Biodiversity response to land use change across scales

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Dedico as minhas mainhas e a meu painho

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Summary

Farmland abandonment and the accompanying natural succession are largely perceived as unwanted (amongst many European conservationists) due to alleged negative effects on biodiversity levels. In this context, it is important to understand how diversity components (alpha, beta and gamma diversity) and species abundance distributions patterns change in habitats on an ecological succession gradient, from extensively managed meadows over scrub-encroached sites to native woodland. For that, macro-moths were light-trapped at 84 fixed circular sampling sites arranged in a nested design within the National Park of Peneda-Gerês, NW-Portugal. This area has undergone a rural exodus since the 1950's, which has increased the turnover of agricultural fields to shrub and forest. In total, 22825 macro-moth individuals belonging to 378 species were collected.

The aims of this thesis are to address the following questions: (chapter 2) how is species richness affected by the habitat amount and landscape configuration (patch size and isolation)? (chapter 3) how does beta diversity vary across scales in different land-uses? And, (chapter 4) how does species abundance change across spatial scale and how can species traits shape the spatial distribution?

Chapter 2 of this thesis shows that habitat amount predicts species richness in multi-habitat landscapes better than do patch size and isolation. Specifically, species richness of forest and meadow macro-moths is impact to a greater extent by forest and meadow habitat amount, respectively, than by patch size and isolation. As such, these results provide evidence supporting the habitat amount hypothesis, which revises the application of island biogeography and metapopulation theory to conservation ecology.

Chapter 3 of this thesis shows that alpha, beta and gamma diversity indicate that farmland abandonment is likely to positively affect the diversity of all species

together as well as the diversity of the forest species alone. However, farmland abandonment likely negatively impact the diversity of non-forest species. Moreover, the results also show that spatial habitat heterogeneity is important to maintain macro-moth diversity, especially for rare non-forest and specialist species for different habitat types. In summary, landscape-scale farmland abandonment can lead to multi-habitat landscapes characterised by high levels of macro-moth diversity, which may translate into a better functioning and more resilient ecosystem than the replaced agricultural system.

Chapter 4 of this thesis shows that the shape of species abundance distributions changes across spatial scale, depending on some species traits. Tchebichef moments predicted the number of species in communities which follow log-normal SADs.

Summing up, this thesis offers new insights about the effects of land-use change on biodiversity, in particular the effect of farmland abandonment. The results show that, in order to maintain high biodiversity in a landscape, it is important to take into account the habitat amount and also the surrounding matrix as well as maintaining a sufficient spatial heterogeneity of the habitats within a landscape. In addition, it suggests that all gradients of farmland abandonment have conservation value for macro-moths, since specialist species were found in all the different habitats. Similarly, it is important to consider multiple scales and species traits for effective macro-moth conservation since each scale or trait might affect macro-moth community composition in different ways.

Chapter 1

Introduction

Land use change and biodiversity

Overall, land-use change has negatively impacted ecological communities (Foley *et al.* 2005). In fact, it has been pinpointed as one of the main factors of global biodiversity change (Pereira *et al.* 2012), reducing species diversity and shifting community composition at various spatial scales and hence modifying species interactions within ecological communities too (Warren *et al.* 2001; Karp *et al.* 2012; Newbold *et al.* 2015). But land-use change is not always negative for biodiversity, as it can also include ecological restoration from intense human land-use back to a more natural state (Clewell & Aronson 2013).

Here, I focus on farmland abandonment which is a type of land-use change whose effects on biodiversity are currently not resolved. On the one hand, abandonment is being perceived as a threat to biodiversity (e.g. Benayas *et al.* 2007; Van Swaay *et al.* 2010; Fischer *et al.* 2012), whilst on the other hand abandonment is being perceived as an opportunity for biodiversity via passive and/or active ecological restoration (Bowen *et al.* 2007; Navarro & Pereira 2012). Several studies described how farmland abandonment affected diversity in different taxonomic groups. Plieninger *et al.* (2014) performed a meta-analysis about the effects of land abandonment on plant and animal species richness and abundance in the Mediterranean Basin. They found that species richness and abundance increased with land abandonment, although their results varied according to the variable. Some studies about impacts of farmland abandonment on moth community structure and population dynamics found that species richness might be affected by land-use change (Conrad *et al.* 2004; Kivinen *et al.* 2006).

In Europe, more than 95% of known lepidopteran species are moths. The total abundance of British macro-moths declined by 28% from 1968 to 2007, with 37% of the 337 species decreasing by at least 50% (Fox *et al.* 2013). Nonetheless, up until now, the effects of farmland abandonment on macro-moth diversity are unclear. Here, I used moths in order to assess the effect of farmland abandonment on biodiversity. Moths are a species-rich group which reacts rapidly to environmental change besides contributing to diversity and ecosystem functioning, such as food resources (Wilson *et al.* 1999), pollinators (Proctor *et al.* 1996) and nutrient recyclers (Merckx *et al.* 2013).

This thesis aims to address the following questions: 1) how is species richness affected by the habitat amount and landscape configuration (patch size and isolation)? 2) how beta diversity varies across scales in different land-uses? And, 3) how species abundance change across spatial scale and how species traits can shape the spatial distribution?

Diversity components: alpha, beta and gamma diversity

Whittaker (1960) defined alpha diversity as the number of species (i.e. species richness) of a given sample and gamma diversity as the species richness of an entire region (also known as the species pool). Beta diversity, i.e. the spatial change in species composition, is considered a key concept to understand how the local community assembly (alpha diversity) is linked to the regional species pool (gamma diversity) (Whittaker 1960). For example, high beta diversity can compensate for low alpha diversity in a region of high gamma diversity (Magurran 2004). However, alpha and gamma diversity can be measured using various metrics such as species richness, exponential of Shannon index, reciprocal of Simpson's index and reciprocal of Berger-Parker index (Hill 1973; Jost 2007) as well as the reciprocal of Simpson evenness (Smith & Wilson 1996). Those indices are all based on the same generalized entropy formula, differing only by an exponent q that determines sensitivity to species relative abundances (Hill 1973). Figure 1 shows in a simple way that diversity values depend on the diversity measure used. For further information about other alpha and gamma diversity indices, see Magurran (2004).

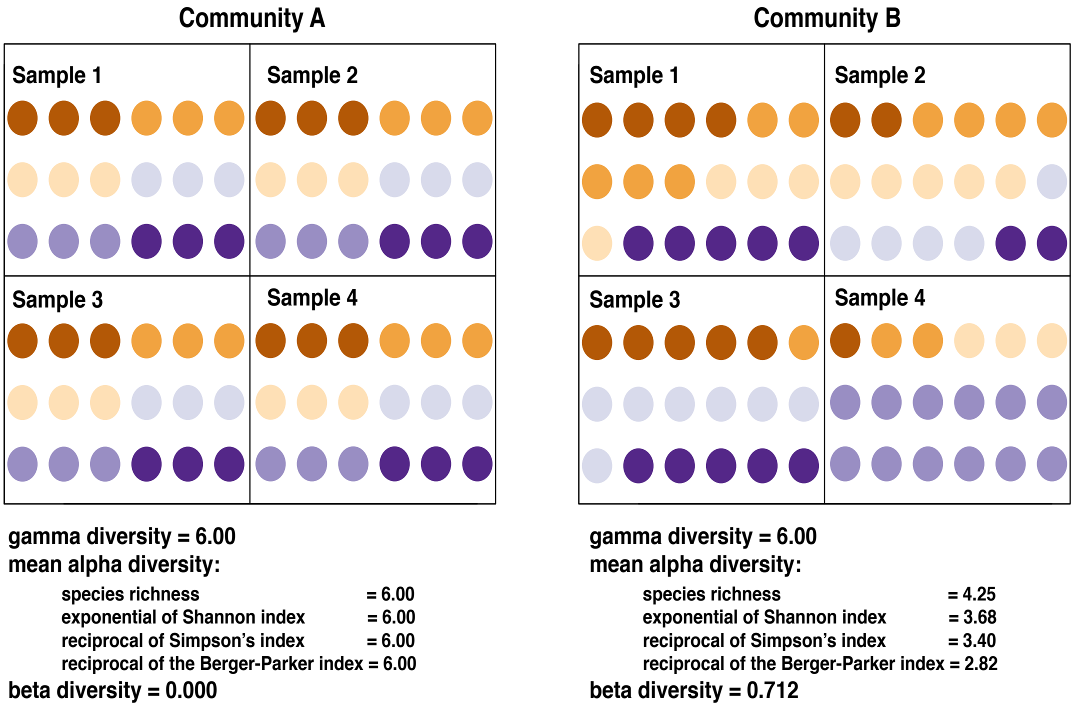

Figure 1: Gamma diversity measured by species richness, mean alpha diversity measured by species richness, exponential of Shannon index, reciprocal of Simpson's index and reciprocal of Berger-Parker index, and beta diversity was calculated by Jaccard dissimilarity. Species richness and abundance in both communities are identical – both have 6 species and 72 individuals. However, individuals are more evenly distributed among samples within the community A than among samples within the community B.

Beta diversity can also be separated into variation in species composition (change in species composition within the dataset) and species turnover (change in species composition along a spatial, temporal or environmental gradient) (Anderson *et al.* 2011). Similar to alpha diversity, there are many different ways of quantifying beta diversity. Here, I use three metrics: mean Jaccard and Sorensen dissimilarity and turnover rate. For further information about other beta diversity indices, see Anderson *et al.* (2011) and Tuomisto (2010a, b).

In addition, beta diversity is not independent of alpha, so it is difficult to compare alpha diversities of different habitats (Tuomisto 2010a). In order to create beta diversity independent of alpha diversity, recent studies have used beta diversity associated with null models to disentangle sampling effects from beta diversity that results from ecological processes (Karp *et al.* 2012; Mori *et al.* 2013; Myers *et al.* 2015).

Species abundance distribution

Species-abundance distribution (SAD) describes the relationship between the number of observed species as a function of their observed abundance. As such, SADs depict the relative abundance of species within a community, a central concept in ecology, and essential for theories on biodiversity and biogeography (McGill *et al.* 2007; Matthews & Whittaker 2014). Arising from this theoretical context, analyses of SADs that enable identifying patterns in the commonness and rarity of species can be useful too in applied ecology and biodiversity management (Matthews & Whittaker 2015). As such, both theoretical and empirical studies have examined the influence of several environmental and biological variables on SADs, such as elevational and latitudinal gradients, niche differentiation, dispersal, and ecological disturbance (Whittaker 1975; Hubbell 1979, 2001; Magurran 2004; Matthews & Whittaker 2015).

There are two graphical methods to represent the SADs: rank abundance plot

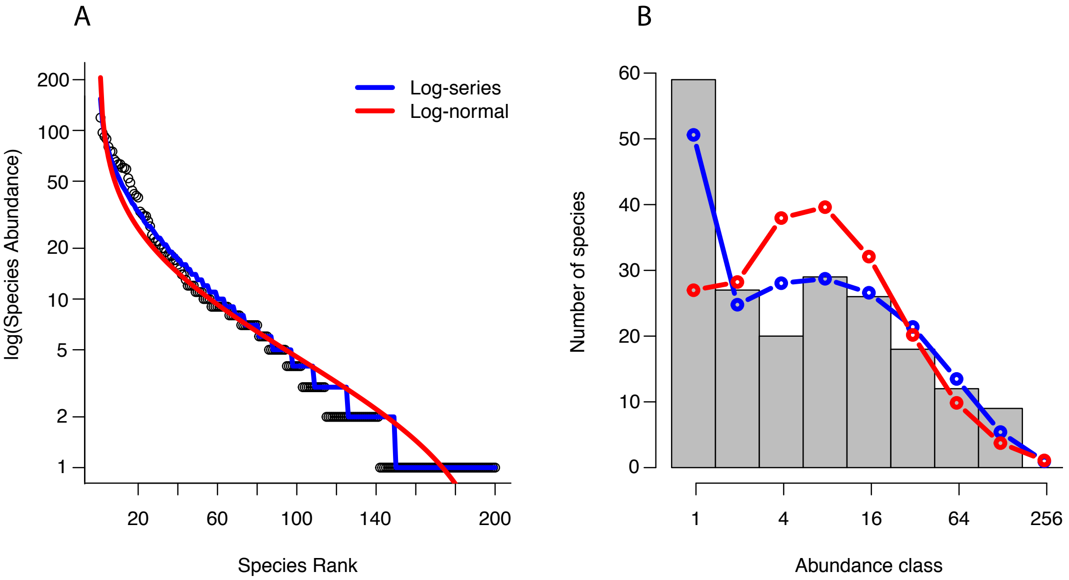

Figure 2: Graphical methods of representing the species abundances distribution models: a) rank-abundance plot and b) histograms. Blue and red lines represent log-series and log-normal distributions, respectively.

and histogram. First method was developed by Whittaker (1965) and consists to plot the abundance (untransformed or log-transformed) against rank order, where rank one corresponds to the species with the highest abundance and last rank corresponds to the species with the lowest abundance (Figure 2A). Another method uses histogram where the species abundances are transformed (Figure 2B). There are various ways to transformed the data; here, I used Preston transformation (Preston 1948).

Recently, McGill *et al.* (2007) list 27 different species-abundance models dividing into five different groups: purely statistical, branching processes, population dynamics, niche partitioning and spatial distribution. Here, I use Ulrich *et al.* (2016) framework which grouped SADs into two classes: the log-series and the lognormal. The log-series shows most individuals belong to a few species and most species are represented by a few individuals (Figure 2B), although the log-normal shows a high number of species with intermediate abundance and smaller numbers of very rare and abundant species (Magurran 2004). Theoretically, SADs should follow log-normal, if the communities are stable and influenced by ecological processes (i.e. intra- and inter-specific interactions), or log-series if the communities are unstable and influenced by random processes (e.g. dispersal and immigration) (MacArthur 1957; Ulrich *et al.* 2010).

Chapter overview

Chapter 2 addresses the theory of island biogeography, the habitat amount hypothesis and countryside biogeography. Species-area relationship (as concept from the island biogeography) has been applied to estimate the number of species in fragmented habitats, where patches of specific habitat are islands surrounded by inhospitable habitats (Levins 1969; Hanski 1982). However, this theory was recently put into check by the habitat amount hypothesis and countryside biogeography (Pereira & Daily 2006; Fahrig 2013) which suggests that the amount of habitat in the surrounding landscape would be a better variable to estimate the species richness. We tested whether the habitat amount hypothesis and countryside biogeography explains species richness patterns better than the species-area relationship.

Chapter 3 focuses on how macro-moth diversity changes across spatial scale. We checked how alpha diversity is linked to gamma diversity through beta diversity which measures how species composition changes across spatial scale. Here, in order to understand the consequences of farmland abandonment, we compared these diversities amongst the three habitat types which represent ecological stages after farmland abandonment: meadow, shrub and forest. Finally, separated analyses include a comparison between forest and non-forest species.

Chapter 4 addresses the species abundance distributions (SAD) and how they change across spatial scale. SAD describes the abundance of all observed species within an ecological community, and a central concept in ecology. In addition, analyses of SADs are able to identify patterns in the commonness and rarity of species which can be useful in applied ecology and biodiversity management. Here, we focused on how regional and local species abundance distributions are related. we used log-normal and log-series distribution in order to characterize the shape of SADs. Moreover, we used family and three other species traits (body size, host-plant specialisation, and hots-plant type) to verify how these species traits affect the species distribution at local and regional scale. Additionally, we also verify the relationship between moments and spatial area and how Tchebichef moments and polynomials might be a good tool to extrapolate the SADs obtained from the local scale to the regional scale.

In chapter 5, I synthesized and discussed the main results from the previous chapters.

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Chapter 2

Habitat amount, not patch size or isolation, drives species richness of macro-moth communities in countryside landscapes

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Abstract

Species richness in fragmented habitats is being estimated using patch size and isolation concepts from island biogeography. Recently, the habitat amount hypothesis and countryside biogeography questioned this approach. They propose that the total amount of habitat in the landscape surrounding a site is a better predictor of species richness, as it better reflects available resources. Using a dataset of macro-moth species in countryside landscapes with multiple habitats, we test and demonstrate that species richness patterns of sampling sites are better explained by the effect of the total amount of habitat in a local neighbourhood than by a combination of patch size and patch isolation effects. Further studies will be needed to confirm the generality of the habitat amount hypothesis, but we suggest that evidence is mounting to revise the application of island biogeography and metapopulation theory to conservation ecology.

Keywords: Habitat patch concept; Lepidoptera; Farmland abandonment; Countryside SAR; Multi-scale approach; Habitat fragmentation; Natural succession; Metapopulation theory; Habitat amount hypothesis; Multi-habitat landscape

Introduction

The theory of island biogeography describes the number of species on an island as a function of the size of the island and its distance to the mainland (i.e. its isolation) (MacArthur & Wilson 1963; 1967). This concept was later adopted by Levins (1969) and Hanski (1982) to create the habitat patch concept, where patch size and isolation correspond to island size and isolation. Recently, Fahrig (2013) called into question the assumption that habitat patches are natural units of measurement for species richness, with distinct effects of both habitat patch size and isolation. Fahrig argued that both these effects are driven by a single 'sample area effect', and she suggested instead that the sum of the amount of habitat in the surrounding landscape – at relevant spatial scales – would be a better indicator for predicting species richness (i.e. the habitat amount hypothesis). Actually, one such 'sample area effect' is widely known as the continental species-area relationship (SAR), where the number of species in a sample increases with increasing total sample area (MacArthur & Wilson 1967; Rosenzweig 1995).

SAR models have often been used to assess and predict the impacts of habitat loss and fragmentation on biotic communities (Pimm *et al.* 1995) assuming habitat patches are islands surrounded by inhospitable farmland or other human-dominated habitats. However, the classic SAR or power model (Arrhenius 1921) is a single-habitat model, which can only take into account one habitat type at a time (Triantis *et al.* 2003). Pereira & Daily (2006) proposed a method for studying patterns of species richness in multi-habitat landscapes: the 'countryside' SAR. This model is not only able to account for different types of habitat in the landscape but it also takes into consideration the differential use of habitats by different groups of species. As such, it has become a useful tool for conservation biology, especially in human modified landscapes (Proença & Pereira 2013). The countryside SAR model provides an interesting framework for the habitat amount hypothesis as it assumes that what drives species richness are the amount of resources available in a given area. Species with higher affinity for a given habitat have higher density of resources available in that habitat (see also Dennis *et al.* 2013).

As different species respond to habitat amount at different spatial scales, it is important to ensure that the spatial scale of the sampled area is appropriate for the taxonomic group under consideration (Fahrig 2013). Some multi-scale methods have been proposed to pin-point the scales at which species richness is expected to respond most strongly to the habitat amount surrounding the sampling site (Holland *et al.* 2004; Jackson & Fahrig 2012, 2015). This is important, as the use of an inappropriate spatial scale may make it impossible to capture the affinity between the species group under consideration and the amount of habitat, which would lead to erroneous conclusions (Holland *et al.* 2005).

Here, we focus on the taxonomically diverse and ecologically well-known group of macro-moths (Lepidoptera), which exhibits rapid response to environmental change (Merckx *et al.* 2013). Macro-moths were collected using a nested sampling design in three countryside landscapes with variable habitat composition, comprising a total of 84 equally sized sites. Our aim is to test whether species richness patterns of local communities are best explained by the effect of the total amount of habitat within the local landscape (i.e. by a simple 'sample area effect'), or instead by a combination of patch size and patch isolation effects. If the habitat amount hypothesis is supported, we predict that (i) species richness will be more strongly related to habitat amount than to patch size and isolation, and (ii) when habitat amount in the local landscape is taken into consideration, the combination of patch size and isolation will no longer have an effect on species richness. Complementary to this, we test whether the countryside SAR explains species richness patterns better than the classic SAR. We predict for species groups that the effective area of habitat, consisting of the sum area of different habitats weighted by the resource density, is a better measure of species richness, as projected by the countryside SAR.

Material and Methods

Study sites

The study was conducted in the Castro Laboreiro area (ca. 42° 2' N, 8° 10' W) within the Peneda-Gerês National Park, NW Portugal (Fig. 3). Within our study area (49.7 km^2; altitude: 750-1155 MASL), shrubland (78.4%) is the dominant habitat, followed by forest (10.5%), agricultural land (9.8%) and urban area (1.3%). The mountainous region of the National Park (altitude: 300-1340 m) lies at a transitional zone between the Atlantic and Mediterranean biogeographic zones.

Sampling design

Macro-moths were light-trapped in two consecutive years (2011 and 2012), across three landscapes (1.64 km^2 each) representing a natural succession gradient, from an agricultural landscape (i.e. meadow-dominated), over a mid-successional landscape (i.e. shrub-dominated) to a landscapes with climax vegetation (i.e. forest dominated) (Fig. 3). For each landscape, 28 fixed circular sampling sites of 300 m^2 were set up using a nested design (Proença & Pereira 2013) (Fig. 3). Sampling sites were labelled according to their habitat type: $n_{meadow} = 24$, $n_{shrub} = 39$ and $n_{forest} = 21$. In total, these 84 fixed sampling sites were each sampled three times a year during peak flight season (May 10 till September 30). For each sampling site, data from the six sampling sessions were lumped.

