Both population size and patch quality affect local extinctions and colonizations

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Both population size and patch quality affect local extinctions and colonizations

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Currently, the habitat of many species is fragmented, resulting in small local populations with individuals occasionally dispersing between the remaining habitat patches. In a solitary bee metapopulation, extinction probability was related to both local bee population sizes and pollen resources measured as host plant population size. Patch size, on the other hand, had no additional predictive power. The turnover rate of local bee populations in 63 habitat patches over 4 years was high, with 72 extinction events and 31 colonization events, but the pollen plant population was stable with no extinctions or colonizations. Both pollen resources and bee populations had strong and independent effects on extinction probability, but connectivity was not of importance. Colonizations occurred more frequently within larger host plant populations. For metapopulation survival of the bee, large pollen plant populations are essential, independent of current bee population size.

Keywords: metapopulation; connectivity; area; pollination; solitary bee; *Andrena hattorfiana*

1. INTRODUCTION

Currently, the habitat of many species is fragmented, resulting in small local populations with individuals occasionally dispersing between the remaining habitat patches (Thomas & Kunin 1999). During the last two decades, the dynamics of such populations have been studied within the metapopulation concept (Hanski & Gaggiotti 2004). Metapopulations survive when local population extinctions are balanced by recolonizations, but there are few studies of these essential processes. Most studies use habitat patch area and isolation in conjunction with occupancy when modelling population viability. Based on general principles, colonization rate is expected to decline with distance to source populations, whereas extinction rate is assumed to increase with declining habitat patch size. Patch size is often used as an easily measured surrogate of habitat quality (available resources) and local population sizes.

Many models have recently been developed to assess the survival of metapopulations, most often based on occupancy patterns of local habitat patches on at least two occasions (Hanski & Gaggiotti 2004). These models have been used in nature conservation, but few studies have examined the basic assumption that habitat patch size is a good surrogate for local population size (cf. Talley 2007). Critics have argued that habitat quality of the patch is as important as patch size *per se* (Thomas *et al*. 2001). This relates to sink–source dynamics, similar to metapopulation dynamics. In sink–source models, some habitats are of lower quality with a low reproductive success, while other habitats are of better quality with higher reproduction success (Pulliam 1988; Pulliam & Danielson 1991).

In a recent study, extinction patterns were predicted more effectively by local population size than by patch area (Pellet *et al*. 2007). However, local population size in a patch may vary strongly between years, even in a stable habitat patch network, especially over many generations (Thomas *et al*. 2002). In years when relatively few individuals inhabit a large patch, the resources *per capita* are larger and may positively influence reproductive success and/or survival for the next generation. Thus, extinction probability may decrease in patches of high habitat quality, patches with large local population sizes and patches of large size. Similarly, when dispersing individuals encounter an empty large or high-quality patch, their propensity to stay and reproduce may be higher than in a small or low-quality patch. Even with random dispersal, a large habitat patch will be colonized by chance more often by dispersing individuals than a small patch. Thus, colonization probability can increase with patch size and/or quality.

As pollinators, solitary bees are key components in terrestrial ecosystems, and they are essential for economic as well as ecological reasons (Matheson *et al*. 1996; Murren 2002; Westphal *et al*. 2003). Recent studies demonstrate that specialized haplodiploid solitary bee species may have high turnover rates for genetic reasons (Zayed & Packer 2005). Here, we explore whether extinction and colonization patterns in a solitary bee metapopulation are related to habitat quality, local bee population size, habitat patch size and isolation over 4 years.

2. MATERIAL AND METHODS

(a) *Study area*

The study area in Stenbrohult parish in southern Sweden (56° 37′ N, 14° 11′ E) is forest-dominated with agricultural land occupying 5 per cent of the study area, mainly consisting of seminatural grasslands. Local bee populations were investigated in all suitable habitats over 4 years in an area of 80 km². The study area is adjacent to the large lake Möckeln in the West and built-up areas and an exploited bog in the

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South. Coniferous forests dominate to the North and East. Thus, the landscape surrounding the study area has a low proportion of agricultural land.

