# Butterfly diversity at the ecotone between agricultural and semi-natural habitats across a climatic gradient

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## ABSTRACT

**Aim** Understanding the response of species to ecotones and habitat edges is essential to designing conservation management, especially in mosaic agricultural landscapes. This study examines how species diversity and composition change with distance from semi-natural habitats, over ecotones into agricultural fields, and how within-site patterns of community transition change across a climatic gradient and differ between crop types.

**Location** A total of 19 sites in Israel where semi-natural habitats border agricultural fields (wheat fields or olive groves) distributed along a sharp climatic gradient ranging between 100 and 800 mm mean annual rainfall.

**Methods** We performed butterfly surveys in 2006. We analysed species richness (α-diversity), diversity, community nestedness and species turnover (β-diversity) within sites and between sites (γ-diversity). We also assessed where species of conservation concern occurred.

**Results** In wheat sites, richness and diversity declined abruptly from ecotones to fields and remained homogenously poor throughout the fields, regardless of climate. In olive sites, despite the sharp structural boundary, richness and diversity remained high from the semi-natural habitat to the grove margins and then declined gradually into groves. Species of conservation concern occurred across all habitats at olive sites, but none were found inside wheat fields or at their ecotones. The contrast in community structure between semi-natural habitats and fields was affected by both climate and field type. Irrigation in arid regions did not augment species diversity.

**Main conclusions** Our results indicate that consideration of crop type, within a climatic context, should receive high priority in biodiversity conservation in agricultural areas. In 'hostile' crops, such as wheat, we suggest favouring a combination of high-intensity management and wide margins over less intensive management without margins, which may merely aid generalist butterfly species. The scarcity of butterflies in arid irrigated fields suggests a need to carefully assess the effects of irrigation and agrochemicals on species' communities.

**Keywords**
Agricultural fields, butterflies, climate, conservation management, diversity, edge effects.

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## INTRODUCTION

Agricultural landscapes comprise a substantial portion of the non-urban landscapes across the world (Ellis & Ramankutty,

2008). While the intensification of agricultural practices accounts for substantial biodiversity loss (Benton *et al.*, 2002; Robinson & Sutherland, 2002; Donald *et al.*, 2006), there is also a growing recognition of the potential of agricultural

landscapes to maintain biodiversity (Tscharntke *et al.*, 2005; Norris, 2008) along with the associated ecosystem services to humans (Allen-Wardell *et al.*, 1998; Kremen *et al.*, 2002). Of particular importance for biodiversity conservation are mosaic landscapes, where agricultural fields are interspersed with natural and semi-natural habitats (Medellin & Equihua, 1998; Harvey *et al.*, 2006; Haslem & Bennett, 2008; Ranganathan *et al.*, 2008). However, a major conservation challenge in such landscapes is the abundance of habitat boundaries, because of which biodiversity is largely shaped by the response of species to edges and ecotones (i.e. transition zones between habitat types)(Risser, 1995; Ries *et al.*, 2004; Kark & van Rensburg, 2006; Kark, 2007).

In a recent review, Ewers & Didham (2006) pointed out that many of the studies that focus on edge effects in agricultural fields take a discrete approach where 'edge' is compared with 'interior' rather than assessing how communities change along a continuum. Of those that did take a continuous approach, many focused only on one side of the ecotone, namely from the borders of agricultural fields to (semi-)natural areas (Ewers & Didham, 2006). Fewer addressed the gradient of species community response along the entire transition, from the natural area through the ecotone and to fields (e.g. Ricketts *et al.*, 2001; Kremen *et al.*, 2002; Ricketts *et al.*, 2002; Ricketts, 2004; Chacoff & Aizen, 2006). Therefore, further studies that address the response of species and communities to edges and ecotones, taking a continuous approach and covering the entire transitional area, can aid conservation efforts in landscape mosaics.

Another challenge in understanding edge effects and the responses of species to ecotones emerges from the inconsistency of the observed patterns. This inconsistency may relate to the rarity of studies across climatic gradients. Studies in (sub)tropical areas often find that species diversity decreases from natural areas to intensively managed agricultural fields, usually with substantial edge effects into the natural areas (Canaday, 1996; Zurita *et al.*, 2006; Tabarelli *et al.*, 2008; Bossart & Opuni-Frimpong, 2009; Zurita & Zuleta, 2009; Norris *et al.*, 2010), whereas studies from arid regions report that irrigated agriculture enriches species richness and abundance (Faisal & Ahmad, 2005; Khoury & Al-Shamlih, 2006). Furthermore, some studies, from various climatic areas, identify a peak in species richness or abundance at the ecotones (e.g. Ewers & Didham, 2006; Vu, 2009; Di Giacomo & de Casenave, 2010).

To address these challenges, this study addresses the questions how community structure (species richness, diversity and composition) changes with distance from semi-natural habitats, over ecotones and into agricultural fields, and how this transition (at the local scale) is influenced by climate (i.e. on a broader scale), as well as by crop type. Considering that conservation should focus not only on richness and diversity but also on species' identity, we also identified where species of conservation concern occurred (sites and habitat).

Our study focused on butterflies (Lepidoptera, Rhopalocera), which are considered good indicators of terrestrial biodiversity (Thomas *et al.*, 2004; Thomas, 2005; Pe'er & Settele, 2008a) and are relatively easy to observe and recognize in the field (Pe'er & Settele, 2008a and references therein). The study was conducted in Israel, along a sharp rainfall gradient from 800 to 100 mm annual precipitation, and in two types of agricultural sites: wheat fields and olive groves.

