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Published in:
Journal of insect conservation

DOI:
[10.1007/s10841-016-9941-3](https://doi.org/10.1007/s10841-016-9941-3)

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Document Version
Publisher's PDF, also known as Version of record

Publication date:
2017

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Wynhoff, I., Kolvoort, A. M., Bassignana, C. F., Berg, M. P., & van Langevelde, F. (2017). Fen meadows on the move for the conservation of *Maculinea (Phengaris) teleius* butterflies. *Journal of insect conservation*, 21(3), 379-392. <https://doi.org/10.1007/s10841-016-9941-3>

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Fen meadows on the move for the conservation of *Maculinea (Phengaris) teleius* butterflies

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Received: 14 June 2016 / Accepted: 23 November 2016 / Published online: 7 December 2016
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Abstract In the Netherlands, a single population of the obligate myrmecophilic butterfly *Maculinea (Phengaris) teleius* has survived on only 3 ha of habitat for more than 25 years, whereas at least 40 ha of habitat are thought to be required for a sustainable metapopulation. Therefore, 170 ha of farmland is being restored to wet meadows within a LIFE+ project by large-scale soil excavation and hay inoculation. For successful restoration, the habitat requirements of the butterfly, with *Sanguisorba officinalis* as host plant and its particular life cycle as parasite of the ant species *Myrmica scabrinodis*, have to be taken into account. We tested whether colonization of nests of this ant species in the restoration areas is facilitated by translocation of sods collected from fen meadows. We divided

54 sods, each sized 1 m², randomly over six patches and measured vegetation development and ant presence in the sods and surrounding control plots for 2 years. In the first summer, significantly more *Myrmica* ants were found in the transplanted sods in comparison to the surrounding area. Herb cover had a significant positive effect on *Myrmica* ant presence while it did not affect the presence of the pioneer ant species *Lasius niger*. In the second year, *Myrmica* ants were found in the surrounding control plots as well. This study contributes to the knowledge-base required for the design of restoration projects aimed at expanding the habitat of the critically endangered butterfly *Maculinea (Phengaris) teleius*.

Keywords Habitat restoration · Myrmecophily · Translocation experiment · *Myrmica* · Fen meadow · LIFE project

Electronic supplementary material The online version of this article (doi:10.1007/s10841-016-9941-3) contains supplementary material, which is available to authorized users.

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Introduction

Until the middle of the last century, wet meadows covered large parts of The Netherlands, while nowadays they are limited to nature reserves which are scattered in an intensively managed agricultural landscape (Schaminée et al. 1996; Jansen et al. 1996; Bakker and Berendse 1999; Reidsma et al. 2006). Wet meadows host many rare plant and animal species, such as butterflies, but population numbers and population sizes have undergone severe declines (Bubová et al. 2015; Van Swaay et al. 2010). For example, many endangered butterflies have suffered from the modernization of agriculture. In addition, their habitats have disappeared through vegetation succession and subsequent penetration by trees and shrubs following cessation

of management and abandonment (Hula et al. 2004; Pöyry et al. 2006).

For butterflies, on the one hand essential elements to fulfil their life cycle may be missing in the remnants of wet meadows, like host plants, nectar sources or host ants. Adaptations of management regimes can certainly improve the habitat quality for common and endangered butterfly species (Batáry et al. 2007; Kruess and Tschardt 2002; Oates 1995; Pöyry et al. 2004; Sawchik et al. 2003; Stewart and Pullin 2006; Tälle et al. 2015; Wenzel et al. 2006). On the other hand, the landscape matrix may have changed with meadows being small and isolated so that exchange between sites is limited and local extinction is no longer compensated for by colonisations. These spatial constraints of the habitat pose additional challenges to conservation measures that are often mainly focused on improving habitat quality (Öckinger et al. 2006; Van Langevelde and Wynhoff 2009). Large conservation projects have attempted to restore vegetation communities and habitats of animal species such as birds (Klimkowska et al. 2007, 2010; Lamers et al. 2015; Tallwin and Smith 2001; Żmihorski et al. 2016) and butterflies (Goffart et al. 2014). In general, however, large-scale restoration projects aimed specifically at insects are rare and the knowledge-base for successful restoration of specific insect species' habitats is limited (Görn and Fischer 2015), especially for butterflies with narrow, specialist, habitat requirements, such as the obligate myrmecophilic *Maculinea (Phengaris)* species (Wynhoff et al. 2008). The caterpillars of this group of species spend most of their development time in nests of specific *Myrmica* host ants, where they feed on ant grubs or are fed by worker ants. This poses additional challenges to restoration projects (Settele and Kühn 2009; Thomas et al. 2009). Conservation actions to improve deteriorated habitat of *Maculinea (Phengaris) arion* in the UK might serve as an example, however this butterfly species occurs on dry chalk grassland (Thomas et al. 2009). The challenge to improve its habitat is different from developing high quality species rich wet meadows suitable for other myrmecophilous species (Settele and Kühn 2009).

In the Netherlands, the LIFE+ project “Blues in the Marshes” aims at enlarging the wet meadow habitat of the rare, iconic butterfly species *Maculinea (Phengaris) teleius* in the nature reserve where the only population in the country occurs. The only host plant of this species, *Sanguisorba officinalis*, is abundant in moist fen meadows, where it has to co-occur with the host ant species *Myrmica scabrinodis* (Witek et al. 2010). After 3 weeks on the host plant on which they feed, caterpillars move to the ant nest, where they hibernate. This Dutch population has survived on only 3 ha of habitat for more than 25 years, whereas at least 40 ha of habitat are thought to be required for a sustainable metapopulation (Wynhoff 2008). To increase its habitat, the

top 40 cm of phosphate enriched former agricultural land in the vicinity of the population was excavated and the vegetation types where the butterfly *M. teleius* occurs, will be restored. However, a major bottleneck for this restoration is that all elements required to fulfil the life cycle of the butterflies have low propensities to colonize the area by natural dispersal (Matus et al. 2003; Elmes et al. 1998). Vegetation establishment was therefore enhanced by distributing hay clipped from the wet fen meadows in the vicinity. The target plant species of the Junco-Molinion vegetation community, amongst them *Sanguisorba officinalis*, are expected to establish in the excavated area, developing a sparse vegetation getting denser and higher over the course of several years. Without interference, the new meadows are expected to be first colonized by the pioneer ant species *Lasius niger*, which occurs almost everywhere in the landscape, disperses easily and is tolerant to extreme microclimatic conditions on sparsely vegetated sandy soils (Peeters et al. 2004; Wynhoff et al. 2011). *Myrmica* ants require a more densely vegetated habitat, later in the vegetation succession, where extreme microclimatic conditions are buffered by the herb layer. Lack of suitable vegetation will therefore prevent an early colonisation of *Myrmica* ants. By the time the vegetation cover would be suitable for these species, they would be forced to compete with the early colonizing pioneer ant species (Wynhoff et al. 2011). To enhance the dispersal of *Myrmica* ants, we used transplanted sods collected in fen meadows to offer habitat islands, enabling the ants to colonize, as yet, inhospitable, recently restored areas earlier than would be possible in the course of natural development.

In this study we investigate the effect of this sod transplantation with Junco-Molinion vegetation (the preferred habitat of *M. teleius*) on the (re)colonisation success of the ant species *M. scabrinodis*. We expect that the ants would colonize the offered habitat islands earlier than the surrounding vegetation which developed after translocation of clipped hay (Hypothesis 1). Differences in vegetation structure were expected to explain differences in colonization rate: the greater the cover and the taller the vegetation, the earlier it should be colonized by *M. scabrinodis* (Hypothesis 2). However, we also expect that the presence of *L. niger* would decrease the colonization rate of the *Myrmica* ant species (Hypothesis 3) (Wynhoff et al. 2011).

