J Insect Conserv (2014) 18:637–642
DOI 10.1007/s10841-014-9667-z

ORIGINAL PAPER

Insect taxa with similar habitat requirements may differ in response to the environment in heterogeneous patches of traditional fruit orchards

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Received: 28 August 2013 / Accepted: 15 July 2014 / Published online: 22 July 2014

Abstract Semi-natural habitats are currently one of the most important environments for many taxa. The main aim of this study was to discover how diurnal butterflies (Lepidoptera) and flower-visiting beetles (Coleoptera) respond to the environment of traditional fruit orchards. In total, 25 orchards were studied in the rural-agricultural landscape in the Czech Republic. Both study taxa were sampled using timed survey walks in 2010. Seven variables in two environmental categories (patch and geography) were evaluated with respect to the species richness of the studied taxa using partial regression, hierarchical partitioning and generalized linear modeling of the best selected variables. Butterflies were highly influenced at a patch level. An increased number of flowering plants, as a reflection of nectar sources for adults, significantly explained a high level of variability, both alone and via interaction with other studied variables. Beetles were influenced by patch and geography to the same degree, although altitude (as a reflection of geographical heterogeneity) significantly negatively explained the highest level of variability. The results indicate that diurnal butterflies and flower-visiting beetles as insect taxa with similar habitat requirements respond differently in heterogeneous environments of traditional fruit orchards. They also indicate the need for multi-taxa studies, even in marginal ecosystems of recent landscapes.

Keywords Altitude · Flower-visiting beetles (Coleoptera) · Diurnal butterflies (Lepidoptera) · Flowering intensity · Geography · Patch

Electronic supplementary material The online version of this article (doi:10.1007/s10841-014-9667-z) contains supplementary material, which is available to authorized users.

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Introduction

Habitat loss is considered one of the major threats to biological diversity throughout the world and this has often led to the instability and reduction of ecosystem function (Steffan-Dewenter and Tscharntke 1999). It is considered that there are currently no remaining patches of natural habitats and that virtually all ecosystems on the planet have been substantially influenced by humans (Cronon 1996; McNeely 2002).

Semi-natural habitats are thus currently one of the most important ecosystems for many taxa (Noordijk et al. 2009). These habitats, which mimic former wildernesses, are shifting (or even have been altered and replaced) from the ecosystem-friendly pressure of traditional land-use, to intensive agricultural management or they have been entirely abandoned (Steffan-Dewenter and Tscharntke 1999; Noordijk et al. 2009). The final loss of semi-natural habitats in agricultural landscapes is leading to a reevaluation of management practices, which often cause low landscape and within patch heterogeneity and will continue to do so in the future (Sjodin et al. 2008).

Insects comprise highly abundant and species-rich taxa with many ecosystem functions (Foottit and Adler 2009). The loss of their biotic interactions within ecosystems (such as pollination) can lead to biodiversity loss not only at a site or local level, but also at the landscape or regional level (Hegland and Boeke 2006; Sjodin et al. 2008; Breeze et al. 2011). Flower-visiting and herbivorous insects are at risk of severe decline due to changes in land use, new diseases or a lower economic significance of similar activities such as beekeeping (Steffan-Dewenter and Tscharntke 1999).

Diurnal butterflies belong to a well-studied taxon and their responses to disparate environmental factors often indicate the actual condition of the studied environment (Binzenhofer et al. 2005; Benes et al. 2006). The study of adult flower-visiting beetles remains largely neglected, even though beetles are one of the most species-rich and abundant taxa in the animal kingdom (Foottit and Adler 2009). Larvae of the studied taxa mostly forage on the tissues of many plant species and the presence and abundance of adults well reflects larval activity as in other insect taxa (Steffan-Dewenter and Tscharntke 1997).

A large portion of former continuous areas of traditional fruit orchards in central Europe has been transformed into more intensively managed grasslands or more often, into fertilized arable land, whereas other areas have been urbanized or abandoned, which has almost caused their transformation into commercial forests (Horak et al. 2013). Traditional orchards, which have persisted in landscapes, have recently become more isolated and in most cases, have gained the status of fragmented marginal habitat types (Kawecki 2008). These areas have faced problems due to a decreased demand for fruit, the declining number of pasture cattle and other domestic animals, the increase in built-up areas and the detrimental activity of mowing with modern machinery (Horak et al. 2013).

