


From pastures to forests: Changes in Mediterranean wild bee communities after rural land abandonment

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Abstract

1. In farmland landscapes worldwide, there are pervasive trends for either intensification or abandonment. Intensification is a widely recognised driver of wild bee declines, but little is known about the consequences of land abandonment, though it involves major habitat shifts from fallows, pastures and meadows, to shrublands and forests.
2. Focusing on a Mediterranean landscape, we investigated long-term changes in wild bee communities during secondary vegetation succession after land abandonment. We used a space-for-time substitution approach, sampling plants and wild bees on five successional stages, from grasslands, through shrublands, to oak woodlands.
3. We recorded 2721 bees, representing over 150 species. Grasslands had the highest wild bee abundance and high diversity of oligolectic species. Moving through successional stages, there was a rapid decline in bee abundance combined with a progressive accumulation of rare species, resulting in maximum diversity of the overall community, ground nesters, polyleges, and oligoleges in oak woodlands. Bee diversity was positively related to plant taxonomic and phylogenetic diversity. There was high turnover in community composition along the succession, with species occurring in grasslands being largely absent from later successional stages, and vice versa. From 21 indicator species, 17 were associated with grasslands, including the only threatened species.
4. Our results suggest that a mosaic of habitats at different successional stages, particularly grasslands and oak woodlands, are necessary to maximise the diversity and abundance of wild bees at the landscape scale. Sustained management is thus needed under land abandonment to retain early-successional herbaceous habitats and to ensure woodland regeneration and protection.

KEYWORDS

biodiversity, community ecology, conservation, functional traits, Hill numbers, pollinator, rewilding, vegetation succession

INTRODUCTION

Worldwide, agriculture is facing two opposite trends with major consequences for biodiversity, involving both rapid intensification in the most productive areas, and also the abandonment of marginal farmland (Kehoe et al., 2017; Li & Li, 2017; Stoate et al., 2009). Much

attention has been given to the link between intensification and the global decline of wild bees (Hymenoptera: Apoidea: Anthophila) and other pollinators, as they provide vital services to crops and wild plants (IPBES, 2016; Potts et al., 2010; Wagner et al., 2021). These declines are mainly related to habitat loss and fragmentation, the expansion and homogenisation of agricultural landscapes, the use of



agrochemicals, and interactions between these and other factors (Goulson et al., 2015; IPBES, 2016; Wagner et al., 2021). It is possible, however, that the abandonment of extensive agriculture and pastoral activities can also have negative consequences, due to the loss of herbaceous habitats such as pastures, fallows, and meadows that are essential for early-successional species (Grundel et al., 2010; Hanula et al., 2015; Potts et al., 2003; Steffan-Dewenter & Tscharntke, 2001; Taki et al., 2013). Yet, abandonment may also be positive in the long term, because it can favour the recovery of species associated with forests and other natural habitats that are poorly represented on farmland (Potts et al., 2006). Understanding these processes is important to promote wild bee conservation under rural land abandonment (Li & Li, 2017; Queiroz et al., 2014).

Mediterranean Europe is one of the global regions with the longest history of agricultural and pastoral activities, and where the rural abandonment trend is most pervasive (Herrando et al., 2016; Moreira & Russo, 2007; Plieninger et al., 2014). Here, the decline of agricultural and pastoral activities is followed by a long process of secondary vegetation succession, with the rapid colonisation of abandoned cultivated fields by an herbaceous layer dominated by annuals, which is replaced after a few years by a layer dominated by perennials and scattered shrubs that progresses over time into dense shrublands and eventually into native forests (Porto et al., 2011; Santana et al., 2011). However, progression from shrublands to forests may take several decades, or even stop, due primarily to soil erosion and depleted fertility, dry climatic conditions, shortage of seed sources, and recurrent fires resetting the succession dynamics (Peña-Angulo et al., 2019; Ritsche et al., 2021; Santana et al., 2010), a condition called arrested succession (Acácio et al., 2007). As a result, abandoned Mediterranean landscapes often become dominated by extensive shrublands, with grassland habitats progressively declining and forest cover remaining sparse unless there is active restoration (Mendes et al., 2015; Rivest et al., 2011). Therefore, the impacts of abandonment on wild bees and other pollinators should be greatly influenced by how communities change over time along the successional gradient.

Little is known about the long-term responses of wild bee communities to land abandonment in the Mediterranean region, despite its importance as a hotspot of wild bee diversity (Herrera, 2020). Studies focusing on post-fire vegetation succession suggest that peaks in Mediterranean wild bee abundance and diversity may occur immediately following disturbance (Potts et al., 2003), though high diversity levels may also occur in mature woodlands due to the presence of many rare species (Potts et al., 2006). In temperate regions, studies have also reported higher bee species richness and abundance in early-successional stages, though with some functional groups reaching higher diversity and/or abundance later in the succession (Grundel et al., 2010; Steffan-Dewenter & Tscharntke, 2001; Taki et al., 2013). These trends are probably influenced to a large extent by changes in the taxonomic and functional composition, richness and abundance of floral communities during succession, which in turn affect nectar and pollen availability for different species and

functional groups (Grundel et al., 2010; Potts et al., 2003, 2006; Steffan-Dewenter & Tscharntke, 2001).

This study investigates long-term changes in Mediterranean wild bee communities during secondary succession after rural land abandonment. Specifically, we hypothesised that during succession there is a marked turnover in wild bee community composition, with peaks in diversity and abundance soon after abandonment, followed by a progressive replacement of early-successional species by rarer and more specialised species at later successional stages. To test this hypothesis, we used a space-for-time substitution approach (e.g. Albrecht et al., 2010; Foster & Tilman, 2000) to describe changes in wild bee communities over five successional stages, from grasslands, through shrublands, to forest habitats. Specifically, we estimated changes during vegetation succession in: (i) community composition; (ii) species diversity and abundance; (iii) diversity and abundance of specialist and generalist species; and (iv) richness of species that are abundant in a given stage, but not in the others (indicator species). In addition, we estimated (v) how temporal changes in wild bee diversity were affected by changes in floral taxonomic and functional richness during succession. Our results were used to discuss management strategies for conserving wild bees under agricultural land abandonment.