Methods

Study site

The study area is located south of the city of 's Hertogenbosch and covers the Natura 2000 area “Vlijmens Ven, Moerputten en Bossche Broek” (931 ha), with the core

site Moerputten (115 ha) in the province Noord Brabant, the Netherlands (51°41'N, 5°15'E, altitude 2 m above sea level). The nature reserve consists of a transition mire, moist meadows with *Junco-Molinion* and other comparable vegetation types, wet forests, and former agricultural land. On most of the former agricultural land the topsoil has been excavated and the historic moist meadow vegetation is in the process of being restored. Geologically, the Natura 2000 reserve is characterized by loamy sands, locally covered with peat or overlying fluvial sediments. The climate is relatively warm (annual temperature 10.1 °C), and wet (annual precipitation 737 mm) (Volkel Meteorological Station, KNMI 2016). For a detailed description of the site see Wynhoff (1998).

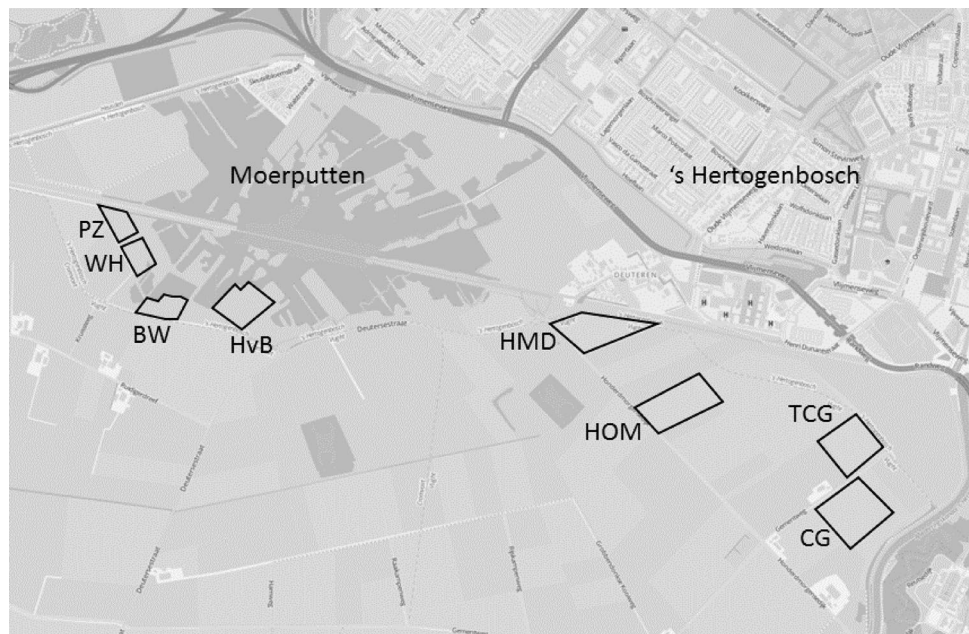
The moist meadows in Moerputten provide the habitat for *M. teleius*. This species is restricted to one core population on the meadow BW (Fig. 1) at the southern border of the core reserve and 2–3 small subpopulations on other meadows within the nature reserve. Since the reintroduction in 1990, *M. teleius* butterflies were recorded on locations at a distance of more than 500 m from the core population only after years with high population densities (Van Langevelde and Wynhoff 2009). When considering only long distance displacements, they covered on average a distance of 1,873 m (SD=1048, n=11, maximum=4,520 m, minimum=900 m), sometimes leading to (temporary) colonization of new habitats. We took the sods from the areas within the normal activity range of the butterflies (Fig. 1). The areas with large-scale soil removal were at distances from these areas within the already observed colonization range (Fig. 1).

The LIFE+ project “Blues in the Marshes” started in 2012 and aims at restoring fen meadows in the area around the nature reserve which have been under intensive agricultural use for about 50 years. After restoring the regional hydrology, the top 40 cm of phosphate enriched soil on a total of 250 ha of corn fields and cattle pastures was excavated. The development of the target vegetation was facilitated by liming (1,000 kg ha⁻¹) and transfer of freshly cut clippings (Hölzel and Otte 2003; Matus et al. 2003; Donath et al. 2007; Török et al. 2011). Clippings were collected after mowing the fen meadows with climax vegetation in Moerputten nature reserve and were spread on the same day in the restoration areas. In 2007, in the area CG soil excavation had already taken place, in 2011 HMD was excavated and finally in spring 2013 the top soil was removed in HOM and TCG (Fig. 1).

Experimental design

In October 2013, 54 sods (1.25×0.85 m each, 10 cm thick) were removed from three fen meadows in Moerputten nature reserve where the vegetation had been mown 1 week before. Sods were cut in rows of 9–13 m length. Each sod sized 1.25×0.85 m was first marked and separated from its surrounding by cutting the edges. Then the 10 cm thick top layer was separated from the underground with a dense prong to avoid tearing. The sods were placed on plastic road plates for transportation. In the restoration area they were allowed to carefully glide into an earlier dug out ditch. Sods were transplanted late in autumn on 23 and 24 October 2013 with normal weather conditions (5–14 °C, average 11 °C, rainy) after a cold period from 9 to 16 October,

Fig. 1 Location of meadows in nature reserve Moerputten (The Netherlands) and soil excavated areas HMD, HOM, TCG and CG



followed by a week with rain. As a consequence of the weather condition *Myrmica* nests were expected to hibernate deep in the soil and hence not be translocated together with the sods.

Thirty sods were removed from HvB, 17 from PZ and 7 from WH (Fig. 1). The transplanted sods were randomly spread over six patches in four restoration areas (CG, HMD, HOM and TCG; Fig. 1). In our study, all target areas for sods received lime and the hay inoculation treatment in different years before sod transplantation. Due to the differences in the history of top soil removal between the restoration areas, sods were moved to sandy soil with sparse vegetation in different densities. At each patch, nine sods were placed in a 3×3 grid, with 3 m distance between the sods, creating a monitoring area of 1.5 m around each sod, which was thought to be enough to prevent interactions of ants between the sods (Fig. 2) (Wynhoff et al. 2013). Control plots of the same dimensions of the sods were established at distances of 3 m around the sods. In 2015, we added eight additional controls per patch at random locations of at least 10 m distance from the patch. To distinguish between them we codified those from 2014 as c-controls and those from 2015 as o-controls.

Data collection

For all six patches in the excavated areas, the plant species composition, abundance, and vegetation height was recorded for all transplanted sods and for eight c-controls in 2014. Vegetation relevés were performed according to the Braun Blanquet method. The cover of all plant species present was estimated, as well as the cover of the total vegetation, trees, shrubs, herbs, mosses, litter (DOM) and bare

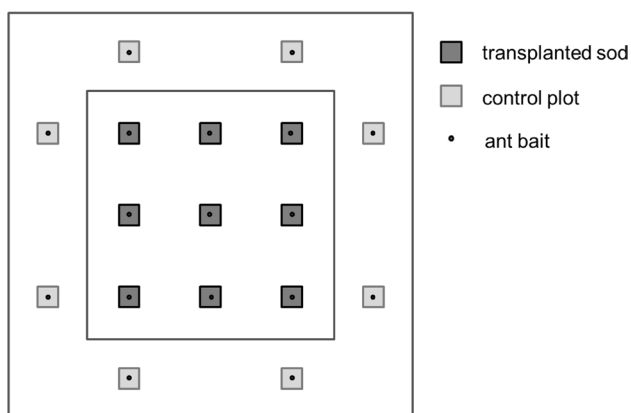


Fig. 2 Positioning of the nine transplanted sods (dark gray) and control relevés (c-controls: light gray) within a patch. Distance between the sods/controls: 3 m. Black dots indicate ant baits. In 2015, an additional eight controls were placed outside each patch at a distance of at least 10 m (o-controls)

soil. With the collected plant data the weighted average Ellenberg indicator values for nitrogen, moisture and pH per relevé could be calculated using the program Turboveg (Hennekens and Schaminée 2001).

