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Ecological meta-networks integrate spatial and temporal dynamics of plant–bumble bee interactions

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Bumble bees can forage on a large number of wild plants and crops. The survival of a colony depends on the availability of suitable food resources within foraging range and throughout their forage season. We studied the spatial and temporal use of floral resources by bumble bees in a set of 30 local plant communities and used these data to model colony survival under different combinations of patch size and bumble bee flight distance. Floral resources vary spatially and temporally at the landscape level, and bumble bees track these resources across the landscape during the season. The simulation model showed that different patterns of resources availability could affect the survival and distribution of bumble bee nests across the landscape. This model can be used to generate hypotheses explaining bumble bee richness and abundance that can be tested in real landscapes. Integrating the spatial and temporal dynamics of the flower resources used by bumble bees provides a new perspective that can be used to inform bumble bee conservation, particularly in the context of their widespread decline in recent decades.

Bumble bees play a central role in many terrestrial ecosystems, as they are the predominant pollinators of a large number of wild plants and crops (Goulson 2003, Klein et al. 2007). As such, they contribute not only to crop yield and to sustaining wild plant populations, but they also generate the seeds and fruits that feed other insects, birds and mammals in the community.

There is mounting evidence of a widespread decline of bumble bees in recent decades, particularly in western Europe, North America and Asia (Williams and Osborne 2009). In the United Kingdom (UK) a dramatic decline in local abundances and regional distributions of many species has been reported, with 3 of the 25 UK species having gone extinct and an additional 8 species having undergone major range declines (Williams 1982, Goulson et al. 2008). These declines have been attributed to the reductions in floral resources, the loss of nest sites, and the exposure to pesticides resulting from agricultural intensification and, particularly for North America, the spread of a non-native parasite (*Crithidia bombi*) from commercial bumble bee hives introduced from Europe (Goulson et al. 2008, Williams and Osborne 2009).

Bumble bees are "central place foragers" (Schoener 1979), that is, they use resources in the landscape within a certain distance of the location of the colony's nest. As a result, bumble bees are "tied to their nests" (Ranta et al. 1981) and survival of a colony depends on the availability of suitable food resources in the landscape within foraging range (Goulson 2003). In addition, there is a temporal aspect to foraging for food: bumble bee colonies require a season-long food supply to complete their life cycle (Ranta and Lundberg 1981). As a result, any gap in the seasonal turnover of flowering plants may cause bumble bee colonies to starve and die (Goulson et al. 2008).

Because bumble bees are easy to observe while foraging and to manipulate, they are a well-studied group of species in a variety of field and laboratory conditions (Heinrich 1979, Goulson 2003). Both spatial and temporal aspects of bumble bee ecology have been studied, including resource partitioning and temporal dynamics in resource use throughout a season (Heinrich 1976, Ranta and Lundberg 1981, Ranta et al. 1981, Ranta and Tiainen 1982, Ranta and Vepsäläinen 1981, Stenström and Bergman 1998), and the influence of landscape structure on local bumble bee richness and abundances (Steffan-Dewenter et al. 2002, Pywell et al. 2005, Hatfield and LeBuhn 2007, Heard et al. 2007, Goulson et al. 2008, Kwaiser and Hendrix 2008, Rundlöf et al. 2008, Ahrné et al. 2009). Although the need to understand the relationship between spatial and temporal resource dynamics has been pointed out (Ranta et al. 1981), these two aspects have never been analyzed together. In this paper we integrate both these aspects of bumble bee ecology by considering a plant–bumble bee

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meta-network in a boreal forest over a three year period. A meta-network is here defined as a set of local plant communities that are interlinked by bumble bees foraging in different communities at different times of the year. In this sense, the concept of meta-network is analogous to the concept of meta-community (i.e. a mosaic of local populations of a given species that are linked by dispersal events; Gilpin and Hanski 1991, Wilson 1992, Leibold et al. 2004). Integrating the spatial and temporal dynamics of the flower resources used by bumble bees provides a new perspective that can be used to inform bumble bee conservation and restoration practices in managed landscapes.

Specifically, we address the following three questions: 1) how do floral resources vary spatially and temporally at the landscape level? 2) Do patterns of resource use by bumble bees relate to spatio-temporal patterns of resource availability across the landscape? 3) How could different patterns of resources availability affect the survival and distribution of bumble bee nests across the landscape?