MATERIALS AND METHODS

Study area

The study was carried out in north-east Portugal (41°21'N, 6°58'W), within the Baixo Sabor Long Term Ecological Research Site (<https://deims.org/45722713-80e3-4387-a47b-82c97a6ef62b>) (Supplementary Figure S1). Climate is transitional between meso- and supra-Mediterranean, with cold winters and dry and hot summers (Monteiro-Henriques, 2010). Topography is characterised by plateaus with maximum altitudes around 600 m a.s.l., which are dissected by deep and narrow stream valleys (Hoelzer, 2003). The peak of agricultural activity occurred in the 1930s and 1940s, due to the availability of subsidies for cereal cultivation (Cepeda, 1999; Pais et al., 1978; Pinto et al., 2019). The area occupied by annual arable crops declined from >60% in the 1940s to <10% in the 2010s (Ana Teresa Pinto, Unpublished Data), due to progressive land abandonment and rural exodus (Cepeda, 1999). In the region, abandoned agricultural land is occupied at first by a range of herbaceous species typical of rough pastures and fallow fields, but after just a few years, there is a rapid colonisation by pioneer shrubs such as *Cistus* spp., *Cytisus* spp. and *Lavandula pedunculata* (Mill.) Cav. (Hoelzer, 2003). Later, fields may turn into tall shrublands dominated by *Juniperus oxycedrus* L. (Curto et al., 2015), which may develop into oak woodlands (*Quercus suber* L., *Q. rotundifolia* Lam.) with a rich understorey including for instance *J. oxycedrus*, *Pistacia terebinthus* L., and *Erica arborea* L. (Hoelzer, 2003). These woodlands have expanded from small, isolated and heavily degraded oak patches that occurred in the region in the 1940s (Ana Teresa Pinto Unpublished Data). At present, the landscape is a mosaic

of arable fields, extensive pastures, perennial crops (mainly olive and almond groves), and patches of natural vegetation at different times since land abandonment. Agriculture throughout the area is low intensity, with little use of agrochemicals, irrigation and mechanisation, and thus unlikely to have negative effects in neighbouring natural habitats.

Study design

Sampling was designed using a space-for-time substitution approach (Albrecht et al., 2010; Foster & Tilman, 2000), taking spatial variation across plots representing different vegetation stages after agricultural land abandonment, to infer temporal changes in wild bee communities during secondary vegetation succession. These stages were selected based on successional patterns described in our region (Hoelzer, 2003; Pinto et al., 2019; Miguel Porto, Unpublished Data) and comparable Mediterranean areas (Porto et al., 2011; Santana et al., 2011), considering in particular shrub cover and height, and cover by late-successional juniper and oak species: 1) grasslands – predominantly fallow lands and other herbaceous habitats with no shrubs or only with scattered shrubs <30 cm high; 2) short shrublands – dominated by shrubs <1 m high, and with <10% cover by juniper and oaks; 3) tall shrublands – dominated by shrubs 1–2 m high, and with <10% cover by juniper and oaks; 4) juniper shrublands – with 10–50% cover by juniper, sometimes also with oaks; 5) oak woodlands – with >50% cover by evergreen oaks, sometimes also with juniper trees.

The temporal succession pathway used in our study is well supported by empirical data (Hoelzer, 2003; Pinto et al., 2019; Porto et al., 2011; Santana et al., 2011), but it cannot be assumed that transitions between consecutive stages occur at regular time intervals. In fact, the speed of transitions is faster between some stages (e.g. from 1 to 2) than others (e.g. from 4 to 5) (Santana et al., 2011), and transitions are likely faster in some areas and slower in others, due to differences in the availability of seed sources and dispersers, soil degradation, and other factors (Acácio et al., 2007). Because of this, vegetation stage cannot be considered a continuous or even interval variable, and so it was treated as an ordinal variable in subsequent analysis. This was considered more adequate than taking stage as a purely categorical variable, because there was an intrinsic ordering of the categories, and we were interested in detecting trends along the succession rather than differences between any particular stages. Moreover, using categories would probably inflate type II errors, because the number of samples per stages was small (see below), and so the power of analysis to detect differences between stages would be low.

Wild bee sampling

Sampling was conducted in six 50 m × 50 m plots per successional stage (total $n = 30$ plots), with a minimum distance between plots of 500 m. Wild bees were surveyed in each plot at monthly intervals, three times in 2014 (May–August) and five times in 2015 (April–August). Four plots were ploughed at the end of 2014, and so they

were replaced in 2015 by nearby plots in the same successional stage and with a similar floristic composition. In these cases, bee community data from the initial and the corresponding replacement plot were pooled, to achieve a similar sampling effort across all plots used in analysis. In each plot and sampling occasion, a single observer (A.P.) conducted a 30-min survey covering the entire area, with bees collected with a hand net. During surveys, no more than 5 min were spent around the same patch of flowering plants to avoid over-sampling. We did not record honeybees (*Apis mellifera* L.) because their abundance is strongly influenced by human management (Herrera, 2020), particularly the spatial distribution of apiaries (Steffan-Dewenter et al., 2002).

After the bee survey, a set of two clusters of pan traps were put at the centre of the plot for 24 h. Each cluster consisted of three pan traps, with each painted in either white, yellow or blue with UV-bright (Sparvar Leuchtfarbe, Germany). The pan traps were filled with water, toxic anti-freeze ethylene glycol in 2014 and non-toxic anti-freeze propylene glycol in 2015, and a drop of detergent. Sampling was conducted in clear and dry weather, between 9:00 h and 16:30 h, with three to six plots sampled per day. To minimise potential biases due to bee activity patterns, plot sampling order was randomised in each survey. The specimens were collected and stored in 70% ethanol, then dried and pinned for taxonomic identification by experts (Supplementary Table S2). All the standard taxonomic methodological data on specimens collected were published by Baldock et al. (2018), and information on species occurrences will be made available through gbif.org in due course. Voucher specimens were mainly deposited in the Natural History and Science Museum of the University of Porto (MHNC-UP), with a few retained in the private collections of taxonomists listed in the study by Baldock et al. (2018).

