The Restoration of Plant–Pollinator Interactions in Hay Meadows

Mikael Lytzau Forup¹,² and Jane Memmott¹,³

Abstract

Whether restoration programs successfully reinstate ecological interactions remains a contentious and largely untested issue. We investigated plant and pollinator interactions on two old and two restored hay meadows, with the aim of evaluating if quantitative patterns of insect visitation and pollen transport were comparable among old and restored meadows. In terms of structural diversity, few species of plants and insects were shared among the webs. In all four meadows, Diptera and Hymenoptera dominated the visitor community in terms of both species richness and abundance. Coleoptera, Hemiptera, and Lepidoptera comprised the remainder of the flower visitors. No significant difference was found between restored and old sites in plant or insect species richness or in plant and insect abundance. In terms of function, the meadows appeared more similar, although a slightly higher proportion of the potential links between plants and insects was realized for old meadows. No difference was found in the proportion of plant species visited, and visited plant species were generalized, with all having more than a single species of insect visitor. We also sampled approximately 400,000 pollen grains from the flower-visiting insects. There were no differences between old and restored sites in the amount of pollen being transported or in the average number of pollen grains per insect. At both types of meadows, Hymenoptera carried most pollen, followed by Diptera. Again, generalization was the norm, with all plants having more than a single species of pollen carrier. No difference was observed in the connectance of pollen transport webs between old and restored sites. Overall, although the four meadows showed considerable structural variation, they showed similarity with regard to the functional processes we studied. Because structural variation is expected among localities, we conclude that the two restoration projects have been successful.

Key words: flower visitation, plant–pollinator interactions, pollen transport, pollination, restoration ecology, structural versus functional diversity.

Introduction

Standard restoration practice often places emphasis on structural aspects of biodiversity. For example, desired plant species are sown or planted on the restoration site and their presence monitored over time. But structural diversity is a problematic measure when evaluating the restoration of entire communities because of the considerable variation, which often exists among localities. This variation relates to a variety of factors, such as soil nutrient levels, hydrology, landscape context, and chance (Kitching 1987; Warren 1989; Tavares-Cromar & Williams 1996; Tscharntke et al. 2002). One of the challenges facing restorationists is to develop tools for assessing acceptable levels of variability among restored populations. Moreover, there is considerable debate over how to assess restoration, including what constitutes a reference site and what metrics are most appropriate (Pratt 1994).

Here we propose that the interactions between species could prove a valuable metric when comparing restored and reference sites. Because we expect structural variation among sites, a complementary measure of restoration outcome should compare sites in functional terms. Although several studies have found that structure influences function (e.g., Tilman et al. 1996; Cadenasso & Pickett 2000; Spehn et al. 2000), some processes relating to system sustainability may be independent of the structural variation in healthy communities. These processes include trophic interactions, disturbance regimes, pollination, and seed dispersal (Hobbs & Norton 1996; Ehrenfeld & Toth 1997; Montalvo et al. 1997). Thus, it may not be important exactly which species is eating or pollinating which other species, as long as trophic interactions and pollination are taking place. Restorationists should therefore investigate whether key species linkages have been reinstated during the restoration process (Ehrenfeld & Toth 1997; Palmer et al. 1997; Holmes & Richardson 1999). We will illustrate this point by considering plant–pollinator interactions.

The majority of interactions between plants and their flower visitors are embedded in a complex web of interactions (Waser et al. 1996). These plant–pollinator webs can be studied in the manner of conventional food webs (Jordano 1987; Petanidou & Ellis 1996; Waser et al. 1996; Elberling & Olesen 1999; Memmott 1999; Dicks et al. 2002). For example, Memmott (1999) and Dicks et al. (2002) presented quantitative visitation webs for meadow

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communities, where the absolute abundance of each insect species and each insect-pollinated plant species was shown, along with the frequencies of interactions between them. Such webs provide a flower visitor’s perspective on the quantity, quality, and regularity in nectar and pollen supplies at a given location. Moreover, if pollen is sampled from the flower visitors, data can also be gathered about which visitors are the likely pollinators at the location. Hence, quantitative pollen transport webs provide the plant perspective on the potential for pollination. The insect and plant perspectives may not imply the same about the outcome of a restoration project. For example, there could be no overlap in the pollinator communities on a restored site and a reference site, but if pollen is transported in a similar manner on both, the restoration project could be successful from the perspective of the plant community.

