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Distribution and abundance of dung beetles in fragmented landscapes

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Abstract Related species utilising similar resources are often assumed to show similar spatial population structures and dynamics. This paper reports substantial ecological variation within a set of *Aphodius* dung beetles occurring in the same patchily distributed resource, livestock dung in pastures. We show how variation in habitat and resource selectivity, in the rate of movements between pastures, and in the distribution of local population sizes all contribute to interspecific differences in spatial population structures. Local dung beetle assemblages are compared between two landscapes with different densities of pastures. In one of the landscapes, we contrast the abundances and regional distributions of *Aphodius* before and after 15 years of rapid habitat loss. Different species show very dissimilar responses to changes in the structure of the landscape. Our results suggest that generalist *Aphodius* species, and specialist species with high dispersal powers, occur as large "patchy" populations in the landscape. In contrast, a strict pasture specialist species with limited dispersal powers (*A. pusillus*) forms classical metapopulations. At the community level, interspecific differences in spatial population structures make the local community composition a function of the structure of the surrounding landscape.

Keywords *Aphodius* · Spatial population structure · Metapopulation · Patchy population · Habitat loss

Introduction

The metapopulation concept has rapidly gained popularity in ecological research (Hanski and Simberloff 1997). Originally, population turnover was considered to be the key feature of metapopulation dynamics (Levins 1969; Gilpin and Hanski 1991), but currently the metapopulation concept is used for any spatially structured population system with local breeding populations connected by migration. Within this wider perspective, the possibility of population reestablishment following extinction is seen merely as an important special case (Hanski and Gilpin 1997, and references therein).

A broad definition of metapopulations will clearly embrace a range of spatially structured populations. Problems are likely to arise if it is assumed, without empirical evidence, that all species within some large taxon or some other grouping conform to some particular type of metapopulation structure, or exhibit particular types of spatial dynamics (Hanski and Simberloff 1997; cf. Doak and Mills 1994; Harrison 1994). A satisfactory understanding of a specific system can only be reached through thorough quantification of system-specific features such as habitat selection, local population sizes and migration rates (Thomas and Harrison 1992; Harrison 1994; Harrison et al. 1995; Harrison and Taylor 1997; Thomas and Kunin 1999). Some insight into metapopulation structure can also be gained indirectly by examining spatial patterns in the abundance and distribution of a species. When extinction-colonisation dynamics govern the dynamics of a metapopulation, local populations are more likely to occur in large and well-connected habitat patches than in small and isolated patches (Hanski 1994, 1999). The rationale is that small patches sustain only small local populations, which are prone to extinction, and that very isolated habitat patches are least likely to be (re)colonised. At the landscape scale, the incidence of a species persisting in a dynamic equilibrium between local extinction and colonisation events is expected to be higher in a dense network of patches than in a sparse one (Hanski 1991a; Hanski et al. 1995). Differences in the density of patch networks are also likely to translate into regional differences in population densities (Hanski 1999). The more local populations there are within migration range from a given population, the more immigrants it will receive. Thus, we expect to find higher lo-

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cal population densities the higher the density of suitable habitat patches in the landscape.

In this paper, we analyse spatial population structures in a set of closely related dung beetles in the genus *Aphodius*. All of these species frequently co-occur in a patchily distributed resource: livestock dung in pastures. Several previous studies have treated these species as a single guild (e.g. Hanski and Koskela 1979; Hanski 1980; Holter 1982; but see Gittings and Giller 1997), and metapopulation-level dynamics have been proposed to be important in many dung beetle species (Hanski and Cambefort 1991). This study has three objectives. First, we describe spatial population structures of different *Aphodius* species, drawing on both new and previous data on habitat selection, resource use and migration rates. Second, we relate the spatial population structures of individual species, and groups of ecologically similar species, to their contemporary abundance and distribution in two landscapes with different densities of pastures. Third, within one of these landscapes, we compare the abundance and distribution of *Aphodius* before and after 15 years of rapid habitat loss. In all cases, we evaluate whether the classical metapopulation concept (*sensu* Hanski and Simberloff 1997) provides a useful description of the actual population structure and consequent dynamics.

Materials and methods

Natural history of *Aphodius*

Beetles in the genus *Aphodius* (Aphodiinae, Scarabaeidae) are the dominant coprophagous beetles in northern Europe (Hanski 1991b). In Finland, a total of 36 species has been recorded, some 10 of which are currently both widely spread and locally abundant (Biström et al. 1991; Silfverberg 1992; the nomenclature of Silfverberg is used throughout this paper).

As a group, *Aphodius* share several ecological characteristics which are likely to translate into similarities in their spatial population structure. General accounts typically describe most species simply as breeding in the dung of domestic livestock (cf. Hanski 1986, 1991b). As such dung occurs only in pastures, individual pastures have the potential to sustain discrete local populations of dung beetles connected by dispersal. Thus described, the whole system conforms well with the classical metapopulation concept.