To explore whether ecological specialisation varied along the successional gradient, we categorised species according to trophic diversity (polylectic or oligolectic) and nesting substrate (ground nesters versus cavity or above ground nesters), based on published literature and personal observations (Supplementary Table S2). Oligolectes were considered the most specialised because they feed on a narrow range of plants, such as a single genus or family. Cavity nesters were also considered the most specialised, because they were assumed to be more limited by the availability of nesting sites than ground nesters, due to their reliance on structures (e.g. snail shells, mouse holes, bramble stems, rock crevices) that may be absent or scarce in some habitats (Potts et al., 2005). We also classified species according to European conservation status (Nieto et al., 2014), to check whether threatened and near-threatened species were associated with any particular successional stage.

Plant sampling

Plants were sampled by a single observer (M.P.) at bee sampling plots, once during a week in June 2014, because this is the month when most plant species are flowering in this region, therefore maximising detectability. Data from this sampling occasion were assumed to be

representative of plant composition in the two bee sampling years, because non-systematic observations indicated that largely the same communities were present in each plot on both years. For plots that had to be replaced in 2015, we used plant data from the corresponding original plot in 2014, because replacement plots were selected to closely match plant composition of the original plot.

At each plot, plant species composition was estimated in three 2-m radius circles placed at a distance of 30 m from each other, in a triangle centred within the plot, with a random rotation (Supplementary Figure S2). Within each circle, we recorded the presence of all vascular plant species, though excluding records that could not be identified with certainty to species level. In subsequent analysis, we only considered plant species potentially providing floral resources to wild bees, thereby discarding species possessing clearly anemophilous flowers like grasses and rushes (families Poaceae, Cyperaceae, Juncaceae), ferns and gymnosperms, and others with similarly reduced flowers with dull colours and absent or reduced corollas (e.g. genera like *Atriplex*, *Pistacia*, *Rumex*). Details are in the Supplementary Table S1.

Diversity metrics

We estimated bee community diversity at the level of each successional stage and each sampling plot, using the Hill diversity framework (Roswell et al., 2021) and the package iNEXT (Hsieh et al., 2016). Specifically, we computed the three forms of Hill diversity most commonly used by ecologists: species richness (Hill number $q = 0$), Hill-Shannon ($q = 1$) and Hill-Simpson ($q = 2$) diversities (Roswell et al., 2021). Increasing the Hill number reduces the leverage given to rare species, that is, rare species have progressively less effect on diversity estimates (Roswell et al., 2021). To estimate bee diversity at the level of successional stages, we pooled all individuals collected in that stage over all sampling plots and occasions, while for diversity estimates at plot level, we pooled across sampling occasions.

Because species richness is highly sensitive to sampling effort, we standardised diversity estimates to equal-coverage, which is preferable to other commonly used methods such as equal-effort sampling, or rarefying datasets to equal sample size (Roswell et al., 2021). Coverage estimates the proportion of individuals in the (whole) community that belong to species present in the sample, recognising that more diverse communities require more sampling in order to be equally well-characterised, and accounting for the underlying species abundance distribution of the community being sampled (Roswell et al., 2021). The procedure involved first estimating variation in sample coverage with increasing number of individuals identified following Chao and Jost (2012), and then fixing the standard coverage value as the minimum coverage obtained when extrapolating each sample to double the number of individuals identified (Chao & Jost, 2012; Roswell et al., 2021). Diversity estimates ($\pm 95\%$ confidence intervals) were then obtained at the standard coverage value, either by extrapolation for samples with coverage lower than the standard value or through rarefaction otherwise (Chao & Jost, 2012). Different standard coverages were used to estimate diversity at stage and plot levels. For

computing the diversity metrics of each trophic group or nesting guild, we did the same procedure, but considering only the species belonging to the given group. Plots with just one species in the given group were removed from analysis, because estimation of diversity metrics in those cases is not robust.

Plant taxonomic richness ($q = 0$) and phylogenetic diversity were also estimated at each plot, to be used as independent variables in models of bee diversity and abundance (see below). Estimates of plant species richness were standardised based on coverage following the procedure described above for wild bees, but using the three circles sampled per plot as replicates rather than the number of individuals collected. Phylogenetic diversity was used as a proxy of functional diversity (Cadotte et al., 2012), and it was estimated by pooling the three samples in each plot and then computing the mean pairwise distance (MPD) separating two species in each plot's community. This metric was used because it is independent of species richness. The distance used for MPD was the cophenetic distance, that is, the sum of the branch lengths between each pair of species in the phylogenetic tree assembled for the whole species pool, based on the GBOTB (GenBank taxa with a backbone provided by Open Tree of Life version 9.1) extended mega-tree included in the 'V.PhyloMaker' R package (Jin & Qian, 2019). The tree was assembled using the function 'phylo.maker' from this package, constructed with scenario 3 (Jin & Qian, 2019). MPD was calculated with the 'mpd' function of the R package 'picante' (Kembel et al., 2010).

