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The restoration of phytophagous beetles in species-rich chalk grasslands

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Abstract

This study focuses on the restoration of chalk grasslands over a six-year period and tests the efficacy of two management practices, hay spreading and soil disturbance, in promoting this process for phytophagous beetles. Restoration success for the beetles, measured as similarity to target species-rich chalk grassland, was not found to be influenced by either management practice. In contrast, restoration success for the plants did increase in response to hay spreading management. While the presence of suitable host plants was considered to dictate the earliest point at which phytophagous beetles could successfully colonise, few beetle species colonised as soon as their host plants became established. Morphological characteristics and feeding habits of 27 phytophagous beetle species were therefore tested to identify factors that limited their colonisation and persistence. The lag time between host plant establishment and colonisation was greatest for flightless beetles. Beetles with foliage-feeding larvae both colonised at slower rates than seed-, stem- or root-feeding species, and persisted within the swards for shorter periods. While the use of hay spreading may benefit plant communities during chalk grassland restoration it did not directly benefit phytophagous beetles. Without techniques for overcoming colonisation limitation for invertebrate taxa short-term success of restoration may be limited to the plants only.

Keywords: Calcareous grassland, Coleoptera, colonisation, hay spreading, hay strewing, persistence, soil disturbance.

Introduction

Throughout Europe, habitat loss and changes in the management of agricultural land have caused dramatic declines in the quality and area of semi-natural grasslands (Bakker & Berendse, 1999; Willems, 2001; Walker et al., 2004). This has been attributed to agricultural improvement, in particular practices such as re-seeding, inorganic fertiliser application, improved drainage and changes to cutting and grazing regimes (Crofts & Jefferson, 1999; Walker et al., 2004). These declines have prompted considerable interest in the development of new management practices for the restoration of biodiversity on agriculturally improved grasslands (Bakker & Berendse, 1999).

While re-establishing the flora is normally seen as the key to grassland restoration (Bakker & Berendse, 1999; Walker et al., 2004), the consideration of other trophic levels has the potential to provide valuable additional information when assessing restoration success (WallisDeVries & Raemakers, 2001; Davis et al., 2002; Perner & Malt, 2003; Pöyry et al., 2005; Ottonetti et al., 2006; Woodcock et al., 2006; Woodcock et al., 2008). For example, in addition to their host plants phytophagous insect are likely to require a suite of suitable environmental conditions to successfully establish once they have successfully colonised (WallisDeVries & Raemakers, 2001; Pöyry et al., 2005; Woodcock et al., 2006).

Here, we consider how the restoration of a primary consumer trophic level is affected by management practices targeted at restoring plant communities. We focus on a group of morphologically and functionally diverse phytophagous beetles (Woodcock et al., 2006; Woodcock et al., 2008). We test two predictions: 1) The re-establishment of host plants – promoted by the management practices of hay spreading and soil disturbance – will indirectly result in an increase in similarity of phytophagous beetles to target species-rich chalk grassland; 2) Following the establishment of suitable host plants subsequent colonization and persistence of beetles will be mediated by individual species traits, that will ultimately act to limit rates of restoration for these grassland communities.

Methods

Study site and experimental design

The experiment was established during 1998 on 1.8 ha of agriculturally improved chalk grassland at Brush Hill, Buckinghamshire, UK (lat 51˚43'27" N, long 0˚48'46" W). Prior to 1998, this grassland had been improved by the application of NPK fertiliser, creating a species-poor sward with *c.* 19 species m^{-2} of vascular plant. In addition to the experimental site, an unimproved species-rich chalk grassland located at Gomm's Wood (lat 51˚37'53" N, long 0˚42'30" W) was used as a donor site for hay used during restoration management (see below) and as a target for measuring restoration success. Gomm's Wood was 12.6 km from the experimental site.