The main aim of this study was to address the question of how the species richness of diurnal butterflies and flower-visiting beetles responds to the environment of traditional fruit orchards situated in lowland area of the rural-agricultural landscape.

The particular aims were the following: (1) which category of environment, namely patch or geography, has the greater effect on species richness of the studied taxa? (2) How large is the effect of the studied variables? (3) Which particular variables best explain the species richness of the studied taxa in traditional fruit orchards?

Materials and methods

Study area and sites

The study area was a rural-agricultural landscape (Czech Republic; Pardubice Region), typical for lowlands of central Europe, which have historically been covered by sparse deciduous woodlands (approximately 60 % arable land, 20 % forests, 5 % grasslands and 5 % of built-up area; European Environment Agency 2006).

Traditional fruit orchards in the study area had a combination of grassland in the understorey and a simulation of open-canopy broadleaved woodland in the overstorey (Horak 2014), often with an admixture of shrubs. Thus, they had high habitat heterogeneity in comparison with most of the surrounding sites that were potentially suitable for the studied taxa (e.g. grasslands). The area of fruit orchards in the studied area was <1 % (ca. 44 ha) of the total area, which seems to be typical for heterogeneous marginal habitat types in recent landscapes (Kawecki 2008). In total, nearly 31 ha of this area were studied, containing 25 traditional fruit orchards, situated within a radius of 10 km (centre: 49.9838 N; 16.1729 E). Sites were selected using recent aerial photographs (GEODIS 2006), followed by field searches.

Study taxa and observations

Adults of day butterflies and burnet moths (Lepidoptera, hereafter referred to as butterflies) and flower-visiting beetles (Coleoptera, hereafter referred to as beetles) have similar habitat requirements in the conditions of the Czech Republic and are dependent on more or less sunny conditions (i.e. avoidance of closed forests), with the presence of flowering plants (Benes et al. 2002; Hurka 2005).

Both study taxa were sampled using timed survey walks. As orchards were relatively small in area (see "Study variables"), each survey lasted no more than 10 min, with the route varying from visit-to-visit to check all available resources for the studied taxa (Benes et al. 2002; Hurka 2005) and to reflect the actual conditions of the studied sites (Kadlec et al. 2012). Study taxa were recorded on eleven occasions from April to early October 2010 during fine weather conditions. All species were identified in the field, except for those from the genus *Leptidea* (Pieridae). These individuals were considered to be *Leptidea* cf. *reali*, because the presence of a second species (namely, *L. sinapis*) in the study area is highly improbable (Benes et al. 2002; pers. obs.). Nitidulid beetles of genus *Meligethes* were excluded from analyses, because adults are often hidden in the blossoms (Hurka 2005).

Study variables

Seven site variables in two categories (geography and patch) were studied with respect to species richness of butterflies and beetles.

Four variables were those that are stable during the time and reflected the long-term perspective of the study site (hereafter referred to as geographical variables): (1) area (mean $\pm$ SE = 1.2 $\pm$ 0.2 ha) as one of the basic biogeographical variables reflecting the amount of potential habitat; (2) altitude (316.7 $\pm$ 8.0 m a.s.l.) also as one of the most-studied biogeographical variables indicating geographical heterogeneity and mostly correlating with climatic conditions; (3) irradiance (88.9° ± 12.4°), reflecting the solar radiation and macroclimatic conditions of the studied site and was measured with south as 0° and north as 180°; the only one unstable variable in this category was (4) autocovariate, as a reflection of potential bias caused by spatial autocorrelation of the dependent variable was computed in R using the package spdep.

Three variables were site characteristics that may change during the time (hereafter referred to as patch variables): (1) management (2.2 ± 0.2) reflected the artificial pressure on the studied sites and was evaluated on an ordinal scale from 1 (abandoned), 2 (managed in a mosaic, site was never fully mowed), 3 (mowed once per season) to 4 (intensively managed, mowed more than once per season). All sites, which have been mown, were mowed in the first half of the summer and some even for the second time in early autumn. (2) Canopy openness (87.0 ± 1.7 %) reflected the light conditions of the study sites and was measured using a Canon EF-8-15 mm f/4L FishEye USM camera. For each site, photographs were taken on 25 May (i.e. under full foliage) in four representative locations at 1.5 m above ground level. All photographs were then evaluated using a Gap Light Analyser 2.0. The mean values from all locations were taken for the analyses. (3) Flowering intensity (1.4 ± 0.1) of plants, which reflected the amount of nectar sources for the studied taxa, was evaluated at each visit on an ordinal scale from 1 (area with a low amount of flowering plants; <25 %), 2 (intermediate flowering intensity; 25–50 %) and 3 (area with many flowering plants; >50 %). The mean from all visits was taken for final analyses.