## METHODS

Wheat and olives are two types of agricultural crops, which are widespread across the Mediterranean region and occur along a wide climatic gradient in Israel. The two crops differ in their architecture and in their management regime. Wheat fields are open monocultures, often under intensive management involving the use of fertilizers, herbicides and pesticides, deep ploughing using heavy machinery, and frequent crop rotation. Olive groves are structurally more heterogeneous (providing both a shaded microhabitat and an open one), and their management is typically less intensive and includes vegetation removal and infrequent application of pesticides. However, from interviews with farmers preceding this study, we found that the management of both crops changes across climate. In olive groves, within mesic environments (> 500 mm mean annual rainfall), the application of agrochemicals is scarce. In semi-arid areas (400–500 mm annual mean precipitation), the groves are often irrigated during summer and pesticides are used more frequently, and in more arid areas (< 400 mm annual rainfall), groves are rare, irrigated year-round and treated frequently by herbicides and pesticides. Wheat fields require more intensive management in Mediterranean areas (> 500 mm) where they are more prone to diseases, whereas in arid areas (especially < 250 mm average annual rainfall), they are either traditionally managed (i.e. applying very shallow ploughing and no agrochemicals) or intensively managed (i.e. irrigated and treated with agrochemicals; see Appendix S1 in Supporting Information).

### Study sites

The study was conducted along the rainfall gradient in Israel, ranging from Mediterranean climate regions in the northern Galilee with mean annual rainfall of 800 mm (32°55′N 35°18′E) to arid sites in the Negev desert with a mean annual rainfall of 100 mm (30°52′N 34°47′E, Fig. 1a). We used detailed orthophotographs (resolution = 80 cm) and a precipitation map of Israel (resolution = 1 km) to identify potential sites and conducted preliminary surveys to select sites and map them (For selection criteria and process see Appendix S2). We selected eleven sites where wheat fields border semi-natural habitats (grasslands or scrublands), at equal intervals across a range from 200 to 650 mm mean annual rainfall, and eight sites where olive groves border semi-
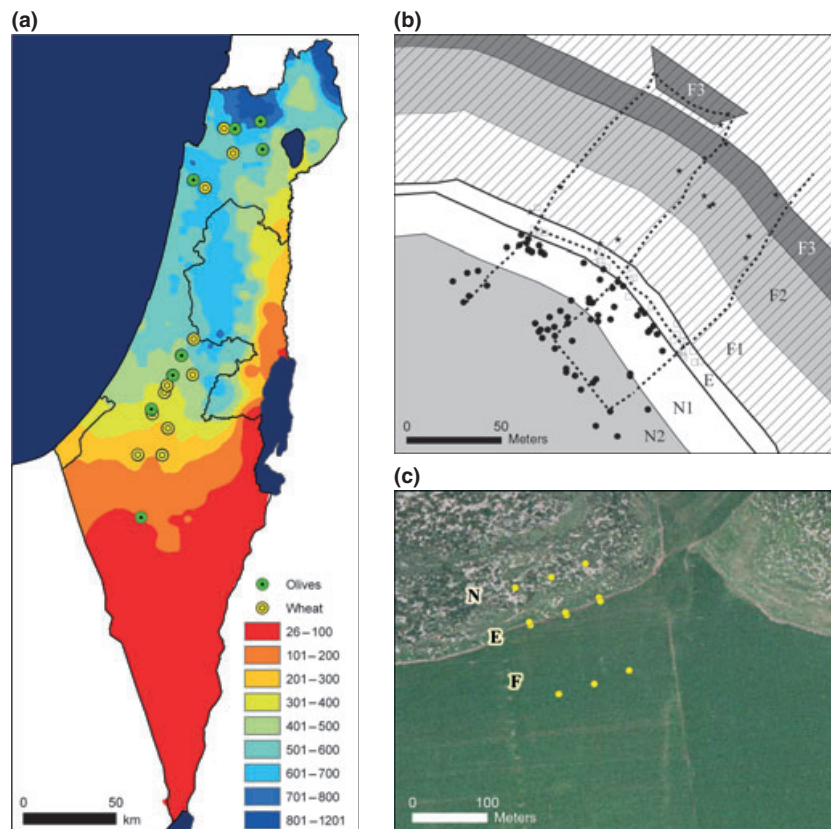
**Figure 1** (a) a map of the mean annual rainfall (mm year$^{-1}$) in Israel and the location of the field sites along the climatic gradient; (b) an example of a transect line in a wheat site (Sdot Micha, 399 mm annual rainfall). Dashed lines represent the transect lines. The points mark the locations of butterfly observations in the semi-natural habitat (full circles), ecotone (empty squares) and inside the field (stars) in a single visit to the site. The six subsections within the site (N2 and N1 in the semi-natural area, E = Ecotone and F1, F2, F3 inside the field) are marked by shadows of grey. The striped zone represents the range of the field itself. (c) an aerial photograph of one of the sites (Yavor), yellow circles signifying marked measure-points along the transect lines. N = semi-natural area, E = ecotone, F = field

natural habitats, at equal intervals from 380 to 790 mm mean annual rainfall and an additional site at 100 mm mean annual rainfall (Fig. 1a and Appendix S1).