(b) Studied species

We studied the specialized bee *Andrena hattorfiana* (Fabricius) for which the main pollen source in Northwest and Central Europe is *Knautia arvensis* (L.) Coult. (Dipsacaceae). In the study area, the bee only collects pollen from *K. arvensis*. The bee species is large with a length of approximately 14 mm and easily identified in the field. Females differ from males in both appearance and behaviour and can easily be sex determined in the field. *Andrena hattorfiana* has declined in several European countries and a pollen budget has been described (Larsson & Franzén 2007*a*). The ecology of *A. hattorfiana* is relatively well known and the bee is active foraging for pollen from mid-June until mid-August and has one generation per year. The pollen plant and bee phenology are well synchronized. The average active foraging span has been estimated at 14.2 days, and the longest recorded foraging span was 44 days (Larsson & Franzén 2007*b*). In a plant population exposed to other flower visitors, *A. hattorfiana* required on average 47 *K. arvensis* stalks (= 16 plant individuals) to produce one offspring (Larsson & Franzén 2007*a*). The reproductive rate is low and one *A. hattorfiana* female produces only five to 10 brood cells each with one egg. It is not known whether a female can make more than one nest in a lifetime. The bee has a sedentary behaviour with short foraging ranges around the pollen resource, usually within 50 m, and only 2 per cent of marked bees dispersing between habitat patches as defined below (Franzén *et al.* 2009). Thus, in the study area, the majority of the bee individuals forage for pollen, mate and nest in the same patch. The males fly around inflorescences of *K. arvensis* in a typical mating flight, searching for females to mate with. Mating takes place on the inflorescence or in the air and lasts only up to a few seconds (M. Franzén 2004, unpublished data). The males hatch some days before the females, are less easy to find and probably have a shorter lifespan compared with the females.

The study species is an example of a highly specialized haplodiploid species with an expected high turnover rate compared with diploid species (Zayed & Packer 2005; Zayed *et al.* 2005). Haplodiploid organisms have been considered immune to genetic load impacts because deleterious alleles are readily purged in haploid males. However, single-locus complementary sex determination ancestral to the haplodiploid solitary bees imposes a substantial genetic load through homozygosity at the sex locus that results in the production of non-viable or sterile diploid males. This increases the risk of inbreeding depression. Thus, haplodiploids are more, rather than less, prone to extinction for genetic reasons.

The pollen resource (plant population size) was estimated by counting all *K. arvensis* stalks with flowers or flower buds at each patch once per season. The plants are at the same phenological stage with new flower heads appearing regularly in the study area from June to August. The number of flower stalks in each habitat patch is a measure of the amount of pollen produced in a patch being the critical reproductive resource for the bee (Larsson & Franzén 2007*a*). To quantify the difference in pollen produced between the local host plant populations owing to gender the frequency of *K. arvensis* females was determined in 15 patches. In 30 randomly

selected plant individuals per patch, we determined the sex, the number of stalks per plant and the number of inflorescences per stalk. In the study area, the female plant proportion was 15 ± 1.7 per cent (min. 5%, max. 21%). Adjusting the female frequency among the 15 sampled *K. arvensis* patches revealed a strong relationship between the number of stalks and the estimated pollen amount ($p < 0.001$, $r^2 = 0.98$). Based on this strong relationship, we decided not to examine the expected loss of pollen owing to the female frequency in each patch/plant population.

The seasonal peak (here called mid-season) period of activity for pollen-collecting females of *A. hattorfiana* was defined each year from our observational data. The mid-season started on the occasion when over 30 per cent of the maximum number of bees were observed and ended the day when less than 30 per cent of the maximum number of bees was observed (Larsson & Franzén 2007*a*). *Andrena hattorfiana* individuals are long-lived, with a long activity period, being active most of the day (Larsson & Franzén 2007*b*).

(c) Habitat patches and survey walks

In the study area, all potentially suitable habitat patches, such as sun-exposed grasslands with more than 50 flower-bearing stalks of *K. arvensis*, were mapped (figure 1) and the number of female *A. hattorfiana* on flowers counted. Habitat patches were defined as separate if the borders were situated 100 m apart or more, based on our study of the movement of individually marked bees. All patches, including small patches where *A. hattorfiana* was never observed, were visited at least three times during mid-season of each year in 2003–2006. For each local bee population, a mean number of observed female bees from each mid-season survey walk was obtained. This mean value was used to estimate the local bee population size according to the equation

$$R = e^{0.642 + 1.61\,\mathrm{Ln}(T)},$$

where T is the number of observed *A. hattorfiana* females per average survey walk (Larsson & Franzén 2007*b*). Survey walks required from 7 to 55 min depending on the *K. arvensis* population size and density. Each survey walk was performed between 09.00 and 17.00. Surveys were not performed in unfavourable weather conditions, such as rain (within 1 h after rainfall), temperatures lower than 17°C or when winds were stronger than approximately 4 m s^{-1}.