Restoration of the chalk grassland at Brush Hill was attempted using two management practices. The first was soil disturbance, which was intended to create germination niches within the grass sward. Soil disturbance was created using a rotovator; a hand-held petrol driven device used by gardeners. The second was the application of hay to introduce local provenance seeds from the donor site (Edwards et al., 2007). The hay was harvested at Gomm's Wood in October 1998 and was applied within 2 days to experimental plots at 20 tonnes ha^{-1}. The four interactions between hay spreading (±) and soil disturbance (±) were tested using a 2 × 2 factorial randomised complete block design. The four treatments levels were: 1) control with no management; 2) hay spreading only; 3) soil disturbance only; 4) hay spreading and soil disturbance. Each treatment levels was allocated randomly to experimental plots within each of five replicate blocks (20 experimental plots in total). Individual experimental plots were 5 × 5 m, and separated from adjacent plots by 10 m. Both management practices were applied in October 1998 only, with soil disturbance applied prior to hay spreading. Throughout the duration of the study Grazing was applied to all experimental plots at rates of between 12 – 15 ewes ha^{-1}. Grazing was initiated in May of each year until the sward reached a height of 4-7 cm, after which grazing was suspended before being restarted in late August. This grazing rate followed recommended stocking densities for UK lowland calcareous grasslands (Crofts & Jefferson, 1999).

Botanical and beetle sampling

Plant community composition was recorded for all experimental plots in July from 1999 to 2004. In the centre of each plot a single 1.0 × 1.0 m quadrat was positioned and the cover abundance of all vascular plant species was recorded. During 1998 a further 15 quadrats were sampled from the hay donor site (Gomm's Wood) using the same methodology.

Beetle sampling was carried out over the same six-year period. Experimental plots were sampled three times a year (May, July and September) using a Vortis (Burkhard Ltd, UK) suction sampler. On each occasion, the sampler was placed in 15 positions (equivalent to 0.3 m^2), each for 10 seconds, within the same 1 × 1 m quadrats used for the botanical surveys. Suction sampling is a quantitative method suitable for the collection of sward active invertebrates (Southwood & Henderson, 2000). Beetle of the Chrysomelidae, Curculionidae and Apionidae were identified to species and counts of individuals were summed for the three sampling dates within each year. Using the same methodology 15 suction samples were also taken in May, July and September 1998 from the hay donor site of Gomm's Wood.

Measuring restoration success

To test prediction 1 restoration success for the plants and phytophagous beetles were compared in response to the same management practices. To provide a measure of restoration success the species composition of the plants and beetles were compared to those of the donor site (Gomm's wood) using Jaccard's similarity coefficient (S_j). This is a binary coefficient that considers only the presence or absence of species (Krebs, 1999) and so considers only species colonisation, not their post colonisation abundance. Jaccard's similarity was calculated for each of the 20 experimental plots in each year. In each case similarity was calculated between the experimental plots and each of the 15 samples collected at the Gomm's Wood donor site to produce an average value. The choice of Gomm's Wood as a target community for restoration success was based on its status as an unimproved species-rich chalk grassland.

Morphology, colonisation and persistence of the beetles

To test prediction 2 the phytophagous beetles were classified according to host specificity (monophagous *vs.* oligophagous / polyphagous) and larval feeding strategy (root-, stem-, foliage- and inflorescence/seed-feeding) (e.g. Hoffman, 1950-58; Woodcock et al., 2006). Species were also classified as being capable of flight (macropterous) or as flightless (brachypterous or apterous). Average beetle mass for each species was determined using Roger et al.'s (1976) mass *vs.* body length equation and was based on mean body lengths of five male and five females.

To determine the effects of these traits on colonisation and persistence over the six years of the study two parameters were calculated for species with 10 or more individuals in the entire data set. 1) Lag time: This was defined as the mean number of years between the establishment of host plants and their colonisation by a beetle species. This was calculated for each plot where a beetle species was found. From this an overall mean lag time was calculated for each beetle species across all experimental plots. 2) Beetle persistence: This was defined as the probability of a beetle persisting as long as their host plants remained within the experimental plots. This probability of persistence was calculated as the ratio of the number of experimental plots where a beetle species went extinct before its host plant to the total number of plots where the beetle was found (out of a maximum of 20). Both of these parameters were derived from information in all 20 experimental plots across all six years and so their analyses will not consider the fixed effects of management or year.