Quantitative interaction webs can be used to study the restoration of pollination processes. Web statistics, such as species number, species abundance, connectance, and linkage density, which are all readily calculated from quantitative interaction webs, can subsequently be compared among restored sites and reference sites. This then allows restoration projects to be described in functional as well as in structural terms. The result is a more comprehensive analysis of the restoration outcome. For example, in food webs where large and small organisms eat each other, connectance should vary between 0.02 and 0.1 (Martinez et al. 1999). Thus, if a restored site has a connectance value differing by an order of magnitude from these values, the restorationist should be suspicious of the success of the project.

Hay meadows represent some of the most species-rich plant communities in the United Kingdom (Rodwell 1992; Blackstock et al. 1999). As many as 97% of the British meadows have disappeared, and some are still threatened (Feltwell 1992). Meadow restoration, along with meadow creation, is an important part of the conservation effort. In this article, we illustrate our interactions approach by quantifying the pattern of insect visitation and pollen movement in two restored and two old hay meadows to assess the efficacy of the restoration programs. We do this by using quantitative visitation and pollen transport webs to characterize the plant–pollinator communities at the four sites and then comparing and contrasting the resulting webs. The specific objectives are 3-fold: (1) to determine whether the pattern of insect visitation is comparable in old and restored meadows; (2) to determine whether the pattern of pollen movement is comparable in restored and old meadows; and (3) to use the data to decide whether pollination has been successfully reinstated.

Methods

Study Sites

Four hay meadows were chosen near Bristol in the southwest of England (Table 1). An annual hay cut and the absence of livestock grazing characterize the management

<table>
<thead>
<tr>
<th>Plants</th>
<th>Insects</th>
<th>Age (year)</th>
<th>Size (ha)</th>
<th>Floral Abundance</th>
<th>Number of Species Found on Flowers</th>
<th>Number of Species Visiting Flowers</th>
<th>Number of Species Found</th>
<th>Number of Species Visiting</th>
<th>Connectance</th>
<th>Linkage Density</th>
</tr>
</thead>
<tbody>
<tr>
<td>Old meadows</td>
<td>Meadow 1</td>
<td>&gt;100</td>
<td>279.5 W</td>
<td>7.5</td>
<td>121,381</td>
<td>26</td>
<td>37</td>
<td>55.2</td>
<td>61.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Meadow 2</td>
<td>&gt;100</td>
<td>234.4 W</td>
<td>2.5</td>
<td>34,131</td>
<td>16</td>
<td>65</td>
<td>36.3</td>
<td>34.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Meadow 3</td>
<td>Approximately 10</td>
<td>239.0 W</td>
<td>9.0</td>
<td>31,650</td>
<td>28</td>
<td>72</td>
<td>51.1</td>
<td>43.0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Meadow 4</td>
<td>Approximately 20</td>
<td>236.4 W</td>
<td>1.0</td>
<td>27,518</td>
<td>26</td>
<td>106</td>
<td>119.7</td>
<td>106.6</td>
<td></td>
</tr>
<tr>
<td>Restored meadows</td>
<td>Meadow 5</td>
<td>Approximately 10</td>
<td>227.2 N</td>
<td>1.0</td>
<td>75</td>
<td>29</td>
<td>79</td>
<td>68.6</td>
<td>69.0</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Meadow 6</td>
<td>Approximately 20</td>
<td>225.2 N</td>
<td>1.0</td>
<td>106</td>
<td>79</td>
<td>79</td>
<td>70.6</td>
<td>70.5</td>
<td></td>
</tr>
</tbody>
</table>

Table 1. Descriptive statistics for four hay meadows in the Bristol area.