The mean number of survey events in each of the 63 patches with the host plant present was 6.46 ± 0.30 (range 3–15) in 2003, 5.45 ± 0.16 (range 3–11) in 2004, 4.51 ± 0.13 (range 3–10) in 2005 and 3.53 ± 0.07 (range 3–7) in 2006.

(d) Connectivity measures

For each patch and year, connectivity was measured as the number of bees occurring in a circle within a radius of 1 and 2 km, respectively, from each patch. The local bee population in the patch for which connectivity was calculated was not included in the calculations. The bee population size as defined above was used to estimate the number of bees in the surrounding area. Connectivity was also analysed with radii of 300–500 m around each patch, but this did not change the result (results not presented). Further, a connectivity measure that includes the distance to the nearest occupied patch was tested with a similar result.
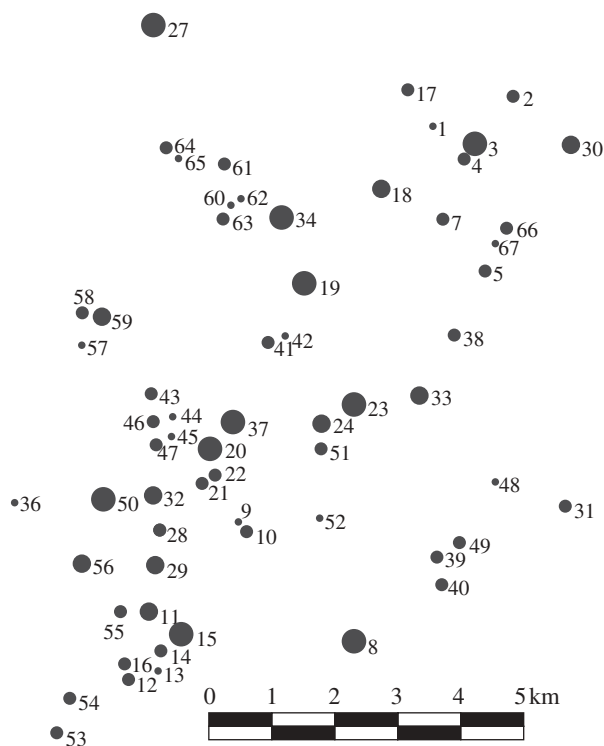
Figure 1. Patches with the host plant *K. arvensis* and occupied by the solitary bee *A. hattorfiana* at least one of the years 2003–2006. The size of the filled circles corresponds to the number of *K. arvensis* stalks (pollen resources) measured in 2004 at each patch (1–100, 101–500, 501–1000 and more than 1000 stalks). The plant population size was measured in 2004, 2005 and 2006 and was relatively constant between the years. No plant population went extinct during the study period. For information about bee populations at each patch, see table S2, electronic supplementary material.

(e) Spatial autocorrelation

The non-independence of data caused by spatial structure can cause analyses to be generous, and even weakly correlated variables may appear to yield significant coefficients owing to the confounding effects of space. The level of significance is important when trying to understand the effect of different predictors on a response variable, such as whether population size will explain spatial variation in extinctions. Testing for the spatial clustering of extinctions, colonizations, plant population size, bee population size and connectivity for each year and patch area was performed using Moran's *I* values (Legendre 1993; Legendre *et al.* 2002). Ten inter-sample distance classes were formed (table S1, electronic supplementary material). The overall significance of the Moran's *I* values was tested by checking whether at least one of the derived Moran's *I* coefficients was significant at the Bonferroni-corrected probability level, here $0.05/4 = 0.013$ (Dale *et al.* 2002). The statistical significance was assessed with 1000 Monte Carlo permutation tests conducted for each distance class separately. For a positive autocorrelation, a negative relationship between the Moran's *I* values and distance classes is expected (Borcard *et al.* 1992; Legendre 1993; Diniz-Filho & Telles 2002; Schiegg 2003). This will detect correlations that are interrupted by source populations and rescue effects entering within the radii of the analysis. Moran's *I* values were calculated for distance classes in order to encompass both the nearest distance between patches (325 m) and the average

distance to all other patches, which is 1200 m (table S1, electronic supplementary material). The distances between the habitat patches were 100–9300 m. In an extensive mark–release–recapture study in the study area, the mean movement distance was less than 100 m and the maximum observed dispersal distance was 1 km (Franzén *et al.* 2009).