Data analyses

Prediction 1 was tested using generalised linear models (GLM) in SAS 9.01. Changes in Jaccard's similarity of the plants and beetles were tested in response to all interactions of hay spreading (± Hay), soil disturbance (± Soil) and year (Schabenberger & Pierce, 2002). Year was considered as a continuous variable in this analysis, and block was included as a covariate. To account for repeated measurements taken within each experimental plot the effects of block, soil, hay, and soil × hay were tested against the mean square error term of block × hay × soil. Based on analyses of the distribution of residuals this GLM used a normal error structure and identity link function (Schabenberger & Pierce, 2002). Non-significant treatment effects were deleted from this maximal model, although the deletion of non-significant treatment effects that were part of significant interaction terms was not permitted.

Prediction 2 tested for the effects of beetle morphology and feeding habits on species colonisation and persistence. The underlying assumption of these analyses was that for phytophagous beetles to become established in experimental plots their host plant had to be present (Woodcock et al., 2006). The response of colonisation lag time to beetle flight (full *vs.* reduced wings), beetle mass and the interaction between these factors was tested using GLM's (Schabenberger & Pierce, 2002). GLM's were used to test for the effect of host plant specificity and beetle larval feeding strategy on colonisation lag times. As species from the same genera often share similar larval feeding strategies it was necessary to account for this potentially confounding effect by including beetle genera as a covariate in this. Where significant effects were found, post-hoc Tukey's tests were performed. These GLM's also used a normal error structure and identity link function.

The effect of host plant specificity and larval feeding strategy on the probability of beetle persistence was also tested using GLM's, using a binomial error structure and logit link function (Schabenberger & Pierce, 2002). The binomial error structure was used to account for the lower (0) and upper (1) boundaries associated with probability data. The confounding effect of beetle genera on the probability of beetle persistence's response to larval feeding strategy was also accounted for by the inclusion of this parameter as a covariate.

Finally, as different beetle species occurred at different abundances within the data set this could have caused systematic biases in lag times and persistence. The extent of this problem was assessed by separately correlating lag time and persistence with beetle abundance. Both analyses were performed using GLM's and the error structures indicated above.

Results

Plant and beetle similarity to the donor site

Prediction 1 was rejected as restoration success for the beetle (as measured by Jaccard's similarity to the donor site) in response to the management practices of hay spreading and soil disturbance did not mirror that of the plants. Plant similarity (S_j) to the target grassland community was found to be greatest where hay had been applied, although this showed no interaction with year (Fig 1). The increase in similarity to the target grassland in response to hay spreading was, however, relatively small (*c.* 2-3 %). Neither block, nor any other individual term or interaction between year, soil disturbance or hay spreading influenced plant similarity (Table 1). In contrast to the plants, the similarity of the beetles to the target grassland was positively correlated with the number of years since restoration began, showing a *c.* 5 % increase over the six years (Table 1, Fig 2). However, no other significant individual or interaction terms were found.

Beetle colonisation and persistence

Following the rejection of prediction 1 the effect of beetle traits on colonisation and persistence during restoration were tested. Of 6,733 phytophagous beetles identified to 67 species, 27 reached the threshold abundance (N > 10 individuals) for inclusion in the analysis. Lag times between the establishment of host plants and their colonisation were found for all but two beetle species.

