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Local-scale factors structure wild bee communities in protected areas

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Summary

1. In the current context of global habitat loss, a fundamental challenge is to understand how ecological processes interact to determine community composition. Despite the accumulating evidence base for global declines in bee populations, few studies have addressed the relative importance of local environmental and large-scale spatial factors in maintaining diverse bee communities outside of agricultural habitats, and particularly in areas protected for nature conservation.

2. We analysed bee community data that we collected from 40 Special Areas of Conservation representing five distinct European Natura 2000 priority habitats in Ireland, quantifying local habitat features within each site and surrounding land-use. Species data were collected in a nested sampling design composed of three hierarchical levels such as 'site', 'habitat' and 'region' and analysed using diversity partitioning. The species–environment relationship was also decomposed into regional-, landscape- and local-scales by variance partitioning using partial canonical correspondence analysis.

3. Wild bee species richness and abundance were highly dependent on habitat type, but the majority of regional diversity was contained within sites, as opposed to species turnover across sites and regions. Bee communities were primarily structured by local-scale factors associated with nesting resources and grazing regime, with non-*Bombus* taxa being more sensitive to landscape-scale differences in adjacent habitats than *Bombus* taxa. Regional-scale processes, such as species sorting along longitudinal gradients, were of minor importance in structuring bee communities in this system.

4. *Synthesis and applications*. Within habitats, local species richness, rather than species turnover at higher spatial scales, accounted for the majority of regional bee diversity. Local environmental factors were powerful determinants of community composition. Therefore, management effort prioritising the maintenance of a diversity of high-quality habitats within a broad network of protected areas best facilitates bee conservation in this system. At a regional level, schemes for conserving and restoring important bee habitats must be habitat- and taxon-specific, as the impact of individual local-scale factors and surrounding land-use on community composition is highly habitat- and taxon-dependent.

Key-words: apoidea, biodiversity, community structure, hierarchical diversity partitioning, insect conservation, semi-natural habitats, variance partitioning

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Introduction

Habitat loss is considered the primary driver of species extinctions world-wide with 40% of all ice-free terrestrial habitats converted to agriculture or urban settlements and 37% of the remaining semi-natural habitats being embedded within this anthropogenic landscape matrix (Ellis *et al.* 2010). Bees, the main animal pollinators of wild and agricultural plants in most ecosystems (Buchmann & Nabhan 1996; Ollerton, Winfree & Tarrant 2011), are currently suffering considerable declines in species richness and abundance (Steffan-Dewenter, Potts & Packer 2005; Biesmeijer *et al.* 2006; NRC 2007). At present, studies from the EU give the strongest evidence base for declines of entire bee communities (Brown & Paxton 2009), where 37–65% of bee species have been identified as being of conservation concern (Patiny, Rasmont & Michez 2009). A recent meta-analysis of 54 published studies affirmed the synergistic negative effects of habitat loss and fragmentation on bee species richness and abundance (Winfree *et al.* 2009). Most bee species rely on a variety of habitats, typically across multiple locations, to provide sufficient floral and nesting resources to complete their life cycle (Westrich 1996; Potts *et al.* 2005). Typically, higher taxa comprise species with broadly similar foraging and nesting requirements, for example, bees have been partitioned into several guilds depending on their nesting requirements such as carpenters, miners, masons and social nesters (Potts *et al.* 2005). Therefore, the focus of bee conservation has shifted from the conservation of single species within a habitat to the conservation of specific taxonomic and functional groups within landscapes, eco-regions or biomes (Brown & Paxton 2009).

The ecological patterns and processes controlling the abundance of species across multiple sites are recognised as being highly scale-dependent (Willis & Whittaker 2002; Tscharntke *et al.* 2005). Consequently, to conserve regional biodiversity effectively, conservationists need to determine how diversity is distributed across a range of spatial scales. Variation in species composition can be studied using a spatial hierarchical sampling design and partitioning a regional or 'gamma' diversity measure into within- and among-group components, 'alpha' and 'beta', respectively (Crist *et al.* 2003; Jost *et al.* 2010). The hierarchical partitioning approach has been used for a range of insect conservation purposes, such as examining bee and wasp diversity across a tropical land-use gradient (Tylianakis, Klein & Tscharntke 2005) and investigating the appropriate scale for conserving ant biodiversity across biogeographical zones (Paknia & Pfeiffer 2011). Furthermore, the relative strength of spatial scale in the species–environment relationship can be determined by explicitly introducing spatial components into statistical models, and environmental and spatial factors identified using variance partitioning (Borcard & Legendre 2002).

A diverse wild bee community contains species that require a variety of nesting and foraging resources within a landscape that facilitates the mobility and dispersal of reproductive individuals. Studies on the requirements of wild bees have historically been biased towards two common genera, the honeybees (*Apis*) and bumblebees (*Bombus*), with the other 425 genera world-wide receiving relatively little research attention (Brown & Paxton 2009; Winfree *et al.* 2009). In terms of bee species' biology, both *Apis* and *Bombus* represent medium-to-large sized social bees and are, therefore, unrepresentative of the majority of bee species in western Europe, which are relatively small and solitary (Westrich 1996). As a consequence of the relationship between body size and foraging range (Greenleaf *et al.* 2007), we may expect marked differences across bee taxa in their sensitivity to environmental change at different spatial scales (Steffan-Dewenter *et al.* 2002; Schweiger *et al.* 2005; Tscharntke *et al.* 2005). Therefore, in temperate wild bee communities, we predict that there are marked differences between *Bombus* and non-*Bombus* populations with regard to the relative strength and spatial scale at which environmental factors impact upon their distribution and abundance.