## Butterfly surveys

Survey transects were comprised of three lines perpendicular to the boundary between fields and the semi-natural area and three lines parallel to the boundary. Transects started at 50 m within the semi-natural area, continued through the ecotone between the semi-natural area and the fields and proceeded 100 m into the agricultural field (Fig. 1b). The asymmetry of depth-sampling stems from the difficulty of finding sites where both the agricultural areas and the semi-natural habitats were large and homogeneous enough (see Appendix S2). Given the relative abundance of studies that focus on community structures from edges to natural or semi-natural habitats, the designed transects allowed deeper sampling into fields.

To define the different habitats at each site, we first set the boundaries of the ecotone: the end of a crop from one side and

the beginning of homogenous semi-natural vegetation from the other side. The ecotone was heterogeneous in nature, including human-related infrastructure (e.g. unpaved roads, fences), organic waste, or ruderal vegetation indicative of frequent disturbances and/or high nutrient levels. The two other habitats were defined as extending outward from the boundaries of the ecotone.

We conducted butterfly surveys in spring 2006, between early March and mid-May, a period in which wheat fields and olive groves receive minimal treatment and butterfly activity is peaking. We performed two visits at each site. Each survey was performed on sunny days (< 50% cloud cover), between 18 and 33 °C, and when wind speed < 10 km h$^{-1}$. A hand-held weather station (Kestrel 3000) was used to record wind and temperature conditions. Surveys were conducted between 10:00 and 15:00 in March and were prolonged to 09:00–16:00 in mid-April. Butterfly surveys were carried out by two observers, at least one of whom was a butterfly expert capable of identifying all species. During surveys, the observers walked at a constant pace of 1 km h$^{-1}$ along the transect line and recorded the identity of each individual seen

within 10 m from the transect line. A sweeping net was used to capture (and immediately release) individuals if necessary for identification. The location of each individual was recorded using a GPS with a spatial accuracy of 5 m. To ensure a constant survey time in all sites (net walking time of 30 min), we halted the surveys during data recording, when the sun was hidden by clouds or if winds exceeded 10 km h$^{-1}$.

## Data analysis

### Characterizing community composition along the distance gradient

We divided each site into six subsections, each comprising 100 m of the transect length. The subsections were defined as: N1 – semi-natural area, 0–33.3 m from the ecotone boundaries; N2 – semi-natural area, > 33.3 m from the ecotone; E – ecotone, F1 – within field, 0–33.3 m from the edge; F2 – 33.3–66.6 m into the field; and F3 – 66.6–80 m into the field along the transect lines perpendicular to the edge plus an additional 50-m transect parallel to it (see Fig. 1b). The latter 50-m section varied in its distance from the nearest edge, ranging from 85 to 100 m depending on field geometry. We assigned butterfly observations to each of the six subsections based on the location of their corresponding GPS points, using ArcGIS 9.2.

Community structure at the subsections and at the site level was characterized by several measures: (1) species richness (number of species, i.e. α-diversity); (2) species diversity according to Shannon index (Shannon, 1948); (3) the level of nestedness within the community (indicating whether butterfly community within a certain zone is a subset of the community observed in another); and (4) β-diversity to assess the turnover of species (community similarity) between subsections in cases where communities were found to be non-nested.

### Nestedness analysis

Nestedness analysis was performed using the Binmatnest software (Rodriguez-Girones & Santamaria, 2006), which uses presence–absence tables of species occurrences to calculate nestedness 'temperatures' (Rodriguez-Girones & Santamaria, 2006). Temperatures range from 0° (perfectly nested) to 100°, where values above 10° are considered to be insignificant. The Binmatnest finds the best minimum temperature matrix using a genetic algorithm (Rodriguez-Girones & Santamaria, 2006). We used it to produce a set of 30 possible solutions, improved by the production of seven new variants and selecting the best-performing ones at each of 2000 'generations'. The algorithm was repeated 100 times to allow significance testing. To identify potential gradients in nestedness along distance within sites, we performed the analysis first for all six subsections, then four and finally for three subsections within a site.

### β-diversity

A non-nested pattern can be found when community structure is uniform across the distance, or alternatively, when species replace each other between habitats, in which case β-diversity would be lower. For this analysis, we selected cases (case = a given visit to a certain site) with nestedness temperature > 10°. For each case, we compared each subsection with all others, using the diversity metrics $\beta_w$ and $\beta_{sim}$. The former was calculated as:

$$\beta_w = \frac{a + b + c}{(2a + b + c)/2}$$

(Whittaker, 1960) and the latter as:

$$\beta_{sim} = \frac{\min(b, c)}{\min(b, c) + a}$$

(Lennon et al., 2001), where a represents the total number of species in both subsections, b is the number of species present in the second but not in the first and c is the number of species present in the first but not in the second subsection. The difference between the two metrics is that $\beta_w$ emphasizes differences in composition that are attributable to species-richness gradients, while $\beta_{sim}$ focuses on compositional differences independent of species richness (Koleff et al., 2003). For each case, we produced a 6 × 6 matrix summarizing the β values of comparison between all subsections and then extracted the average $\beta_w$ and $\beta_{sim}$ from each matrix.