(f) Statistics

Multiple logistic regressions (logistic-likelihood ratio significance, enter selection procedure) were used to analyse extinctions and colonizations in separate analyses for colonizations and extinctions. In the analyses of extinction patterns, occupancy was recorded for year *t* and *t* − 1 for all patches that were occupied in year *t* − 1. Each patch was classified as occupied (0) or extinct (1) in year t. In the analysis of colonization patterns, occupancy was recorded for year *t* and *t* − 1 for all patches that were unoccupied in year *t* − 1. Each patch was classified as unoccupied (0) or colonized (1) in *t*. Logistic regressions were performed for extinctions in 2004 (2003–2004) and 2006 (2005–2006) and for colonizations in 2005 (2004–2005). All possible combinations of years were not analysed because there was not enough (more than five) colonization and extinction events represented. Additionally, if turnover data from 2 consecutive years are analysed, there will be a strong dependence in the data. Thus, to avoid pseudoreplication, we only analysed independent data points. Response variables were patch area, bee population size, the local host plant population size and the number of bees in the surrounding landscape. For the variables included in analysis of extinctions and colonizations, see table 1.

The response variables were correlated to each other to explore patterns of multicollinearity using the Pearson correlation (table 2).

To evaluate whether the method is appropriate for the analysis of turnover rates, we tested whether extinctions and/or colonizations were related to the number of transect counts performed in mid-season at each patch using the *t*-test. Colonizations and extinctions occurred independent of the number of transect counts performed in mid-season (colonizations; $t = -0.55$, $p = 0.59$, d.f. = 71 and extinctions; $t = 0.93$, $p = 0.35$, d.f. = 114). To test whether there is a higher probability of detection at intensively visited patches, extinctions and colonizations were related to intensively (over six transect surveys in mid-season) and extensively visited (3–6 transect surveys in mid-season) habitat patches. No such effect was found (colonizations; $t = 0.75$, $p = 0.27$, d.f. = 71 and extinctions; $t = 0.43$, $p = 0.65$, d.f. = 114). All statistical analyses were performed in SPSS 14.0. Means are presented with ±1 s.e.

3. RESULTS

The pollen plant *K. arvensis* occurred at 63 patches, covering 1.83 per cent of the total study area, with a mean patch area of 1.28 ± 0.19 hectares (figure 1). In 2003–2006 the bee occurred at 54 (totally 1266 individuals), 24 (313 individuals), 40 (568 individuals) and 13 (75 individuals) habitat patches. The bee occupied 10 (16%) of the 63 habitat patches all 4 consecutive years (2003–2006) (figure 2, table S2, electronic supplementary material). The largest local population was the one consisting of more than 20 female individuals all 4 years (334, 132, 233 and 23 individuals). In total,

Table 1. Colonizations and extinctions was analysed against patch characteristics using the listed variables and years. Variables in brackets (x) analysed as alternatives to the connectivity measure (bees in surrounding 3 km^2 year t) and were included in the same model instead of another connectivity measure.

analyses	colonizations 2005 (2004–2005)		extinctions 2004 and 2006 (2003–2004 and 2005–2006)	
year	t	$t-1$	t	$t-1$
patch area (log 10-transformed)	x		x	
bee population size (log 10-transformed)				x
plant population size (log 10-transformed)	x			x
bees in surrounding (3 km^2)	x	(x)	x	(x)
bees in surrounding (12 km^2)	(x)	(x)	(x)	(x)

Table 2. Correlation matrices presenting significance levels (*p*-value) and correlation coefficients (slope) between the independent variables. Correlation based on data from 2004 for all 63 patches.

