10) New Zealand; (11) Canada1; (12) Canada2; (13) USA1; (14) USA2; (15) USA3; (16) Chile1; (17) Chile2; and (18) Argentina. The network Norway1 contained only nine species of bees when *Apis mellifera* was excluded and was therefore not included in the analyses of bee biogeography. See Appendix S1 for details [Colour figure can be viewed at wileyonlinelibrary.com]

final tree therefore contained branch length information: from Hedtke et al. (2013) at the genus level; from Hines (2008) for all 54 *Bombus* species; from COI genes for 221 species; and no branch lengths for the remaining species. Because branch lengths were estimated from different sources and genes, we used a metric that does not require branch length information to test the influence of phylogenetic relatedness on niche overlap. For the biogeographic analyses, branch lengths were required and we therefore restricted these analyses to the genus level, where branch lengths had been estimated from one source.

2.1 | Niche overlap versus phylogenetic distance

We tested if the degree of niche overlap between bee species, and the niche breadth (i.e. the number of plant species a bee species was observed to visit), within each network displayed a phylogenetic signal.

We estimated the dissimilarity of the floral associations of bees by placing all species in a non-metric multidimensional scaling (NMDS) trait space defined by their Jaccard's dissimilarities in resource use. This allowed us to quantify the dissimilarities among species on several uncorrelated, continuous gradients of resource use. The more similar scores species had on a NMDS axis the more similar they were in that specific niche-dimension. We applied the NMDS analysis as it is suitable when the underlying data are binary (occurrence), in contrast to weighted average-based approaches, such as (CA) and detrended correspondence analysis (DCA) and that it more accurately compresses the variation in dissimilarity matrices into a few axes, than principal coordinate analysis (PCoA) (Legendre & Legendre, 1998). Prior to the NMDS analyses, we removed disconnected species (i.e. bee species observed on flowers that no other species were observed on) from each network as these did not provide any information on dissimilarities in patterns of floral associations compared to other species. At the most, two species had to be removed from a network to ensure connectedness among network members and thus it is unlikely that this influenced the results (network abbreviation = removed species/species in full network; Argentina = 1/11, Norway2 = 1/12, New Zealand = 1/13, Spain = 1/47, Japan = 1/57, USA3 = 2/83, Greece = 2/238). The NMDS ordinations were run using the step-across function to account for 100% dissimilarities within pairs of species. We set the maximum number of random starting points and iterations to 1,000, which ensured that the final NMDS reached a convergent solution. For each bee-flower network, we initially ran the NMDS with three dimensions to maximize the representation of the data. If no solution was reached with a three dimensional NMDS we reduced the number of dimensions to two, and finally one if necessary. An exception to this rule was made for the largest bee-flower network (236 species) where a convergent solution could only be reached when the NMDS was conducted on four dimensions.

Each NMDS gradient thus reflected a unique part of the niche-space covered by the bees in the bee-flower network. For each bee-flower network, we used the species-specific scores on each NMDS axis as well as the number of number of plant species visited (i.e. links) to calculate Abouheif's C_{mean} (Abouheif, 1999) which is a measure of phylogenetic signal. We used this metric because it performs well compared to other indices of phylogenetic signal, and does not depend on branch lengths (Münkemüller et al., 2012; Pavoine et al., 2008). Our phylogeny included information on branch lengths from different sources at the genus and species levels making this a relevant issue. Significance tests of the C_{mean} values were conducted using permutation tests with 9,999 iterations of the species found within the bee-flower network being tested. The C_{mean} was calculated using the R package phylosignal (Keck, Rimet, Bouchez, & Franc, 2016).

Biogeographic processes are expected to lead to a decreased phylogenetic diversity (dispersion) when the distance the location of a taxa's origin increases (Warren et al., 2014). The most common species within a region are therefore likely to belong to the same phylogenetic clade. The phylogenetic signal in terms of the floral visitation patterns of bees are therefore likely to be underestimated in under-sampled bee-flower networks. To test this hypothesis, we used Spearman's rank correlation on the *p*-values of the individual C_{mean} estimates and the phylogenetic diversity (i.e. Faith's PD; Faith, 1992) within the community (i.e. bee flower network). Phylogenetic diversity was calculated as the sum of phylogenetic branch lengths of the genus level phylogeny, and was thereby related to the number of genera within each network while also including information on the shared ancestry between the genera. In one case *Bombus* was the only genus present, and the phylogenetic diversity was set to zero. We used the *p*-values (i.e. the rank order of the observed phylogenetic signal compared to the null distribution) as C_{mean} estimates cannot be compared directly among different phylogenies (Münkemüller et al., 2012).