### Species of conservation concern

Two types of species were considered to be of conservation concern: rare species (according to Table 1 in Pe'er & Benyamini (2008)) and 'indicators of natural habitats'. The latter were defined as species that are not threatened in Israel, but are known to avoid urban and disturbed landscapes (GP & Dubi Benyamini, unpublished data) and/ or are considered rare or endangered in neighbouring countries (Katbeh-Bader et al., 2003; Table 3 in Pe'er & Benyamini, 2008). We registered the localities and abundance of these species and inspected in which habitats they occurred within wheat site and olive site.

### Analysing the climatic effect

To characterize how the local patterns within sites change with the climatic gradient, we first compared the interior of the semi-natural area (subsection N2) with the interior of the fields at a comparable depth of 33–66 m from the edge (F2). We then assessed how differences in richness and diversity between the two subsections (i.e. the contrast between 'field' and 'semi-natural habitat') change across the rainfall gradient, for wheat and olive sites. In a second analysis, we summed up

Table 1 Nestedness levels (temperature and significance) for different subsections within sites, first for six subsections (F3, F2, F1 within fields, E = ecotone, N1, N2 within the semi-natural habitat), and then after removal of sections to inspect for nestedness patterns within habitats. Analysis presented (a) for all fields irrespective of climatic area; and (b) divided to three climatic zones: Mediterranean (mean annual rainfall > 500 mm), semi-arid (380–500 mm) and arid (≤ 370 mm). Significance values are based on the output 'p3' of the Binmatnest software (Rodriguez-Girones & Santamaria, 2006) after 100 simulation repeats. Order of nestedness was characterized visually, marking '>' when the number of species clearly differed between two subsections; otherwise, subsections are separated by a comma.

| Field type | Model | Temp. | Sig. | Nestedness order |
|---|---|---|---|---|
| (a) | | | | |
| Wheat | All six subsections | 17.96 | < 0.001 | E > N1 > N2 > F2 > F1 > F3 |
| | Without F3, F2 | 25.57 | < 0.001 | E > N1 > N2 > F1 |
| | Without F3, F2, F1 | 43.38 | 0.28 | |
| Olives | All six subsections | 10.43 | < 0.001 | N1 > N2 > E>F1 > F2 > F3 |
| | Without F3, F2 | 19.44 | < 0.001 | N1 > N2 > E > F1 |
| | Without F3, F2, F1 | 16.32 | < 0.001 | N1 > N2 > E |
| | Without N2, N1 | 15.4 | < 0.001 | E > F1 > F2 > F3 |
| | Without N2, N1, F3 | 37.08 | 0.1 | |

| Field type | Climate | Model | Temp. | Sig. | Nestedness order |
|---|---|---|---|---|---|
| (b) | | | | | |
| Wheat | Mediterranean | All six subsections | 23.22 | < 0.001 | E > N2 > N1 > F2 > F1 > F3 |
| | | Without F3, F2 | 33.56 | 0.06 | N1, N2, E, F1 |
| | | Without F3, F2, F1 | 43.84 | 0.44 | |
| | Semi-arid | All six subsections | 10.86 | 0.05 | N2 > E > N1 > F2 > F1 > F3 |
| | | Without F3, F2 | 17.55 | 0.01 | N2, E, N1 > F1 |
| | | Without F3, F2, F1 | 39.3 | 0.31 | |
| | Arid | All six subsections | 19.78 | 0.03 | E > N1 > N2 > F2 > F3 > F1 |
| | | Without F3, F2 | 24.89 | 0.1 | |
| | | Without F3, F2, F1 | 46.05 | 0.61 | |
| Olives | Mediterranean | All six subsections | 14.78 | < 0.001 | N1 > F1 > N2 > E > F2 > F3 |
| | | Without F3, F2 | 25.73 | < 0.001 | N1 > F1 ≥ N2 ≥ E |
| | | Without F3, F2, F1 | 24.99 | 0.05 | N1 > N2 > E |
| | | Without N1, N2 | 14.53 | < 0.001 | F1, E, F2 > F3 |
| | | Without N1, N2, F3 | 31.68 | 0.05 | F1 > E > F3 |
| | Semi-arid | All six subsections | 16.92 | < 0.001 | N1 > N2 > E > F2 > F1 > F3 |
| | | Remove F3, F2 | 26.47 | 0.02 | N1, N2, E > F1 |
| | | Without F3, F2, F1 | 40.37 | 0.24 | |
| | | Without N1, N1 | 10.97 | < 0.001 | E, F2, F1 > F3 |
| | | Without N1, N2, F3 | 31.43 | 0.11 | |
| | Arid* | All six subsections | 25.79 | na | na |

*Not enough individuals observed (see Appendix S1).

the observations per site and inspected how richness and diversity at the site level change across the rainfall gradient (γ-diversity) and between the crop types. To ensure that each habitat receives the same sampling effort, we selected one subsection from each habitat: the interior of the semi-natural area (N2), the fields' interior at a comparable depth (F2) and the ecotone (E). Lastly, we evaluated how patterns of nestedness change across the climatic gradient and between the two crop types. Here, as a result of limitations of the Binmatnest test, which requires a sufficient number of individuals and species, we clustered the presence–absence data from several sites (and both visits) into three climatic zones relating to the above-mentioned differences in management.

In all statistical analyses and the results presented hereafter, we treat each visit to a given site as if it was an independent observation: this was done as a conservative measure, which considers (and maintains) the variation in species richness, diversity and community structure between visits to a given site.