	patch area	host plant population size	connectivity (3 km)
host plant population size			
slope	0.259		—
p-value	0.038		
connectivity (3 km)			
slope	−0.187	−0.246	
p-value	0.139	0.050	
bee population size			
slope	0.212	0.613	−0.112
p-value	0.093	0.001	0.380

72 local extinction events and 31 (re)colonization events were observed (figure 3). No extinction or colonization event was observed in local *K. arvensis* populations between 2004 and 2006 and the local plant population size in 2006 was strongly correlated with the size of the same plant populations in 2004 (local plant population size 2006 = 0.43 + 0.80 * 2004. $p < 0.001$, $r^2 = 0.63$). Between 2004 and 2006, 40 local plant populations increased in size and 23 decreased in size. On average, a local plant population had increased by 12 per cent between 2004 and 2006.

The local bee extinction rate was strongly dependent both on local bee population size and patch habitat quality, the latter measured as pollen plant population size, but habitat patch size had no additional predictive power (figure 3). Colonizations occurred more frequently in larger host plant populations (logistic regression with all variables included in the model: patch area: $B = -0.63$, $p = 0.57$, plant population size: $B = 4.45$, $p = 0.004$, bees in surrounding 3 km^2: $B = -0.25$, $p = 0.24$). Extinctions and colonizations were not associated with connectivity, measured as the number of bees in the surrounding area (measured both at the 3 and 12 km^2 areas). Spatial autocorrelation was not found for extinctions, colonizations and independent factors, except for our connectivity measure mainly at distances up to 1000 m (table S1, electronic supplementary material).

4. DISCUSSION

Both the size of the local pollen plant population and the local bee population had strong and independent effects on the local extinction probability of the solitary bee (figure 3). Solitary bees provide the opportunity to explore the interacting effects on extinction risks of patch area, population size and resource availability that are impossible to explore in most other insects. For metapopulation survival of the bee, large host plant populations are essential. These results are important since a general decline of both bees and insect-pollinated plants has been found (Biesmeijer *et al.* 2006). For the integrity of ecosystems and survival of both bees and plants, attention should be given to crucial factors for viable metapopulations of bees. Our results emphasize the importance of large local populations of those plant species on which specialized pollinators depend. Further, our results carry a general message to metapopulation studies: patch quality and local population sizes are not surrogates for each other, but both may be important factors in metapopulation dynamics.

Other studies separating the effects of habitat patch size and local population size on colonization and extinction probabilities are few (cf. Talley 2007). Our results stress that the factors generating population turnover can be additive and complex. Patch area might be more important than population size (or vice versa) for extinction and colonization patterns in different situations and species. Between-patch dispersal could balance local extinctions by colonizations. In our study area, no evidence for a rescue effect *sensu* (Brown & Kodric-Brown 1977) was evident.

The mechanism of a higher bee extinction risk in small host plant populations, even when bee population size has been accounted for, could be that bees are pollen-limited in small host plant *K. arvensis* populations to a much larger extent compared with larger host plant populations. Other pollen-foraging flower visitors might have a higher visitation frequency in small plant populations. This has been found in the plant *Viscaria vulgaris*, also visited by a diverse insect fauna (Jennersten & Nilsson 1993). Additionally, a possible high visitation frequency of other flower visitors in small *K. arvensis* populations may induce bee dispersal. We suggest that relatively low pollen availability in small *K. arvensis* populations could be the determining factor influencing both extinction and colonization processes in *A. hattorfiana*.
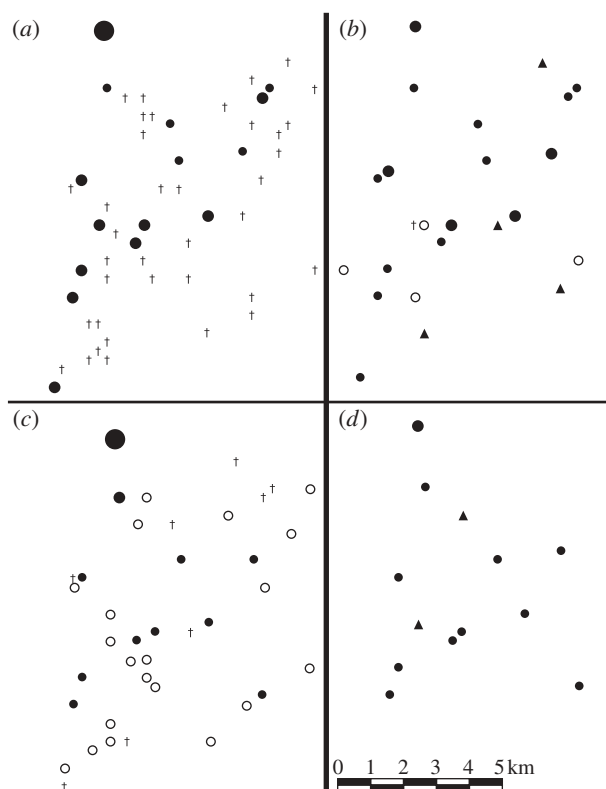
Figure 2. Occurrence pattern of the solitary bee *A. hattorfi-ana* in (*a*) 2003, (*b*) 2004, (*c*) 2005 and (*d*) 2006. Filled black dots represent estimated population sizes in increasing size classes: 1–10, 11–50, 51–100 and more than 100 female bee individuals. Dagger denotes patches where the bee became extinct the subsequent year. Triangle denotes colonized patches. Open dots denote patches with extinction followed by colonization or vice versa for the previous and subsequent year. Note that information is missing for (*a*) colonizations in 2003 and (*d*) extinctions in 2006. Filled circle, present; dagger, extinct; filled triangle, colonized; open circle, colonized and extinct.