Although the degree by which macro-moths are attracted to light is known to differ among families, the used light-trap type (Heath pattern 6W actinic; Heath 1965) has an effective attraction radius of typically 10 m, with only very low percentages of moths drawn in from further away (Merckx & Slade 2014). This

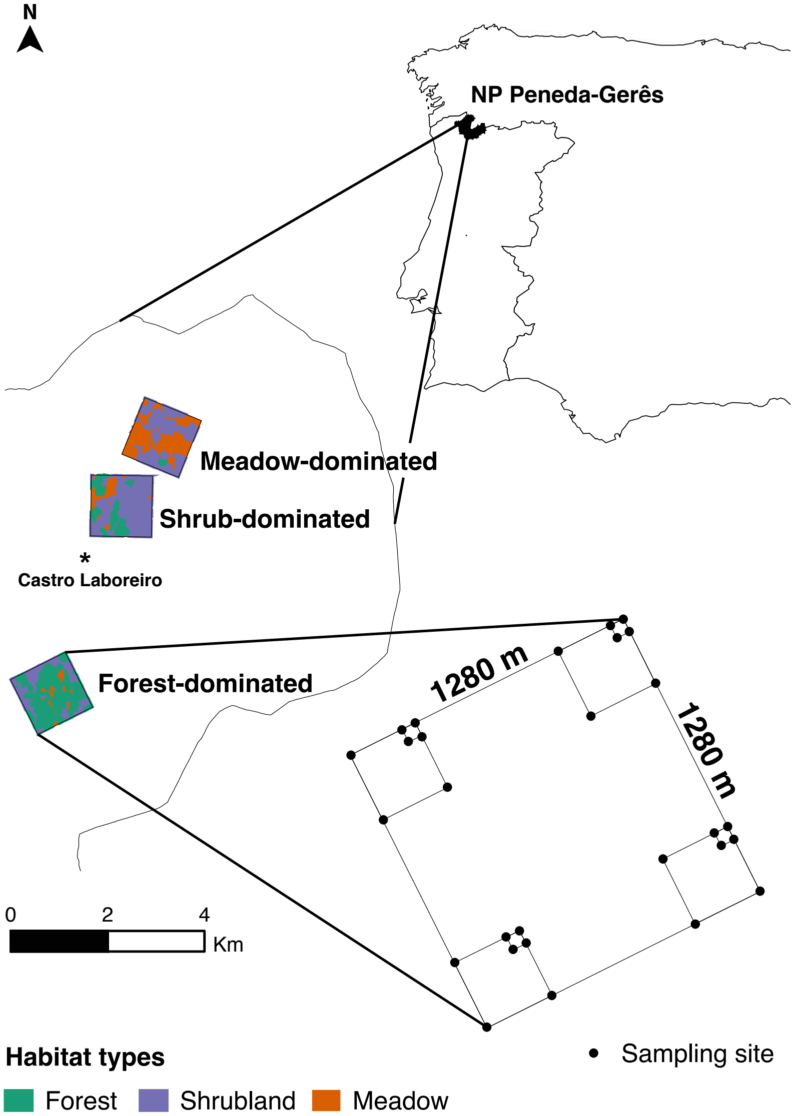

Figure 3: Study area and sampling design. Map of study area and sampling sites near the town of Castro Laboreiro in Peneda-Gerês National Park, NW Portugal. 84 fixed light-trap sampling sites were part of a nested sampling design covering three study landscapes that represented a natural succession gradient.

attraction radius hence translates in a local sampling area of ca. 300 m^2. Moreover, the possible bias, due to intrinsic differences in flight-to-light behaviour among individuals, species and families, is identical for each of the 84 sites, as they were all sampled with identical light-traps. As such, although local absolute light-trap samples are biased with respect to the local community, the observed relative differences among trap sites are not biased.

Sampling was only conducted during suitable weather conditions, with light traps operated from dusk until dawn. At dawn, macro-moths in and on the trap were enumerated and identified to species-level. Specimens which could not be accurately determined on the spot were collected and identified later on, sometimes with the help of another expert.

Species were grouped into forest, shrub or meadow species according to in which habitat they displayed the highest relative abundance, corrected for the sampled amount of habitat types. Nonetheless, for species with low observed abundance (N $\leq$ 5), the classification was instead based on literature and expert knowledge, with 23 of the 378 sampled species eventually not retained for analyses as they could not be clearly classified in one of the three groups. As such, 205 species were classified as forest species, 84 as shrub species, and 66 as meadow species (see Table 3 in Supporting Information).

SAR models

The classic SAR was fitted using the power model:

$$S = cA^z \tag{1}$$

where S is the number of species, A is the sampled area, and c and z are parameters that depend on the taxonomic group and sampling design. The countryside SAR model (Pereira & Daily 2006) builds on this power model but accounts for the differential use of habitats by species. Here, the richness of forest and meadow species is estimated by:

$$S_i = c_i \left(\sum_j h_{ij} A_j \right)^{z_i} \tag{2}$$

where S_i is the number of species in group i, h_{ij} is the affinity of the group i to habitat j, and A_j is the area covered by the habitat j. Finally, the total number of species in the landscape is given by the sum of the number of species in each group:

$$S = \sum_i S_i. \tag{3}$$

The fit of both models to the data was evaluated using corrected Akaike's Information Criteria (AICc) and the coefficient of determination (R^2), which indicates the proportion of the variance explained by the (effective) area. In order to verify the effect of the effective areas on each species group i, the area of habitat A_j was multiplied by the affinity of the species group to habitat h_{ij}. Areas, effective areas and species richness were log-transformed before model analyses.

Scale of effect

In order to test the effect of landscape composition on macro-moth species richness, we used a GIS (ArcGIS, vs. 10.2.1, ESRI, Redlands, CA) to calculate the area of forest, shrub and meadow within concentric buffers around each sampling site. Land-use covers were obtained by manually digitising aerial photographs (IGP 2007; year 2000; the minimum mapping unit was around 10000 m^2) into the following classes: forest, short shrub, tall shrub, meadow and urban. Because the most appropriate spatial scale for the local landscape was unknown, we tested multiple buffers (i.e. 20, 40, 80, 160, and 320 m radii), with 320 m as maximum to prevent substantial overlap of the circles at larger scales.

For each buffer radius, Pearson's correlation coefficients were calculated between the amount of habitat (forest, shrub and meadow) and species richness of (forest, shrub and meadow) macro-moths. Then, Pearson's correlation coefficients were plotted against their respective radii (Ricketts *et al.* 2001; Horner-Devine *et al.* 2003; Eigenbrod *et al.* 2008). If there is an effect of habitat amount on species richness, it is expected that the relation between species richness and habitat amount should increase until the best spatial scale (i.e. scale of effect) and then decrease again (Fahrig 2013).

Landscape configuration was also measured: for each sampling site, we estimated both the patch size into which the sampling site was inserted as well as the distance to the nearest neighbouring patch of the same habitat type.

Autocovariate Models

In order to evaluate the effect of (i) habitat amount (forest, shrub and meadow), (ii) patch size, and (iii) distance to the nearest patch (and their interactions of (ii) and (iii) with habitat amount), we used the Information-Theoretic (IT) approach and autocovariate models in order to account for potential spatial autocorrelation (Dormann *et al.* 2007; Bolker *et al.* 2009). The IT-approach is used to simultaneously compare several competing hypotheses in order to identify the confidence set of models based on Akaike's information criterion (AICc) (Burnham & Anderson 2002). In order to avoid collinearity among explanatory variables, only combinations of fixed effects with up to two-way interactions were used. After that, we ranked the models using AICc to select the best model, and model differences were calculated so as to assess the relative strength of support for each model (Burnham & Anderson 2002). We applied this approach separately for forest and meadow habitat with and no spatial autocorrelation.

All statistical analyses were performed in the statistical software environment R version 3.1.1 (R Core Team 2014), using the MuMIn (Bartoń 2015) package.

Results

SAR models

The AICc value for the countryside SAR model was considerably smaller than the value for the classic SAR model (Table 1), which shows that the former outperformed the latter. In the countryside SAR, the z-value was higher (+38%) for forest species than for meadow species (Table 1). This indicates that forest species have a higher spatial turnover than meadow moths. Similarly, the c-value was higher (+87%) for the forest group, which shows that, on average, there were more species in a forest than in meadow sampling units (300 m^2). Forest species showed a much stronger affinity towards shrub habitat than meadow species (Table 1).

Table 1: Fit output of both classic and countryside species-area relationship (SAR) models. Countryside SAR clearly outperforms the classic SAR, given its much smaller model-corrected Akaike's Information Criterion (AICc) value. *c* and *z* are model parameters that depend on the taxonomic group and the sampling design (Eqn 1 and 2), respectively; h_f, h_s and h_m represent the affinity of the species groups to forest, shrub and meadow habitat (Eqn 2), respectively.

Group	c	z	h_f	h_s	h_m	AICc
SAR	17.54	0.192	-	-	-	1072.89
cSAR$_{Forest}$	14.69	0.183	1	0.190	0.055	811.30
cSAR$_{Meadow}$	7.84	0.133	0.001	0.021	1	

The response of species richness to area (classic SAR) versus effective area (countryside SAR) differed. With regard to area *per se*, the relationships between forest species richness and total area as well as between meadow species and total area were statistically significant (Fig. 4). However, a much better fit was obtained when using effective areas instead of areas *per se*, with the increase in fit stronger for meadow ($\Delta R^2 = 0.28$) than for forest species ($\Delta R^2 = 0.10$) (Fig. 4).

Scale of effect

The range of correlation coefficients varied greatly depending on species group and habitat type. At all five spatial scales, species richness of forest macro-moths was positively correlated with the amount of forest habitat in the landscape surrounding the sample sites, and significantly so at intermediate radii scales (i.e. 80 and – most strongly so – 160 m) (Fig. 5A and 6A). By contrast, the species richness of shrub macro-moths was not significantly correlated with the amount of shrub habitat (Fig. 5B). Additionally, the species richness of meadow macro-moths was positively correlated with the amount of meadow habitat at spatial scales higher than 80 m, but only significantly so at the 320 m radius scale (Fig. 5C and 6B). Summarised, forest moth species richness was significantly correlated with forest habitat at the 160 m radius scale, whilst meadow moth species richness was significantly correlated with meadow habitat at the 320 m radius scale (Fig. 5). As a result, and for further analyses, we identified the 160 m radius as the scale which maximizes the relationship between species richness and forest habitat amount, and 320 m for meadow habitat amount.

Autocovariate models

Given these different 'scales of effect', we separated the autocovariate models into four groups: forest habitat at the 160 m radius scale for forest species (Table 2A), and meadow habitat at the 320 m radius scale for meadow species (Table 2B), with and without a spatial autocovariate.

Sampling sites surrounded by a higher amount of forest habitat within a 160 m radius were characterised by a higher number of forest species (top-ranked model: $\mathrm{Hab}_{for} = 17.62$; df = 4; $P < 0.05$) (Table 2A). This top-ranked model, containing

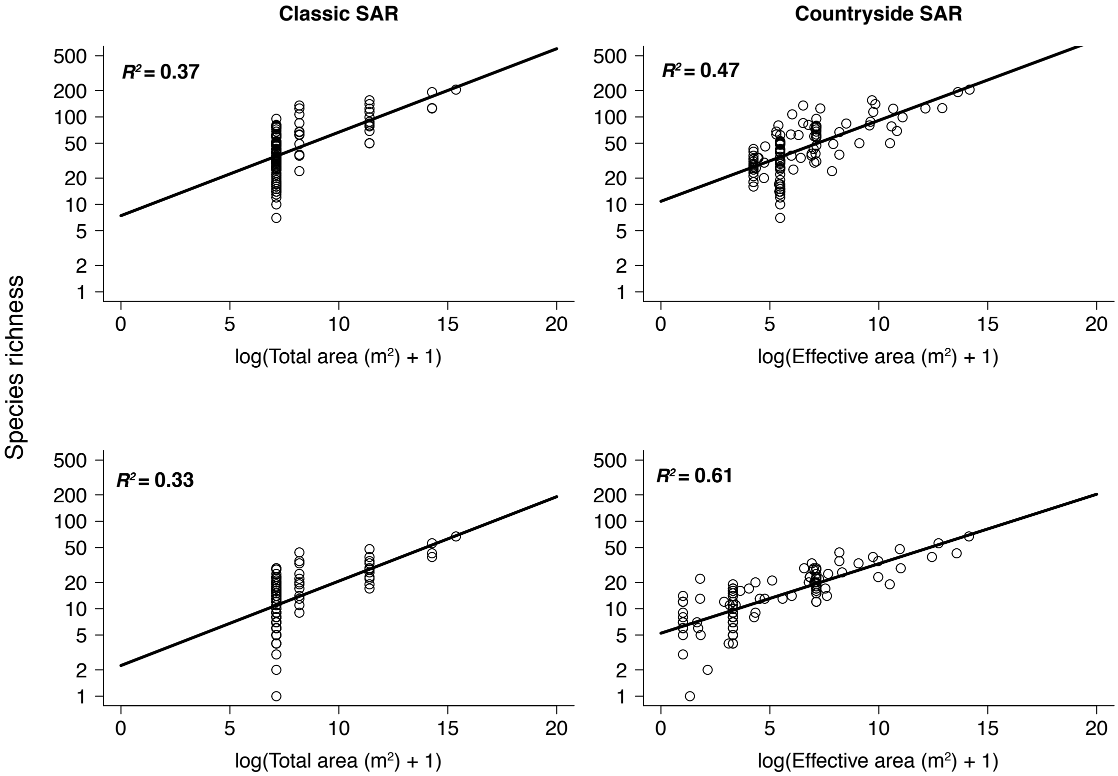

Figure 4: Classic and countryside species-area relationship (SAR) models. Effects of area on species richness of forest (top row) and meadow (bottom row) macro-moths following classic (left columns) versus countryside (right columns) SAR models. Countryside SAR models consistently provided a better fit than classic SAR models. R^2-values are given for each model. Bold values indicate significant ($P < 0.05$) relationships. Remark that both area and species richness are log-transformed.

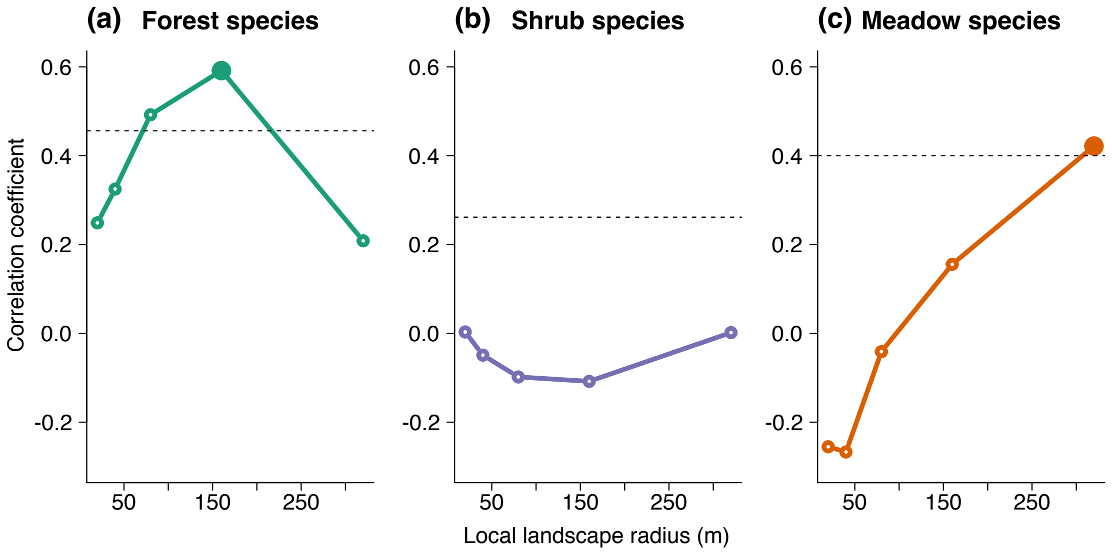

Figure 5: Multi-scale richness-habitat amount relationship. Correlation between the amount of habitat and species richness of (a) forest species, (b) shrub species and (c) meadow species, at five spatial scales for the local landscape (radii: 20, 40, 80, 160, 320 m). Each point represents a Pearson's correlation coefficient. Horizontal lines mark the critical value for significant correlation at $P = 0.05$. Significant relationships for the forest habitat were strongest at the 160 m radius scale, whilst for the meadow habitat they were strongest at the 320 m radius. Hence, these radii, indicated by a large dot, were used for further analyses.

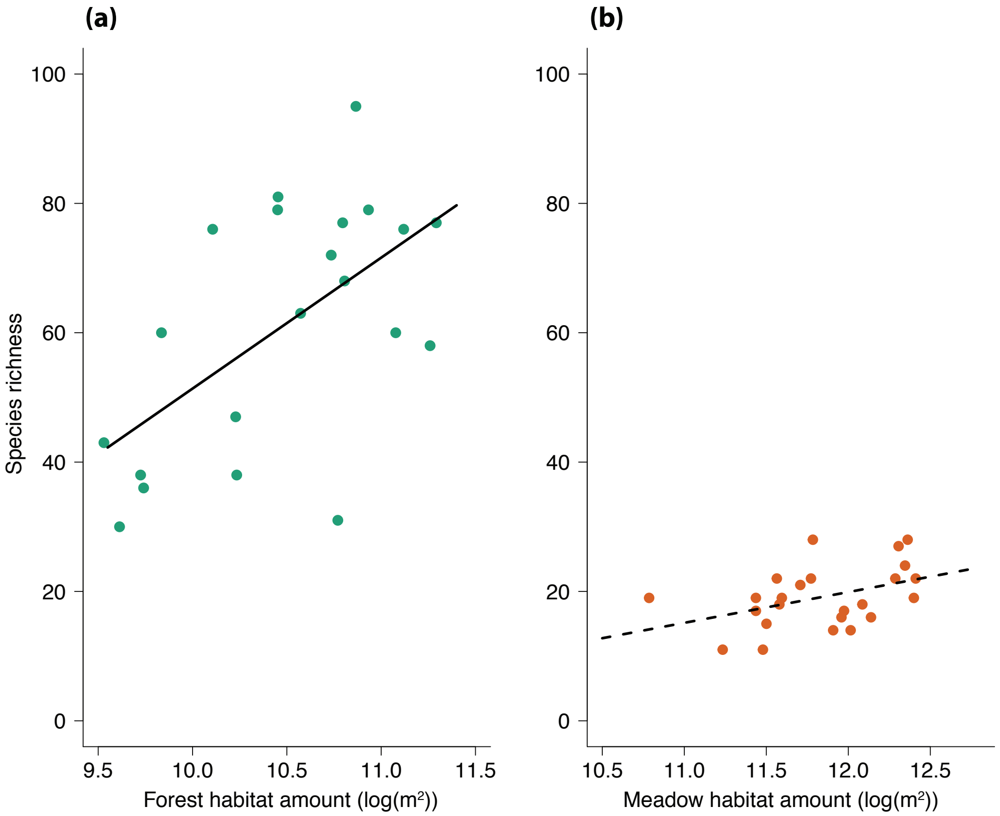

Figure 6: Scale of effect for forest and meadow habitat. (a) Relationship between the amount of (a) forest habitat (m^2) within an area with a radius of 160 m (see Fig. 5) around the sampling sites and species richness of forest (green dots and line) moths. (b) Relationship between the amount of meadow habitat (m^2) within an area with a radius of 320 m (see Fig. 5) around the sampling sites and species richness of meadow (orange dots and dashed line) moths. Remark that both area is log-transformed.

only forest habitat amount as a variable, was strongly supported (AICc = 184.2) in contrast with models additionally containing patch size and patch distance (i.e. AICc > 2) (Table 2A).

Meadow species richness increased, both for models with and without a spatial covariate, with increasing amount of meadow habitat surrounding the sampling site (Table 2B). Neither for forest nor for meadow species, patch size and patch distance were not significant ($P > 0.05$). Spatial autocorrelation did not greatly influence the analyses, except for meadow species in three models contending patch size and habitat amount.

Discussion

Our analyses demonstrate that habitat amount predicts species richness in multi-habitat landscapes better than do patch size and isolation. This suggests that both the habitat patch size and isolation effects are driven by a single underlying ‘sample area effect’ as suggested by Fahrig (2013). Specifically, we found that species richness of forest and meadow macro-moths is to a greater extent affected by forest and meadow habitat amount, respectively, than by patch size and isolation.

Recently, the relevance of the amount versus configuration of habitat for species richness has been discussed. Hanski (2015) challenged the habitat amount hypothesis, arguing that some of Fahrig (2013) considerations were based on a narrow perspective of the ‘local landscape’, which ignores important information on habitat configuration (e.g. fragmentation effects). In return, Fahrig (2015) draws attention to the need for rigorous testing of her hypothesis, before rejecting it prematurely. So far, to our knowledge, only two studies have tested, and rejected, the habitat amount hypothesis. Coudrain *et al.* (2014) explored the effects of habitat amount and isolation on host-parasitoid interactions (*in casu* solitary bees and wasps and their parasitoids), whilst Evju & Sverdrup-Thygeson (2016) did so

Table 2: Ranking and autocovariate model output following the Information-Theoretic approach of five statistical models explaining species richness (A) for forest species as a function of forest habitat amount (Hab) at the 160 m radius scale, patch size (Size), distance to nearest patch (Dist), and their interactions with habitat amount (Hab:Size and Hab:Dist), both with (A1) and without (A2) spatial autocorrelation (AS), and (B) for meadow species as a function of meadow habitat amount (Hab) at the 320 m radius scale, Size, Dist, Hab:Size, and Hab:Dist, both with (B1) and without (B2) AS. Both forest habitat at the 160 m radius scale and meadow habitat and 320 m radius scale were selected because the 'scale of effect' displayed the highest correlation at these spatial scales (see Fig. 5). Bold values indicate significant effects ($P \leq 0.05$). df represents the number of estimated parameters; AICc and ΔAICc represent the model-corrected Akaike's Information Criterion values and the difference in AICc with the top-ranked model, respectively. Models are ranked in descending order with reference to the AICc. For each group, only one model was retained in the confidence set of models as the second-best models had ΔAICc-values > 2. The best model of the forest habitat amount models (A) contains habitat amount whereas the best model of the meadow habitat amount models (B) contains habitat amount and spatial autocorrelation. Models are based on Dormann *et al.* (2007) and assess spatial autocorrelation by adding an extra variable (i.e. autocovariate), which is a distance-weighted function of neighbouring response values to the model's explanatory variables.

Rank	Variable*						df	AICc	ΔAICc
	Hab	Size	Hab:Size	Dist	Hab:Dist	AS(e^{-5})			
(A) Forest habitat amount at the 160 m radius scale									
(A1) Forest species - with spatial autocovariate									
1	**17.62**					1.926	4	184.2	0.00
2	16.31			0.08		-201.3	5	187.1	2.96
3	**19.66**	-3.17				2.900	5	187.2	3.04
4	181.90	125.5	-13.16			5.223	6	189.6	5.43
5	-4.38			-1.28	0.13	-15.93	6	190.6	6.45
(A2) Forest species - without spatial autocovariate									
1	**20.24**						3	181.4	0.00
2	**16.30**			0.08			4	183.6	2.23
3	**22.09**	-1.74					4	184.3	2.93
4	-4.42			-1.28	0.13		5	186.6	5.23
5	110.30	68.04	-7.07				5	187.3	5.87
(B) Meadow habitat amount at the 320 m radius scale									
(B1) Meadow species - with spatial autocovariate									
1	3.07					**5.322**	4	140.6	0.00
2	2.16	0.43				**5.809**	5	143.6	3.05
3	3.06			0.001		5.481	5	143.8	3.22
4	13.07			0.800	-0.07	4.588	6	144.6	4.07
5	-23.94	-24.80	2.16			**5.375**	6	145.4	4.82
(B2) Meadow species - without spatial autocovariate									
1	**15.92**			0.94	-0.08		5	143.8	0.00
2	**4.76**						3	144.0	0.21
3	4.16			-0.02			4	144.2	0.37
4	**6.29**	-0.87					4	146.1	2.34
5	-26.71	-32.3	2.70				5	147.0	3.24

*Intercepts of the models were omitted

for vascular plants in dry calcareous grasslands. However, in the first study, habitat amount may have failed to explain species richness because the authors did not verify whether, as recommended by Fahrig (2013), the species were associated to the specific habitat type, neither did they test the scale at which species respond to habitat amount. In the second study, the focal taxon is generally known to be rather insensitive to environmental change in surrounding environmental conditions, given the low mobility of vascular plants, a characteristic which is being reflected by their considerable extinction debt (Helm *et al.* 2006; Vellend *et al.* 2006).