To address these questions we used a combination of field observations in an area of the native pine woodlands of Scotland (question 1 and 2) and a computer simulation (question 3). The ultimate goal of this study is to generate hypotheses explaining bumble bee richness and abundance that can be tested in real landscapes.

Methods

Field site

The study was undertaken in the pine woodlands of Scotland. These woodlands represent modified remnants of the original natural boreal forest in Scotland (Steven and Carlisle 1959, Peterken 1996), and so have an important conservation status (Peterken et al. 1992, Anonymous 1998, 2000). Despite this there is a paucity of research on the impact of management practices on their insect populations (Hunter 1977, Humphrey et al. 1999). The study was conducted in the Cairngorms National Park in northern Scotland (grid reference NH931098; 57°10′N, 3°44′W).

Scottish pinewoods are dominated by Scots pine *Pinus sylvestris* var. *scotica*. The understory is dominated by *Calluna vulgaris* and, to a lesser degree, by *Erica cinerea, E. tetralix*, *Vaccinium vitis-idaea* and *V. myrtillus*. Commercial plots of Scots pine *Pinus sylvestris* var. *scotica* are mostly grown as stands of a single age class (McVean 1963, Gimingham 1977), resulting in a distinctly patchy landscape. There is evidence that the structure of the plant community in the forest understory is strongly influenced by changes in the structure of the tree cover along succession (Aubin et al. 2008, Devoto et al. 2012). As a result, plots of different ages have different plant compositions that will offer flower resources for bumble bees at different times of the season.

Sampling protocol

Within Cairngorms National Park, thirty circular 1-ha plots (radius = 56.5 m) were selected for sampling. Plot selection was based on multiple criteria (spatial independence, accessibility, availability of management information on the forest stands, etc.), but most importantly that the plots covered the full range of managed successional stages: restocking (clear felled ca 5 to 15 years before the start of the study), thicket (16–45 years), pole (46–75 years), mature (76–120 years) and old-growth pine forests (135–200 + years old), with six replicates of each stage.

Plots were sampled from May to August in three consecutive years (2007–2009). This covered the entire activity period of bumble bees (from the presence of nest-seeking queens in May to the emergence of males in August). Each of the 30 plots was sampled five times in 2007, six times in 2008 and four times in 2009. A blocked design was used with six blocks, each consisting of five plots, so that all successional stages (restocking, thicket, pole, mature and old-growth) were represented in each block. In 2007 sampling was done along fixed transects (following Memmott 1999). Thereafter, and because of the low sample size in the fixed transects, the sampling was changed to a 40-min random walk within the boundaries of the plot (Westphal et al. 2008). When sampling the plots all bumble bees visiting flowers were collected and the identity of the host plants recorded. At the end of the collecting period the number of flowers of each plant species was counted in eight quadrats (0.5 × 0.5 m) placed randomly in the plot. Racemes of *Calluna vulgaris* and flower heads of *Erica cinerea* and *E. tetralix* were counted as a single floral unit. Plots within a block were sampled on the same day and sampling was done in dry weather and light to moderate wind conditions. Bumble bees were identified to species by taxonomists (see Acknowledgements).

Data processing

To describe the spatial distribution of floral resources, the data on local flower abundance was pooled across years for each plot separately (Supplementary material Appendix A1 Fig. 1). To describe the temporal dynamics of flower resources, data were pooled across years and plots, and then divided into ‘time slices’ of 15 days each from mid May to August (Supplementary material Appendix A1 Fig. A2). These time slices cover the flowering periods of all dominant species in the community. As in Devoto et al. (2012) data were pooled across years in order to increase the overall sample size. Floral abundances from samplings in all three years were pooled for these analyses. To describe the spatial use of resources by bumble bees the number of visits received by each plant species at different times of the season was pooled across years and plots.

Spatial and temporal variation of floral resources

To analyze temporal changes in flower resources a constrained canonical correspondence analysis (CCA) was performed on the temporal resource-availability matrix. CCA is a multivariate ordination method to elucidate the relationships between biological assemblages of species and their environment (ter Braak 1987). The method is designed to extract environmental gradients from ecological data-sets. In its constrained form the method does not try to display all variation in the data, but only the part that can be explained by the constraints used (Oksanen et al. 2010). In this case, the temporal resource–availability matrix was used as the assemblage of species and the constraining variable was a 'time' vector. The time vector consisted of numbers 1 to 7 which were assigned in chronological order to each time slice (1 = second half of May, 2 = first half of June, and so on until 7 = second half of August). A permutation test was used to test for the effect of time on the variance of the matrix (function 'anova.cca' in the R package 'vegan'; Oksanen et al. 2010). If the effect of the constraining vector is significant, this means there is a marked change through the season in the availability and identity of resources; if it is not, flowering phenology does not follow a clear seasonal pattern. Floral abundances were log-transformed prior to analysis. Although some floral abundances did not meet the assumptions of normality and unimodality, CCA is robust to deviation from these assumptions (ter Braak and Verdonschot 1995).