We used the Barkman stick method to measure the vegetation height (Barkman 1979). A Styrofoam disk (Ø 10 cm, 6 g) with a central hole was placed around a stick placed inside the vegetation relevé, after which the disk was dropped. The height where the disk settled was measured with the indicated scale on the stick (to the nearest cm). In total five measurements were taken per relevé and were averaged. We used the standard deviation as a proxy for variation in vegetation structure.

To collect data on ant presence in all six patches, we placed plastic pitfall tubes (15 ml, Ø 1.7 cm, 12 cm long) filled with fruit wine (mixture of raspberry, blackcurrant, cherry, 8.5% alcohol) in the soil in the middle of the sods and control plots, with the top of the tube level with the ground surface. Tubes were collected 24 h after positioning to be sure all periods of daily activity of the ants were covered. We placed the baits on 16-7-2014 and on 20-7-2015. Identification of ants was performed using Boer (2010). Each baited tube monitored an area of maximally 3 m in diameter (Elmes et al. 1998), therefore it was chosen to place all control plots around the 3×3 grid. The distance of 3 m between the c-control locations and the sods was thought to prevent interference with baits in the transplanted sods (Elmes et al. 1998). We expected therefore that worker ants from the same colony could only be found in one bait. Thus the frequency of ant occurrences within a patch is independent of species' activity densities (Dahms et al. 2010).

Data analysis

To assess differences in vegetation composition, we performed a detrended correspondence analysis (DCA) in the statistical software R (using the package “vegan”, Oksanen et al. 2016), ordinating relevés along DCA axes based on their similarities in plant species composition. The environmental factors and the deduced Ellenberg values were added to the relevé data with the function ‘envfit’ of vegan to test if the ordination could be explained by these factors. We used the DCA axes scores as a proxy for vegetation composition in further analyses. The environmental factors that were important in differentiating vegetation composition between relevés, were detected using Spearman correlation tests between the environmental factors and the scores of the first and second DCA axes.

Next, we tested whether the source sites of the transplanted sods (as fixed factor) determined the presence/absence patterns of ants in the transplanted sods (as dependent variable), using generalized linear models

(GZLM) with a binomial distribution and logit link function. At the source sites, only *M. scabrinodis* and *M. gallieni* were found, and in low densities. *M. gallieni* occurred locally only on wet locations in PZ and WH. We did the test of the impact of the source sites for *L. niger*, *M. scabrinodis*, all *Myrmica* species combined, and all ant species. No significant difference in occurrence of all ant species, all *Myrmica* species combined, *M. scabrinodis* or *L. niger* at the restoration sites was found between the source strip of the transplanted sods (Supplementary Electronic Material S1a) or between the source meadows (Supplementary Electronic Material S1b). These results suggest that if differences in occurrence of any of the tested ant species between the sods are found, they cannot be related to the meadows or the strips where these sods were cut. Hence, the source of the sods was excluded from any further analysis.

Then, we analysed the differences in the presence/absence of *L. niger*, *M. scabrinodis*, all *Myrmica* species combined, and all ant species (dependent variables in separate tests) between the sods and the c-controls (fixed factor) using a generalized linear mixed model (GLMM) with a binomial error distribution and logit link function. We used a GLMM as the ants and vegetation in the sods and c-controls were repeatedly measured: once in 2014 and once in 2015. The differences in the presence or absence of the respective (group of) ant species between the treatments were tested for 54 sods and 48 c-control plots over 2 years and 48 o-control plots over 1 year. In the GLMM, we applied patch ID (combination of sods, c-controls and o-controls) as random factors. The random factor ‘patch ID’ was not significant in any of the models, but we kept it in the model as it was part of our experimental design. The best fitting models were selected by choosing the random effect covariance matrix with the lowest Akaike’s Information Criterion (AICc, corrected for small data sets) value. This was achieved by selecting Variance Components. For the repeated covariance type, mixed autoregressive moving averages ARMA 11 gave the best model, accounting for autocorrelation due to repeated measurements (Hannan 1980). For all GLMMs, differences between the treatments were tested using the post hoc sequential Sidak test (Sokal and Rohlf 2012).

Finally, we analysed which independent variable could be best related to the detected variation in the occurrence of (groups of) ants. Therefore we used GLMMs with the presence-absence of the ant species as dependent variable and one-by-one we added the independent variables (thus one model for each of the independent variables). First, the year of excavation of the location was tested (as independent variable) as vegetation succession following excavation could explain the vegetation and its structure. For *M. scabrinodis* (as dependent variable), the

correlation of *L. niger* presence was tested (as independent variable), whereas the correlation of *M. scabrinodis* presence (as independent variable) was tested for the model with *L. niger* as dependent variable. We tested the correlation with vegetation structure, such as the cover of the various layers and the height (as independent variables). As a proxy for variation in vegetation structure, the standard deviation of the mean of the vegetation height was also tested as independent variable. Finally we also tested the correlation with the Ellenberg indicators and DCA axis scores, that indicate differences in abiotic conditions and vegetation composition respectively. All tests were done using IBM SPSS Statistics version 22.

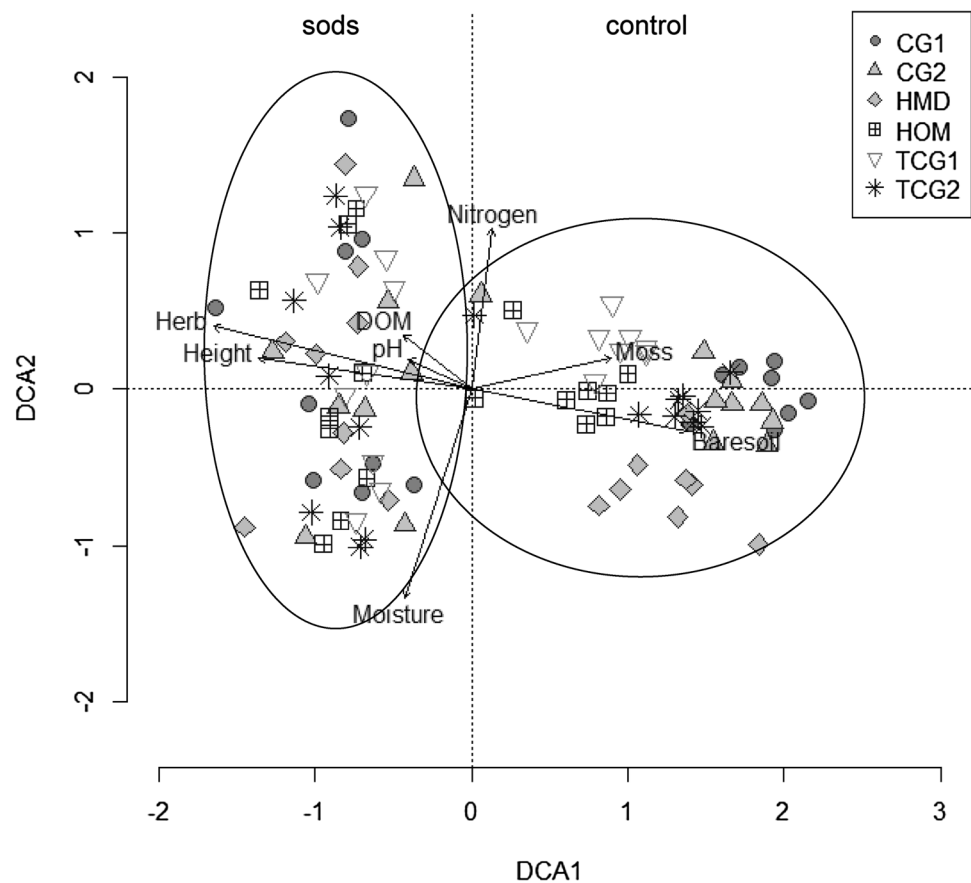
Results

Vegetation

All sods survived the transplantation in October 2013 and the subsequent winters, and no dead plant material was found in the subsequent year. In most areas, even in the second year, the edges of the transplanted sods were clearly distinguishable from the surrounding area. The depth of 10 cm of the sods that were transplanted seemed to be enough for plants to recover from the transplantation since no dead plants were found.

