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Incidence and population dynamics of the leaf beetle *Gonioctena olivacea* in dynamic habitats

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In natural as well as in cultural landscapes, disturbance and succession are responsible for the emergence and subsequent disappearance of suitable habitat patches. The dynamics of habitat patches has important consequences for the spatial structure and dynamics of regional populations. However, there are only few studies quantifying both patch dynamics and incidence of insect species in a dynamic landscape over several years. I studied the incidence and population dynamics of the leaf beetle *Gonioctena olivacea* in a system of dynamic patches of the host plant Scotch broom *Cytisus scoparius*. The incidence of the beetle was most strongly affected by patch area, whereas connectivity, patch quality, patch age, and landscape context had no or only a minor effect when analysed with logistic regression. The size of local beetle populations was highly fluctuating between the years; however, the population dynamics of the local populations was not synchronous. Adjacent patches did not show higher degrees of synchrony than patches separated by large distances. In the three years of study, local populations became extinct through demographic or environmental stochasticity and patch destruction. Each year >10% of the patches disappeared. The extinction rate of beetles in persistent patches was decreasing with increasing patch area. On the other hand, patches newly emerged and were rapidly colonized by the beetle. The colonization rate depended on patch connectivity. Obviously, *Gonioctena olivacea* was capable of persisting in this system with high turnover of patches owing to its high dispersal power.

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The spatial dynamics of regional insect populations has gained much attention in ecological research. Especially, metapopulation theory has given deep insights into the effects of fragmentation on the spatial dynamics of species (Hanski 2001). The persistence of metapopulations depends on an equilibrium between extinction and colonization of habitat patches (Harrison and Taylor 1997, Hanski 1998). Numerous studies on insects attempted to quantify extinction and colonization in a set of patches linked by dispersal (Hanski 1994a, Hanski et al. 1995, Appelt and Poethke 1997, Biedermann 2000, Fleishman et al. 2002). A common feature of all these studies was the analysis of a static network with constant spatial distribution and area of patches. However, the assumption of stable habitats is not very realistic, neither in natural nor in cultural landscapes. In real landscapes natural and anthropogenic disturbances as well as succession may be responsible for the emergence and subsequent disappearance of suitable habitat patches and thus affect population structure (Remmert 1991, Harrison 1994, Nürnberger 1996, Thrush and Whitlatch 1996, Harrison and Taylor 1997, van der Meijden and van der Veen-van Wijk 1997, Stelter et al. 1997, White and Jentsch 2001, Eber and Brandl 2003). As a consequence, patches are present only for a limited period of time. Insect species inhabiting landscapes

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with short-lived habitat patches have to compensate extinction, which may happen through the disappearing of patches, by rapidly colonizing newly emerged patches (Stelter et al. 1997).

Despite the ubiquity of dynamic landscapes, there are comparably few studies focussing on the spatial dynamics of species in such dynamic landscapes, which is in a system of habitat patches changing in number, area, and quality over time. Although a number of theoretical studies have examined the effect of dynamic patches on metapopulation dynamics and persistence (Brachett et al. 1999, Johnson 2000a,b, Keymer et al. 2000, Amarasekare and Possingham 2001, Johst et al. 2002, Ellner and Fussmann 2003), quantitative empirical studies are rare up to now (Stelter et al. 1997, Briers and Warren 2000, Wahlberg et al. 2002). However, such studies are necessary to examine the effect of patch turnover on the occupancy and persistence of species living in dynamic patch systems, in particular because a further cause of extinction – besides extinction through environmental or demographic processes on population dynamics – acts on local populations in dynamic landscapes: the destruction of entire patches through succession or disturbance. Consequently, it is of crucial importance to analyse and quantify the emergence and disappearance of the habitat patches, when analysing the dynamics of species in such a dynamic landscape (Eber and Brandl 2003).