In this study, we examine simultaneously the environmental and spatial components of bee community variance in Special Areas of Conservation (SACs), representing five distinct Natura 2000 Annex I habitats across the island of Ireland (Fig. 1). SACs are areas of

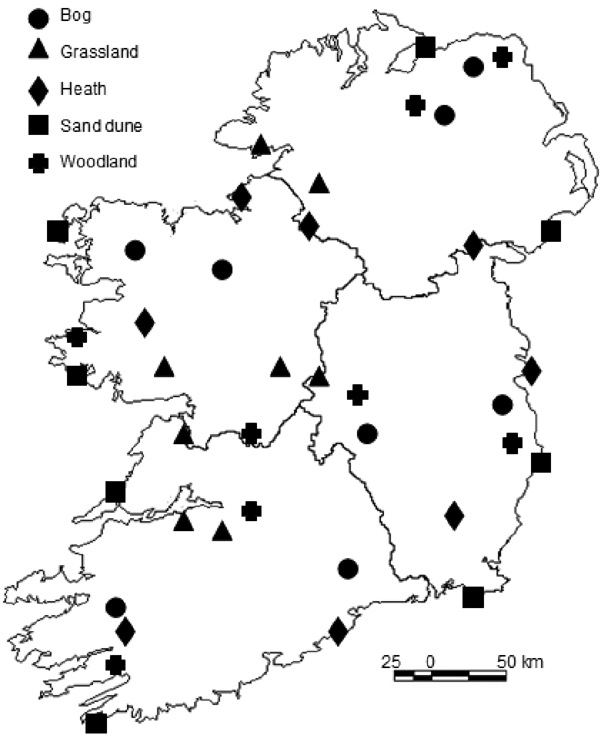

Fig. 1. Map of the study area with each Special Area of Conservation site and habitat type surveyed.

prime conservation value that receive legal protection under the 1992 EU Habitats Directive (92/43/CEE) and form part of the Natura 2000 network of protected habitats across Europe. Given the extent of the Natura 2000 network of conserved areas across Europe and the functional importance of bees as pollinators, there is a pressing need to systematically compare priority habitats in the structure of bee communities. We did so by focusing on four key questions: (i) How do habitats differ in terms of bee species richness and abundance, and is this related to the area of protected habitat? (ii) Do patterns of diversity partitioning differ among habitats? (iii) What is the relative influence of local-, landscape- and regional-scale factors on bee community structure? (iv) How do specific factors within each spatial scale affect *Bombus* and non-*Bombus* bee community composition? Answers to these questions will help prioritise bee conservation management within a network of reserves at local and regional scales and identify taxon- and habitat-specific factors determining bee community composition.

Materials and methods

STUDY REGION AND SAMPLING DESIGN

Our study system consisted of 40 sites representing five distinct Annex I habitats (Natura 2000 code in parenthesis): active raised bogs (7110) and blanket bogs (7130), hereafter 'bogs'; semi-natural dry calcareous grasslands (6210), 'grasslands'; European dry heath (4030), 'heaths'; fixed dunes with herbaceous vegetation (2130) and dunes with *Salix repens* ssp. *argenta* (2170), 'sand dunes'; old sessile oak woods with *Ilex* and *Blechnum* (91A0), 'oak woodlands'. Eight sites of each habitat type were sampled over 2004 (bogs, grasslands and sand dunes) and 2005 (heaths and oak woodlands; Fig. 1; Table S1, Supporting Information). To minimise spatial autocorrelation across assemblages, two sites of each habitat type were chosen from each of the four provinces, henceforth 'regions', of Ireland (Fig. 1). All sites were >16 km apart, which is beyond the typical foraging range of the bees in the study (Greenleaf *et al.* 2007).

Each site was visited three times across the year (spring, early summer and late summer). Bees were sampled using standardised observation transects and pan traps. In each site, a 1-km transect located in the centre of the habitat was walked in a random direction not following tracks or landscape features over a 2-h period between 09:00 and 13:00. All bees encountered within 1 m on either side of the observer were recorded. Specimens that could not be identified in the field were collected using aerial netting and identified to species in the laboratory (identification key: G. Else, personal communication). Three yellow water-filled pan traps were also installed haphazardly in the vicinity of each transect (min. of 150 m between traps) for 8 h on each visit. When inclement weather disrupted sampling, pan traps remained in place until sufficient periods of good weather had accumulated to 8 h. Workers, queens and males of the *Bombus lucorum* complex cannot be reliably differentiated in the field and were therefore collectively recorded as *B. lucorum agg*. (Carolan *et al.* 2012). All specimens have been archived for future reference at Queen's University Belfast and Trinity College Dublin.

ENVIRONMENTAL VARIABLES

In parallel with the standardised observation transects, we recorded environmental variables in a hierarchical design of three main sets and five subsets covering three spatial scales (Table 1; Table S2, Supporting Information). Spatial relationships across sites were quantified using principle coordinates of neighbour matrices (PCNM; Borcard & Legendre 2002). For landscape-scale analyses, the habitat composition and diversity surrounding each study site was characterised using the Irish and Northern Irish CORINE Land Cover Data (http://gis.epa.ie). We grouped 44 land-cover types into six categories of interest: agricultural, bog, grassland, heath, sand dune, woodland and urban. Analyses using ArcGIS 9 (ESRI, Redlands, CA, USA) were conducted at four radii encompassing both the transect and pan traps: 500 m, 1, 5 and 10 km from the centroid of the area surveyed in each site, and the following were calculated for all radii: percentage cover of each land-cover type; percentage cover of semi-natural habitats (summation of all land-cover types, excluding agricultural and urban land classes); landscape diversity (H_s) according to Krebs (1989), where $H_s = -\sum p_i * \ln p_i,$ and where p_i is the proportion of each land-cover type i.

