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Restoration of riverine inland sand dune complexes: implications for the conservation of wild bees

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Summary

1. The evaluation of restoration measures is an important task of conservation biology. Inland sand dunes and dry, oligotrophic grasslands have become rare habitat types in large parts of Central Europe and their restoration and management is of major importance for the preservation of many endangered plant and insect species. Within such habitats, it is important to restore key ecosystem services, such as pollination networks. As wild bees are the most important pollinators in many ecosystems, they represent a suitable key group to evaluate restoration measures. Furthermore, the recent decline of many bee species and the potential ecological and economic consequences are currently topics of strong scientific interest.

2. We studied the succession of bee communities in response to restoration measures of sand dunes and sand grasslands and compared these communities with those of old sand dune complexes.

3. Our results show that wild bees respond rapidly to restoration measures indicated by a high species richness and abundance. The community structure of bees at restoration sites converged only slightly to those of the target sites. A higher similarity was found between bee communities at the restoration sites (sand dunes and grasslands), indicating that their close proximity was an important determinant of species overlap. Environmental factors such as the number of entomophilous plant species and moisture had a strong influence on wild bee species composition.

4. *Synthesis and applications*. The restoration of inland sand dune complexes provides opportunities for colonization by a diverse wild bee community. Although it is difficult to establish a given target community, restoration measures gave rise to a high pollinator diversity and abundance, suggesting that community function can be re-established.

Key-words: colonization, community structure, grassland management, pollination, succession

Introduction

Habitat destruction, alteration, degradation and fragmentation are key threats to biodiversity throughout the world (Primack 2002). Changes in land use and particularly the intensification of agricultural practices, are considered to be the main reason for the decline of many plant and animal species (Carvell 2002). In Central Europe, inland sand dunes and dry oligotrophic grasslands were widespread on Pleistocene and alluvial soils until the end of the 19th century (Muller *et al.* 1998; Hochkirch, Gärtner & Brandt 2008). These habitats have been extensively grazed by sheep and cattle for centuries and supported a highly specialized flora and invertebrate fauna, many species of which are nowadays threatened (Hochkirch *et al.* 2007). Meanwhile, oligotrophic grasslands and inland sand dunes have become rare in large parts of Central and Northern Europe (Muller *et al.* 1998). Furthermore, a loss of natural dynamics because of regulation and canalization of rivers has threatened pioneer species adapted to floodplain habitats (Gröning, Krause & Hochkirch 2007; Exeler, Kratochwil & Hochkirch 2008). The restoration and appropriate management of such habitats is, therefore, important for the conservation of many endangered species.

The restoration of habitats generally aims to recreate ecosystem structure and recover ecosystem function (Primack 2002). Pollinators are suitable for analysing the effects of restoration measures on both of these aspects, as they represent a species-rich and behaviourally diverse group which provides key services in ecosystems. A high pollinator diversity

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*Correspondence author. E-mail: nina.exeler@gmx.de supports a species-rich plant community (Fontaine *et al.* 2006) and a decline in the number of pollinators may cause increased competition among plants and a reduction in the reproductive success of many plant species (Vamosi *et al.* 2006). Wild bees (Apoidea) are known to be the most important pollinators in many ecosystems (Winfree *et al.* 2008). The recent decline of many bee species and the potential ecological and economic consequences is, therefore, a topic of major interest (Biesmeijer *et al.* 2006; Butler, Vickery & Norris 2007).

A typical wild bee community contains generalized and specialized species (Williams, Minckley & Silveira 2001). While generalized bee species may pollinate a high number of different plant species, specialized bee species utilize pollen of only few plant species as larval food and/or nest only in habitats with special substrate or exposition. The strong specialization of many wild bee species on specific pollen sources and nesting sites makes them particularly vulnerable to local extinction. A third group consists of parasitic bee species that lay their eggs in the nest of a specific host instead of provisioning their own nests. Wild bee communities are usually composed of species covering a great range of different body sizes, which are assumed to be correlated with their flight radius (Araújo *et al.* 2004). Most species are thought to have a small foraging flight radius (Gathmann & Tscharntke 2002). Even bumblebees (*Bombus* Latr.) prefer to forage within 200-m distance around their nests (Osborne *et al.* 1999).

A diverse wild bee community requires a variety of nesting sites and foraging areas and is an indication of species-rich vegetation and heterogeneous habitat structure. Although there is strong evidence for a decline of wild bees (Biesmeijer *et al.* 2006), only few attempts have been made to initiate restoration activities for pollinators to date (Carvell *et al.* 2007; Forup *et al.* 2008).