We found two main axes in the DCA analyses of the vegetation data of all six restoration areas with eigenvalues of 0.57 for axis 1 and 0.29 for axis 2 respectively (0.86 combined). The vegetation composition clearly differed between sods and controls since all transplanted sods are ordinated on the left-hand side of the DCA axis 1 while those of the controls are clustered at the right-hand side (Fig. 3). The sods had a greater herb cover, had taller vegetation and contained more litter relative to the controls. DCA axis 1 correlated with vegetation structure characteristics, such as herb cover ($\rho = -0.657$, $p < 0.0001$, $n = 78$), total vegetation cover ($\rho = -0.504$, $p < 0.0001$, $n = 78$), bare soil cover ($\rho = 0.504$, $p < 0.0001$, $n = 78$) and mean vegetation height ($\rho = -0.557$, $p < 0.0001$, $n = 78$), while DCA axis 2 correlated with the Ellenberg moisture value ($\rho = -0.467$, $p < 0.0001$, $n = 78$) and the Ellenberg nitrogen value ($\rho = 0.369$, $p < 0.0001$, $n = 78$). The average Ellenberg pH had no significant linear correlation with the DCA axes. The controls contained a higher bare soil cover and a higher moss cover relative to the sods. Moss species were not determined in this study, however moss encountered at the controls were predominantly *Polytrichum sp.* or the common liverwort *Marchantia polymorpha*.

Fig. 3 Detrended correspondence analysis (DCA) of the vegetation relevés of all transplanted sods as well as the c-control relevés in 2014 in the restoration areas, with the vectors of the environmental variables. Nitrogen, Moisture and pH refer to the respective Ellenberg indicator values calculated from the relevés. Herb, Moss, Baresoil and DOM refer to the cover (in %) of herbs, mosses, bare soil and dead organic matter respectively. Each different symbol indicates the sods and control relevés of one restoration area. Control relevés and transplanted sods are indicated with the circles. Left circle: transplanted sods, right circle: control relevés



Ants

We found eight different species of ants (Supplementary Electronic Material S2). *Myrmica scabrinodis*, *M. sabuleti*, *M. gallienii* and *L. niger* occupied one or more sods or controls in both years. In 2014 only, we found *Myrmica rugulosa* and *Lasius umbratus* in one of the sods in HMD. *Myrmica ruginodis* and *Myrmica rubra* were only found in 2015 on the c-controls in TCG2 and CG2. The species richness was usually low. In the sods we found up to three species, with a mean (\pm SD) species richness between 1.1 ± 1.2 (HMD 2014) and 0.2 ± 0.4 (HOM 2015) per patch and year. In the c-control plots we found at most two species with an average between 0.75 ± 0.71 (CG2 2014 and HMD 2015) and 0 (TCG1 2014). The o-controls were poorest in ant diversity with never more than one ant species. *L. niger* was most abundant on CG2 where we found the species on every o-control plot.

We found differences in presence/absence of the analysed groups of ants between the 2 years and between the treatments (Table 1). *M. scabrinodis* was affected by both year and treatment while the occurrence of *L. niger* was found to be independent from both factors. The treatment affected the distribution of all *Myrmica* species combined and all ants, but there was no effect of the year on the ants.

Table 1 Results of the generalized linear mixed models for the effect of the treatment (sods, c-controls and o-controls) and the year on the occurrence of *Myrmica scabrinodis*, all *Myrmica* species, all ant species and *Lasius niger* ants in the restoration areas after sod translocation in 2013

Model	F	p	df1	df2
<i>Myrmica scabrinodis</i>				
Year	5.431	0.021	1	270
Treatment	10.127	<0.001	2	270
Year \times treatment	5.431	0.021	1	270
<i>Myrmica spec</i>				
Year	3.849	0.051	1	270
Treatment	14.229	<0.001	2	270
Year \times treatment	6.179	0.014	1	270
All ant species				
Year	2.594	0.108	1	270
Treatment	11.009	<0.001	2	270
Year \times treatment	0.250	0.617	1	270
<i>Lasius niger</i>				
Year	0.008	0.928	1	270
Treatment	0.789	0.456	2	270
Year \times treatment	2.652	0.105	1	270

For each variable in the model, the F- and P-value and the degrees of freedom of the fixed factors (df1) and the error (df2) are given. The model was built using the Variance Components covariance structure