In addition, our study shows that the countryside SAR outperformed the classic SAR. This corroborates earlier findings on other taxa: plants (Proença & Pereira 2013), birds (Guilherme & Pereira 2013), and amphibians, reptiles and passerine birds (Martins *et al.* 2014) in multi-habitat landscapes. Whist the classic SAR focuses only on the size and isolation of the habitat (MacArthur & Wilson 1967), the quality of the landscape matrix is nevertheless known to be able to influence species richness, as overly demonstrated (Kupfer *et al.* 2006; Prevedello & Vieira 2010). Unlike the classic SAR, the countryside SAR aims to draw attention to the effective amount and variety of habitats used by different species groups, facilitating the estimation of species richness in those habitats. Although the countryside SAR and habitat amount hypothesis both stress the idea that each species group uses available resources in the landscape, they use a different approach. While the countryside SAR explains how the number of species in a given region changes with habitat area (i.e. gamma and beta diversity), the habitat amount hypothesis explains the number of species in specific habitat types (i.e. alpha diversity). As such, both approaches are complementary.

Our results also highlight the importance of landscape heterogeneity, providing sufficient cover of forest, shrub and meadow, in order to cater for both forest and meadow macro-moths. Whereas forest species use shrub and meadow habitat to some degree (see also Dolman *et al.* 2007 for birds), meadow species appear more, but not fully, restricted to their preferred habitat (i.e. meadows). Nevertheless, because we here show that forest species display higher spatial turnover and are characterised by a considerably higher species richness per sampling unit than meadow species, a high proportion of woodland cover appears beneficial for overall moth diversity at the landscape scale. Similarly, Marini *et al.* (2008; 2009) show that a high proportion of woody vegetation at a landscape-scale positively affects Orthopteran species richness, whereas a high proportion of grasslands did so negatively. Densities of birds of prey which obtain resources from both farm- and woodland increase too with forest cover (Sánchez-Zapata & Calvo 1999). Such results can be interpreted as forests providing resources for non-forest species, such as shelter, roosting sites, and food to name a few. Similarly, Ricketts *et al.* (2001) found that species richness of macro-moths in agricultural habitats was strongly influenced by the presence of nearby forest. Many moth species utilise both forest and agricultural habitats, and frequently move between them (Woiwod & Stewart 1990), with forest species typically relying on forest connectivity –for instance provided by hedgerows– when crossing the agricultural matrix (Slade *et al.* 2013).

Our test of the habitat amount hypothesis rigorously followed Fahrig's (2013; 2015) recommendations, such as that sample sites should be equally sized and sampled identically, that samples should be distributed over a large area, that the species group tested should be associated with a given cover type, and that the appropriate spatial scale needs to be pin-pointed correctly. In addition, relatively mobile taxa –such as moths– are more likely to exhibit a strong effect of habitat amount at the landscape scale than sessile taxa which may depend more significantly on the local conditions. Moreover, Hanski (2015) suggested that for habitats which were originally (almost) land-covering (e.g. native woodland), fragmentation makes anyway little or no difference if the amount of habitat is larger than roughly 20-30%

of the landscape area (Lande 1987; Fahrig 1998). Consequently, testing the habitat amount hypothesis for such habitat types should preferentially be done in landscapes where the habitat cover is less than 20%, and when fragmentation effects are presumed to start kicking in. Woodland cover within our study area amounted to only 10.5%, so that habitat fragmentation effects –if important– would be detectable.

Although our results of both the SAR and autocovariate models provide support for the habitat amount hypothesis, it is important other tests follow suit in order to better assess the applicability of this hypothesis. Responses of various taxonomic groups to habitat amount should be compared, each at their appropriate scale of effect, in order to determine whether habitat amount is indeed a good and sufficient predictor for species richness. In conclusion, results from our large-scale study show that species richness of both forest and meadow macro-moths respond more strongly to the total amount of habitat in the local landscape surrounding the sample site than to the precise habitat patch configuration. As such, these results provide evidence supporting the habitat amount hypothesis, which revises the application of island biogeography and metapopulation theory to conservation ecology.

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Supporting Information

Table 3: List of 378 macro-moth species, indicating species group classification in chapter 2 (SG1) (F: forest species; S: shrub species; M: meadow species) and in chapter 3 (SG2) (F: forest species; N: non-forest species), the raw number -not yet weighted in line with numbers of sampled habitat types- of observed individuals, both in the three different habitat types as well as overall, family (FM - G: Geometridae; N: Noctuidae), host-plant specialisation (HPS - O: oligophagous species; P: polyphagous species), larvae host-plant (LHP - H: herb-feeder; S/T: shrub/tree-feeder; G: grass-feeder; HT: heather-feeder; L: lichen-feeder; F: fern-feeder), average wingspan (WNG; mm) and size group (SIZE - L: large species; S: small species). Individuals of cryptic species were aggregated into four species-groups (*Caradrina selini* and *C. wullschlegeli*; *Cilix glaucata*, *C. hispanica* and *C. algirica*; *Stilbia anomala* and *S. andalusiaca*; *Watsonalla uncinula* and *W. binaria*). For the chapter 2, 21 low-abundance (N $\leq$ 5) species were not retained for analyses as the observed habitat preference and ecological literature suggested classification into more than one habitat type class. Two species -*Panolis flammea* and *Thaumetopoea pityocampa*- were not retained because they are associated with (non-native) pine trees.

Species	SG1	SG2	Forest	Shrub	Meadow	Total	FM	HPS	LHP	WNG	SIZE
Abraxas grossulariata	S	N	1	11	3	15	G	P	S/T	40	L
Acronicta aceris	F	F	3	3	1	7	N	P	S/T	40	L
Acronicta auricoma	S	N	4	10	2	16	N	P	S/T	38.5	L
Acronicta euphorbiae	S	N	0	1	0	1	N	P	H	35	L
Acronicta leporina	S	F	0	1	0	1	N	P	S/T	39	L
Acronicta psi	S	F	0	1	0	1	N	P	S/T	38	L
Acronicta rumicis	F	F	20	14	3	37	N	P	-	34.5	L
Adactylotis gesticularia	F	F	40	1	0	41	G	O	S/T	35	L
Aethalura punctulata	S	F	0	1	0	1	G	P	S/T	27.5	S
Agriopis marginaria	S	F	0	1	0	1	G	P	S/T	33	L
Agrotis bigramma	F	F	21	14	5	40	N	P	H	44	L
Agrotis chretieni	M	N	2	26	38	66	N	P	H	42	L
Agrotis exclamationis	M	N	3	24	69	96	N	P	H	35	L
Agrotis ipsilon	S	N	3	13	4	20	N	O	H	42.5	L
Agrotis puta	-	N	1	2	0	3	N	P	H	31	S
Agrotis segetum	F	F	46	59	13	118	N	P	H	35	L
Agrotis trux	F	N	115	200	78	393	N	O	H	38.5	L
Alcis repandata	F	F	115	104	11	230	G	P	S/T	47.5	L
Aleucis distinctata	S	N	0	1	1	2	G	O	S/T	28	S
Amphipyra pyramidea	F	F	18	5	1	24	N	P	S/T	46	L
Anarta myrtilli	S	N	2	21	1	24	N	O	HT	22	S
Antitype chi	S	N	0	10	2	12	N	P	H	36	L

Species	SG1	SG2	Forest	Shrub	Meadow	Total	FM	HPS	LHP	WNG	SIZE
Apamea lithoxylaea	M	N	1	3	6	10	N	P	G	47	L
Apamea monoglypha	M	N	29	72	99	200	N	P	G	46.5	L
Apamea remissa	S	N	2	11	3	16	N	P	G	38	L
Apamea scolopacina	M	N	0	1	1	2	N	P	G	34	L
Aplocera efformata	F	F	4	4	0	8	G	O	H	30.5	S
Aplocera plagiata	F	N	3	2	0	5	G	O	H	34	L
Aporophyla nigra	M	N	2	3	3	8	N	P	H	43	L
Arctia caja	M	N	2	4	5	11	-	P	H	68.5	L
Aspitates gilvaria	M	N	0	0	3	3	G	P	H	30	S
Atlantarctia tigrina	F	F	34	33	0	67	-	P	H	45.5	L
Autographa gamma	S	N	1	18	5	24	N	O	H	37.5	L
Autophila cataphanes	S	N	1	1	0	2	-	O	S/T	38.5	L
Biston betularia	S	N	4	9	4	17	G	P	S/T	50	L
Biston strataria	S	F	0	1	0	1	G	P	S/T	50	L
Brachylomia viminalis	M	N	3	3	4	10	N	O	S/T	29.5	S
Bryophila domestica	-	N	1	2	1	4	N	P	L	22.5	S
Bryophila ravula	F	F	18	9	8	35	N	P	L	27	S
Cabera exanthemata	F	F	5	3	0	8	G	P	S/T	30.5	S
Cabera pusaria	F	F	10	3	1	14	G	P	S/T	30	S
Calamia tridens	M	N	0	0	4	4	N	P	G	39.5	L
Calliteara pudibunda	S	N	3	6	1	10	-	P	S/T	50	L
Callopistria juventina	F	F	1	0	0	1	N	O	H	36	L
Callopistria latreillei	F	F	1	0	0	1	N	P	F	28	S
Calophasia hamifera	F	F	1	1	0	2	N	O	H	25	S
Calophasia platyptera	-	N	1	0	0	1	N	P	H	28	S
Campaea margaritaria	F	F	40	9	2	51	G	P	S/T	43	L
Camptogramma bilineata	F	F	14	3	9	26	G	P	H	27	S
Caradrina AGGseliniwullschlegeli	F	F	256	147	55	458	N	P	H	27.5	S
Caradrina aspersa	F	F	86	15	1	102	N	P	H	29.5	S
Caradrina clavipalpis	-	N	1	1	0	2	N	P	H	31	S
Caradrina flavirena	S	N	1	3	0	4	N	P	H	31	S
Caradrina morpheus	S	N	2	34	19	55	N	P	H	35	L
Catarhoe rubidata	-	N	0	0	4	4	G	O	H	26.5	S
Catephia alchymista	F	F	1	0	0	1	-	O	S/T	44	L
Catocala nupta	F	F	2	3	1	6	-	P	S/T	72.5	L
Catocala optata	S	N	1	3	1	5	-	O	S/T	62	L

Species	SG1	SG2	Forest	Shrub	Meadow	Total	FM	HPS	LHP	WNG	SIZE
Catocala promissa	F	F	36	4	0	40	-	P	S/T	62.5	L
Catocala sponsa	F	F	5	2	0	7	-	P	S/T	65	L
Cerastis rubricosa	S	N	5	32	11	48	N	P	H	34.5	L
Cerura iberica	-	N	0	0	1	1	-	P	S/T	75	L
Charanyca ferruginea	F	N	121	213	60	394	N	P	H	35.5	L
Charissa avilarius	F	F	8	0	0	8	G	P	H	31.5	S
Charissa mucidaria	F	F	27	14	1	42	G	P	H	25	S
Charissa obscurata	F	F	51	33	2	86	G	P	-	29	S
Charissa predotae	F	F	89	32	1	122	G	P	H	28.5	S
Chemerina caliginearia	S	N	0	1	0	1	G	P	S/T	35	L
Chesias isabella	M	N	6	14	10	30	G	O	S/T	26	S
Chloantha hyperici	S	N	0	1	0	1	N	O	H	30	S
Chloroclysta siterata	F	F	1	0	0	1	G	P	S/T	30	S
Chloroclystis v-ata	F	F	3	1	1	5	G	P	H	17	S
Cilix AGGglaucatahispanicaalgirica	F	F	5	0	0	5	-	O	S/T	21.5	S
Cleonymia diffluens	F	F	28	21	2	51	N	O	S/T	22	S
Cleora cinctaria	-	N	1	2	1	4	G	P	S/T	37.5	L
Cleorodes lichenaria	F	F	6	1	1	8	G	P	L	30	S
Clostera pigra	S	F	0	1	0	1	-	P	S/T	28	S
Colocasia coryli	F	F	4	3	2	9	N	P	S/T	31.5	S
Colostygia hilariata	M	N	0	1	1	2	G	O	H	26.5	S
Colostygia pectinataria	-	N	0	2	2	4	G	P	H	25.5	S
Comibaena bajularia	F	F	1	0	0	1	G	O	S/T	28	S
Compsoptera opacaria	F	F	8	4	0	12	G	P	S/T	39.5	L
Conisania andalusica	F	F	12	1	1	14	N	O	H	37	L
Conistra rubiginea	F	F	4	4	3	11	N	P	S/T	32.5	L
Coscinia cribraria	F	F	196	131	40	367	-	P	H	34	L
Cosmia trapezina	F	F	9	5	0	14	N	P	S/T	30.5	S
Cosmorhoe ocellata	M	N	12	20	23	55	G	O	H	25	S
Crocallis albarracina	F	F	17	11	0	28	G	P	S/T	30.5	S
Crocallis dardoinaria	F	F	36	9	0	45	G	O	S/T	40	L
Crocallis elinguaria	F	F	9	0	1	10	G	P	S/T	39	L
Crocallis tusciaria	S	N	1	0	0	1	G	P	S/T	35.5	L
Cryphia algae	F	F	15	3	0	18	N	P	L	26.5	S
Cryphia pallida	F	F	3	0	0	3	N	P	L	22	S

Species	SG1	SG2	Forest	Shrub	Meadow	Total	FM	HPS	LHP	WNG	SIZE
Cucullia umbratica	M	N	0	0	2	2	N	P	H	49	L
Cybosia mesomella	S	N	4	17	4	25	-	P	L	30	S
Cyclophora albipunctata	F	F	3	2	1	6	G	O	S/T	24	S
Cyclophora linearia	F	F	1	0	0	1	G	P	S/T	25	S
Cyclophora porata	F	F	24	7	0	31	G	P	S/T	25	S
Cyclophora punctaria	F	F	38	11	2	51	G	O	S/T	26.5	S
Cyclophora puppillaria	F	F	9	8	4	21	G	O	S/T	29	S
Cyclophora ruficiliaria	F	F	91	11	1	103	G	O	S/T	24	S
Cymatophorina diluta	F	F	1	2	0	3	-	O	S/T	35.5	L
Cymbalophora pudica	F	F	14	14	2	30	-	P	H	38.5	L
Deilephila porcellus	M	N	0	2	4	6	-	P	H	49	L
Denticucullus pygmina	F	F	18	2	1	21	N	P	G	26	S
Diachrysia chrysitis	F	N	1	1	0	2	G	O	H	29	S
Diacrisia sannio	S	N	3	57	12	72	-	P	H	41.5	L
Diaphora mendica	F	F	27	10	7	44	-	P	H	35	L
Diarsia brunnea	F	F	3	2	0	5	N	P	S/T	40	L
Diarsia guadarramensis	S	N	4	10	3	17	N	O	H	33.5	L
Diarsia rubiD	F	N	1	0	0	1	N	P	H	30.5	S
Drepana curvatula	F	F	0	2	2	4	-	O	S/T	34	L
Drymonia querna	S	N	1	4	2	7	-	O	S/T	38	L
Drymonia ruficornis	F	F	4	4	2	10	-	O	S/T	40	L
Drymonia velitaris	F	F	5	0	1	6	-	O	S/T	37.5	L
Dryobotodes roboris	S	N	2	7	0	9	N	O	S/T	31	S
Dypterygia scabriuscula	F	F	4	2	4	10	N	P	H	37.5	L
Dyscia distinctaria	S	N	0	5	3	8	G	P	H	34.5	L
Dysgonia algira	F	F	9	0	0	9	-	P	S/T	41.5	L
Dyspessa ulula	-	N	2	2	0	4	-	O	H	23	S
Dysstroma citrata	F	F	5	4	0	9	G	O	-	31.5	S
Dysstroma truncata	F	F	2	3	1	6	G	P	-	31.5	S
Ectropis crepuscularia	F	F	3	4	0	7	G	P	S/T	37.5	L
Egira conspicillaris	F	F	6	2	0	8	N	P	S/T	40	L
Eilema caniola	F	F	59	30	12	101	-	P	L	31.5	S
Eilema complana	M	N	84	115	174	373	-	P	L	34	L
Eilema lurideola	F	N	20	32	22	74	-	P	L	34.5	L
Eilema pygmaeola	S	N	1	12	5	18	-	P	L	26	S
Eilema uniola	F	F	455	56	7	518	-	P	L	21.5	S

Species	SG1	SG2	Forest	Shrub	Meadow	Total	FM	HPS	LHP	WNG	SIZE
Elaphria venustula	M	N	0	0	1	1	N	P	H	20.5	S
Electrophaes corylata	F	F	1	1	0	2	G	P	S/T	28	S
Ematurga atomaria	S	N	1	4	0	5	G	P	HT	28.5	S
Ennomos alniaria	F	F	4	1	3	8	G	P	S/T	36.5	L
Ennomos erosaria	F	F	1	0	0	1	G	P	S/T	35	L
Entephria cyanata	-	N	2	0	0	2	G	O	H	30.5	S
Epilecta linogrisea	F	F	19	0	0	19	N	P	H	36.5	L
Epirrhoe alternata	M	N	10	16	14	40	G	O	H	25.5	S
Epirrhoe galiata	F	F	14	17	4	35	G	O	H	26	S
Episema glaucina	S	N	0	2	0	2	N	P	H	36	L
Eublemma ostrina	S	N	0	1	0	1	-	P	H	21.5	S
Eublemma polygramma	M	N	0	0	1	1	-	O	H	17	S
Eublemma purpurina	M	N	1	1	0	2	-	O	H	24.5	S
Eugnorisma arenoflavida	F	F	21	4	1	26	N	P	H	32.5	L
Eugnorisma glareosa	F	N	208	355	120	683	N	P	-	33	L
Euphyia frustata	S	N	2	0	1	3	G	P	H	27	S
Eupithecia abbreviata	F	F	2	1	0	3	G	O	S/T	19	S
Eupithecia centaureata	F	N	1	1	1	3	G	P	H	21	S
Eupithecia dodoneata	F	F	0	1	0	1	G	P	S/T	17	S
Eupithecia extraversaria	F	F	3	0	0	3	G	P	H	18	S
Eupithecia icterata	M	F	6	0	7	13	G	P	H	22	S
Eupithecia innotata	S	N	0	1	0	1	G	P	-	21	S
Eupithecia laquaearia	F	F	12	4	1	17	G	O	H	18	S
Eupithecia nanata	S	N	14	33	1	48	G	O	HT	19	S
Eupithecia pantellata	F	F	1	0	0	1	G	O	H	15	S
Eupithecia pulchellata	F	F	16	14	10	40	G	O	H	20	S
Eupithecia pyreneata	F	F	8	0	0	8	G	O	H	17	S
Eupithecia scopariata	F	F	287	260	34	581	G	P	HT	17	S
Eupithecia subfuscata	S	N	10	22	8	40	G	P	H	18	S
Eupithecia venosata	F	F	4	2	1	7	G	P	H	22.5	S
Eupithecia vulgata	F	F	17	18	7	42	G	P	H	19	S
Euplagia quadripunctaria	F	F	44	12	1	57	-	P	H	57	L
Euplexia lucipara	M	N	1	4	3	8	N	P	H	34	L
Euproctis chrysorrhoea	F	F	155	6	3	164	-	P	S/T	34	L
Euproctis similis	F	F	0	1	1	2	-	P	S/T	35.5	L
Euxoa obelisca	F	F	18	19	8	45	N	P	-	35	L

Species	SG1	SG2	Forest	Shrub	Meadow	Total	FM	HPS	LHP	WNG	SIZE
Euxoa tritici	S	N	10	20	3	33	N	O	G	33	L
Falcaria lacertinaria	M	F	3	1	4	8	-	O	S/T	32.5	L
Geometra papilionaria	F	F	1	0	0	1	G	P	S/T	50	L
Gnophos furvata	S	N	4	0	0	4	G	P	S/T	45	L
Gnophos obfuscata	M	N	0	0	1	1	G	P	-	37.5	L
Griposia aprilina	F	F	2	0	0	2	N	O	S/T	45.5	L
Gymnoscelis rufifasciata	F	F	257	188	215	660	G	P	H	16.5	S
Habrosyne pyritoides	M	N	2	2	5	9	-	P	S/T	37	L
Hadena albimacula	M	N	1	0	1	2	N	O	H	33	L
Hadena bicruris	M	N	2	2	1	5	N	P	H	35	L
Hadena confusa	M	N	0	1	0	1	N	P	H	32	S
Hadena filograna	S	N	3	7	0	10	N	O	H	31.5	S
Hadena perplexa	F	F	7	1	4	12	N	O	H	31.5	S
Harpyia milhauseri	F	F	5	6	0	11	-	P	S/T	49	L
Helicoverpa armigera	M	N	0	2	0	2	N	P	H	35	L
Heliothis nubigera	M	N	1	0	0	1	N	P	H	40	L
Heliothis peltigera	M	N	0	1	1	2	N	P	H	38	L
Heterogynis paradoxa	S	N	0	1	0	1	-	O	S/T	24.5	S
Hoplodrina ambigua	F	F	52	73	15	140	N	P	H	33	L
Hoplodrina hesperica	F	F	333	111	52	496	N	P	H	29	S
Hoplodrina octogenaria	M	N	105	286	196	587	N	P	H	31	S
Hydriomena furcata	F	F	48	3	7	58	G	P	-	32	S
Hydriomena impluviata	F	F	4	2	0	6	G	P	S/T	30	S
Hyles livornica	M	N	0	1	2	3	-	P	H	76	L
Hyphoraia dejeani	M	N	26	41	40	107	-	P	H	39	L
Hypomecis punctinalis	F	F	4	0	0	4	G	P	S/T	43	L
Hypomecis roboraria	F	F	1	0	0	1	G	P	S/T	53.5	L
Idaea alyssumata	F	F	7	0	0	7	G	P	H	18.5	S
Idaea aversata	F	F	30	7	1	38	G	O	H	30	S
Idaea belemiata	-	N	1	0	1	2	G	O	H	16.5	S
Idaea biselata	-	N	1	2	2	5	G	P	-	21	S
Idaea calunetaria	F	F	4	2	0	6	G	O	H	17.5	S
Idaea cervantaria	S	N	0	0	1	1	G	O	H	17.5	S
Idaea contiguaria	F	F	151	81	47	279	G	P	-	19.5	S
Idaea degeneraria	F	F	68	40	2	110	G	P	-	26	S
Idaea deversaria	F	F	33	1	0	34	G	O	H	25	S
Idaea dromikos	F	F	1	0	0	1	G	P	-	20.5	S

