The restoration of ecological interactions: plant-pollinator networks on ancient and restored heathlands

Article (Unspecified)

The restoration of ecological interactions: plant–pollinator networks on ancient and restored heathlands

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Summary

1. Attempts to restore damaged ecosystems usually emphasize structural aspects of biodiversity, such as species richness and abundance. An alternative is to emphasize functional aspects, such as patterns of interaction between species. Pollination is a ubiquitous interaction between plants and animals. Patterns in plant–pollinator interactions can be analysed with a food web or complex-systems approach and comparing pollination webs between restored and reference sites can be used to test whether ecological restoration has taken place.

2. Using an ecological network approach, we compared plant–pollinator interactions on four pairs of restored and ancient heathlands 11 and 14 years following initiation of restoration management. We used the network data to test whether visitation by pollinators had been restored and we calculated pollinator importance indices for each insect species on the eight sites. Finally, we compared the robustness of the restored and ancient networks to species loss.

3. Plant and pollinator communities were established successfully on the restored sites. There was little evidence of movement of pollinators from ancient sites onto adjacent restored sites, although paired sites correlated in pollinator species richness in both years. There was little insect species overlap within each heathland between 2001 and 2004.

4. A few widespread insect species dominated the communities and were the main pollinators. The most important pollinators were typically honeybees (*Apis mellifera*), species of bumblebee (*Bombus* spp.) and one hoverfly species (*Episyrphus balteatus*). The interaction networks were significantly less complex on restored heathlands, in terms of connectance values, although in 2004 the low values might reflect the negative relationship between connectance and species richness. Finally, there was a trend of restored networks being more susceptible to perturbation than ancient networks, although this needs to be interpreted with caution.

5. *Synthesis and applications.* Ecological networks provide a powerful tool for assessing the outcome of restoration programmes. Our results indicate that heathland restoration does not have to occur immediately adjacent to ancient heathland for functional pollinator communities to be established. Moreover, in terms of restoring pollinator interactions, heathland managers need only be concerned with the most common insect species. Our focus on pollination demonstrates how a key ecological service can serve as a yardstick for judging restoration success.

Key-words: complex system, ecological restoration, food web, heathland, network, pollination web, pollination

Introduction

Terrestrial restoration projects focus normally on some basic core of the target community, usually the dominant plant species, in the hope that natural processes will subsequently steer the community on a trajectory towards complete restoration (Palmer, Ambrose & Poff 1997). However, ecologists

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rarely possess complete records of the structure of a historical community, let alone regional species pools. This makes it difficult to define an exact target community for the restoration process and to evaluate later if the community has been returned to its original state. Moreover, an approach that aims to restore some historical community structure is fundamentally flawed where landscape properties have changed and can no longer sustain the target community (Cairns & Heckman 1996; Palmer, Ambrose & Poff 1997; Ehrenfeld 2000). Similarly, the use of reference communities as targets to aim for in the restoration process can be inappropriate, because species composition is expected to vary between localities in response to variations in soil type, hydrology, aspect, disturbance frequency, size and composition of the local species pool, landscape connectivity, priority effects and chance events (Jordano 1994; Williams *et al.* 1996; White & Walker 1997; Potts *et al.* 2003; Young, Petersen & Clary 2005). In planning and evaluating restoration projects, therefore, a purely structural focus is inadequate. An alternative is to consider function, i.e. what constituent species do rather than simply recording whether or not they are present (Ehrenfeld & Toth 1997). Indeed, a direct functional comparison of successfully restored and target habitat is possible when considering ecological processes that should not vary between localities, such as processes needed for target plants to survive and reproduce.

Pollination is one of several ecosystem services that must be reinstated for ecological restoration to be successful. Pollination by animals is ubiquitous in terrestrial habitats, involving 67% of flowering plant species (Kearns & Inouye 1997) and an equivalently high diversity of insect species (Nabhan & Buchmann 1997). However, plant–pollinator interactions may not re-establish automatically themselves in communities undergoing restoration management, because pollinators establish populations only once their habitat requirements have been met. For example, in addition to food resources, bees require nesting sites and nesting materials (e.g. Kearns, Inouye & Waser 1998; Gathmann & Tscharntke 2002). These features make pollination a useful functional bio-indicator for comparing restored communities to reference communities.

Connections between plants and pollinators can be analysed for entire ecological communities using a food web approach (Jordano 1987; Waser *et al.* 1996; Memmott 1999; Dicks, Corbet & Pywell 2002; Memmott & Waser 2002; Vázquez & Aizen 2003) or, more generally, a complex systems approach (Bascompte *et al.* 2003; Jordano, Bascompte & Olesen 2003; Memmott, Waser & Price 2004). The recent surge in work investigating the properties and consequences of network structure has yielded many new insights (Jordano, Bascompte & Olesen 2006), some of which have implications for restoration ecology. For example, the way interaction webs assemble is relevant for restoration projects, and both Dunne, Williams & Martinez (2002) and Jordano *et al.* (2003) have shown that the build-up of ecological interaction networks is not explained adequately by 'preferential attachment' to highly connected nodes, as seen in many other real-world networks (Barabási & Albert 1999).

In addition to providing a target community structure, information on interaction networks also enables the robustness of a whole community to be ascertained, providing a powerful tool to test the impact, on community structure, of 'that most insidious type of extinction, the extinction of ecological interactions' (Janzen 1974). For example, modelling the removal of pollinator species from two plant–pollinator networks, Memmott, Waser & Price (2004) found that the greatest effect on plant survival occurred when generalist pollinators were removed. By comparing the robustness of networks from restored sites to those from ancient sites, the ability of restored sites to withstand future natural and man-made perturbations can be assessed.

Here we use a network approach to evaluate the outcome of heathland restoration in the county of Dorset, southern England. We focus on the following three questions: (1) has pollination been reinstated in restored heathlands; (2) do insect species which visit flowers on restored heaths originate from adjacent ancient heathland; and (3) do ancient heaths have a more complex network structure than restored heaths and is any variation in complexity linked to the resilience of the networks to future perturbation?