Nevertheless, there are also important ecological differences among the species. First, one of us (Roslin 2000) has found significant differences in the movement patterns of different species. Second, local population densities typically differ between species. In studies of local dung beetle communities, some species are typically found to be highly abundant, whereas others are uniformly rare (Hanski 1986, 1991b). Third, habitat preferences and resource use differ between species. Some *Aphodius* are most abundant on open pasture habitats, whereas others prefer shady forest habitats (Landin 1961; Rainio 1966; Koskela and Hanski 1977). Some species are strict specialists on the dung of livestock, whereas others also breed or feed on rotting plant material (White 1960; Landin 1961; Gittings and Giller 1997).

In Table 1, we have grouped the 18 different *Aphodius* species encountered in this study into four guilds, based on independent information on their natural history: (1) “generalists”, species which are regularly found to breed or feed in all kinds of habitats; (2) “pasture specialists”, species which are more or less exclusively found on open pastures; (3) “intermediate species”, which are more common on open pasture habitats than in shady forest habitats, but frequently occur in both (according to Gittings and Giller 1997, some of these species have saprophagous larvae); and (4) “forest specialists”, species which mainly reproduce in shady habitats, whereas adults are regularly found in open pastures. For species belonging to guilds 1, 3 and 4, local populations are unlikely to be as discrete as in guild 2, and we may a priori expect to see rather different types of spatial population structures and dynamics in each guild (cf. Harrison 1994; Harrison and Taylor 1997). Classical metapopulation structures seem most plausible among pasture specialists.

Table 1 *Aphodius* species encountered in this study, divided into four guilds based of their habitat preferences. Within guilds, species are listed in alphabetical order. Species shown in **bold type** belong to the late summer fauna (Finn et al. 1998, 1999), and were excluded from the analyses. For all other species, a *three-letter abbreviation* is introduced for use in subsequent figures. The “+” and “–” signs indicate the presence or absence, respectively, of the species in dung beetle samples from Åland and Uusimaa

Guilds and species	Species abbreviation	Presence in samples	
		Åland	Uusimaa
Generalists			
A. depressus	*dep*	+	+
A. fimetarius	*fim*	+	+
A. rufipes		+	+
A. scybalarius		+	–
Pasture specialists			
A. erraticus	*err*	–	+
A. foetens		+	–
A. fossor	*fos*	+	+
A. ictericus		+	–
A. merdarius	*mer*	–	+
A. pusillus	*pus*	+	+
Intermediate species			
A. ater	*ate*	+	+
A. distinctus	*dis*	+	+
A. haemorrhoidalis	*hae*	+	+
A. prodromus	*pro*	+	+
A. punctatosulcatus	*pun*	+	–
Forest specialists			
A. borealis	*bor*	+	+
A. lapponum	*lap*	–	+
A. tenellus	*ten*	–	+

This classification is based on personal comments kindly provided by Bengt Ehnström, Gunnar Gustavsson, Jyrki Muona, and Karolina Vessby, on our own previous experience, and on the following written sources: White (1960); Landin (1961); Rainio (1966); Koskela and Hanski (1977); Gittings and Giller (1997). We acknowledge the fact that the ecological characteristics of a species may differ in different parts of its range; thus, this classification is likely to be valid for Fennoscandia only

Study areas

Two study areas were selected close to each other in southern Finland: Western Uusimaa, and the largest of the Åland islands (Fig. 1). Both areas are approximately 50×50 km^2 in size. By the mid-20th century, they each had a dense network of livestock farms, but during the last few decades, local herds of cattle, sheep and horses have rapidly decreased (National Board of Agriculture 1920–1985; Information Center of the Ministry of Agriculture and Forestry 1986–1996). The decline has been somewhat sharper in Uusimaa than on Åland, and as a consequence, the current network of farms is much denser on Åland than in Uusimaa (Fig. 1). Within Åland, the mean distance between neighbouring livestock farms is 0.75 km