Methods

Study Sites

Four hay meadows were chosen near Bristol in the southwest of England (Table 1). An annual hay cut and the absence of livestock grazing characterize the management...
of these meadows. Each meadow was within 6 km of the other meadows. Meadow 1 and Meadow 2 were old meadows dating back to before agricultural intensification, and they were therefore reference sites. Meadow 1 was adjacent to a quarry but set in a mosaic of woodland, farmland, and a golf course, whereas Meadow 2 was surrounded by suburban development and farmland. In contrast, Meadow 3 and Meadow 4 were recently restored meadows. Meadow 3 was set in the same mosaic as Meadow 1, which was 1 km away. Meadow 3 was restored in the early 1990s. Prior to this, the meadow formed part of a golf course. It was frequently mowed, and fertilizers were likely used to improve the sward. The restoration of this meadow simply involved the return to traditional management, that is, an annual hay cut. Meadow 4 was established in 1981 in a section of a formal city park, surrounded mainly by residential houses and gardens. The park, which originally consisted of steep slopes grazed by sheep, was landscaped in the 1920s and 1930s. In the time between landscaping and restoration, Meadow 4 was a frequently mowed lawn where soil fertility was maintained by fertilizer application. The restoration of Meadow 4 consisted of the translocation of turfs from another meadow to a section of Meadow 4, some planting of wild flower plugs, some sowing of flower seed, and a return to an annual hay cut (H. Hall 2000, Avon Wildlife Trust, personal communication). Pollinators were plentiful at each site, moving through the landscape via hedges, gardens, and other seminatural corridors.

Quantitative Flower Visitation Webs

A 100 × 100-m plot was established in each of meadows 1, 2, and 3. All of Meadow 4 was used because of the small size of this meadow (Table 1). On each sampling occasion, two 50 × 2-m transects were chosen at random within the plot. Sampling began in early May 2000, when the plants were beginning to flower, and was carried out every 13–15 days until the end of July when three of the meadows were cut. The hay was cut in Meadow 2 at the end of June, and therefore only four samples were obtained from this meadow, compared with the six from the other three meadows. Sampling was carried out on "good" pollinator days, here defined as dry, sunny days with no more than moderate wind speeds.

In each transect, the identity of all insect-pollinated plant species was recorded, along with the number of flower heads. Following plant identification, the transect was left for a minimum of 5 minutes to allow insects to re-disperse into the area. After this period the transect was walked again, but this time all insects observed visiting flowers up to 1 m ahead of the recorder were captured. No a priori decisions were made concerning if an insect was likely to be a pollinator; rather, all insects visiting flowers were collected. They were either caught using a sweep net or captured directly into a killing tube (2.5 × 8.5 cm), which contained a shallow (1–2 cm) layer of plaster of Paris in the bottom, into which was added a few drops of ethyl acetate. The killing tube was lined with a small paper bag and this, together with a paper disk that lined the vial cap and was replaced after each catch, prevented insects from touching the sides of the glass vial, which could subsequently be used for new catches with a low risk of pollen contamination. Once an insect was anesthetized, the bag containing the insect was removed from the glass tube, folded shut, marked with host flower species, and transferred to a larger killing jar. Hoverflies, butterflies, and moths were identified to species by the authors; all other insects were identified to species by taxonomists at the National Museum of Wales.

Pollen Transport Webs

A pollen reference collection was made of all insect-pollinated plant species found in or near the meadows during the field season. Flower buds were collected in the field and left to mature and open in the laboratory. Once the flower opened and the anthers dehisced, pollen was collected, stained with fuchsin pink, and mounted on a microscope slide (Fægri & Iversen 1975). The resulting reference collection was used for identifying the pollen on the coats of the insects.

Each sampled insect was systematically dabbed with a 5 × 5-mm square of fuchsin pink gel (Kearns & Inouye 1993). Pollen storage areas were avoided, for example, pollen baskets on bumblebees, because these contain pollen unlikely to be available for pollination. The forceps used for holding the square of staining gel were sterilized over a flame between handling insects. After allowing at least 24 hour for the stain to work, the pollen samples were identified under the light microscope. However, certain pollen grains were not easily distinguished under the light microscope. Hence, the composites Rough hawk’s-beard (Crepis biennis), Smooth hawk’s-beard (C. capillaris), Beaked hawk’s-beard (C. vesicaria), and Cat’s-ear (Hypochaeris radicata) were amalgamated into one species group, whereas the buttercups Meadow buttercup (Ranunculus acris), Bulbous buttercup (R. bulbosus), and Creeping buttercup (R. repens) were amalgamated into another. Pollen not matching any grains in the reference collection was recorded as "unknown." Only pollen grains recorded five or more times from an insect were used in the analysis. This reduced the risk of pollen contamination, potentially occurring in the insect net or subsequent handling of the insect, biasing the results.