Colonisation lag time was not correlated with the number of individuals collected of each beetle species ($F_{1,25}$=2.43, p=0.13). Phytophagous beetles capable of flight were found to have significantly reduced colonisation lag times ($F_{1,25}$=10.0, p<0.01, R^2=0.29; Fig. 3). However, neither beetle body mass ($F_{1,24}$=0.14, p=0.71) nor the interaction between mass and flight ($F_{1,23}$=0.28, p=0.60) had a significant effect. Larval feeding strategy also significantly influenced colonisation lag times ($F_{3,23}$=12.1, p<0.001; R^2=0.61; Fig. 4), although the covariate coding for beetle genera had no effect ($F_{8,15}$=1.04, p>0.05). The shortest lag time was associated with root-feeding strategies, and the longest with the foliage feeders. Colonisation lag time was not dependent on the degree of host plant specificity (monophagous *vs.* oligophagous / polyphagous) shown by the beetles ($F_{1,25}$=1.12, p=0.30).

Out of the 27 species considered, only two were always found to persist as long as their host plants. In contrast to colonisation lag times, the probability of beetles persisting as long as their host plants was positively correlated with individual species abundance ($F_{1,25}$=11.0, p>0.01). Individual species abundance was thereafter included as a covariate in subsequent analyses of beetle persistence to account for this bias. Host plant specificity did not predict the probability of beetles persisting as long as their host plants ($F_{1,24}$=1.12, p=0.30). However, larval feeding strategy did have a significant effect on beetle persistence ($F_{3,22}=4.12$, $p<0.05$; Fig. 5), although the confounding effect of beetle genera did not ($F_{8,14}=5.82$, $p>0.05$). Beetles with concealed larval feeding strategies (i.e. root-, stem- or inflorescence / seed-feeding) were more likely to persist within the sward than the foliage feeding species.

Discussion

While the addition of seeds within hay overcomes limitations associated with the remnant seed bank of the restoration site for the plants (Walker et al., 2004), this effect was not mirrored for the phytophagous beetles. The rejection of prediction 1 demonstrates that the establishment of host plants alone does not represent the only factor limiting restoration success for the phytophagous beetles. This finding indicates that simply restoring the plants will not necessarily result in the restoration of other trophic levels, and the ability of species to colonize and subsequently persist are factors of key importance. There are a variety of factors which may act to limit the successful establishment of beetle species, for example local suitability of microclimate (Davis et al., 2002; Perner & Malt, 2003), cutting and grazing regimes (WallisDeVries & Raemakers, 2001; Pöyry et al., 2005; Woodcock et al., 2006) and patch quality (Bonte et al., 2003; Krauss et al., 2005). Landscape scale effects such as isolation are also likely to limit colonisation, both for the plants as well as insects in general (Tscharntke & Brandl, 2004). However, while hay spreading can be used to overcome dispersal limitation issues for the plants (Willems, 2001; Walker et al., 2004; Edwards et al., 2007), there exists no equivalent management practice to achieve the same goal for the beetles. That said, it was possible that some individuals were transferred via the hay (Wagner, 2004), although given the fragility of invertebrates mortality resulting from such a dispersal mechanism would be likely to be high. While mechanisms that restrict rates of colonisation and establishment have been widely investigated for plants (e.g. Soons & Heil, 2002; Pywell et al., 2003), they often remain poorly understood for the invertebrates (Ottonetti et al., 2006).

For the beetles, restoration success increased with the number of years since restoration was initiated, independently of the management practices. This suggests that the establishment of species is a gradual process reflecting colonisation from source populations present in other grasslands within the local landscape (Bonte et al., 2003; Tscharntke & Brandl, 2004; Krauss et al., 2005). Ultimately the establishment of phytophagous species will be limited by their requirements for suitable host plants. Given the greater plant similarity of the hay spreading treatments to the target grassland community, it was expected that similarity for the beetles would continue to increase for the hay spreading treatment after that of the control had levelled off. However, there is no evidence for this over the six year period, suggesting that such a divergence point has not yet occurred, possibly reflecting slow rates of colonisation for the beetles. Given that the difference in similarity for the plants between the hay spreading and control treatments were small (*c.* 2-3 %) such a divergence may be hard to detect.