2.2 | Geographic and climatic influences on biogeography

We analysed how the phylogenetic beta-diversity was related to both geographical distance (a proxy for migration distance) and dissimilarities in climatic conditions (an environmental filter). We used the function "unifrac" in the Picante (Kembel et al., 2010) library in R to calculate the fractions of unshared branch lengths between bee-flower networks as a measure of phylogenetic beta-diversity between networks (Lozupone et al., 2006). Measures of phylogenetic beta-diversity depend on branch length information, and we therefore restricted the analysis to the genus level phylogeny by placing species at the nodes of their respective genera. The fact that we did not have a fully resolved phylogeny at the species level—combined with the coarse spatial resolution of our study— prevented us from distinguishing between the role of speciation and migration on local bee species diversity. Instead, we interpreted the gradient in phylogenetic beta-diversity as the product of both speciation, migration and continental scaled ecological filtering (i.e. biogeographic processes). We included the 17 networks with at least ten species, excluding the domesticated *Apis mellifera* (L.)

because its distribution depends on beekeeping practices and not biogeographic processes, and used only the ten most widely sampled species in each network (i.e. with the highest rank-abundance, in terms of number of plant species visited). This was done because the relative occurrences and niche-width of flower visiting species, in terms of the number of plant species visited, tends to be relatively stable, irrespective of sampling intensity (Hegland et al., 2010) and that the number of plant species visited (i.e. the "observed linkage") is correlated with bee abundance and a good predictor of bee occurrences within a region (Winfree et al., 2014). We therefore viewed the ten most widely sampled species within networks as being central constituents of the regional species pool. In cases where the number of ties in frequency-classes prevented us from ranking the ten most common species, we included all species belonging to the same frequency-class, assuming their detectability was qualitatively similar. Although this selection criterion may have removed some common, but highly specialized (monolectic) species, we deemed it as appropriate as specialization on a single plant species rarely occurs. Indeed, specialization is generally confined to the family or genus level (oligolectics) of plants (Michener, 2007). The final dataset consisted 165 bee species from 17 networks.

The geographical distance between each network-pair within the 17 networks was calculated based on their GPS locations. In cases where the exact GPS-locations of the study sites were unavailable, we used the coordinates of the nearest known location obtained from the site-descriptions in the studies. At each location, we extracted information on climatic conditions from the BioClim models from the WorldClim database (Hijmans et al., 2005). The climatic conditions at each site were defined according to the categories: annual mean temperature (BIO1); mean diurnal range (BIO2); maximum temperature of warmest month (BIO5); minimum temperature of coldest month (BIO6); annual range of temperature (BIO7); mean temperature of driest quarter (BIO9); mean temperature of warmest quarter (BIO10); and annual precipitation (BIO12). As the climate variables were on different scales they were rescaled to a zero-one scale before calculating the Euclidean distance between all site pairs, using the climatic variables as input data. We used the climate distances between pairs of sites as a proxy for the ecological filter posed by dissimilarities in climatic conditions.

We tested if the phylogenetic beta-diversity increased with the geographical distance between bee-flower networks, and with dissimilarity in the climatic conditions between the sites where the bee-flower networks had been sampled. The relationships between phylogenetic beta-diversity and geographical distance and climatic conditions were tested using Mantel tests with Spearman's rank correlation coefficient and 10,000 permutations. The analyses were done with the R package "Vegan" (Oksanen et al., 2013). In addition to the Mantel tests, we also conducted a multiple regression on distance matrices (MRM) with rank correlations, allowing us to estimate the relative explanatory power of the geographical distance and climatic conditions. This was done because climatic dissimilarities were correlated with geographical distances (rho = 0.27, p = .02).The

MRM was conducted using the R package "Ecodist" (Goslee & Urban, 2007).