Statistical analyses

Species richness was used as a dependent variable and its normality was tested using the Shapiro–Wilks test—beetle species richness was square-root-transformed to achieve normality. As species richness and abundance of beetles were rather low, bootstrapping in EstimateS 8.2 was used for control as a comparison method due to potential sampling bias. To avoid the effect of multi-colinearity among variables, the variance inflation factor (VIF < 2) of environmental variables was computed using the HH package in R language. The variability explained by the studied categories was calculated using partial regression in SAM v4.0. Hierarchical partitioning of the studied variables was computed via R^2 using the package hier.part in R. Model scenaria were selected by ΔAICc ≤ 2, using the packages nlme, pgirmess and MASS in R. Comparison of selected models was performed using ANOVA with a χ^2 distribution. If ΔAICc did not drop significantly ($P > 0.05$) then the model with fewer variables was chosen. Generalized linear model (GLM) with the normally distributed dependent variable was used and computed in R.

Results

In total, 50 species of butterflies with 1,853 individuals (Table S1) and 13 species of beetles with 105 individuals (Table S2) were observed.

Partial regression of patch and geography

The total explained variability by all studied variables was relatively high (76.8 %) for butterflies. Geography alone explained 5.7 % of the total variation, whereas patch accounted for 39.2 %, which was higher than the variability shared by both study categories (31.9 %; Fig. 1a).

Beetles showed more than a two-fold lower total explained variability (34.7 %) than butterflies. Geography and patch explained the same percentage of variability (14.8 %), whereas the shared variability was only 5.1 % (Fig. 1b). Nearly the same result was reached for estimated species richness (36.5 %).

Hierarchical partitioning of the studied variables

Flowering intensity explained the highest total variability (67.0 %) of species richness of butterflies, followed by altitude (14.5 %), canopy openness (12.8 %), irradiance (12.1 %), area (6.7 %), autocovariate (3.0 %) and management (1.1 %; Fig. 2a).

Altitude explained the highest percentage of the explained variability (16.5 %) for beetles, followed by management (11.7 %), autocovariate (7.9 %), flowering intensity (6.1 %), area (1.4 %), canopy openness (0.6 %) and irradiance (0.1 %; Fig. 2b). The results for estimated richness indicated the same order of environmental variables.

Response to the best selected studied variables

Flowering intensity as a variable of patch category was the best selected studied environmental variable for butterflies (Fig. 3a) and significantly positively explained 65.5 % of the adjusted variability (estimate = 11.7; $F = 46.6$; $P < 0.001$).

Altitude as the best selected variable of the geographical category (Fig. 3b), significantly negatively affected the species richness of beetles and explained 12.9 % of adjusted variability (estimate = −0.1; $F = 4.6$; $P < 0.05$). The selection and final result for estimated beetle richness was quite the same with significant negative effect of altitude.

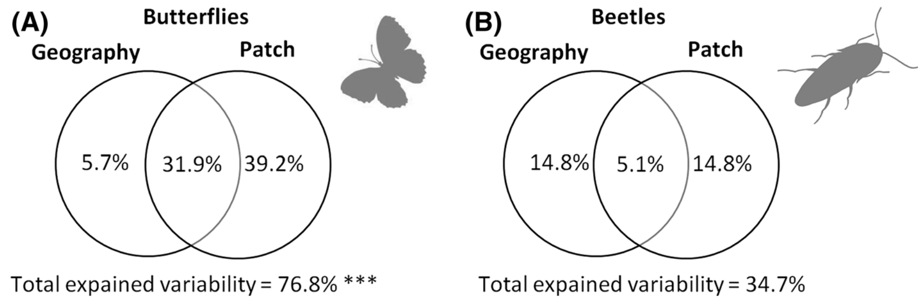

Fig. 1 Venn diagrams showing the results of partial regression with values of explained variability of the studied categories with respect to the species richness of **a** butterflies and **b** beetles in traditional orchards (***$P < 0.001$)

