Asymmetrical responses of forest and ''beyond edge'' arthropod communities across a forest–grassland ecotone

(Article begins on next page)

13 September 2024

UNIVERSITÀ DEGLI STUDI DI TORINO

The final publication is available at Springer via

Title: Asymmetrical responses of forest and "beyond edge" arthropod communities across a forest-grassland ecotone

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Abstract

Historically, where forest habitats are deemed as the pristine landscape state, anthropogenic habitats such as managed grasslands or open spaces are often perceived to be antagonistic and of secondary conservation priority. Traditionally, studies on biodiversity responses to ecological variation, i.e. edge effect, have mostly focused on forest habitats. Yet recently there has been increased attention on communities beyond the forest edge in an effort to better understand how interactions between forests and adjacent habitats may potentially affect regional biodiversity. However, in Europe and the Mediterranean basin (a biodiversity hotspot), areas with high landscape heterogeneity and high edge density, there is a paucity of studies analysing the community responses across forest and "beyond edge" habitats across ecotones. In a protected area of central Italy, we investigated the responses of ground-dwelling arthropods (Araneae [spiders], Chilopoda [centipedes] and Carabidae [ground beetles]), which were differentiated into habitat-specific guilds (forest, edge and grassland species) across a forest-grassland ecotone. We investigated the extent to which a habitat edge influenced communities of arthropods associated with either the forest or grassland, and how far from the edge this effect penetrated into each habitat. Twelve 150 m-transects perpendicular to a forest-grassland edge were established and arthropods were sampled at nine progressive distances across the ecotone. An indicator species analysis (ISA) was used to detect species significantly associated with forest, edge-belt or grassland habitats, which were assumed representative of the respective communities. Logistic models of indicator species richness and abundances were used to describe responses of grassland and forest communities across the ecological boundaries. We found that grassland and edge habitats had habitat specialists and higher species richness compared to the forest habitat. Moreover, the occurrence of grassland-specific species was influenced by the presence of an edge up to 15 m from the habitat border. In contrast forest-associated indicator species were not affected by proximity to the habitat edge, rather individuals typical of forest habitats tended to "spill over" into grassland habitats. These findings support the hypothesis that in a forest-grassland mosaic, forest species are less sensitive to an edge and influence the community beyond the forest edge and into the grassland more than the reverse, i.e. the effect was asymmetric. From these data, we estimated that a minimum grassland habitat width of 600 m is necessary for grassland species to maintain a core area that is relatively unaffected by the spillover of species from adjacent forest habitats. Incorporating the directional influences of adjacent communities on each other allows for an empirical

assessment of habitat vulnerability that doesn't *a priori* value the conservation of one habitat over another.

Introduction

Conservation biologists and environmentalists have often perceived forest habitats and their associated wildlife as a conservation goal, particularly in those areas where forests are seen as the desirable "pristine" state of the landscape (Murcia 1995; Vera 2000; Bond and Parr 2010; Willis and Bhagwat 2010). With some notable exceptions aside (e.g., USA prairies, Serengeti), grasslands are commonly given a lower priority for conservation in both temperate and tropical areas and are often assumed to be highly anthropogenically influenced and suboptimal habitats for species conservation (Andres and Ojeda 2002; Bremer and Farley 2010; Putz and Redford 2010; Willis and Bhagwat 2010). However tropical and temperate grasslands often have high levels of endemism and habitat specialists (Watson 1999; Bond et al. 2008; Taboada et al. 2011; Dengler et al. 2012; Wilson et al. 2012), suggesting that both prior to modern human activities and presently they play a non-trivial role in shaping current patterns of biodiversity. Consequently, these habitats are essential for maintaining present levels of biodiversity (Svenning 2002; Van Swaay 2002; Habel et al. 2013).

Many studies of biodiversity responses across environmental gradients have focused on forest-grassland ecotones with particular emphasis on edge effects. The edge effect occurs when biotic and abiotic conditions change along the interface between two habitats, affecting the distribution of species and with consequences for overall biodiversity and ecosystem functionality in both habitats (Murcia 1995). If edge effects are strong and spatially pervasive penetrating into a habitat, then total habitat area may not be representative of its capacity to support species typical of that habitat (Laurance and Yensen 1991). Without information about the residual core area, (area safe from edge effect), it is difficult to predict how regional species diversity will respond to reductions or increases in habitat area (Laurance and Yensen 1991; Didham and Ewers 2012). Although a rich literature is available examining forest community responses to edge effects (Ranney et al. 1981; Murcia 1995; Riesans Sisk 2004; Harper et al. 2005; Tian et al. 2011), little is known about how edges affect grassland communities (Samways and Moore 1991; Hänggi and Baur 1998; Bieringer and Zulka 2003; Pinheiro et al. 2010; Pryke and Samways 2012).

Although edge effects can have consequences on both the adjacent habitats and communities, ecological patterns and processes have usually been analysed from an edge to the interior of one habitat (one-sided approach) and not the whole gradient from the interior of one habitat to the interior of the

other habitat (two-sided approach) (Ewers and Didham 2006; Fonseca and Joner 2007; Bond and Parr 2010; Harper and Macdonald 2011; Bieringer et al. 2013). Most importantly, in Europe and the Mediterranean basin (a biodiversity hotspot, Myers et al. 2000), areas with high landscape heterogeneity, high edge density (Naveh 1994), and extraordinary richness of grassland species (WallisDeVries et al. 2002; Dengler et al. 2012; Wilson et al. 2012), there is a paucity of studies on two-sided edge effects at the forest-grassland ecotones (but see Hänggi and Baur 1998; Bieringer and Zulka 2003; Roume et al. 2011; Bieringer et al. 2013). European countries currently are undergoing declines of a wide range of grassland species (Santos et al. 2008; Van Swaay et al. 2010; Taboada et al. 2011), mainly due to agricultural intensification and forest encroachment (Preiss et al. 1997; Debussche et al. 1999; Falcucci et al. 2007; Wigley et al. 2010). Conservation of biodiversity in such complex landscapes will depend on the ability to preserve both forest and open habitats within the landscape.