Materials and methods

BRITISH HEATHLANDS

Dry lowland heathland is a relatively species-poor, seminatural plant community dominated by the ericaceous shrubs *Calluna vulgaris* Hull, *Erica tetralix* L. and *E. cinerea* L., and the fabaceous shrubs *Ulex minor* Roth, *U. europaeus* L. and/or *U. gallii* Planch. The habitat is an important focus for conservation and ecological restoration efforts, because heathlands have a limited distribution internationally, are associated with a number of rare or threatened species of vertebrates and invertebrates (Usher 1992; Anonymous 2002) and have considerable aesthetic and cultural significance (Webb 1986; Usher 1992; Anonymous 2002). The Dorset heathlands were once extensive: a survey in the 1750s listed some 40 000 ha, but by 1978 only 6000 ha remained (Webb & Haskins 1980). This reduction was caused predominantly by afforestation, conversion to agriculture, urban spread and a lack of appropriate management to halt succession (Rose *et al.* 2000). The heathland that remains is highly fragmented but ecological restoration is currently being carried out to increase the total heathland area and link up heath fragments.

THE FIELD SITES

We used a paired design to study restored heathlands and compare their vegetation and visitation networks to those of ancient heathlands (> 250 years old). Thus each of the four restored sites (R1–R4) was paired with an ancient site (A1–A4). Paired sites were adjacent, except pair 2, where the sites were separated by 3 km (although R2 was adjacent to ancient heathland, the ancient site could not be sampled because of an asbestos pollution there. A2 was the nearest alternative site of ancient heathland). All the heathlands were located within a 100-km^2 area with a similar climate and soils (Table 1). The restored sites were heathlands before being afforested with pine. The pine trees prevent sufficient light reaching the heathland, which then dies off. Restoration began in 1990 when the pine plantations were cleared.

Table 1. The location and size of the four pairs of restored and ancient dry lowland heaths in the Poole Basin, Dorset, South England, along with the web statistics for each heathland: plant and insect diversity, insect abundance and network connectance for 2001 and 2004

Pair	Code	Latitude and longitude	Size (ha)	Plants		Insects				Network connectance		
				2001	2004	2001		2004		2001		2004
				Spp.	Spp.	*N*	Spp.	*N*	Spp.	Visitation	Pollen transport	Visitation
1	R1	50°41·3′ N 2°02·0′ W	8	8	4	212	23	336	34	0·18	0·17	0·32
	A1	50°41·2′ N 2°02·0′ W	30	5	4	463	34	468	27	0·28	0·32	0·41
2	R2	50°43·5′ N 2°03·7′ W	15	8	6	352	38	457	44	0·17	0·17	0·26
	A2	50°42·6′ N 2°06·3′ W	25	7	6	367	43	425	38	0·24	0·23	0·30
3	R3	50°42·9′ N 2°10·4′ W	2	10	7	205	41	162	32	0·15	0·18	0·20
	A3	50°43·1′ N 2°09·7′ W	18	6	4	422	48	194	29	0·26	0·24	0·36
4	R4	50°43·8′ N 2°07·6′ W	8	6	5	351	28	424	52	0·23	0·24	0·26
	A4	50°43·7′ N 2°07·2′ W	16	6	4	351	32	362	34	0·27	0·30	0·37

SAMPLING PROTOCOL

Plants, pollinators and their interactions were collected every 3 weeks from late April until late September in 2001 and from early May to late September in 2004. Thus each site was sampled eight times throughout each season. Slightly different sampling methods were used in the 2 years, because the methods in 2004 were changed to conform to methods used in other ongoing pollination projects. In 2001 the centre of a circular plot was marked with a pole at each site, and sampling was carried out along two 100-m-long transects laid out in random directions from the pole. In 2004, circular plots were changed to square plots (100 × 100 m), with the centre of the new plots being coincident with the centre of the old plots. Sampling was again carried out along two 100-m-long transects. One of the four 100-m edges of each square plot was established as a baseline. From this, 10 transect lines, spaced equally at 10 m apart, extended at right-angles across the plot for 100 m. These were then split into two blocks of five transects each. At any given sampling event, one transect was selected randomly from each of the two blocks. The methods in 2001 and 2004 both sampled the same location in each heathland (eight sampling sessions, two transects each of 100 m² in length) but from plots that differed in size between the two censuses (31 416 m² in 2001 vs. 10 000 m² in 2004).

In both years, sites were sampled alternately in the morning and in the afternoon to avoid differences emerging between sites that could reflect patterns in insect day activity. Sampling was conducted only in calm, sunny weather, although in 2004 a wet summer prevailed. While sites were never sampled in the rain, in 2004 the weather was not as consistent between the samples as in 2001. Each transect was sampled twice, allowing at least 30 min between samples. All flower-visiting insects in a 2-m-wide swathe of vegetation were sampled along the 100 m long transect, with insects up to 1 m ahead being recorded. No *a priori* decision was made concerning if an insect was likely to be a pollinator; rather, all flower-visiting insects were collected. They were caught using a sweep-net, or captured directly into a killing tube. Each 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, reducing the risk of pollen contamination between insects. Insects were identified to species or morphotype by taxonomists at the National Museum of Wales. Workers of *Bombus lucorum* L. and *B. terrestris* L. are difficult to tell apart and these species were therefore grouped as *B. lucorum/terrestris*, similar to Dicks, Corbet & Pywell (2002).

Following insect sampling, all entomophilous plant species blooming in each transect were recorded together with their floral abundance. In 2001 flowers were counted along the entire transect, until the copious flowering of the ericaceous shrubs in July, August and September when counting individual flowers was unrealistic. The abundance of these species was therefore estimated from six 1-m quadrats placed along the transect line at the 15 m, 30 m, 45 m, 60 m, 75 m and 90 m marks. These data were used to calculate the average number of floral units per m². In 2004 floral abundance was measured along the two 100 m long transects using a 0·5 × 0·5 m quadrate placed at 0, 15, 30, 45, 60 and 75 m along each transect. At each point the number of floral units were recorded and used to calculate the average number of floral units per m².