Data Analysis

The interaction web from each meadow was drawn using a program written in Mathematica (Wolfram Research, Inc., Champaign, IL, U.S.A.). In order to compare insect visitation in the restored and old meadows, the following statistics were calculated for each visitation web: (1) the number of flowering plant and insect species; (2) the
abundance of flowers and insects; (3) the proportion of plant species visited; (4) the median number and range of insect species visiting each plant species; (5) the median number and range of plant species visited by each insect species; (6) linkage density; (7) web connectance; and (8) the Berger–Parker dominance index for the number of plants visited by each insect species.

Because pollinator sampling is unlikely to be complete (Lande 1996), we compared the number of observed insect species to estimates of the “true” species diversity generated by nonparametric richness estimators. Colwell and Coddington (1994) evaluated the performance of eight such estimators and concluded that the Chao 2 (Chao 1987) and second-order jackknife (Smith & van Belle 1984) estimators performed best for a small number of samples, followed by the first-order jackknife estimator (Burnham & Overton 1979; Heltsh & Forrester 1983) and the Michaelis–Menten method (Raaijmakers 1987). Consequently, we calculated all four statistics using software written by Colwell (1997). For comparison, we calculated the same statistics for the visitation data in Memmott (1999), which were obtained from an old meadow close to Meadow 1 but sampled at a much higher intensity (2,722 recorded interactions) over a shorter period (1 month).

In order to compare pollen movement in the old and restored meadows, the following statistics were calculated for each pollen transport web: (1) the number of pollen species groups; (2) pollen abundance; (3) the proportion of pollen groups being carried at each site; (4) mean pollen abundance per insect species; (5) the median number and range of pollen species found on each insect species; (6) the median number and range of pollen transporters per plant species; (7) linkage density; (8) web connectance; and (9) the Berger–Parker dominance index for the number of pollen groups carried by each insect species. Linkage density and connectance are statistics that index the level of interactions, potential competition, and overall interconnectedness of food webs (May 1974; Pimm 1982). The ratio of links per species, linkage density, $L$, has the formula

$$L = \frac{l}{i + p} \tag{1}$$

where $l$ is the number of observed linkages, $i$ is the number of insect species in the sample, and $p$ is the number of plant species. Thus, the potential range of $L$ is sensitive to the number of species. Connectance, $C$, is the fraction of realized links in the web, and in these plant–pollinator webs it has the following formula (Jordano 1987)

$$C = \frac{l}{ip} \tag{2}$$

The number of links ($l$) is counted simply as present or absent and does not involve any measure of the frequency. Consequently, this statistic could hide a difference in visitation pattern because an insect could specialize in a particular plant and occasionally visit others, or it could divide its visits equally between species. To overcome this problem, we calculated a plant dominance index for each insect species, quantifying the equitability of both their flower choices and the pollen species they transported. We used the Berger–Parker dominance index, $d$, which has low sensitivity to sample size, is conceptually simple (Southwood 1996), and characterizes the distribution at least as well as most other indexes (May 1975). It simply expresses the proportion of the total catch that is due to the dominant species. In this situation, it provides a measure of the equitability of the interactions that each insect species makes with plants; thus, if an insect visited five plant species, does it mostly visit one species, or does it visit most species equally? We calculated $d$ from the formula

$$d = \frac{N_{\text{max}}}{N_t} \tag{3}$$

where $N_{\text{max}}$ is the frequency of the most common interaction, which each insect species made, and $N_t$ is the total abundance of interactions recorded for that insect species.

We used repeated measures analysis of variance (Sokal & Rohlf 1995) to investigate the effect of meadow status (old or restored) on plant and insect species richness, plant and insect species abundance, the proportion of plant species visited, and the number of pollen grains per insect. Where necessary, data were either log or arcsine transformed to meet the assumptions of normality, and the two missing samples from Meadow 2 were treated as missing values. Kruskal–Wallis tests were used to determine the impact of meadow status on the median number of insect species visiting each plant species, the median number of plant species visited by each insect species, the median number of pollen species found on each insect species, and the median number of pollen transporters per plant species. If a significant difference was found between the four meadows, an adaptation of the Tukey test was used to test for differences between the four meadows (Daniel 1990). Connectance and linkage density were compared among old and restored meadows in two-sample $t$ tests (Sokal & Rohlf 1995). The visitation webs were analyzed using Mantel tests (Mantel 1967), which estimate the association between two independent matrices describing the same set of entities (here matrices of interactions between plants and insects). All four matrices were tested against each other.