## RESULTS

### Richness and diversity along the distance gradient

Overall, we recorded 2074 butterflies belonging to 42 species. Of these, 1187 butterflies of 36 species were observed within the six subsections and were included in our analyses (see

Appendix S3). Significantly fewer species were observed in wheat field than in olive grove sites: 5.69 ± 2.89 (Average ± SD) species per site and 8.65 ± 4.57 ($T$ = 2.602, d.f. = 41, $P$ = 0.013), respectively.

Butterfly richness and diversity decreased from the semi-natural areas to the fields in most sites: ANCOVA for the impacts of field type, subsection and rainfall (as a covariant) found the effect of subsection to be highly significant for both richness (d.f. = 5, $F$ = 10.061, $P$ < 0.001) and diversity (d.f. = 5, $F$ = 11.317, $P$ < 0.001), yet this pattern differed significantly according to the field type (i.e. the subsection × field type interaction was significant as well (d.f. = 5, $F$ = 4.257 and $P$ = 0.001 for richness; $F$ = 4.461 and $P$ = 0.001 for diversity). We found no separate effect of field type on richness (d.f. = 1, $F$ = 2.13, $P$ = 0.146), but it did affect diversity (d.f. = 1, $F$ = 4.461, $P$ = 0.033). These results reflect the different pattern of change in community structure along the transition from semi-natural habitats to fields. In wheat sites, species richness and diversity increased mildly but insignificantly from the semi-natural habitat towards the ecotone (N2 ≤ N1 ≤ E), then dropped sharply to the interior of the fields and remained evenly low throughout the fields (F1 = F2 = F3; Fig. 2a,b). By contrast, a gradual pattern was observed in olive sites, where richness and diversity were high throughout the semi-natural habitat, the ecotones and the field margin (F1), peaking at the subsections N2 and F1 and then decreasing gradually with distance into the groves (F1 > F2 > F3; Fig. 2c,d).
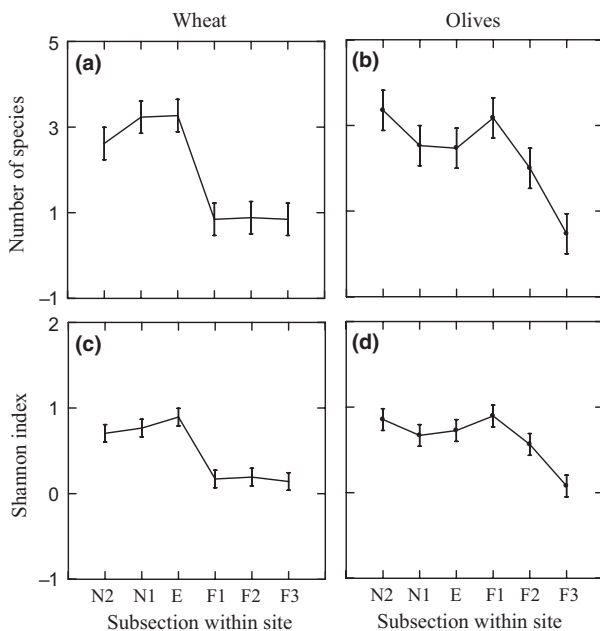


**Figure 2** Least square mean (±SD) for species richness (a,c) and Shannon index of diversity (b,d), against the distance gradient (six subsections: N2 and N1 in the semi-natural area, E = Ecotone and F1, F2, F3 inside fields) from semi-natural area through the ecotone and to fields, in wheat sites (a,b) and in olive sites (c,d).

Butterfly communities inside wheat fields were significantly nested within the semi-natural and ecotone communities, indicating that they were a subset of the outside community (Table 1a). Results were distance independent, as signified by the fact that significant nestedness remained after removal of the two deepest subsections of the field (F2, F3). No significant nestedness was found between the semi-natural and the ecotone community (i.e. once removing the three subsections within the fields). Butterfly communities in olive sites were also significantly nested, but the ranking order was different: communities inside the olive groves were nested within the ecotone community, and the latter was nested within the community at the semi-natural area (Table 1a). This time, significant nestedness remained after removing the grove subsections (F1, F2, F3) as well as after removing the subsections within semi-natural habitats (N1, N2), indicating that the nested pattern prevailed across all habitats and across distance.

## Beta diversity

Analysing community structure for non-nested sites, we found $\beta_w$ to be significantly lower in wheat sites than in olive sites ($T_{d.f. = 27}$ = −3.344, $P$ = 0.0012), but no significant difference was found for $\beta_{sim}$ ($T_{d.f. = 27}$ = −1.105, $P$ = 0.139). These results indicate that species communities in wheat sites were either nested or relatively homogeneous, whereas communities in olive sites exhibited higher species turnover (i.e. they were patchier in terms of species composition), which was attributable also to species-richness gradients (hence the lack of significance for $\beta_{sim}$).

## Species of conservation concern

We recorded ten species of conservation concern, four of which were rare and six were indicators of natural habitats (see Appendix S4). Of these ten species, three occurred in wheat sites but only within the semi-natural area. By contrast, we observed nine species of conservation concern in olive sites, and these were observed in all three habitats (Appendix S4). We note that most of the species of conservation concern were observed at the sites with the highest annual rainfall.