In this study, the incidence and population dynamics of the leaf beetle *Gonioctena olivacea* were analysed in a system of dynamic patches of its host plant Scotch broom *Cytisus scoparius*. The number of broom patches varied during the three years of study. Some patches disappeared, while others emerged newly. The number and spatial distribution of broom patches were examined in order to quantify patch dynamics and to analyse the spatial redistribution of newly emerged patches. The presence of the beetle was recorded over the three years. Additionally, the population size of selected patches was monitored to test for spatial synchrony of local population dynamics. The occupancy as well as the extinction and colonization rates were analysed with respect to quality, spatial configuration, and landscape context of the habitat patches. Special attention was given to the role of connectivity in the colonization of newly emerged patches to test whether the colonization of patches follows a random process or depends on the connectivity to other local populations of the beetle.

Methods

Study system

The leaf beetle *Gonioctena olivacea* (Coleoptera, Chrysomelidae) has one generation per year (some adults occasionally overwinter into the next year) with a peak of adult occurrence at the end of July/beginning of August. *Gonioctena olivacea* lives exclusively on Scotch broom *Cytisus scoparius* (Richards and Waloff 1961) and is part of the food web on broom (Memmott et al. 2000). The biology and population dynamics of *G. olivacea* have been extensively studied by Waloff and Richards (1958), Richards and Waloff (1961) and Waloff (1968).

Scotch broom is a perennial leguminous shrub of 0.5–2 m height and is especially found in disturbed sites. The lifespan of individual plants is 10–15 yr, occasionally up to 20 yr (Peterson and Prasad 1998, Paynter et al. 2003). Patches of broom may die of old age or during winter by hard frosts (see also Fickeler 1958, Richards and Waloff 1961). Additionally, some patches were destroyed in the study area each year by the mowing of road verges.

The occurrence of the leaf beetle *G. olivacea* was investigated in a network of broom patches within an agricultural landscape south of Oldenburg in Lower Saxony, Germany (52°59′N, 8°14′E). At the beginning of this study in 2000 a landscape ("Huntlosen") with an area of 20.5 km^2 was chosen for the analysis of the effects of patch area and connectivity on patch occupancy. A part of that landscape ("Hegel", Fig. 1) served

Fig. 1. The distribution of patches (dots) of Scotch broom *Cytisus scoparius* and occupancy (2002) of the beetle *Gonioctena olivacea* (dark dots) in the study area "Hegel". The crosses indicate destroyed patches; the shaded areas show the forests.

as study area for the detailed analysis of habitat quality and spatial dynamics. It comprises 8.8 km^2 and is characterized by fields (29%), grasslands (8%), and forests (51%). There were no large patches of *Cytisus scoparius* immediately outside the edge of the "Hegel" study area. The population dynamics, i.e. the fluctuation in populations size, of the beetle was studied from 1999 to 2001 in 8 patches distributed over a study area of 74.7 km^2, which comprised both the "Huntlosen" and "Hegel" areas.

Field surveys

In both landscapes ("Huntlosen" and "Hegel") the entire study area was surveyed for patches of the host plant *Cytisus scoparius* that occurred predominantly on road verges (Fig. 1). The patches were mapped and their area was measured in the field. Patches were regarded as discrete when at least 10 m apart. The survey was done in May when *C. scoparius* shows its conspicuous yellow flowering and patches were easily detected. In the "Huntlosen" area the survey was conducted only in 2000. In the "Hegel" area repeated surveys each year from 2000 to 2002 resulted in a documentation of patch turnover. The exact and complete documentation of the fate of each patch is of crucial importance for the analysis of patch dynamics and consequently for the analysis of the metapopulation dynamics of *G. olivacea*, especially the colonization in relation to patch connectivity (see below). From one year to the next, each patch undergoes one of five transitions: 1) patch destroyed (by environmental or human impact), 2) patch area decreased, 3) patch area constant, 4) patch area increased, and 5) patch newly emerged (mostly by germination of seeds). The mean growth rate of decreasing or increasing patches was calculated as the ratio of patch size in one year to the size in the following year.