Species	SG1	SG2	Forest	Shrub	Meadow	Total	FM	HPS	LHP	WNG	SIZE
Idaea eugeniata	F	F	33	9	0	42	G	P	H	22.5	S
Idaea fuscovenosa	F	F	14	4	3	21	G	O	H	19	S
Idaea humiliata	-	N	0	2	0	2	G	O	H	19	S
Idaea infirmaria	F	N	1	0	0	1	G	P	H	15.5	S
Idaea joannisiata	-	N	2	2	0	4	G	P	H	19	S
Idaea litigiosaria	S	N	1	2	0	3	G	O	H	19.5	S
Idaea lutulentaria	F	F	7	1	0	8	G	P	H	16	S
Idaea macilentaria	M	N	1	4	23	28	G	P	H	22.5	S
Idaea moniliata	M	N	1	0	0	1	G	P	H	19	S
Idaea obsoletaria	F	F	12	1	0	13	G	P	H	16	S
Idaea ostrinaria	F	F	4	3	0	7	G	P	H	17.5	S
Idaea rubraria	-	N	2	0	0	2	G	P	H	23.5	S
Idaea sardoniata	F	N	1	3	0	4	G	P	H	17.5	S
Idaea straminata	F	F	15	2	0	17	G	P	H	27	S
Idaea subsaturata	M	N	1	1	0	2	G	P	H	16.5	S
Idaea subsericeata	F	F	12	15	10	37	G	P	H	23.5	S
Isturgia miniosaria	S	N	22	173	50	245	G	O	S/T	34.5	L
Jodis lactearia	F	F	5	1	0	6	G	P	-	22	S
Lacanobia contigua	S	N	1	10	5	16	N	P	-	37	L
Lacanobia oleracea	F	N	1	3	1	5	N	P	H	37	L
Lacanobia thalassina	S	N	11	21	6	38	N	P	H	37	L
Lacanobia w-latinum	S	N	6	13	1	20	N	P	H	40	L
Laothoe populi	S	N	0	5	1	6	-	O	S/T	78	L
Lasiocampa quercus	M	N	2	7	8	17	-	P	S/T	70	L
Lasiocampa trifolii	S	N	2	14	0	16	-	P	S/T	60	L
Leucania loreyi	S	N	0	2	0	2	N	P	G	39	L
Leucania putrescens	F	F	29	20	6	55	N	P	G	34	L
Leucochlaena oditis	M	N	5	5	14	24	N	P	G	32	S
Leucoma salicis	F	N	0	1	0	1	-	P	S/T	46.5	L
Litoligia literosa	M	N	1	2	0	3	N	P	G	27.5	S
Lomaspilis marginata	F	F	13	4	2	19	G	P	S/T	23	S
Lophoterges millierei	F	F	9	3	0	12	N	O	S/T	30	S
Luperina nickerlii	M	N	2	5	4	11	N	P	G	37	L
Luperina testacea	M	N	71	139	280	490	N	P	G	35	L
Lycophotia erythrina	F	F	326	342	73	741	N	O	HT	29.5	S
Lycophotia molothina	F	F	54	73	3	130	N	O	HT	42.5	L
Lycophotia porphyria	S	N	23	159	25	207	N	O	HT	28.5	S

Species	SG1	SG2	Forest	Shrub	Meadow	Total	FM	HPS	LHP	WNG	SIZE
Lymantria dispar	F	F	4	1	0	5	-	P	S/T	65	L
Lymantria monacha	F	F	18	0	1	19	-	P	S/T	47.5	L
Macaria alternata	F	F	33	26	2	61	G	P	-	26	S
Macaria notata	F	F	1	0	0	1	G	P	S/T	30	S
Macrothylacia rubi	F	N	4	7	4	15	-	P	S/T	53.5	L
Malacosoma castrensis	M	N	0	0	1	1	-	O	H	32	S
Malacosoma neustria	S	N	1	4	1	6	-	P	S/T	34.5	L
Mamestra brassicae	M	N	0	1	0	1	N	P	H	41	L
Meganola strigula	F	F	19	3	1	23	-	P	S/T	21	S
Melanchra persicariae	F	N	1	1	0	2	N	P	H	38.5	L
Melanchra pisi	M	N	0	4	6	10	N	P	S/T	37	L
Menophra abruptaria	F	F	23	13	9	45	G	P	S/T	38	L
Menophra nycthemeraria	F	F	4	2	0	6	G	P	S/T	40	L
Mesapamea secalis	M	N	4	5	8	17	N	P	G	31.5	S
Mesoligia furuncula	M	N	3	3	8	14	N	P	G	25	S
Mesotype didymata	M	N	0	7	5	12	G	P	H	21	S
Miltochrista miniata	F	F	1	0	0	1	-	O	L	28	S
Mimas tiliae	F	F	1	0	0	1	-	P	S/T	69	L
Minucia lunaris	F	F	1	0	0	1	-	O	S/T	57	L
Mormo maura	F	F	4	0	0	4	N	P	H	60	L
Mythimna albipuncta	F	F	13	16	5	34	N	P	G	32.5	L
Mythimna conigera	M	N	8	67	87	162	N	P	G	32.5	L
Mythimna ferrago	F	F	59	67	59	185	N	P	G	38.5	L
Mythimna impura	S	N	25	148	65	238	N	P	G	31.5	S
Mythimna l-album	F	N	2	0	2	4	N	P	G	34	L
Mythimna sicula	F	F	15	17	15	47	N	P	G	37	L
Mythimna unipuncta	M	N	2	0	0	2	N	P	G	44.5	L
Mythimna vitellina	S	N	55	156	30	241	N	P	G	39.5	L
Noctua comes	S	N	12	33	13	58	N	P	H	43	L
Noctua interjecta	M	N	4	17	16	37	N	P	H	33.5	L
Noctua janthe	F	F	7	8	4	19	N	P	H	35	L
Noctua orbona	F	F	6	3	0	9	N	P	H	41.5	L
Noctua pronuba	S	N	94	304	44	442	N	P	H	50	L
Noctua tirrenica	F	F	14	13	1	28	N	P	H	51	L
Notodonta dromedarius	F	F	0	0	1	1	-	P	S/T	45	L
Nychiodes andalusiaria	F	F	46	13	5	64	G	P	S/T	38.5	L

Species	SG1	SG2	Forest	Shrub	Meadow	Total	FM	HPS	LHP	WNG	SIZE
Nycteola revayana	F	F	2	1	0	3	-	P	S/T	23	S
Nycteola siculana	F	F	1	0	0	1	-	O	S/T	25	S
Nyctobrya muralis	F	F	9	0	0	9	N	P	L	30.5	S
Ochropleura leucogaster	M	N	0	3	4	7	N	O	H	35.5	L
Ochropleura plecta	M	F	5	5	6	16	N	O	H	27.5	S
Ocneria rubea	F	F	12	3	0	15	-	P	S/T	39	L
Odice pergrata	S	N	1	3	0	4	-	O	H	28	S
Oligia strigilis	M	N	39	47	64	150	N	P	G	23.5	S
Oligia versicolor	F	N	1	0	0	1	N	P	-	25.5	S
Olivenebula xanthochloris	F	F	20	2	0	22	N	P	G	41	L
Omphaloscelis lunosa	M	N	38	64	569	671	N	P	G	35	L
Opisthograptis luteolata	F	F	2	0	0	2	G	P	S/T	34.5	L
Orthosia cerasi	F	N	5	9	3	17	N	P	S/T	37	L
Orthosia gothica	S	N	21	95	44	160	N	P	S/T	34	L
Orthosia incerta	S	N	9	18	7	34	N	P	S/T	38.5	L
Orthosia miniosa	S	N	2	6	2	10	N	P	S/T	33.5	L
Ourapteryx sambucaria	F	F	2	0	0	2	G	P	S/T	50	L
Pachycnemia hippocastanaria	F	F	661	753	161	1575	G	O	HT	28.5	S
Pachycnemia tibiaria	F	F	131	151	14	296	G	O	HT	26	S
Paidia rica	F	F	2	1	0	3	-	P	L	27.5	S
Panolis flammea	-	F	0	1	0	1	N	O	S/T	34.5	L
Paracolax tristalis	F	F	5	0	0	5	-	P	-	27	S
Pasiphila rectangulata	F	F	1	0	0	1	G	P	S/T	19.5	S
Perconia baeticaria	S	N	22	76	30	128	G	O	S/T	36	L
Peribatodes ilicaria	F	F	37	12	7	56	G	P	S/T	32.5	L
Peribatodes rhomboidaria	F	F	51	21	38	110	G	P	S/T	39	L
Peridea anceps	F	F	11	4	3	18	-	O	S/T	64	L
Peridroma saucia	F	F	5	8	1	14	N	P	H	50.5	L
Perizoma hydrata	F	F	3	3	0	6	G	O	H	21	S
Petrophora chlorosata	S	N	34	68	8	110	G	O	H	29	S
Phalera bucephala	F	F	4	0	1	5	-	P	S/T	59	L
Pharmacis lupulina	F	F	5	1	0	6	-	P	G	31.5	S
Phlogophora meticulosa	S	N	0	5	1	6	N	P	H	50	L
Photedes minima	M	N	0	2	2	4	N	O	G	21.5	S
Phragmatobia fuliginosa	S	N	4	24	14	42	-	P	H	34	L

Species	SG1	SG2	Forest	Shrub	Meadow	Total	FM	HPS	LHP	WNG	SIZE
Plagodis dolabraria	S	F	0	1	0	1	G	P	S/T	31.5	S
Polia nebulosa	F	F	6	2	0	8	N	P	-	49.5	L
Polymixis argillaceago	S	N	1	3	0	4	N	P	H	36.5	L
Polymixis dubia	F	F	23	12	0	35	N	P	H	35.5	L
Polymixis flavicincta	M	N	0	0	1	1	N	P	H	45	L
Polymixis lichenea	M	N	2	8	7	17	N	P	H	37.5	L
Polymixis xanthomista	S	N	3	30	7	40	N	P	H	41	L
Polyploca ridens	S	N	2	4	1	7	-	O	S/T	37	L
Pseudenargia ulicis	F	F	14	12	0	26	N	O	S/T	39.5	L
Pseudoips prasinana	F	F	3	0	1	4	-	P	S/T	32.5	L
Pseudoterpna coronillaria	F	F	92	96	41	229	G	P	S/T	36	L
Psilogaster loti	S	N	0	1	0	1	-	O	S/T	30	S
Rhodometra sacraria	S	N	0	1	0	1	G	P	H	25	S
Rhodostrophia calabra	F	F	25	9	0	34	G	O	S/T	28	S
Rhodostrophia vibicaria	F	F	11	10	0	21	G	P	-	28	S
Rhoptria asperaria	S	N	64	197	4	265	G	O	S/T	22.5	S
Rivula sericealis	F	N	0	1	1	2	-	P	G	20	S
Saturnia pavonia	S	N	0	2	1	3	-	P	HT	70	L
Scoliopteryx libatrix	-	N	0	0	2	2	-	O	S/T	42.5	L
Scopula asellaria	S	N	0	3	0	3	G	P	H	19	S
Scopula imitaria	F	F	59	14	0	73	G	P	H	27.5	S
Scopula marginepunctata	-	N	1	0	0	1	G	P	H	22	S
Scopula rufomixtaria	-	N	1	0	0	1	G	P	H	23.5	S
Scotopteryx coelinaria	F	N	20	36	14	70	G	O	S/T	35	L
Scotopteryx luridata	S	N	0	11	3	14	G	O	S/T	32.5	L
Scotopteryx peribolata	S	N	13	80	17	110	G	O	S/T	30.5	S
Selenia dentaria	S	N	2	11	1	14	G	P	S/T	38.5	L
Selenia lunularia	F	F	8	2	1	11	G	P	S/T	36.5	L
Selidosema pyrenaearia	F	F	21	22	1	44	G	P	S/T	32.5	L
Selidosema taeniolaria	F	F	63	38	12	113	G	P	S/T	32.5	L
Sesamia nonagrioides	M	N	2	0	0	2	N	P	G	35	L
Sideridis reticulata	M	N	0	0	1	1	N	P	H	37.5	L
Sideridis rivularis	S	F	2	4	0	6	N	P	H	28.5	S
Sphinx ligustri	F	N	1	2	0	3	-	P	S/T	105	L

Species	SG1	SG2	Forest	Shrub	Meadow	Total	FM	HPS	LHP	WNG	SIZE
Spilosoma lutea	F	F	17	13	6	36	-	P	H	38	L
Spudaea ruticilla	M	N	2	4	4	10	N	O	S/T	31	S
Stauropus fagi	F	F	1	1	0	2	-	P	S/T	61.5	L
Stilbia AGGanomalaandalusiaca	F	F	54	84	19	157	N	O	G	32.5	L
Tephronia lhommaria	F	F	13	2	0	15	G	P	L	25	S
Tephronia sepiaria	M	N	0	0	15	15	G	P	L	23	S
Thalera fimbrialis	F	F	5	1	0	6	G	P	-	31	S
Thalpophila vitalba	S	N	11	65	35	111	N	P	G	35	L
Thaumetopoea pityocampa	-	F	1	1	1	3	-	O	S/T	37.5	L
Thera obeliscata	S	N	0	3	0	3	G	P	S/T	29.5	S
Tholera decimalis	M	N	4	47	110	161	N	P	G	38.5	L
Thyatira batis	F	F	2	0	0	2	-	O	S/T	33.5	L
Timandra comae	M	N	0	1	1	2	G	O	H	29.5	S
Trichiura castiliana	F	F	7	5	0	12	-	O	S/T	30	S
Trichoplusia ni	F	N	1	0	0	1	N	P	H	35	L
Trichopteryx carpinata	-	N	0	0	1	1	G	P	S/T	27.5	S
Trigonophora crassicornis	S	N	1	0	0	1	N	P	S/T	41.5	L
Trigonophora flammea	F	F	36	30	9	75	N	P	-	48	L
Trigonophora haasi	M	N	25	129	97	251	N	P	S/T	36	L
Trigonophora jodea	F	F	14	22	2	38	N	P	-	40	L
Watsonalla AGGuncinulabinaria	F	F	11	5	0	16	-	O	S/T	26.5	S
Watsonarctia deserta	S	N	0	3	1	4	-	P	H	29	S
Xanthia icteritia	F	N	1	3	0	4	N	P	S/T	33.5	L
Xanthia togata	F	F	2	0	0	2	N	P	S/T	32.5	L
Xanthorhoe fluctuata	-	N	0	2	2	4	G	P	H	26	S
Xanthorhoe iberica	F	F	5	4	1	10	G	P	H	29	S
Xestia agathina	S	N	455	1226	197	1878	N	O	HT	32	S
Xestia baja	F	F	53	70	21	144	N	P	H	37.5	L
Xestia c-nigrum	F	F	2	3	1	6	N	P	H	38.5	L
Xestia castanea	F	F	164	62	7	233	N	O	HT	38	L
Xestia xanthographa	M	N	108	474	318	900	N	P	H	34	L
Xylocampa areola	F	N	1	1	3	5	N	O	S/T	36	L
Zanclognatha lunalis	F	F	2	0	0	2	-	O	S/T	28.5	S
Zanclognatha tarsipennalis	-	F	1	2	0	3	-	P	S/T	32.5	L

Chapter 3

Moth diversity patterns under farmland abandonment

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Abstract

Farmland abandonment and the accompanying natural succession are largely perceived as unwanted (amongst many European conservationists) due to alleged negative effects on biodiversity levels. Here, we test this assumption by analysing alpha, beta and gamma diversity patterns of macro-moth communities in habitats on an ecological succession gradient, from extensively managed meadows over scrub-encroached sites to native woodland. Macro-moths were light-trapped at 84 fixed circular sampling sites arranged in a nested design within the National Park of Peneda-Gerês, NW-Portugal. In total, we collected 22825 individuals belonging to 378 species. Alpha, beta and gamma diversity indicate that farmland abandonment is likely to positively affect the diversity of all species together and forest species, and to negatively affect the diversity of non-forest species. However, our results also show that spatial habitat heterogeneity is important to maintain macro-moth diversity, especially for rare non-forest and specialist species for different habitat types.

Keywords: Habitat heterogeneity, Null models, Species richness, Beta diversity, Lepidoptera; Rewilding, Multi-habitat landscapes

Introduction

Land-use change has been pinpointed as one of the main factors of global biodiversity change (Pereira *et al.* 2012), reducing species diversity at various spatial scales and modifying species interactions within ecological communities (Karp *et al.* 2012; Newbold *et al.* 2015). However, land use change is not always negative for biodiversity, as it can also include ecological restoration from intense human land-use back to a more natural state (Clewell & Aronson 2013).

Here, we focus on farmland abandonment, which is a type of land-use change whose effects on biodiversity are currently unresolved. Whilst abandonment is perceived as a threat to biodiversity amongst many European conservation biologists (Benayas *et al.* 2007; Van Swaay *et al.* 2010; Fischer *et al.* 2012), some see the accompanying ecological succession as an opportunity for ecological restoration with positive effects on biodiversity (Bowen *et al.* 2007; Navarro & Pereira 2012). We here test which of both assumptions is correct by analysing diversity patterns of macro-moth communities in three habitat types on a gradient of ecological succession, from extensively managed meadows, over scrub-encroached sites, to native woodland.

The focus of our study is on macro-moths –an abundant and species-rich insect group– as they react swiftly to environmental change and play key roles in ecosystem functioning (Merckx *et al.* 2013). Beta diversity –the spatial change in species composition– is considered a key concept to understand how local community assembly (alpha diversity) is linked to the regional species pool (gamma diversity) (Whittaker 1960; Margules & Pressey 2000). Because a comprehensive analysis of these three aspects of diversity is needed to fully understand the consequences of farmland abandonment, we thus compare alpha, beta and gamma diversity levels amongst the three habitat types. We also separate analyses contrasting forest versus non-forest species, as both groups are expected to show markedly different responses to farmland abandonment. Our hypothesis is that farmland abandonment will affect species richness and composition between different habitat types.

Material and Methods

Study area

The study area is located nearby the town of Castro Laboreiro (42.031 N, -8.155 W) within the National Park of Peneda-Gerês, NW-Portugal (Fig. 3 in chapter 2), which is a mountainous region situated in the transitional zone between the Atlantic and Mediterranean ecoregions. The study area (49.7 km^2; 750-1155 MASL) consists of shrub (78.4%), forest (10.5%), agricultural land (9.8%) and urban land (1.3%). It has undergone a rural exodus since the 1950's, which has increased the turnover of agricultural fields to shrub and forest (Rodrigues 2010).

Sampling design

Field work was performed across three landscapes of each 1.64 km^2 representing ecological succession stages after farmland abandonment: meadow-, shrub- and forest-dominated landscape (Fig. 3). For each landscape, 28 fixed circular sampling sites of 300 m^2 (radius ca. 10 m) were set up using a nested design (Proença & Pereira 2013) (Fig. 3). Each landscape varied in the relative cover of the three habitats, but all landscapes had some sites in each of the habitats. The total number of meadow, shrub, and forest sites were 18, 40, and 26, respectively. Each site was sampled six times during the main flight season of moths (i.e. May-September) in 2011 and 2012. For analyses, samples of these six sessions were lumped.

Macro-moths were sampled using light traps, which were activated from dusk until dawn. All macro-moth individuals inside and on the trap were enumerated and identified to species-level, with collection for later identification of specimens that could not be identified immediately. Sampling was only conducted during sufficiently favourable weather conditions for moth flight activity (see Merckx *et al.* 2012a). Although the degree by which macro-moths are attracted to light is known to differ among families, the used light-trap type (Heath pattern 6W actinic; Heath 1965) has an effective attraction radius of typically 10 m, with only very low percentages of moths drawn in from further away (Merckx & Slade 2014). This attraction radius hence translates in a sampling area of ca. 300 m^2. The possible bias, due to intrinsic differences in flight-to-light behaviour among individuals, species and families, is identical for each of the 84 sites, as they were all sampled with identical light-traps. As such, although local absolute light-trap samples are biased with respect to the local community, the observed relative differences among trap sites are not biased.

Species were grouped as either forest or non-forest species according to whether they displayed a higher relative abundance –corrected for the relative amount of habitat types– in forest vs. non-forest (i.e. meadow/shrub) habitat, respectively. Species with five or fewer individuals were classified based on literature and expert knowledge. As such, 196 species were classified as forest species and 182 as non-forest species (Table 3 in Supporting Information - chapter 2).

Gamma and alpha diversities

Effective species numbers were also used to characterize the taxonomic diversity each habitat type at regional and local scales. Effective species numbers are all based on the same generalized entropy formula, differing only by an exponent q that determines sensitivity to species relative abundances (Hill 1973), with low order q sensitive to rare species, and high order q sensitive to abundant species. We used the following effective species numbers: species richness ($q = 0$), the exponential of Shannon diversity ($q = 1$), the reciprocal of Simpson's diversity ($q = 2$) and the reciprocal of the Berger-Parker index ($q \to \infty$, i.e. reciprocal of the proportional abundance of the commonest species). At sampling site level, we tested for effects of habitat type on each of these metrics and on Simpson's evenness, by using a bootstrap procedure of 4000 runs and comparing confidence intervals (95%) around the bootstrapped mean of metrics. Simpson's evenness was included as it is mathematically independent from the reciprocal of Simpson's diversity (Smith & Wilson 1996).

Beta diversity

We looked at two aspects of beta diversity: (i) the mean dissimilarity of species composition between any pair of sites for each habitat type, and (ii) how that dissimilarity changes with distance between sites. For the former, we calculated mean Jaccard dissimilarities (hereafter 'observed beta diversity'; see Supporting Information for mean Sørensen dissimilarities). For the latter, the spatial turnover rate was calculated for each habitat type as the slope of a linear least-squares regression of dissimilarity on geographic distance (Anderson *et al.* 2011). We used a bootstrap procedure with 4000 runs to test whether observed beta diversity and turnover rate differed between the three habitat types.