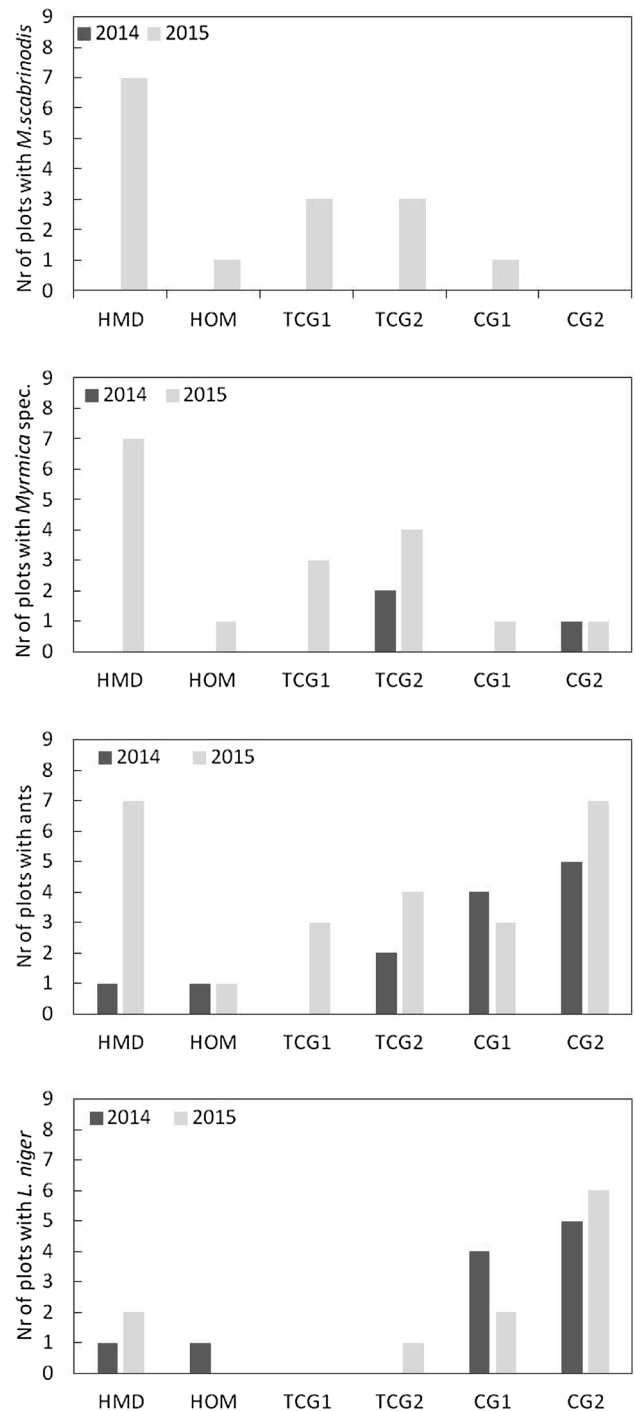
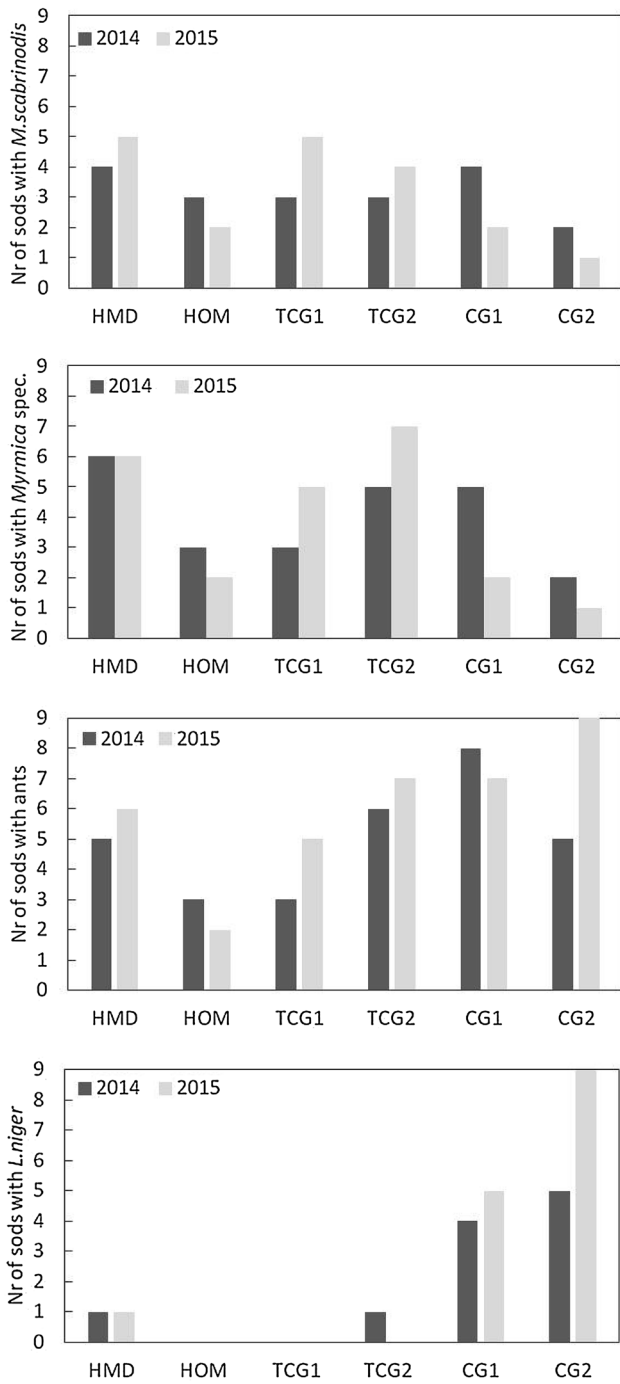


Fig. 4 Number of transplanted sods (left column) and control plots (right column) per patch per year for all ant species, all *Myrmica* species, *Myrmica scabrinodis* and *Lasius niger*. The maximum achievable number is nine since each patch consists of nine sods

Fig. 4 (continued)

The year effect on the *Myrmica* species combined was almost significant.

In the first year of the experiment, 2014, *M. scabrinodis* was restricted to the sods but was not present in the c-controls (Fig. 4). One year later, the species was also present in

the c-control plots surrounding the sods, while it was still missing in the distant o-controls (Figs. 4, 5) indicating that the species had not colonized the restoration area before the transplantation of the sods. The same pattern was found for all *Myrmica* species combined except for a few c-control plots in TCG2 and CG2, which were colonized by *M. ruginodis* and *M. rubra*. However, the difference between the

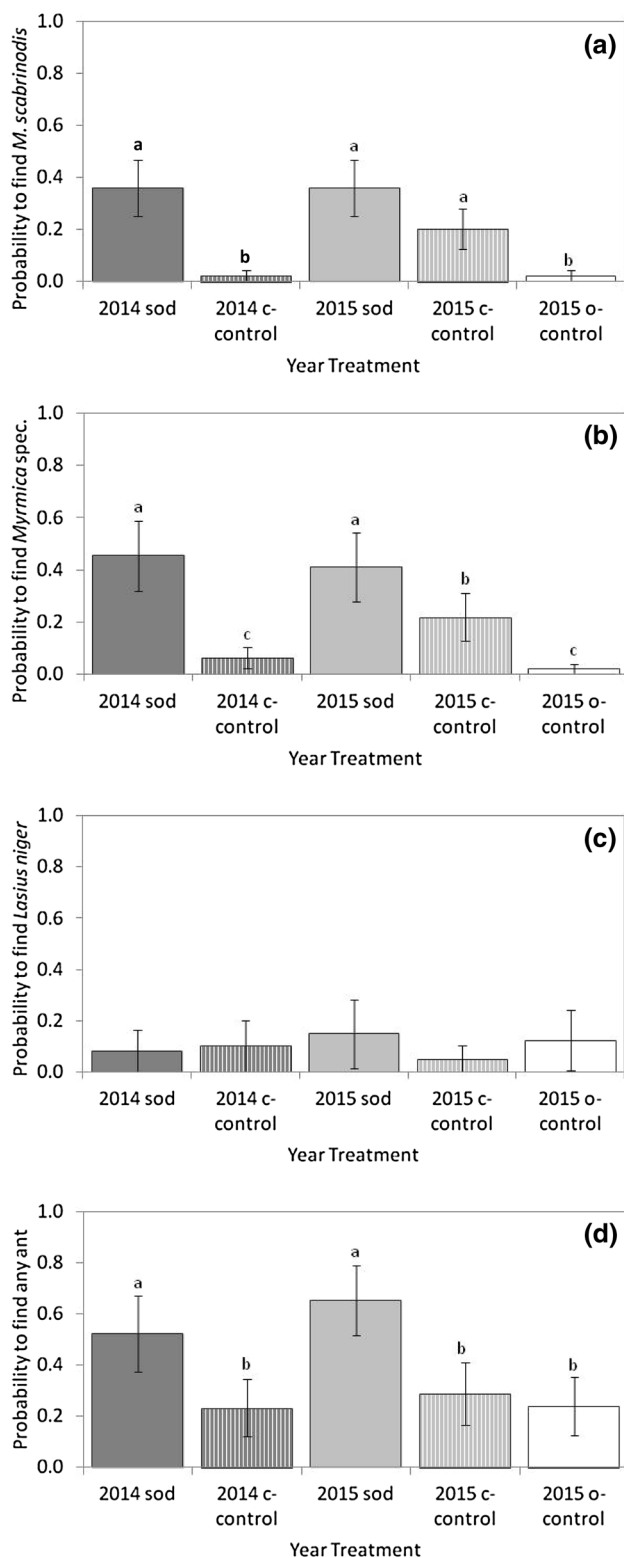


Fig. 5 Occurrence of *Myrmica scabrinodis* (a), any *Myrmica* species (b), *Lasius niger* (c) and any ant species (d) with standard error per treatment (sod, c-control and o-control). Letters indicate significant differences between the treatments, see text for statistics

Table 2 Results of the generalized linear mixed models for the effect of various parameters on the occurrence of *Myrmica scabrinodis* ants in the restoration areas after sod translocation in 2013