## The climatic gradient

Comparing the semi-natural interior (N2) with the comparable zone within fields (F2), we found that in wheat sites the contrast between the two, both in richness and in diversity, was positively correlated with rainfall (Fig. 3a): The decrease in species richness and diversity from semi-natural habitats to fields was greater in sites of higher precipitation (Linear regression: Richness: $F$ = 7.247, d.f. = 24, $P$ = 0.013, $R^2$ = 0.232; Diversity: $F$ = 6.545, d.f. = 24, $P$ = 0.017, $R^2$ = 0.214). In olive sites, we could not find such a relationship ($F$ = 0.018,
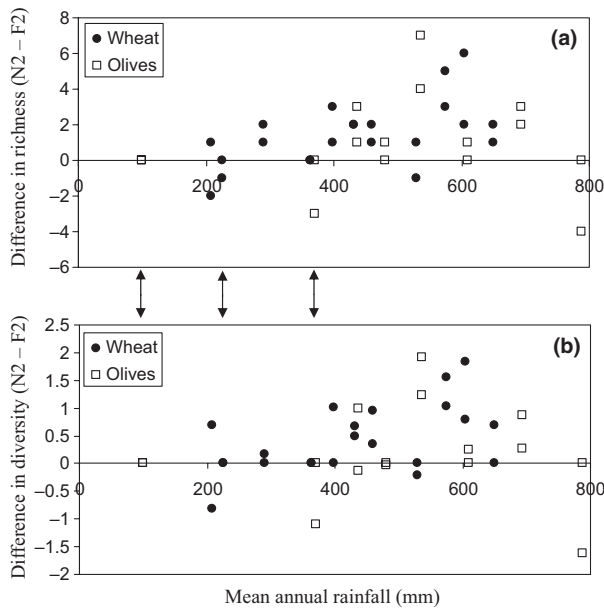
**Figure 3** Difference in (a) species richness and (b) species diversity (based on Shannon index) between the natural area (section N2) and the field (F2), in wheat sites (black circles) and in olive sites (empty squares) along the climatic gradient. Arrows signify irrigated fields.



**Figure 4** Overall species richness (a) and Shannon index of diversity (b) on the site level (summing up sections N2, E and F2) against the mean annual precipitation, for wheat sites (full circles) and olive sites (empty squares). Arrows signify irrigated fields.

d.f. = 17, $P = 0.896$ for richness; $F = 0.006$, d.f. = 17, $P = 0.940$ for diversity; Fig. 3b), and despite the seemingly unimodal pattern, a quadratic regression did not yield significant results either.

We did not find an effect of climate on nestedness patterns in wheat sites: the community within fields was always nested in that of the surroundings (semi-natural habitat and ecotone), and no significant nestedness was found between the semi-natural subsections and the ecotones (Table 1b). In olive sites, however, different nestedness patterns were found in each of the three climatic regions. In Mediterranean olive groves, the communities inside the groves were nested within the ecotone, and the latter was significantly nested within the semi-natural communities (Table 1b). In semi-arid areas, the order of nestedness remained, but levels of nestedness between subsections were very much reduced (i.e. nestedness disappeared when removing subsections, especially the semi-natural area), indicating that the effects of the distance gradient diminished. In arid areas, the scarcity of butterflies in olive groves did not allow this analysis.

## Gamma diversity

Pooling the observations at each site from all three habitats, we found that butterfly richness increased significantly with rainfall with no significant difference between wheat and olive sites (Fig. 4a), whereas butterfly diversity was significantly affected by rainfall in olive sites but only near significantly in wheat sites (Fig. 4b and Table 2). Nonetheless,
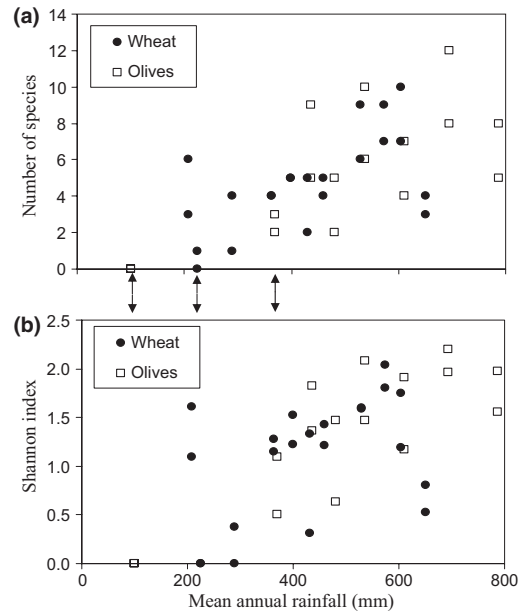
we did not find a significant interaction between field type and rainfall.

Lastly, we note that all results presented in this study were independent of the selection of richness metrics. This is demonstrated in Appendix S5, where we provide complementary results for Figs 2–4 for two commonly used indices of species richness, Chao1 (Chao, 1984) and $S_{obs}$ ('Mao Tau'; Colwell *et al.*, 2004).