Corrected beta diversity

As the different habitat types had different values of both mean alpha and gamma diversity, we used a null model to remove the effect of alpha diversity on beta diversity (Kraft *et al.* 2011). For each habitat type, we randomised species in the observed data using a null model with 2000 iterations that shuffled species between sampling sites while maintaining the species total fixed (e.g. SIM2 in Gotelli (2000)). We then calculated the expected beta diversity between all sampling sites from the same habitat type using the Jaccard index (Sørensen index in Supporting Information). Next, beta deviations were calculated for each habitat type as the difference between observed and mean expected beta diversity, divided by the standard deviation of the expected beta diversity (Kraft *et al.* 2011). A bootstrap procedure with 4000 iterations was used to test whether the expected beta diversity and beta deviation differed between the three habitat types. The beta deviation represents the beta diversity not accounted for in the random sampling of the meta-community. In other words, the beta deviation represents a standard effect size with positive and negative values indicating more and less beta diversity, respectively, than expected by chance. All analyses were performed using R version 3.1.1 package 'vegan' (R Core Team 2014; Oksanen *et al.* 2015).

Results

Gamma diversity

A total of 22825 macro-moth individuals from 378 species were collected (Table 3 in Supporting Information - chapter 2). Gamma diversity decreased from 313 species (8355 individuals) in forest, over 301 species (9870 individuals) in shrub, down to 226 species (4600 individuals) in meadow habitat. The gamma diversity profile indicate that farmland abandonment is likely to positively affect the diversity of all species together and forest species in particular, whereas less likely, or at least to a smaller degree, to negatively affect the diversity of non-forest species (Fig. 7A-C).

Alpha diversity

Overall, there was no difference in species richness nor in the reciprocal of Berger-Parker index among the three habitat types (Fig. 7D/G). However, both the exponential of Shannon index and the reciprocal of Simpson's index were higher in forest habitat than in meadow habitat, with shrub habitat values similar to meadow habitat values for the exponential of Shannon index and not dissimilar from both forest and meadow habitat values for the reciprocal of Simpson's index (Fig. 7E/F).

For forest species, forest habitat was characterised by higher species richness and higher exponential of Shannon, reciprocal of Simpson's and Berger-Parker indices than both shrub and meadow habitat, which did not differ amongst them (Fig. 7D/E/F/G).

For non-forest species, species richness and the exponential of Shannon index were higher in meadow than in forest habitat, with shrub habitat values similar to meadow habitat values for species richness and not dissimilar from both meadow and forest habitat values for the exponential of Shannon index (Fig. 7D/E). There was no difference in the reciprocal of Simpson's index nor in the Berger-Parker index among the three habitat types (Fig. 7F/G).

Simpson's evenness did not differ among the three habitat types, neither overall, nor for forest and non-forest species separately (Fig. 7H).

Beta diversity: within habitat variation in species composition

Observed within-habitat beta diversity of macro-moths overall was slightly higher in shrub than in forest, and lowest in meadow habitats (Fig. 8A). This pattern is similar to the expected beta diversity pattern, although the observed beta diversity is consistently higher than the expected beta diversity, which suggests a higher dissimilarity between communities from different locations of the same habitat than what would be expected by chance based upon the observed alpha and gamma diversity of these habitats (Fig. 8A/B). The positive beta deviation values for all three habitat types do indeed show that their beta diversity is much higher than what would be expected from a random sampling model, but now with the highest value for forest, an intermediate value for shrub, and the lowest value for meadow habitat (Fig. 8C). This means that the compositional variation of macro-moths overall is largest in forest and smallest in meadow habitats, after accounting for the observed alpha and gamma diversity.

Although forest species had lowest observed and expected beta diversity in forest habitat (Fig. 8A/B), their beta deviation was almost three times higher in forest than in shrub and meadow habitat (Fig. 8C). Similarly, non-forest species displayed lowest observed and expected beta diversity in meadow habitat and intermediate values in shrub habitat (Fig. 8A/B), whilst their beta deviations at meadow and shrub habitat were almost double the value at forest habitat (Fig. 8C).

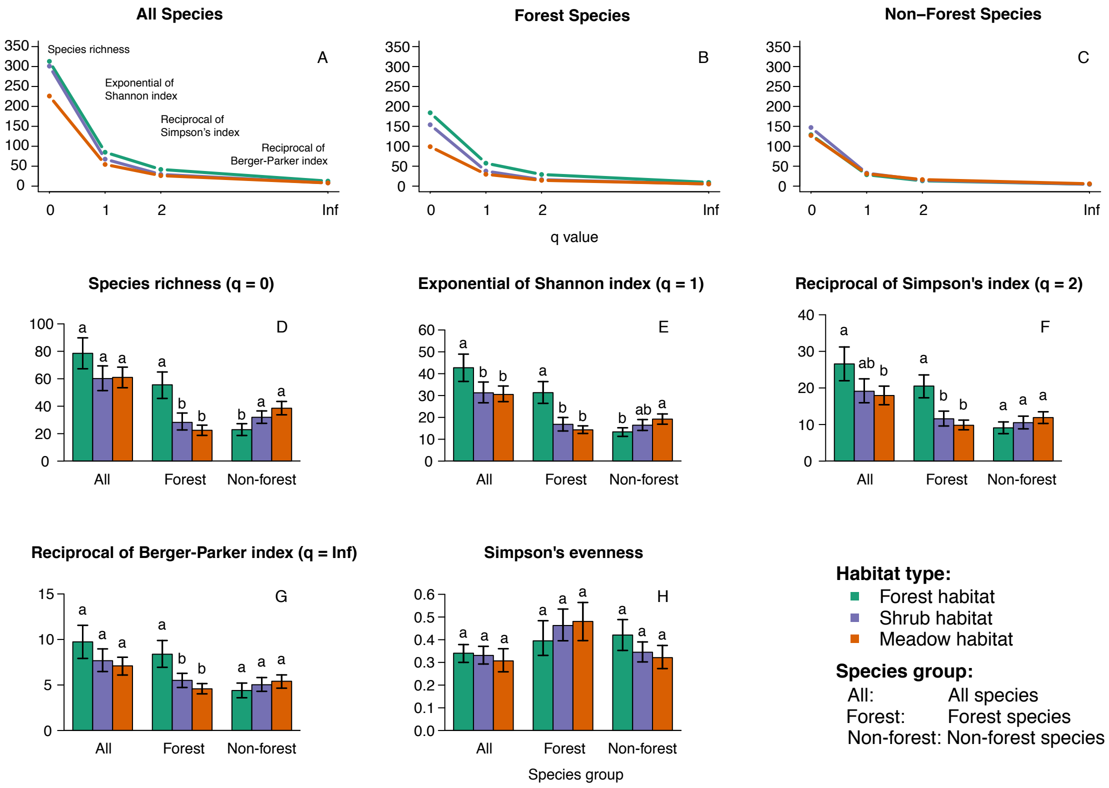

Figure 7: Comparison of effective species numbers between habitats. Effective species numbers are based on the same generalized entropy formula, differing only by an exponent q which vary between 0 and positive infinite: low values indicate rare species are taken into account, while high values abundant species are taken, so species richness ($q = 0$), the exponential of Shannon diversity ($q = 1$), the reciprocal of Simpson's diversity ($q = 2$), the reciprocal of the Berger-Parker index ($q \to \infty$). Effective species numbers for all species (A), for forest species (B) and for non-forest species (C) at regional scale. Mean species richness (D), mean exponential of Shannon index (E), mean reciprocal of Simpson index (F), mean reciprocal of Berger-Parker index (G) and mean Simpson's evenness (H) for the three species groups at local scale. Green, lilac and orange colours represent forest, shrub and meadow habitats, respectively. Error bars are 95% confidence intervals based on 4000 bootstrap replicates. Different letters represent statistic differences.

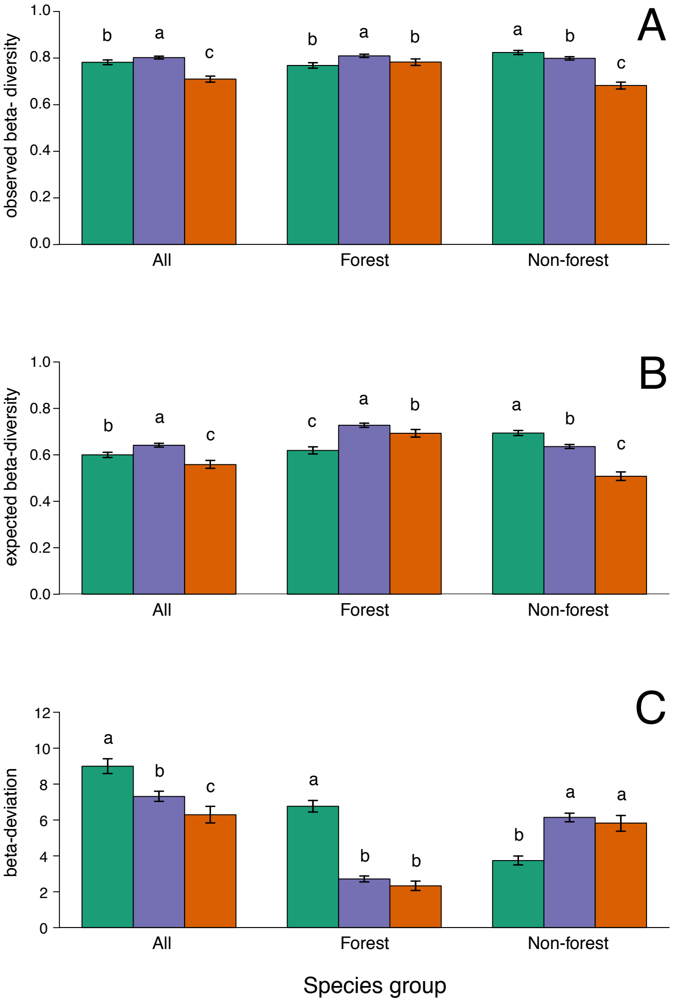

Figure 8: Beta diversity across habitats and species groups. (A) Observed beta diversity (*in casu* Jaccard index), (B) expected beta diversity from a null model based on random sampling from the regional species pool, and (C) beta deviations (standardized effect sizes which represent the difference between observed beta diversity and expected beta diversity) for all species (left), forest species (centre), and non-forest species (right). Beta deviations are positive, indicating beta diversity higher than expected by chance. Green, lilac and orange bars represent forest, shrub and meadow habitats, respectively. Error bars are 95% confidence intervals based on 4000 bootstrap replicates. Different letters represent statistic differences. Similar results were obtained using the Sørensen index (Figure 10 in Supporting Information).

Hence, compositional variation –corrected for alpha diversity– is highest in forest habitat for forest species, whilst it is highest at both shrub and meadow habitat for non-forest species.

Beta diversity: spatial turnover rates

Overall, observed beta diversity of macro-moth communities increased with increasing distance between sites. This positive turn-over rate pattern –for all species lumped– was strongest for meadow, intermediate for forest, and weakest for shrub habitat (Fig. 9A). Forest species displayed high turn-over both for forest and meadow habitat, whilst no turn-over for shrub habitat (Fig. 9B). Turn-over of non-forest species was highest for meadow, intermediate for shrub and lowest for forest habitat (Fig. 9C).

Discussion

Having compared species diversity of macro-moth communities in three different habitats, representing a gradient of farmland abandonment, we found –using a range of indices– that both alpha and beta diversity were overall considerably higher in forest than in both shrub and meadow habitats. Nevertheless, meadow habitat showed the highest spatial turnover rate, although forest habitat was characterised by a high turnover rate too, especially so for forest species.

The alpha diversity profiles indicate that farmland abandonment is likely to positively affect the diversity of macro-moths overall and forest species in particular. These findings strongly suggest that multi-habitat landscapes, characterised by a substantial heterogeneity of meadow, shrub and forest habitat, are able to reach high levels of macro-moth diversity, also because many species are able to use several habitat types to a varying extent. In the same vein, Merckx *et al.* (2012b) showed that the retention of open habitats within English broadleaved woodlands increases

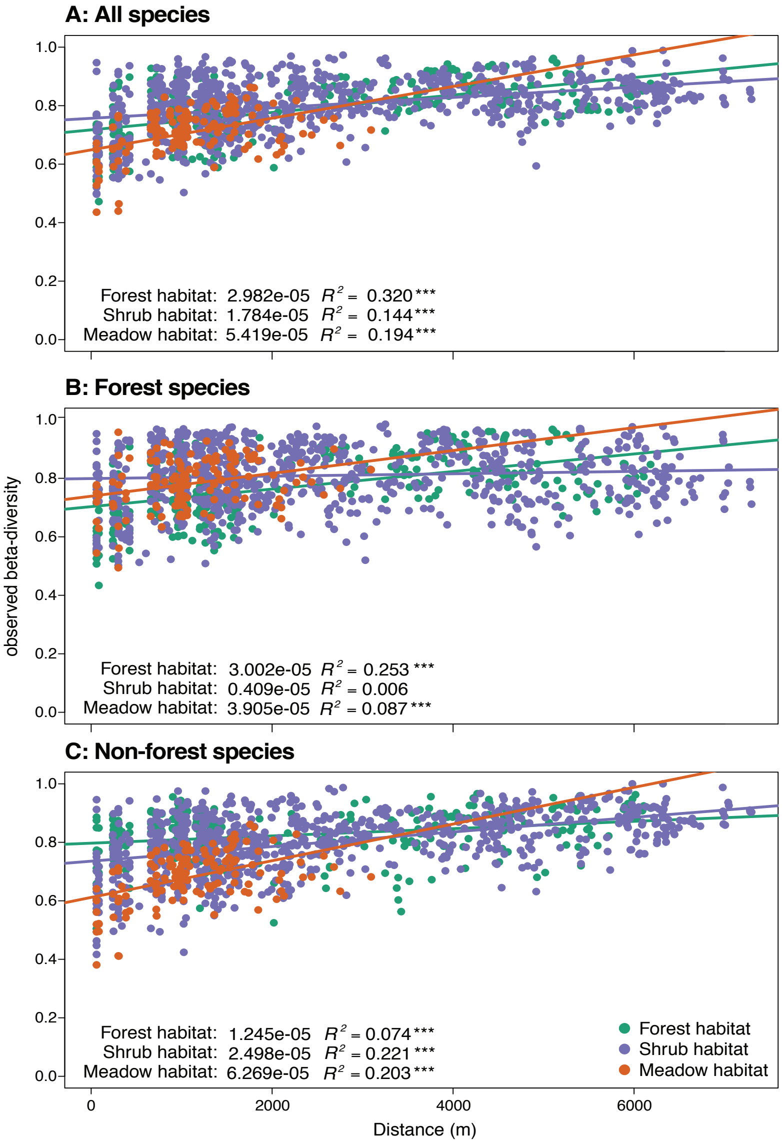

Figure 9: Relationships between geographic distance and beta diversity (*in casu* Jaccard index) for pairs of sampling sites across habitats and species groups. Observed beta diversity for all species (top), forest species (middle), and non-forest species (bottom). Green, lilac and orange dots represent forest, shrub and meadow habitats, respectively. The solid lines represent the best-fit lines from linear regression. The turnover rates (slopes), R^2-values and significance levels of turnover rates (*** $P < 0.001$, ** $P < 0.01$ and * $P < 0.05$) are given within each panel. Similar results were obtained using the Sørensen index (Figure 11 in Supporting Information).

the overall diversity of macro-moths, since they allow open-biotope specialists to occur, even though their alpha diversity is much lower than the alpha diversity of the closed woodland habitat. Similarly, and especially given the high spatial turnover rate for meadows, this habitat too is important for diversity levels at the landscape and regional scales. As such, our findings show the importance of retaining habitat diversity during farmland abandonment. Whilst abandonment poses risks regarding the long-term presence of meadow habitats, especially if the process happens sudden at the landscape-scale, rewilding is able to cater for sufficient landscape heterogeneity including meadows (e.g. via large grazers) (Merckx & Pereira 2015; Navarro *et al.* 2015).

At local and landscape scales, forest habitat displayed higher alpha and gammadiversity than both shrub and meadow habitat. Similarly, Beck *et al.* (2002) showed that primary and old-grown regenerated forest sites in Borneo are characterised by a much higher diversity of geometrid moths than agricultural sites. Kivinen *et al.* (2006) too found that forest cover correlated positively with macro-moth species richness, whilst agricultural field cover correlated negatively, demonstrating that overall species richness was lower in homogenous agricultural landscapes. However, focusing on non-forest species, we show that their diversity, as expected, decreases with ecological succession; the highest diversity was observed in meadow habitat, with lower but statistically similar levels for shrub, and lowest diversity in forest habitat. This pattern is fully explained by the observation that ecological succession more strongly affects rare than common non-forest species. By contrast, intensification of meadow habitats and agricultural landscapes is known to drastically reduce overall moth diversity levels (Merckx *et al.* 2012a). One aspect of agricultural intensification is a reduction in woody cover, which is known to be of importance at the landscape scale for moths, even for open-biotope species (Warren & Key 1991; Wagner *et al.* 2003; Kivinen *et al.* 2006). Trees and shrubs indeed provide essential resources to open-biotope species too, such as a more sheltered micro-climate (Merckx *et al.* 2008, 2010).

Our results show that the inter-habitat differentiation in species diversity –both for all species and forest species only– occurred for all q values, which indicates that the differentiation occurred for both rare and common species. For non-forest species however, the inter-habitat differentiation only occurred at low values, indicating that the diversity differences are due to differences in the diversity of rare species only. Summerville *et al.* (2003), who also used the first three q values in order to study spatial variation in species diversity and composition of forest Lepidoptera, found that species richness changed equally across all spatial scales due to the large amount of rare species ($> 50\%$).

Although the observed beta diversity for all species was higher in shrub than in forest and meadow habitats, the pattern completely changed after taking into account gamma and alpha diversity with the highest beta deviation for forest, intermediate beta deviation for shrub, and the lowest beta deviation for meadow habitat. Hence, the forest habitat is not only characterised by the highest gamma and alpha diversity, but by the highest beta diversity too. An explanation for this high forest beta diversity is that although the native forest habitat in our study area is largely composed of *Quercus robur* and *Q. pyrenaica*, many other tree and plant species are part of the native forest community. The spatial heterogeneity and vertical layering of host-plant species within the forest habitat type can lead to a high variation in community composition between sampling sites (Kessler *et al.* 2009). By contrast, layering and among-site heterogeneity are reduced for the meadow habitat, reducing moth beta diversity. Nonetheless, the meadow habitat displayed the steepest spatial turnover rate overall, but it was largely explained by the distribution of rare non-forest species, which although important for conservation in their own right may be less important in terms of their contribution to natural processes and ecosystem functioning (Grime 1998; Gaston & Fuller 2008). Another explanation for the steepest spatial turnover in meadow is that there are no dissimilarity values between sampling sites which are more distant than 3000 m, consequently this might influence the spatial turnover in meadow making it higher than in forest and shrub.

Our results also showed that the observed beta diversity was consistently larger than the beta diversity expected by chance, which translated in positive beta deviation values for all habitat types and species groups. This observation suggests that the size of the regional species pool (i.e. gamma diversity) for the three habitat types cannot entirely explain the geographical distribution of their beta diversity, and that macro-moth communities were additionally shaped by ecological assembly mechanisms (e.g. habitat filtering and biological interactions) and/or random processes (e.g. dispersal, colonization and extinction), producing higher beta diversity (Chase 2014; Tucker *et al.* 2016).

Understanding the effect of farmland abandonment on diversity levels of native biodiversity is important in order to design mitigation measures for possible negative ecological impacts. Although we here demonstrate that a late stage of ecological succession following farmland abandonment (i.e. native woodland) is characterised by the highest diversity levels of macro-moths, our results also show the importance of retaining sufficient spatial habitat heterogeneity for macro-moth diversity, especially for rare non-forest species. Mitigation may entail the release of large grazers when regional monitoring of habitat heterogeneity in abandoned regions highlight heterogeneity has become too low because natural disturbances, such as grazing, turn out to be insufficient yet (Merckx & Pereira 2015). As macro-moths are an indicator group for other terrestrial invertebrates (Merckx *et al.* 2013), our main findings are likely to be relevant for other invertebrate taxa too. Moreover, moths are key to ecosystem functioning. For instance, the herbivore caterpillars are important nutrient cyclers, flying adults are nocturnal pollinators, and both larvae and adults are important food resources for several other trophic levels (Merckx *et al.* 2013).

Summarised, we here show that landscape-scale farmland abandonment can lead to multi-habitat landscapes characterised by high levels of macro-moth diversity, which may translate in a better functioning and more resilient ecosystem than the replaced agricultural system.