Model	AICc	Coeff.	StD E	t	p
Year excavation	1320.8	–	–	1.81	0.039
<i>L. niger</i> presence	1306.0	0.734*	0.499	1.49	0.139
Total vegetation cover	1342.8	0.022	0.007	2.98	0.003
Shrub cover	1309.8	–0.010	0.017	–0.57	0.566
Herb cover	1339.3	0.022	0.006	3.73	<0.001
Moss cover	1315.7	–0.009	0.008	–1.16	0.247
Litter cover	1318.2	0.008	0.01	0.81	0.421
Bare soil cover	1317.4	–0.022	0.008	–2.88	0.004
<i>S. officinalis</i> cover	1313.5	0.005	0.012	0.43	0.669
Vegetation height	1314.9	0.014	0.014	0.97	0.334
StD vegetation height	1311.0	–0.016	0.027	–0.60	0.551
Ellenberg productivity	935.6	–0.003	0.004	–0.82	0.413
Ellenberg moisture	935.3	0.004	0.003	1.09	0.276
Ellenberg pH	936.5	0.006	0.003	1.59	0.101
DCA axis 1	986.5	–0.788	0.207	–3.82	<0.001
DCA axis 2	928.6	0.432	0.351	1.23	0.220

Each independent variable refers to one model. For each variable in the model, the AICc, the coefficient F- and P-value are given. Degrees of freedom for the year of excavation $df=2$, all others $df=1$. We used a binomial error distribution with logit link function. The model was built using the repeated covariance type ARMA 11 (Autoregressive moving average 11) and the Variance Components covariance structure

* Change relative to *L. niger* absence

years was non-significant when lumping all *Myrmica* species (Fig. 5). When all ants were combined, most ants were found in the sods. Finally, the presence of *L. niger* showed no difference between the treatments and years. However, the occurrence of this ant species increased with the number of years since excavation. The same effect was found in *M. scabrinodis* but much weaker.

Distribution of ants in relation to vegetation characteristics

The distribution of ants was related to the cover of the vegetation, herbs and the percentage of bare soil. The probability of finding ants increased with total vegetation cover and herb cover of the sods, irrespective of ant species or group of ant species. The effect of the cover of the total vegetation was only small for *L. niger* and absent when considering only the cover of herbs (see Tables 2, 3, 4, 5; Fig. 6). The reverse relationship was found between ants and the cover of bare soil. The vegetation composition when expressed as the DCA axis 1 score explained the occurrence of *Myrmica* species but not of *L. niger*. *Myrmica* species preferred vegetation with a higher number of plant species, which had a negative DCA axis 1 score. More important factors

Table 3 Results of the generalized linear mixed models for the effect of various parameters on the occurrence of all *Myrmica* ant species in the restoration areas after sod translocation in 2013

Model	AICc	Coeff.	StD E	t	P
Year excavation	1289.9	–	–	1.14	0.275
<i>L. niger</i> presence	1280.3	0.803*	0.479	0.68	0.095
Total vegetation cover	1306.1	0.020	0.007	2.94	0.004
Shrub cover	1283.9	–0.007	0.016	–0.43	0.669
Herb cover	1311.4	0.018	0.005	3.34	<0.001
Moss cover	1295.5	–0.013	0.007	–1.74	0.083
Litter cover	1289.4	0.006	0.009	0.61	0.544
Bare soil cover	1299.6	–0.018	0.007	–2.65	0.009
<i>S. officinalis</i> cover	1287.4	0.014	0.011	1.35	0.180
Vegetation height	1287.8	0.011	0.014	0.83	0.406
StD vegetation height	1283.7	–0.030	0.027	–1.11	0.268
Ellenberg productivity	948.8	–0.009	0.004	–2.24	0.026
Ellenberg moisture	924.7	0.005	0.003	1.65	0.101
Ellenberg pH	916.1	0.002	0.003	0.47	0.636
DCA axis 1	999.1	–0.0001	0.000	–4.15	<0.001
DCA axis 2	935.2	0.000	0.000	1.04	0.298

Each independent variable refers to one model. For each variable in the model, the AICc, the coefficient F- and P-value are given. Degrees of freedom for the year of excavation df=2, all others df=1. We used a binomial error distribution with logit link function. The model was built using the repeated covariance type ARMA 11 (Autoregressive moving average 11) and the Variance Components covariance structure

* Change relative to *L. niger* absence

explaining *Myrmica* presence/absence are herb cover, vegetation height and, contrastingly, the percentage of bare soil. The Ellenberg indicator values had little effect: all *Myrmica* combined were more likely to be found in mesophilic rather than poor vegetation (see Fig. 3).

We found no indication of competition by *L. niger* expressed as a negative correlation with the other ant species (see Tables 2, 3). The more years have passed since excavation the more likely *L. niger* has colonised and spread over the area, resulting in a higher frequency of occurrence in the plots. However, *L. niger* apparently does not limit the probability of finding *M. scabrinodis* or any other *Myrmica* ant species, neither does the presence of *Myrmica* ants discourage *L. niger* from colonizing the area.

Discussion

Butterflies need host plants to lay their eggs on and flowers or other resources to feed on. In addition, both adult and larval instars are sensitive to microclimate and vegetation structure. When habitats have deteriorated, and special requirements are not met, management changes can improve the situation significantly, as was documented for

Table 4 Results of the generalized linear mixed models for the effect of various parameters on the occurrence of all ant species in the restoration areas after sod translocation in 2013

Model	AICc	Coeff.	StD E	t	p
Year excavation	1207.6	–	–	1.54	0.094
<i>L. niger</i> presence	1353.7	–4.920*	0.901	–5.462	<0.001
Total vegetation cover	1247.3	0.021	0.005	3.90	<0.001
Shrub cover	1210.5	0.011	0.013	0.84	0.404
Herb cover	1237.8	0.016	0.005	3.29	0.001
Moss cover	1212.2	–0.004	0.006	–0.68	0.496
Litter cover	1215.8	0.017	0.009	2.04	0.043
Bare soil cover	1252.6	–0.023	0.006	–3.94	<0.001
<i>S. officinalis</i> cover	1215.4	0.024	0.011	2.12	0.035
Vegetation height	1224.3	0.033	0.012	2.61	0.010
StD vegetation height	1209.3	0.001	0.021	0.05	0.960
Ellenberg productivity	883.8	–0.007	0.004	–1.91	0.058
Ellenberg moisture	883.7	0.005	0.003	1.54	0.126
Ellenberg pH	882.0	0.004	0.003	1.17	0.243
DCA axis 1	932.1	–0.0001	0.000	–4.16	<0.001
DCA axis 2	892.4	0.000	0.000	0.37	0.715

Each independent variable refers to one model. For each variable in the model, the AICc, the coefficient F- and P-value are given. Degrees of freedom for the year of excavation df=2, all others df=1. We used a binomial error distribution with logit link function. The model was built using the repeated covariance type ARMA 11 (Autoregressive moving average 11) and the Variance Components covariance structure

* Change relative to *L. niger* absence

the rare and endangered *Lycaena helle* and *Euphydryas aurinia*, but also for common butterfly species (Goffart et al. 2014; Öckinger et al. 2006; consult; Bubová et al. 2015 for more case studies). Parasitic butterfly species, such as *M. teleius*, impose additional challenges on habitat restoration because of the specific habitat requirements necessary for successful population establishment. Both the host plant, *Sanguisorba officinalis* for the butterflies, and the host ant, *Myrmica scabrinodis* for the caterpillars, should be present in sufficient densities and in close proximity to each other (Witek et al. 2010). Huge efforts have been made to conserve the obligate myrmecophilous *M. arion* in Britain by restoring deteriorated habitat by changes in the management in combination with assisted colonization (Thomas et al. 2009). Our project makes a start in an even more difficult situation after the habitat has completely been destroyed. Starting conditions were created by removing the phosphate enriched topsoil to create nutrient poor conditions for the desired vegetation and by restoring the hydrology. While it is comparatively easy to restore the vegetation with the host plant, even when starting on bare soil, there is almost no knowledge on how to aim for a specific ant community in which the host ant species of the butterfly is present. We show that transplanted