Dry, oligotrophic habitats with a high diversity of flowering plant species are among the most important habitat types for the conservation of bees. It has been shown that wild bees benefit from extensive grassland management (Carvell 2002; Kohler *et al.* 2007). Mowing and extensive grazing have been shown to increase plant species richness and thus the availability of pollen and nectar (Carvell 2002). We therefore hypothesize that the restoration of extensively managed inland sand dunes and oligotrophic grasslands will promote a diverse wild bee community. We compared the succession of bee communities in restoration sites with that of similar vegetation communities in an old nature reserve and a nearby sand grassland (target areas). Our aims were (1) to test whether the bee communities increase in species richness and abundance as a result of restoration measures to levels similar to those found in old habitats, and (2) to examine whether the bee communities of restoration and target sites converge after the restoration management. As it has been suggested that the degree of specialization and the body size of bees might influence their dispersal ability (Tscharntke *et al.* 2002), (3) we also examined whether generalized or large-bodied species are the initial colonizers.

Materials and methods

STUDY AREA AND RESTORATION METHOD

The study area was located in the subatlantic zone of north-western Germany (Lower Saxony), which is characterized by temperate humid climatic conditions with mild winters and cool-rainy summers (Fig. S1). Restoration sites were situated at two meander cores of the river Hase close to the town of Haselünne and comprise a total area of 49 hectares. Prior to restoration, these sites were used as maize fields and intensive grasslands, and intensive agriculture and forestry are the predominant land use in the surrounding area. In the immediate vicinity (radius 1000 m), the landscape is characterized by pine plantations (*c.* 50%), intensive farmland (*c.* 25%) and intensive grasslands used mainly for cattle grazing (*c.* 20%). Restoration measures were carried out from 2001 to 2002 to convert these intensively used agricultural areas into species-rich, extensive, oligotrophic grasslands. The two target vegetation types were (1) Diantho-Armerietum (plant communities typically characterized by the presence of *Dianthus deltoides* and *Armeria elongata*) and (2) Corynephoretum sand dune complexes (plant communities composed of typical pioneer species found on oligotrophic sandy soils such as *Corynephorus canescens* and *Carex arenaria*). The restoration measures included the removal of dykes and the creation of new artificial inland sand dune complexes, fluviatile sand layers and permanent or temporarily flooded hollows (Stroh *et al.* 2005). The removal of dykes led to occasional flooding of restoration sites and helped to achieve the open character of a typical alluvial landscape. In addition, restoration sites were managed by extensive cattle grazing. In 2002, parts of the newly created dune complexes were spread with mown and raked hay from a target site to accelerate the colonization of a typical oligotrophic vegetation. The hay was weighed to guarantee an even distribution at all sites.

A nature reserve near the river Ems (24 ha) served as target area for the Corynephoretum sites (C) of the restoration project. This alluvial pasture/woodland vegetation complex has been extensively grazed by cattle for centuries and is characterized by inland sand dunes, heathlands, seasonally flooded wetland and riparian willow shrubs and pasture woodlands. A second target area for the Diantho-Armerietum sites (D) was located next to restoration sites (Fig. S1).

WILD BEE AND VEGETATION SURVEY

In 2002, 10 permanent plots (exclosures) were established on the target and restoration sites to study the succession of the vegetation and the bee communities [Spergulo-Corynephoretum: three target plots (CT) and three restoration plots (CR); Diantho-Armerietum: two target plots (DT) and two restoration plots (DR)]. The number of Diantho-Armerietum plots was lower as the availability of potential target sites was limited. From April to September 2003, 2005 and 2006, two yellow and two white traps (diameter: 16 cm, height: 8·5 cm), filled with ethylene glycol, were installed on each plot 0·4 m above the ground and separated by 5 m. In order to assess the status quo prior to the restoration measures, four pan traps (two yellow and two white traps) were installed at the restoration site in 2001 (two at a former dyke and two at a relict dune fragment). In the first year after the restoration (2002), the census was conducted as described above, but using just two pan traps (one white and one yellow in each plot). Because of the reduced sampling effort, these data were only used in the analysis of similarity (Renkonen analysis). All traps were emptied fortnightly and the bees were identified in the laboratory. In addition, the vegetation in each plot was quantified in a subplot of 25 m^2 once a year in spring (M. Stroh, unpublished data), using the Braun-Blanquet method (Braun-Blanquet 1964). Estimates of vegetation abundance were made according to Barkman, Doing & Segal (1964). In addition, the vegetation structure (vegetation cover, bare ground cover, forb cover, grass cover, the number of plant species and the number of entomophilous plant species) was recorded. The cover of each plant species was used to calculate a weighted moisture indicator value (Ellenberg *et al.* 1992) for each plot.

STATISTICAL ANALYSIS

Species richness (total number of species) and the abundance of each species were calculated for each year and plot. A repeated measures ANOVA was used to detect differences between habitat types (C vs. D), treatments (target and restoration) and years in each of the following response variables: total species richness, total wild bee abundance, number and abundance of generalized, specialized and parasitic bee species, respectively, number of small (<7 mm), medium (7–12 mm) and large species (>12 mm) as well as abundance of single-threatened bee species (according to the Red Data List of Germany) with sufficiently high abundance (average >5 individuals). We determined the degree of specialization based on the number of plant species used as larval food as reported in the literature (Westrich 1989). Species specialized on a single plant family, genus or species were assigned as specialists, while polylectic species were assigned as generalists. Furthermore, we tested for differences in environmental factors, such as the number of plant species and the number of entomophilous plant species, the cover of forbs, grasses and bare ground as well as moisture. These analyses were performed by using R 2.7.0 (R Development Core Team 2007).