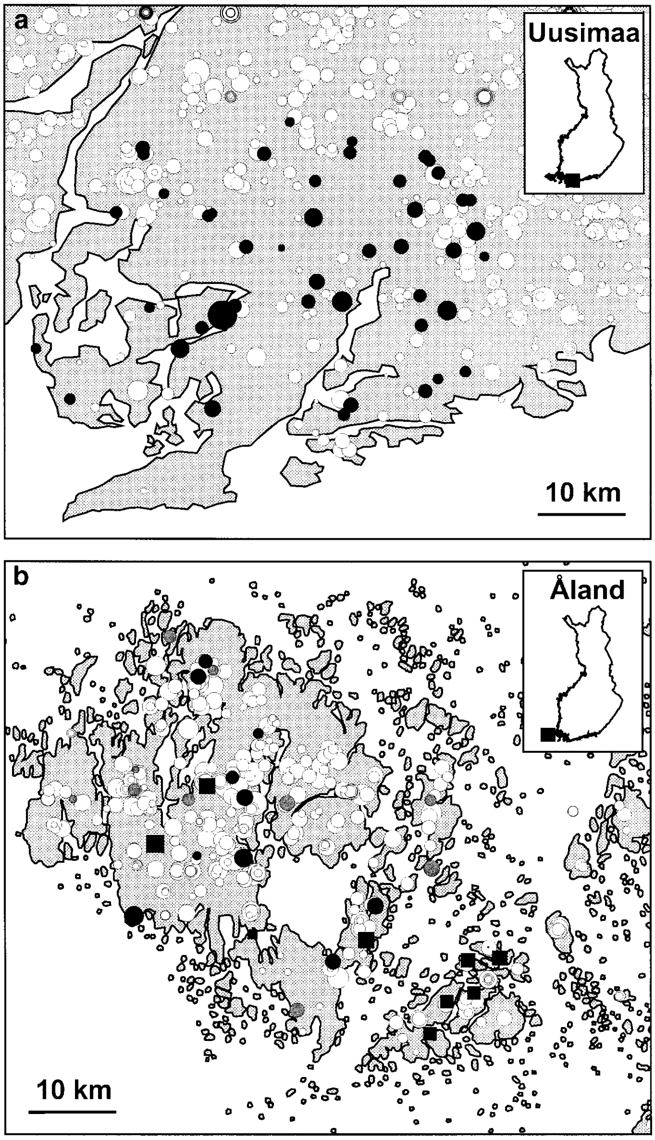

Fig. 1 Maps of the current distribution of livestock farms **a** in Uusimaa and **b** on Åland. Individual farms are shown as *circles*; the *size* of each circle is proportional to the "effective livestock" on the respective farm (see Materials and methods for a description of this measure). In both maps our sampling sites are indicated by *solid symbols*. **b** On Åland, nine farms previously sampled by Hanski and Kuusela (1983) are shown as *squares*. All sites sampled between 31 May and 20 June are shown by *darker solid symbols*, whereas sites sampled between 27 June and 7 July are shown as *lighter solid symbols*

(SE=0.05, median=0.47, n=326), compared to 1.41 km in Uusimaa (SE=0.07, median=1.17, n=208). By comparing the abundance and distribution of dung beetles in these two areas, we may thus identify potential effects of a change in the landscape composition.

Sampling design

Characterisation of habitat patch size and isolation

To establish the effect of "patch size" and "isolation" in the dung beetle systems, these concepts were first operationalised as follows. Our size metric was based on the resource most likely to limit the size of local dung beetle populations, i.e. dung and thus livestock. Farm-specific data were obtained from an official agricultural data base documenting, for each farm, its livestock (stratified by species and age) and location (with an accuracy of 10 m) (figures from 1995; Anonymous 1996), and from personal communication with farmers. As animals of different species and age are likely to produce different amounts of dung, each farm i was assigned a size corresponding to its "effective livestock":

$$N_i=[cows_i+bulls_i+horses_i+0.5(heifers_i)+0.25(calves_i+foals_i)\\ +0.2(sheep_i)+0.1(lambs_i)],$$

(hereafter simply referred to as the "size" of a farm). Only animals let out to graze were considered (data collected from the farmers).

The connectivity (the opposite of isolation) of each farm i was measured by a simple index, proportional to the expected numbers of beetles immigrating from populations on surrounding farms at maximum patch occupancy:

$$S_i=\sum_{j\neq i} e^{\alpha d_{ij}} N_j$$

where d_{ij} is the distance (km) between farms i and j, N_j is the effective livestock on j, and α is a parameter describing how fast the number of migrants from patch j decline with increasing distance (index modified from Hanski 1994, 1999; Hanski and Simberloff 1997). A rough estimate of α=–1.9 was adopted from a study of dispersal distances in *A. pusillus* (Roslin 2000). The current analyses and results are insensitive to species-specific variation in the value of α, as S_i measures remain highly correlated across tenfold variation in α (cf. Hanski 1999).

Sampling of farms

We used the following randomisation procedure to sample the full range of farm sizes and connectivity values encountered in Åland and Uusimaa. Within both areas, all farms were divided into sixteen size-connectivity classes, with class limits defined by the quartiles of each variable's distribution. From each class, two or three farms to be sampled were then chosen at random. However, on Åland, nine farms were selected nonrandomly for comparisons with older material collected by Hanski and Kuusela (1983; see below under Historical data). All sampled farms had neat cattle (cows, bulls and/or heifers) only.

Field work was scheduled to coincide with the peak abundance of the early summer *Aphodius* assemblage (Finn et al. 1998, 1999). Farms on Åland were sampled in two periods in 1995: between 31 May and 20 June (19 farms), and between 27 June and 7 July (10 farms). In Uusimaa, a total of 47 farms were sampled between 3 and 19 June 1996. The sampling on Åland was thus more protracted than in Uusimaa. To minimise any phenological bias in the Åland data set, we split the data according to sampling periods. For early species hibernating as adults, we analysed only data from the first sampling period; for species with a protracted flight period, we included data from both periods. Late summer species (*sensu* Finn et al. 1998, 1999), which emerged in low numbers towards the end of the second sampling period, were excluded from the analyses (Table 1).

On each farm, we collected an average of five to seven cow pats. As cattle droppings attract maximum numbers of *Aphodius* a few days after deposition (e.g. Koskela and Hanski 1977), we carefully selected pats with the physical appearance typical of that stage. To exclude any effect of habitat and resource heterogeneity, the sampling effort was focused on cow dung in a single habitat type, i.e. open field pasture. Beetles were extracted by flotation of the pats in water. Koskela and Hanski (1977) have found that this method retrieves more than 95% of the beetles present in a dung pat.