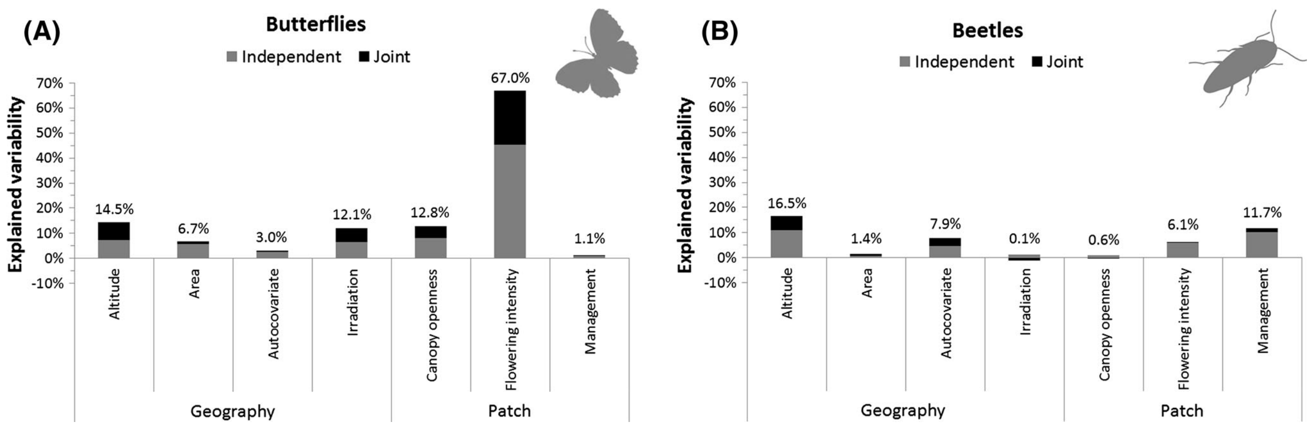

Fig. 2 Hierarchical partitioning on independent- and joint-explained variability of all studied variables in traditional orchards with species richness of **a** butterflies and **b** beetles as dependent variables

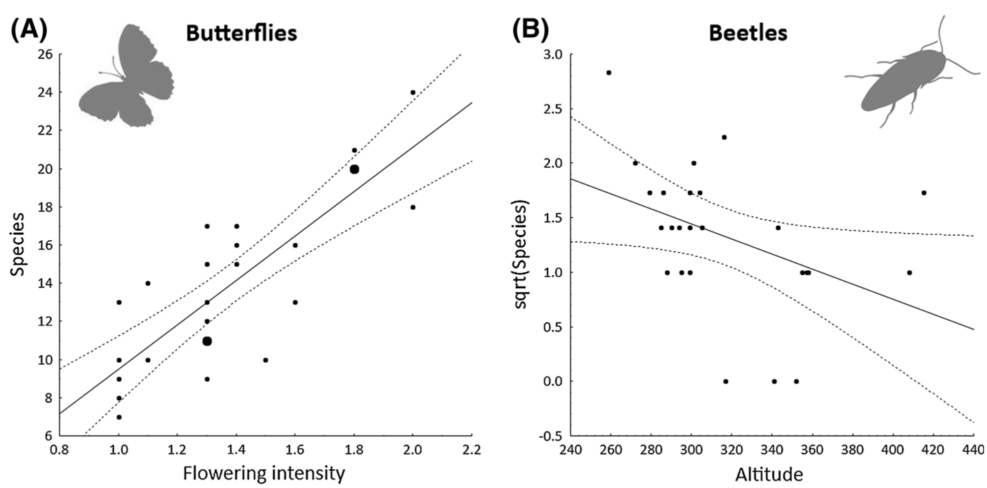

Fig. 3 Response of species richness of **a** butterflies and **b** beetles with 95 % confidence intervals to the best selected variables in traditional orchards