LABORATORY METHODS

In 2001 pollen carried by insects was identified and quantified in order to distinguish the probable pollinators. It was sampled from each insect specimen by dabbing the left-hand side of the body systematically with a 5 × 5 mm square of fuchsin pink gel (Kearns & Inouye 1993). Both the dorsal and the ventral surfaces were sampled, but pollen storage areas were avoided; for example, pollen baskets on bumblebees, as these contain pollen unlikely to be available for pollination. Pollen samples were identified under the light microscope using a pollen reference collection of all the insect-pollinated plant species found in or near the plots. Sub-sampling was carried out on *Apis mellifera* and *B. lucorum/terrestris* when a high number of bees belonging to one of these species was caught in the same transect and on the same flower species. When this was the case, only the first eight individuals were sampled for pollen and their average load used to estimate the remainder of that species' sample. Pollen species represented on a specimen with fewer than five grains were removed from analysis, as was pollen from plant species growing outside the transects and the small amount of pollen that could not be identified.

DATA ANALYSIS

Has pollination been reinstated in restored heathlands?

In order to compare pollination on restored and ancient heathlands, we used the data to construct two types of network for each site: quantitative flower visitation networks from both the 2001 and 2004

data, and quantitative pollen transport networks from the 2001 data. Visitation networks show how insects respond to the diversity, quantity and regularity in nectar and pollen supplies (Memmott 1999). Constructing pollen transport networks is a recently developed approach (Forup & Memmott 2005; Gibson *et al*. 2006) that shows which insect species carry which pollen species. These 'pollen vectors' are considered the potential pollinators. We used the pollen transport data to calculate pollinator importance, *PI*, following Gibson *et al*. (2006), as a measure of the importance of individual insect species in pollinating the plant species. The measure combines both the 'quality' and 'quantity' components of each pollinator's potential value to a given plant species, using the following equation:

$$PI = [\text{Relative abundance of pollinator}] \times [\text{Pollen fidelity}]$$

where [Relative abundance of pollinator] is the proportion of all insects carrying a given pollen species that belong to the pollinator species and [Pollen fidelity] is the average proportion of individual pollen loads on the pollinator species that originate from the given plant species.

Do the pollinators on restored heaths originate from adjacent, ancient heathland?

The percentage overlap in species was calculated for each pair of sites using the raw data on species richness for each site and for both 2001 and 2004. Species richness was then weighted for insect abundance and the percentage overlap recalculated. To measure the amount of temporal variation, we also compared the pollinator community within each site between the 2 years. As before, the overlap in species between 2001 and 2004 was calculated using the raw data on species richness. Species richness was subsequently weighted for abundance and the percentage overlap recalculated.

Do ancient heaths have a more complex network structure and is this linked to the robustness of the networks in the face of future perturbation?

Connectance, *C*, was calculated for each network. This measures the generalization of each network by looking at the actual number of connections as a proportion of the possible pairwise connections between plant and insect species (Jordano 1987; Lundgren & Olesen 2005).

To model the response of the networks to species loss, we used three different algorithms to remove species from the eight data sets. For random removal we removed increasing proportions of all species chosen at random and without replacement. This process was repeated 300 times for each web. Random removal represents a 'null model' with which to contrast two types of systematic removal of the number of links of pollinator species, i.e. the number of plant species that they visit. We removed systematically species from the least linked (most specialized) species to the most linked (most generalized); and conversely from the most to least linked. After each primary removal, the most or least connected species was recalculated. The analysis was run twice, first ranking all species, i.e. both plants and pollinators and secondly ranking only the pollinators. The first approach was that used by Dunne, Williams & Martinez (2002) and the second approach that of Memmott, Waser & Price (2004). The approach used by Dunne *et al.* (2002) is used widely in network analysis and is useful for comparison with other networks. In contrast, the approach used by Memmott *et al.* (2004) is tailored specifically for the probable order of extinction in plant–pollinator communities. We calculated the 'robustness' of each

network to species loss by using the method of Dunne *et al.* (2002). This calculates the fraction of species that needs to be removed to result in a loss of 50% or more of the species (i.e. primary species removals plus secondary extinctions). The maximum possible robustness is 0·50 and minimum is 1/*S*, where *S* is the number of species (Dunne *et al.* 2002). These measures of robustness were compared between ancient and restored sites using paired *t*-tests.

Results

In both 2001 and 2004 we recorded abundant heath vegetation on all eight sites, with the low species diversity characteristic of heathlands. All sites were dominated by the ericoids *C. vulgaris* and *E. cinerea*. In 2001 restored sites generally contained more plant species than their paired sites (Fig. 1, Table 1), but their additional species were ruderal plants present at low abundance. In 2004 the plant diversity levels were similar,
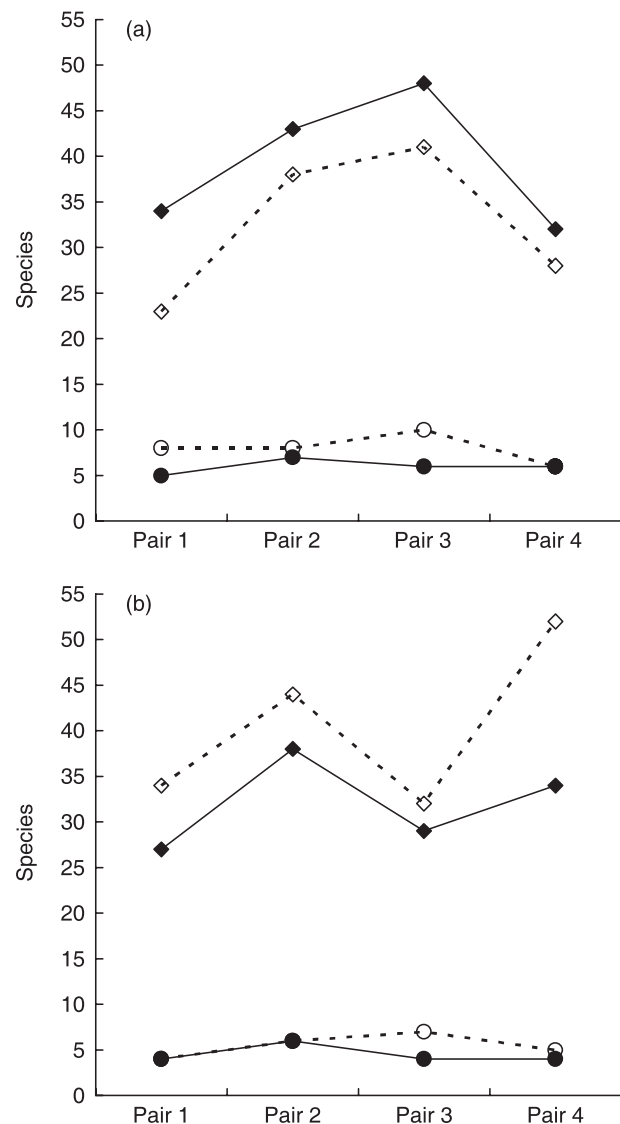