Historical data

To assess the persistence of local dung beetle communities, and the effect of the recent decline in the livestock herd on Åland, we compared the samples collected in 1995 to an extensive data set collected 15 years earlier (between 15 May and 14 June 1980) by Hanski and Kuusela (1983; I. Hanski, personal communication). Of the 24 sites sampled in 1980, 9 were identified as dairy farms still active in 1995, and they were therefore specifically included in the sampling design. All of these farms were visited during the first sampling period in the early summer of 1995. In cases where Hanski and Kuusela (1983) had sampled a particular site on several different occasions, we compared our data to a single sample taken at a similar date and under similar, sunny weather conditions in 1980. Every individual sample from 1980 and 1995 comprised beetles from five cow pats, selected by the same criteria in both years. As the weather conditions were similar in 1980 and 1995, all samples were considered directly comparable between years (I. Hanski, personal communication).

Statistical models

Data were analysed using generalised linear models (McCullagh and Nelder 1989). For data that met the assumptions of a normal distribution and equality of variance, we used ANOVAs (and *t*-tests). For data on proportions, we fitted logistic models with binomial errors (Hosmer and Lemeshow 1989), and for count data, we built models with Poisson errors of the natural logarithm of the observed counts. Here, we first fitted a constant-only model, and then sequentially added variables of interest, and relevant interactions. The significance of each term was tested as the difference in deviance (*D*) between a model with and without it, against a χ^2 distribution with the appropriate degrees of freedom.

Results

Contemporary analyses

Sampling on 29 livestock farms on Åland yielded a total of 3,684 *Aphodius* beetles, whereas 18,080 dung beetles were found on the 47 farms sampled in Uusimaa. The large difference in sample size between areas was mainly due to the disproportionate abundance of three species in Uusimaa: *A. fimetarius*, *A. erraticus* and *A. depressus*, together accounting for 15,000 individuals. With the exception of *A. erraticus*, every species considered in this study is known to occur both in Uusimaa and on Åland (Biström et al. 1991; T. Roslin, personal observation). Nevertheless, in our sampling, we encountered only ten of the species in both areas. Another eight species were found in samples from one of the areas, but not from the other (Table 1).

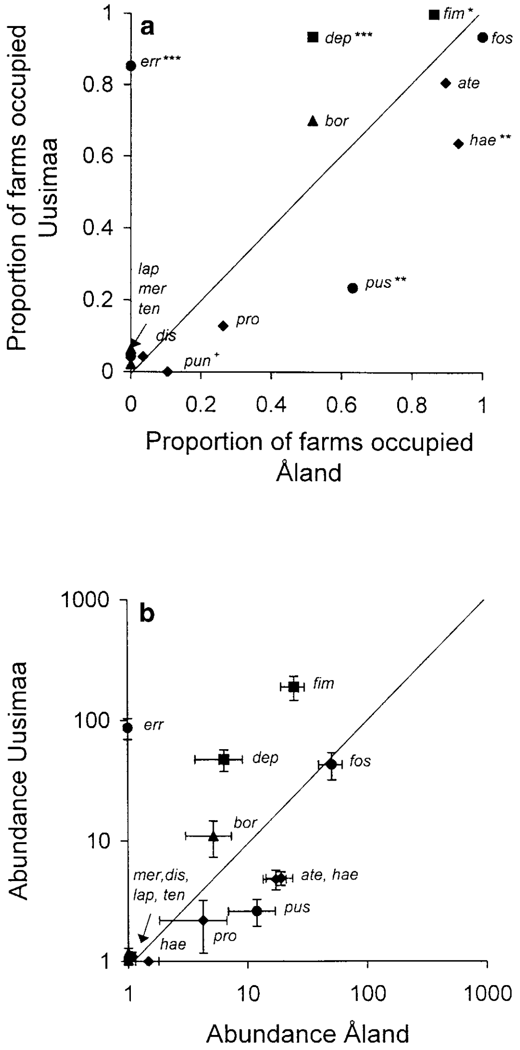

Fig. 2 **a** The proportion of sampled farms occupied by individual *Aphodius* species on Åland and in Uusimaa. *Species names* are abbreviated as in Table 1 (■ generalist, ● pasture specialist, ▲ forest specialist; ◆ intermediate species). Species for which significant differences were observed between areas are marked with *asterisks* (****P*<0.001, ***P*<0.01, **P*<0.05, $^{+}$*P*<0.1). Comparisons are based on 2×2 tables of numbers of occupied and unoccupied sites in the respective area (Fisher exact tests). **b** The abundance of *Aphodius* species in Åland and Uusimaa, measured as the average count of individuals per farm. Each data value had 1 added to allow plotting of zero values on this logarithmic scale. *Error bars* indicate SEM. The *1:1 line* has been drawn for comparison. Differences between areas were significant at the *P*<0.01 level for all species except *A. distinctus*, *A. fossor, A. punctatosulcatus*, and *A. tenellus* (see Materials and methods for a description of the statistical models)

Patterns of abundance and distribution

The regional distribution and local abundance of individual species differed widely between areas (Fig. 2). Spearman's rank correlation between a species' incidence on Åland and in Uusimaa, respectively, was only r_s=0.61. For local abundance, the rank correlation was even lower, r_s=0.57 (*n*=14 species in both cases). The most striking difference was found in *A. erraticus,* which was totally absent on Åland, but present on 40 out of 47 farms in Uusimaa, where it was highly abundant as well. Two generalist species, *A. fimetarius* and *A. depressus*, were also more widely distributed in Uusimaa than on Åland, whereas the opposite was true for the pasture specialist *A. pusillus* and the intermediate species *A. haemorrhoidalis* (Fig. 2a).