While management was not found to have a direct affect on restoration success for the beetles, there was strong support for prediction 2 that individual species traits were responsible for mediating colonisation and persistence during restoration. The establishment of host plants is arguably a simple basis for assessing habitat quality, and indeed it is likely that many other factors may play an important role in limiting site suitability for colonisation. For example, local microclimate in relation to North or South facing slopes, or sensitivity to cutting or grazing regimes

(WallisDeVries & Raemakers, 2001; Pöyry et al., 2005; Woodcock et al., 2006). Ultimately, however, niche breadth for the phytophagous beetles will have its limits set by the availability of host plants (Woodcock et al., 2008).

Perhaps the most obvious morphological trait found to limit colonisation rates of the phytophagous beetles was their ability to fly (St Pierre et al., 2005; Woodcock et al., 2006). Such evidence for dispersal limitation does highlight the need to consider sites intended for restoration within a landscape context, in particular their proximity to existing areas of species-rich chalk grassland (Bakker & Berendse, 1999). Targeting funding aimed at restoration specifically at sites characterised by low levels of isolation may therefore be an efficient was of promoting restoration of trophic levels other than the plants (Bonte et al., 2003; Tscharntke & Brandl, 2004). While neither colonisation lag times nor the persistence of beetles within the experimental plots was influenced by the degree of host plant specificity (monophagous *vs.* oligophagous / polyphagous), this was not the case for larval feeding strategy. In general, species that fed in a concealed manner, in particular within roots or plant stems, were more likely to colonise host plants and subsequently persist on them once established. The poor colonisation and persistence of beetles with larvae feeding on exposed plant structures, principally the foliage, may have been caused by damage to these structures resulting from grazing management. However, as this study did not specifically test the effects of grazing intensity its effects of colonisation and persistence rates can only be supposition.

Sampling for both the plants and the beetles within this study was limited to a relatively small area (1 m^2) within each experimental plot. This has potential implications for the measurements of similarity made between the experimental plots and the target grassland. Similarity will be affected not only by the species composition of plants and insects, but also by the underlying distribution of plant and insect species, the extent of conspecific aggregation and sample size (Plotkin & Muller-Landau, 2002). While the sample areas within each experimental plot represented 4.0 % of the overall area of each plot, it is probable that different patterns of similarity with the target grassland may have been encountered had sampling occurred at different spatial scales or had larger sampling areas been used. In addition to this issue, the reference community of plants and phytophagous beetles was only surveyed once in the six-year period. Given that it was unlikely that the composition of plants and beetles of this grassland were to remain static from year to year, the validity of this community as a target for measuring restoration success may have limitations (Crofts & Jefferson, 1999; Willems, 2001). However, the target grassland community was sufficiently dissimilar to the experimental plots so that yearly variation in its community structure was not unlikely to be large enough to distort the overall patterns of restoration success described.

In conclusion, it appears that while soil disturbance and hay spreading were not of direct importance in the restoration of chalk grassland phytophagous beetles, the colonization and subsequent persistence of individual species was found to be a function of individual species traits. This effect reflects similar findings in studies investigating species invasion into new communities, where species traits can be used to predict establishment (e.g. Duyck et al., 2007; Ward & Masters, 2007). Importantly, competitive ability can play as important a role as colonisation and thus the long term persistence of species (Duyck et al., 2007), a factor not directly considered here. Ultimately, the rate at which beetles were able to colonise grasslands during restoration represents a limiting factor to the successful enhancement of biodiversity on agriculturally improved grassland. Interestingly, it seems that the establishment of host plants represent only the most basic requirement for the restoration of phytophagous insects. Factors that influence the capacity of individual species to colonise and persist may therefore be acting as an additional filter limiting what assemblage of phytophagous beetles that ultimately becomes established. Understanding what these limitations are provide a first step to developing management strategies that can be used to overcome them and so promote restoration success in these chalk grasslands.

Implications for Practice

- Increased similarity of plants to target species-rich chalk grasslands during restoration was achieved by introducing seeds within green hay.
- Similarity of phytophagous beetles to the target grassland was not influenced by either hay spreading or soil disturbance, but it did increase over time.
- Evidence for dispersal limitation highlighted the need to consider sites intended for restoration within a landscape context, in particular their proximity to existing areas of unimproved species-rich chalk grassland may be vital to achieve restoration success.