**Results**

**Structural Diversity**

Overall, 42 plant species and 85 flower-visiting insect species were found in the meadows. Aside from Meadow 2, which was mown early and therefore sampled less, the number of plant species was similar among the meadows (Table 1). However, there was little species overlap: only 8
of the 42 insect-pollinated plant species recorded in trans-
sects grew on all four meadows. There was more variation
in the number of insect species per meadow (Table 1), but
again with only a modest species overlap: just 7 of the
overall 85 flower-visitor insect species were recorded in
all four meadows. No insects were specific to old mead-
ows, and although two insect species were only found in
the restored meadows, these species were rare and their
association with restored meadows probably reflects the
fact that very few were caught. Diptera and Hymenoptera
always dominated the insect communities, whereas the
remainder belonged to Coleoptera, Hemiptera, and Lepi-
doptera. The four visitation webs are shown in Figure 1.
The purpose of these webs is to provide overviews of the
quantitative differences between webs, and it is apparent
that there was considerable variation in the abundance of
flowers and insects among the meadows. The meadow
with the highest floral abundance was Meadow 1, but here
the flower count was inflated by Black medick (Medicago
lupulina), a small fabaceous plant, whose flowers were not
visited by any insect during sampling. This species aside,
the four meadows showed similar floral abundances.
Insect abundance was more varied across the meadows.
However, because Meadow 1 (old) and Meadow 4
(restored) had most insects, these differences were not
clearly related to meadow status. In all cases, the observed
number of insect species was much lower than the diver-
sity suggested by the nonparametric estimators (Table 1).
For the two old meadows, the observed number of visitor
species was about two-thirds of those estimated by Chao 2
and the two jackknife estimators, whereas for the restored
meadows the observed species richness was closer to half
the predicted values. In all four cases, the Michaelis–
Menten estimator predicted even higher diversity. The
considerable extra sampling effort in Memmott (1999) re-
sulted in a closer agreement between the observed and
estimated insect diversity. The observed value of 79
species was about four-fifths of the estimated values.

Functional Diversity
The number of interactions in the visitation webs was
related to the abundance of insects, and it was therefore
greatest on the old Meadow 1 and the restored Meadow 4
(Table 2). However, the proportion of plant species actu-
ally visited was similar across the four meadows. Less than
half of the plant species in each web were visited during
the study, and the least abundant plants were unlikely to

Table 2. Food web statistics for the visitation webs.

<table>
<thead>
<tr>
<th></th>
<th>No. of Interaction Types</th>
<th>Proportion of Plants Visited</th>
<th>Median (Range) Insect spp./Plant sp.</th>
<th>Median (Range) Plant spp./Insect sp.</th>
<th>C</th>
<th>L</th>
<th>Berger–Parker Index</th>
</tr>
</thead>
<tbody>
<tr>
<td>Old meadows</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Meadow 1</td>
<td>69</td>
<td>0.39</td>
<td>1 (0–14)</td>
<td>1 (1–5)</td>
<td>0.0717</td>
<td>1.1129</td>
<td>0.8309</td>
</tr>
<tr>
<td>Meadow 2</td>
<td>34</td>
<td>0.41</td>
<td>0 (0–11)</td>
<td>1 (1–3)</td>
<td>0.0885</td>
<td>0.8500</td>
<td>0.8824</td>
</tr>
<tr>
<td>Restored meadows</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Meadow 3</td>
<td>40</td>
<td>0.30</td>
<td>0 (0–13)</td>
<td>1 (1–4)</td>
<td>0.0510</td>
<td>0.7143</td>
<td>0.8851</td>
</tr>
<tr>
<td>Meadow 4</td>
<td>71</td>
<td>0.43</td>
<td>0 (0–20)</td>
<td>1 (1–4)</td>
<td>0.0515</td>
<td>0.8987</td>
<td>0.8816</td>
</tr>
</tbody>
</table>