Fig. 1. Plant and insect species richness on the restored and ancient heathlands in each of the four pairs in (a) 2001 and (b) 2004, respectively. ○ = plants, ◇ = insects, stippled lines = restored sites, solid lines = ancient sites.

because the weeds had disappeared. Similarly, plant abundance was successfully restored and there was no significant difference in the overall floral abundance between paired sites (2001: paired *t*-test, *t* = 0·90, *P* = 0·44; 2004: Mann–Whitney *U*-test, *U* = 6, *P* = 0·67). In contrast, restored sites contained fewer insect species than their paired, ancient sites in 2001 but more species in 2004 (Fig. 1). In 2001 we collected a total of 112 insect species (*n* = 2723) from flowers of eight plant species across the eight heathlands and in 2004 we collected 105 species of insect (*n* = 2828) from seven plant species.

Has pollination been reinstated in restored heathlands?

In 2001 and 2004 plants and pollinators were linked in complex visitation networks on restored and ancient sites. An example of such a network is shown in Fig. 2a. Hymenoptera and Diptera dominated all communities, and *A. mellifera* and *B. lucorum/terrestris* were the dominant flower visitors on most sites, regardless of whether a site was a restored or ancient heathland. In 2001 we sampled and identified over 1 million pollen grains from insects captured on flowers and the data were used to construct pollen transport webs (Fig. 2b). Hymenopterans were responsible for 97% of the pollen transport (Fig. 2b). The network statistics for the visitation and

pollen transport webs are shown in Table 1. Using the data from the visitation and pollination transport networks, we calculated pollinator importance values for all insects visiting the plant species on each of the eight heathlands in 2001. Many insects in the networks had extremely small *PI* values, reflecting either their low abundance and/or the fact that they carried little pollen. Only for *C. vulgaris* and *E. cinerea* were *PI* values large enough to be meaningful, and these two species made up an average of 93% of the floral abundance at each site. Table 2 shows the *PI* values for the highest-scoring and most abundant flower visitors. Pollinator importance was correlated with pollinator abundance (Spearman's rho = 0·379, *P* < 0·001), and given that pollinator abundance is one of the two components in our *PI* index, this result is not unexpected. However, nor can it be taken for granted, because if the values for the other component, pollen fidelity, are allocated randomly to each insect, the correlation becomes very weak (Spearman's rho = 0·135, *P* < 0·001). Moreover, *PI* values for species shared between paired sites were, with one exception, moderately or strongly correlated (*C. vulgaris*; pair 1: Spearman's rho = 0·72, *P* < 0·01, pair 2: Spearman's rho = 0·704, *P* < 0·001, pair 3: Spearman's rho = 0·649, *P* < 0·001 and pair 4: Spearman's rho = 0·599, *P* < 0·05. *E. cinerea*; pair 1: Spearman's rho = 0·388, *P* > 0·05, pair 2: Spearman's rho = 0·891,

(a)

Calluna vulgaris

Erica cinerea

Erica tetralix
Ulex minor
Rhododendron ponticum
Polygala serpyllifolia

(b)