We tested if the biogeography of bees led to bee species assemblages consisting of increasingly phylogenetic clustered subsets of species from the global (i.e. 165 species, following the subsampling of the 10 most widely sampled species per network) species pool as the distance to the equator increased. We calculated the phylogenetic diversity (sum of phylogenetic branch lengths on the genus level phylogeny) within each bee flower network (Faith, 1992). We used the R function "ses.pd" in the "Picante" (Kembel et al., 2010) package to standardize the phylogenetic diversity (PD) according to a null model whereby taxa names where shuffled across the phylogeny through 999 permutations to correct for the varying number of species between networks. The standardized PD was calculated as ses.PD = $(PD_{obs} - PD_{random\ mean})/PD_{random\ standard\ deviation}$, where PD_{obs} was the observed PD within the bee flower network, $PD_{random\ mean}$ and $PD_{random\ standard\ deviation}$ were the mean and standard deviation of the PD calculated from the 999 permutations. We tested if bee flower networks consisted of species that were more closely related than would be expected by chance by comparing the observed phylogenetic diversity against the null models distribution. We then used a linear regression model to test if the phylogenetic dispersion decreased with latitude (i.e. towards the poles). Although the linear model yielded a strong effect size (t = −5.9) and a seemingly good explanatory power (df = 15, R^2 = 0.7, p < .001) graphical validation plots revealed that a linear model did not fit the data well even after log-transforming latitude. We therefore refitted the model using the second order polynomial of the absolute latitude as an explanatory variable, which normalized the residual plots. All statistical analyses were conducted in R version 3.1.1 for windows (R development core team 2014).

3 | RESULTS

3.1 | Niche overlap versus phylogenetic distance

We constructed COI phylogenies for 20 genera (Appendix S3). The bootstrap values provided limited support for several of the nodes in the largest phylogenies, which was likely due to the phylogenies being constructed from a single gene. The remaining genera contained only few species: 31 contained 1; 10 contained 2; 8 contained 3; 3 contained 4; 2 contained 6; and 1 genus contained 12 species.

The niche overlap—i.e. floral associations among bee species—was related to the phylogenetic distance among them (Table 1). This relationship was most prevalent for the first niche dimension (NMDS1) and for the number of plant species bee species were observed to visit (# visits). For these traits, eight and nine of the 18 networks showed statistically significant phylogenetic signal (C_{mean}). In contrast, when evaluating the niche overlap among bees on the second niche dimension (NMDS axis 2) a significant phylogenetic signal occurred in only four of 17 networks (all networks, except USA1, see Table 1); and when evaluating the niche overlap among bees on

the third NMDS axis, a significant phylogenetic signal occurred in only three out of 13 networks (networks that were best described by more than 2 NMDS axes (see Table 1).

The proportion of bee-flower networks displaying a significant phylogenetic signal depended on the phylogenetic diversity of bees within the bee flower networks. We found that for the NMDS1, NMDS2 and #Visits the strength (i.e. p-values) of the phylogenetic signal compared to the null models, were related to the phylogenetic diversity within the local bee phylogenies (Figure 2). Similarly, of the bee flower networks with more than 20 species, six of eight networks showed a significant phylogenetic signal on NMDS1. In contrast, for networks with fewer than 20 species, only three out of ten networks showed a significant phylogenetic signal for NMDS1 (Table 1).

3.2 | Geographical and climatic influences on bee biogeography

The biogeographical analyses based on the ten most generalist bee species in each network showed that geographical distance and climatic conditions influenced the global distribution of bee taxa and thereby the phylogenetic composition within bee communities. The phylogenetic beta-diversity between bee communities increased with geographical distance (Mantel rho = 0.32, p = .019, Figure 3). The

phylogenetic beta-diversity also increased with the dissimilarity in climatic conditions (rho = 0.34, p = .002, Figure 3). The MRM revealed that the geographical distance and the dissimilarity in climatic conditions together explained 17% of the variation in phylogenetic beta-diversity among bee communities (MRM, $\beta_{geographical\ distance}$ = 0.24, p = .06, $\beta_{dissimilarity\ in\ climatic\ conditions}$ = 0.27, p = .01, R^2 = 0.17, F-test = 13.5, p-model = .005).

In addition to driving changes in the phylogenetic beta-diversity amongst bee communities, the location of communities also determined the phylogenetic diversity within them. Specifically, the phylogenetic diversity decreased towards the poles (Figure 4: df = 14, R^2 = 0.79, p-model < .001, $\beta_{absolute\ latitude}$ = −5.3, $t_{absolute\ latitude}$ = −6.8, $p_{absolute\ latitude}$ < .001, $\beta^2_{absolute\ latitude}$ = 1.9, $t^2_{absolute\ latitude}$ = 2.4, $p^2_{absolute\ latitude}$ = .03) and all communities located at latitudes above 40 degrees displayed a significantly lower phylogenetic diversity than expected by chance (Table 2, Figure 4).