The presence of *G. olivacea* in the broom patches was surveyed during 2000 in the "Huntlosen" area and from 2000 to 2002 in the "Hegel" area by searching for adult beetles at their peak density in July/August. The search effort was proportional to the patch area and took ca 2 min m^{-2}. Each year the survey was conducted by a single field worker.

The population size at peak density was estimated in 8 selected patches using removal trapping (Zippin 1958, Andrzejewska 1966). The beetles were fairly sessile on the broom plants and were collected by hand from all individual plants of a patch using a common entomologist exhauster. The number of beetles caught was counted in time periods of 2 min. The population size was not extrapolated from a few samples as is usually done in removal trapping, but the sampling was conducted until no more beetles were caught in three subsequent time periods. The number of beetles sampled at the end of the sampling was taken as an estimate of the population size. After this, the beetles were released on the broom plants.

Characteristics of the host plant patches

The percentage of dead twigs (measured in 2001 and 2002) was used to characterize the condition of *Cytisus scoparius*, following the observation that decaying plants have a higher proportion of dead biomass (Richards and Waloff 1961, Peterson and Prasad 1998). In each patch, the mean diameter (at the base of the stems) of 5 randomly chosen *C. scoparius* plants was measured in 2002. The diameter was used as an index of patch age, following Parker (2000) and Paynter et al. (2003) who documented a close relationship between age and stem diameter of this woody plant. The area of the patches was measured (in m^2) and the shading of the patches was recorded in three categories: forest interior (or at least one half of the patch shaded by trees), forest edge or unshaded. Additionally, in 2002, the influence of landscape context (Steffan-Dewenter et al. 2002, Thies et al. 2003) on occupancy was analysed. For that purpose the land use of the study area was mapped and the proportion of the three major land use types fields, grasslands, and forests in a circle around each patch was calculated using GIS. A radius of 50 m was used, however, the proportions were strongly correlated when using a radius of 20 m or 100 m (Spearman correlation coefficient $r > 0.77$).

The connectivity S (Hanski 1994b) of a patch i to all occupied patches j (distance d_{ij} in m and area A_j in m^2) was calculated using eq. (1)

$$S_i = \sum \exp(-\alpha \cdot d_{ij}) \cdot A_j^b \qquad (1)$$

where $\alpha = 1$ to represent the maximum colonization distances (the three highest distances at least covered in patch colonization were 584, 651 and 1004 m); and $b = 0.5$ to account for patch-size dependent emigration (see also Moilanen and Nieminen 2002).

Statistical analysis

The effect of patch properties on patch occupancy of *G. olivacea* was analysed using logistic regression (Hosmer and Lemeshow 2000) using SPSS (SPSS, Chicago, IL). In a stepwise forward procedure, all variables that made a significant ($p < 0.5$) contribution to explaining the presence–absence pattern were entered into the regression model. Patch destruction as well as extinction and colonization of *G. olivacea* were analysed in a similar way, using the three variables as the binary response in logistic regression.

To test for spatial aggregation of newly emerged patches to existing patches, the connectivity of newly emerged patches to existing patches was compared (using t-test) to the connectivity of 100 random points to existing patches in the study area. As it seems likely that patches newly emerge due to dispersal of *C. scoparius* seeds – according to Peterson and Prasad (1998) no vegetative reproduction occurs – the connectivity measure S was again used for calculating the connectivity to all patches.

The degree of synchrony in population fluctuations between patches was measured using an approach that is based on counting correlated changes in the direction of two time series (for details Buonaccorsi et al. 2001). The degree of synchrony τ_{ij} (ranging from -1 to 1) between two time series i and j was calculated with eq. (2)

$$\tau_{ij} = 2\cdot\left(\frac{s_{ij}}{T-1}\right) - 1 \qquad (2)$$

where s_{ij} gives the number of times the two series i and j show the same direction in change (increase or decrease); and T is the length of the time series. A value of $\tau_{ij} = 1$ indicates that all changes of the two time series are in the same direction, whereas a value of $\tau_{ij} = -1$ means that all changes are in the opposite direction. A value of $\tau_{ij} = 0$ occurs when there is the same number of changes in the same direction as in the opposite direction comparing two time series. The index τ_{ij} appears to be especially suitable to measure the correlation of ups and downs of local populations within a metapopulation, where the independence of local extinction events is of fundamental interest.