Calluna vulgaris

Erica cinerea
Erica tetralix
Ulex europaeus

Ulex minor

Rhododendron ponticum

Scale bars

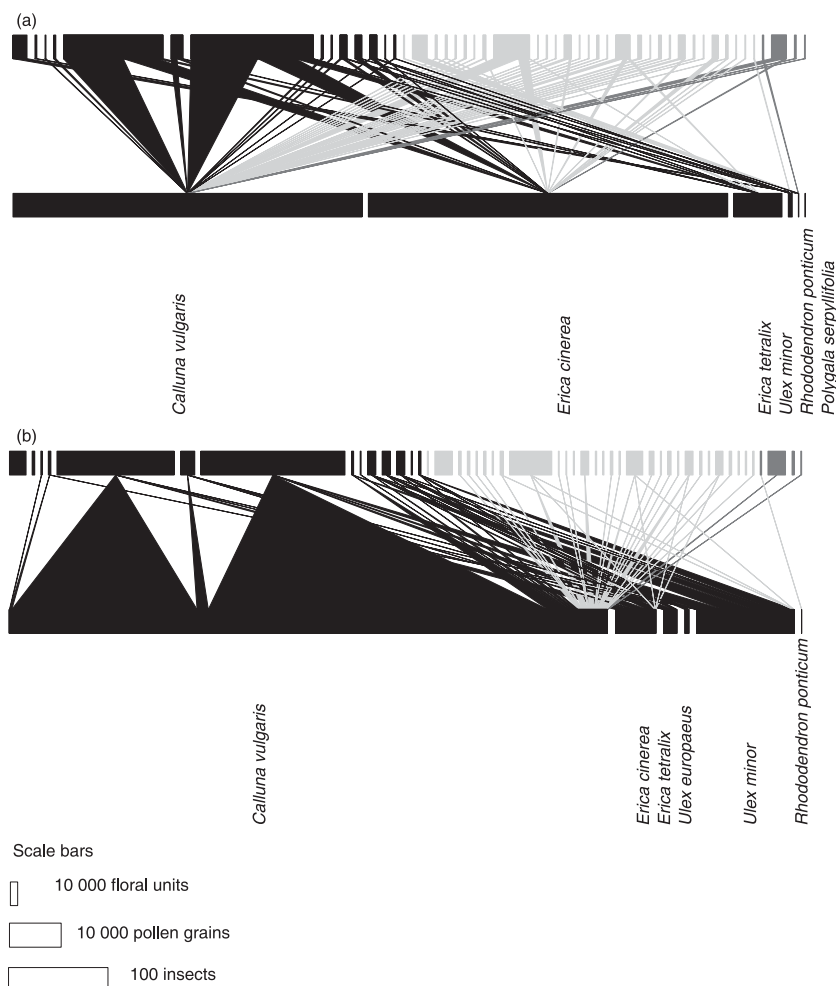☐ 10 000 floral units

☐ 10 000 pollen grains

☐ 100 insects

Fig. 2. Ecological networks: (a) quantitative flower visitation network for an ancient heathland (A3). In the network each species of plant and insect is represented by a rectangle: the lower line represents flower abundance, the upper line represents insect abundance (note scale bars at bottom of figure). The width of the rectangles and the size of the interaction between them are proportional to their abundance at the field site. Hymenoptera are shown in black, Diptera in light grey, Lepidoptera and Coleoptera in dark grey; (b) quantitative pollen transport network for an ancient heathland (A3). In the network each species of pollen and insect is represented by a rectangle: the lower line represents the pollen abundance sampled from the insects' bodies, the upper line represents insect abundance (scale bars at bottom of figure). The width of the rectangles and the size of the interaction between them are proportional to their abundance at the field site. Insects with no interactions are flower visitors, but not pollen transporters. Colour codes as in Fig. 2a.

Table 2. Pollinator importance (*PI*) values of the highest-scoring insects visiting *Calluna vulgaris* and *Erica cinerea* across the eight heathlands in 2001; r.a. (relative abundance) is the proportion of all insects carrying a pollen species that belong to the given insect species

| Plant species | Site | Insect species | | | | | | | | | | | |
| | | *Apis mellifera* | | *Bombus jonellus* | | *B. lucorum/ terrestris* | | *B. pascuorum* | | *Colletes succinctus* | | *Episyrphus balteatus* | |
		r. a.	*PI*	r. a.	*PI*	r. a.	*PI*	r. a.	*PI*	r. a.	*PI*	r. a.	*PI*
Calluna vulgaris	R1	0·62	0·21	0·03	0·01	0·04	0·04	–	–	0·01	0·01	0·10	0·06
	A1	0·67	0·28	0·01	< 0·01	0·09	0·05	0·00	0·0	0·01	0·01	0·11	0·09
	R2	0·66	0·37	0·04	0·03	0·11	0·05	0·04	0·03	–	–	0·02	0·01
	A2	0·15	0·06	0·02	0·01	0·39	0·18	0·05	0·01	0·06	0·05	0·06	0·02
	R3	0·21	0·12	0·02	0·01	0·24	0·16	0·04	0·02	0·01	0·01	0·01	0·02
	A3	0·30	0·20	0·04	0·03	0·31	0·21	0·02	0·01	0·01	< 0·01	0·06	0·03
	R4	0·36	0·19	< 0·01	< 0·01	0·43	0·34	0·01	0·01	0·02	0·02	0·04	0·03
	A4	0·52	0·28	0·01	0·01	0·28	0·09	0·02	< 0·01	0·01	0·01	0·05	0·04
Erica cinerea	R1	0·90	0·56	0·03	0·03	0·00	0·00	–	–	0·01	< 0·01	0·01	< 0·01
	A1	0·85	0·64	0·03	0·02	0·06	0·01	< 0·01	< 0·01	0·00	0·00	0·00	0·00
	R2	0·74	0·23	0·04	< 0·01	0·12	0·03	0·04	< 0·01	–	–	0·00	0·00
	A2	0·27	0·10	0·05	0·01	0·44	0·10	0·05	0·01	0·01	< 0·01	0·01	0·00
	R3	0·32	0·11	0·07	0·04	0·37	0·07	0·07	< 0·01	0·00	0·00	0·00	0·00
	A3	0·43	0·11	0·06	0·01	0·39	0·06	0·02	< 0·01	0·00	0·00	0·01	< 0·01
	R4	0·59	0·24	0·00	0·00	0·29	0·04	0·01	< 0·01	0·00	0·00	0·01	< 0·01
	A4	0·53	0·14	0·00	0·00	0·34	0·08	0·01	< 0·01	0·00	0·00	0·00	0·00

Table 3. The overlap in insect species between the eight sites in 2001 and 2004, respectively. Overlap between a pair of ancient and restored sites are shown in bold type; (a) unweighted by insect abundance, (b) weighted by insect abundance

| (a) | | | | | | | | (b) | | | | | | | |
	A1	R1	A2	R2	A3	R3	A4		A1	R1	A2	R2	A3	R3	A4
2001															
R1	**26·67**							R1	**93·86**						
A2	31·03	30·00						A2	88·35	85·84					
R2	26·32	27·08	**31·15**					R2	94·49	89·89	**89·43**	88·11			
A3	20·59	24·56	34·33	28·36				A3	86·44	82·49	88·47	88·11	**86·12**		
R3	22·95	30·61	29·69	36·21	**36·92**			R3	86·44	83·45	87·76	88·51	**86·12**	88·31	
A4	26·92	30·95	37·04	29·63	29·03	30·36		A4	86·23	87·03	93·45	93·03	90·04	88·31	
R4	17·74	27·50	27·27	24·53	24·59	27·78	**30·43**	R4	84·32	87·92	90·39	90·47	86·80	85·79	**93·59**
2004															
R1	**32·61**							R1	**92·66**						
A2	32·65	28·57						A2	91·38	86·99					
R2	26·79	21·88	**34·43**					R2	86·81	88·15	**90·14**				
A3	43·59	36·96	45·65	37·74				A3	92·75	91·89	90·31	92·17			
R3	31·11	24·53	32·08	38·18	**41·86**			R3	89·37	86·35	84·33	92·41	**90·17**		
A4	38·64	33·33	44·00	32·20	37·21	34·69		A4	92·77	91·98	91·99	90·72	92·27	87·98	
R4	19·70	26·47	28·57	35·21	32·79	27·27	**30·30**	R4	80·61	85·66	87·75	88·20	85·60	82·42	**88·55**

P < 0·001, pair 3: Spearman's rho = 0·797, *P* < 0·001 and pair 4: Spearman's rho = 0·632, *P* < 0·05). Overall, these results suggest no systematic difference in pollination on restored and ancient heathlands. *A. mellifera* and *B. lucorum/terrestris* were always the main pollinators of *E. cinerea*. Similarly, they were the main pollinators of *C. vulgaris*, with the exception of pair 1, where the hoverfly *Episyrphus balteatus* ranked higher than *B. lucorum/terrestris* (Table 2). Indeed, *E. balteatus* often ranked higher than many bee species as a pollinator of *C. vulgaris*.