4 | DISCUSSION

Increased phylogenetic beta-diversity with geographical distances suggests that biogeographic processes (i.e. speciation and subsequent migrations) determine the global distribution of bees. Moreover, as phylogenetic beta-diversity between bee-flower networks

TABLE 1 Bee diversity and phylogenetic signal in floral associations within bee flower networks. The phylogenetic signal in the floral associations of bees measured as the number of plant species visited (# visits) and the species specific scores along each non-metric multidimensional scaling (NMDS) axis in bee-flower networks with ≥10 species. The phylogenetic signal was estimated using Abouheif's C_{mean}, a measure of the autocorrelation in trait values between species adjacent in the phylogeny, and the significance tested using 9,999 permutations. Significant values are marked in bold. See Appendix S4 for bar plots of the network specific phylogenies and species scores on each NMDS axis and # visits

	Bee diversity			# visits		NMDS1		NMDS2		NMDS3		NMDS4	
Network	Genera	Species[a]	PD_{genus}	C_{mean}	p	C_{mean}	p	C_{mean}	p	C_{mean}	p	C_{mean}	p
Norway2	1	11	0.00	−0.33	.96	−0.17	.74	−0.24	.78	−0.07	.35		
Norway1	2	10	0.23	−0.25	.80	**0.26**	**.02**	−0.32	.93	−0.18	.60		
England2	4	12	0.82	0.06	.17	**0.35**	**.02**	−0.15	.63				
England1	5	11	0.92	0.06	.13	−0.11	.48	−0.15	.56				
New Zealand	5	12	0.87	−0.11	.51	0.09	.16	−0.08	.42				
Canada1	5	15	1.00	0.10	.16	−0.02	.33	−0.04	.41	−0.02	.35		
Chile1	6	11	0.83	**0.45**	**.02**	−0.23	.70	0.18	.08	0.02	.20		
Canada2	8	28	1.29	**0.20**	**.03**	0.02	.30	0.12	.11	−0.03	.46		
USA1	9	16	1.28	**0.39**	**.01**	0.05	.22						
Argentina	10	10	1.08	**0.29**	**.04**	0.09	.18	0.02	.27				
Canary Islands	10	12	1.83	−0.12	.52	**0.24**	**.03**	−0.10	.47	−0.08	.45		
USA2	10	31	1.59	−0.12	.77	**0.18**	**.05**	0.01	.36	0.03	.28		
Norway3	11	35	1.64	0.16	.06	**0.31**	**.00**	0.05	.22	**0.21**	**.02**		
Japan	11	56	1.85	**0.31**	**<.01**	0.01	.34	**0.19**	**.01**	**0.25**	**.00**		
Chile2	16	25	2.15	**0.21**	**.04**	**0.31**	**.01**	0.12	.11	−0.02	.42		
Spain	21	46	2.72	0.08	.15	**0.27**	**.01**	**0.27**	**<.01**	−0.01	.44		
USA3	21	81	2.75	**0.48**	**<.01**	**0.38**	**<.01**	**0.18**	**.01**	0.02	.31		
Greece	42	236	4.01	**0.14**	**.01**	**0.45**	**<.01**	**0.27**	**<.01**	**0.11**	**.01**	0.05	.11