The principal aim of this study was to understand and quantify the mutual influences of adjacent terrestrial habitats on animal species abundances and distributions. We worked within a protected area in the central Italian Apennines, characterized by a mosaic of forest and grasslands with well-defined and abrupt habitat boundaries (Fig.1a, b). Here we focused on epigeic arthropods, which are widely used due to their sensitivity to environmental variation at small spatial scales (Pearce and Venier 2006). We selected three groups: spiders (Araneae), centipedes (Chilopoda) and ground beetles (Carabidae). These taxa (mostly predators) have intermediate trophic positions, feeding on soil invertebrates and serving as prey for small mammals, amphibians and birds. As a consequence, they may play key roles in the maintenance of ecosystem functions (Pearce and Venier 2006). Ground-dwelling arthropod species were first categorized into habitat-specific assemblages (forest, edge and grassland-associated species, irrespective of taxonomic categories, following the "habitat guild" approach of Bieringer et al. 2013). We then used these categories to compare how arthropod assemblages associated with a specific habitat type changed across the grassland-forest ecotone and the magnitude of these changes (i.e., edge effect) on both forest and grassland-assemblages. We also examined how far an edge effect permeated into the alternate habitat and whether this effect was symmetrical.

Because of the traditional focus on forested areas in conservation planning in Europe, we hypothesized that forest-associated arthropod assemblages would be more affected by proximity to forest-grassland edges than grassland assemblages, although species diversity of these groups would be high in

both habitats. This information can help identify the spatial scale and directionality of cross-habitat associated effects and can be used in conservation planning.

Methods

Study area and sampling design

This study was conducted within the Monti Simbruini Regional Park (13.0356° E – 13.3838° E and 41.833° N – 42.0267° N), a 29 990 ha natural reserve located in the Apennines mountains of central Italy. The park contains 4 874 ha of grasslands, embedded within large and virtually continuous temperate and warm temperate forests (21 425 ha), with highlands potentially covered by snow between October and April. Low intensity grazing by domestic animals, principally cattle, horses and sheep (< 0.05 animals ha^{-1}) occurs within the park boundaries, except in "Special protection zones" (areas not used in this study).

We selected sampling locations at the ecotone of the dominant mountain beech forest and adjacent grassland openings typical of the calcareous soil of the central Apennine. In order to reduce the variability among forest or grassland sampling locations, we used an available digital phytosociological map for the park (Attorre et al. 2005), and selected the *Koelerio splendentis-Brometum erecti* plant association as representative of grassland habitat and *Polysticho aculeati-Fagetum sylvaticae* plant association as representative of forest habitat. The grassland habitat consists of dry secondary grasslands, mainly used as pasture for extensive grazing. The selected forest habitat constitutes nearly pure forest of *Fagus sylvatica* (beech), with dense and homogeneous canopy closure (83 - 96%), almost absent understory, deep leaf litter and a sharp tree line edge that demarcates the boundary of this habitat (Fig. 1a). All these features make the ecotone between these two habitats a good experimental system since detecting habitat boundaries was easy, and plant communities were homogeneous even in proximity to the edge.

Six study sites located at least 1 km from each other were established at the ecotone between forest and grassland habitats at 1 300-1 700 m a. s. l. (Fig. 1b). At each study site two 150 m transects were positioned perpendicular to the forest/grassland interface. Transects at a sampling site were at least 18 m from each other, except for one site (distance: 13 m). Nine sampling plots were placed along each transect at 0, 12.5, 25, 50 and 75 m from the edge (Fig. 1c) into the forest and grassland habitats with

higher plot density in the proximity of the edge in order to detect steeper gradients of assemblage changes occurring in this transition zone (Digweed et al. 1995; Ewers and Didham 2006; Larrivèe et al. 2008).

Arthropod sampling

Within each plot we placed two pitfall traps, spaced 2 m apart, consisting of 500 ml plastic cups each 9.5 cm in diameter and filled with 100 ml vinegar to retain, kill and preserve individuals (Koivula et al. 2003), and partially covered opening with a flat stone set approximately 3 cm above each trap in order to prevent rainwater from entering the trap. Traps were run continuously for eight weeks between 3 June and 31 July 2009, in the period of the highest arthropod activity and when the greatest diversity and species abundance were expected. A high spatial sampling effort (216 traps) during peak activity for most arthropod species is expected to capture the essence of the species assemblages in this area, allowing us to make inferences on arthropod assemblage responses (Larrivée et al. 2008; Lövei 2008). Arthropod collections occurred monthly, and upon collection, pitfall samples from a plot (two traps) were strained, transferred to 70% ethanol, and pooled together to obtain a single pitfall sample per plot. Captures were later sorted in laboratory and individuals identified and enumerated at the species level (or closest higher taxonomic level, e.g., genus). Nomenclature and classification follow Minelli (2006) for Chilopoda, Vigna Taglianti (1993, 2005) for Coleoptera: Carabidae and Platnick (2011) for Araneae.

Data analysis

Arthropod taxonomic groups (Carabidae, Chilopoda, Araneae) were analysed together as an assemblage to establish groups of species that were most typically associated with a particular habitat (Bieringer et al. 2013). This habitat-guild delineation approach assumes that there are species assemblages associated with homogenous ("pure") habitats that can be used as reference conditions to which assemblages from other locations can be compared. By using this approach, patterns of assemblages at edges can be more clearly interpreted (although the taxon-specific contributions to this pattern become less apparent). For example, ignoring habitat-specific associations of species could show peaks in species diversity at edges, even though this may be due to an additive effect of species belonging to two adjacent habitats, an effect that doesn't clarify the existence of an edge-specific group. Thus, the

habitat guild approach allows disentangling such ecological patterns and can give a clearer picture of complex interactions existing between adjacent communities (Bieringer et al. 2013).

Spider, centipede and ground beetle counts from each plot were summed over the two sampling periods to detect and describe patterns of community turnover across the forest-grassland ecotone. Within a 150 m transect, we identified *a priori* three sequential habitats: grassland (plots 1-3), the transition "edge belt" (plots 4-6, ± 12.5 m from the edge, Fig. 1c), and forest (plots 7-9). To examine whether trap locations were sufficiently spaced to be independent replicates, we tested our data for autocorrelation by performing a Mantel test based on Pearson's product-moment correlation (permutations: 9 999), between Bray-Curtis distances in assemblage composition and the geographical distances of samples collected at the same distance from the edge and far from a source of disturbance (75 m from the edge). The tests were performed separately on both grassland and forest samples (for each habitat: 1 plot × 12 transects). We found that spatial correlation in assemblages between samples was low (grassland: Person's $r = 0.23$; forest: Person's $r = 0.20$) and not significant ($p \geq 0.05$). Therefore, we assumed all sampling plots as statistically independent (inter-sample distance ≥ 13 m). Baker and Barmuta (2006) similarly found no evidence of autocorrelation in pitfall traps located at between 1 - 100 m.