To test for intraspecific differences in local abundance between areas, we assessed the change in deviance when area (dummy coded) was added to a Poisson regression model. As slightly more dung pats were sampled per farm in Uusimaa (average 6.9±0.2 pats; ±SE) than on

Table 2 Species-specific logistic regression models of the probability of a species being present on a farm as a function of sampling area (A; Åland=0 versus Uusimaa=1), and the connectivity (S_i) and size (N_i) of a farm (see Materials and methods for a description of these measures). Models were built starting from a constant-only model, and successively adding terms in the order indicated in the table. Coefficients (and SEs) are shown for those terms which resulted in a significant reduction in deviance (critical D=3.85 with df=1). Interactions $S_i \times N_i$ and $S_i \times N_i \times A$ were not significant in any of the species; hence, these terms are excluded from the table. *INF* indicates that there was a significant difference between regions, but any estimate of the coefficient would be dubious, as the species was either absent from or present on all farms within either region. The information value of each species is reflected by *n*(Ala) and *n*(Uus), i.e. the number of farms occupied by the species per the number of farms sampled within Åland and Uusimaa, respectively. Species present on or absent from a few farms only should be considered uninformative. Species are sorted by their functional group (Table 1)

Guild	Species	Term						
		A	S_i	N_i	$A \times S_i$	$A \times N_i$	*n*(Ala)	*n*(Uus)
Generalists	*A. depressus*	2.62 (0.70)					15/29	44/47
	A. fimetarius	INF					25/29	47/47
Pasture specialists	*A. pusillus*	–1.77 (0.61)		0.04 (0.03)			12/19	11/47
	A. erraticus	INF					0/29	40/47
	A. fossor						29/29	44/47
	A. merdarius						0/29	2/47
Intermediate species	*A. ater*				–0.11 (0.04)		17/19	38/47
	A. haemorrhoidalis	–2.03 (0.79)					27/29	30/47
	A. prodromus					–0.12 (0.06)	5/19	6/47
	A. punctatosulcatus	INF					2/19	0/47
Forest specialists	*A. borealis*		–0.04 (0.02)				15/29	33/47
	A.lapponum		–2.88 (2.14)				0/29	3/47
	A. tenellus						0/29	1/47

Åland (5.3±0.2), area was added to a model which already included the exact number of dung pats sampled on each farm. With the notable exception of *A. fossor* and three rare species (*A. distinctus*, *A. punctatosulcatus*, and *A. tenellus*), the difference was significant in every species (P<0.01; Fig. 2b). Interestingly, several pasture specialist and intermediate species were more abundant on Åland than in Uusimaa, whereas all species classified as generalists were more abundant in Uusimaa. Overall, the proportion of individuals belonging to pasture specialist species was thus higher in local dung beetle communities on Åland than in Uusimaa (logistic regression, D=211, df=1, P<0.00001).

Effects of farm size and isolation

To assess the effects of study areas, farm size and connectivity on the probability of a species occurring on a farm, we sequentially added these terms and their two- and three-way interactions to species-specific logistic regression models. For species which were either absent or present on the vast majority of farms, there was an obvious lack of power in these analyses. The information value of each species may be gleaned from the fraction of farms which it occupies (Table 2).

As already noted, the probability of a particular species occurring on a farm frequently differed between the two study areas (Table 2; see also Fig. 2a). Effects of the precise connectivity and size of a farm were less consistent; in only two species did the probability of local presence change significantly with connectivity (Table 2). Farm size had an impact on the occurrence of one species only; the pasture specialist *A. pusillus*. As expected, this species was more likely to be present the larger the farm (Table 2). For *A. ater*, the effect of connectivity was different in different areas, and for *A. prodromus*, the effect of farm size varied between areas (Table 2).