**Table 2** ANCOVA for the impact of field type and average annual rainfall on (a) species richness; and (b) species diversity (Shannon index) on the site level, clustering the data from subsections N2, E and F2. Separate linear regressions for wheat and olive sites yielded a significant effect of rain on species richness in both wheat and olives ($P = 0.008$, $P = 0.004$, respectively), and an effect on species diversity in olive sites ($P = 0.04$), but only a near-significant effect on diversity in wheat sites ($P = 0.08$). All values are after Bonferroni correction.

| Source | d.f. | MS | F-ratio | P |
|---|---|---|---|---|
| **(a)** | | | | |
| Rain | 1 | 134.78 | 24.61 | < 0.001 |
| Field type | 1 | 0.764 | 0.139 | 0.711 |
| Field type × rain | 1 | 0.560 | 0.102 | 0.751 |
| Error | 34 | 5.477 | | |
| **(b)** | | | | |
| Rain | 1 | 5.913 | 22.353 | < 0.001 |
| Field type | 1 | 0.165 | 0.624 | 0.435 |
| Field type × rain | 1 | 0.261 | 0.987 | 0.328 |
| Error | 34 | 0.265 | | |

## DISCUSSION

### Butterfly community patterns across the transition from semi-natural habitats to fields

A recent review by Prevedello & Vieira (2010) found ample evidence that the degree of edge contrast is inversely related to matrix quality for various taxa. Accordingly, one may anticipate that the sharp structural contrast between olives and their surroundings (grasslands or scrublands) should translate into a sharp alteration in butterfly community structure, whereas the smaller structural difference between wheat fields and neighbouring grasslands or scrublands should dictate a less abrupt alteration in community structure with distance. This, however, was not the case here (Fig. 2 and the significant subsection × field type interaction): In wheat sites, richness and diversity peaked at the ecotone and declined sharply and abruptly when moving into fields (within one metre. GP and CM, unpublished data). By contrast, in olive sites, the community was as rich and diverse at the semi-natural habitat as it was at the groves' margins (subsection F1); and a gradual decrease in richness and diversity was observed once moving into the groves. These results indicate that a strong response of community structure to habitat edges may also take place in the absence of a sharp structural boundary, whereas a sharp structural contrast may not invoke a sharp alteration in community structure (see also Schultz & Crone, 2001). Therefore, while Prevedello & Vieira (2010) suggested that increasing the structural similarity between agricultural fields and neighbouring (semi-)natural habitats should enhance the conservation value of the fields, our observations suggest a need for caution when assigning matrix permeability or attempting to predict community responses to edges based on structural contrast alone.

The higher richness and diversity at wheat field ecotones could be explained by the high abundance of nectar resources along the field edges, as well as by the tendency of some species to establish territories along linear landscape attributes, whereas the sharp fall in richness and diversity is attributable to strong avoidance behaviour. Similarly, Merckx et al. (2009a) found that sharp changes in moth abundance and richness between wheat fields and their edges was explained by the presence of nectar sources along edges and the absence of resources within fields. In olive groves, however, butterflies were often observed to enter the groves at least to a certain distance before flying back to the open. These results indicate that the intensity of response of community structure to habitat edges is primarily resource induced.

Additionally, our observations reveal that butterfly richness and diversity may peak at a different location than one may perceive as the ecotone. In olive groves, the structural edge was utilized by 'ravining' butterflies (species that establish territories along rivers, streambeds or other linear elements (Tennent, 1995)), the grove margins were used by territorial species for roosting or perching (e.g. *Satyrium spini*), and yet other species utilized the shady environment provided by the trees, especially

during warm days, for thermal regulation (Dennis & Sparks, 2005, 2006; Dennis et al., 2006; Grundel & Pavlovic, 2007). Thus, analyses of ecotonal changes in species diversity and composition should take a resource-based approach (Dennis et al., 2006; Vanreusel & Van Dyck, 2007) and consider the functionality and potential complementarity of the different habitats with respect to species' needs, rather than assign suitability according to the inherent structure of each habitat separately (see also Walker et al., 2003; Levanoni et al., 2010).

The gradual decrease in species richness and community with distance into olive groves also suggests a need for caution when sampling species' communities in a given land type or biotope. While in some cases one can assume that species community is homogeneous within a given biotope, in other cases this may not be valid. Such gradients should be taken into account also when modelling animal movements, species distribution and diversity patterns in heterogeneous landscapes, since the microscale effect of distance is likely to affect larger-scale patterns of connectivity and biodiversity (Pe'er & Kramer-Schadt, 2008).

### The climatic gradient

The local-scale pattern of community change across the transition from semi-natural habitats to fields was clearly affected by both field type and the climatic area in which sites were located. The contrast between the semi-natural habitat and the field interior decreased towards arid areas, because of the diminishing species pool towards the desert, as well as the changes in field management with climate. However, we were surprised to identify that irrigation did not have any enrichment effect on species richness or diversity (Figs 3 and 4): in the irrigated wheat field, we observed only one passing butterfly in two visits (Pieris rapae), and in the most arid olive grove, we found none. As indicated from our interviews with farmers, this was likely because of the heavy use of pesticides and herbicides. Therefore, given the potential of irrigation to aid biodiversity in arid regions, we strongly recommend reducing the application of agrochemicals when biodiversity is of interest or concern. Concomitantly, it is necessary to assess whether this can be carried out without accompanied undesired effects of pests or invasion of mesic species.

The decrease in contrast between semi-natural habitats and wheat fields with aridity relates to a decrease in agricultural intensiveness. Particularly, most fields in arid regions belong to traditional Bedouin societies and are managed by shallow ploughing and without agrochemicals. Nevertheless, species richness and diversity were not particularly high in less intensively managed fields (two sites in the desert and two in Mediterranean areas), and species of conservation concern did not occur there. Instead, a nested community pattern prevailed across climate and managements, suggesting that a monoculture such as wheat simply provides few resources and poor habitat (see also Appendix S5, Fig. S4, and Liu et al., 2010).