Listed Berger–Parker indexes are site averages.
be visited (Fig. 1). As a consequence, the median values of insect species per plant species are very low (1, 0, 0, and 0 for meadows 1, 2, 3, and 4, respectively). However, the ranges vary widely for the individual plant species, and when only those species that were visited during the study are considered, the medians are 3.5 and 5.5 for meadows 1 and 2, respectively, and 2.0 and 3.5 for meadows 3 and 4, respectively. Therefore, pollinator generalization appears to be the norm for these visited plant species. In contrast, insect species were more specialized, visiting a median of one species of plant on all sites, although this is almost certainly a consequence of the high number of insect species represented by a single individual. Obviously, if an insect species is only collected once, the species is recorded as visiting a single plant species, and a large number of such insects can therefore bias the sample toward appearing specialized. Connectance in all the meadows was low, between only 5 and 9% of potential interactions were realized (Table 2). The old meadows had slightly higher connectance than the two restored meadows; thus, a higher proportion of potential links was realized (Table 2). However, this difference was statistically weak (two-sample \( t = 4.52, p = 0.069 \)). There was no suggestion of systematic differences in linkage density or in the Berger–Parker dominance indexes among the four sites (Kruskal–Wallis \( H = 9.14, p = 0.031 \)). However, looking at the mean index per site (Table 4) it is apparent that this difference is independent of site status.

Pollination process appears to be the norm for both plants and insects because all insect species carried a median number of pollen species greater than one, and all plants had more than a single pollen carrier (Table 4). These data for insects contrast with the visitation data where many insects appeared to be specialized.

There were no systematic differences in connectance or linkage density between old and restored meadows. When comparing connectance or linkage density between the visitation and pollen transport webs, the pollen transport webs had significantly higher values: between 20 and 46% of potential interactions were realized in the pollen transport webs compared to 5 and 9% in the visitation webs (connectance: two-sample \( t = 9.26, p = 0.001 \); linkage density: two-sample \( t = 6.71, p = 0.003 \)). Thus, pollen transport webs are significantly more complex than visitation webs. This reflects the fact that the pollination data provide a qualitative summary of past visitation rather than the snapshot provided by the visitation data.

Discussion

Our data show that although the four meadows were structurally very different, they were apparently similar in other respects: there were no significant differences between restored and reference meadows in plant or insect species richness, in the proportion of flower species visited by insects, in the numbers of pollen grains being moved by flower visitors, or in the number of links per species.

In this section, we first outline potential sources of bias in the construction of the webs. We then discuss the success of the restoration programs and the structure of the plant–pollinator community at the four sites. Next, we use our data to consider whether or not pollination processes have been restored successfully. We end by discussing
whether it matters if particular species are restored or whether it is more important that a function (here pollination) is restored.

Limitations in the Construction of the Webs

The results showed that old and restored meadows were similar in some respects. However, the methodology used may not have been rigorous enough to pick up subtle differences among old and restored meadows. For example, it would have been preferable to sample more than just four meadows. This would overcome such management-related differences as the timing of the annual hay cut. Thus, old meadows could perhaps turn out to be more similar than suggested in our study, where Meadow 2 was cut much earlier than Meadow 1. However, food webs in general are rarely replicated (Cohen et al. 1993) due to the huge amount of work involved in their construction, and restoration ecology in particular is subject to experimental design difficulties (Simberloff 1990; Michener 1997). Therefore, the fact that the webs are replicated at all has been an improvement on traditional approaches.

Other limitations with the dataset are 3-fold. First, we recorded only diurnal flower visitors, even though we were aware that night-flying moths were present at the sites. However, there are practical problems associated with obtaining visitation data for moths because when light is used as an attractant, moths are likely to be attracted from outside the meadow. Second, we did not sample very small flower-visiting insects found deep within the flowers, such as thrips (Thysanoptera) and pollen beetles (Coleoptera: Kateretidae and Nitidulidae). Few pollination studies include these groups, although they may be important pollinators, particularly in systems where they are superabundant (Hagerup 1950; Hagerup & Hagerup 1953; Ananthakrishnan 1993; Roubik 1993; Williams et al. 2001). However, studies frequently identify Hymenoptera as the most important pollinators (Corbet et al. 1991), and this group, together with the Diptera, might have been better sampled in this study, relative to Lepidoptera, Thysanoptera, and Coleoptera. Third, it would have been ideal to sample more insects from each site: overall a total of 344 visitation interactions and 879 pollen transport interactions between plants and insects were recorded. Although we sampled 85 insect species, 42 plant species, and approximately 400,000 pollen grains, many interactions were undoubtedly missed. Indeed, the observed diversity was much less than that predicted by the