Simulation model of the patterns of resource use by bumble bees

To investigate concordance between flower availability and their use by bumble bees at our field sites, we performed a Procrustes analysis using the 'protest' function of package vegan implemented in R 2.11. Procrustes analysis is a multivariate exploratory technique that attempts to maximize the similarity (i.e. minimize the sum of squared difference) between two matrices (Oksanen et al. 2010). Although originally developed for a different purpose (Gower 1975), it is suitable for community-scale ecological comparisons (Jackson 1995, Peres-Neto and Jackson 2001, Alarcón et al. 2008). A matrix describing the temporal availability of resources was compared to a matrix describing the use of resources. Significance of the statistic was determined by a Procrustean randomization test (999 randomizations; Jackson 1995).

We used the information obtained from field observations to model the survival of bumble bee nests in a landscape in response to two factors: (a) patch size, and (b) bumble bee foraging range. The survival of the nests was assessed under different scenarios (Fig. 1). Each scenario consisted of a combination of a landscape of a given patch size (square patches with side lengths of 100, 200, 500, 1000, 2000, 4000 or 5000 m) and a bumble bee type of a given foraging range (100, 200, 400, 1000 and 1500 m), resulting in 35 different scenarios (7 patch sizes × 5 foraging ranges). We used foraging distances in the range 100–1500 m in accordance with those recorded for bumble bees in mark–recapture experiments (see Table 1 in Zurbuchen et al. 2010). The patch sizes we considered are within the range of patch sizes commonly found for both natural and planted *Pinus sylvestris* boreal forests (Peterken 1996). Each scenario was run 100 times. At the beginning of each run a thousand bumble bee nests (all with the same foraging range) were randomly distributed in a virtual landscape of 10 × 10 km in which all patches were the same size (using the combinations of foraging range and patch size mentioned above). Patches were assigned to one of five successional stages (restocking, thicket, pole, mature or old-growth). The proportion of landscape occupied by each stage was based on actual data for Glenmore Forest (David Jardine, Forestry Commission, pers. comm.),

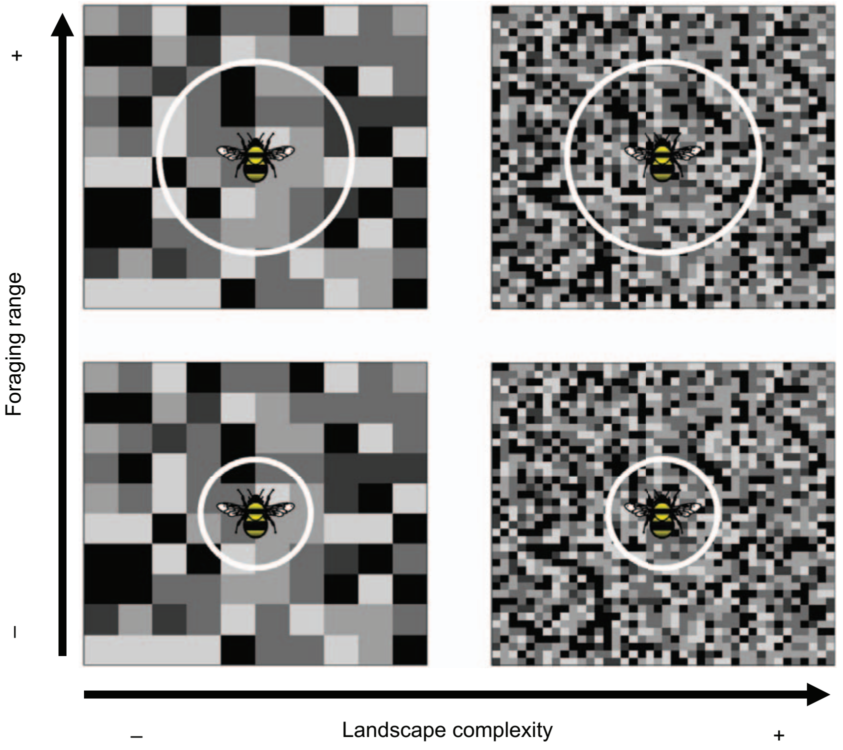

Figure 1. Pictorial representation of the scenarios used in simulations of the survival of bumble bee nests. Scenarios resulted from the combination of different levels of landscape complexity (patch sizes ranging 100–5000 m of side length) and bumble bee foraging ranges (100–1500 m). Squares of different colours represent plots assigned to one of five successional stages (restocking, thicket, pole, mature or old-growth).