Acknowledgements

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Supporting Information

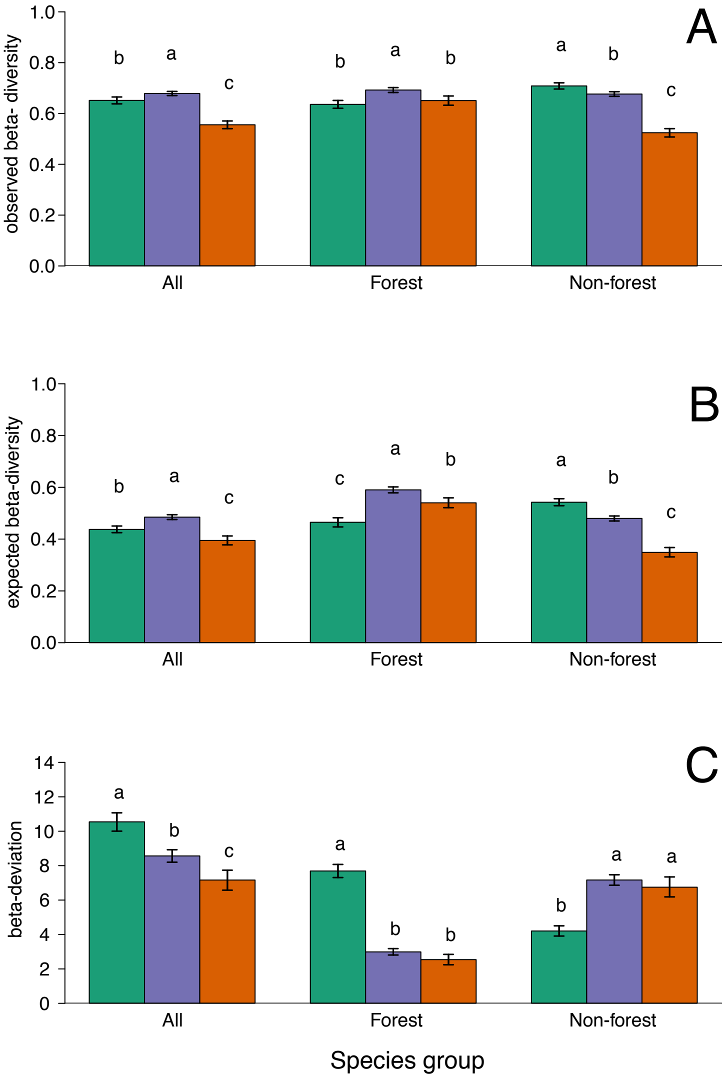
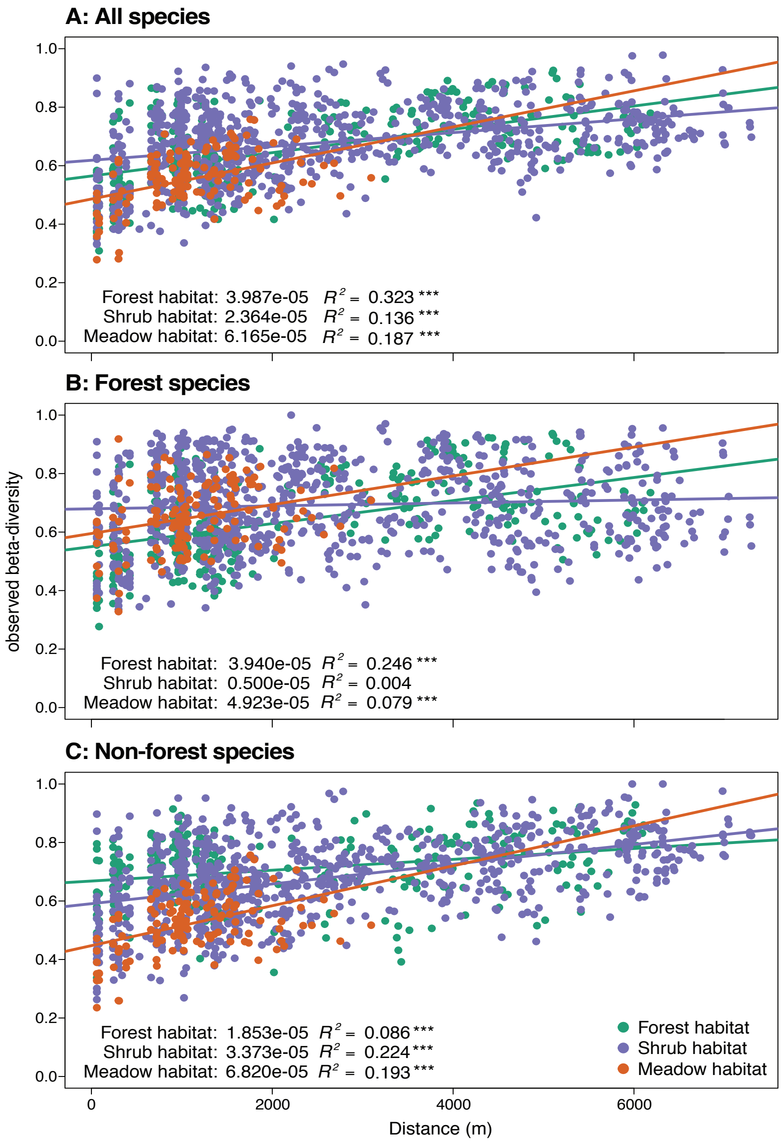


Figure 10: Beta diversity across habitats and species groups. (A) Observed beta diversity (*in casu* Sørensen index), (B) Expected beta diversity from a null model based on random sampling from the regional species pool and (C) beta deviations (standardized effect size which represent the difference between observed beta diversity and expected beta diversity) for all species (left), forest species (centre) and non-forest species (right). Beta deviations are positive, indicating higher beta diversity than expected by chance. Green, lilac and orange represent forest, shrub and meadow habitats, respectively. Error bars are 95% confidence intervals based on 4000 bootstrap replicates. Different letters represent statistically differences.



A: All species

B: Forest species

C: Non-forest species

Figure 11: Relationships between geographic distance and beta diversity (*in casu* Sørensen index) for pairs of sampling sites across habitats and species groups. Observed beta diversity for all species (top), forest species (middle) and non-forest species (bottom). Green, lilac and orange represent forest, shrub and meadow habitats, respectively. The solid lines represent the best-fit lines from linear regression. The turnover rate (slope), R^2-value and significance levels of turnover rate (*** $P < 0.001$, ** $P < 0.01$ and * $P < 0.05$) are given within each panel.

Chapter 4

Species traits shape the relationship between local and regional species abundance distributions

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Abstract

The species-abundance distribution (SAD) describes the relationship between the number of observed species as a function of their observed abundance. We test whether SADs are more likely to follow a log-normal versus a log-series distribution and how that may change with scale. We test if and how family (Geometridae and Noctuidae) and species traits (body size, host-plant specialisation, and host-plant type) affect SADs. We analyse how SAD moments respond to spatial scale. Finally, we assess the performance of Tchebichef moments to scale SADs from the local plot scale to the landscape. For that, we collected macro-moth within the Peneda-Gerês National Park, NW-Portugal using 84 light-traps set up in a nested design. Next, we fitted log-normal and log-series distribution, then we used Akaike information criteria to select the best fitting model. In addition, we upscaled SADs using Tchebichef moments and polynomials. Our results show that the shape of SADs changes across spatial scale, depending on some species traits. This suggests that some traits influence the spatial distribution of individuals of macro-moth species.

Keywords: Lepidoptera; Moths; Raw moments; Species abundance distributions; Tchebichef moments and polynomials; Multi-habitat landscapes; Forest; Meadow; Shrubs

Introduction

The species-abundance distribution (SAD) describes the relationship between the number of observed species and the abundance of each species. As such, SADs depict the relative abundance of species within a community, a central concept in ecology, and essential for theories on biodiversity and biogeography (McGill *et al.* 2007; Matthews & Whittaker 2014). Analyses of SADs that enable identifying patterns in the commonness and rarity of species can be useful too in applied ecology and biodiversity management (Matthews & Whittaker 2015). As such, both theoretical and empirical studies have examined the influence of several environmental and biological variables on SADs, such as elevational and latitudinal gradients, niche differentiation, dispersal, and ecological disturbance (Whittaker 1975; Hubbell 1979, 2001; Magurran 2004; Matthews & Whittaker 2015).

In their review on SADs studies, McGill *et al.* (2007) criticised the strong proliferation of models trying to explain the shape of SADs. Here, we use Ulrich *et al.*'s (2016) framework, which summarises SADs into two groups only: SADs following a log-series versus a log-normal distribution. The log-series SAD implies that most individuals belong to a few species and that most species are represented by a few individuals, whereas the log-normal SAD implies a higher number of species with intermediate abundance and smaller numbers of both very rare and abundant species (Magurran 2004). It has been hypothesized that SADs should be of the log-normal type if communities are stable and influenced by ecological processes (e.g. intra- and inter-specific interactions), and should instead be of the log-series type if communities are unstable and influenced by random processes (e.g. dispersal and immigration) (MacArthur 1957; Ulrich *et al.* 2010).

A key point that will move the study of SADs forward is understanding how they are affected by spatial scale (McGill *et al.* 2007). In this context, some studies have focused on how dispersal limitation and species aggregation affect the relationship between local and regional SADs (Dewdney 1998; Green & Plotkin 2007), whilst others have tried to predict the regional SAD from SADs obtained at smaller scales using various upscaling methods, such as maximum-entropy and Bayesian methods (Magurran 2005; Harte *et al.* 2009; Zillio & He 2010). Another upscaling method is the Tchebichef moments method. Borda-de-Água *et al.* (2012) applied this method using local SADs built with data of tree and shrub species occurrence in a 50 ha plot of tropical rain forest. They tested the method within the 50 ha plot, and then extrapolated the SAD for areas up to 5 km^2, which showed advantages over other upscaling methods such as that the number of singletons is maintained across scale, and that there is no need to normalise the data.

Here, we test whether SADs are more likely to follow a log-normal or a log-series distribution and how that may change with scale. We test if and how family (Geometridae and Noctuidae) and species traits (body size, host-plant specialisation, and host-plant type) affect SADs. We analyse how SAD moments respond to spatial scale. Finally, we assess the performance of the Tchebichef moments to scale SADs from the local plot scale to the landscape scale. We focus on macro-moths, a species-rich group of flying insects, and do so using a nested multi-site design in three multi-habitat landscapes.

Material and Methods

Study area

We gathered species abundance data on macro-moths in the Castro Laboreiro area (ca. 42°2’ N, 8°10’ W) within the Peneda-Gerês National Park, NW-Portugal (Fig. 3 in chapter 2). The landscape within our study area consists mainly of scrubland (78.4%), forest (10.5%) and meadows (9.8%). Sampling was conducted in three 1.6 km^2 multi-habitat landscapes between May and September of both 2011 and 2012 (three times per year) using Heath pattern actinic light traps (6W). For each landscape, 28 fixed light-traps were set up using a nested design with four levels corresponding to a spatial scale (Proença & Pereira 2013) (Fig. 3). First scale is the sampling site, second scale has the four nearest sampling sites, third scale has the seven nearest sampling sites and fourth scale represents a landscape.

Species abundance distribution models

Macro-moth abundance data at each scale was lumped and then fitted with log-series and log-normal distributions using maximum-likelihood tools with the *sads* package for R (Prado *et al.* 2016). In order to select the best fitting model, we used corrected Akaike information criteria (AICc). Specifically, we calculated the difference between the AICc values (ΔAICc) corresponding to the log-normal and the log-series distributions, using the threshold of $\Delta\text{AICc} > |2|$ to establish when two distributions were significantly different (Burnham & Anderson 2002; Slik *et al.* 2015). Accordingly, the log-normal SAD model is considered to provide a better fit when $\Delta\text{AICc} \leq -2$ whilst $\Delta\text{AICc} \geq 2$ indicates a better fit for the log-series model. Models characterised by $-2 < \Delta\text{AICc} < 2$ were classified as intermediate ones, with both the log-normal and log-series providing an equally good fit. We then created ordinal logistic models to test the relation between spatial scale (ln (m^2)) and the probability for these log-normal, intermediate, and log-series SADs. Ordinal logistic regression assumes that the response variable is categorical and follows an order. It has been used in a few ecological studies (Guénette & Villard 2004; Rutherford *et al.* 2007). Next, we evaluated the goodness-of-fit and deviance. The strength of the association (McFadden's R^2) was calculated as 1 - (L_{model}/L_{null}), where L_{model} is the log-likelihood value for the fitted model and L_{null} is the log-likelihood for the null model which includes only an intercept.

The same approach was used to test how family (Geometridae vs. Noctuidae) and three species traits (body size, host-plant specialisation, and host-plant type) affect the SAD. Wingspan (mm) was used as a proxy for body size. For each species, wingspan range was obtained from www.lepidoptera.eu, topped up by data from other sources for a few species were info was missing. We then calculated the average wingspan for each species. Species with average wingspan smaller than the overall median were classified as small, the others as large. Host-plant specialisation was classified into two classes: oligophagous species, whose larvae only feed on a few plant species from the same family, and polyphagous species, which are able to feed on several plant species from different families. Host-plant type was classified as species whose larvae are either herb-feeders or shrub/tree-feeders. The data on host-plant specialisation and host-plant type were obtained from the same sources as above. An overview of all species classifications can be found in supplementary material (Table 3 in Supporting Information - chapter 2). All statistical analyses were run in the statistical software environment R version 3.1.1 (R Core Team 2014).

SAD moments, Tchebichef moments and polynomials

The moments of order n of the SAD from a given community were estimated as:

$$M_n = \frac{1}{S} \sum_{j=1}^{S} x_j^n \tag{4}$$

where S is the number of species, and x_j is the log_2-transformed number of individuals of species j. For each spatial scale, we calculated the average of the moments obtained from each set of lumped sampling sites, and then plotted this average as a function of the corresponding spatial scale. Although in our analysis the number of moments varied between 0 and 11 –because there were 12 bins in the histogram of all landscapes– we limited the number of moments to 9, both separately for each landscape and for all landscapes together, as higher moments presented significant variation.

For each site, data were lumped, and for each species the number of individuals was log_2-transformed. We calculated the moments for each sampling site, which corresponds to the smallest scale, i.e. 400 m^2 (20 x 20 m based on an attraction-to-light radius of ca. 10 m; Merckx & Slade 2014). For each moment, we then calculated the average from all sampling sites. For the next spatial scale (i.e. 6400 m^2), we lumped all sampling sites within these areas, we then calculated the moments for each area, and for each moment we then averaged the values from all these areas. This procedure was repeated one more time for the next spatial scales (i.e. 102400 m^2). The next step was to fit a linear regression in order to assess the relationship between the ln-transformed area and the ln-transformed moment, $ln(M_n(A)) = a_n + b_n ln(A)$, where a_n and b_n are parameters estimated from the regression. Next, we extrapolated the moments for larger areas (i.e. 163840 m^2 or the individual landscapes, and 4915200 m^2 which corresponds to the sum of the three landscapes) using the moments obtained at the 400 m^2, 6400 m^2 and 102400 m^2 spatial scales (hereafter: 'extrapolated moments'). Finally, we reconstructed the probability density function using the estimated Tchebichef moments and polynomials. In principle, a probability distribution can be reconstructed directly from its moments. However, in practice this is not viable, and other upscaling methods have to be sought (Borda-de-Água *et al.* 2012). Here, we used a method based on Tchebichef moments and polynomials, which consists of estimating the SAD moments and based on these the Tchebichef moments as follows:

$$T_n = \frac{1}{N^n \rho(n, N)} \sum_{k=0}^{n} C_k(n, N) \sum_{i=0}^{k} s_k^{(i)} M_i \tag{5}$$

where N is the number of bins in the histogram, M_i is the moment of order i, $s_k^{(i)}$ are the Stirling numbers of the first kind, $C_k(n, N)$ is

$$C_k(n, N) = (-1)^{n-k \frac{n!}{k!}} \begin{pmatrix} N-1-k \\ n-k \end{pmatrix} \begin{pmatrix} n+k \\ n \end{pmatrix},$$

and $\rho(n,N)$is

$$\rho(n,N) = \frac{N\left(1-\frac{1}{N^2}\right)\left(1-\frac{2^2}{N^2}\right)...\left(1-\frac{n^2}{N^2}\right)}{2n+1}; \, n = 0, 1, ..., N-1.$$

The Tchebichef moments are then the "weights" in the following formula,

$$f(x) = \sum_{n=0}^{N-1} T_n t_n(x) \tag{6}$$

where $t_n(x)$ are the Tchebichef polynomials (Mukundan et al. 2001). The reconstruction of a distribution becomes relevant when we extrapolate the SAD for larger areas than the sampling area, as we explain in the next section. For further information, we refer to Mukundan *et al.* (2001) and Borda-de-Água *et al.* (2012).

Comparison and evaluation of distribution

We used the log-series and log-normal distributions to fit the macro-moth data for the three different landscapes and for all landscapes together in order to evaluate whether the predicted values from the extrapolated moments followed the log-series or the log-normal distribution. For that, we measured the sum absolute error, SAE $= \sum_i |B_i$ - $\hat{B}_i|$, where B_i is the number of species expected by the lognormal or log-series fits in the bin i and $\hat{B}_i$ is the number of species predicted by the extrapolated moments in the bin i. We also used SAE to verify the efficiency of the predictions made by the moments, with a low value means good prediction.

Results

SADs

In total, we collected 22825 individuals belonging to 378 species. Most species belonged to two families: Noctuidae (39.4%) and Geometridae (38.9%). The two most abundant species were the noctuid *Xestia agathina* and the geometrid

Pachycnemia hippocastanaria, comprising 8.2% and 6.9% of all individuals collected, respectively. Most species were singletons or had between two and five individuals (15.3% and 23.0% of the species, respectively).

For all macro-moth species, ordinal logistic regression showed that the odds of moving from log-series to intermediate/log-normal distribution (or from log-series/intermediate to log-normal) increased as ln-area increases (Fig. 12). This means that the probability of being log-series distributed is highest at small areas, and that the probability of being log-normal is highest at large areas (ln-area = 0.395; t = 4.435; P = 9.17e-6) (Fig. 12; Fig. 15 in Supporting Information shows more details).

Our results also show the importance of host-plant specialisation ($R^2_{Oligophagy}$ = 0.14; $R^2_{Polyphagy}$ = 0.00) and body size (R^2_{Small} = 0.27; R^2_{Large} = 0.01) as high R^2-values indicate that the models are well fitted. Furthermore, host-plant specialism and body size have better fit than family and host-plant type as the intermediate probability fall at larger scale. For example, ordinal logistic regression showed that the odds of moving from log-series to intermediate/log-normal (or from log-series/intermediate to log-normal) increased as ln-area increased for oligophagous species, and for small species, respectively (Fig. 12). This shows that for oligophagous and small species a log-series distribution is more likely at small areas, and a log-normal distribution is more likely at large areas (ln-area$_{Oligophagy}$ = 0.412; t = 4.463; $P < 0.0001$; ln-area$_{Small}$ = 0.717; t = 5.786; $P < 0.0001$). The polyphagous and large body size species groups did not change their SAD models, which means that the log-series distribution fitted well both at small and large spatial scales (Fig. 12). For family ($R^2_{Geometrids}$ = 0.06; $R^2_{Noctuids}$ = 0.02) and host-plant type ($R^2_{Herb-feeders}$ = 0.05; $R^2_{Shrub/Tree-feeders}$ = 0.01) there was only little relationship between area and model type (Fig. 12 - first and second row).

Plotting the *ln*-transformed moments of order 1 to 11 as a function of the

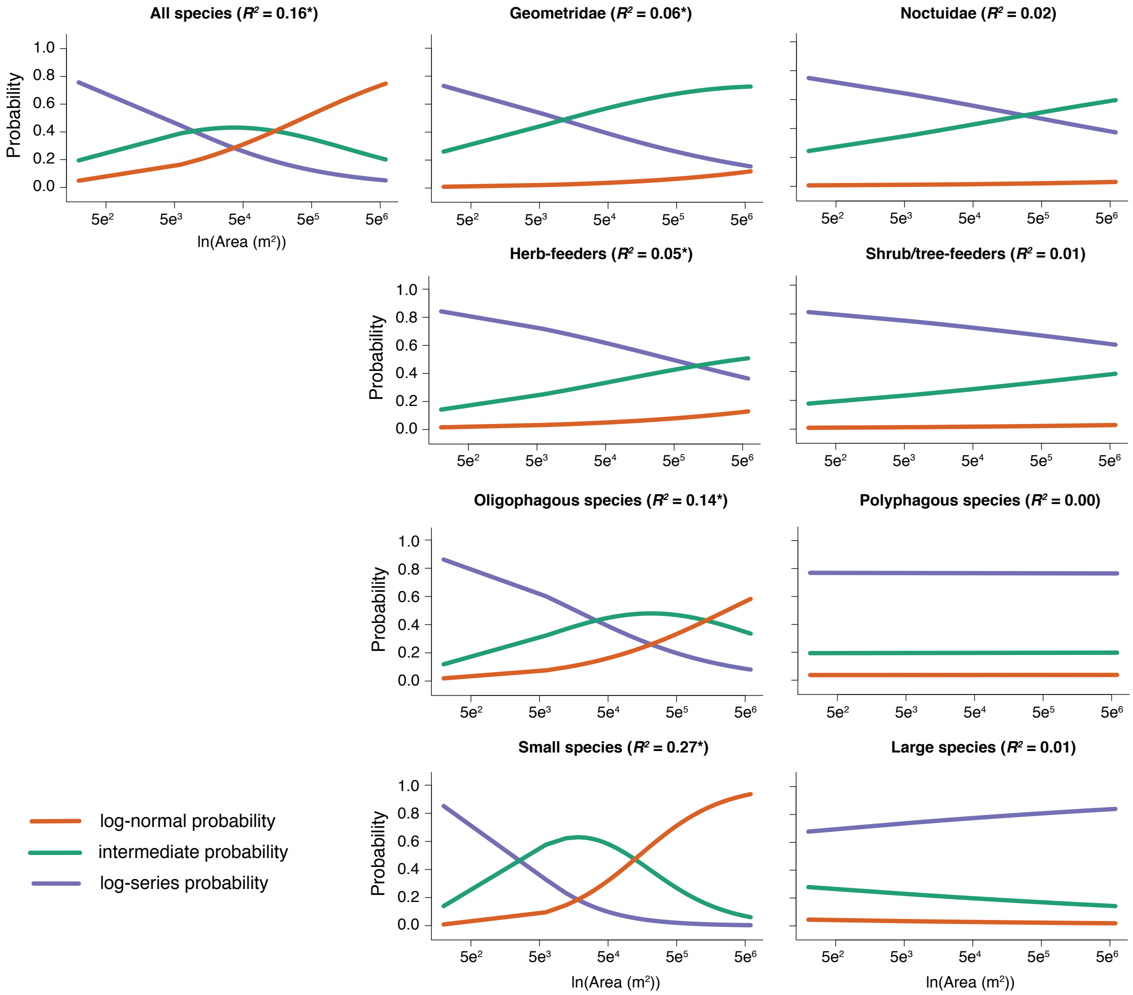

Figure 12: Probabilities for three types of species abundance distribution (SAD) –log-normal, log-series, or a combination of both ($-2 < \Delta\text{AIC} < 2$)– as a function of area (ln m^2). Panels depict relationships for all macro-moth species as well as for separate groups, contrasting geometrids versus noctuids, herb-feeding versus shrub/tree-feeding species, oligophagous versus polyphagous species, and small versus large species. Orange, green and lilac lines represent log-normal, intermediate and log-series SADs, respectively, based on ordinal logistic regression model output. R^2-values and significance levels of the odds moving distribution as function of ln-area ($* \; P < 0.05$) are given for each panel.

ln-transformed area, shows that there is an almost linear relationship (Fig. 13; Table 5), similar to previous findings (Borda-de-Água *et al.* 2012). This relationship can be used to extrapolate the SAD to larger scales. Tchebichef moments and polynomials predicted well the SADs in meadow- and shrub-dominated landscapes at the landscape scale based on the SADs at the smallest scales. However, they did not capture the rare species in the forest-dominated landscape nor in all landscapes together (Fig. 14; Fig. 16/17 in Supporting Information). The comparison of predictions from the moments with the observed distribution of species shows that SAE was smaller for small and for oligophagous species than for large and for polyphagous species (Fig. 16/17). The shrub- and meadow-dominated landscapes obtained lower SAE values than the forest-dominated landscape (Table 4).