Recent studies have highlighted that extinction risk in haplodiploid organisms can be extremely high, especially for specialized species occurring in small local populations (Zayed & Packer 2005; Zayed *et al.* 2005). It cannot be excluded that genetic factors generate a high rate of local extinctions, in particular when many local populations consist of less than 10 individuals as observed in our study system (Wade & McCauley 1988; Franzén *et al.* 2009). Single-locus complementary sex determination ancestral to the haplodiploid solitary bees imposes a substantial genetic load through homozygosity at the sex locus that results in the production of non-viable or sterile diploid males. Thus, in small local populations, either sterile males or a biased sex ratio can increase the extinction risk. Specialized solitary bees are more, rather than less, prone to extinction for genetic reasons such as inbreeding depression (Zayed *et al.* 2005). Over the period of the study, the bees declined from 54 local populations (1266 individuals) in 2003 to 13 local populations (75 individuals) in 2006. The situation for the bees in the study area is alarming. Even if patch area and resources were stable throughout the studied period, the bee declined. Clearly, populations with few individuals suffer from a high

extinction risk, reducing the number of occupied patches over time (figure 2).

Colonization probability increased with pollen resources measured as host plant population size. It is more probable that large patches become colonized by chance (Simberloff 1978) and large plant populations might be found more easily if dispersal is non-random (Thomas 1994; Conradt *et al.* 2000). We did not find any effect of connectivity on colonization probability. The lack of connectivity effects suggest that the bees are relatively good at finding suitable patches over the distances covered in this study (Moilanen & Hanski 2001; Moilanen & Nieminen 2002; With 2004). However, connectivity measures used in models might not reflect how the species perceive connectivity. Patch area, population size and matrix influence real connectivity (Moilanen & Hanski 2001; Ricketts 2001; Fleishman *et al.* 2003; Sutcliffe *et al.* 2003). A tendency towards a more frequent extinction occurring at patches surrounded by many bees was observed, suggesting that the bees temporarily colonize patches with low habitat quality (figure 3). It is possible that the bee has a source–sink dynamic where some patches are of lower quality with a high turnover rate and other source populations have a high quality with high reproductive success (Pulliam 1988; Pulliam & Danielson 1991). In fact, the 10 local populations that occupied 4 consecutive years (2003–2006) might represent source populations. The temporary use of low-quality habitats are important to consider when assessing the conservation status and modelling population persistence. More studies are required to understand whether and how connectivity and source–sink dynamics influence the studied population.

Extinctions and colonizations showed no evidence of spatial synchrony (table S1, electronic supplementary material). The connectivity measure was spatially structured with a significant spatial autocorrelation. This was expected because areas surrounding the patches are considered in the connectivity measure. This procedure increases the spatial correlations and is similar to the reducing degrees of freedom, since the patches depend on each other (Moilanen & Nieminen 2002; Brooks 2003). We judged it unnecessary to integrate the spatial information into the regression models because the patches were spatially independent of each other (table S1, electronic supplementary material).