where nearly half of our sampling plots are located. These proportions were: restocking 23%; thicket 9%; pole 26%; mature 23%; old growth 19%. We used our measurements of availability and abundance of floral resources at each plot to generate the model's assumptions regarding spatial resources patchiness. The model assumed that pole and mature stages, dominated by *Vaccinium* spp., provided early season resources, while restocking and old-growth stages, dominated by *Calluna vulgaris* and *Erica* spp., provided late season resources. Because of its closed canopy and low flower abundance, the thicket stage was assumed to provide no significant food resources to sustain bumble bees colonies. This assumption is deliberately simplistic in order to gain a general understanding of the way the species respond to spatial and temporal variability in resources.

The survival of each nest was assessed at the end of each run; only nests that had both early and late resources available within foraging range (i.e. that could find food through the whole season) survived. This assumption is based on the fact that all bumble bee species seen in the field seemed to depend on both early (e.g. *Vaccinium* spp.) and late (e.g. *Calluna vulgaris*) floral resources for feeding (Supplementary material Appendix A1 Fig. A3) and that no additional food sources were found there. After each run the number of surviving nests and the distance of the nests to the nearest plot edge were recorded. These values were then averaged across runs to obtain an estimate of the mean response under each scenario.

Results

A total of 909 interactions between 13 plant and 8 bumble bee species were recorded in the field. The most abundant bumble bee species were *Bombus jonellus* and *Bombus lucorum*, each of which accounted for ca 32% of all visits to flowers recorded through the whole study, while the most abundant plants were *Calluna vulgaris* and *Vaccinium vitis-idaea*, which received 61% and 20% of all bumble bee visits recorded.

Temporal and spatial variation of floral resources

Temporal variation

The availability of flower resources in our ca 36 km^2 landscape changed markedly throughout the season. One group of species produced flower resources early in the season (May–June) and a second, more species-rich group, produced flower resources later in the season (July–August; Supplementary material Appendix A1 Fig. A1). In terms of flower abundance, the first group was dominated by *Vaccinium myrtillus* and *V. vitis-idaea*, while the second group was mainly dominated by *Erica cinerea* and *E. tetralix* in early summer and by *Calluna vulgaris* in late summer. Time explained a significant proportion of the variation in resource dynamics (constrained correspondence analysis; resource availability ~time vector, $F_{1,5} = 1.38$, $p = 0.005$, 21.7% of variance explained). Species of *Vaccinium* were most abundant in mid-successional plots and *Calluna vulgaris* and *Erica* spp. were most abundant in early and late successional stages (Supplementary material Appendix A1 Fig. A2).

Resource use by bumble bees

There was a highly significant correlation between resource availability and resource use by bumble bees along the season (Procrustes correlation = 0.97, p = 0.001). In May and June, bumble bees' main food sources were *Vaccinium vitis-idaea* and *Vaccinium myrtillus*, which accounted for 78.7% and 11.1% of all bumble bee visits recorded in that period (Supplementary material Appendix A1 Fig. A3, top). In July and August, bumble bees mainly visited *Calluna vulgaris* and, to a lesser degree, *Erica cinerea* and *E. tetralix*, which accounted for 79%, 9.5% and 1.8% of all bumble bee visits recorded in that period (Supplementary material Appendix A1 Fig. A3, bottom). As a result of this foraging pattern, a large proportion of bumble bees (84%) were caught either on *Vaccinium* spp. in mid-successional plots in spring (May, and first half of June) or on *Calluna*/*Erica* spp. in early/late successional plots in summer (second half of June, July and August).