To determine the independent effect of each environmental variable on total species richness and abundance, the richness and abundance of specific groups of wild bees (generalists, specialists and parasites) and selected species, we performed a hierarchical partitioning analysis using the 'hier.part' package for R (Walsh & Mac Nally 2003). This method is particularly suited to identifying those variables having the most independent effect on the response variable and thus avoiding multicollinearity among predictor variables (Mac Nally 2002).

We calculated the Renkonen index as a measure of similarity of the wild bee communities using the programme ECOSIM 7.0 (Gotelli & Entsminger 2007). This index gives the percentage similarity of two or more data sets. It is calculated as $P = \Sigma(p_{1i}, p_{2i})$. where p_{1i} is the percentage of species i in community sample 1 and p_{2i} is the percentage of species I in community sample 2. The Renkonen index is particularly useful for the comparison of the community prior to the restoration with the data after the restoration as it is relatively unaffected by sample size and species diversity (Krebs 1999). We used this index for comparing pairs of restoration and target sites per year, the two types of restoration sites per year and for comparing the wild bee communities of restoration sites compared to the situation prior to restoration (2001).

To analyse compositional differences in the wild bee community, we performed multivariate ordination analyses. Because of a long gradient length ($>2{\cdot}9$ SD) in the wild bee community data, estimated in a detrended correspondence analysis, we applied a canonical correspondence analysis (CCA) including the environmental variables mentioned above. CCA is a non-linear, direct ordination method that estimates the structure in the main matrix, which is usually composed of species abundance data in specific sample units, in relation to a second matrix providing environmental explanatory variables of the same sample units. The significance of the correlation with environmental variables was assessed by a Monte-Carlo permutation test (9999 permutations) as implemented in CANOCO version 4.5 (Ter Braak & Smilauer 2002).

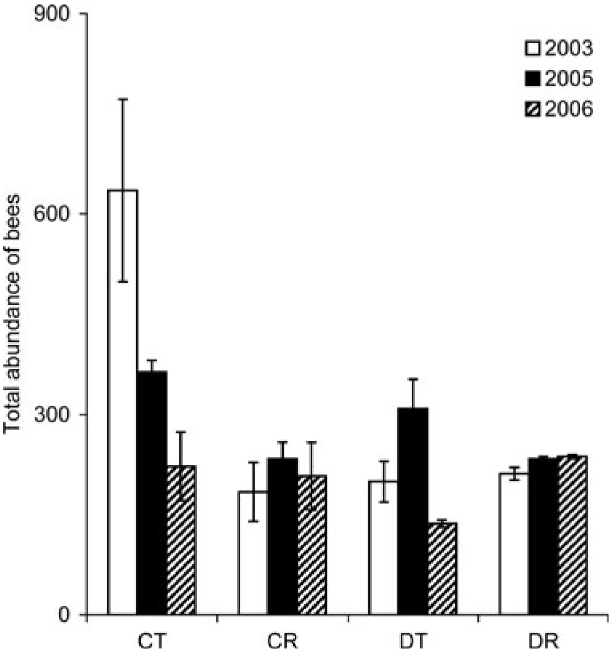

Fig. 1. Variation of total bee abundance between the two vegetation types and restoration treatments (CT, Corynephoretum target; CR, Corynephoretum restoration; DT, Diantho-Armerietum target; DR, Diantho-Armerietum restoration) and years.

Results

Between 2001 and 2006, a total of 8735 individuals belonging to 90 wild bee species were detected at the target and restoration sites. A total of 17·9% of the species were oligolectic with nine species specialized on Asteraceae, four species on willow pollen (*Salix*), one species on *Vaccinium*, one species on *Ranunculus* and one species on Fabaceae. At all sites, the wild bee communities were characterized by a high number of species with a low abundance (67·5% of all species occurred with a relative abundance of $<5\%$).

MAIN EFFECTS OF THE VEGETATION TYPE

We found almost no significant difference in the number and abundance of wild bee species (or subsets of this group) between sand dunes (Corynephoretum) and sand grasslands (Diantho-Armerietum; Fig. 1, Tables 1 and 2). However, the abundance of the Red List species differed between these two habitats: *Lasioglossum sexnotatum* had a higher abundance at the Corynephoretum sites, whereas *Lasioglossum quadrinotatum* was more frequent at the Diantho-Armerietum sites (Table 1, Fig. 2a, b).