Results

Occupancy of *Gonioctena olivacea*

In the "Huntlosen" landscape 237 patches of broom were found, of which 101 (occupancy = 0.46) were occupied by *G. olivacea* in 2000. Patch area and connectivity had a significant effect on patch occupancy of *G. olivacea* (Table 1). The incidence was increasing with increasing patch area and connectivity, however, the explained variance was low.

In "Hegel" between 79 and 88 patches were found each year (Table 2). The area of the patches ranged from 1 to 160 m^2. The distribution of patch areas showed a high proportion of small patches (Fig. 2). The occupancy of the patches was fairly stable over time, about one third to one half of the patches was occupied in the three years (Table 2). Habitat quality had virtually no effect on the occupancy of *G. olivacea*. Patch shading (unshaded, forest edge or forest interior), host plant properties (stem diameter, percentage of dead twigs), and landscape context (proportion of fields, grasslands or forests within 50 m around the patch) showed no significant effect on the presence of *G. olivacea* (Table 1); except for patch shading in 2002, where the incidence was significantly higher in patches at forest edges. In all three years, the occupancy was positively affected by patch area (Table 1), whereas connectivity had no effect on occupancy in the "Hegel" area.

Patch dynamics

High dynamics in the number of patches occurred in the system. Some patches were destroyed and new patches emerged in the "Hegel" area (Table 3). In all years more new patches emerged than were destroyed. Patch destruction was not affected by habitat quality or area, when tested with logistic regression ($\chi^2 \leq 1.838$, $p \geq 0.175$). Patch emergence depended on connectivity to other patches (Fig. 3), that is, new patches predominately emerged in the vicinity of existing patches. The connectivity of newly emerged patches was significantly higher than that of random points within the study area (t-test, 2001: $t = 4.43$, $p < 0.001$; 2002: $t = 2.75$, $p = 0.007$).

Table 1. Logistic regression analysis of the effects of habitat quality, landscape context, and spatial configuration on the presence of the beetle *Gonioctena olivacea* in Scotch broom *Cytisus scoparius* patches.

Significant parameters	β_1	β_0	χ^2	p	$R^2_{Nagelkerke}$
Shading 2002 (n = 88, reference = forest interior)			7.8	0.020	0.11
forest edge	−0.2428	−0.5108			
unshaded	1.0906	−0.5108			
Area 2000 (Huntlosen, n = 237)	0.0132	−0.5479	13.6	<0.001	0.08
Area 2000 (n = 79)	0.0808	−1.3624	10.8	0.001	0.18
Area 2001 (n = 82)	0.1404	−1.7419	21.6	<0.001	0.32
Area 2002 (n = 88)	0.0916	−0.7272	10.8	<0.001	0.16
Connectivity 2000 (Huntlosen, n = 237)	0.0138	−1.5575	17.0	<0.001	0.09
Non-significant parameters					

Shading 2000 and 2001, percentage dead twigs 2001 and 2002, mean stem diameter 2002, landscape context (50 m) 2002: proportion of fields, grasslands and forests, connectivity 2000, 2001 and 2002.

Table 2. Number of Scotch broom *Cytisus scoparius* patches in the "Hegel" area and incidence of the beetle *Gonioctena olivacea*.

	2000	2001	2002
Number of patches	79	82	88
Total area of patches (m^2)	818	755	770
Number of occupied patches	28	29	42
Occupancy	0.35	0.35	0.48

Table 3. Patch dynamics of Scotch broom *Cytisus scoparius* in the "Hegel" area.