Table 5 Results of the generalized linear mixed models for the effect of various parameters on the occurrence of *Lasius niger* presence in the restoration areas after sod translocation in 2013

Model	AICc	Coeff.	StD E	t	p
Year excavation	1551.4	–	–	5.22	<0.001
<i>Myrmica spec.</i> presence	1506.9	0.269*	0.468	0.58	0.566
<i>M. scabrinodis</i> presence	1508.8	0.244*	0.492	0.50	0.620
Total vegetation cover	1556.9	0.015	0.006	2.51	0.012
Shrub cover	1508.5	0.027	0.016	1.65	0.101
Herb cover	1525.0	0.005	0.005	1.05	0.293
Moss cover	1516.1	0.011	0.008	1.41	0.159
Litter cover	1562.2	0.023	0.013	1.82	0.070
Bare soil cover	1572.4	–0.018	0.006	–2.73	0.007
<i>S. officinalis</i> cover	1520.0	0.007	0.012	0.56	0.573
Vegetation height	1547.8	0.039	0.017	2.24	0.026
StD vegetation height	1516.4	0.040	0.029	1.36	0.174
Ellenberg productivity	1123.1	0.006	0.005	1.22	0.224
Ellenberg moisture	1095.4	0.001	0.004	0.39	0.699
Ellenberg pH	1143.5	0.006	0.004	1.55	0.123
DCA axis 1	1130.4	–0.0001	0.000	–1.15	0.251
DCA axis 2	1117.2	–0.0001	0.000	–1.56	0.120

Each independent variable refers to one model. For each model, the AICc, the coefficient F- and P-value are given. Degrees of freedom for the year of excavation $df=2$, all others $df=1$. We used a binomial error distribution with logit link function. The model was built using the repeated covariance type ARMA 11 (Autoregressive moving average 11) and the Variance Components covariance structure

* Change relative to *Myrmica spec./Myrmica scabrinodis* absence

sods in sparsely vegetated nature restoration areas enhance the colonization of *Myrmica* ants into an area which would otherwise be rapidly colonized by *L. niger* ants. Vegetation structure characteristics were found to be important for ant colonization.

Where do the ants come from?

We did not expect to find ants already in the sods in July of the first summer, not even a year after translocation in October the previous year. The question arises: where did the *M. scabrinodis* found in the sods might come from? The sods were transplanted in October 2013 and checked for ants in July 2014, while nuptial flights occur from the end of July until mid-September, months before the sods were removed (Elmes et al. 1998; Seifert 2007). Nuptial flights in summer 2013 could have occurred very late but it is unlikely that this caused high occurrence of ants after only 1 year. The summer of 2014 was very warm with a first period of high temperatures already in the beginning of June. The month of July was also very warm. The high temperatures may have induced early nuptial flights which resulted in the colonization of our experimental patches.

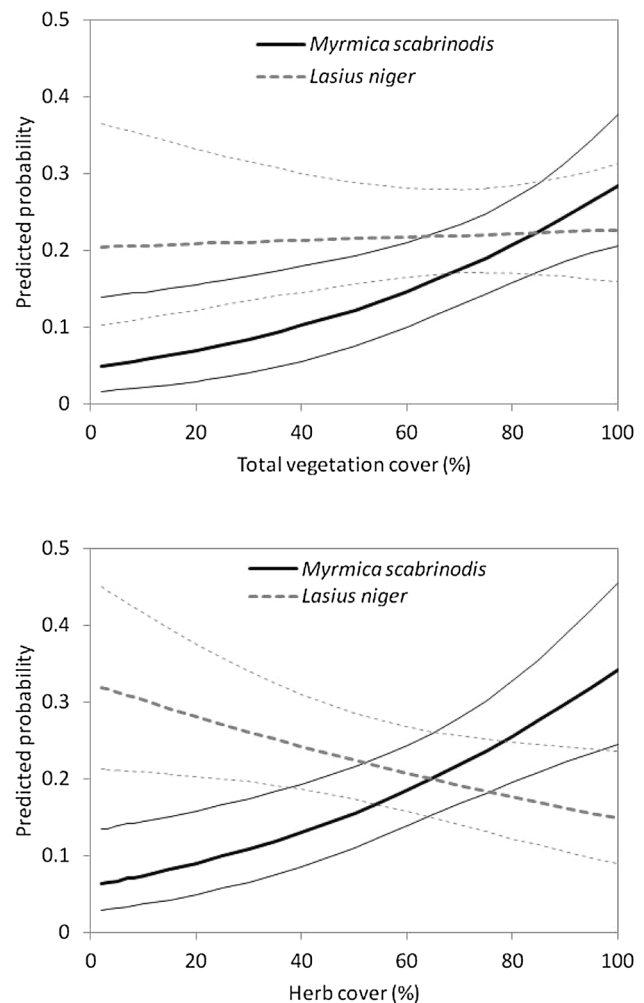


Fig. 6 Predicted probabilities (thick lines) with the 95% confidence intervals (thin lines) of *Myrmica scabrinodis* or *Lasius niger* as a function of the total vegetation cover, herbs and bare soil (%), and the scores of the first DCA. For statistics see text

However, nuptial flights from *Myrmica* ants generally cover only 10 m and only occasionally are larger distances covered (Elmes et al. 1998, but see; Seifert 2007). Moerpotten nature reserve is quite far away for the young colonizing queens, this holds especially for the sites CG and TCG. Colonisation through budding, which is not limited to the period of nuptial flights, would be another possibility. In this case, however, only short distances of several meters can be covered and thus the colonies would have to originate from the edges of the excavation areas or the vegetation surrounding them, for example from the road verges nearby. CG and HMD were excavated in 2007 and 2011 respectively. In 2013 *M. scabrinodis* was only found occasionally at CG and not at all at HMD which makes it unlikely that *Myrmica* ant nests were already present before transplantation and moved into the sods. This is supported

by the low numbers of worker ants captured in the o-controls far away from the experimental patches. The other areas HOM and TCG were excavated in 2013 and therefore it is even more unlikely that high densities of ant nests were already present. The absence of *Myrmica* nests in the o-controls indicated that this was indeed not the case. Source populations near restoration areas are thought to be of great importance for facilitation of colonisation (Dauber and Wolters 2005; Knop et al. 2011). If the surroundings of an area have only a few source populations, the chance of colonisation is low (Knop et al. 2011). In our situation road verges and edge vegetation surrounding the excavated field are the most likely locations of the source population. The monitoring data collected between 1990 and 2012 (Wynhoff et al. 2013) show that in 2012, at the road verges around HMD, a high density of *L. niger* was found, but no *M. scabrinodis*, turning budding from this population pool into an unlikely option. If it did occur, one would expect to also find *Myrmica* nests in the control plots which was not the case.