[a]The number of species included in each network after removal of disconnected species.
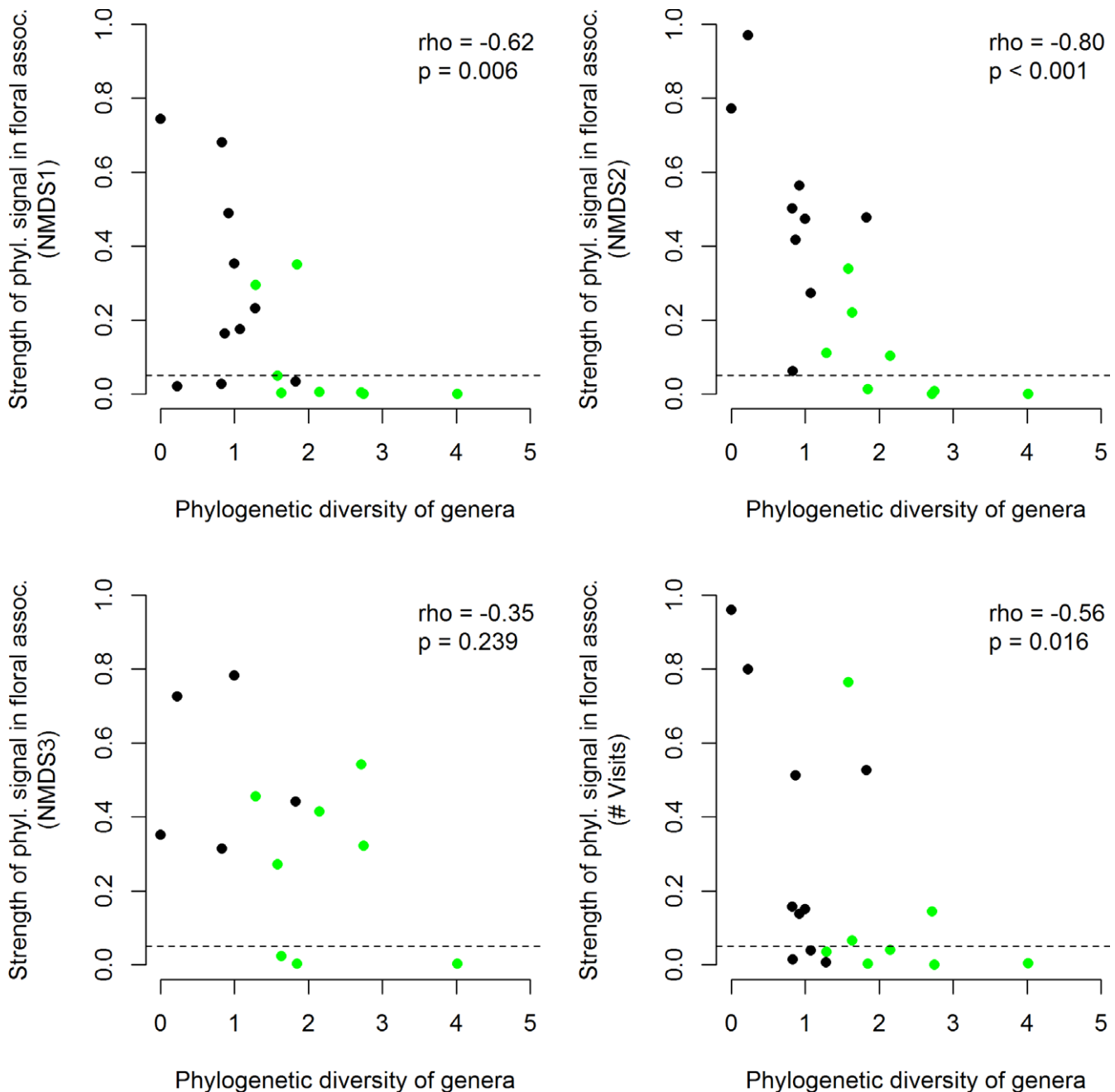
FIGURE 2 Relationship between the strength of the phylogenetic signal in the floral associations of bees (*p*-values associated with Abouheif's C_{mean}) and the phylogenetic diversity within bee flower networks (i.e. Faiths PD based on the genera phylogeny). The floral associations of bees was quantified both as the dissimilarity in flower visitations between species pairs—NMDS1–3—and as the total number of plant species each bee species was observed to visit—# visits. Black dots show the *p*-values for networks with <20 species, green dots show the *p*-values for networks with ≥20 species. Tests statistics show the Spearman rank correlation (rho) and its associated *p*-value [Colour figure can be viewed at wileyonlinelibrary.com]

also increased with climatic differences we hypothesize that the immigration of species into new regions can be hindered by ecological filtering. Once present within communities, similarity in floral resource use between bee species is related to their phylogenetic relatedness, so that ecological similarity increases with relatedness. Because both the global distribution of bee species, and their ecological similarity in terms of both floral visitation patterns and climatic preferences seem related to the evolutionary history, our

findings indicate that phylogenic distances can potentially provide the analytical basis for linking processes occurring at both biogeographic and ecological scales.