PRELIMINARY ANALYSIS

Across all sites, we found no spatial autocorrelation among sites with respect to bee abundance (Moran's $I = -0{\cdot}041$, $P = 0{\cdot}639$) or bee species richness (Moran's $I = -0{\cdot}067$, $P = 0{\cdot}213$). For each habitat, the scale at which the surrounding land cover had the most explanatory power was found by correlating bee abundance

Table 1. Nested framework of environmental variables utilised in hierarchical partitioning models after controlling for multicollinearity

Main set (scale: min.–max)	Subset	Variable (s)
Regional (40 557–161 943 km^2)	–	Principle coordinates of neighbour matrices spatial predictors
Landscape (3–314 km^2)*	Composition	% Habitat: agriculture, contiguous, semi-natural, urban
	Diversity	Krebs (1989) landscape diversity index
Local (<2 km^2)	Management	Drainage ditches, anthropogenic disturbance, grazing (cattle, deer, rabbit, sheep)
	Microclimate	Cloud cover, min. temperature, wind speed, min. altitude.
	Nesting resources	Exposed soil (calcareous, gravel, mineral, peat, sand); grass tussocks, trees, wooden fences.

*Habitat-dependent scale at which the surrounding land-cover best predicted the abundance of bees (see Table S1, Supporting Information).

against the proportion of adjacent habitat surrounding each site at radii of 50, 1000, 5000 and 10 000 m. The resulting Spearman's rank coefficients of determination were then compared, and the scale with the highest coefficient of determination was used in all subsequent analyses for that habitat (Holland, Bert & Fahrig 2004; Table S1, Supporting Information).

STATISTICAL ANALYSES

Species richness (total number of species per site) and abundance per sampling period were pooled for each site. Differences in species richness and abundance across habitats were assessed using general linear modelling with habitat type and the logarithm of area under protection as fixed factors, and year as a random factor, as implemented in the 'nlme' package v3.1-100 (Pinheiro *et al.* 2011) with Tukey's HSD *post hoc* test ('multcomp' v1.2-6; Hothorn, Bretz & Westfall 2008), in R v.2.12.1 (R Development Core Team 2011). For each habitat, data were pooled across the season per site and rarefied using 1000 randomisations without replacement in EcoSim v7.0 (Gotelli & Entsminger 2001) to produce the rarefied species richness estimates. The Sørensen abundance-based estimator L_{abd} was used to assess compositional similarity among habitats (Table S3, Supporting Information), as well as species turnover by distance between sites within habitats, with 95% confidence intervals calculated using 1000 randomisations in EstimateS v8.0 (Chao *et al.* 2005; Colwell 2006).

The multiplicative model of beta diversity ($\gamma = \alpha \times \beta$), measured by species richness and Shannon diversity, was partitioned across hierarchical scales of site, habitat and region (Crist *et al.* 2003; Jost *et al.* 2010). Partitions of species richness are purely the effect of the number of species, whereas Shannon diversity accounts for the combined effect of richness and relative abundance and has been shown to be a robust measure of partitioned diversity (Jost *et al.* 2010). The significance of partitions was assessed by comparison with null model distributions for each component of species richness and Shannon diversity generated using 1000 randomisations, as implemented in the program partition 3.0 (Veech & Crist 2009). The total observed species richness and diversity was initially partitioned into its components across sites, regions and habitats, followed by separate analyses for each habitat type across sites and regions.

Variance in bee community data was hierarchically partitioned according to specific sets of environmental data by means of partial canonical correspondence analysis (pCCA; ter Braak 1988), as implemented in the 'vegan' package v1.17-11 (Oksanen *et al.* 2011) in R. Using pCCA, the 'marginal' and 'conditional' effects of the main sets and subsets of environmental variables could be calculated and compared across habitats and spatial scales. Marginal effects represent the community variability explained by a given set of environmental variables without considering other environmental variables, whereas conditional effects account for community variability explained by a given set of environmental variables after removing the confounding effect of one or more other environmental variables. Both marginal and conditional effects were tested for significance on the first and all canonical axes (global) by 999 Monte Carlo permutations on residuals within a pCCA (ter Braak 1988). pCCAs were conducted on all species, and on *Bombus* and non-*Bombus* taxa separately.

Unlike previous studies utilising the hierarchical partitioning approach (e.g. Schweiger *et al.* 2005), the final analyses could not be conducted on the entire data set with habitat type coded as a dummy variable because of the over-parameterisation of the initial pCCA model (see Table S4, Supporting Information). Instead, marginal models of each main set of environmental variables were simplified by subjecting the explanatory variables to forward selection and retaining a subset using Akaike's information criterion (AIC; Oksanen *et al.* 2011). Once simplified, the selected environmental variables from each marginal model were then incorporated into a final conditional pCCA model for each habitat. Hence, we initially simplified models using a 'bottom-up' approach, before constructing the final 'top-down' model. Owing to differences across habitats and taxa in the set of explanatory environmental variables, we followed Okland (1999) and focussed on the explainable variability only of our models, decomposing total variance explained into proportions of variance explained by the main sets and subsets of environmental variables. Thus, the relative, as opposed to absolute, impact of sets of environmental variables could be compared across habitats and taxa.

For each taxon (*Bombus* and non-*Bombus*) and habitat, the environmental variables selected in the pCCA models were examined in more detail using randomisation tests; qualitative factors were assessed using the mean difference in species richness and abundance between sites with and without the factor, quantitative factors were tested using Spearman's rank correlation. Pairwise similarity in community composition was quantified using the Chao-Sørenson abundance-based similarity index (Chao *et al.* 2005). Qualitative factors were tested using anova, comparing pairs of sites lacking the factor against pairs of sites where one site contained the factor; quantitative variables were assessed using Mantel tests of pairwise matrices of community similarity and Bray–Curtis similarity of the factor across sites. Two-tailed statistical significance was assessed using 999 Monte Carlo permutations as implemented in PopTools v3.2.5 (Hood 2010).