The higher occupancy of *Myrmica* ants in the sods can also be explained if the ants had been transplanted with the sods. This is not very likely, because ant nests are mostly located deeper in the soil than the top 10 cm. During winter, ant nest development slows down and nests move deeper into the ground to endure the winter. Sometimes hibernating *Myrmica* colonies are found in the winter in tussocks of purple moorgrass (*Molinia caerulea*) (pers. comm. P. Boer), but before transplantation the source meadows of the sods were cut and thus colonies in tussocks were removed. In addition, in order to start a new colony it is necessary that the queen is transplanted with the sods together with some worker ants (Pontin 1963; Bradley 1972; Sovari et al. 2007). It seems unlikely that a total of 21 ant colonies were unknowingly translocated in the sods. Furthermore, only nests of *M. scabrinodis* and *M. gallienii* could have been translocated together with the sods as they were found to be present in the source sites, all other ant species are true colonizers. In conclusion, we think that the ants found in 2014 in the sods had colonized the restoration areas after early nuptial flights induced by the relatively high temperatures in the early summer of that year. While most young queens found a new colony in the vicinity of their maternal colonies, some may have covered longer distances and reached the nature restoration areas where the sods were waiting for them. However, when repeating this experiment the question of the origin of the ants deserves more attention.

Effect of sod transplantation on vegetation characteristics

The most successful restoration method for wetland vegetation starts with excavation of the nutrient-rich top soil

followed by hay inoculation, obtained from sites with the target vegetation (Klimkowska et al. 2007). After soil excavation it usually takes 5–10 years for fen meadows to establish the target Junco-Molinion vegetation, and only if a seed bank is still available (Jansen and Roelofs 1996; Jansen et al. 2000; Van der Hoek and Heijmans 2007). Hay inoculation or transplantation using sods with the target vegetation potentially provides an easy and quick development of wet fen meadow vegetation with the desired vegetation structure and the host plant *S. officinalis* in the excavated areas. If only hay inoculation is applied, this does not provide suitable habitat for *Myrmica* ants, i.e. a dense and tall vegetation, within a short period of time before pioneer ant species settle and spread in the area and later compete with the target ant species.

Effect of sod translocation on ants

Application of vegetation sods cut from habitat of *M. telieus* into restoration areas appears to have had a positive effect on the presence of its host ant species, *M. scabrinodis*. The large advantage of sod transplantation is that, as well as the desired vegetation composition, the suitable vegetation structure for *M. scabrinodis* is also introduced. In all of the excavated areas, in the first year *M. scabrinodis* was already present in the transplanted sods, but was not found in the control plots. The absence of *M. scabrinodis* in the control plots during the first year after transplantation indicates that the restoration areas were not yet colonized by the species, as was confirmed by the absence of the ant species in the additional controls located a substantial distance from the sods in the second year. Only one of these controls was colonized by *M. scabrinodis* and the others were empty while only a few control plots nearer to the sods hosted *L. niger*. In the landscape around the study area, *M. scabrinodis* is the second-most abundant ant species on road verges, though it occurs mainly in nature reserves (Wynhoff et al. 2011). Even though being a general species, colonization of restoration areas does not occur most likely due to the lack of suitable habitat. It thus seems that the transplanted sods form suitable habitat islands, attracting *M. scabrinodis* colonizers.

We cannot rule out the possibility that worker ants found in a sod came from a nest in one of the neighboring sods. Although the distance between the sods was thought to be large enough to prevent such foraging distances, the territory of a nest in a resource poor environment with sods of limited size could be larger than average, allowing worker ants to access neighboring sods. However, the spatial pattern of occupied sods within a patch and the associated control plots gives no indication of a higher probability of ant captures in neighboring sods or controls.

Several vegetation characteristics could explain the occurrence of our target ant species *M. scabrinodis*. A high cover of relatively tall vegetation or herbs with only a small amount of bare soil increases the probability of encountering *M. scabrinodis*. The great difference in vegetation structure between the densely vegetated sods and the sparsely vegetated control plots can explain our results; i.e. that in this early phase of restoration sods, with suitable vegetation structure and composition, provide suitable habitat for host ants. This colonization was not found to be hindered by the presence of the competitive species *L. niger*. However, at larger spatial scales, a negative correlation with the host ant of *M. teleius* was found (Wynhoff et al. 2011). Although *L. niger* is better able to colonize areas with bare soil (Dekoninck et al. 2008; Elmes et al. 1998; Wynhoff et al. 2011), *M. scabrinodis* has still managed to establish in these areas as well. This might indicate that at least at the very local scale of the sod, *L. niger* is not limiting the establishment of *M. scabrinodis*. It is also possible, that enough space might still be available for both species to co-occur and competition for nest sites is not yet present. It is worth mentioning that the results of the experiment only cover a two-year period. On the one hand, once the abundance of *L. niger* nests has increased, a shortage of space and resources might result in competition between ant species and lower colonization and dispersal of *Myrmica* ants. On the other hand, as vegetation development continues, and cover becomes more extensive and the canopy closes, more habitat becomes available for *Myrmica* ants. Monitoring in the coming years will show if the presence of *L. niger* in the excavated area obstructs the colonization by *M. scabrinodis*.

As herb cover becomes increasingly dense, *M. scabrinodis* may be able to colonize more of the surroundings of the sods more quickly (Elmes et al. 1998) since the first control plots were already colonized within 2 years. The transplantation experiment had no effect on the occurrence of *L. niger*. Even for this pioneer species (Wynhoff et al. 2011), it takes a while to colonize vacant habitat. We found a strong effect of the time since excavation on the probability of finding its workers at the baits. The highest probability of ant occurrence was found in the areas excavated first. The ability to easily cross open spaces and reach high altitudes during nuptial flights enable rapid colonization anywhere in the landscape. With strongly synchronized nuptial flights and pleometrosis during the initial founding phase of a new colony, rapid expansion in newly colonized areas is possible (Hölldöbler and Wilson 1990; Noordijk et al. 2008). The nest density of *L. niger* might increase for several years but will finally decrease due to the closing of the vegetation cover and the stable management of mowing that will follow the restoration. Finally, when the targeted vegetation covers the soil, *L. niger* is expected to be very rare or even

absent as it is in the meadows in the nature reserves where *M. teleius* is found (Wynhoff et al. 2011).

Dahms et al. (2010) found an effect of time on the whole ant community after restoration of abandoned grassland by tree cutting and grazing, mainly affecting the open-habitat species richness. However, the observed time span was much longer and the starting conditions were quite different. For our study sites, we expect that once the vegetation covers most of the excavated soil the ant community will be dominated by *Myrmica* ants while *L. niger* will be restricted to landscape elements with regular disturbance, such as road verges and stream borders, as has been found by Wynhoff et al. (2011).

Conclusion

Large-scale restoration of wet fen meadows, when restricted to soil excavation and hay inoculation, does not expand the habitat of *Maculinea teleius* butterflies for many years because it only facilitates the establishment of the host plant *Sanguisorba officinalis*. Colonization of the restoration areas by the equally needed host ant *Myrmica scabrinodis* can be supported by offering densely vegetated habitat islands. Our experiment shows that translocation of sods with the target vegetation results in a higher probability of finding *Myrmica* ants in comparison to the sparsely vegetated habitats on sandy soils. An effect of offering sods on the pioneer ant species *Lasius niger* was not found, neither was there any evidence for competition between the species as this would have resulted in a negative correlation between *L. niger* and *M. scabrinodis*. Sod translocation helps to enhance colonisation of *Myrmica* ant nests and further studies in the coming years will monitor the development of the ant community.

Acknowledgements This study was performed within the LIFE+Project “Blues in the Marshes” (LIFE 11 NAT/NL/000770/Action C1 and D1). National State Forestry and Natuurmonumenten gave us permission to access their nature reserves and carried out the transplantation experiment. Kars Veling helped in the field and documented the actions. Sicco Ens assisted collecting vegetation data. Peter Boer helped identifying the ants. IW’s work was partly funded by the Province of Northern Brabant. MPB’s work was partly funded by the Uyttenboogaart-Eliasen Society.

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