Patterns of species richness, abundance and occurrence

To investigate patterns of species richness for the overall arthropod assemblage, we first calculated rarefaction-standardized number of species (Gotelli and Colwell 2001) to account for the effect of abundance on species richness estimates. Sample-based (i.e., plot-level) rarefied estimates of species richness (± 95% CI) were performed for each habitat type, with 500 iterations being conducted independently, using ''EstimateS 8.2'' (Colwell 2009) and re-scaled by average abundance.

Patterns of species composition were explored using non-metric multi-dimensional scaling (NMDS) of species assemblage data. To account for the possibility of different assemblage patterns due to variation in species composition or density, two NMDS ordinations were conducted on a Bray-Curtis distance matrix calculated between sampling plots with either presence-absence and fourth-root transformed species abundance data. Permutational multivariate analyses of variance (PERMANOVA, Anderson 2001) in Primer 6 (PRIMER-E 2008) was employed to test for significant inter-group differences in multivariate community structure using a 3-factor nested model with pairwise post-hoc

comparisons. Analyses were performed on both presence-absence and fourth-root transformed data, incorporating the factors: (1) habitat (fixed factor with three levels: forest, edge belt and grassland; 2) site (random factor with six levels); 3) transect (random factor with two levels nested within site). P-values were calculated from 9 999 unrestricted permutations of the data.

Edge effect estimations and comparison between forest and grassland habitats

To describe and quantify the potential bi-directionality of effects between arthropod assemblages from adjacent habitats we used the following approach: first, we defined the characteristic arthropod assemblages of the two main habitats (i.e. forest *vs.* grassland); second, a general logistic model was used to describe continuous response functions of forest and grassland assemblages from the non-habitat (matrix) into the focal habitat; finally, the first and the second derivatives of the functions were used to calculate the magnitude and extent of edge effects on both forest and grassland communities (see Ewers and Didham 2006). Such an approach allowed us to quantitatively compare the magnitude and extension of effects that forest habitat had on the grassland arthropod assemblages and vice versa.

To define the two characteristic assemblages, we assumed that the grassland, as well as the forest, is best characterized by those species showing a preference for that particular habitat (i.e. indicator species). The responses of both forest and grassland indicator species were assumed representative of their respective communities. Although habitat preferences based on the autoecology of some species are available in literature, these categorizations are not universally shared by experts. Therefore we used an Indicator Species Analysis (ISA) implemented in PC-ORD 6 (McCune and Mefford 2011) to objectively identify species' habitat preference on the basis of their relative abundance (specificity) and occurrence (fidelity) (Dufrêne and Legendre 1997). This analysis generates an Indicator Value (IV) relative to a specific habitat for each species, that ranges from 0 (no indication) to 100 (perfect indication). We evaluated the statistical significance of the maximum IV using a Monte Carlo randomization test (10 000 runs).

To describe the responses of forest and grassland communities across the ecotonal boundaries, from the non-habitat (matrix) into the focal habitat (forest or grassland), we selected two biotic variables: the richness of habitat indicators and the abundance of habitat indicators (Larrivée et al. 2008). Before running analyses abundance data of habitat indicators were fourth-root transformed in order to

9

downweight the effects of dominant species. Analyses were run twice, firstly considering as indicators only species with IV > 25% and significant ($p < 0.05$) (Dufrêne and Legendre 1997), secondly using all species with significant IV. We expected a progressive decrease in both the variables from the innermost to the outermost habitat plots, following a sigmoid trend (Downie et al. 1996; Cadenasso et al. 2003; Ries and Sisk 2004). For each variable, we modelled the pattern of changes across the ecotone using nonlinear mixed effect models, in which the hierarchical nature of the data was specified (i.e. transects nested within site). Data were analysed in R (version 3.0.2, R Development Core Team, 2013) using the *nlme* package (Pinheiro et al. 2014). Following Ewars and Didham's (2006) recommendations we used the first and second derivatives of the functions and a bootstrap technique of resampling of the errors (Davison and Hinkley 1997; Toms and Lesperance 2003) to objectively estimate the underlying parameters of edge effect and their confidence intervals ($\pm$ 95% CI). The parameters estimated were the magnitude of edge effect, midpoint, extent of edge zone and depth of edge influence. Magnitude of edge effect, ranging between 0 (no edge effect) and 1 (maximum edge effect), was defined as the difference between the maximum and minimum values of the standardized response variable (richness or abundance of indicators), relativized by maximum. The midpoint is the point across the ecotone where the most abrupt effect is observed and was detected by local maximum of the first derivative of the function. The extent of edge zone is the edge effect's spatial range in both the adjacent habitats, whose start and end points were identified by local maximum and minimum of the second derivatives of the function. Finally, the depth of edge influence is the distance from the edge at which the variable (richness or abundance of indicators) ceased to be different to habitat interior (forest or grassland), i.e., the portion of the edge zone falling within a single habitat.

The 95% CIs of the edge parameters were calculated using the bootstrap resampling of residuals from the fitted models. Residuals from each fitted model were randomly sampled (with replacement) and then added to the fitted values to create a bootstrap sample. The model is then refitted to the bootstrap sample, and all edge effect parameters recalculated. The process was repeated 1 000 times and a 95% CI was calculated as the 2.5[th] and 97.5[th] percentiles of the bootstrapped estimates (Toms and Lesperance 2003; Ewars and Didham 2006). Since our models showed heteroskedastic errors, we used the wild bootstrap method (Wu 1986), implemented in fANCOVA package version 0.5-1 (Wang 2010).

Results

Patterns of species richness, abundance and occurrence

We identified a total of 8 727 arthropods, including 143 taxa (with 124 identifiable species, see Online Resource ESM 1), recording 12 endemics (restricted to Italy or central Apennine,). There were 1 439 individuals and 67 species in the grassland habitat, 3 720 individuals and 98 species in the edge belt, and 3 546 individuals and 48 species in the forest habitat.