To reduce the number of explanatory environmental variables and resultant multicollinearity within the pCCA models, variables were correlated using the phi coefficient and Pearson product-moment coefficient, respectively, and all but one of the significantly correlated variables removed. All *P*-values were adjusted for repeated testing using Storey & Tibshirani's (2003) R package 'Q-value' v1.0. Where necessary, logarithmic or square-root transformation of environmental variables was used to achieve normality and proportional data were arcsin-square-root transformed. Counts of bees were pooled for the entire year per site, and the data transformed using $\log_{10}(x + 1)$. To exclude casual occurrences and enhance the detection of relationships between community composition and environmental factors, species occurring in <5% of sites were excluded from pCCAs (McCune & Grace 2002).

Results

SPECIES RICHNESS AND ABUNDANCE ACROSS HABITATS

A total of 4608 individual bees (4327 from transects; 281 from pan traps) representing 54 species were recorded from the 40 sites. The most abundant taxon was the Bombini, representing 81% of our data, followed by the Colletidae (11%) and the Halictidae (5%). Using our abundance data, a jackknife estimate of total species richness for all habitats was 61·8 ± 5·6 (mean ± 95% CI).

There were marked differences in species richness ($F = 4{\cdot}65$; d.f. = 4, 29; $P = 0{\cdot}005$) and abundance across habitats ($F = 3{\cdot}82$; d.f. = 4, 29; $P = 0{\cdot}013$; Table 1), but these were unrelated to area of protected habitat (species richness, $F = 0{\cdot}02$; d.f. = 1, 29; $P = 0{\cdot}884$; abundance, $F = 0{\cdot}03$, d.f. = 1, 29; $P = 0{\cdot}868$). Grasslands harboured the highest species richness in comparison with bogs ($Z = 4{\cdot}69$, $P < 0{\cdot}001$), dry heaths ($Z = 2{\cdot}49$, $P = 0{\cdot}094$), sand dune ($Z = 3{\cdot}52$, $P = 0{\cdot}004$) and oak woodland ($Z = 2{\cdot}69$, $P = 0{\cdot}055$). In contrast, dry heaths had twice the abundance of bees compared to the other habitats studied: bogs ($Z = 3{\cdot}74$, $P = 0{\cdot}002$), grassland ($Z = 2{\cdot}73$, $P = 0{\cdot}049$), sand dunes ($Z = 2{\cdot}86$, $P = 0{\cdot}035$) and oak woodland ($Z = 3{\cdot}79$, $P = 0{\cdot}014$). After controlling for disparate abundance across habitats, the highest rarefied species richness per site was recorded in calcareous grasslands (39·5 ± 2·5) and the lowest in bog habitats (11·8 ± 0·8). In terms of compositional similarity of species between habitats, bogs were the most similar to dry heaths (L_{abd} ± 95% C.I.; 0·778 ± 0·055) and oak woodlands (0·747 ± 0·043), whereas the greatest dissimilarity was found between sand dune and oak woodland assemblages (0·576 ± 0·049; Table S3, Supporting Information). Within habitats, there was no significant difference in the compositional similarities across sites, but sites were more dissimilar with increasing geographical distance in both calcareous grassland ($r = -0{\cdot}35$, $P < 0{\cdot}05$) and sand dune habitats ($r = -0{\cdot}55$, $P < 0{\cdot}01$; Table 2).

SPECIES RICHNESS AND DIVERSITY PARTITIONING

Partitioning species richness and diversity across five habitats revealed qualitatively identical results; therefore, only the results from species richness will be presented (the Shannon diversity analyses appearing in the Table S5, Fig. S1, Supporting Information). All diversity components deviated from a null distribution, and the majority of within-habitat diversity was contained in the alpha component (Fig. 2; Table 3). Species richness within sites was typically lower than expected, whereas turnover across sites and regions was greater than predicted by null distributions. Bog habitats had the largest fraction of α_{site} species richness (72·1%) compared to grasslands (70·3%), heaths (63·9%), sand dunes (68·3%) and woodlands (71·0%; Fig. 2). Overall, β-diversity accounted for 45% of species richness among sites, habitats and regions (Fig. 2). Significantly, more β-diversity was observed across sites, habitats and regional scales than expected from null distributions, with the greatest species β-diversity being observed across habitats ($\beta_{\mathrm{habitat}} = 2{\cdot}86$; Table 3). In all habitats, β_{region} was higher than β_{site}.

HIERARCHICAL PARTITIONING OF COMMUNITY VARIANCE

Of the 54 species recorded across all sites, 36 (13 *Bombus*; 23 non-*Bombus*) met the criterion for inclusion in the

Table 2. Mean bee abundance and species richness with 95% CI in parenthesis, the median area conserved and distance between sites, and associated Mantel test using distance between sites and the Sørensen abundance-based similarity index (L_{abd}) for the five habitats studied

Parameter	All data	Bog	Calcareous grassland	Dry heath	Sand dune	Oak woodland
Abundance (individuals/site)	115·2 (89·5–140·8)	93·5 (43·9–143·1)	97·6 (83·7–111·6)	200·5 (114·2–286·8)	105·6 (65·5–145·7)	78·8 (62·2–95·3)
Observed species richness (species/site)	9·0 (7·4–10·5)	5·6 (1·8–9·4)	13·6 (8·9–18·5)	9·4 (5·2–13·6)	7·7 (4·1–11·3)	9·6 (5·6–14·4)
Observed species richness (species/habitat)	–	11·0 (4·9–17·1)	41·0 (31·3–50·7)	33·0 (23·5–42·5)	20·0 (12·6–27·4)	24·0 (14·7–31·3)
Rarefied species richness (species/habitat)†	–	11·8 (11·0–12·6)	39·5 (37·0–42·0)	26·0 (22·0–30·0)	20·0 (18·0–21·0)	24·0 (0·0–0·0)
Median area of conserved habitat (‘00 ha)	2·1 (0·1–221·8)‡	18·8 (1·8–99·4)	0·6 (0·1–11·3)	14·0 (0·1–221·8)	1·5 (0·1–22·5)	1·7 (0·2–3·0)
Median distance between sites (km)	174·8 (16·5–470·6)‡	198·6 (32·6–399·4)	106·5 (19·3–227·3)	191·1 (37·9–307·9)	260·9 (75·9–454·2)	209·9 (44·0–436·1)
Mantel r of L_{abd} and geographical distance	−0·01 (−0·13–0·05)	−0·09 (−0·36–0·18)	−0·35* (−0·31–0·39)	−0·05 (−0·26–0·33)	−0·55** (−0·51–0·59)	−0·22 (−0·48–0·04)

†Rarefied to 631 individuals in Oak woodland
‡Min.–max.
*$P < 0{\cdot}05$, **$P < 0{\cdot}01$.