Caution is needed in interpreting these results. Although the average size of sampled farms were equal among the two study areas (13.3 effective livestock units±1.9 on Åland vs. 17.2±4.4 in Uusimaa, ±SE; t_{61}=0.82 with unequal variances, P=0.4), mean connectivity values did differ between the areas (23.1±4.1 on Åland vs. 13.3±1.9 in Uusimaa; $t_{34.5}$=3.5 with unequal variances, P=0.01). To some extent, the effects of study area and connectivity are thus confounded, and care should be taken not to ascribe effects due to one factor to the other. In Table 2, we conservatively test for an effect of isolation *beyond* effects confounded with area, by assessing the change in deviance when connectivity is added to a model already including area. Here, connectivity was found to have an effect only for two forest specialists, *A. lapponum* and *A. borealis*. The effect was negative in both species, and a trend of decreasing incidence with increasing connectivity was also evident within each region (data not shown). To uncover *any* effect of connectivity, confounded or not, we built another set of models with connectivity added as the first term to a constant-only model (data not shown). This time, a significant effect was again found in *A. lapponum* and *A. borealis*, and in two more species; *A. pusillus* (positive effect), and *A. depressus* (negative effect). However, for the latter two, we found no relationship between connectivity and distribution within areas. In conclusion, general differences between the two farm networks, such as the mean density of farms, seem more important than the exact connectivity of individual farms within each network.

Comparisons over time

Contrasting the data collected on livestock farms on Åland in 1995 to data collected in 1980 by Hanski and Kuusela (1983) revealed significant changes in local community composition over time. At the nine dairy farms sampled in both years, species richness appeared stable over time (mean difference between 1995 and 1980=–0.56±SE 0.65; paired *t*-test, t=0.86, df=8, P=0.42). However, this community-level statistic masked many changes in the distribution and abundance of individual dung beetle species (Fig. 3).

Overall, the correlation of the rank order of a species' distribution between years was r_s=0.56 (n=11 species). *A. haemorrhoidalis* occurred on significantly more farms in 1995 than in 1980, whereas *A. punctatosulcatus* and *A. pusillus* markedly decreased in frequency (Fig. 3a). Of the 11 species observed by Hanski and Kuusela in 1980, 3 were not found at all in 1995. Of these, *A. distinctus* and *A. tenellus* were very rare in 1980, but the third one, *A.punctatosulcatus*, was formerly widespread (Fig. 3a). Its disappearance must thus reflect a true population decline within Åland. *A. pusillus* was not observed on four of the nine sites where it had been encountered in 1980. Quite remarkably, these were the four populations with the lowest population density in 1980. There was also a trend of an increase in the probability of local extinction in *A. pusillus* with decreasing farm size (logistic regression, D=3.13, df=1, P=0.08).

In most species, changes in distribution were associated with changes in abundance. *A. fossor* and *A. haemorrhoidalis* were slightly more abundant in 1995 than in 1980, whereas the other species were more or less rarer (Fig. 3b). These differences in overall abundance were partly due to changes in the fraction of patches occupied by each species (Fig. 3a). However, the same difference was evident when sites unoccupied by a species in either year were excluded from the comparison. In a majority of species, persisting local populations had slightly lower densities in 1995 than in 1980, but the difference was significant only within the two species with largest sample size (*A. ater* and *A. fimetarius*, Fig. 3c). Taken together, the correlation of a species' ranked mean abundance between years was low, only r_s=0.35 (n=11 species).