EFFECTS OF THE RESTORATION

The differences between restoration and target sites (i.e., the effects of 'treatment') were pronounced. Treatment effects were

Table 1. Results of the repeated-measures ANOVAS showing the effects of vegetation (Corynephoretum or Diantho-Armerietum), treatment (restoration or target) and year (2003, 2005 and 2006) (a) on wild bee species richness and abundance, the number and abundance of specialist, generalist and parasitic species, the number of large (< 13 mm), medium (8–13 mm) and small (> 8 mm) species and the abundance of the Red List species *Lasioglossum sexnotatum* and *L. quadrinotatum*

	Error: site (d.f. = 1, 6)				Error: within (d.f. = 2, 12)		
Wild bee response	Vegetation	Treatment	Vegetation × treatment	Year	Vegetation × year	Treatment × year	Vegetation × treatment × year
Species richness	NS	NS	NS	F = 4·18*	NS	NS	NS
Of specialist sp.	NS	NS	NS	NS	NS	NS	NS
Of generalist sp.	NS	NS	F = 10·07*	NS	NS	NS	NS
Of parasite sp.	NS	F = 13·32*	NS	F = 5·94*	NS	NS	F = 5·10*
Of large sp.	NS	NS	NS	F = 5·41*	NS	NS	F = 7·69**
Of medium sp.	NS	NS	F = 10·99*	NS	NS	NS	NS
Of small sp.	NS	NS	NS	F = 5·78*	NS	NS	NS
Total abundance	NS	F = 9·50*	F = 7·78*	F = 4·58*	NS	F = 6·30*	NS
Of specialist sp.	NS	F = 7·5*	F = 6·9*	NS	NS	F = 4·37*	NS
Of generalist sp.	NS	NS	NS	F = 7·15**	NS	NS	NS
Of parasite sp.	NS	NS	NS	F = 9·44**	NS	NS	NS
Of *Lasioglossum sexnotatum*	F = 7·68*	NS	F = 17·35**	F = 4·33*	NS	F = 9·42**	NS
Of *L. quadrinotatum*	F = 31·69**	F = 187·03***	F = 24·39**	F = 6·33*	NS	F = 5·96*	F = 8·48**

NS, not significant; *$P \leq 0{\cdot}5$; **$P < 0{\cdot}01$; ***$P < 0{\cdot}001$.

Table 2. Results of the repeated measure ANOVAS on the effect of vegetation (Corynephoretum or Diantho-Armerietum), treatment (restoration or target) and year (2003, 2005 and 2006) on environmental variables

	Error: site (d.f. = 1, 6)				Error: within (d.f. = 2, 12)		
Environmental variables	Vegetation	Treatment	Vegetation × treatment	Year	Vegetation × year	Treatment × year	Vegetation × treatment × year
Total number of plant sp.	NS	NS	NS	NS	NS	NS	NS
No. entomophilous plant sp.	NS	NS	NS	NS	NS	NS	NS
Proportion of bare ground	NS	NS	NS	F = 5·81*	F = 3·94*	NS	NS
Forb cover	F = 7·57*	NS	$F_{1,6}$ = 6·70*	F = 6·75*	F = 15·01**	F = 15·05**	F = 8·58*
Grass cover	NS	NS	NS	F = 13·22**	NS	F = 5·93*	NS
Moisture	F = 18·55**	NS	NS	F = 11·00**	NS	NS	NS

NS, not significant; *$P \leq 0{\cdot}5$; **$P < 0{\cdot}01$; ***$P < 0{\cdot}001$.

found for the total abundance of bees and for the abundance of specialized bee species, both of which were greater at the target sites (Table 1, Fig. 1). The opposite was true for the number of parasitic species and the Red List species *L. quadrinotatum*, which occurred more frequently at restoration sites (Table 1, Fig. 2a). Furthermore, we found significant interactions between the vegetation type and the treatment, indicating that the different habitats responded differently to the restoration measures. At the Corynephoretum sites, the total bee abundance and the abundance of specialists was higher at the target sites (averages: $\mathrm{CT}_{\mathrm{total}} = 407{\cdot}0$; $\mathrm{CR}_{\mathrm{total}} = 208{\cdot}3$; $\mathrm{CT}_{\mathrm{specialists}} = 240{\cdot}3$; $\mathrm{CR}_{\mathrm{specialists}} = 51{\cdot}4$), whereas at the Diantho-Armerietum sites the total bee abundance was similar on both restoration and target sites (DT = 215·0; DR = 227·3; Fig. 1), while the abundance of specialists was significantly higher at restoration sites (DT = 44·0; DR = 62·7). The number of generalist species was higher at the Corynephoretum restoration (CR) sites than at target sites (CT = 17·4; CR = 19·7), whereas the opposite was true for the Diantho-Armerietum sites (DT = 18·7; DR = 17·0). In addition, a significantly higher number of medium-sized bee species was found at the Corynephoretum target (CT) sites than at the corresponding restoration sites (CT = 14·3; CR = 11·9), while the reverse was found at the Diantho-Armerietum sites (DT = 9·8; DR = 13·1). No effects were found for small- and large-sized species.