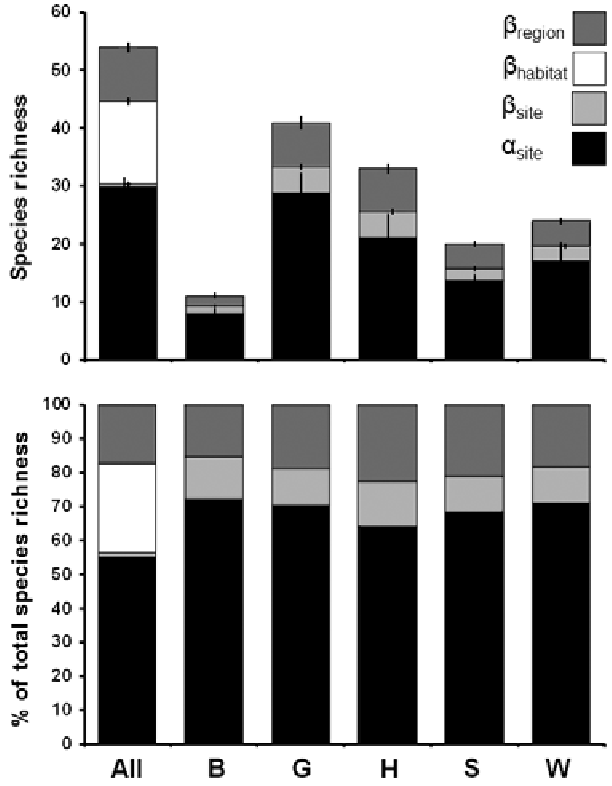

Fig. 2. Mean α- and β-diversity (between sites, habitats and regions) values and the proportion of each diversity component expressed as a percentage of total γ-diversity for species richness; error bars are ±2 SE of the mean. The multiplative model of diversity was transformed to an additive model using $\log_2$ before calculating the number of species and percentage represented by each partition. Hierarchical diversity partitions are shown for all data, and separately for bogs (B), grasslands (G), heaths (H), sand dunes (S) and woodlands (W).

Table 3. Hierarchical multiplicative partitioning of α- and β-components for bee species richness. *P*-values were obtained by comparing the observed values with the distribution of expected values from 1000 randomisations

	Species richness		
Diversity	Observed	Expected	*P*
All data			
α_{site}	9·02	12·65	<0·001
β_{site}	1·05	1·13	<0·001
$\beta_{habitat}$	2·86	2·04	<0·001
β_{region}	1·99	1·86	<0·001
γ	54		
Habitat			
Bog			
α_{site}	5·64	8·52	<0·001
β_{site}	1·35	1·13	<0·001
β_{region}	1·44	1·14	<0·001
γ	11		
Grassland			
α_{site}	13·62	19·77	<0·001
β_{site}	1·50	1·31	<0·001
β_{region}	2·01	1·58	<0·001
γ	41		
Heath			
α_{site}	9·37	16·54	<0·001
β_{site}	1·60	1·32	<0·001
β_{region}	2·13	1·47	<0·001
γ	33		
Sand dune			
α_{site}	7·74	12·84	<0·001
β_{site}	1·37	1·18	<0·001
β_{region}	1·88	1·32	<0·001
γ	20		
Woodland			
α_{site}	9·56	12·12	<0·001
β_{site}	1·40	1·31	<0·001
β_{region}	1·80	1·51	<0·001
γ	24		

pCCAs (Table S6, Supporting Information). After correcting for multicollinearity, nine quantitative and 19 qualitative explanatory environmental variables were included and subjected to forward selection in the marginal pCCAs (Table 1; Table S7, Supporting Information). In the final conditional pCCA models (Table S8, Supporting Information), the composition of bee communities appeared to be largely determined by local factors (28·0–52·0%), compared to landscape (7·0–22·5%) and region (7·2–12·1%; Table 4; Fig. 3). Factors associated with site management explained the majority of total community variance in bog, sand dune and woodland habitats (22·7%, 21·2% and 27·1%, respectively), whereas nesting resources explained 27·9% and 36·5% of the variance in grassland and heath habitats (Fig. 3). Habitat diversity surrounding heath sites (22·5% of total community variance) was the only statistical significant landscape-scale factor.

Owing to the dominance of *Bombus* across the habitats in this study, it is unsurprising that many factors found to have the highest explanatory power when analysing the entire community data are also of primary importance to the *Bombus* community data. Site management explained 17·8%, 12·7% and 31·0% of bumblebee community variance in grassland, sand dune and woodland habitats, and nesting resources accounted for 21·5%, 29·6% and 19·3% in bog, grassland and heath habitats (Fig. 3). In contrast, non-*Bombus* communities were more sensitive to landscape-scale factors, with landscape composition being of primary importance in sand dune (30·8%) and woodland habitats (17·8%), and of secondary importance in heath habitats (12·5%). Furthermore, the microclimate at each site contributed significantly to structure the non-*Bombus* communities in both grassland (9·3%) and sand dune (19·4%) habitats, and nesting resources explained a further 8·5% of community variance in grasslands.