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Tables

	Plants	Phytophagous beetles
Whole plot fixed effects		
Hay	$F_{1,18}$= 26.3 ***	$F_{1,17}$= 4.02 ns
Soil	$F_{1,13}$= 1.09 ns	$F_{1,17}$= 1.78 ns
Hay × Soil	$F_{1,12}$= 0.55 ns	$F_{1,16}$= 0.76 ns
Block	$F_{4,14}$= 2.41 ns	$F_{4,12}$=0.42 ns
Error term for tests of whole plot effects = Hay × Soil × Block		
Repeated measurements and interactions		
Year	$F_{1,99}$= 3.51 ns	$F_{1,99}$= 38.6***
Year × Hay	$F_{1,98}$= 2.59 ns	$F_{1,97}$= 1.34 ns
Year × Soil	$F_{1,97}$= 2.58 ns	$F_{1,98}$= 3.80 ns
Year × Hay × Soil	$F_{1,96}$= 0.00 ns	$F_{1,96}$= 0.13 ns

Table 1. Jaccard's similarity of plants and beetles to a target species-rich chalk grassland in response to the management practices of hay spreading (Hay) and soil disturbance (Soil). To account for repeated measurements from the same experimental plots the whole plot treatment effects of Hay, Soil and block were tested against the error term Hay × Soil × Block. F-values and degrees of freedom have been given for non-significant parameters at the point of deletion. Where: ns = non-significant (p>0.05); *** = p<0.001.

Figure legends

Figure 1. Similarity of plant species to a species-rich chalk grassland in response to restoration management of soil disturbance and hay spreading. Means with the same letter do not differ significantly (P> 0.05).

Figure 2. Similarity of plant (□) and phytophagous beetle (■) species to a species-rich chalk grassland in response to year. Where: ns = non-significant; *** = p<0.001.

Figure 3. Differences in the colonisation lag times for phytophagous beetles according to the flight ability of individual species. Where: n = number of species in each group.

Figure 4 The effect of larval feeding ecology on colonisation lag times for the phytophagous beetle. Means with the same letter do not differ significantly (P> 0.05). Where: infl.= inflorescences; n = number of species in each larval feeding strategy.

Figure 5. The effect of larval feeding ecology on the probability of phytophagous beetles persisting as long as their host plants. Means with the same letter do not differ significantly (P> 0.05). Where: infl.= inflorescences; n = number of species in each larval feeding strategy.

Figures

Figure 1.