The overall decrease in species richness and diversity across the climatic gradient is in accordance with various studies

(Delsinne *et al.* (2010); Kutiel *et al.*, 2000; Pugnaire & Lazaro, 2000; Davis *et al.*, 2008), yet the overall low species richness in wheat sites and the weaker effect of climate on species diversity in wheat sites (Fig. 4) warrant further attention. These results suggest that the overall species pool in a site, as well as the climatic effect on the site level, may dwindle in the presence of a 'hostile' crop. An explanation may be that poor-quality sites support generalist species that occupy not only a wide range of habitats but also a range of climates. Therefore, targeted conservation planning should consider both crop and management within the more general contexts of landscape and climate.

## Further implications for conservation

The protection of biodiversity in agricultural landscapes is receiving increasing attention and funding in recent years. Agro-Environmental Schemes (AES), where farmers are paid for environmental services to enhance biodiversity in agricultural landscapes (DEFRA - Natural England, 2008), have become one of the most important tools for conservation on agricultural landscapes (MacDonald *et al.*, 2007; Farmer *et al.*, 2008). However, the success of such schemes is equivocal (Kleijn & Sutherland, 2003; Kleijn *et al.*, 2006; Konvicka *et al.*, 2008; BirdLife International & RSPB, 2009; Spitzer *et al.*, 2009), and there is ample scope to improve their efficiency (Merckx *et al.*, 2009b). Within this context, an important discussion involves the question of land sparing versus wildlife-friendly farming (Hole *et al.*, 2005; Rundlof & Smith, 2006; Fischer *et al.*, 2008; Hodgson *et al.*, 2010). However, noting that most conservation studies in an arable context focus on questions of how to manage fields (e.g. organic versus conventional) or their margins (e.g. how wide, what vegetation and how), our study offers a different perspective by sampling communities across scales, climates and crops. Our results suggest that one should first of all ask what crop type should be prioritized, as this selection would determine the observed pattern at the local scale. In our case, wheat fields supported overall less species, and locally, it was the boundary area that maintained the richest and most diverse community, whereas in olive groves it was the combination of contrasting habitats that supported biodiversity. As a second step, it is important to consider the size and spatial configuration of fields, as demonstrated by the decrease in species richness and diversity with distance into olive groves. The actual management may come last. Here, we note that in wheat fields we recognized three habitats that could potentially be managed (field, ecotone and semi-natural habitat), whereas in olive groves the ecotone often did not exist as such but was merely a transitional area between two other habitats. Obviously, in the latter case, field boundaries or set-aside regions may be less important or even impossible to manage. Our results also suggest that, when hostile crops or monocultures are considered, wide strips or areas of set-aside land could support species of conservation concern, while reduced intensity without enlarging margins could only aid generalist species.

## CONCLUSIONS AND OUTLOOK

Our study demonstrates that the quality of an agricultural matrix matters with strikingly different responses of butterfly communities to field type (wheat versus olives), across various scales. Our results suggest that conservation of biodiversity in agricultural landscapes should first of all consider the nature of alternative potential crops (Jones *et al.*, 2005) within the wider context of the ecosystem and climate in question. Second should be the design of fields in terms of size and spatial structure (Weibull *et al.*, 2003), and lastly, the management of the field and the set-aside areas. Specifically for the studied region and crops, our results indicate the potential conservation value of olive groves for biodiversity and even for species of conservation concern (see also Potts *et al.*, 2006; Scalercio *et al.*, 2007). Results of this study have facilitated an experimental AES in Israel (Amdur, 2009), where wheat fields were replaced by a carefully designed olive grove in Menashe Highlands (Northern Israel; see Pe'er & Settele, 2008b), and monitoring transects have been established to assess the long-term effects of crop replacement on butterflies.

Given the multitude of factors that affect management decisions in agricultural systems, it is obvious that a single study can only address some of the many remaining questions. A comparative study of different management schemes in a given climatic area was beyond the scope of this study, yet clearly needs to be conducted and repeated across different climatic regions, and particularly in arid regions were relevant data are scarce. This may be particularly valuable in the context of climate change, since both land uses and ecosystems alter in response to climate.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Summary of study sites, average annual rainfall at the site, irrigation management, dates of visit (dd/mm/yy) and the number of species observed in three of the site's subsections: N2, E and F2, for (a) wheat sites and (b) olive sites.

**Appendix S2** Selection of study sites.

**Appendix S3** List of observed species.

**Appendix S4** Butterflies of conservation concern observed during surveys, divided into sites, numbers and habitats (N = nature, E = ecotone, F = field).

**Appendix S5** Complementarily to Figures 2-4, we present further results based on $S_{obs}$ (Mao Tau) and Chao Index for a) species richness along the distance gradient (Figure S1); b) the difference in species richness between the natural area and the field along the climatic gradient (Figure S2); and the overall species richness on the site level (pooling all six subsections) along the climatic gradient (Figure S3). In addition, Figure S4 depicts overall species richness per habitat (semi-natural habitat, ecotone, field) and along the climatic gradient, based on based $S_{obs}$ (Mao Tau).

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## BIOSKETCH

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Author contributions: G.P. and S.K. conceived the ideas; G.P. and C.v.M. collected the data; G.P., C.v.M., A.T. and Y.G.M. analysed the data; and G.P. led the writing, with contributions from all co-authors.

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