FACTORS STRUCTURING BEE COMMUNITIES

Overall, the net effect of factors identified from pCCA models was mostly associated with changes in the composition of bee species within a community, rather than to variation in total species richness or abundance (Table S9, Supporting Information). Across taxa, nesting resources

Table 4. Proportion of total variability explained by conditional effects of regional, landscape and local habitat factors for each habitat type and for all bee species, *Bombus* only, and non-*Bombus* bees. Statistical significance of each partial canonical correspondence analysis model was evaluated by 999 Monte Carlo permutations under the reduced model

				Spatial scale								
				Regional			Landscape			Local		
Habitat	Taxon	No. Sites	No. Species	% Community variance	d.f.	Global *F*-ratio	% Community variance	d.f.	Global *F*-ratio	% Community variance	d.f.	Global *F*-ratio
Bog	All taxa	8	12	10·64	1,4	1·13	21·09	2,2	1·26	38·82	2,4	2·07*
	Bombus	8	8	6·73	1,2	1·24	24·17	2,2	2·22	41·54	2,2	2·37*
	Non-*Bombus*	4	4	–	–	–	–	–	–	–	–	–
Calcareous grassland	All taxa	8	30	9·93	1,4	1·75	15·53	2,2	0·77	27·98	2,4	2·39*
	Bombus	8	12	7·52	1,2	1·17	14·60	2,2	1·14	47·66	2,2	3·70*
	Non-*Bombus*	8	18	14·02	1,2	0·72	17·46	2,2	0·75	18·61	2,4	1·93*
Dry heath	All taxa	8	24	7·21	1,3	1·33	22·52	1,3	4·16*	36·48	2,3	3·37**
	Bombus	8	9	7·35	1,3	0·79	3·53	1,3	0·38	26·64	2,4	1·93*
	Non-*Bombus*	6	15	12·42	1,3	1·34	12·54	1,3	1·55*	48·04	2,4	2·34*
Sand dune	All taxa	8	18	7·66	1,4	0·81	6·95	2,2	0·68	30·06	1,5	1·99*
	Bombus	8	11	9·40	1,4	2·88†	12·07	2,2	0·84	22·55	2,4	2·09*
	Non-*Bombus*	7	7	15·53	1,3	0·12	30·82	1,3	3·98*	19·41	1,3	3·86*
Oak woodland	All taxa	8	22	12·12	2,1	3·17	16·56	1,1	4·64	51·99	2,4	6·64*
	Bombus	8	7	20·05	1,5	2·11†	29·95	2,3	1·72	31·00	1,5	3·23*
	Non-*Bombus*	7	15	7·99	1,2	0·79	35·33	2,3	2·18**	8·38	1,2	0·82

Monte Carlo permutation test: *P < 0·05; **P < 0·01; †P < 0·06; all other P-values > 0·1.

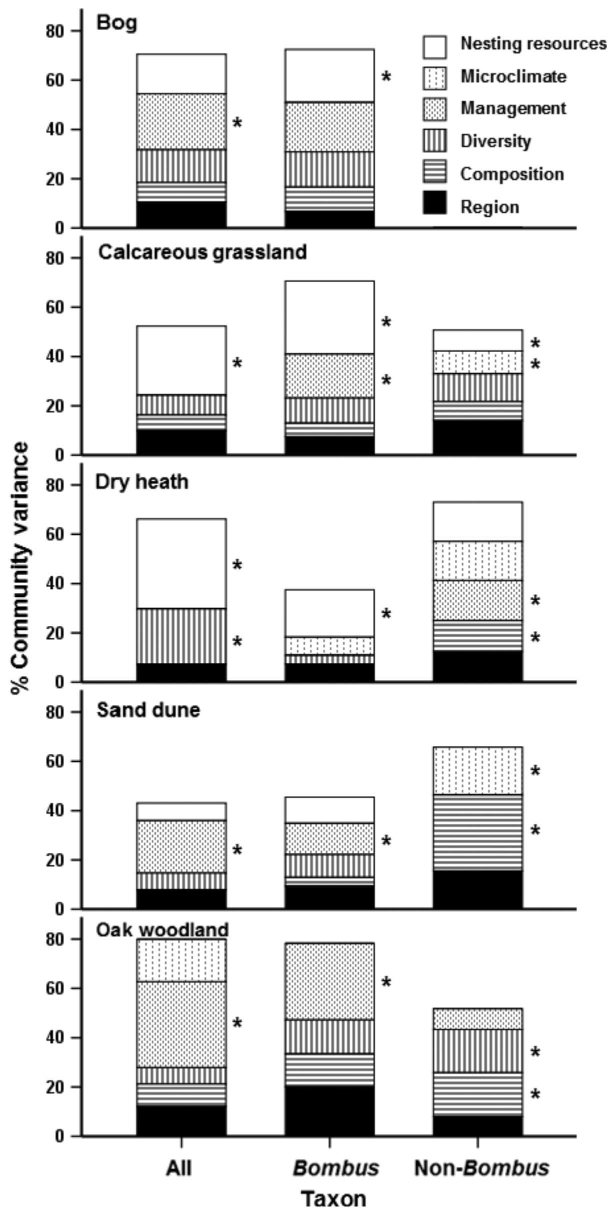

Fig. 3. Hierarchical variability partitioning of conditional partial canonical correspondence analysis models identifying the proportion of variance associated with regional-scale (region), landscape-scale (composition, diversity) and local-scale (management, microclimate, nesting resources) environmental factors on the total bee, *Bombus* only, and non-*Bombus* bee communities in each Special Areas of Conservation habitat. Statistical significance ($^*P < 0{\cdot}05$) of each factor was determined by 999 Monte Carlo permutations under the reduced model.

such as exposed calcareous soil increased bee species richness (mean ± SE) in grassland and heath habitats by 8·14 ± 5·24 ($P = 0{\cdot}023$) and 10·90 ± 5·85 ($P = 0{\cdot}018$) species per site, respectively. Grass tussocks, exposed calcareous soil and tree cover also slightly increased the abundance of bees per site by 2·25 ± 1·61 ($P < 0{\cdot}001$), 1·47 ± 1·05 ($P < 0{\cdot}001$) and 1·95 ± 1·50 ($P = 0{\cdot}048$) species in bog, grassland and sand dune habitats, respectively.