The probability of detection is crucial in metapopulation studies (e.g. Moilanen 2002). In species with a low probability of detection, apparent extinction and colonization patterns can be an effect of pseudo-turnover (Nilsson & Nilsson 1985; Moilanen 2002), i.e. small populations still occur at a patch but are not detected. Even small *A. hattorfiana* populations appear to be easily detected, and our data suggest a high probability of detection. The discrepancy between different surveyors was very low. Comparing the occupancy pattern of bees in habitat patches between two different independent surveyors reveal that within 40 visited patches with three or more mid-season visits by two independent surveyors, only six patches (15%) differed in occupancy between the surveyors. These were observations of single bee females and thus detection error is low.
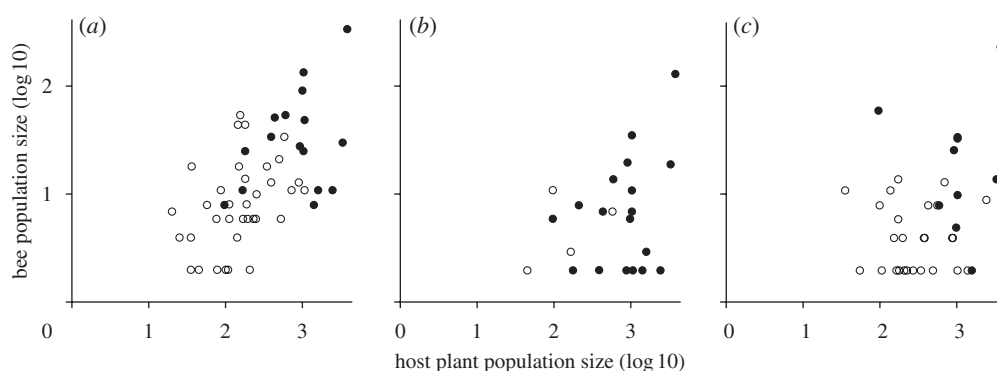
Figure 3. The relationship between local extinctions and the size of local female bee *A. hattorfiana* populations the year before the extinction events occurred, and the local pollen plant population size (number of *K. arvensis* stalks), over 3 consecutive years ((a) 2003–2004, (b) 2004–2005 and (c) 2005–2006). Extinct local bee population are denoted by an open dot and local bee population present both years are denoted by a filled dot. Logistic regression 2003–2004, all variables included in the model: patch area: $B = -0.24$, $p = 0.82$; bee population size: $B = -2.99$, $p = 0.035$, plant population size: $B = -4.58$, $p = 0.003$; bees in surrounding 3 km^2 in 2003: $B = -0.009$, $p = 0.24$. Logistic regression 2005–2006, all variables included in the model: patch area: $B = -2.87$, $p = 0.15$; bee population size: $B = -5.39$, $p = 0.009$; plant population size: $B = -5.83$, $p = 0.044$; bees in surrounding 3 km^2 in 2005: $B = -0.06$, $p = 0.34$. Extinctions in 2005 were not analysed statistically owing to few observations.

5. CONCLUSION

Determining the factors influencing local extinction and colonization events are of crucial importance to understanding the regional dynamics of populations as well as developing sound conservation measures. Indeed, many rare and endangered species occur in small local populations in highly fragmented habitats. Our study highlights that in a species where only 1.8 per cent of the landscape consists of suitable habitat patches, patch quality and local population size were important factors independent of each other, influencing metapopulation dynamics. On the other hand, habitat patch size had no additional predictive power. We, therefore, suggest metapopulation studies to explore these three important potential factors for extinction and colonization probabilities.

We tentatively suggest that the extinction risk of local populations of solitary bees may be high compared with many other taxa. In the German region studied in detail, Baden-Württemberg, 57 per cent of the recorded 429 bee species are endangered or close to extinction (Westrich 1990). Over 5 per cent (15 species) in Sweden of the Apoidae fauna have become extinct, with similar or higher values in several other countries (Matheson *et al.* 1996). The indicated elevated extinction proneness of solitary bees, combined with the keystone pollinator services that they provide, makes them valuable when assessing the health of natural and agricultural ecosystems. For metapopulation survival of bees, large pollen plant populations appear to be essential.

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