Data analysis

Bee diversity metrics estimated per plot and the mean number of individuals recorded per plot across sampling occasions, were related to plant species richness and plant phylogenetic diversity, and to vegetation stage using generalised linear models (GLMs), with Gaussian errors and identity link. Separate analyses were conducted for the total wild bee community and for species categorised according to nesting substrate and trophic specialisation. Vegetation stage was fitted using orthogonal polynomial contrasts up to the fourth order, to assess the presence of linear and non-linear trends in bee diversity and abundance across the successional gradient. For each bee metric, we first analysed the univariate relation with each plant diversity variable. Then, we considered the full model including both the succession stage (the main variable of interest), and the two plant diversity variables. Finally, we built GLM also using orthogonal polynomial contrasts to relate plant species richness and phylogenetic diversity to vegetation stage. This modelling strategy was used to gain a better understanding of the effects of plant diversity and vegetation stage on bees, given that plant diversity is also expected to be highly related to vegetation stage (Porto et al., 2011; Santana et al., 2011).

Patterns of variation in species composition of the wild bee communities were examined using non-metric multi-dimensional scaling (NMDS), based on Bray-Curtis dissimilarities (Legendre & Legendre, 1998). We

TABLE 1 Wild bee diversity estimates in each of five successional vegetation stages sampled in north-eastern Portugal in 2014–2015

Successional vegetation stage	Individuals recorded	Species recorded	Sampling coverage (%)	Standardised diversity estimates		
				Species richness	Hill-Shannon	Hill-Simpson
Grasslands	1141	100	96.7	58.6 (55.0, 62.2)	17.7 (16.3, 19.1)	7.5 (6.7, 8.3)
Short shrublands	737	70	97.6	46.5 (43.1, 50.0)	14.9 (13.2, 16.6)	7.6 (6.8, 8.3)
Tall shrublands	366	58	94.3	48.7 (44.2, 53.1)	19.4 (16.5, 22.2)	9.7 (8.1, 11.3)
Juniper shrublands	208	49	86.6	71.7 (58.6, 84.8)	23.7 (18.4, 29.0)	12.4 (9.8, 14.9)
Oak woodlands	207	69	83.6	93.4 (76.4, 110.3)	50.3 (41.5, 59.1)	29.3 (22.1, 36.5)

Note: For each stage, we indicate the total number of individuals and species recorded, the sampling coverage, and species richness, Hill-Shannon and Hill-Simpson diversity estimates ($\pm 95\%$ confidence intervals) at a standard coverage of 91.3% (details in diversity metrics section).

tested whether there were differences in dispersion around the centroids of stages using PERMDISP, and then tested for differences in the location of stage centroids using PERMANOVA, both with 999 permutations (Anderson & Walsh, 2013). To evaluate whether there was a turnover of species associated with the successional gradient, we related dissimilarity in community composition between plots to the corresponding dissimilarities between vegetation stages using Mantel correlations between matrices (Legendre & Legendre, 1998). Successional dissimilarity was calculated as the absolute value of the difference between plots of the ordinal variable coding the vegetation stage.

To estimate the association of individual bee species with particular vegetation stages we used the indicator value (IndVal) method of Dufrêne and Legendre (1997), which combines the specificity and fidelity of a species, and tests for the statistical significance of the associations ($\alpha = 0.05$). Species with IndVal > 0.25 were classified as indicator species because they were present in at least 50% of plots of only one stage, and its relative abundance in that stage reached at least 50% (Dufrêne & Legendre, 1997).

Analyses were performed using the packages *ecodist* for Bray-Curtis dissimilarity and NMDS (Goslee & Urban, 2007), *vegan* for PERMDISP and PERMANOVA (Oksanen et al., 2016), and *labdsv* for species indicator values (Roberts, 2019) in R 4.0.4 (R Development Core Team, 2021).

RESULTS

We captured 2721 wild bees, representing 154 species plus three morphospecies (Table 1, Supplementary Table S2). Most species (64%) were rare (≤ 5 individuals), with singletons comprising 28% of species. The three most abundant species accounted for 51% of the wild bees recorded: *Lasioglossum malachurum* (Kirby, 1802) (21% of individuals), *Halictus gemmeus* Dours, 1872 (21%) and *Panurgus calcaratus* (Scopoli, 1763) (9%). More bees were captured in pan traps (69%) than in hand-net surveys (31%), and more bees were captured in yellow (46%) than in white (16%) or blue (7%) pan traps. The

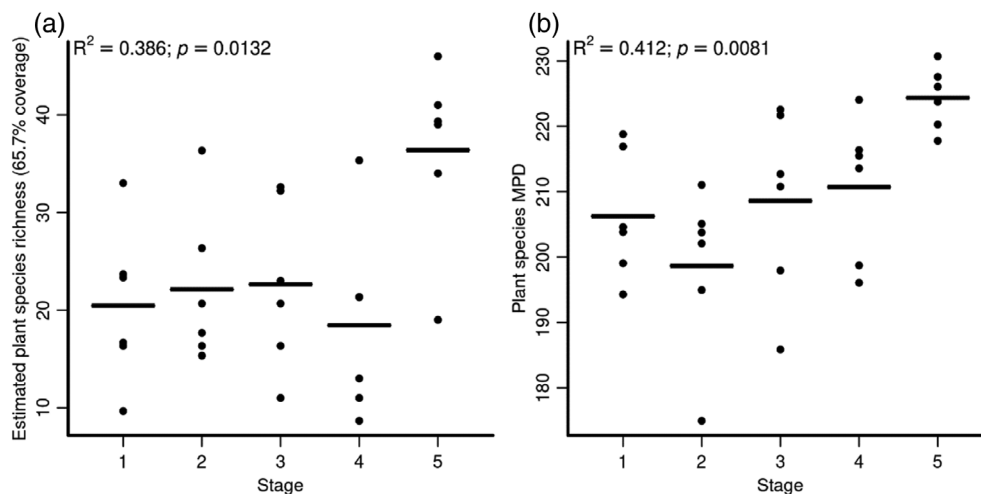


FIGURE 1 Variation in species richness standardised for sampling coverage (a) and phylogenetic diversity, measured as the mean pairwise distance, (MPD; b) of flowering plant species (Table S1) in relation to vegetation succession stages (1-grasslands to 5-oak woodlands) after land abandonment, estimated in 30 plots surveyed in NE Portugal in June 2014. In each panel, dots are values estimated for each plot, and lines are mean values predicted by a generalised linear model (GLM) relating plant richness and phylogenetic diversity to vegetation stage, coded as an ordered factor with polynomial contrasts. The coefficient of determination (R^2) and the significance of the full model are also provided. Details of GLM models are provided in Table S3