With respect to bumblebees, management factors such as grazing changed the composition of communities in bogs (cattle grazing; $F = 7{\cdot}349$, $P = 0{\cdot}015$) and grasslands (sheep grazing; $F = 3{\cdot}551$, $P = 0{\cdot}045$) and decreased the number of species in sand dune habitats by 2·2 ± 1·03 (rabbit grazing; $P < 0{\cdot}001$) per site. Specifically, the relative abundance of *Bombus lapidarius* and *Bombus sylvarum* increased with sheep grazing in grasslands, while the relative abundance of *Bombus rupestris* decreased with rabbit grazing in sand dunes (Table S10, Supporting Information). The presence of grass tussocks, exposed mineral soils and tree cover changed the composition of bumblebee communities in bog ($F = 3{\cdot}425$, $P = 0{\cdot}054$), heath ($F = 4{\cdot}946$, $P = 0{\cdot}036$) and sand dune ($F = 42{\cdot}002$, $P < 0{\cdot}001$) habitats, respectively. In bogs, this appears to be primarily due to *Bombus jonellus* avoiding sites with grass tussocks. In contrast, in sand dunes, *B. jonellus* and *B. lucorum* agg. were positively associated with tree cover, while *B. lapidarius* was negatively associated with tree cover (Table S10, Supporting Information).

Sheep grazing, and landscape factors such as the proportion of urban habitat and semi-natural habitats, altered the non-*Bombus* community in heath ($F = 2{\cdot}149$, $P = 0{\cdot}042$), sand dune ($z = -0{\cdot}852$, $P = 0{\cdot}029$) and woodland habitats ($z = -0{\cdot}334$, $P = 0{\cdot}042$), respectively (Table S9, Supporting Information). In terms of individual bee species, sheep grazing in heaths excluded *Nomada panzeri*, and the proportion of urban areas was positively associated with *Colletes succinctus* and *Halictus rubicundus* in sand dune habitats (Table S10, Supporting Information). In parallel to the analysis of the entire community, exposed calcareous soil increased non-*Bombus* species richness per site by an average of 7·01 ± 4·90 ($P < 0{\cdot}018$) species.

Discussion

This is the first study to examine factors influencing bee species diversity in a network of protected areas. Our fundamental finding is that factors operating at the upper scale of our study, such as climate, have little impact on community composition, whereas habitat type, a local-scale factor, does; specifically, calcareous grasslands and dry heaths support higher species diversity relative to bogs and sand dunes. Furthermore, across habitats, local-scale environmental factors such as the availability of nesting resources are most closely related to high species diversity, while bumblebees are relatively insensitive to surrounding land-use compared to non-bumblebee taxa.

Owing to the high spatiotemporal variation in bee community composition, previous studies investigating processes regulating bee biodiversity across multiple sites have rather concentrated on quantifying species turnover itself (Tylianakis, Klein & Tscharntke 2005; Clough *et al.* 2007). Our findings add to this growing body of the literature by demonstrating that species turnover at broad spatial scales contributes significantly to total regional bee species richness. Specifically, we could account for 45% of species richness by the turnover of species among sites (1%), habitats (27%) and regions (17%; Fig. 2), indicating that habitat-based strategies would be the most appropriate framework for conserving bee diversity in Ireland. However, bumblebees, a highly mobile taxon, dominated the SAC habitats in this study (26% of species richness; 81% of total abundance). Therefore, it may be unsurprising that local species richness accounts for the majority of regional diversity in these SACs as a result of reduced species turnover across sites and regions of the same habitat type (Clough *et al.* 2007). Ultimately, within habitats, the significant contribution of within-site diversity (64–72% of species richness; 68–84% of Shannon diversity) relative to among-site species turnover (11–13%; 7–13%) strongly suggests that prioritising protection of high-diversity sites within each habitat type would maximise the number of species conserved in this system.

A recent meta-analysis found that bee community composition was extremely sensitive to changes in land-use (Winfree *et al.* 2009). Our data reinforce this view and conclusively show that, relative to large-scale spatial relationships (4–16 × 10^4 km^2), localised environmental factors are powerful determinants of bee biodiversity in protected habitats. Moreover, these environmental factors can be highly taxon and habitat specific. For example, we found that non-*Bombus* bees were more sensitive to surrounding land-use than *Bombus*, but in a highly habitat-specific manner, whereby the proportion of urban habitats within 0·5 km of sand dunes and the proportion of semi-natural habitats within 5 km of woodlands altered the abundance distribution across species, but not species richness *per se*, in these SACs (Table S9, Supporting Information). Although intensely managed landscapes are detrimental to bee diversity (Schweiger *et al.* 2005), the variability in bee community response to landscape context stems from the fact that some species benefit from human-mediated disturbance compared to others (e.g. suburban habitats, Chapman, Wang & Bourke 2003; extensive agricultural habitats, Tylianakis, Klein & Tscharntke 2005). As an example, the abundance of three endangered bumblebees in calcareous grasslands responded differentially to local factors, with *B. sylvarum* abundance being positively associated with sheep grazing, while *B. rupestris* benefited from the absence of trees, and *Bombus distinguendus* was excluded from sites with trees (Table S10, Supporting Information).