	2000–2001	2001–2002
Destroyed patches	11 (13.9%)	12 (14.6%)
Newly emerged patches	14	18

The total area of all patches was similar in the three years (Table 2). From 2000 to 2001 of the 68 surviving patches 13.2% decreased in area (mean growth rate = 0.4), 85.3% were constant, and 1.5% increased in area (mean growth rate = 2.0), from 2001 to 2002 the rates were 24.3% (0.5), 48.6%, and 27.1% (2.1), respectively. Negative growth rates were not consistently correlated with initial area of the patches (Spearman correlation, 2000 to 2001: $r = 0.75$, $p = 0.020$, $n = 9$; 2001 to 2002: $r = 0.22$, $p = 0.403$, $n = 17$), while positive growth rates were high in small patches and decreased with patch area (Spearman correlation, 2000 to 2001: not applicable, $n = 1$; 2001 to 2002: $r = -0.63$, $p = 0.004$, $n = 19$).

Spatial dynamics of *Gonioctena olivacea*

Two kinds of extinction events occurred, namely stochastic extinction (through demographic or environmental stochasticity) of *G. olivacea* in persistent patches and extinction through the destruction of a patch. Six stochastic extinction events were observed during all the study years. The extinction rate was 21.4% from 2000 to 2001 and 20.7% from 2001 to 2002. The stochastic extinction rate was significantly (logistic regression, 2000 to 2001: $\beta_1 = -0.1676$, $\beta_0 = 0.8439$, $\chi^2 = 6.24$, $p < 0.013$, $R^2 = 0.35$; 2001 to 2002: $\beta_1 = -0.1514$, $\beta_0 = 0.1217$, $\chi^2 = 5.80$, $p < 0.016$, $R^2 = 0.28$) decreasing with increasing patch area (Fig. 4). Extinction through patch destruction only occurred from 2000 to 2001, when 5 occupied patches were destroyed.

The colonization of previously empty patches was high (Table 4). From 2000 to 2001 a total of 12 colonization events (colonization rate = 18.5%) were recorded, from 2001 to 2002 in total 19 colonization events (colonization rate = 29.2%) occurred. In all years a large number of newly emerged patches were colonized (Table 4). Applied to single years, the logistic regression revealed no or only a marginally significant relationship between connectivity of a patch and its colonization (2000 to 2001: $\chi^2 = 0.92$, $p = 0.337$; 2001 to 2002: $\chi^2 = 2.99$, $p = 0.084$), probably due to small number of colonization events (Table 4). Pooling the colonization events from all years revealed a significant relationship ($\beta_1 = 0.0693$, $\beta_0 = -3.4533$, $\chi^2 = 5.73$, $p = 0.017$, $R^2 = 0.07$). The colonization rate was high in patches well connected to other occupied patches (Fig. 5). This relationship especially held when the colonization of newly emerged patches was analysed separately ($\beta_1 = 0.1553$, $\beta_0 = -6.4344$, $\chi^2 = 4.4$, $p = 0.035$, $R^2 = 0.17$). Landscape context (proportion of fields, grasslands and forests in 50 m radius) had no significant effect on the colonization of the patches, neither in single years nor in the pooled data (logistic regression, $\chi^2 \leq 1.035$, $p \geq 0.309$).

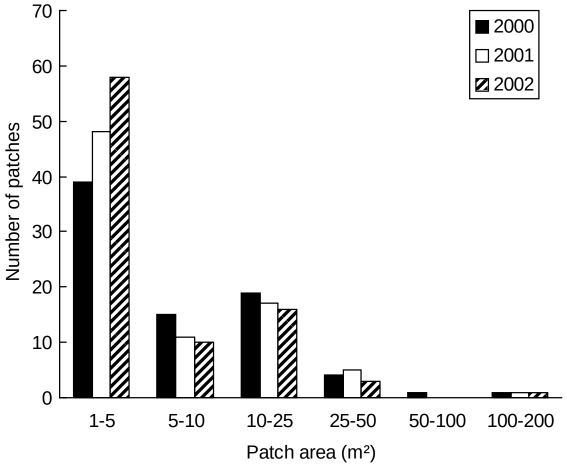

Fig. 2. The distribution of patch area of the Scotch broom *Cytisus scoparius* patches in the "Hegel" area.