4.1 | Niche-overlap versus phylogenetic distance

We found that the niche overlap among bee species—in terms of floral associations within bee-flower networks—displayed a
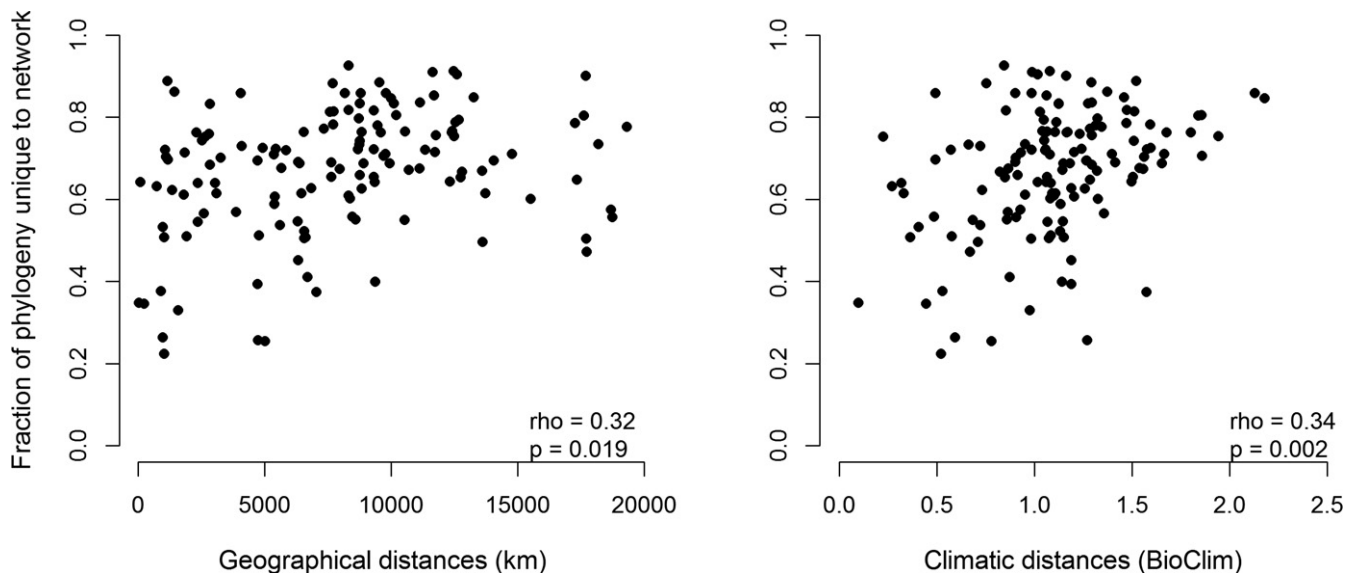
FIGURE 3 Relationships between the phylogenetic beta-diversity and the geographical distance and climatic dissimilarity between bee flower networks. The relationships were tested using mantel tests with Spearman's rank correlation (rho)
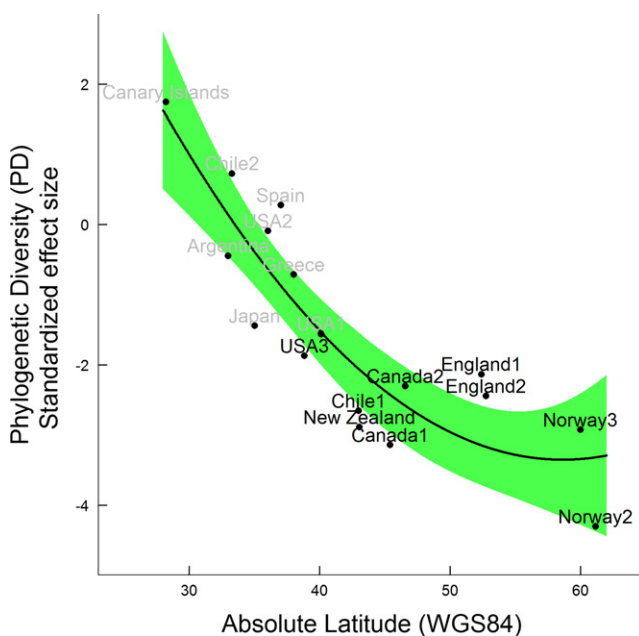
FIGURE 4 The relationship between the phylogenetic diversity within bee flower networks and the absolute latitude of their geographical position. The geographic location (country names) of each network is given above its point in the plot. Networks in which bee species ranked as the ten most common bee species (i.e. highest number of plant species visited) were more closely related than expected by chance (i.e. the phylogeny is smaller than would be expected from the number of species) are shown in black. See Table 2 for test statistics on the phylogenetic diversity [Colour figure can be viewed at wileyonlinelibrary.com]

phylogenetic signal in the most phylogenetically diverse networks (Table 1, Figure 2). Our findings are in accordance with Darwin's (1859) hypothesis that ecological similarity is related to the evolutionary history of the species. Following this hypothesis, it is