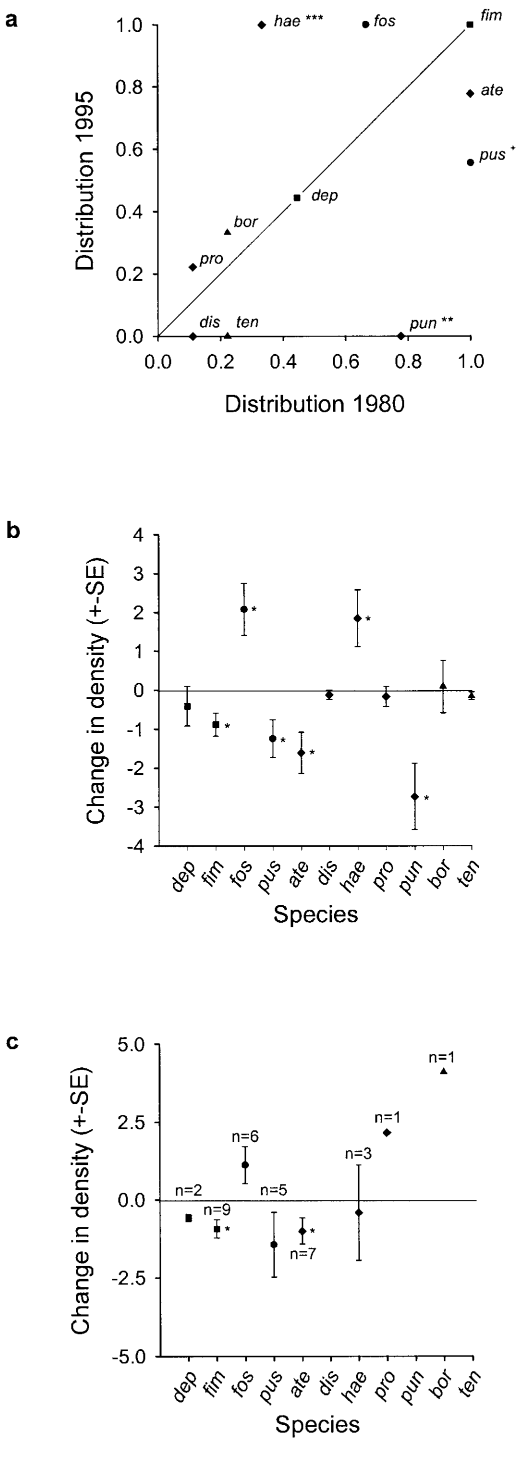

Fig. 3a–c Comparisons of local dung beetle communities in 1980 and 1995. **a** The distribution of individual species expressed as the number of farms occupied by the species in 1980 and 1995 (species names abbreviated as in Table 1). The *1:1 line* has been drawn for comparison. Species for which significant changes were observed between years are marked with *asterisks* (***P<0.001, **P<0.01, *P<0.05, ^+P<0.1). Comparisons are based on 2×2 tables of numbers of occupied and unoccupied sites in different years (Fisher exact tests). **b** Temporal changes in intraspecific densities, expressed as the average of $d_i(1995)$-$d_i(1980)$, where $d_i(1995)$ and $d_i(1980)$ are the natural logarithms of the number of individuals found on farm i in 1995 and 1980, respectively. *Asterisks* denote significant changes, based on paired *t*-tests (n=9 in all cases). **c** Changes in density within those local populations which persisted in both years (significance levels based on paired *t*-tests; n given above or below each *data point*)

Discussion

Related species using similar resources are often assumed to show similar spatial population structures and dynamics (Murphy et al. 1990; Hanski and Kuussaari 1995; Wahlberg et al. 1996), but our study identifies several important sources of variation even within a congeneric set of dung beetles. Although these species co-occur within the same resource patches, variation in habitat and resource selectivity (Table 1), in the rate of movement between pasture habitats (Roslin 2000), and in the distribution of local population sizes (Hanski and Cambefort 1991; Roslin 1999; this study) all contribute to interspecific differences in spatial population structures. That these differences are large enough to cause different types of dynamics at the landscape level was demonstrated both by interspecific differences in the response to contemporary landscape composition, and variation in species' responses to habitat destruction over time. For some species, dynamics at the metapopulation level are clearly important, whereas for others, the classical metapopulation concept provides a poor description of the actual population structure.

Farm size and connectivity

Contrary to expectations under extinction-colonisation dynamics (Hanski 1994, 1999), we detected no positive association between a species' incidence and connectivity. A positive effect of farm size was found for one species only (*A. pusillus*). However, this general lack of effects may be more suggestive of an "absence of evidence than the evidence for an absence" (van Noordwijk 1998). Several alternative explanations prevent us from interpreting the current results as critical evidence against the existence of classical metapopulation structures among *Aphodius* (cf. Roslin 1999). Most importantly, a clear-cut relationship between the occurrence of the species and the size and connectivity of habitat patches is only expected under equilibrium conditions. Drastic habitat destruction within both study areas may have created a state of disequilibrium in patch occupancy patterns. Thus, the current distribution of a species may partly reflect landscape composition decades ago, not the current landscape (cf. Harrison 1994; Tilman et al. 1994; Hanski et al. 1996). Differences in the mean connectivity of farms across landscapes can still be detected, as described below for pasture specialist species. Thus, we note that at least for *A. pusillus*, the spatial distribution patterns are not *incompatible* with metapopulation persistence, but turn to other data for more solid evidence.

Comparisons between generalist and specialist species

The habitat preference of a species will clearly have a major effect on its spatial population structure. Whereas specialist species with a strong preference for pasture habitats are structured into assemblages of more or less discrete local populations, generalist species are more evenly distributed within and between pastures. Dynamically, these differences should translate into dissimilar sensitivity to landscape composition, with specialist species reacting to changes which affect migration rates between patches of suitable habitat. This expectation was borne out by our results. Differences in farm density across two landscapes were associated with significant differences in the abundance and distribution of dung beetles with different types of habitat preferences. Dung beetles specialised on pasture habitats were significantly more abundant on Åland than in Uusimaa. This difference was evident both in the relative abundance of all pasture specialist species within local dung beetle assemblages, and in the absolute abundance and distribution of one important pasture specialist species, *A. pusillus*.

Interspecific differences in sensitivity to landscape composition were also evident in temporal comparisons within Åland. During 15 years of rapid habitat loss, *A. pusillus* declined in both abundance and distribution. Yet, the "intermediate" species *A. punctatosulcatus* decreased even more, being common and widespread in 1980, but entirely absent in 1995. In part, this may be due to phenological differences between years. *A. punctatosulcatus* is most abundant in the spring (Finn et al. 1998, 1999), and its occurrence in early summer will be very sensitive to the progress of the season. Nevertheless, no drastic differences in abundance or distribution between years were observed in *A. prodromus*, a closely related species with similar phenology. As the larvae of this subgenus (*Melinopterus*) are evidently saprophages (Gittings and Giller 1997), it remains unclear to what extent population declines in *A. punctatosulcatus* have been caused by changes in the density of livestock farms.

In summary, the habitat and resource specificity of different dung beetle species appears to explain a part of, but far from all, interspecific variation in their abundance, distribution and dynamics. The significance of other ecological traits is illustrated by a comparison among specialist species with the same habitat requirements.