Discussion

The principal goals of this study were to assess whether spatial scale and species traits affect the shape of SADs, and how well Tchebichef moments and polynomials predict the regional SAD using SADs from smaller spatial scales. We determined that the shape of SADs changes across spatial scales, although some species groups maintain the shape of the SAD independent of the scale. Tchebichef moments predicted the number of species well in communities which follow log-normal SADs.

Complexity arises as different species traits may interact to determine SADs (Gaston *et al.* 2000). For instance, although some polyphagous moth species may have wider distribution ranges than oligophagous species (Quinn *et al.* 1997), the latter are typically smaller than polyphagous species, and their distribution is patchier given the patchy spatial configuration of their host-plant resources (Lindström *et al.* 1994). Also, large species tend to be more widespread and hence occur at lower densities at the local scale than small species (Blackburn *et al.* 1993; Nieminen *et al.* 1999).

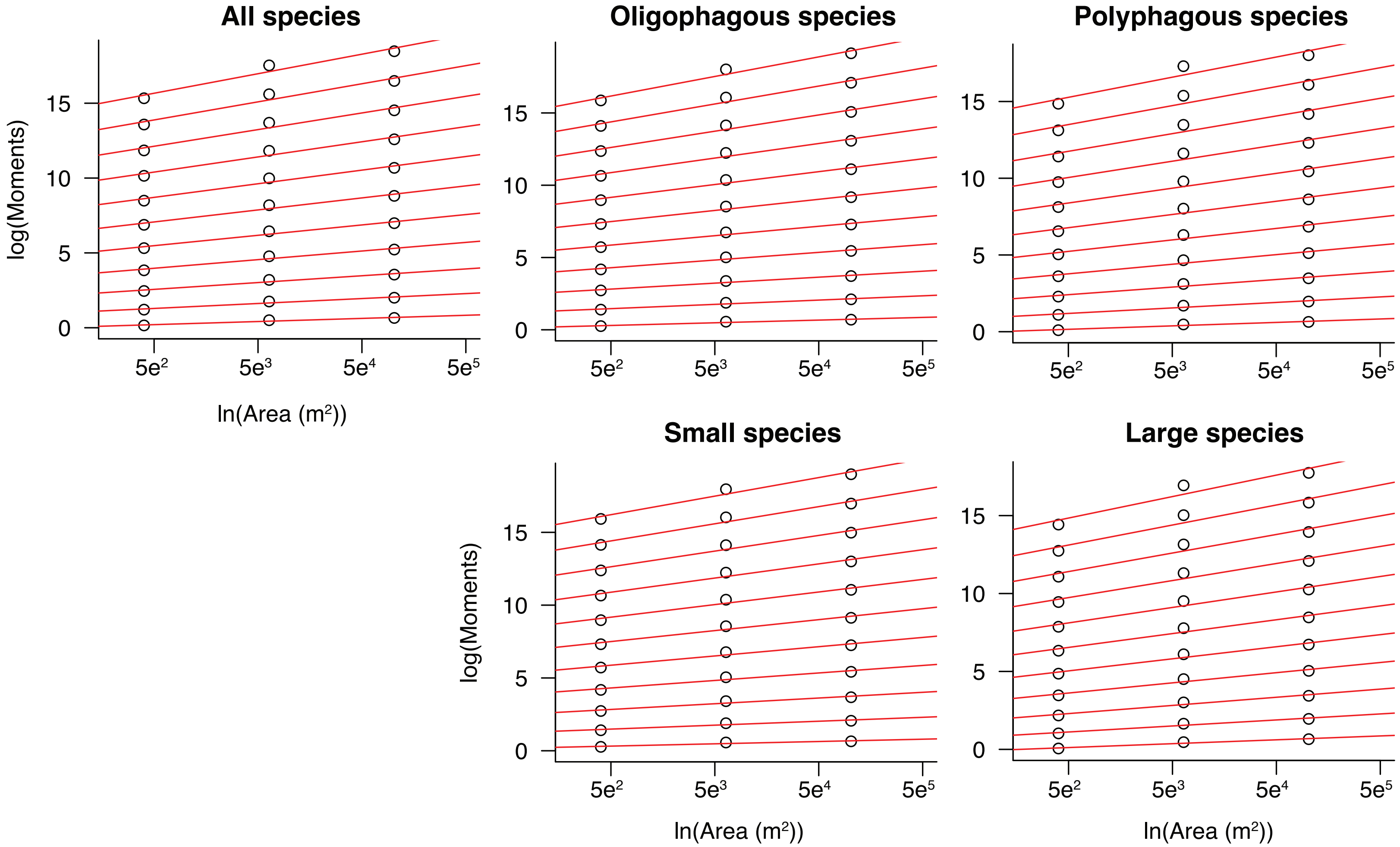

Figure 13: Plots of ln-transformed moments (1-11) of the species abundance distribution as a function of spatial scale (ln m^2). Panels depict relationships for all macro-moths as well as for separate groups, contrasting oligophagous versus polyphagous species, and small versus large species. Red lines represent the best fit of linear regression models.

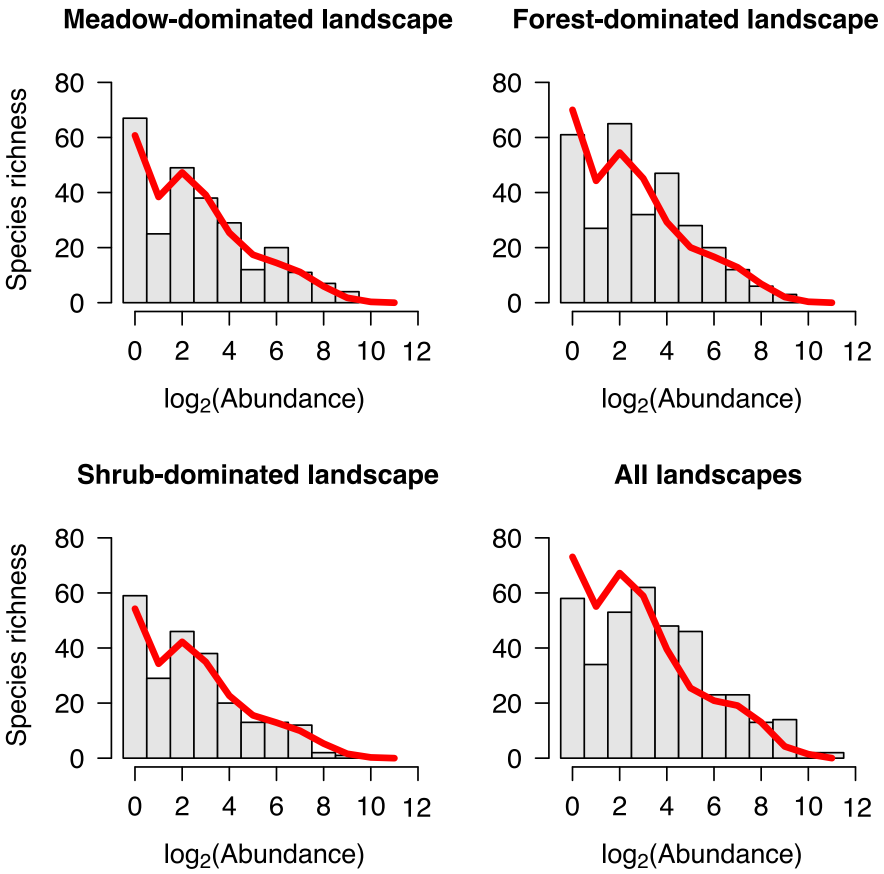

Figure 14: Species abundance distribution (SAD) for all macro-moth species, both separated according to landscape type (forest-, shrub- and meadow-dominated) as well as for all three landscapes combined. Red lines represent the number of species as predicted by the moments (n = 9) of the SAD for all species combined.

Moreover, large species are typically more mobile (Öckinger *et al.* 2010; Sekar 2012; Slade *et al.* 2013). This may explain why the SADs of small species followed the log-series distribution at the local scale, and changed to the log-normal distribution at larger scales, whilst the SADs for the large moth species followed the log-series distribution at all spatial scales. The higher dispersal capacity of large species tends to homogenise them in the metacommunity, making the SAD steeper and mode in rare species. On the other hand, small species tend to be more aggregated, and hence

Table 4: Overview of Corrected Akaike Information Criteria (AICc) to determine the best fitted between log-series and log-normal, and Sum Absolute Error (SAE) between the predicted number of species by moments and the expected number of species by log-series or log-normal distributions separated by body size and host-plant specialism in three different landscapes and all landscapes. The total number of species observed of each species group in each landscape type; by body size, 177 and 201 species are classified as small and large, respectively, and by host-plant specialism, 105 and 273 species are oligophagous and polyphagous, respectively. Bold values indicate best fitted (i.e. ΔAICc > $|2|$).

Landscape	Log-series	Log-normal	Moments
	AICc	AICc	SAE
All species			
Forest-dominated	2286.3	2287.4	82.16
Shrub-dominated	1621.0	**1612.6**	28.83
Meadow-dominated	1923.1	1921.9	40.81
All landscapes	3287.3	**3282.3**	100.76
Small species			
Forest-dominated	1128.33	**1125.70**	46.87
Shrub-dominated	659.32	**647.87**	22.01
Meadow-dominated	1180.66	**1184.01**	63.06
All landscapes	1806.10	**1808.17**	80.29
Large species			
Forest-dominated	**1153.82**	1162.46	71.03
Shrub-dominated	**960.99**	967.53	55.65
Meadow-dominated	**1180.66**	1184.01	63.06
All landscapes	**1806.10**	1808.17	80.29
Oligophagous species			
Forest-dominated	650.96	650.62	25.83
Shrub-dominated	496.25	**492.84**	20.22
Meadow-dominated	523.91	**520.43**	22.74
All landscapes	912.92	**906.86**	29.48
Polyphagous species			
Forest-dominated	**1636.65**	1640.78	110.03
Shrub-dominated	**1117.29**	1121.46	61.32
Meadow-dominated	**1400.82**	1403.89	71.61
All landscapes	**2375.09**	2379.44	125.28

more common at a given spatial scale, due to their low to intermediate mobility levels. As a consequence, the SADs of this species group show a log-normal shape. Likewise, Mouquet & Loreau (2003) observed that species rank-abundance distributions were strongly affected by the level of dispersal between spatial scales. Dornelas & Connolly (2008) also showed that spaced species are rare in abundance and dominate the rare mode of the SAD, whilst clustered species dominate the intermediate mode. Nieminen *et al.* (1999) showed that moth size and abundance tended to be negatively correlated, which suggests that small species indeed tend to be more abundant than large ones.

Some studies have shown that plant species distributions are important predictors of moth abundance, diversity and distribution (Kitching *et al.* 2000; Hilt & Fiedler 2006; Novotny *et al.* 2006). If host-plants are characterised by a patchy distribution, we would expect that oligophagous species are more aggregated than polyphagous ones. This interpretation would explain why the shape of the SADs for the oligophagous species did also change from log-series at a local scale to log-normal at larger scales, whilst it did not change for the polyphagous species.

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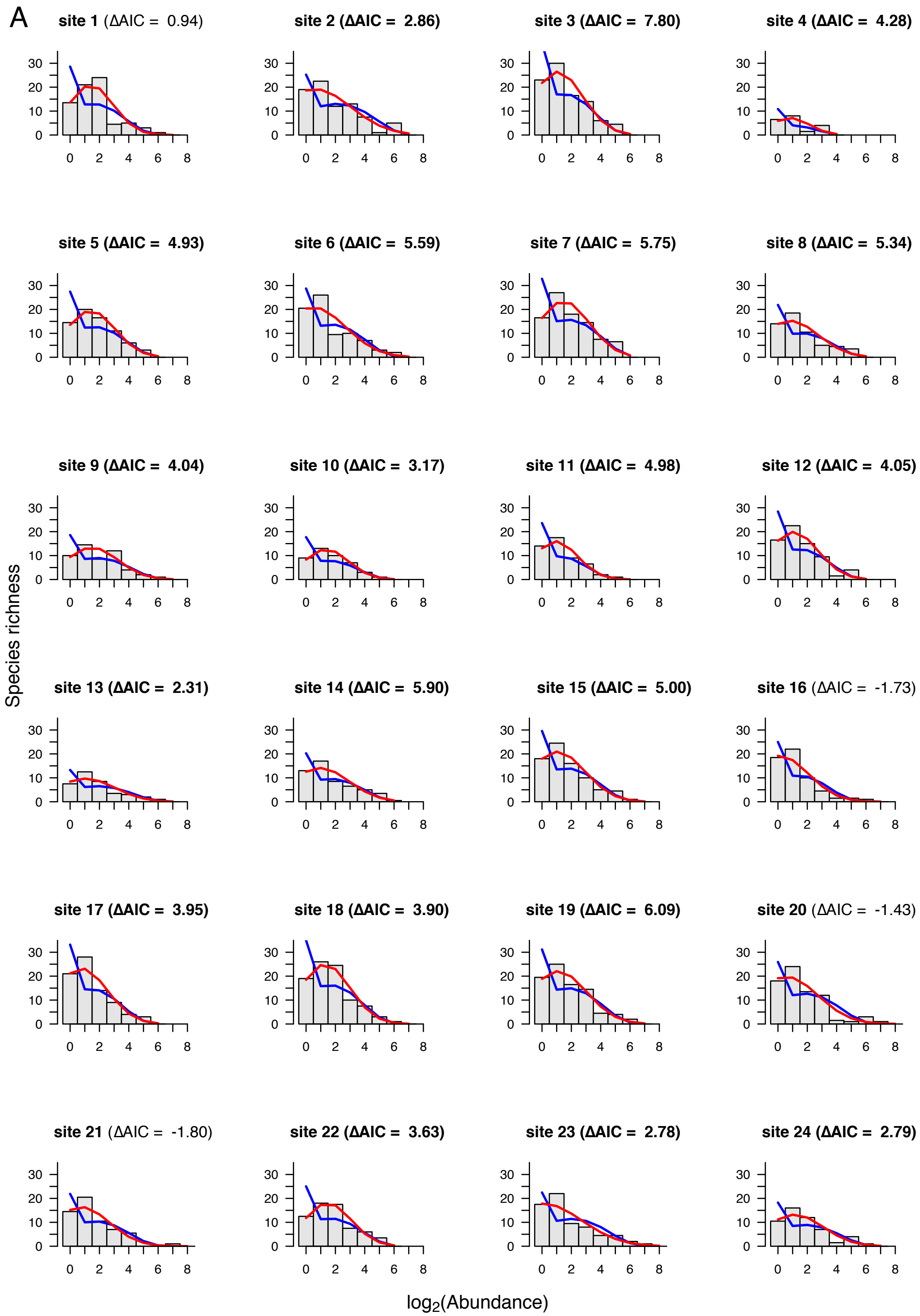
Supporting Information

Table 5: Overview of parameter output -intercepts, slopes and coefficients of determination (R^2)- of the linear regressions of the species abundance distribution moments (ln-transformed) on spatial scale (ln m^2) (see Fig. 13).

M_n	All macromoths			Oligophagous			Polyphagous			Small			Large		
	Interc.	Slope	R^2	Interc.	Slope	R^2	Interc.	Slope	R^2	Interc.	Slope	R^2	Interc.	Slope	R^2
1	-0.354	0.090	0.903	-0.200	0.080	0.955	-0.451	0.100	0.952	-0.107	0.068	0.901	-0.554	0.108	0.959
2	0.399	0.143	0.914	0.663	0.129	0.964	0.224	0.156	0.953	0.757	0.117	0.928	0.073	0.168	0.964
3	1.336	0.198	0.920	1.700	0.179	0.968	1.077	0.215	0.953	1.778	0.170	0.942	0.884	0.227	0.966
4	2.418	0.250	0.922	2.858	0.231	0.970	2.082	0.272	0.952	2.921	0.224	0.950	1.851	0.284	0.966
5	3.615	0.301	0.921	4.101	0.283	0.970	3.215	0.325	0.949	4.157	0.276	0.955	2.947	0.336	0.964
6	4.900	0.349	0.919	5.406	0.335	0.970	4.454	0.374	0.945	5.468	0.327	0.958	4.147	0.385	0.960
7	6.255	0.395	0.916	6.760	0.386	0.970	5.781	0.419	0.940	6.840	0.375	0.961	5.433	0.431	0.955
8	7.667	0.440	0.912	8.152	0.437	0.970	7.183	0.461	0.933	8.262	0.422	0.962	6.787	0.475	0.947
9	9.123	0.483	0.908	9.578	0.488	0.970	8.648	0.500	0.926	9.728	0.468	0.964	8.195	0.517	0.939
10	10.618	0.525	0.904	11.033	0.539	0.968	10.166	0.536	0.918	11.233	0.511	0.965	9.644	0.558	0.929
11	12.145	0.567	0.899	12.513	0.588	0.968	11.729	0.570	0.706	12.770	0.554	0.965	11.125	0.598	0.919


A
site 1 (ΔAIC = 0.94)
site 2 (ΔAIC = 2.86)
site 3 (ΔAIC = 7.80)
site 4 (ΔAIC = 4.28)
site 5 (ΔAIC = 4.93)
site 6 (ΔAIC = 5.59)
site 7 (ΔAIC = 5.75)
site 8 (ΔAIC = 5.34)
site 9 (ΔAIC = 4.04)
site 10 (ΔAIC = 3.17)
site 11 (ΔAIC = 4.98)
site 12 (ΔAIC = 4.05)
site 13 (ΔAIC = 2.31)
site 14 (ΔAIC = 5.90)
site 15 (ΔAIC = 5.00)
site 16 (ΔAIC = -1.73)
site 17 (ΔAIC = 3.95)
site 18 (ΔAIC = 3.90)
site 19 (ΔAIC = 6.09)
site 20 (ΔAIC = -1.43)
site 21 (ΔAIC = -1.80)
site 22 (ΔAIC = 3.63)
site 23 (ΔAIC = 2.78)
site 24 (ΔAIC = 2.79)
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10
20
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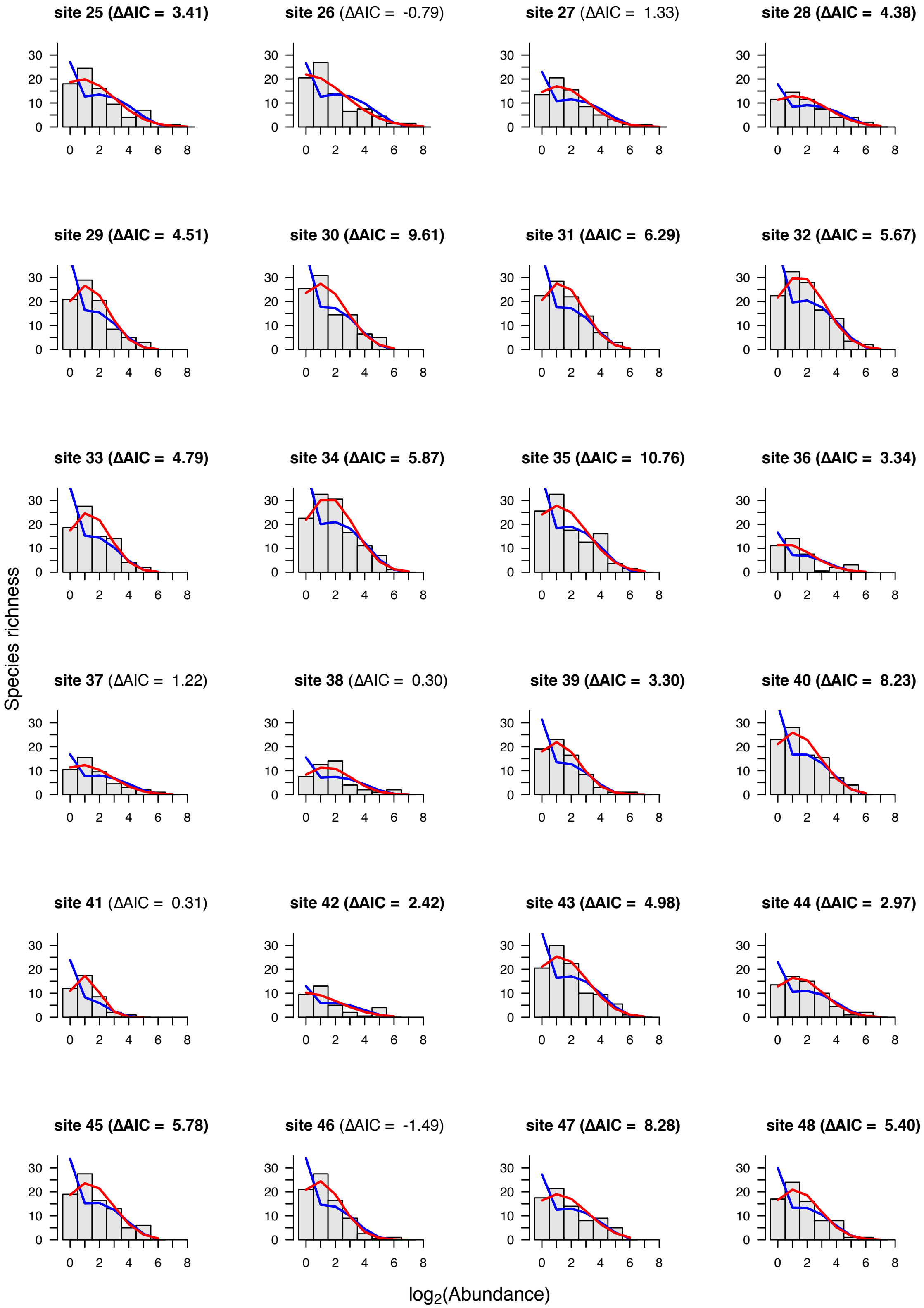
0
2
4
6
8
Species richness
$\log_2$(Abundance)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site 26 (ΔAIC = -0.79)
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site 28 (ΔAIC = 4.38)
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site 30 (ΔAIC = 9.61)
site 31 (ΔAIC = 6.29)
site 32 (ΔAIC = 5.67)
site 33 (ΔAIC = 4.79)
site 34 (ΔAIC = 5.87)
site 35 (ΔAIC = 10.76)
site 36 (ΔAIC = 3.34)
site 37 (ΔAIC = 1.22)
site 38 (ΔAIC = 0.30)
site 39 (ΔAIC = 3.30)
site 40 (ΔAIC = 8.23)
site 41 (ΔAIC = 0.31)
site 42 (ΔAIC = 2.42)
site 43 (ΔAIC = 4.98)
site 44 (ΔAIC = 2.97)
site 45 (ΔAIC = 5.78)
site 46 (ΔAIC = -1.49)
site 47 (ΔAIC = 8.28)
site 48 (ΔAIC = 5.40)
Species richness
0
10
20
30
0
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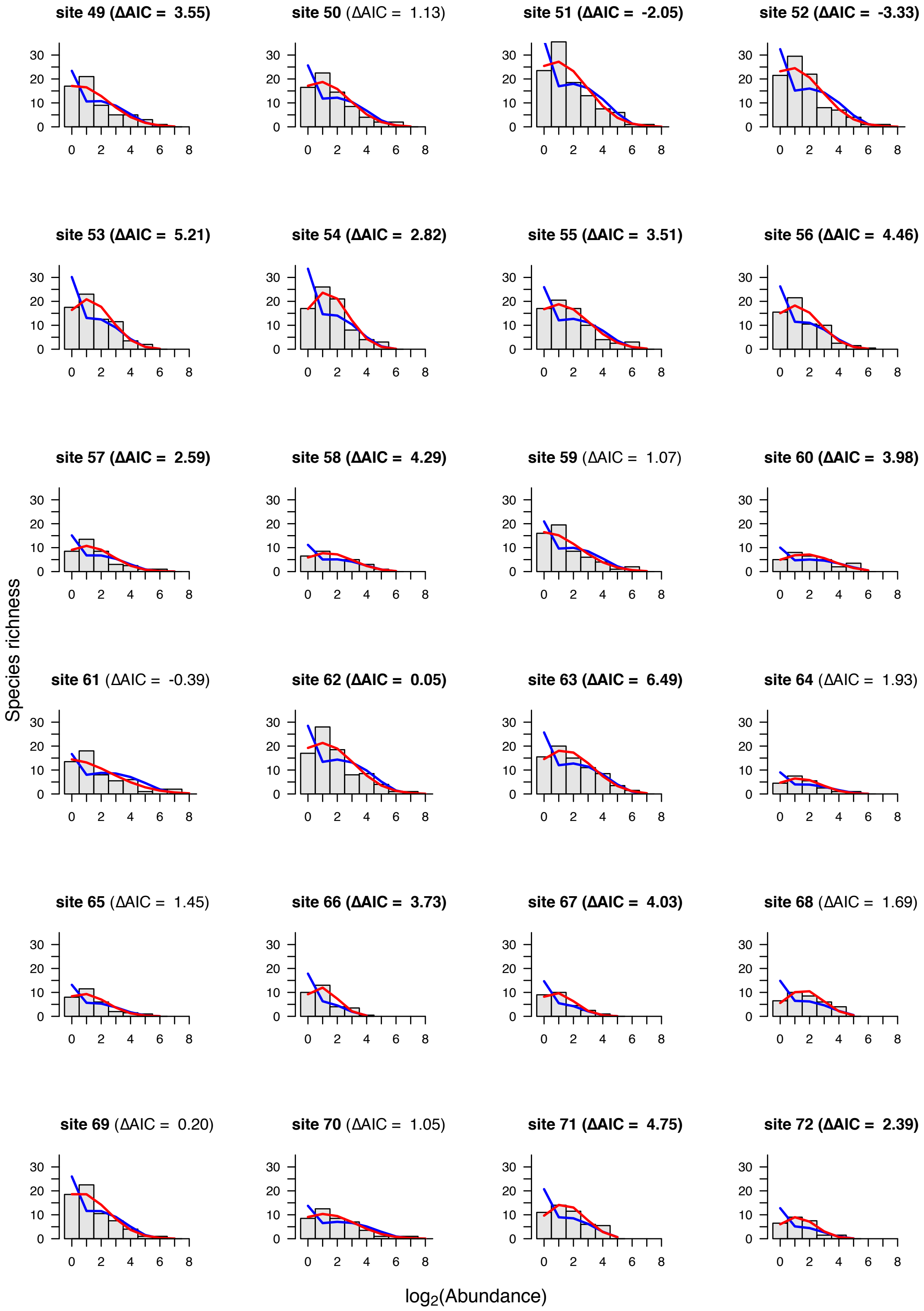
8
log$_2$(Abundance)