Rarefaction estimates of species richness indicated that traps in the grassland and the edge belt captured significantly more species than the forest traps, although the forest and the edge belt had the highest number of individuals (Fig. 2).

The overall species richness was highest in the edge belt and decreased toward the two core habitats (75 m from the edge into the grassland or into the forest), with a faster decline toward the forest core (Fig. 3a). Even when considered separately, the two dominant taxa, spiders (68 species) and ground beetles (43 species), showed comparable peaks in species richness at the grassland-side of the edge belt, a pattern similar to that obtained for the combined assemblage (overall species richness) (Fig. 3a). Centipedes (13 species) showed the lowest species richness within the grassland habitat, while edge belt and forest habitat had comparable values.

Similar to the overall species richness, total abundance of ground-dwelling arthropods peaked in the edge belt (Fig.3b). However, there was a more rapid decrease in total abundance toward the grassland core due to the greater abundance of individuals found in edge and forest habitats across all three taxonomic groups (Fig. 3a, Fig. 2). In the forest habitat, total abundance values remained relatively high and dominated by ground beetle individuals, while spiders were more common in the grassland habitat, where centipedes were almost absent.

Non-metric multidimensional scaling ordinations of arthropod assemblages showed forest and grassland plots were significantly distinct, with the edge belt plots intermediate between the two, though edge habitat assemblages showed a greater overlap with species in the forest habitat. This pattern was consistent when analysed with either presence-absence (Fig. 4a) or fourth-root transformed abundance data (Fig. 4b), suggesting that it is not merely based on differences in species abundance. In both cases, there was a gradual change in the arthropod assemblage toward the ecotone. For subsequent analyses we show only the results based on fourth-root transformed data.

PERMANOVA results showed significant differences in arthropod assemblage structure between forest, edge belt and grassland habitat (habitat: pseudo-F= 15.06, $p < 0.001$) (see table 1). Significant differences were also detected among sites, although the composition of the assemblages was more variable among habitats than among sites (site: pseudo-$F = 4.78$, $p < 0.001$). Both habitat typology and site interacted to determine the arthropod community structure (habitat × site: $p < 0.001$), while no effect of transect was detected (transect (si), transect (si) × ha: $p > 0.05$). The largest difference in arthropod assemblage was between grassland and forest plots (pairwise PERMANOVA pseudo-$t = 4.40$, $p < 0.01$), followed by grassland and edge belt plots (pseudo-$t = 3.34$, $p < 0.01$). The smallest difference in arthropod assemblages was between the forest habitat and the edge belt (pseudo-$t = 3.32$, $p < 0.01$).

Edge effects and comparison between forest and grassland habitats

Indicator Species Analysis (ISA) found 31 indicators (IV range: 10.4-74.5, $p < 0.05$), 17 associated with grassland, 6 associated with the edge-belt (with 1 endemic, *Calathus fracassii*), and 8 indicators associated with forest (with 2 endemics, *Lithobius tylopus* and *Parachtes vernae*) (Online Resource ESM 2). Spiders and ground beetles were the taxa that most affected habitat characterizations, with spiders (especially wolf spiders, e.g., *Pardosa aenigmatica, P. mixta, Lycosa tarantula*) being good indicators of the grassland while ground beetle species (e.g., *Pterostichus micans, Abax parallelepipedus* and *Nebria tibialis*) were mainly associated with the forest habitat. Among centipedes, only two species, *Lithobius castaneus* and *L. tylopus,* showed significant preferences for a particular habitat (forest).

For forest and grassland habitats, the percentage of indicator species across transects decreases in the proximity of the edge (plot 5), hence within the 25 m edge belt (plots 4 - 6, Fig. 5). In both cases, once across the edge, the percentage of indicators approaches zero, indicating edge effects of comparable magnitude (Table 2). The same trends were observed also when only indicators with IV > 25 were used (data not showed). For subsequent analyses we show only the results based on all indicators with significant IVs ($p < 0.05$).

The changes in richness and abundance of habitat indicators as a function of distance from the matrix to the interior of a habitat type showed sigmoid trends (Fig. 5). The models obtained for both variables (richness and abundance) showed that grassland species changed earlier and more abruptly than forest species (Fig. 5, Table 2). The point along the ecotone at which the edge effect most influenced the

richness of indicators (the midpoint) was at 6 m from the edge, and within the habitat, for the grassland species, and at 5 m beyond the edge, outside of the habitat, for the forest species. Hence, the location at which grassland species' midpoint is detected coincides approximately with forest species' midpoint (5-6 m beyond the forest edge into the grassland). The patterns in richness of habitat indicators showed grassland community having an edge zone of 8 m, all included within the grassland border; forest community had an edge zone of 17 m, extending 4 m within and 13 m beyond the forest borders (Table 2). The depth of edge influence into the habitat was 10 m for grassland and 4 m for forest communities. These results are in general agreement with those obtained by the analyses on the patterns of abundances, but no difference in depth of edge influence was observed between forest and grassland communities (see Table 2).

Discussion

Working across a grassland-forest mosaic in the central Apennines of Italy, we found a diverse assemblage of ground-dwelling arthropods of high species richness. Of this diverse community, some arthropod species were typically associated with either the grassland habitats, forest habitats or the ecotonal edge itself. These habitat specific guilds, however, changed with proximity to the ecotonal edge. The grassland assemblage of ground-dwelling arthropods was more sensitive to the proximity of the ecotone than the assemblage of species associated with the forest habitat. Separate logistic models of species richness and abundance as a function of distance through the grassland-forest ecotone showed that the species richness and abundance of grassland-associated arthropods changed more abruptly (i.e., shorter extent of edge zone) than that of forest species. In addition, the point along the ecotone at which the loss in grassland and forest species was strongest occurs about 5- 6 m beyond the forest edge. It is interesting to note that this location falls within the range of tree shadow (about 5 m beyond the forest boundary, Fig. 1a). It is possible that this narrow zone could supply microclimatic conditions (e.g. temperature, light and humidity) that are more favourable to forest arthropods than to grassland species (Cadenasso et al. 1997). This "depth of edge" effect indicates that the occurrence of grassland species is affected up to 15 m (upper 95% CI) from the ecotonal boundary. In contrast, we found that forest species are not as affected within the habitat (95% CI distance of edge influence: 0 - 8 m) and individuals tend to "spill over" into grassland habitats (Roume et al. 2011; Schneider et al 2013). These findings support the

hypothesis that in a forest-grassland mosaic, forest species are less sensitive to an edge effect and influence the community beyond the forest edge more than the reverse, with potential detrimental effects on the trophic interactions and/or ecosystem functioning of the adjacent habitats (Schneider et al 2013; Gaublomme et al. 2014). Moreover, the encroachment of forest-associated arthropods into the grassland habitat, and the decline of grassland species near the ecotonal boundary, suggests that a habitat mosaic is therefore not merely the sum of its component parts since interactions among the habitats via edge effects can change the species composition of adjacent habitats.