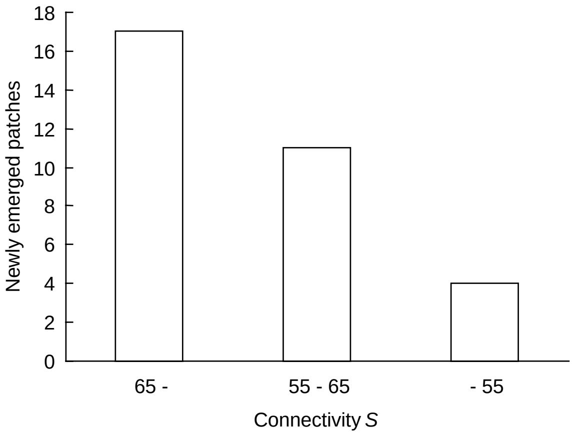

Fig. 3. Number of newly emerging patches of Scotch broom *Cytisus scoparius* in relation to the connectivity S to other patches.

Table 4. Spatial dynamics (number of turnover events) of the beetle *Gonioctena scoparius* in patches of Scotch broom *Cytisus scoparius* in the “Hegel” area.

	2000–2001	2001–2002
Stochastic extinction	6	6
Colonization		
All patches	12	19
Persistent patches	9	10
Newly emerged patches	3	9

Population dynamics of *Gonioctena olivacea*

The size of local populations fluctuated over the years (Fig. 6). The estimated population sizes range from 1 to 60 individuals. The mean and maximum density was 4.4 and 24.4 individuals m^{-2}, respectively. The population dynamics of the local populations of *G. olivacea* showed a low degree of synchrony. Further, the degree of synchrony did not depend on the distance between patches (Pearson correlation, $r = 0.13$, $p = 0.526$). Adjacent patches did not show higher degrees of synchrony than patches separated by large distances (Fig. 7).

Discussion

This study is among the few investigations that both quantify the dynamics of habitat patches (emergence and destruction) on a landscape scale and the spatial dynamics of an insect inhabiting these patches. The results demonstrate how the leaf beetle *Gonioctena olivacea* copes with a permanently changing number and distribution of host plant patches. The local populations fluctuated not synchronously. Thus, the local processes seem to be more or less independent of each other. Each year >10% of the *Cytisus scoparius* patches disappeared and local populations became extinct through patch destruction. On the other hand, patches newly emerged and were rapidly colonized by the beetle. Thus, *G. olivacea* was capable of persisting in this system with high turnover of patches.

The main determinant of occupancy was patch area, which is explained by the reduced extinction rate of larger patches. Patch quality and landscape context seem to be of minor importance for the occurrence of *G. olivacea*. Especially, the age of the patches (indexed as mean stem diameter of the host plant) was not relevant, a finding concordant to the results of Richards and Waloff (1961). In contrast, an association between the age of *Cytisus scoparius* and the incidence of the treehopper *Gargara genistae* was found in a study within the same system (Biedermann unpubl.). The landscape context around the patches did not affect occupancy or colonization, indicating that *G. olivacea* reaches all