Comparisons among pasture specialist species

Although the occurrence of pasture specialist species is confined to the same network of habitat patches (pastures), their abundance and distribution showed large differences both within areas, across areas and over time. Good ecological data allow for particularly interesting comparisons between two species, *A. fossor* and *A. pusillus*. Here, interspecific differences seem large enough to allow for different modes of persistence at the landscape level. Several observations suggest that *A. fossor* persists as one large patchy population (Harrison 1991, 1994; Harrison and Taylor 1997), whereas *A. pusillus* may depend on classical metapopulation persistence (Hanski and Kuussaari 1995; Hanski et al. 1995).

First, movements between local populations are much more frequent in *A. fossor* than in *A. pusillus*. In a mark-release-recapture study by Roslin (2000), 35% of recaptured *A. fossor* individuals moved between experimental pastures, compared to only 8% in *A. pusillus*. (*A. pusillus* was actually found to be the least mobile of the ten *Aphodius* species examined.) In the current study, a thinning-out of the farm network seem to interfere with movements between pastures in *A. pusillus*, but not in *A. fossor*. Local population densities of *A. pusillus* were higher on Åland than in Uusimaa, whereas no differences were observed in *A. fossor*. Similarly, densities of *A. pusillus* decreased over time with habitat destruction progressing within Åland, whereas densities of *A. fossor* remained stable over time or actually increased.

Second, local population density, reflecting local population size, was significantly larger in *A. fossor* than in *A. pusillus* (Fig. 2b); in *A. fossor*, an average of 47±8 (*n*=73, ±SE) individuals were encountered in samples from occupied sites, compared to 12±4 (*n*=23) in *A. pusillus*. If we assume that the extinction probability increases with decreasing population size across ecologically similar species, local populations should be less persistent in *A. pusillus* than in *A. fossor*. High levels of movement in *A. fossor* should also make local extinctions unlikely (Roslin 2000, 2001; Stacey et al. 1997), and considerable heterozygosity at genetic marker loci further testify against frequent turnover in this species (Roslin 2001; cf. Hedrick and Gilpin 1997). In *A. pusillus*, small populations seemed particularly prone to extinction: sparse populations, and populations on small farms frequently disappeared between 1980 and 1995, and the present-day incidence of the species increased with increasing farm size.

Taken together, these differences between *A. fossor* and *A. pusillus* seem to account for their different fates in recent years. Whereas a change in the balance between local extinction and colonisation events at the metapopulation level may explain the decline of *A. pusillus* in Uusimaa, and a decrease in its distribution on Åland, movements between pastures in *A. fossor* should still be frequent enough to maintain more or less continuous populations over large areas (Roslin 2001). Similar population trends have been found at larger spatial scales: whereas *A. fossor* is still widespread and highly abundant in southern and central Finland, the distribution of *A. pusillus* has recently declined (Roslin 1999).

The spatial population structure of a third pasture specialist species, *A. erraticus*, seems similar to that of *A. fossor*. *A. erraticus* was widely distributed in the sparse network of livestock farms in Uusimaa, and local abundances were high. Migration rates between pastures are also high: in the mark-release-recapture experiment of Roslin (2000), *A. erraticus* was found to be the most dispersive species, with 50% of recaptured individuals moving between pastures. Nevertheless, the species was completely absent from the dense network of pastures on Åland. This apparent paradox is obviously explained by historical chance events. Due to recent glacial history, the fauna of Åland is still relatively young. As these islands lie isolated from the mainland by tens of kilometers of open sea, colonisation events from the mainland must be extremely rare – even in the most dispersive dung beetle species. A more or less random subset of species is hence lacking from the islands, including *A. erraticus* (cf. distribution maps in Biström et al. 1991).

The fourth pasture specialist species with a seasonal occurrence adequately covered by our sampling was *A. merdarius*. This species was formerly widespread in all of Finland, but over the last few decades, its population has rapidly dwindled (Biström et al. 1991). Our data do not allow for any critical assessment of potential causes for this decline, as we found only one individual on each of two farms. Nevertheless, given its small size, the species is likely to be a relatively weak flyer (Roslin 2000), and recent changes in the agricultural landscape may have affected its population dynamics much as in *A. pusillus* (cf. Biström et al. 1991).

Landscape effects on community structure

At the community level, dissimilar responses to landscape composition in different *Aphodius* species will translate into variation in local community composition. In this study, differences were found at two different spatial scales. At the landscape scale, the overall proportion of individuals representing pasture specialist species was higher on pastures in a dense network of farms (Åland) compared to a sparse network (Uusimaa). At the scale of individual farms within landscapes, two species typical of forest habitats (*A. borealis* and *A. lapponum*) had a high incidence at the most isolated sites, which were mainly surrounded by forest. Both observations support the prediction of Holt (1997) that the rarer a habitat, the more the structure of local communities within this habitat will be influenced by the spillover of generalist species from other habitats (cf. Harrison 1997, 1999). We conclude that analyses of local community composition without any consideration of the surrounding landscape may be misleading (Holt 1993, 1997; see also Kruess and Tscharntke 1994; Didham et al. 1998), and that only by appreciating species-specific idiosyncrasies in spatial population structures can we understand the regional distribution, local abundance and spatial dynamics of each species in the landscape.

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