**Table 4. Food web statistics for the pollen transport webs.**

<table>
<thead>
<tr>
<th>Pollen Groups</th>
<th>Pollen Abundance</th>
<th>Proportion of Plants Carried</th>
<th>Interaction Types</th>
<th>Median (Range) Carrier spp./Plant sp.</th>
<th>Median (Range) Pollen spp./Insect sp.</th>
<th>Berger–Parker Index</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Old meadows</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Meadow 1</td>
<td>20</td>
<td>106,055</td>
<td>0.95</td>
<td>185</td>
<td>6 (1–32)</td>
<td>4 (1–13)</td>
</tr>
<tr>
<td>Meadow 2</td>
<td>11</td>
<td>93,175</td>
<td>0.65</td>
<td>82</td>
<td>4 (1–22)</td>
<td>3 (1–8)</td>
</tr>
<tr>
<td><strong>Restored meadows</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Meadow 3</td>
<td>18</td>
<td>86,231</td>
<td>0.72</td>
<td>168</td>
<td>4 (1–13)</td>
<td>3 (1–11)</td>
</tr>
<tr>
<td>Meadow 4</td>
<td>23</td>
<td>111,032</td>
<td>0.96</td>
<td>254</td>
<td>5.5 (1–25)</td>
<td>4 (1–14)</td>
</tr>
</tbody>
</table>

Listed Berger–Parker indexes are site averages.

Figure 2. Quantitative pollen transport webs for the four hay meadows. The pollen groups are shown as rectangles at the top of each web, whereas insects are shown at the bottom. Interactions link the pollen and insect species. The relative abundance of the species is indicated by the width of the rectangles, and the frequency of each interaction type is indicated by the width of the line. Hymenoptera are shown in black, and the webs are drawn to the same scale.
nonparametric estimators. The larger dataset in Memmott (1999) showed a much better agreement between observed and estimated insect diversity. However, the data in Memmott (1999) come from a meadow in close proximity to Meadow 1, and we would expect the predicted diversity values for these two meadows to be more similar than they were. It is therefore possible that the estimators do not perform well on these time series. For example, it seems extreme when the Michaelis–Menten estimator suggests a true species diversity of almost twice the number of individuals caught on Meadow 4. At any rate, the observed visitor richness cannot be regarded as near-complete representations of the diversity on the four meadows. Thus, we emphasize that these webs do not represent complete pollination webs but that they provide comparative insights into the food base of insects foraging on flowers as well as quantitative estimates of the potential pollinators for the meadow plant species.

The most obvious problem with the limited sampling is that we cannot assess the importance of any missed species for the pollination of the meadow plants. However, this problem would be more relevant if the restored webs had showed markedly reduced connectance values because we would then be unable to assess whether this was a true pattern or whether it reflected incomplete sampling.

The Restoration Outcome

The two restored meadows were structurally very different from the old meadows, but although our samples do not represent the complete interaction webs, they do indicate that processes of visitation and pollen transport occur at rates comparable to those of old sites. Thus, insects find forage on the restored meadows, and they provide an important part of the pollination service, namely pollen transport. However, if the goals were to copy the community structure of a given old meadow, the restoration projects were clearly unsuccessful. In practice though, restorationists are unlikely to attempt building exact copies, given that many unknowns, coupled with financial and social constraints, make the undertaking extremely unlikely to succeed (Ehrenfeld 2000). Moreover, the present study confirms that reference information must be treated cautiously: the two old meadows were so structurally different that selecting either community as the restoration target should be done only if a detailed comparison confirmed similar physical and biological factors acting on this and the restoration site. However, restorationists are more likely to restore some basic community structure and let restored communities mature in response to local physical factors, species pool, landscape connectivity, etc. (Pratt 1994; Parker 1997; Callicott 2002). Therefore, if the restoration goals were, more realistically, to restore hay meadows with at least some of the species observed in existing hay meadows and with similar patterns of flower visitation and pollen transport, then these restoration projects have been successful.