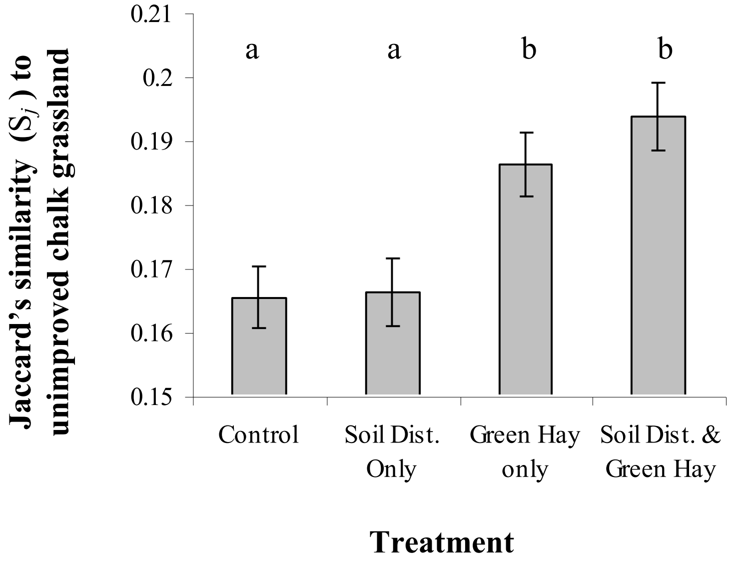


Figure 2

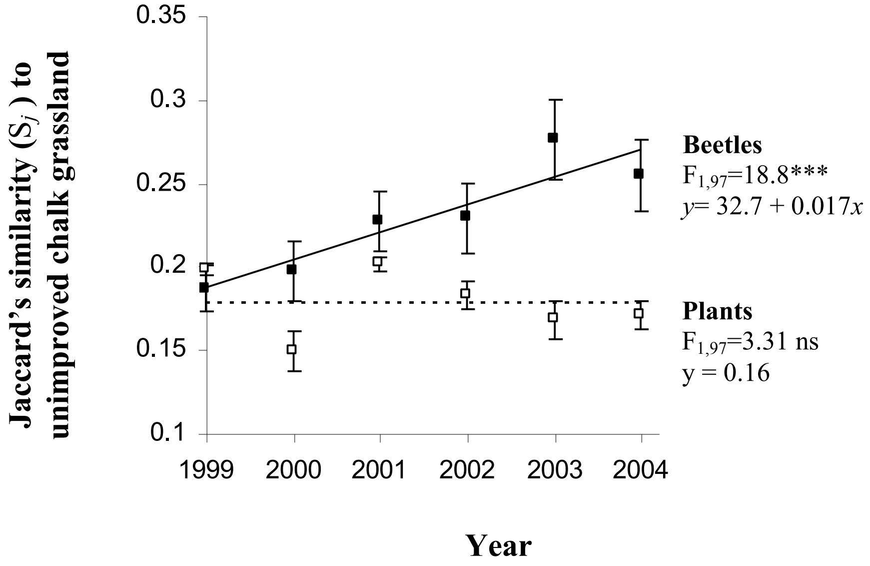
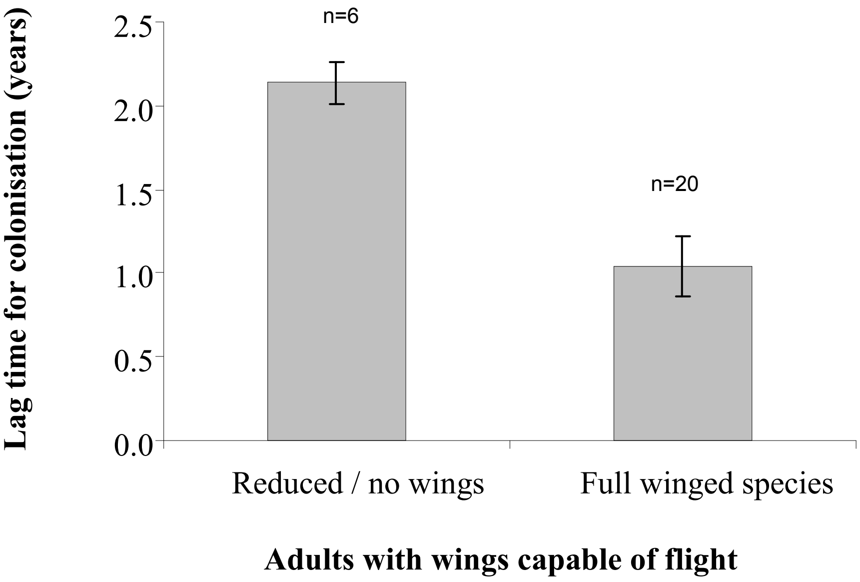

Jaccard's similarity (S_j) to unimproved chalk grassland
0.35
0.3
0.25
0.2
0.15
0.1
1999
2000
2001
2002
2003
2004
Year
Beetles
$F_{1,97}$=18.8***
y= 32.7 + 0.017*x*
Plants
$F_{1,97}$=3.31 ns
y = 0.16

Figure 3



Lag time for colonisation (years)
2.5
2.0
1.5
1.0
0.5
0.0
n=6
n=20
Reduced / no wings
Full winged species
Adults with wings capable of flight

Figure 4.