The value of grassland and edge habitats for arthropod biodiversity

In some parts of the world, grassland habitats and their edges are often regarded as disturbed habitats and potential sources of exotic and generalist species (Cadenasso and Pickett 2001; Cardoso et al. 2009; Hansen and Clevenger 2005), and therefore are considered of secondary conservation value (Bond and Parr 2010; Bremer and Farley 2010; Willis and Bhagwat 2010). Grasslands have been often undervalued since they are frequently associated with human activities, such as grazing, cultivation, or deforestation, considered detrimental to persistence of native species (Bond et al. 2008). Yet our findings show that mountain grasslands in the Apennine region of central Italy have a greater number of associated arthropod species (indicators = 17) and a higher species richness compared to forest habitats (Fig. 2). Two grassland indicators, *Lycosa tarantula* and *Steatoda albomaculata*, were never found in both edge belt and forest habitats. This pattern of specialization and high species richness in grasslands support similar findings for other areas (Taboada et al. 2004; Negro et al. 2009; Pawson et al.2010; Taboada et al. 2011) and for other taxa (Kotze and Samways 1999; Pino et al. 2000). It is also notable that we never recorded any exotic species in grasslands, the edge-belt, or in the forest. The lower number of individuals found in the grassland compared to edge belt and forest habitats could be explained by the low primary production of these habitats (Pringle et al. 2007).

In the "edge belt", the transition zone between grassland and forest habitats, we found an elevated number of species. The diversity found there was comparable to grassland habitat, and the abundance of arthropods was as high as that found in forest habitat. This pattern suggests that grassland and forest assemblages may merge in this transition area (Leopold 1933; Downie et al. 1996), with a bias towards higher abundance rather than a shift in composition so as to become more forest-like

(Gaublomme et al. 2014). Additionally, in the narrow transition area between the two habitats (25 m belt), we found 6 species significantly associated with edge habitat including two specialists (*Amara curta* and *Drassylus praeficus*) and an endemic species (*Calathus fracassii*) with a very restricted range (central Apennines). For these species, the abundance patterns across the ecotone show a clear preference for the edge (unimodal pattern; see Online Resource ESM 3). The low, but significant, IVs observed for some species are mainly due to their low fidelity (sensu Dufrêne and Legendre, 1997); that is, they didn't occur in all edge belt plots. These findings are consistent with previous studies (Magura et al. 2001; Máthé 2006; Yu et al. 2007) and highlight the edge belts as a unique habitat that is not merely the sum of the two adjacent habitats, but an emergent property of the forest-grassland interface.

The decrease in the occurrence and abundance of grassland-associated arthropod species in proximity of the grassland-forest interface indicates that there is a certain amount of grassland habitat adjacent to edges that has different characteristics than habitat near the "core". We found that this "depth of edge influence" can reach 15 m into the grassland habitat. A consequence of this finding is that patches smaller than 30 m diameter surrounded by forest could lack sufficient interior area to maintain grassland-associated arthropods (Hänggi and Baur 1998; Bieringer and Zulca 2003; Pryke and Samways 2012). Scaling this finding up suggests that an idealized circular patch of grassland of 300 m in radius (about 25 ha) would result in about 10% of the patch area influenced by an edge effect from the adjacent forest (core area model, Laurance and Yensen 1991). This effect is expected to increase for patches that have greater edge to area ratios (Didham and Ewers 2012). This also suggests that ignoring potential interactions between habitats overestimates the value of grassland habitats within mosaics for biodiversity conservation. That is, the total amount of habitat area itself in not sufficient to predict its value as a habitat for grassland species. Thus, because of the edge-based interaction between forest and grassland habitats, with grassland species being significantly more sensitive to the edge than forest species, the size and proximity of habitat patches in a mosaic landscape can affect the conservation value of habitat areas.

The patterns observed, and the conclusions we draw, are likely strongly dependent on the specific taxa that were used as indicators in this study, ground-dwelling arthropods. The life histories and dispersal abilities of spiders, centipedes and ground beetles make them sensitive to changes in environmental conditions at relatively small scales (10s of meters). Different taxa may respond differently to habitat edges. For example, wild bees are frequently positively related to edge density, since they

depend upon the presence of forest habitat for nesting and open habitat for foraging (Diaz-Forero et al. 2013). In contrast, European butterflies are mainly associated with open habitats (Van Swaay et al. 2006) and are negatively affected by forest presence (Ricketts 2001). Plants (more sessile than arthropods) are strongly influenced by abiotic variables (e.g., soil composition, radiation and moisture; Murcia 1995). On the other extreme of dispersal abilities, bird communities are often affected by characteristics of the landscape at the scale of 100s m to kilometers (O'Connell et al. 2000). Thus, the applicability of the general finding of this study to other systems, that is the sensitivity of habitat specialist guilds to edge habitats (which is sometimes asymmetrical), needs to be scaled to the average life histories and dispersal ranges of the species assemblages in question.

Implications for biodiversity conservation in complex European landscapes

Historically, the conservation of forest and open habitats has been considered separately. One view has been to preserve forest habitats, discouraging within protected areas all those activities, including traditional land uses such as grazing and logging, considered non-natural disturbances and therefore not forest-friendly (Spitzer et al. 2008; Leroux et al. 2010). Yet, the cessation of traditional human activities from areas with a millennial history of human-environment interaction, such as the European continent, has not necessary yielded positive results for biodiversity (Sala et al. 2000; Fonderflick et al. 2010; Lenda et al. 2011).