SUCCESSIONAL PATTERNS

Significant variation in the response variables was found among years, with a general increase in the number and abundance of wild bee species in 2005 followed by a decline in 2006. Only rarely did we find significant interactions between treatment and year, e.g. for the total and the specialists abundance, which declined gradually at the target sites. The abundance of Red List species also differed between the years. An increase

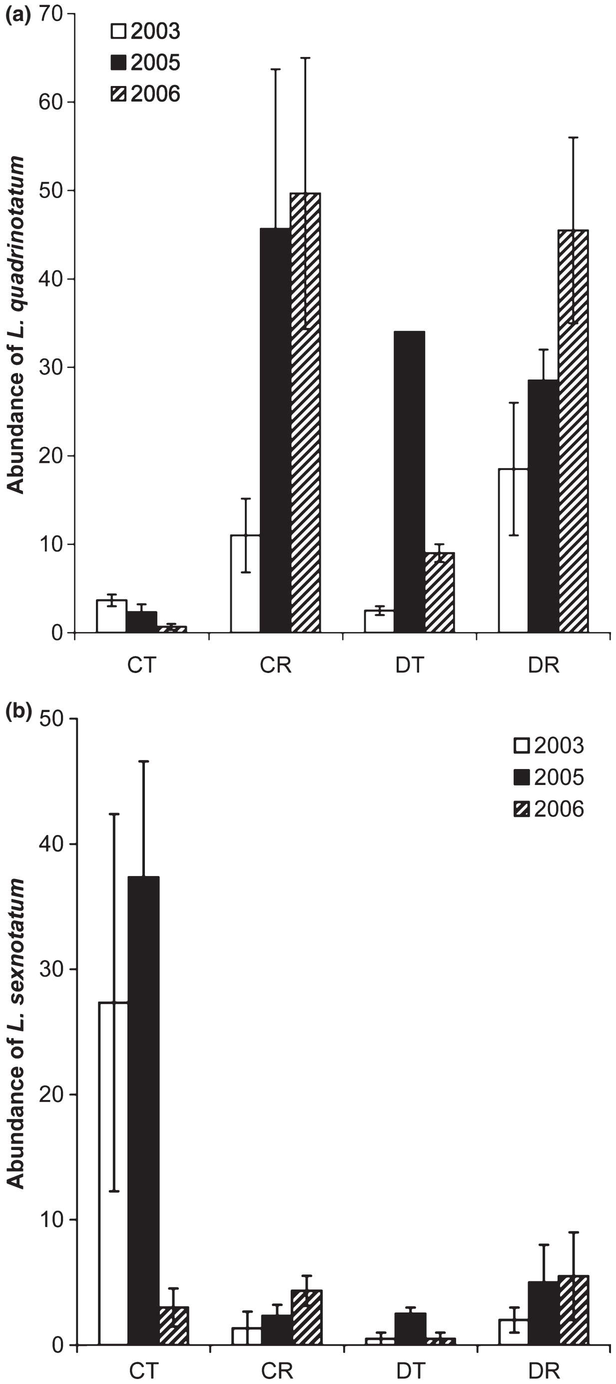

Fig. 2. (a) Variation in the abundance of *Lasioglossum quadrinotatum* between the two vegetation types and restoration treatments (CT, Corynephoretum target; CR, Corynephoretum restoration; DT, Diantho-Armerietum target; DR, Diantho-Armerietum restoration) and years. (b) Variation in the abundance of *Lasioglossum sexnotatum* between the two vegetation types and restoration treatments (CT, Corynephoretum target; CR, Corynephoretum restoration; DT, Diantho-Armerietum target; DR, Diantho-Armerietum restoration) and years.

was recorded for *L. quadrinotatum* at restoration sites and a decline of *L. sexnotatum* in the target areas (Table 1). A *post-hoc* test revealed that the increase of *L. quadrinotatum* was significant at restoration sites (pairwise *t*-tests with Bonferroni correction, $P = 0·04$), but not at target sites. The abundance changes at DR correlated strongly with the pattern at DT ($r^2 = 0·50$) and with the pattern at CR ($r^2 = 0·91$), while the abundance changes at CR showed no significant correlation with the pattern found at CT ($r^2 = 0·016$) but with DT ($r^2 = 0·54$). Species numbers at DR increased from 32 species in 2003 to 47 species in 2005 (and 46 in 2006). At CR the number of species remained constant between years (44 species in 2003 and 2005, 45 species in 2006).