Discussion

Day-active butterflies belong to one of the most-studied insect taxa, especially due to their conspicuousness and relatively well-known habitat preferences (Benes et al. 2002). Existing studies of butterfly communities range from a comparison of several species to single species requirements (Binzenhofer et al. 2005; Horak 2013), and from a continental to a site perspective (Zimmermann et al. 2005; Hamback et al. 2007). In contrast, studies on flower-visiting beetles are more scarce, even though the usefulness of this ecological group has been recently more studied (Sjodin et al. 2008). Although studies involving beetles have relatively lot of potential, this study showed the potential disadvantage with respect to the studies with butterflies—that is, their lower species richness. Most studies on diurnal butterflies and flower-visiting beetles deal with more or less homogenous habitats with prevailing grasslands without woody vegetation. Studies that have focused on more heterogeneous habitats such as coppices, shrublands or military training areas might contribute better insights into taxa preferences (Benes et al. 2006; Binzenhofer et al. 2005; Cizek et al. 2013). Relatively the same is the situation with studies that use more taxa and that thus better reflect which characteristics influence most taxa (Sjodin et al. 2008; Cizek et al. 2013). These studies also reveal possible varied and even contrasting response to the characteristics of the environment. In the case of potentially changing environmental conditions (e.g. management), such studies might better to say whether there is any way to avoid decreasing biodiversity.

The effect of changing characteristics of the study sites

It is well-known that unstable conditions at a patch level influence many insect species. Management intensity and heterogeneity belong to the most frequently studied phenomena in insect conservation biology (Grill et al. 2008; Noordijk et al. 2009). It has been suggested that most butterflies and beetles thrive on spatial and temporal diversification of management activities such as mowing in strips or rotation pasture (Sjodin et al. 2008; Cizek et al. 2012), which mimic high habitat heterogeneity. In traditional orchards, which show a high diversification in management activities, only beetles showed a negative response, although non-significant, to increasing management intensity. Surprisingly, butterflies, did not show any association with management activity and furthermore, management showed the lowest contribution to the explained variability. The importance of this studied variable at the patch level was probably exceeded by flowering intensity of plants. The traditional orchards studied, had a low area and thus management activities were not so critical with respect to the effect of the surrounding landscape (Horak et al. 2013). Moreover, due to relatively high spatial heterogeneity (especially presence of fruit trees), nectar sources were not generally negatively affected by mowing, as the dominant management type in the studied area, because of the existence of alternative nectar sources such as the flowering of fruit trees or fruit fermentation. Surprisingly, there was no response of flower-visiting beetles to flowering intensity, as a reflection of the abundance of nectar sources for adults (Hegland and Boeke 2006), which probably resides in the higher interaction with geography, which might cause a higher micro-regional diversification. Butterflies showed a positive but non-significant response to the openness of canopies in traditional orchards, probably due to interaction with other studied variables. The lower association of beetles with strictly non-woodland areas (as they might reach a high abundance in sparse woodlands) might reflect non-preference for a particular light condition.

The influence of stable characteristics

Rising altitude showed a negative influence on both studied taxa, although for butterflies this was not significant, even though it showed the second highest level of variability. This might reflect a high overlap in geographical categories in the partial regression of butterflies. Beetles showed the same negative pattern in response to altitude as butterflies, as is known for high altitude areas, whereas in most lowland areas, many taxa showed the opposite pattern (Lomolino 2001)—especially due to intensified land use (Konvicka et al. 2003; Horak et al. 2011). This opposite response to altitude with respect to the known global pattern suggests that studies in biotopes with higher environmental heterogeneity might more accurately reflect organismal requirements. Area and irradiance only showed a weak influence on the beetle species richness, whereas the response of butterflies was approximately the same as that for canopy openness as the patch category. Although it is well known that species richness of most taxa increases with an increase in the patch area (Krauss et al. 2003), the results here were non-significant. One of the main reasons may be the fact that majority of the studied orchards was small and with relatively same size. A similar, non-significant result was found for the influence of irradiance, even though the studied taxa are typical ectothermic organisms. The reason for the lack of effect of both variables (area and irradiance) on the species richness of the studied taxa might again reflect the higher within site environmental heterogeneity of the traditional orchards.

Conclusions

The results showed that insect taxa with similar ecological requirements responded differently to conditions of vertically and horizontally heterogeneous environments of traditional fruit orchards. Butterflies were highly influenced by patch characteristics and the intensity of flowering plants as a reflection of nectar sources for adults significantly explained a high level of variability, both for solitary studied variables and their interaction. Beetles were influenced by patch and geography to the same extent, although altitude as a reflection of geographical heterogeneity significantly explained the highest level of species richness variability.

Acknowledgments This study was supported by the Internal Grant Agency (IGA No. A10/14), Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague. Mr. Besitzer corrected the English and an anonymous referee helped to improve this paper.

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