Modelling resource availability and bumble bee nest survival

Both patch size and foraging range had a marked effect on nest survival. As patch size increased, the proportion of surviving nests decreased (Fig. 2). Nests of bumble bees with longer foraging ranges were less affected by increases in patch size. Conversely, the survival of nests where the bee species had a short range decreased rapidly even at small increases in patch size (Fig. 3). There was also an effect of landscape structure on nest location: although patch size increased, surviving nests were only found close to the edges of patches (< 700 m; Fig. 3). Here too there was a partially compensatory effect of foraging range on the impact of increasing patch size: the longer the foraging range, the farther from the plot's edge the surviving nests could be found. In addition, as patch size increased, surviving colonies of all species,

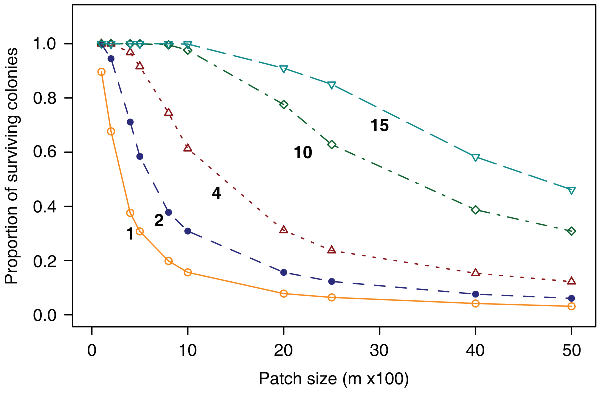

Figure 2. Bumble bee colony survival dependence on patch size (square patches, measure given is that of one side × 100 m). Each curve corresponds to a different foraging range, from 100 to 1500 metres. Values of foraging distance for each curve (in metres × 100) are given.

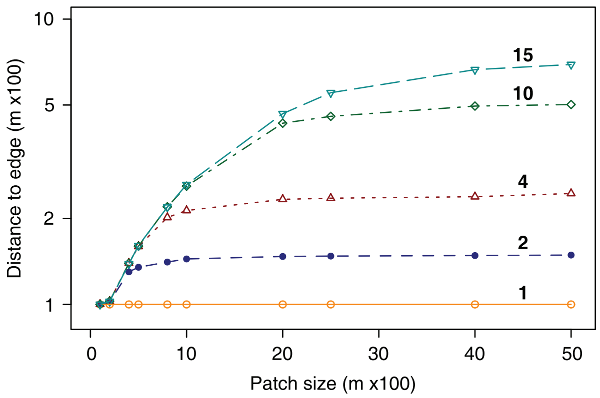

Figure 3. Effect of patch size (square patches, measure given is that of one side × 100 m) on the distance to the nearest patch edge of surviving nests. Each curve corresponds to a different foraging range, from 100 to 1500 m. Values of foraging distance for each curve (in metres × 100) are given.

irrespective of foraging range, were increasingly confined to plots' edges (Fig. 3).

Discussion

This study used a combination of field observations and a computer simulation to understand the spatio-temporal dynamics of the flower resources used by bumble bees in an area of the native pine woodlands of Scotland. Field observations revealed that floral resources vary spatially and temporally at the landscape level, and that bumble bees respond to these variations by tracking floral resources across the landscape during the season. The simulation model showed that different patterns of resources availability could affect the survival and distribution of bumble bee nests across the landscape.

In this section we will first address the main limitations and potential sources of bias of the study, and then discuss the relevance of the results in the context of the three questions of this study.

Limitations

First, there is the potential bias caused by the sampling technique. By walking randomly in the plots, plants were sampled proportionally to their abundances. As a result, there is the possibility that more bumble bees were recorded on the dominant plants because they were more common (Gotelli and Graves 1996) rather than because they represented a resource of particularly good quality. The lack of correlation between flower abundance of each plant species at each site and the number of bumble bees captured on them (Procrustes analysis; correlation between matrices $= 0.12$, $p = 0.48$) suggests that, even if this effect was present, it was unlikely to bias the results. If timed observations had been used, then a much lower number of interactions would have probably been recorded (Gibson et al. 2011).

Second, temporal and spatial pooling of data has been identified as a potential source of bias causing spurious results in ecological studies (Fox and Morrow 1981, Vázquez and Aizen 2004, Medan et al. 2006, Jordán and Osváth 2009). This study pooled flower abundance and insect visitation data obtained over three seasons of field work. Replicate samplings of each site in individual years were too few to allow for an analysis of each year separately. Although there was some variation in flowering times among years, it is unlikely that analysing each year separately would have rendered a different result as the same flowering sequence and a lack of overlap between early and late floral resources was observed each year (Supplementary material Appendix A1 Fig. A4).