predicted that competitive exclusion should prevent the co-occurrence of closely related species within species assemblages, unless other environmental filters select for ecological similarity (Webb, 2000). However, as bees depend on both nesting (Potts et al., 2005) and foraging resources, which may be further subdivided into nectar and pollen resources (Potts et al., 2003), it is possible that competitive exclusion only occurs between species that use the same resources along several niche dimensions. In addition, the tendency for closely related species to utilize the same resource may be due to filtering processes operating on resource acquisition, as found for mammalian ectoparasites (Krasnov et al., 2014) and flower-visitor networks spanning across several taxonomic orders (Rezende et al., 2007). In this case, one would expect bee species assemblages (sensu Fauth et al., (1996)) to be phylogenetically under-dispersed if resource acquisition requires evolutionarily conserved functional traits. Our results suggest that phylogenetically conserved traits may govern the partitioning of foraging resources within bee communities. Such traits could include tongue-length, which determine whether bees can access the nectar from concealed flowers (e.g. legumes) (Michener, 2007); phenology, which determines if the bees are active during the flowering of particular plant species (Oertli et al., 2005); foraging preferences related to floral rewards (Potts et al., 2003), and the capability of digesting pollen toxins (Sedivy et al., 2013). Although our tests of phylogenetic signal were conducted at a taxonomically coarse scale (across bee families) it is not unlikely that differences in floral visitation patterns display a phylogenetic signal even within genera. For instance within the short-tonged genus *Andrena* species within the subgenus *Taeniandrena* (e.g. *A. intermedia* and *A. wilkella*) are atypical in that they specialize on plants within the Fabaceae family (Scheuchl & Willner, 2016).

The tendency for floral associations to be phylogenetically confined within taxa offers a mechanistic explanation for the frequent

TABLE 2 Phylogenetic diversity within networks included in the biogeographic analyses. Only the 165 most widely sampled bee species were included in the analysis. For each network, Faith's PD was calculated (PD.obs) and standardized against the mean (PD.rand.mean) and standard deviation (PD.rand.sd) of the values obtained from the null models to obtain the standardized effect size of the phylogenetic diversity (Ses.PD). Networks with a significant phylogenetic underdispersion are marked in bold

Network	Species[a]	PD.obs	PD.rand.mean	PD.rand.sd	Ses.PD	*p* value
Argentina	10	1.113	1.211	0.194	−0.50	.307
Canada1	**11**	**0.642**	**1.264**	**0.210**	**−2.95**	**.002**
Canada2	**13**	**0.908**	**1.400**	**0.207**	**−2.38**	**.006**
Canary Islands	11	1.621	1.278	0.200	1.72	.954
Chile1	**10**	**0.699**	**1.211**	**0.201**	**−2.55**	**.007**
Chile2	16	1.744	1.565	0.227	0.79	.793
England1	**10**	**0.789**	**1.206**	**0.196**	**−2.13**	**.014**
England2	**12**	**0.834**	**1.339**	**0.208**	**−2.43**	**.010**
Greece	10	1.059	1.207	0.196	−0.75	.221
Japan	11	0.986	1.281	0.203	−1.46	.077
New Zealand	**12**	**0.734**	**1.343**	**0.212**	**−2.87**	**.003**
Norway2	**12**	**0.443**	**1.337**	**0.208**	**−4.29**	**.001**
Norway3	**11**	**0.676**	**1.266**	**0.200**	**−2.95**	**.002**
Spain	12	1.404	1.337	0.200	0.33	.642
USA1	15	1.147	1.506	0.221	−1.63	.055
USA2	11	1.264	1.270	0.201	−0.03	.486
USA3	**11**	**0.872**	**1.279**	**0.205**	**−1.98**	**.027**

[a]The number of species ranked as the ten commonest species within a network were included in the analyses. Note that ties within ranks led to the inclusion of >10 species in some networks.

finding that the diversity in bee species assemblages is associated with different aspects of floral diversity (Potts et al., 2003; Roulston & Goodell, 2011; Winfree et al., 2011). Our results also have management implications as they suggest that entire clades of bees may be negatively affected if the predicted impact of land use and climate change on plant diversity (Pompe et al., 2008) shifts the floral composition towards plants not accessible to those bee taxa. Such changes have historically included the introduction of soil fertilizers and industrial fixation of atmospheric nitrogen, which both reduced legume rotations in agriculture. These changes coincided with an increased rate of bee extinctions in both Britain (Ollerton et al., 2014) and the Netherlands, where long-tongued bees have declined more than short-tongued bees during the past century (Biesmeijer et al., 2006).