One possible explanation for the relative insensitivity of *Bombus* communities to surrounding land-use is that individual bees are generally larger and have a greater dispersal capacity than non-*Bombus* species (Greenleaf *et al.* 2007). Species with enhanced dispersal capacity are hypothesised to be more able to move between habitat patches and use fragmented resources more effectively (Hanski & Ovaskainen 2000). In agreement with this view, Bommarco *et al.* (2010) found that large-bodied generalist bees, such as bumblebees, were less sensitive to patch size compared to small-bodied specialist bee species across five temperate European grassland systems. Therefore, the high proportion of bumblebees recorded in Irish bee communities may explain the lack of a relationship between protected patch area and species richness or abundance observed in this study. Additionally, SAC habitats may be legally, but not biologically, discreet entities in which the predominant habitat within the SAC also exists in unprotected fragments adjacent to the SAC, where it is typically of poorer quality and smaller size. Hence, depending on the distribution and quality of the neighbouring unprotected habitats, arthropod communities within the protected area may make use of these suboptimal habitats.

The lack of landscape-scale correlations with bee diversity in this study may be primarily due to the relatively high heterogeneity of the land cover surround our focal SAC habitats. Therefore, compared to landscape context, we found that the availability of critical local-scale environmental factors largely dictated the structure of bee communities. In general, floral and bee diversity and abundance are positively associated (e.g. Potts *et al.* 2003 ; Biesmeijer *et al.* 2006), but data on the importance of nesting resources in structuring communities are lacking (recently reviewed in Murray, Kuhlmann & Potts 2009). Our results indicate that the local factor grazing explained considerable variance in the composition of the community of bumblebees in bogs (20·1%), grasslands (17·7%) and sand dunes (12·7%) and the composition of the community of non-*Bombus* species in heaths (16·3%). For example, sheep grazing in grasslands and heaths did not alter the bee species richness or abundance *per se*, but did change the abundance distribution across *Bombus* species in grasslands and non-*Bombus* bees in heaths (Table S9, Supporting Information). In contrast, rabbit grazing on sand dunes was found to decrease the number of bumblebee species by 20%. The response of bees to grazing is, however, highly dependent on the intensity of grazing (Winfree *et al.* 2009). Intermediate levels of grazing can increase plant species richness by preventing dominance of competitive species, subsequently benefiting bee diversity (Carvell 2002). Where grazing is associated with a decrease in floral abundance and diversity, it negatively effects bee populations (Kruess & Tscharntke 2002; Xie, Williams & Tang 2008), but intense grazing can also increase the amount of exposed soil and compacted ground for ground-nesting bee species, overall benefiting bee diversity (Vulliamy, Potts & Willmer 2006). In Ireland, grazing on SAC habitats is typically unregulated and, in the past 10 years, excessive grazing is known to be one of the principle drivers of decline in the area of bog (−1·2%), heath (−1·1%), sand dune (−4%) and woodland (−0·2%) habitats, whereas lack of grazing reduces the area of calcareous grassland through scrub and woodland encroachment (−5%; NPWS 2007). It is notable that grazing has emerged as one of the strongest drivers of bee diversity within this study of Irish protected habitats.

Finally, in terms of bee nesting habitat, the presence of exposed calcareous soil in grasslands and heaths, grass tussocks in bogs, woody habitat in sand dunes and drainage ditches in woodlands were all significant explanatory factors (they explained 7–36%) of bee community variance (Table 4; Table S8, Supporting Information). Specifically, species richness in sites with exposed calcareous soils was 27% higher in calcareous grasslands and 45% higher in heaths, whereas drainage ditches in woodlands modestly increased richness by 6%, and grass tussocks in bogs increased abundance by 2%. Compared to floral resources, relatively few data exist on the nesting requirements of many bee species and the impact of nest site limitation on bee populations (Murray, Kuhlmann & Potts 2009). Our data suggest that nesting resources in calcareous grassland and heath habitats are limiting. As this inference is based on correlational results, experimental studies demonstrating an increase in population size with increasing nesting resources are necessary to determine whether nesting resources are limiting bee populations. The only experimental study conducted on nest limitation found that trap nest augmentation increased *Osmia rufa* populations 35-fold (Steffan-Dewenter & Schiele 2008).

Habitat loss is non-random and the spatial arrangement of remaining habitat fragments can have an equally large impact on extinction rate as the absolute amount of habitat loss (Seabloom, Dobson & Stoms 2002; Ewers & Didham 2006). Extinctions within fragments lower the amount of α-diversity and high levels of β-diversity among fragments represent a much greater proportion of total species richness at higher spatial scales (Crist *et al.* 2003). As bumblebees appear to dominate the SAC habitats in this study, local species richness of this highly mobile taxon may approach regional species richness as a result of increased community homogeneity among sites within each habitat type (Clough *et al.* 2007). Indeed, across a diverse array of protected habitats, we found that 55% of bee species richness was contained within sites, compared to 45% produced by the turnover of species across sites, habitats and regions. In addition, by integrating explicit spatial models into a hierarchical partitioning framework by means of pCCA, we find that the majority of species turnover is explained by specific local- and landscape-scale factors relating to nesting resources and grazing, rather than regional-scale spatial variance in community composition. Future management of SACs for bee conservation should prioritise habitat- and taxon-specific schemes that focus on the interaction of local-scale forage and nesting resources, with the intensity of grazing and surrounding land-use.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1. Hierarchical partitioning of α- and β-components for bee Shannon diversity.

Table S1. Description of the sites surveyed.

Table S2. Environmental data set indicating those included in pCCA.

Table S3. Between habitat compositional similarity.

Table S4. Summary of initial marginal and conditional pCCA models.

Table S5. Hierarchical partitioning of α- and β-components for bee Shannon diversity.

Table S6. Species abundance per habitat.

Table S7. Summary of AIC-selected marginal pCCA models.

Table S8. Summary of conditional pCCAs models.

Table S9. Summary of randomisation tests conducted on explanatory variables.

Table S10. Relative abundance of species in response to factors identified from pCCA analyses.