Finally, although our simulation was spatially explicit, the size, shape and distribution of plots were not based on a real landscape. In real landscapes, patch size and shape are heterogeneous and there are many linear elements which can sustain bumble bee populations; the influence of these, however, were not considered in the present study. Moreover, in our study there is some evidence (Devoto and Memmott unpubl.) to suggest that ruderal plant communities in disturbed areas (road sides, landslides, forestry timber roads) may act as reservoirs of flower resources that bumble bees can exploit during gaps in flower availability elsewhere in the landscape.

Variation in floral resources and their use by bumblebees

Our results suggest that early and late flower resources were not randomly distributed across the landscape; rather, each group of plant species was associated with plots at certain points in the successional gradient. For instance, *Vaccinium vitis-idaea* and *V. myrtillus* (spring resources) were associated with late successional plots (+80 year since last clear-cut), whereas *Calluna vulgaris, Erica cinerea* and *E. tetralix* (summer resources) were associated to early and late successional plots but tended to be less abundant in mid-successional plots. This has significant implications for forest management aimed at conservation targets, as it suggests the proportion of plots at different successional stages in a given area might strongly affect the availability of resources for local bumblebees along the season.

The temporal segregation of resources has significant implications in the context of climate change. Spring resources are critical for bumble bee queens that have just emerged from wintering and are searching for a nesting site, laying eggs or starting to feed the first brood of workers (Goulson 2003). In a study of 385 British plant species, spring flowers were more affected by climate warming than those that flowered later (Fitter and Fitter 2002), i.e. they flowered disproportionately earlier. Thus, if a warm spring advances the flowering date of *Vaccinium* spp. or shortens their phenophases there is the potential for a resource gap occurring in early summer before *Calluna* blooms. Although there is a lot of variation in rates between species, this situation is potentially risky since it would affect the fitness and survival of bumble bee colonies which, in turn, may deprive other plant species in the area of pollination services later in the season (Memmott et al. 2007, Hegland et al. 2009).

The high correlation between resource availability and resource use suggests bumble bees tracked flower resources available in plots at different successional stages at different times of the season. This is evidence that movement between fragments is essential for the persistence of bumble bees, a behaviour which is particularly common in fragmented habitats for species with limited mobility (Debinski and Holt 2000).

In the simulation model, as landscape structure became simpler (i.e. as patch size increased) there were less areas suitable for nest establishment because in many areas access to early and late season resources within foraging range is not possible. As a result, bumble bee species with short foraging ranges ("doorstep foragers" sensu Goulson and Stout 2001) were, on average, less successful at establishing colonies than long-range species. These results suggest that both landscape complexity and bumble bees' foraging range could affect the survival of bumble bee nests and thus constrain the distribution of nests at the landscape level. The results of our simulation are perhaps not surprising in light of the simplicity of the model used. However, the model is a first step towards using spatially explicit simulations to generate hypotheses about the landscape-level effect of forest management practices on bumble bee populations. For instance, our approach could be used to predict local bumble bee abundances based on the structure of the surrounding landscape and then test predictions against field measurements. Furthermore, the model could be used to test the hypothesis that bumble bee queens assess the complexity of the landscape (and thus the likeliness of finding season-round food resources) when searching for a nesting site. While simple, our model could readily be applied to other landscapes, such as farmland, where it may provide some explanations for the causes underlying bumble bee declines (Kosior et al. 2007, Goulson et al. 2008, Rundlöf et al. 2008, Williams and Osborne 2009).

Conclusion

The field observations and the results from the simulation indicate the importance of considering the temporal and spatial scale of plant-visitor interactions when planning and testing successful pollinator management strategies in intensively managed and fragmented landscapes. Our study used a meta-community approach to integrate the spatial and temporal dynamics of resource availability and resource use at the landscape level. It also showed that spatially-segregated ecological networks within a landscape actually function as a meta-network linked by animal species foraging across the landscape. This approach provided an insight into the foraging ecology of bumble bees that wouldn't have been gained from observing the individual plots on a one by one basis. Both conservation and restoration of pollination may benefit from a better understanding of the dynamic interplay between space and time in ecological interactions. Overall, our results highlight the complex interplay between spatially and temporally segregated resources in sustaining bumble bee populations in the native pine woodlands of Scotland. Understanding this complexity will be essential for integrating pollinator conservation into habitat management practices.

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Supplementary material (available online as Appendix oik-01251 at <www.oikosjournal.org/readers/appendix>). Appendix A1.