We found that the presence of a phylogenetic signal depended on the phylogenetic diversity of the species comprising the bee community, the number of bee species, and the number of NMDS axes (i.e. niche dimensionality) present (Table 1). Community size may influence the probability of observing significant relationships between phylogenetic distance and niche overlap (Rezende et al., 2007; Slingsby & Verboom, 2006). Moreover, Blomberg et al. (2003) showed that the statistical power of phylogenetic randomization tests is most robust in communities with >20 species. However, the lack of statistical significance from the randomization tests in this study may also reflect the nature of the ecological patterns in the data. For instance small plant–pollinator networks tend to be dominated by relatively common and highly inter-connected species,

whereas larger networks include a higher proportion of rare and less-connected species (Hegland et al., 2010). It is therefore possible that functionally or behaviourally distinct groups of bees are underrepresented in the smaller networks (i.e. low phylogenetic diversity), and in the networks where the niche width of species has been underestimated (i.e. displays a low dimensionality), and do not fully account for the niche differentiation among species. Indeed, the *p*-value of the C_{mean} tests on the number of plant species visited and the first two NMDS axes decreased with the phylogenetic diversity within the recorded bee flower networks. The low phylogenetic resolution of our phylogeny combined with the modest bootstrap values of our phylogenies and the reliance on a single gene for constructing the genera phylogenies could potentially have influenced our results. However, we do not believe this to have been the case because a low phylogenetic resolution at the tip of the phylogeny only has limited impact on phylogenetic diversity metrics (Swenson, 2009) and that the genus level phylogeny used in this study is highly resolved (Hedtke et al., 2013).

4.2 | Geographical and climatic influences on bee biogeography

The phylogenetic beta-diversity among bee species assemblages increased with geographical distances (Figure 3) and we suggest that this reflects the migration history (Cavender-Bares et al., 2009) and regional radiations of bee taxa. Although the low resolution of our phylogeny did not allow us to distinguish between these two

processes (e.g. speciation and migration), our results suggest a high degree of regional endemism that ultimately creates the foundation for speciation and dispersal events. However, in addition to biogeographic processes, other factors also contribute to the distribution of taxa, i.e. some of the observed relationships between phylogenetic beta-diversity and distance were caused by the presence of introduced taxa in non-native regions. The presence of *Hylaeinae* species in networks from New Zealand and Japan (Appendix S1) can partly be explained by natural dispersal events from Australia (Kayaalp et al., 2013), whereas the presence of *Bombus* in New Zealand is due to anthropogenic introductions in the 20th century (Michener, 2007). The introduction of non-native species may therefore have introduced some additional variation into the relationship between the phylogenetic beta-diversity and geographical distances and the exact positioning of individual pairs of bee communities according to their phylogenetic beta-diversity should therefore be interpreted with some caution. Despite this potential limitation we also found a significant increase in phylogenetic beta-diversity with dissimilarity in present day climatic conditions (Figure 3), suggesting that environmental filtering pose barriers to the global distribution of bee taxa. Indeed, the northern regions (North-America and North-Eurasia) share many taxa from the genera *Hylaeus* (Kayaalp et al., 2013), *Andrena* (Michener, 2007) and *Bombus* (Hines, 2008), due to past speciation and migration events that were likely restricted to the Holarctic.

The increase in phylogenetic beta-diversity with dissimilarities in climatic conditions may reflect past migrations of bee taxa into areas of favourable climates (e.g. ecological filtering). Regional radiations in species diversity within genera and subsequent phylogenetic clustering at the continental scale (Harmon-Threatt & Ackerly, 2013) may then further have increased the phylogenetic beta-diversity at large spatial scales. For instance the predominantly northerly distributed genus *Bombus* originated at high elevations and migration events between and across continents coincide with global cooling periods and subsequent habitat expansions (Hines, 2008). Moreover, *Bombus* species have been shown to be less affected by climatic filters associated with elevation and latitude than other bees within the regional species pool (Hoiss et al., 2012; Sydenham et al., 2015). That the migration of bees into—and out of—northern regions is limited by phylogenetically conserved climatic tolerances, may explain why the phylogenetic dispersion amongst the most widely sampled bee species decreased with the absolute latitudinal position of the bee community (Table 2, Figure 4).

5 | CONCLUDING REMARKS

Our findings suggest that local scale processes related to the distribution of species among floral resources, and broad scale biogeographic processes related to the distribution of species among regions and biomes, are restricted by the species phylogenetic history. The inclusion of phylogenetics into the theory of community ecology thereby allows for a link to biogeography. Specifically, our study demonstrates that the degree of niche overlap between species pairs within species assemblages depends on the phylogenetic distance between them (hypothesis 1) and that speciation and migration history, as well as ecological filtering (hypothesis 2), are important determinants of community composition at the global scale. A further understanding of such distributional patterns will aid the conservation of phylogenetically diverse species assemblages of bees.

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