One potential reason why biodiversity benefits have not been realized is that anthropogenic influences historically produced not only changes in the landscape through land clearing and farming for crops, but also caused regional extinctions of many wild large herbivores (Vera 2000). These wild grazers, which included auroch and tarpan wild horse, created heterogeneity in the landscape through their grazing and disturbances, and promoted the persistence of grasslands. These species were gradually replaced with their domesticated descendants (Bengtsson et al. 2000; Vera 2000; Sutherland 2002). Given that current European ecosystems lack many native large herbivores, they are not able to easily retain their biodiversity: changes in traditional land use have resulted in woodland closure and conversion of open habitats into forest through succession (Debussche et al. 1999; Vera 2000; Falcucci et al. 2007). The persistence of open habitats and their associated wildlife depends on the ability to manage the dynamic equilibrium between forest and open habitat (Fischer et al. 2012). The high diversity of arthropod and

other animal and plant species associated with grasslands depends on the maintenance of areas that are sufficiently large enough to maintain populations of species, and that are not overwhelmed by edge effects. In European landscapes, a potential strategy for preserving grassland habitats would be to use low density domestic animal stocks as surrogates for wild herbivores as a way to prevent forest encroachment and canopy closure (Vera 2000, Svenning 2002, Weigl and Knowles 2014).

In summary, management measures aimed at effectively preserving species in landscape mosaics require an understanding of the degree to which habitats interact and the spatial extent of that interaction. Our finding of an asymmetrical effect among habitats (with grassland species more affected by an edge effect than forest species) and the spatial extent of that interaction (up to 15 m for grassland) allows us to better predict and manage the effect of changes in habitat area on ground-dwelling arthropod species. We highlight that these insights were possible through the simultaneous examination of cross-ecotonal edge effects. Furthermore, given that alterations in arthropod biodiversity can lead to changes in food web interactions or ecosystem functioning (Schneider et al. 2013), a more effective conservation of arthropods can have indirect positive effects on other taxa as well. We propose that similar approaches examining the effects of adjacent communities are taken across other habitats, natural or managed, in close proximity to each other (e.g., forest plantations, agricultural, grassland and forest habitats (Barlow et al. 2007; Larrivée et al. 2008; Karp et al. 2012). By taking a view of habitat composition that examines the reciprocal effects of adjacent habitats and the spatial extent of their interactions, we can better develop successful conservation strategies for the long-term persistence of biodiversity in complex landscapes.

Acknowledgments

Supporting Information

Abundance data of the taxa recorded (ESM 1.pdf), significant results for ISA (Indicator Species Analysis) (ESM 2.pdf) and Barplots showing the abundance distributions across the ecotone of the six edge species (ESM 3.pdf) are available online.

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Figure captions

Fig. 1 Study area and sampling design showing (a) the sharp edge along the ecotone between the mountain beech forest and the grassland; (b) map of the study area in Italy showing the distribution of the selected forest (*Polysticho aculeati-Fagetum sylvaticae*) and the grassland (*Koelerio splendentis-Brometum erecti*) habitats (note the grasslands embedded in the continuous beech forest), and the position of the six study sites in the forest-grassland interface; and (c) a representation of a 150 m transect, perpendicular to the grassland-forest interface, showing the relative placement of pairs of pitfall traps in the nine sampling plots along the three ecotonal zones (grassland, edge-belt and forest).

Fig. 2 Sample-based rarefaction curves rescaled by average abundance for arthropod species in forest (dashed-dotted line), edge-belt (dashed line) and grassland (line) respectively. Fitted dotted lines indicate 95% CI (from Monte Carlo randomizations) of species richness.

Fig. 3 (a) Number of epigeic arthropod species and (b) number of individuals collected in pitfall samples across all grassland (-75 m) to forest (+75 m) transects in the central Apennine mountains, Italy, in 2009, for ground beetles (Carabidae, black), spiders (Araneae, dark gray) and centipedes (Chilopoda, light gray) and combined totals (line).

Fig. 4 Non-metric multi-dimensional scaling (NMDS) ordinations of arthropod community structure across forest (triangles), edge belt (4, 5, 6) and grassland (circles) based on the presence-absence (a) and fourth-root transformed abundance (b) data. Stress values (≤ 0.15) indicate a good 2-dimensional representation of the multivariate data.

Fig. 5 Patterns of the number of forest and grassland indicator species (from indicator species analysis, ISA) (proportion of maximum) changes across the 150 m transects (from plot 1 to 9, see Fig. 1c), where 5* is the plot on the edge.

TABLES

Table 1 Results of PERMANOVA tests (n=9,999 permutations) on the effects of 'habitat' (fixed factor), 'site' (random factor), and 'transect' (random factor nested within site), on the structure of ground-dwelling arthropod assemblages collected with pitfall traps along transects at the forest-grassland ecotone in the central Apennine mountains, Italy. The analysis is based on Bray–Curtis dissimilarities of fourth-root transformed abundances.

Source of variability	df	MS	Pseudo-F	p (perm)
habitat (ha)	2	54701	15.061	0.001
site (si)	5	7623.7	4.7818	0.001
transect (si)	6	1594.3	0.95855	0.566
ha x si	10	3632.1	2.2351	0.001
transect (si) x ha	12	1625	0.97699	0.559
Res	72	1663.3		

Table 2 Estimates (and 95% bootstrapped CI) of edge effect parameters from a logistic fit of indicator species richness and abundance for forest and grassland-associated indicator species. Abundance of habitat indicators were previously fourth-root transformed in order to down-weight the effects of dominant species. The "midpoint" is the point across the transect where the edge effect is more intense (i.e., point of greatest change, local maximum of the first derivatives of the fitted model). The "extent of edge zone" is edge effect's spatial range in both of the adjacent habitats (identified by local maximum and minimum of the second derivatives of the fitted model). The "depth of edge influence" is that portion of the edge zone falling within a single habitat (focal habitat or the alternate matrix habitat). Finally, the "magnitude of edge effect", ranging between 0 (no edge effect) and 1 (maximum edge effect), is the difference between the maximum and minimum values of the standardized response variable. The midpoint and depth of edge influence are measured as the distance in meters from the edge; negative edge distances are inside the matrix, positive edge distances are in the habitat.