EFFECTS ON THE ENVIRONMENTAL PARAMETERS

For the environmental variables, the repeated measures ANOVAS revealed a significant decline in bare ground cover over the years, which was mainly true for Corynephoretum sites (averages: 2003 = 25·7%; 2005 = 2·8%; 2006 = 2·0%; Table 2). The cover of forbs and grasses also changed over time. While forb cover declined at restoration sites (2003 = 21·8%; 2005 = 8·6%; 2006 = 11·2%), grass cover increased (2003 = 39·2%; 2005 = 68·6%; 2006 = 64·0%). Moreover, there was a significant difference in the moisture indicator values among the vegetation types, with Diantho-Armerietum sites being moister at both restoration and target sites (averages: D = 5·03; C = 3·54). In addition, the moisture index increased significantly over time at all sites (2003 = 3·99; 2005 = 4·12; 2006 = 4·30). The hierarchical partitioning analyses revealed that moisture was the most important factor explaining bee species richness (with dry sites promoting more species, independent effect 26·03%) and bee abundance (also promoted by dry conditions, independent effect 37·27%) followed by the cover of bare ground (being most relevant for the presence of specialized species, independent effect 38·12%). The number of entomophilous plants and forb cover had also a high explanatory power for some variables (Table 3).

SIMILARITIES IN WILD BEE ASSEMBLAGES

The Renkonen index of similarity in wild bee assemblage revealed a high similarity between restoration sites as well as between the Diantho-Armerietum target sites and the respective restoration sites. In contrast, the similarities between CT and restoration and between Corynephoretum or Diantho-Armerietum target sites were low. The similarity index between restoration sites and the situation prior to restoration increased until 2003 followed by a continuous decline (Fig. 3) suggesting an ongoing change in wild bee community composition after the restoration measures.

Multivariate analyses of the wild bee communities using CCA showed a clear grouping of the wild bee assemblages sampled at the CT sites. A greater variability was found for the bee communities from restoration sites and from the Diantho-Armerietum sites. However, for both habitat types a slight convergence of restoration sites with the respective target sites was found (Fig. 4). The inclusion of environmental variables in the model explained 47% of the variance in the species data with moisture being the most important factor (Monte Carlo Permutation test, $F = 3·81$, $P < 0·001$). At the Diantho-

Table 3. Hierarchical partitioning analysis

	Moisture		Bare ground		Entomophil. plant species		Forb cover		No. plant species		Grass cover	
Response/predictor	Effect	Sign	Effect	Sign	Effect	Sign	Effect	Sign	Effect	Sign	Effect	Sign
Species richness	**26·03**	–	13·15	–	7·8	–	**44·27**	–	3·22	–	5·51	+
Of specialist sp.	**34·55**	–	**38·12**	–	13·7	+	3·67	–	6·62	+	3·33	+
Of generalist sp.	**39·34**	–	**22·51**	–	8·87	–	2·94	–	6·15	+	20·19	+
Of parasite sp.	**42·11**	+	1·76	+	10·32	–	**28·18**	–	10·03	–	7·61	+
Of large sp.	**54·66**	–	**16·26**	–	8·33	–	2·86	–	13·6	–	7·29	–
Of medium sp.	**16·38**	–	3·35	+	7·53	–	**62·67**	–	2·25	–	7·82	+
Of small sp.	**14·68**	–	**34·33**	–	6·85	–	17·48	–	2·36	+	14·3	+
Total abundance	**37·27**	–	9·71	–	**31·94**	–	4·33	–	10·87	+	5·88	–
Of specialist sp.	**24·83**	–	–0·27	+	**53·23**	–	6·22	–	15·94	+	0·05	+
Of generalist sp.	8·73	+	**34·61**	–	**24·75**	–	3·63	–	6·08	+	22·2	+
Of parasite sp.	**34·43**	+	**26·29**	–	12·16	–	5·56	–	11·14	–	10·42	+
Of *L. sexnotatum*	**30·06**	–	9·09	–	11·21	–	2·21	–	**35·52**	+	11·91	–
Of *L. quadrinotatum*	15·48	+	**38·84**	–	**22·45**	+	11·1	–	4·33	+	7·81	+

Independent effect (%) of each predictor variable on the variance in the response variables. The sign indicates a positive (+) or a negative (–) correlation. Bold numbers indicate the two most important predictor variables for each response variable.

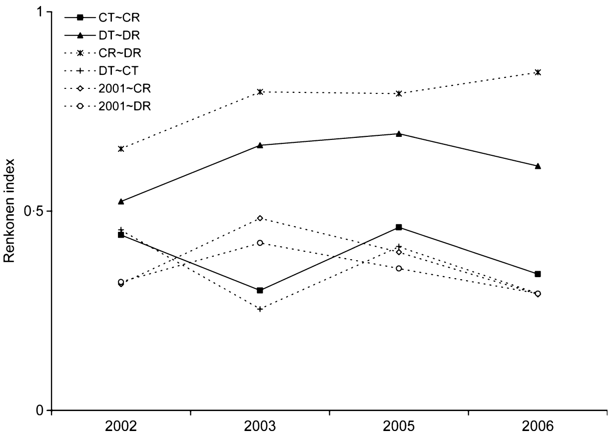

Fig. 3. Changes in species overlap (Renkonen-index) of the wild bee communities over time. CT~CR: similarity between Corynephoretum target (CT) and restoration (CR); DT~DR: Diantho-Armerietum target (DT) and restoration (DR); CR~DR: comparison of restoration sites D and C; DT~CT: comparison of target sites D and C; 2001~CR and 2001~DR: comparison of restoration sites with the situation before the restoration measures were started (2001).