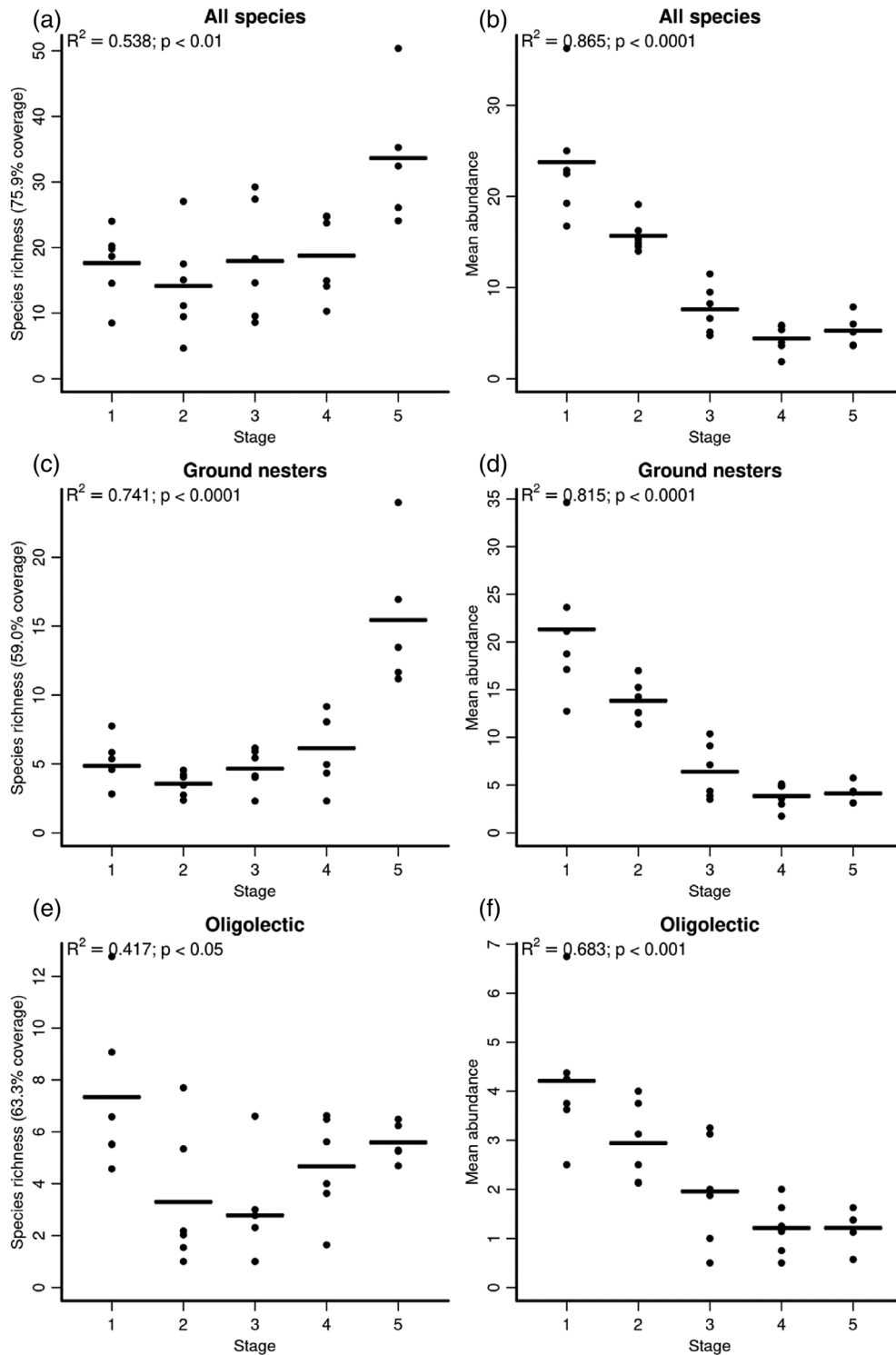


FIGURE 2 Variation in standardised species richness of wild bees per plot (a,c,e) and mean number (abundance) of wild bees recorded per plot per visit (b,d,f) in relation to vegetation succession stages (1-grasslands to 5-oak woodlands) after land abandonment, estimated at 30 plots surveyed in NE Portugal in spring and summer 2014 and 2015. In each panel, dots are values estimated for each plot, and lines are mean values predicted by a generalised linear model (GLM) relating bee richness/abundance to vegetation stage coded as an ordered factor with polynomial contrasts, at average values of plant species richness and phylogenetic diversity per stage. Separate GLMs were built for the overall community (a,b), ground nesters (c,d) and oligolectes (e,f). The coefficient of determination (R^2) and the significance of the full model are also provided. Details of GLMs are provided in Table S4

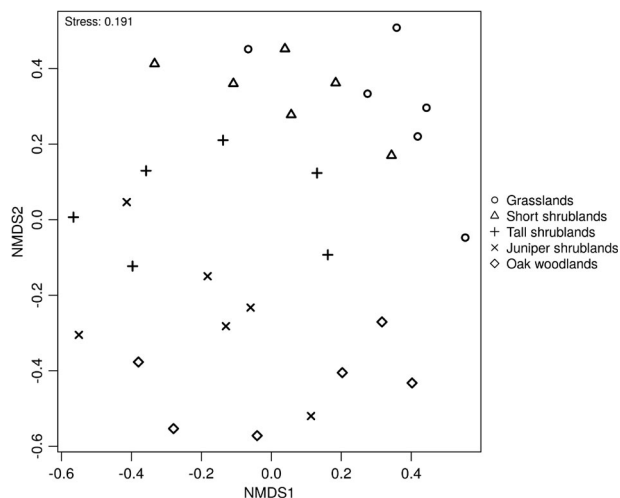


FIGURE 3 Plot of a non-metric multidimensional scaling (NMDS) ordination on a dissimilarity matrix (Bray–Curtis distance) of wild bee communities at 30 plots sampled across a gradient of successional vegetation stages in north-eastern Portugal in 2014–2015. Each point is a sampling plot, with the symbol corresponding to its vegetation stage

number of species recorded per month peaked in May and June, and the numbers of bees captured per survey were highest in June and July (Supplementary Figure S2). There was only one Vulnerable

(*Systropha planidens* Giraud, 1861) and one Near Threatened (*Dufourea halictula* [Nylander, 1852]) species, while 25% of species were data deficient (Supplementary Table S2).