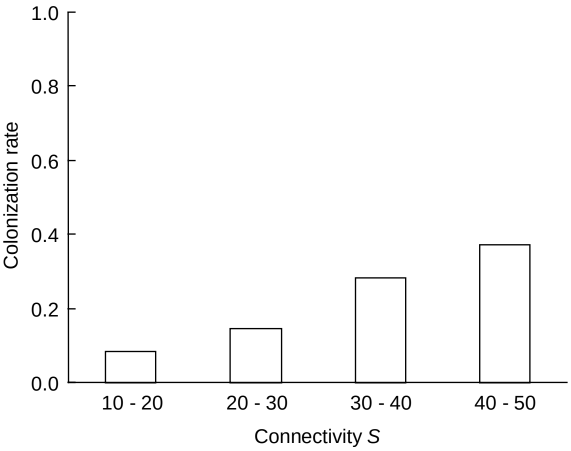

Fig. 5. Colonization rate of Scotch broom *Cytisus scoparius* patches by the beetle *Gonioctena olivacea* in relation to patch connectivity S to other occupied patches (pooled data from 2000 to 2001 and 2001 to 2002, n = 118 patches).

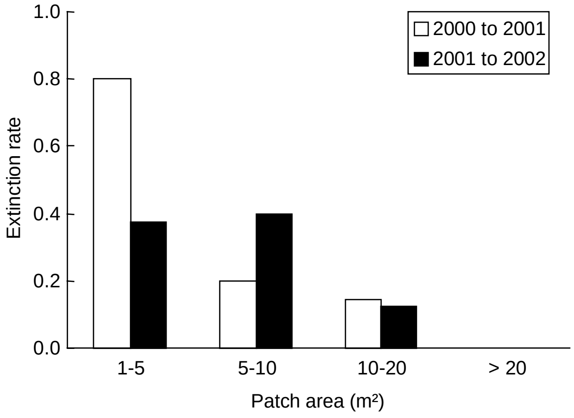

Fig. 4. Stochastic extinction rate of the beetle *Gonioctena olivacea* in persistent patches of Scotch broom *Cytisus scoparius* in relation to patch area (2000 to 2001: n = 23 patches; 2001 to 2002: n = 29).

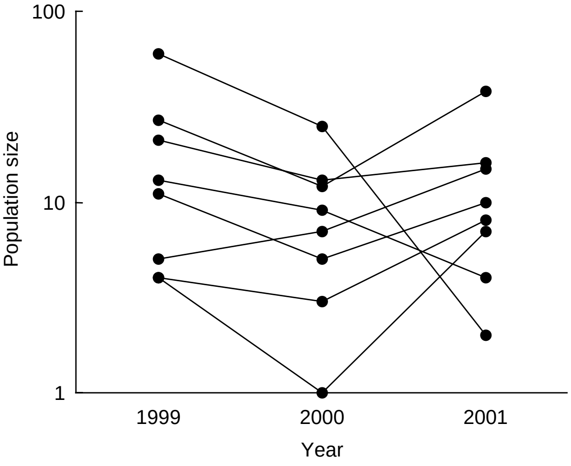

Fig. 6. Population dynamics of the beetle *Gonioctena olivacea* in 8 patches from 1999 to 2001.

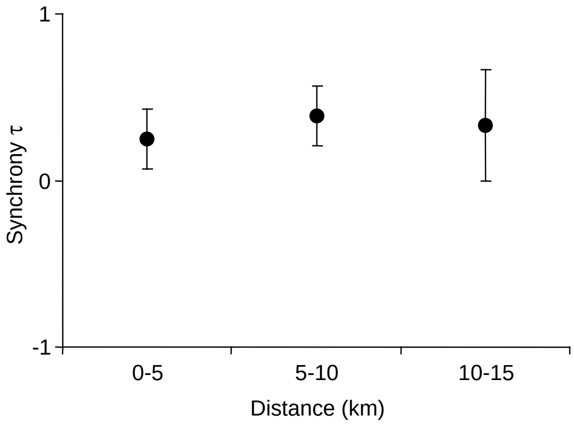

Fig. 7. Mean degree of synchrony τ (with standard error) in population dynamics of the beetle *Gonioctena olivacea* in different classes of pair wise distances between patches.

patches with equal probability. There seem to be no critical barriers (e.g. forests) to the dispersal of the beetle, in contrast to other studies on insects in heterogeneous landscapes (Schmitt et al. 2000, Berggren et al. 2001).