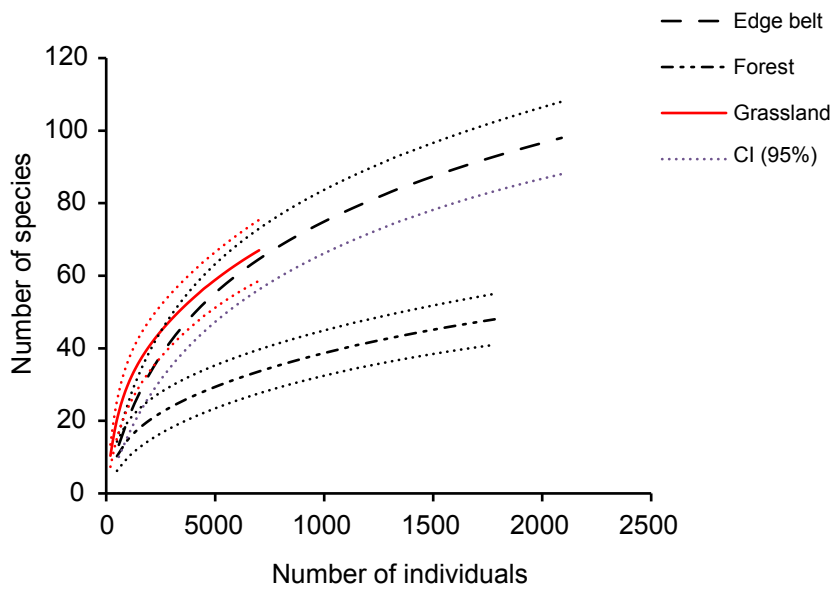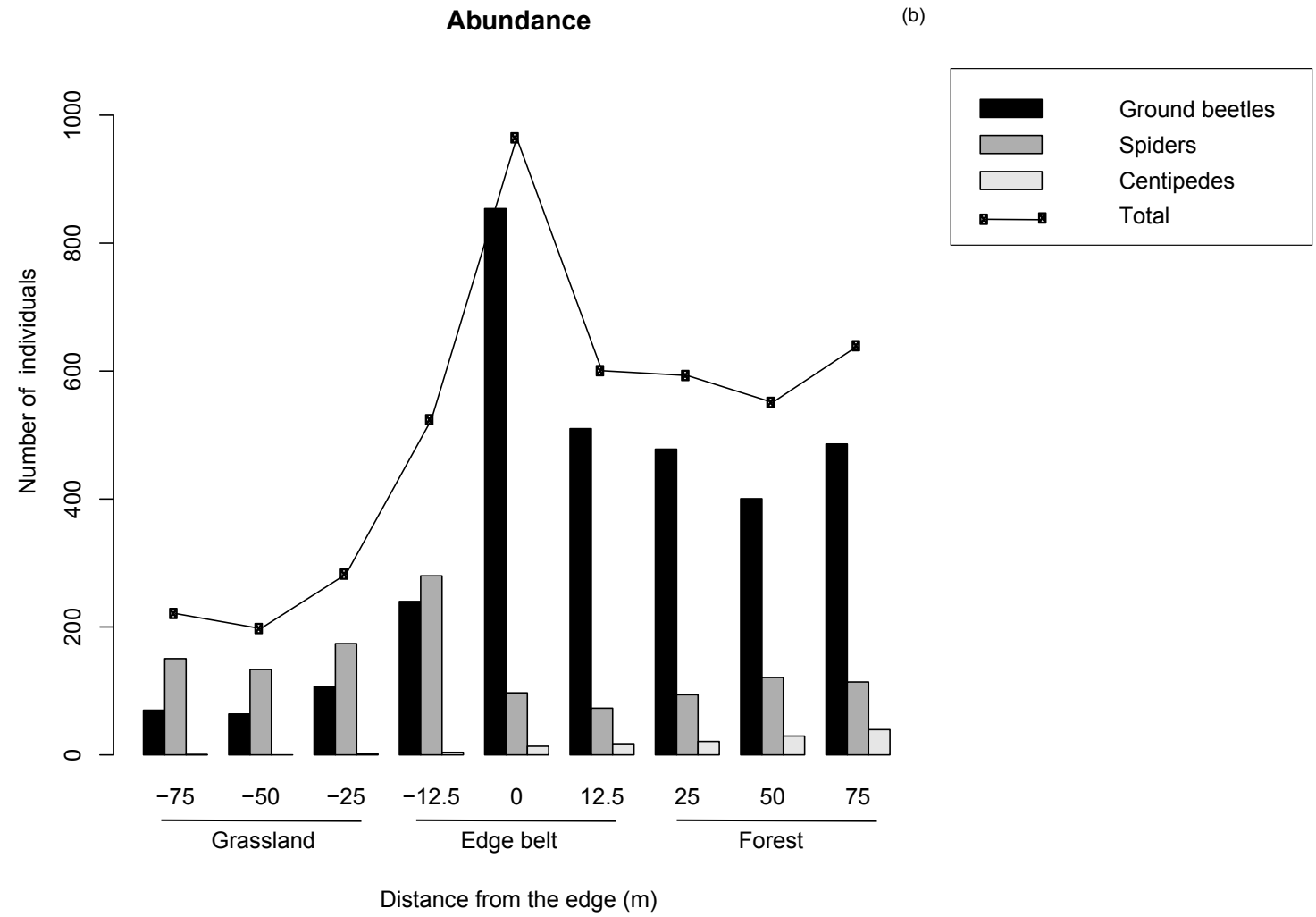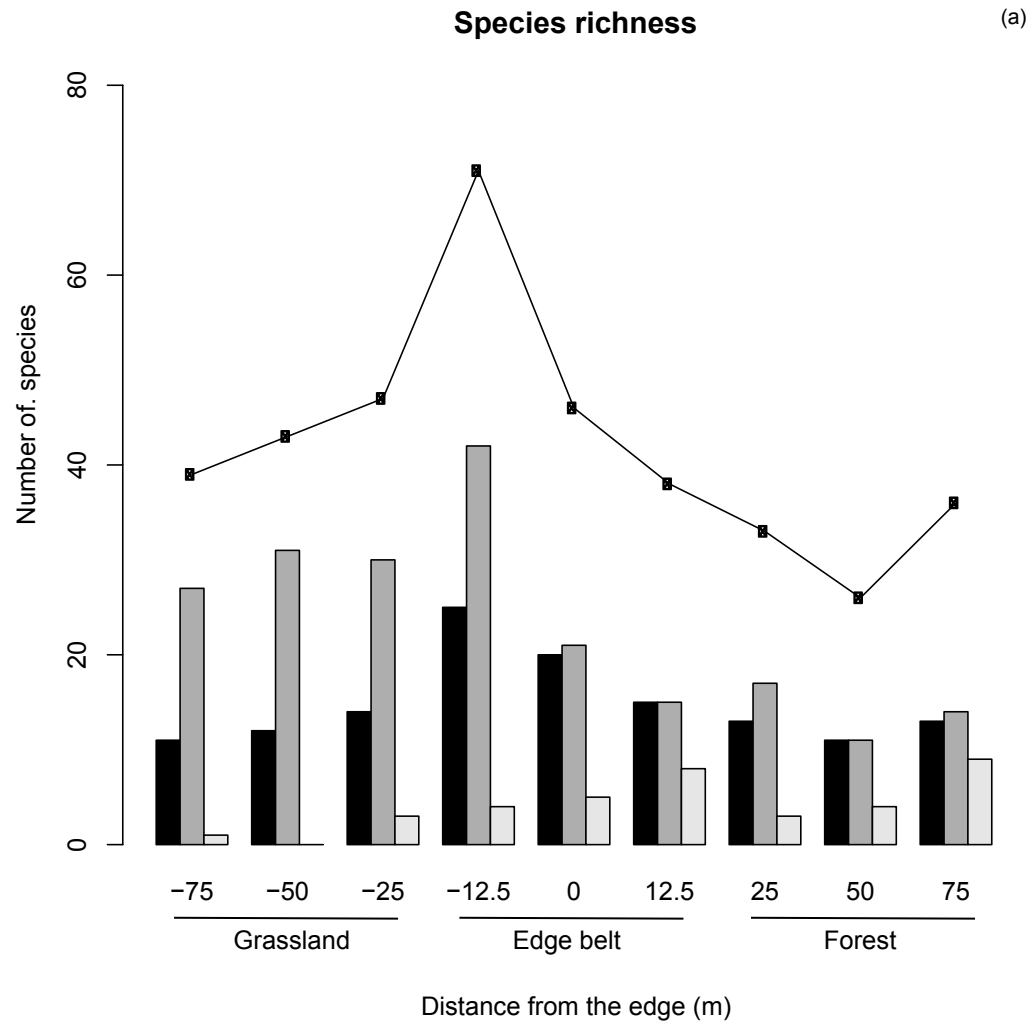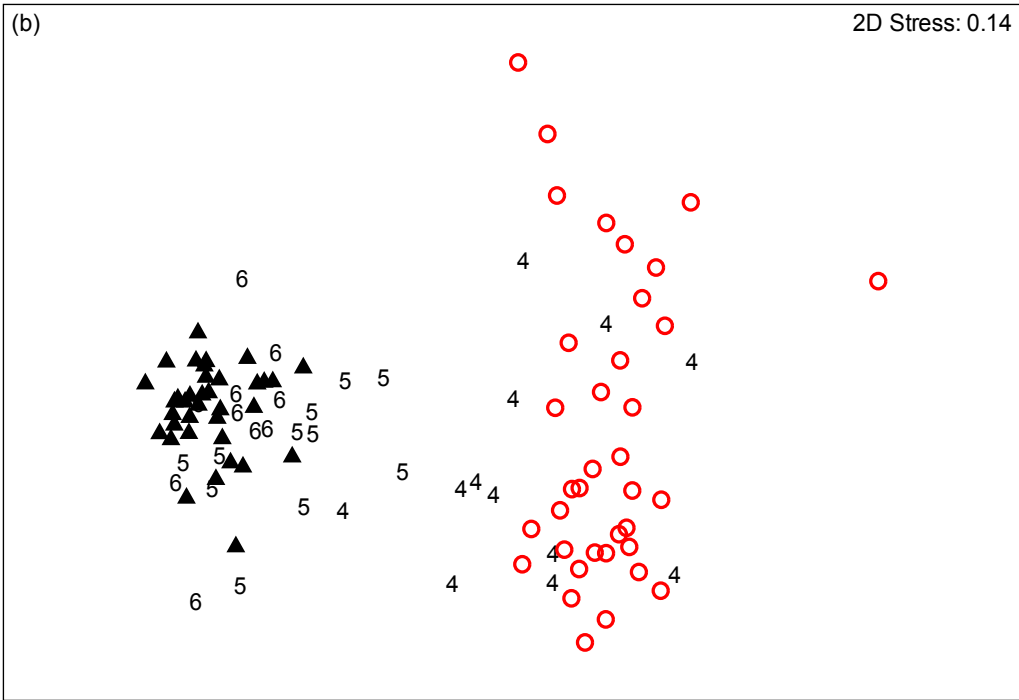| Response variable | Midpoint (m) | Depth of edge influence (m) | | Strength of edge effect | |
		Habitat	Matrix	Extent of edge zone (m)	Magnitude
Richness of grassland indicators	6 (4,9)	10 (6,15)	0 (0,0)	8 (0,15)	1 (1,1)
Richness of forest indicators	-5 (-8,-2)	4 (0,8)	-13 (-19,-8)	17 (8,27)	1 (1,1)
Abundance of grassland indicators	5 (3,8)	8 (6,13)	0 (0,0)	6 (2,13)	1 (1,1)
Abundance of forest indicators	-2 (-5,1)	8 (4,13)	-11 (-15,-8)	19 (12,28)	1 (1,1)

Fig. 2

Fig. 3

(a) **Species richness** — Number of species vs. Distance from the edge (m); grouped by Grassland (−75, −50, −25), Edge belt (−12.5, 0, 12.5), and Forest (25, 50, 75).

(b) **Abundance** — Number of individuals vs. Distance from the edge (m); grouped by Grassland (−75, −50, −25), Edge belt (−12.5, 0, 12.5), and Forest (25, 50, 75).

Legend: Ground beetles, Spiders, Centipedes, Total.

Fig. 4

Fig. 5