The total number of bee species recorded per successional stage was highest in grasslands and then in short shrublands, where estimated sampling coverage was also the highest (Table 1, Supplementary Figure S3). After standardisation at a fixed coverage, the estimated bee species richness was highest in oak woodlands and then in juniper shrublands, which were the habitats with the lowest sampling coverage. The lowest standardised bee species richness was found in short and tall shrublands, with non-overlapping confidence intervals in relation to estimates in grasslands, juniper shrublands, and oak woodlands (Table 1). Patterns for Hill–Shannon diversity were largely similar to those of species richness, while Hill–Simpson diversity increased monotonically along the entire succession (Table 1).

The model relating plant species richness to vegetation stage showed significant linear and quadratic terms (Supplementary Table S3), revealing little variation in richness from grasslands to juniper shrublands, but then increasing markedly in oak woodlands (Figure 1). The model for phylogenetic diversity (MPD) also showed significant linear and quadratic terms (Supplementary Table S3), revealing a small decline in MPD from grasslands to a minimum in

TABLE 2 Summary results of the indicator value analysis testing the association of each wild bee species with each successional vegetation stage in north-eastern Portugal in 2014–2015

Species	Conservation	Stage	IndVal	P	Plots
<i>Halictus fulvipes</i>	LC	Grasslands	0.68	0.001	15
<i>Eucera cineraria</i>	LC	Grasslands	0.67	0.002	4
<i>Hoplitis acuticornis</i>	LC	Grasslands	0.67	0.004	4
<i>Lasioglossum malachurum</i>	LC	Grasslands	0.56	0.001	33
<i>Eucera clypeata</i>	LC	Grasslands	0.50	0.005	3
<i>Hoplitis annulata</i>	LC	Grasslands	0.50	0.004	3
<i>Hoplitis mucida</i>	LC	Grasslands	0.50	0.006	3
<i>Osmia melanogaster</i>	LC	Grasslands	0.50	0.013	3
<i>Systropha planidens</i>	VU	Grasslands	0.50	0.006	3
<i>Hoplitis adunca</i>	LC	Grasslands	0.46	0.013	4
<i>Lasioglossum pauperatum</i>	LC	Grasslands	0.44	0.013	21
<i>Panurgus canescens</i>	LC	Grasslands	0.44	0.025	16
<i>Halictus gemmeus</i>	LC	Grasslands	0.43	0.021	32
<i>Eucera elongatula</i>	DD	Grasslands	0.39	0.018	5
<i>Lasioglossum interruptum</i>	LC	Grasslands	0.39	0.021	5
<i>Lasioglossum villosulum</i>	LC	Grasslands	0.37	0.035	10
<i>Lasioglossum leucozonium</i>	LC	Grasslands	0.36	0.049	5
<i>Xylocopa cantabrita</i>	LC	Short Shrublands	0.42	0.022	8
<i>Andrena senecionis</i>	LC	Oak woodlands	0.51	0.004	5
<i>Lasioglossum punctatissimum</i>	LC	Oak woodlands	0.43	0.024	7
<i>Protosmia asensioi</i>	DD	Oak woodlands	0.43	0.016	3

Note: For each species, we provide the IUCN conservation status, the vegetation stage with which it was associated, the indicator value estimated (IndVal), its significance level (p), and the number of plots where the species occurred.

short shrublands, followed by a steady increase thereafter, up to a maximum in oak woodlands (Figure 1).

In univariate models, the total and polyleges richness were positively related to plant species richness and phylogenetic diversity (Supplementary Table S4, Figure S4, S5). The richness of ground nesting bees was also significantly and positively related to plant phylogenetic diversity, and marginally related ($p < 0.10$) to plant species richness. There were no significant relations between plant species richness and bee abundance, but in all cases except cavity nesters, there was a significant decline in bee abundance with increasing plant phylogenetic diversity (Supplementary Table S4, Figure S4, S5). In the full model containing vegetation stage and plant diversity variables, the latter showed only a marginally significant positive relation ($p < 0.10$) between total bee species richness and plant species richness (Supplementary Table S3). In contrast, the linear and/or quadratic terms of stage in the orthogonal polynomial models were always significant, except for the richness of cavity nesting species (Figure 2, Supplementary Table S3, Figure S6). Only the linear term was significant for total and polyleges richness, revealing a linear increase along the succession. The quadratic component was also significant for ground nesters, revealing little variation in early vegetation stages followed by a marked increase in oak woodlands, and for oligoleges, revealing a marked decline in richness from grasslands to shrublands, followed by an increase in juniper shrublands and, in particular, oak woodlands. In terms of abundance, only the linear term was significant for oligoleges and cavity nesters, revealing a marked decline along the vegetation succession. For the other groups, the quadratic contrast was also significant, showing a steep decline from grasslands to tall shrublands, but little change thereafter. Analysis based on Hill-Shannon and Hill-Simpson diversities showed results largely similar to those obtained using species richness (Tables S3, S4, Supplementary Figures S7–S9).