Visitation and Pollen Web Data

The summary statistics from the visitation webs can be compared to values in published visitation webs. The connectance values lie between the published values of 0.036 for a conifer forest and grassland web in Colorado (Waser et al. 1996) and the average connectance of 0.294 for the several webs listed in Jordano (1987). Although a few studies have investigated pollen loads in a flower-visiting assemblage, these have previously been within taxonomic subgroups of flower visitors, e.g., hawkmoths (Kislev et al. 1972), hoverflies (Haslett 1989), or hummingbirds (Feinsinger et al. 1987). We are not aware of any published studies describing pollen loads quantified for a whole community.

Although the difference was statistically weak, it is interesting that connectance was higher on the old meadows. Dunne et al. (2002) found that food web robustness increases with connectance. The lower connectance values of the restored meadows may suggest that these communities are in a greater state of flux than the old meadows and still changing in response to the restoration management (Jordano et al. 2003). The reason why the connectance and linkage densities were significantly higher for the pollen transport webs than for the visitation webs is that the pollen transport data provide a history of past flower visitation. The pollen transport data show that the visitation data do not adequately predict pollination. For example, interactions that occurred at high frequencies in the visitation web, occurred at low frequencies in the pollen transport web, or failed to appear (e.g., interactions between Ranunculus spp. and the Anthomyiidae). Looking at the data overall, 18% of individual insects did not carry pollen from the plant species they had just visited. However, pollen transport is not a complete predictor of pollination either; future work might consider the more ambitious task of constructing true pollination webs in which the interactions between insects and plants equate to seed production, rather than the number of foraging bouts to the various plant species or the movement of their pollen.

The Restoration of Pollination Processes

Mutualistic interactions, such as pollination and seed dispersal, presumably play a pivotal role in population establishment, reproduction, migration, and community development (Montalvo et al. 1997). Leong (1994) reported that in a Californian pollination system consisting of andrenid bees and annual plants, visitation rates, numbers of taxa, and seed set were all lower in restored habitats in comparison with pristine habitats. This suggests that the restoration of pollination processes may not automatically follow the reinstatement of target plant species. In contrast, we have found no quantitative differences in the functional biodiversity of plant and flower visitors on the old and restored meadows, aside from a slight difference in visitation web connectance.
Does It Matter that Few Species Are Shared Among Webs?

Our data suggest that it does not matter for the overall processes of flower visitation and pollen transport that few species were shared among the webs. However, because the data do not consider pollinator effectiveness, they cannot adequately evaluate if the low species overlap causes the meadows to function differently. Rather they indicate differences at larger taxonomic scales. For example, the pollen transport webs clearly show that Hymenoptera are much more efficient pollen transporters than any other group, and rare bee species could therefore turn out to be much more important pollinators than common species of fly. Fundamentally, however, we should expect considerable variation among the four meadows. For example, pollinator communities can exhibit considerable spatial and temporal variation (e.g., Herrera 1988; Gilbert & Owen 1990; Potts et al. 2003), and entomophilous flowers in temperate areas often have diverse pollinator faunas and thus appear well buffered against a disruption in pollinator services (Bond 1994). This could be particularly evident in temperate meadow communities, such as these, which experience a major annual disturbance when the hay is cut.

Using Species Interactions in Restoration Ecology

Although there has been a recent spate of studies investigating species interactions at the community level (e.g., Reed 1995; Dicks 2002; references in Ollerton & Cranmer 2002; Potts et al. 2003), this approach is rare in restoration research. However, communities of interacting species have been used to investigate the impact of habitat fragmentation upon community structure (Krueiss & Tscharntke 1994; Gilbert et al. 1998), nontarget effects in biological control (Henneman & Memmott 2001), and the impact of insecticide spraying on pest populations in rice ecosystems (Cohen et al. 1994). Reproductive mutualisms, such as pollination and seed dispersal, epitomize the subtle, complex web of interactions, which, if broken by human actions, could cause a cascade of extinctions (Bond 1994). Community-level approaches such as the one described here can start to reveal whether restored sites are “working” from a functional as well as a structural point of view. We hope that ecological restorations will increasingly be designed with respect to later evaluations of both structural and functional aspects because this will provide a more comprehensive measure of their sustainability.

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