Do the pollinators on restored heaths originate from adjacent, ancient heathland?

While Fig. 1 showed that paired sites correlated in diversity, there was little proof that insect species on restored sites originate from adjacent, ancient heathland. In 2001 paired sites shared between 26·67% and 36·92% of their species (Table 3a), but only in pairs 3 and 4 did the restored site share more species with its paired site than with another site and this increased similarity was very minor. Two ancient sites, A2 and

Table 4. The overlap in insect species within sites between 2001 and 2004, unweighted (upper line) and weighted by insect abundance (lower line)

	A1	R1	A2	R2	A3	R3	A4	R4
Species shared 2001–04 (%)	27·08	39·02	32·79	22·39	30·51	23·73	34·69	21·21
Specimens in shared species (%)	90·98	92·15	88·76	84·18	82·95	75·48	90·60	79·10

A4, had the highest overall overlap in insect species but shared only 37·04% of their species. In 2004 paired sites shared slightly more species than in 2001, ranging from 30·30% to 41·86% of their species (Table 3a), but only in pair 3 did the restored site share more species with its paired ancient site than with another site.

When the data were weighted in terms of insect abundance, sites were much more similar: in 2001 between 86·12% and 93·86% of all specimens on paired sites belonged to shared species (Table 3b). These results are largely explained by the abundance of honeybees, *A. mellifera*, which dominated the insect community on six of the eight sites, followed by various species of bumblebee, notably *B. lucorum/terrestris*. Of the four restored sites, only R4 was more similar to its paired site than to any other site (Table 3b). Weighting the 2004 data revealed that between 88·55% and 92·66% of all specimens on paired sites belonged to shared species, but of the four restored sites only R1 was more similar to its paired site than to any other site (Table 3b). Again, these results are explained largely by the abundance of social bees.

In three of the four pairs, the restored site retained slightly fewer species between 2001 and 2004 than did the ancient site (Table 4), but the species overlap between years was modest for all sites and ranged from only 21·21% for R4 to 39·02% for R2. When the data were weighted in terms of specimens belonging to species found in both years, the same relative pattern emerged, although similarity coefficients were much higher, ranging from 75·48% for R3 to 92·15% for R2. However, there was a change in dominance from *Apis* to *Bombus* between 2001 and 2004. This was caused by a significant decrease in honeybees, whereas the increase in bumblebees was not significant (honeybees: paired *t*-test, $t = 5·09$, $P = 0·0015$; all bumblebees: paired *t*-test, $t = 0·64$, $P = 0·54$, *B. lucorum/terrestris* alone: paired *t*-test, $t = 1·01$, $P = 0·35$).

Do ancient heaths have a more complex network structure and is this linked to the robustness of the networks in the face of future perturbation?

For the visitation networks connectance was higher for the ancient site within each pair in both 2001 (paired *t*-test, $t = 5·06$, $P = 0·015$) and in 2004 (paired *t*-test, $t = 4·03$, $P = 0·028$) (Table 1). Because connectance in flower-visitation networks usually declines as the number of species increases (Jordano 1987), and because the networks had very different levels of diversity, connectance values have been plotted against species richness to determine whether the significant difference between the ancient and restored connectance values is due to

species-rich ancient sites being compared to species-poor restored sites. Interestingly, the relationship between the two variables is different in 2001 and 2004. Thus, in 2001 there was no evidence of the expected negative association between connectance and species richness (Fig. 3a). In contrast, the significant difference in connectance values for ancient and restored networks in 2004 could just reflect the higher number of species found on restored sites, because ancient and restored networks appear to fit the expected relationship of C to S (Fig. 3b). The 2001 pollen transport networks were similar to the visitation networks, with connectance values significantly higher for the ancient site within each pair (paired *t*-test, $t = 2·97$, $P = 0·025$). As before, however, the plot of connectance against species richness does not follow the expected negative association between connectance and species richness, suggesting different relationships between these two variables for ancient and restored pollen transport networks (Fig. 3c).

Using the method of Dunne *et al.* (2002) and removing the most connected plants and pollinators first from the network (most to least in Fig. 4a) led to a rapid collapse of both ancient and restored heathlands: once about 20% of species were removed in primary extinctions, a cascade of secondary extinctions was elicited, leading to 100% extinction (Fig. 4a). Removing the least connected species first reduced drastically the collapse of the networks (Fig. 4a). Using the method of Memmott *et al.* (2004) and removing only the pollinators from the community caused far fewer secondary extinctions (Fig. 4b) for both most to least connected, and least to most connected algorithms. Analysing data from all the sites though, there was some evidence of a trend towards a greater robustness in the ancient sites vs. the restored sites when using the method of Dunne *et al.* (2002) and that of Memmott *et al.* (2004) (Wilcoxon's signed-rank tests, Dunne method: extinction order most to least, $W = 3·0$, $P = 0·584$; least to most, $W = 0$, $P = 0·100$; random, $W = 2$, $P < 0·361$; Memmott method: most to least, $W = 0$, $P = 0·100$; least to most, $W = 0$, $P < 0·100$, random, $W = 3$, $P < 0·181$).