Armerietum sites, wild bee community composition was determined by moisture, the number of entomophilous plant species and the cover of forbs, whereas at the Corynephoretum sites bare ground cover and drier conditions were more important for the wild bee species composition.

Discussion

RESTORATION SUCCESS

Our results show that wild bee communities may change rapidly within the first few years following restoration measures. Based on previous studies, one would expect a gradual increase in the number of wild bee species at restoration sites (Brown & Gange 1992), reaching the level of the target sites after some years. However, the number of wild bee species at restoration sites did not differ from the target sites in any study year, and differences between restoration and target sites were seen only in the total abundance of wild bees and in the abundance of specialist species, both of which were greater at the target sites. These results differ from those of other studies, which showed a rapid increase in flower and insect diversity during the first 2 years followed by a decline in species richness in subsequent years (e.g. Potts *et al.* 2003a; Tyler 2008). Of course, a certain level of variation in bee diversity and abundance occurred at both target and restoration sites. However, this was mainly caused by a great number of species with low abundance, some of which may not be indigenous to the study sites (see also Williams *et al.* 2001; Potts *et al.* 2003b). In our study plots, 67·5% of the species occurred with a relative abundance of < 5%, while the most abundant bee species were similar at both restoration and target sites.

Pollination is a key component of ecosystems as it regulates the succession of plant communities. It has been shown that the reproductive success of many plant species in agricultural landscapes decreases with increasing distance to the next semi-natural habitat (i.e., extensive grassland), which maintain a high number of pollinators (Steffan-Dewenter & Tscharntke 1999). As bees are known to be the most important pollinators in many ecosystems, a rapid recovery of bee communities is important for the success of restoration projects. Many bee species require patches of bare ground as nesting habitats, characteristics of the first successional years (Potts *et al.* 2003a). In our study, no decline in diversity occurred in subsequent years, possibly because of the ongoing disturbance by cattle grazing or flooding. The co-occurrence of different successional stages and a strong heterogeneity in soil types are important in retaining high pollinator diversity (Sjödin, Bengtsson & Ekbom 2008).

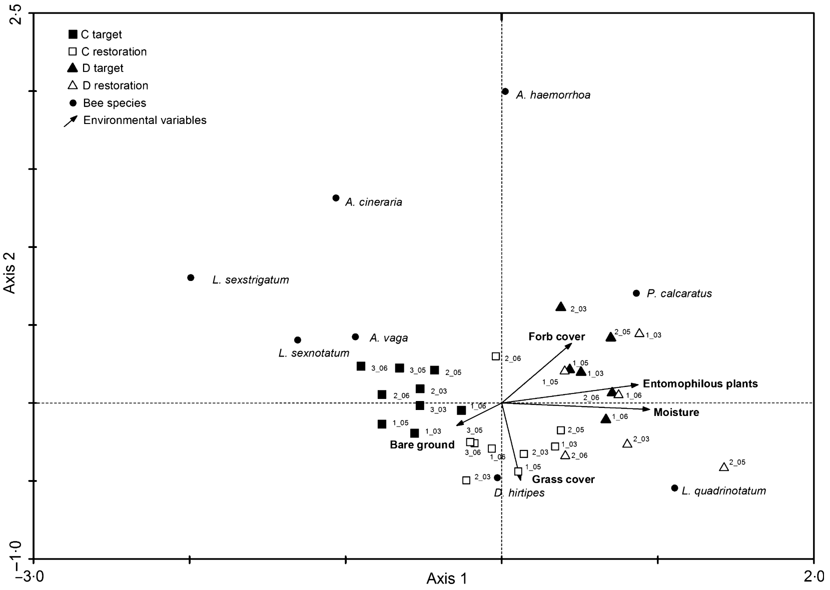

Fig. 4. Canonical correspondence analysis (CCA) biplot showing the average loadings of bee species (*A.* = *Andrena*, *D.* = *Dasypoda*, *L.* = *Lasioglossum*, *P.* = *Panurgus*) and the vectors of environmental variables (first axis eigenvalue = 0·26; second axis eigenvalue = 0·07). The loadings of specific sites are annotated by the plot number and the year.

A major goal of restoration is to promote the establishment of endangered species. We recorded the population development of two Red List bee species both of which increased in abundance on the restoration sites. In particular, *L. quadrinotatum* was present in greater numbers on the restoration sites than at the target sites. However, it should be noted that both species need bare sand for their nests, and bare ground was common during the first years after restoration, but declined continuously thereafter. It is possible that nesting conditions will deteriorate over time for both species, depending on the degree of disturbance by flooding and grazing.