In the study area, patches were destroyed or died off due to environmental, demographic or anthropogenic causes. Patch destruction did not depend on habitat quality, area, connectivity or landscape context. More than 10% of the patches disappeared from one year to the next. Without the emergence of new patches of *C. scoparius*, the number of patches would have steeply decreased from 79 in 2000 to only 56 in 2002. Assuming a constant rate of patch destruction, broom patches would no longer be available after five more years. The stochastic extinction rate of *Gonioctena olivacea* in persistent patches was area-dependent; the extinction rate rapidly decreased with patch area and was already low in patches of only some tens of square meters. Mowing of road verges destroyed some of the patches. But even in landscapes with no such human impact the extinction by patch eradication will be of importance, as the maximum life-span of an individual broom plant does not exceed 10–15 yr.

On the other hand, each year a large number of new patches emerged, probably by germination of seeds. The emergence of new patches depended on the connectivity to existing patches, resulting in a clumped distribution of patches. A considerable number of the new patches was colonized by *G. olivacea* within one year, covering up to hundreds of meters between patches. Although other studies indicated a high dispersal power of *G. olivacea* – Fowler et al. (2000) and Waloff and Richards (1977) reported a rapid colonization of newly emerged *Cytisus* patches; Richards and Waloff (1961) mention the trapping of an adult beetle at least 400 yards (= 366 m) from the next broom plant – the results presented here quantitatively demonstrate the connectivity-dependent dispersal of *G. olivacea*. The newly emerged patches are smaller than average as they had less time to grow. In 2001, three newly emerged patches were colonized by *G. olivacea*. These three patches were also occupied in 2002. As this sample was to small to test whether the new patches have different extinction dynamics compared to more established patches, long-term studies on the turnover of *G. olivacea* in new patches would be necessary.

This study revealed that virtually no effect of connectivity was detected in the analysis of the occupancy although both patch emergence and patch colonization clearly depend on connectivity. Even in the "Huntlosen" area, which comprised 237 patches, only a small amount of variance was explained by connectivity. The explanation for this apparent contradiction most probably lies in the dynamic nature of the patches. Obviously no equilibrium conditions were achieved, because a considerable number of patches disappear from the landscape in each year. The process of patch dynamics obscures the expected connectivity-dependence regularly found in metapopulations in static landscapes (Hanski 2001). In dynamic landscapes, however, the lack of connectivity effects on the incidence of insect species does not inevitably mean that no connectivity-dependent colonization is acting in a system. In other words, the pattern of occupancy is not solely a function of the current landscape configuration, but also depends on landscape history (Petit and Burel 1998, Wahlberg et al. 2002). This "obscured connectivity" phenomenon has been confirmed by a modelling study (Biedermann 2004) and is suggested to have implications on conclusions drawn from occupancy patterns. In general, the analysis of patch connectivity in structured populations may yield misleading results in dynamic landscapes and may explain the lack of connectivity effects on occupancy as observed in some systems (Fleishman et al. 2002). Further, this phenomenon may have substantial consequences upon the estimation of metapopulation parameters (extinction and colonization rates) from snap-shot data on patch occupancy (Wahlberg et al. 2002).

It is expected that in a large number of phytophagous insects the spatial dynamics of the host plant has severe effects on structure and persistence of populations. Concerning the analysis of such effects of patch dynamics, this study revealed that it appears useful to revisit the concepts of patch dynamics (Remmert 1991, White and Jentsch 2001) and to study the population structure of insects in such dynamic systems. Integrating the metapopulation concept with patch dynamics as exemplified in the *Cytisus*-*Gonioctena* system seems to be a promising approach to enhance our knowledge on insects in dynamic habitats. Further, the addition of a landscape ecological point of view on more complex systems of dynamic habitats (e.g. mosaics of dry grassland types undergoing succession and management, Kleyer et al. 2002), in contrast to the comparatively simple *Cytisus*-*Gonioctena* system, would be helpful to extend this approach to insects other than phytophagous specialists.

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