The distribution of plots on the plane extracted through NMDS showed a marked gradient in species composition associated with the vegetation succession gradient (Figure 3). The PERMDISP test indicates that there was no significant difference in dispersion among groups ($F_{4,25} = 1.7855$, $p = 0.1633$), while PERMANOVA revealed significant differences in the location of groups ($F_{1,28} = 9.2066$, $p = 0.001$). The Mantel test also indicated a major turnover of species composition along this gradient, with a significant positive correlation between the matrices of community dissimilarity and successional dissimilarity among plots ($r = 0.641$, $p < 0.001$). The indicator value analysis revealed that 17 out of 21 indicator species were associated with grasslands, including the single threatened species (Table 2). The other indicator species were associated with either short shrublands or oak woodlands.

DISCUSSION

Our results support the hypothesis that land abandonment strongly influences wild bee communities, with a marked turnover in community composition along the vegetation successional gradient, and peaks in wild bee abundance in grasslands followed by marked declines in shrublands and later successional stages. In addition, we

found that total standardised species richness at stage level declined from grasslands to shrublands, but in contrast to expectations, it increased again in juniper shrublands, and peaked at much higher values in oak woodlands. A similar pattern, albeit weaker for early stages, was found for Hill-Shannon diversity, while Hill-Simpson diversity increased throughout the successional gradient. Also in contrast to expectations, bee diversity at plot level increased along the successional gradient and peaked in oak woodlands, mainly due to the accumulation of rare species in later stages. Notwithstanding, grasslands had the highest concentration of species associated with a single habitat, and together with oak woodlands had the largest number of oligoleges. Taken together, these results have important implications for wild bee conservation under land abandonment, supporting the need to maintain a heterogeneous mosaic of vegetation at different successional stages, where both grasslands and oak woodlands need to be represented, to sustain diverse communities at the landscape scale.

The observed peak abundance of wild bees in grasslands followed by marked declines in more mature vegetation stages has been reported elsewhere (Grundel et al., 2010; Potts et al., 2003; Steffan-Dewenter & Tschamtkke, 2001; Taki et al., 2013), including in the Euro-Mediterranean region (Potts et al., 2003). In our system, this pattern was observed when considering both the entire wild bee community, and each functional group categorised according to either feeding specialisation or nesting substrate. Curiously, there were negative relations between bee abundance and plant phylogenetic diversity, but this was probably spurious because the relation became non-significant when considering the effects of vegetation stage. Our results are probably a consequence of high cover by flowering herbaceous annuals in grasslands (e.g. Hoelzer, 2003; Porto et al., 2011), and thus to the high availability of nectar and pollen forage (Potts et al., 2003; Steffan-Dewenter & Tschamtkke, 2001). When succession progresses, cover by annual flowering herbs declines and vegetation turns into dense shrublands that are often monospecific or at least largely dominated by a single shrub species such as *Cistus* spp. or *Cytisus* spp. (Hoelzer, 2003; Mendes et al., 2015; Rivest et al., 2011), with reductions in food resources probably causing the observed marked declines in wild bee abundance (Potts et al., 2003; Stout, 2000). Cover by flowering herbs remains relatively low in juniper shrublands and oak woodlands (Porto et al., 2011; Miguel Porto, unpublished), which likely justifies the continued low wild bee abundance later in the succession (Potts et al., 2003, 2006). It cannot be ruled out from our data, however, that the observed patterns were influenced to some extent by the distribution of honey bees, as previous studies have shown that they may deplete floral resources and contribute to wild bee declines in the Mediterranean region where beekeeping is widespread (Herrera, 2020; Torné-Noguera et al., 2016). This possibility should be further investigated, though non-systematic observation suggested that honey bees occurred consistently across successional stages, and so were unlikely to have particularly high negative impacts on wild bees at any particular stage.

The decline in standardised bee species richness from grasslands to shrublands in analysis at stage level was in line with expectations,



as previous studies have shown that many bee species favour open habitats characterised by little shade, abundant food resources provided by fast-growing annual herbs, and patches of bare soil that are required by ground-nesting species (Grundel et al., 2010; Polatto et al., 2014; Potts et al., 2003; Tylianakis et al., 2006). In the Mediterranean region, this pattern has also been observed in other insect groups such as butterflies and orthopterans that are mainly associated with open habitats and early-successional stages (Vasconcelos et al., 2019; Verdasca et al., 2012). The decline in wild bee richness was probably also affected by a higher number of rare species in grasslands than in shrublands, because the pattern was attenuated and disappeared when considering Hill-Shannon and Hill-Simpson diversities, respectively, which give progressively less leverage to rare species (Roswell et al., 2021). It should be noted that analysis at plot level did not show the initial decline in wild bee richness detected in analysis at stage level. This is probably because analysis at stage level integrates information on diversity within plots (alpha diversity) and differentiation in composition between plots of the same stage (beta diversity), though this should be confirmed in future studies with larger sample sizes (e.g. Santana et al., 2017). Irrespective of the scale and diversity metric used, however, bee diversity increased again later in the succession, up to the much higher values in oak woodlands, which contrasts with other studies showing peak diversity in early successional stages. The differences between ours and previous research may be because few studies corrected diversity estimates for sample coverage, thereby producing underestimates where coverage was lower (Roswell et al., 2021). In fact, we actually observed far more species in grasslands than in any other stage, but this was an artefact due to the presence in grasslands of many abundant species, which were easier to tally than in late successional vegetation stages characterised by a large number of rare species. Overall, therefore, it is possible that the pattern revealed in our study may be widespread, following the increase in diversity with successional age expected from ecological theory (e.g. Brown & Southwood, 1987).