Discussion

The four restoration projects established successfully heathland plant and pollinator communities. Using the networks to calculate pollinator importance indicated that the key pollinators are in place on the restored heaths and that these pollinators are also the most abundant ones. Unexpectedly, adjacent heathlands did not share more species than more distant ones, which suggests that adjacency to ancient habitat need not be a criterion when choosing heathlands to restore.
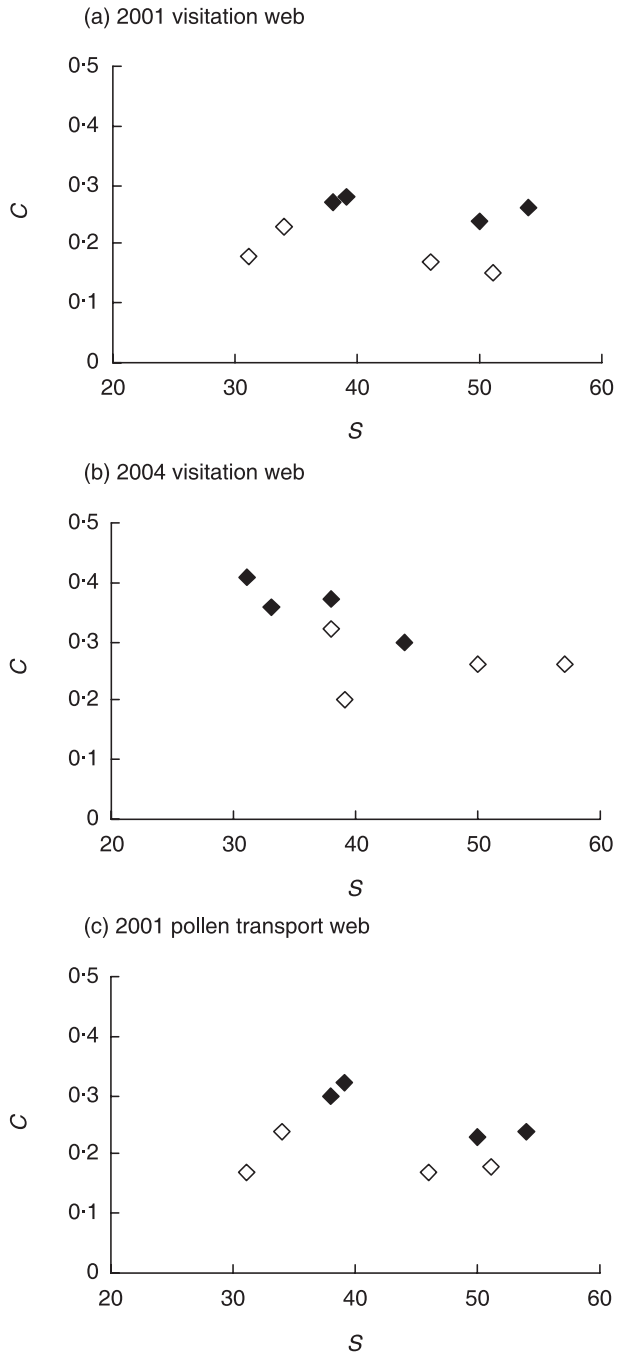
(a) 2001 visitation web

(b) 2004 visitation web

(c) 2001 pollen transport web

Fig. 3. Connectance (C) plotted against species richness (S). (a) Visitation networks for 2001; (b) visitation networks for 2004; (c) pollination networks for 2001. Open symbols = restored sites, filled symbols = ancient sites.

Fig. 4. Community robustness analysis. The proportion of species lost to secondary extinctions as a function of proportion of species removed (primary extinction) from A3 and R3. The diagonal dashed lines connect points at which all species in the network are lost. (a) Plants and pollinators are equally at risk of being removed (c.f. Dunne *et al.* 2002); (b) pollinators alone are removed, and secondary extinctions are solely of plants (c.f. Memmott *et al.* 2004). Each curve in the random removals represents 300 replicate simulations; the error bars are smaller than the symbols and are not shown. These curves dip downwards as they approach the diagonal as not all of the replicate simulations persist equally long before the whole pollination web becomes extinct. Those that persist longest have slower accumulation of secondary extinctions, so the mean of the cumulative secondary extinctions tends to be lower towards the end.

While the restored heathlands were functionally less complex than ancient heathlands in 2001 (i.e. connectance was significantly lower), this did not correspond to a reduction in their robustness towards perturbation, and in 2004 the apparent differences in connectance could be explained by differences in species richness. The results are discussed below with respect to our approach and the implications of our data for the restoration of British heathlands.
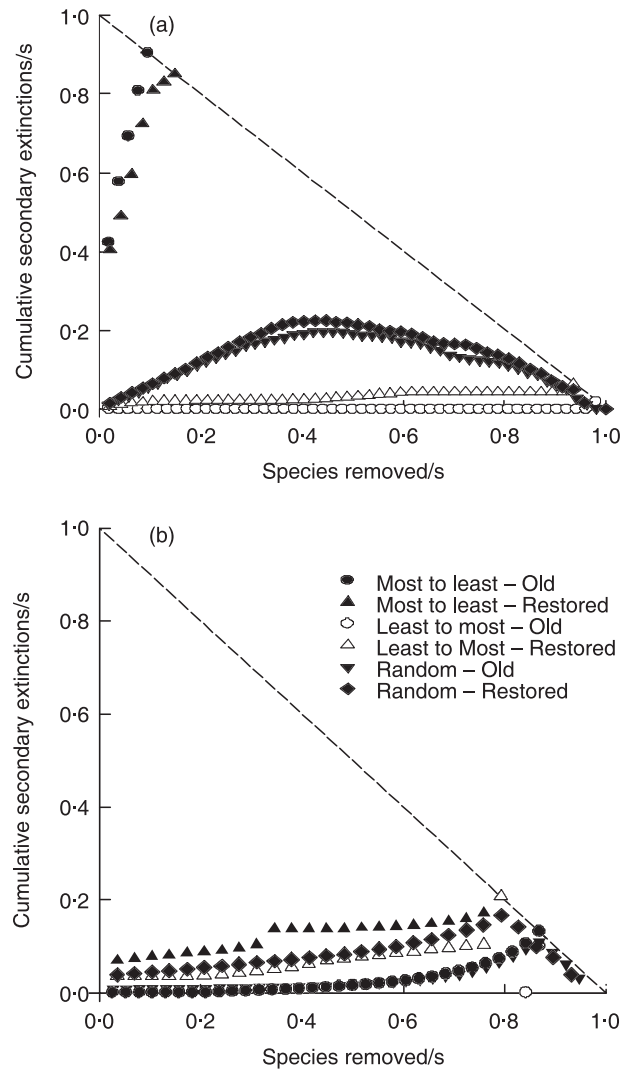
THE NETWORK APPROACH

In this study, we have analysed species interaction data rather than simply described species presence and abundance. This has provided an understanding of the actual workings of restored communities and how this compares to ancient communities. A sampling protocol with replication is uncommon (especially at

the community level) in restoration ecology; this study has provided one of the few examples of a replicated design in the analysis of ecological restorations. Moreover, in addition to spatial replication, our study has demonstrated the value of temporal replication. For example, data from only 2001 would have led to the erroneous conclusion that ancient sites were more species rich with regard to pollinators, when the opposite was true in 2004. Finally, by investigating an essential ecosystem service, we have overcome the main problem of using reference sites; pollination must be comparable between restored and ancient habitat despite any variation in species structure.