COLONIZATION PATTERNS

It has been suggested that colonization patterns of bees might be influenced by their body size, which is correlated with flight radius and movement patterns (Gathmann & Tscharntke 2002). Smaller species disperse over shorter distances than large-bodied bees and therefore are expected to take longer to reach new sites (Tscharntke *et al.* 2002). However, bees are generally strong fliers and body size might not influence succession patterns in newly colonized sites (Beil, Horn & Schwabe 2008). Our results support this view, as we did not find any stepwise colonization of large, medium and small species. It has also been proposed that populations of strongly specialized bee species are highly fragmented (Packer *et al.* 2005) and thus might have a reduced colonization ability. A similar pattern might also be true for parasitic bees which depend on large populations of their host species. However, in our study, species richness and abundance of both groups did not differ between restoration and target sites. Population genetic studies on two highly specialized *Andrena* species from the study sites revealed a high degree of genetic exchange among populations (Exeler *et al.* 2008) supporting the hypothesis that the degree of specialization does not influence dispersal abilities. Hence, movement patterns calculated from mark-recapture studies seem not be transferrable to colonization patterns (Hochkirch & Damerau 2009)

INFLUENCE OF SPATIAL AUTOCORRELATION AND ENVIRONMENTAL FACTORS

We found a marked difference in the bee communities of the two habitat types in response to the restoration measures. While the wild bee communities of the Diantho-Armerietum restoration and target sites were rather similar, the CR and target sites differed strongly. This is probably explained by the close proximity of Diantho-Armerietum target and restoration sites leading to spatial autocorrelation patterns. The CT site was located *c.* 15 km from the restoration sites, whereas the Diantho-Armerietum was located *c.* 500–1500 m from the restoration sites. The regional species pool might influence the local species composition (Potts *et al.* 2003b). This might also explain why the CR sites were more similar to the Diantho-Armerietum target site than to the CT site. Nevertheless, in both habitat types the wild bee communities at the restoration sites converged towards the respective target communities. The effect of spatial autocorrelation is illustrated by the colonization pattern of the two Red List species. *L. quadrinotatum* decreased in abundance at CT and increased at the other three sites (Fig. 2a), while *L. sexnotatum* was highly abundant at CT in 2003 and 2005, but was rare at the three closely situated sites CR, DT and DR (Fig. 2b).

Environmental factors had a strong influence on the structure of the wild bee communities. Wild bee species richness and abundance showed a negative correlation with moisture, which was the most important environmental factor explaining the differences between both habitat types. Corynephoretum sites were characterized by drier conditions and a higher cover of bare ground, whereas Diantho-Armerietum sites were moister with a greater cover of forbs and a greater number of entomophilous plant species. It has been shown that changes in the bee community are strongly correlated to changes in the vegetation structure (Corbet 1995). In particular, the abundance of flowers and the availability of sandy soil have a strong influence on bee species richness and abundance (Sjödin *et al.* 2008).

Conclusions

In order to evaluate the success of restoration projects, it is crucial to assess not only species composition but also ecosystem function. Pollinators such as wild bees provide key services in ecosystems. In this study, we evaluated the success of the restoration measures and analysed which factors influenced colonization of the sites by wild bees. Our results show that species-rich wild bee communities establish rapidly after restoration measures have been carried out. Although the bee communities differed structurally from the target sites, the functional aspects (number of generalists, specialists and parasites, body-size distributions) of the communities were similar, indicating that ecosystem function may be restored rapidly.

A key factor in the restoration of riverine dunes is the creation of natural dynamics that increases natural sand movement and leads to a rapid development of new habitats for pioneer species. Most riverine systems in Central Europe are heavily regulated and most dunes have been stabilized by pine plantations or flattened for agricultural purposes. In our study area, great effort was made to reconstruct the former dune relief, but due to the use of heavy machinery most artificial dunes have been stabilized too much. Furthermore, eutrophication of the sands can represent a problem. At our restoration sites, the artificial dunes would probably have become invaded by ruderal plants if the hay spreading had not been carried out. The most successful restoration measure was the relocation of the dykes, which has substantially increased the number and intensity of flooding events. The flooding was particularly effective, where a large fallen willow had created a deep hollow. During a flood, this hollow has been further deepened and fine sand has been churned up, leading to the formation of young primary dunes. In contrast to the artificial creation of dunes, the creation of flooded hollows was much more successful. During the first years, a number of endangered species colonized these habitats, including the shoveller duck *Anas clypeata* and Cepero's grasshopper *Tetrix ceperoi* (Gröning *et al.* 2007). The heterogeneity of the site, including wet habitats as well as dry grassland and dunes, promoted the establishment of a diverse fauna and flora. However, careful management including the use of cattle grazing is necessary to keep the sites open. Our results should encourage conservationists to conduct similar restoration projects in order to re-establish species-rich ecosystems that contain a high number of plants and insects.

In future, long-term monitoring is needed to assess the stability of the newly established diverse communities. Large-scale strategies need to be developed in order to reduce eutrophication, for example oligotrophic grasslands cannot be restored if nitrogen deposition continues. In addition, the interactions between plants and pollinators during the colonization process still need to be studied experimentally by excluding groups of pollinators from a study site.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1. Map of the study area and the locations of restoration and target plots in north-western Germany.