The peak in rare wild bee species in more mature vegetation stages has been reported elsewhere in the Mediterranean region (Potts et al., 2006), and it may be a consequence of higher structural vegetation heterogeneity and long-term habitat stability (e.g. Santana et al., 2011), which possibly favours the progressive colonisation by species with contrasting ecological requirements. Also, this was probably influenced by the positive relation between bee species diversity and both plant species richness and phylogenetic diversity, which peaked in late successional stages. The positive effect of plant species richness is likely related to more plant species providing a wider range of niches for wild bees, while the effect of plant phylogenetic diversity is probably mediated by functional diversity, with a wider range of floral traits providing more foraging opportunities for more bee species (Potts et al., 2003; Steffan-Dewenter & Tschamtkke, 2001; Tylianakis et al., 2006). It should be noted, however, that while plant species richness and phylogenetic diversity positively affected the total community, ground nesters, and polyleges, they had no significant effects on cavity nesters and oligoleges. Cavity nesters were also not related to vegetation stage, which may be a consequence of imprecise

estimates of diversity due to the relatively small number of individuals detected per plot, or to the operation of other factors not measured in our study. Oligoleges peaked in grasslands, which may be because many species specialising on annual herbs could only be present early in the succession, and peaked also in woodlands, possibly because high plant species richness and phylogenetic diversity promoted species packing and smaller niche breadth (Grundel et al., 2010; Potts et al., 2006; Steffan-Dewenter & Tschamtkke, 2001).

During the succession, there was also a marked turnover in bee species, with community composition in early-successional herbaceous habitats differing from late-successional stages. This was likely a consequence of habitat affinities of different bee species, with each species represented in a given section of the successional gradient due to their particular requirements in terms of, for instance, food plant species, nesting site availability, microclimate and other factors (Grundel et al., 2010; Odanaka & Rehan, 2020; Rubene et al., 2015). For instance, in the Mediterranean post-fire succession, there are changes in floral reward reflecting the general shift from annuals (generally low-reward open access flowers) to perennials (mostly high-reward and restricted access flowers), which in turn affect the composition of wild bee communities (Potts et al., 2003). Given this marked turnover and the increase in diversity along the succession, it might seem surprising that about 80% of the bee species associated with just a single habitat type were found in grasslands, whereas only 15% were in oak woodlands, 5% were in short shrublands, and none were in the other stages. This may be partly an artefact of species rarity in late successional stages, as a much larger sampling effort would probably be needed to correctly assess the indicator value of species that occur in few plots and at low numbers (Dufrêne & Legendre, 1997). Nevertheless, the observed uniqueness of grasslands may also be real, reflecting for instance the presence of species specialising on annual herbs (Steffan-Dewenter & Tschamtkke, 2001), which tend to decline rapidly during the succession (Porto et al., 2011). It should be noted that the indicator values observed were never very high (<0.70), which means that even indicator bee species may occur in more than one stage and/or in only some plots of the stage with which they are primarily associated (McGeoch et al., 2002).

Our results have important implications for wild bee conservation under land abandonment in the Euro-Mediterranean region, by showing that the conservation of wild bee diversity is critically dependent on keeping a landscape mosaic of patches representing different succession stages, as observed for other species groups (e.g. Porto et al., 2011; Santana et al., 2011, 2012; Vasconcelos et al., 2019; Verdasca et al., 2012). This is a consequence of the marked species turnover observed along the succession gradient, with many unique species occurring in early-successional stages and rare species accumulating through the succession up to a peak in oak woodlands, implying that not even the richest vegetation stage can capture the entire bee diversity represented across the successional gradient. The preservation of grassland patches may be particularly difficult in these landscapes, because of shrub encroachment soon after land abandonment (Mendes et al., 2015; Rivest et al., 2011; Santana et al., 2011). This may be prevented in some areas through some kind of agri-



environment subsidies and other schemes supporting extensive agricultural and pastoral land uses (Moreira & Russo, 2007; Stoate et al., 2009). Many other areas, however, are sparsely occupied by an ageing population, and the rural depopulation trend is unlikely to be reverted in the foreseeable future, thereby requiring other management solutions. These can include active management involving for instance prescribed burning or mechanical vegetation removal (Verdasca et al., 2012), but also a more hands-off approach advocated by rewilding strategies (Perino et al., 2019). Such strategies assume that early-successional habitats may be maintained through grazing by large wild herbivores or their feral surrogates (Garrido et al., 2019; Navarro et al., 2015; Perino et al., 2019), though their ability to control shrub encroachment in Mediterranean landscapes has been questioned (Calleja et al., 2019), and, in some circumstances, they may have direct negative impacts on wild bees (Griffin et al., 2021). Maintaining late-successional stages also involves some challenges, because the progression of the succession into oak woodlands may be arrested by a number of factors (Acácio et al., 2007; Mclachlan et al., 2005; Santana et al., 2010; Peña-Angulo et al., 2019), including large and recurrent wildfires due to fuel accumulation (Porto et al., 2013). Overcoming these challenges may involve public or private support to actively restore forests, though a more hands-off approach may be possible in more productive environments (Rey Benayas & Bullock, 2012). Efforts to recover Mediterranean forests will likely benefit from the ambitious ecological restoration targets set by the European Union Biodiversity Strategy for 2030 (EC, 2020), involving for instance a roadmap for planting at least 3 billion additional trees in the EU, though care should be taken for not replacing the early-successional herbaceous habitats that are also critical for biodiversity conservation. Overall, we suggest that the conservation of very diverse groups such as wild bees under land abandonment may require due consideration of a portfolio of alternative approaches, including both active management and rewilding, which need to be carefully tailored to the actual socio-ecological conditions of each particular region (Perino et al., 2019; Plieninger et al., 2014; Rey Benayas & Bullock, 2012, 2015).

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR'S CONTRIBUTIONS

Andreia Penado, Hugo Rebelo, and Pedro Beja designed the study, Andreia Penado and Miguel Porto collected the bee and plant data,

respectively, Andreia Penado and Miguel Porto analysed the data, Andreia Penado and Pedro Beja wrote the manuscript. All authors contributed to manuscript writing, editing, and approved the manuscript.

DATA AVAILABILITY STATEMENT

Data is available from the authors upon request. Species occurrence data will be published in gbif.org.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Appendix S1: Supporting Information

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