Has pollination been reinstated in restored heathlands?

Despite considerable differences in the visitation networks, the key pollinators were the same on ancient and restored sites after 11 years. Moreover, these key pollinators were also the most abundant flower visitors 14 years after restoration, suggesting that the service of pollination was relatively stable. Our findings support the conclusion by Vázquez, Morris & Jordano (2005) that the most common flower visitors are also the most important pollinators. Particularly important were the honeybees (*A. mellifera*) and bumblebees (mainly *B. terrestris/lucorum*) that dominated most communities in both years. Given their abundance, it is not surprising that honeybees score highly, even though they are less efficient pollinators relative to many other bee species (Westerkamp 1991). It is perhaps a greater surprise that a hoverfly, *E. balteatus*, often scored higher than bees as a pollinator of the dominant heath species, *C. vulgaris*. Overall, the pollination services on restored sites were equivalent to those of ancient sites.

Do the pollinators on restored heaths originate from adjacent, ancient heathland?

Contrary to our prediction that more insects would be shared between adjacent heaths than between more distant heaths, paired sites did not have more species in common than they did with other sites, although they correlated in the level of diversity. This suggests an effect of landscape and site conditions, combined with chance events. It is well known that landscape setting has a marked influence on how great a subset of the regional species pool can be found locally (e.g. Tscharntke *et al.* 2002; Steffan-Dewenter 2003; Steffan-Dewenter & Kuhn 2003), but some of the factors causing pollinator assemblies to vary dramatically between years may also account for differences between nearby localities within seasons. In a 15-year-long study of hoverflies in an urban garden, Gilbert & Owen (1990) concluded that species fluctuated independently in response to resource availability but that competition played no role in structuring the species assemblage. The variation they observed between years was so great that Gilbert & Owen (1990) questioned the notion of 'community'. It seems likely that some of the species in our study behaved in similar ways on a spatial scale in response to varying site conditions. In addition, the regional insect species pool contains a high number of uncommon species, which are more suscep-

tible to chance events than are common species. Consequently, it may be invalid to expect a great overlap in pollinator species even between nearby heathlands. Instead, a more appropriate focus may be the relative abundance of species. When we weighted species by abundance, the heathlands in our study emerged as being remarkably similar; the same few species dominating the pollinator guild on most sites. Those are species which are abundant in the landscape surrounding these heathlands, or species that are able to travel the distances and cross the barriers between the sites in this study. Overall, our results imply that restoration of species structure is less relevant than the restoration of functionality.

Do ancient heaths have a more complex network structure and is this linked to the robustness of the networks in the face of future perturbation?

While the robustness of networks is currently a very active area of research (e.g. Dunne *et al.* 2002; Tanizawa *et al.* 2005; Buzna, Peters & Helbing 2006; Fortuna & Bascompte 2006), to our knowledge this is the first time the method has been used in an applied context. In 2001 we found the insect foraging networks were less generalized (i.e. connectance was significantly lower) on restored heathlands than on ancient heaths. The same result was seen in the measure with most relevance for plant reproduction, namely the pollen transport networks. In their analysis of 16 food webs, Dunne *et al.* (2002) reported that increasing connectance also leads to a greater robustness towards secondary extinctions following perturbation. Although we found no significant difference in network robustness on ancient and restored heathlands, there was evidence of a trend. However, our statistical power is very low when interpreting trends, and in reality we can conclude only that the comparison of ancient and restored sites is inconclusive with respect to robustness. By 2004 network generalization appeared equivalent between ancient and restored heathlands, because the values for both heathland types appeared to follow the same relationship with species richness. In other words, the reduced level of functioning on restored sites in 2001 did not affect robustness to a large degree and its effect had disappeared by 2004. While these results are inconclusive, the question of whether restored habitats are as robust as ancient habitats to perturbation is central in restoration ecology, and our approach (using a larger sample size) could prove very useful in future studies assessing the efficacy of ecological restoration.

PRACTICAL IMPLICATIONS

Our findings have practical implications for the management of heathland restoration schemes. First, heathland restoration is evidently a relatively rapid process for both plants and pollinators: 11 years after restoration, highly functional communities had established that appeared as robust as ancient communities. Secondly, heathland restoration sites may not need to be immediately adjacent to intact habitat to be successful. The functionally important pollinators are mobile,

abundant and able to traverse other habitat than heathland. This makes pollination likely even where heathlands are more isolated and likely to host fewer pollinator species. However, a note of caution should be sounded for other systems or projects with a special focus on invertebrate conservation, because some species are unlikely to travel even short distances. For example, even though we recorded few butterflies on either the ancient or the restored heathlands, some species, such as the silver-studded blue (*Plebejus argus*), are restricted to mainly this habitat. Working in North Wales, Thomas & Harrison (1992) found that the silver-studded blue was unlikely to colonize new habitat more than 1 km away.

Concluding remarks

As a practical tool, ecological restoration is widespread and used in a range of contexts. In contrast, its scientific basis has been slow to develop. Here we have shown the value of applying a network approach to restoration ecology. Although habitat restoration is an essential component of conservation ecology (Dobson, Bradshaw & Baker 1997), our current understanding of the ecological processes underlying successful habitat restoration is both incomplete and poorly integrated across different systems. Developing a 'general template' that will help to run ongoing projects and provide direction for future restoration projects is crucial (Montalvo *et al.* 1997). Species interaction networks, whether they be pollination networks, as described here, or predation, parasitoid or seed dispersal networks, can provide such a general template, allowing assessment of whether ecosystem processes such as pollination are restored. Interactions between species can provide a superior yardstick for judging restoration success in comparison to species richness and abundance. This is because they characterize what species actually do, in addition to whether or not they are present. Moreover, by working with species interactions, ecologists are working in the currency of ecosystem services; the restoration of these services remains one of the most exciting and challenging areas of restoration ecology.

Acknowledgements

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