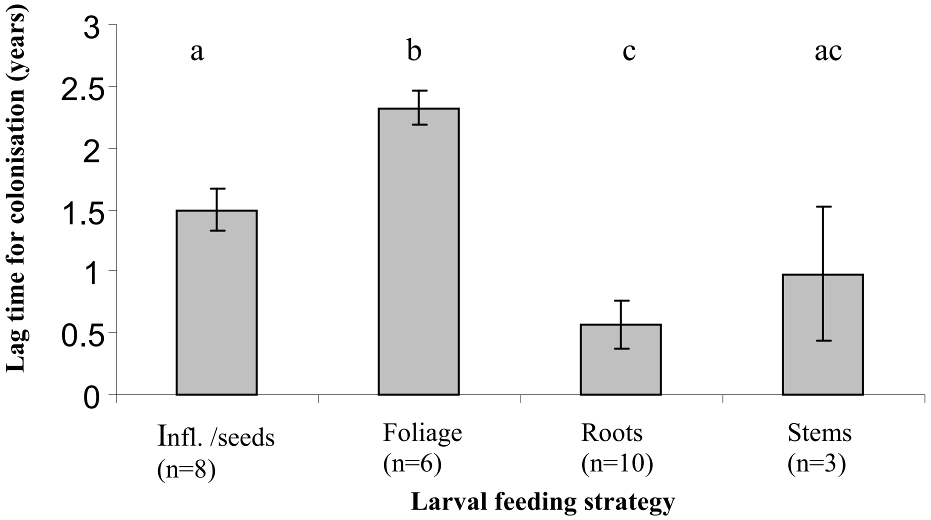
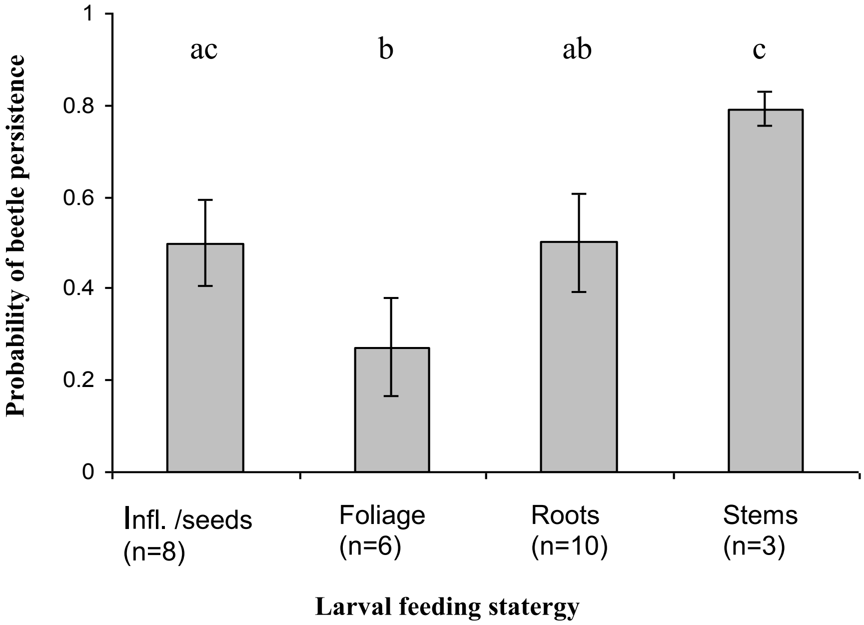

Lag time for colonisation (years)
3
2.5
2
1.5
1
0.5
0
a
b
c
ac
Infl. /seeds
(n=8)
Foliage
(n=6)
Roots
(n=10)
Stems
(n=3)
Larval feeding strategy

Fig. 5



1
0.8
0.6
0.4
0.2
0
Probability of beetle persistence
ac
b
ab
c
Infl. /seeds (n=8)
Foliage (n=6)
Roots (n=10)
Stems (n=3)
Larval feeding statergy