site 49 (ΔAIC = 3.55)
site 50 (ΔAIC = 1.13)
site 51 (ΔAIC = -2.05)
site 52 (ΔAIC = -3.33)
site 53 (ΔAIC = 5.21)
site 54 (ΔAIC = 2.82)
site 55 (ΔAIC = 3.51)
site 56 (ΔAIC = 4.46)
site 57 (ΔAIC = 2.59)
site 58 (ΔAIC = 4.29)
site 59 (ΔAIC = 1.07)
site 60 (ΔAIC = 3.98)
site 61 (ΔAIC = -0.39)
site 62 (ΔAIC = 0.05)
site 63 (ΔAIC = 6.49)
site 64 (ΔAIC = 1.93)
site 65 (ΔAIC = 1.45)
site 66 (ΔAIC = 3.73)
site 67 (ΔAIC = 4.03)
site 68 (ΔAIC = 1.69)
site 69 (ΔAIC = 0.20)
site 70 (ΔAIC = 1.05)
site 71 (ΔAIC = 4.75)
site 72 (ΔAIC = 2.39)
Species richness
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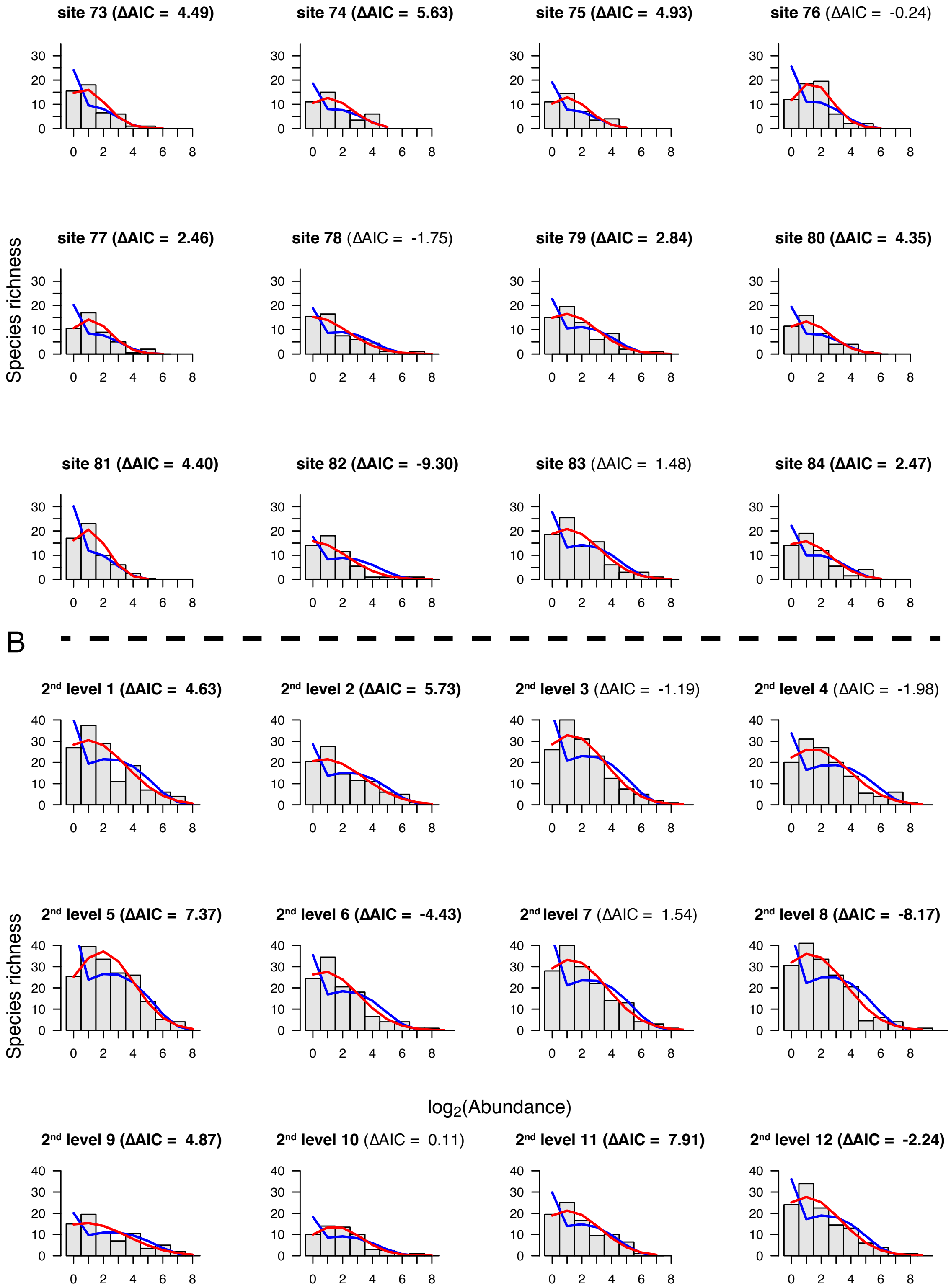
log2(Abundance)


site 73 (ΔAIC = 4.49)
site 74 (ΔAIC = 5.63)
site 75 (ΔAIC = 4.93)
site 76 (ΔAIC = -0.24)
site 77 (ΔAIC = 2.46)
site 78 (ΔAIC = -1.75)
site 79 (ΔAIC = 2.84)
site 80 (ΔAIC = 4.35)
site 81 (ΔAIC = 4.40)
site 82 (ΔAIC = -9.30)
site 83 (ΔAIC = 1.48)
site 84 (ΔAIC = 2.47)
Species richness
0
10
20
30
0
2
4
6
8
B
2nd level 1 (ΔAIC = 4.63)
2nd level 2 (ΔAIC = 5.73)
2nd level 3 (ΔAIC = -1.19)
2nd level 4 (ΔAIC = -1.98)
2nd level 5 (ΔAIC = 7.37)
2nd level 6 (ΔAIC = -4.43)
2nd level 7 (ΔAIC = 1.54)
2nd level 8 (ΔAIC = -8.17)
2nd level 9 (ΔAIC = 4.87)
2nd level 10 (ΔAIC = 0.11)
2nd level 11 (ΔAIC = 7.91)
2nd level 12 (ΔAIC = -2.24)
Species richness
0
10
20
30
40
log$_2$(Abundance)

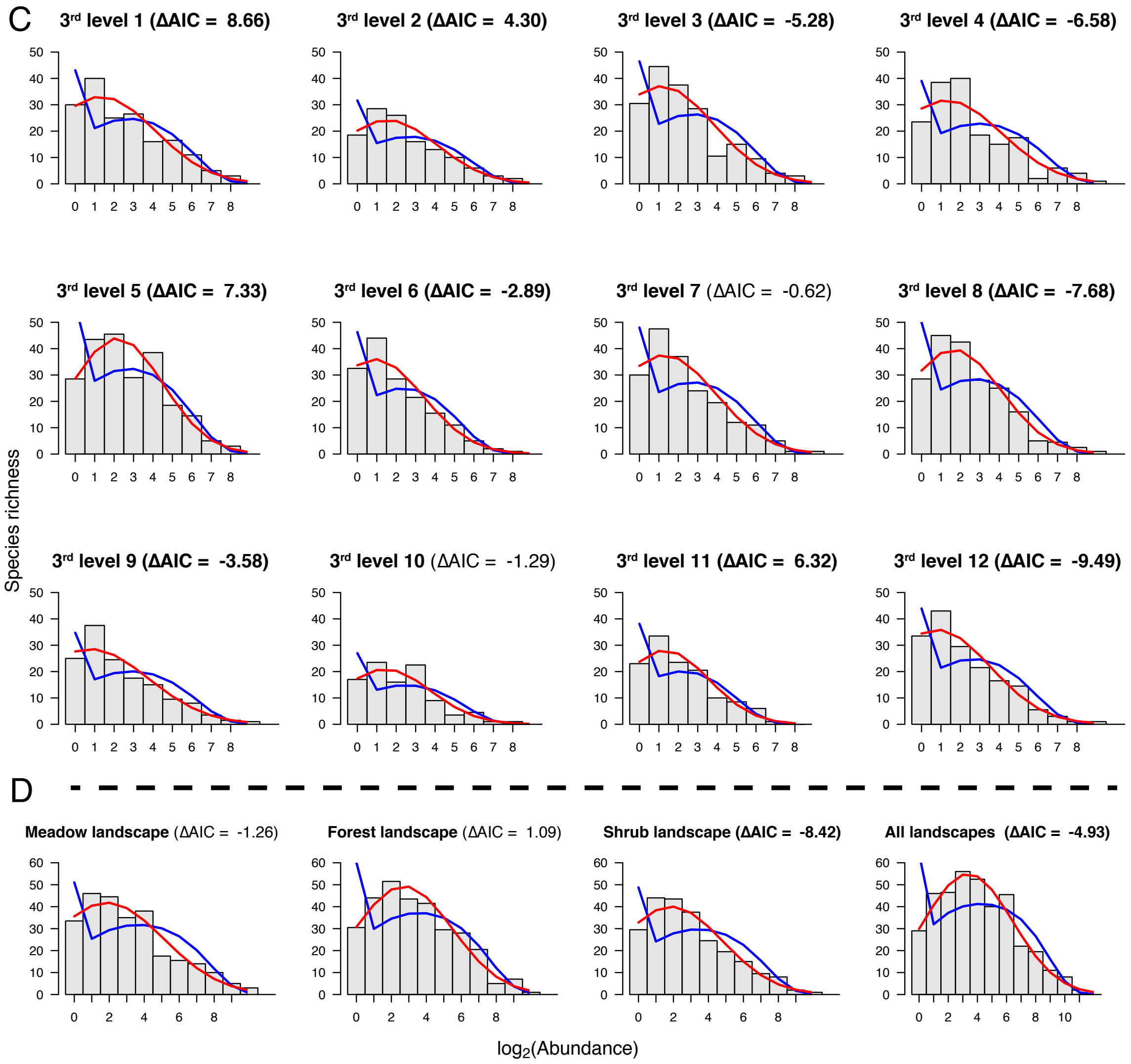


Figure 15: Histograms correspond to the species abundance distribution through spatial scale. (A) 84 sampling site which represent the first scale, (B) 12 second scale, (C) 12 third scale, (D) 3 landscapes which represent the fourth scale and an extra scale with all landscapes together. Blue and red lines represent log-series and log-normal distributions, respectively. Bold value indicates difference between log-normal and log-series (ΔAICc $> |2|$). When ΔAICc ≤ -2 the log-normal SAD model is considered to provide a better fit, whilst ΔAICc ≥ 2 indicates a better fit for the log-series model. Models characterised by $-2 < \Delta$AICc < 2 were classified as intermediate ones, with both the log-normal and log-series providing an equally good fit.

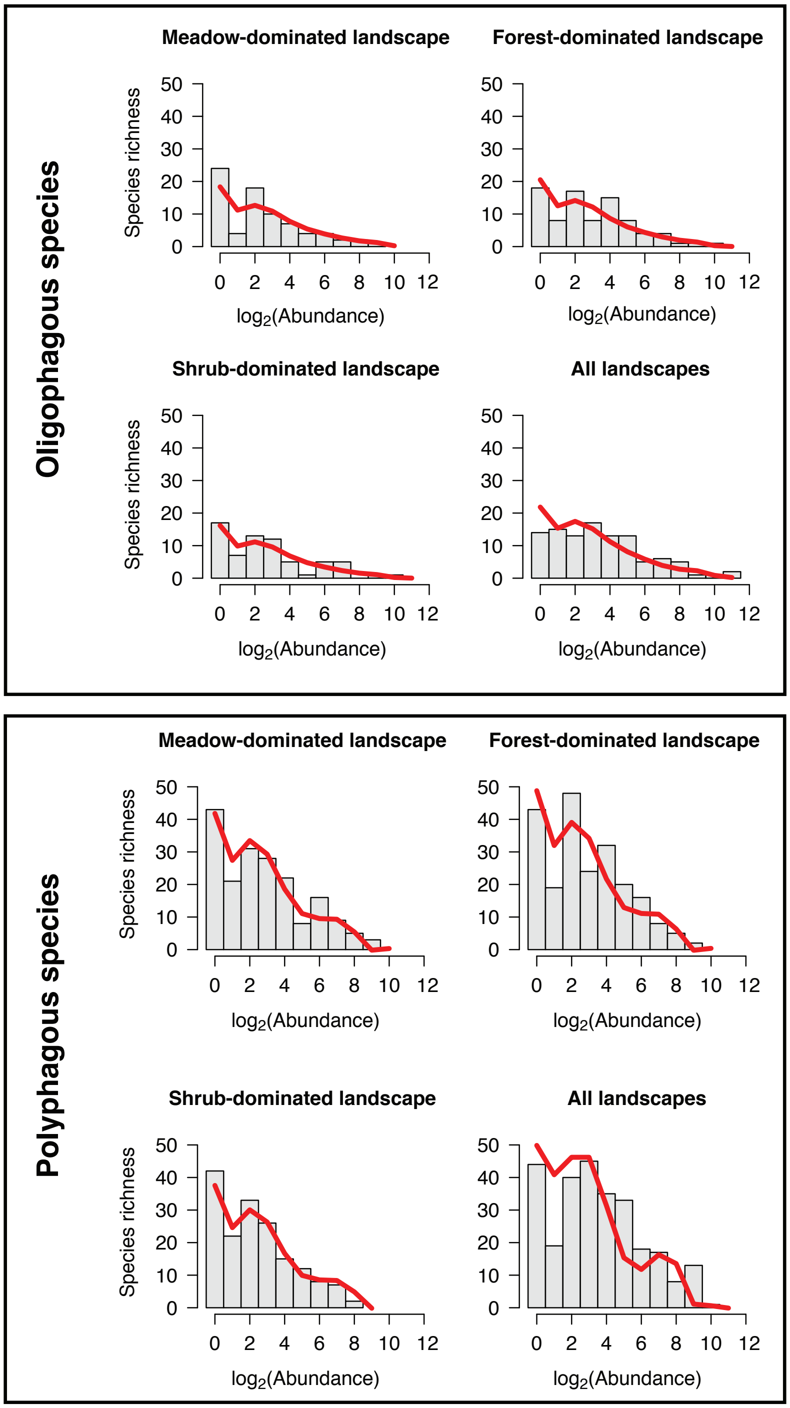


Figure 16: Histograms correspond to the species abundance distribution for host-plant specialism separated into four panels: three different landscapes (forest, shrub and meadow) and for all landscapes. Red line represents the number of species predicted by moments (n = 9).

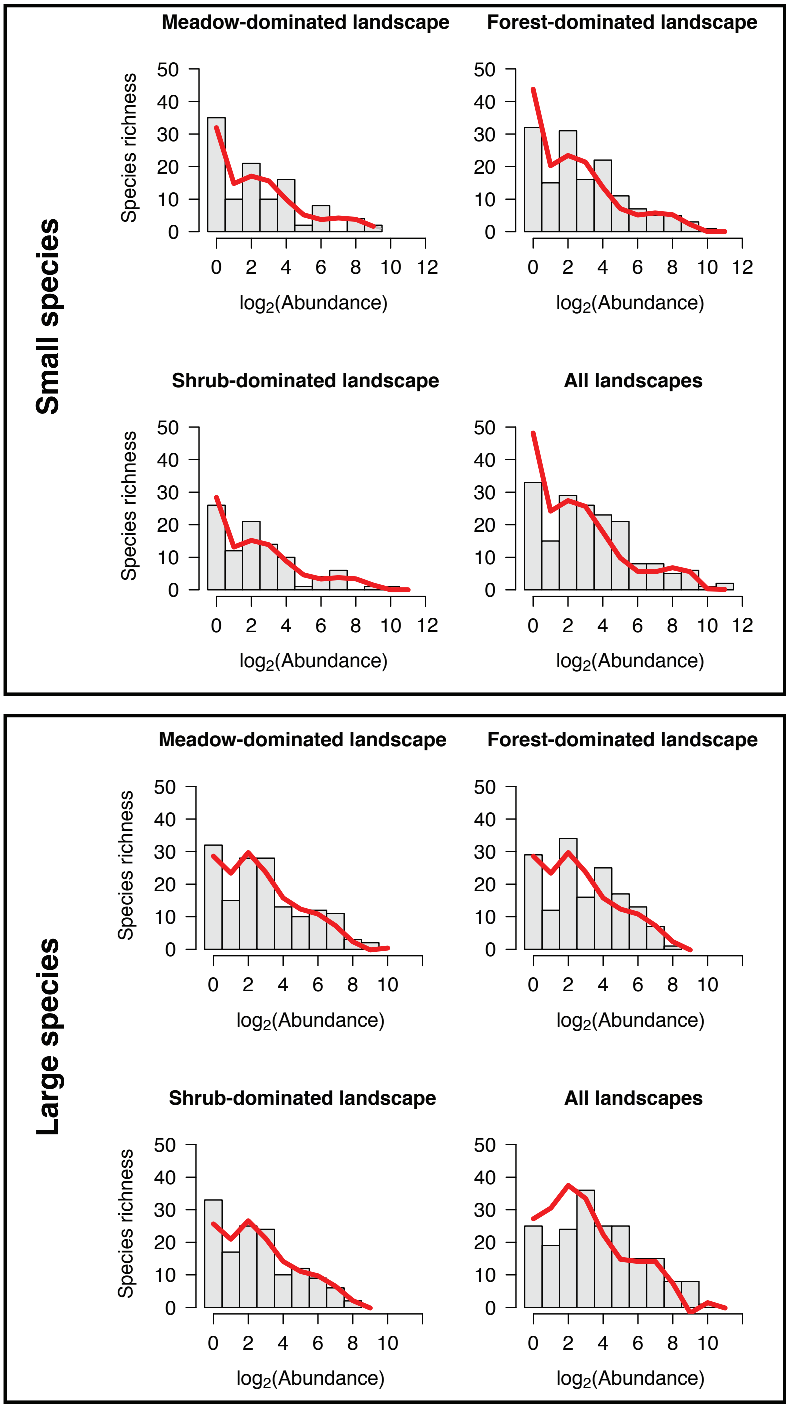


Figure 17: Histograms correspond to the species abundance distribution for body size separated into four panels: three different landscapes (forest, shrub and meadow) and for all landscapes. Red line represents the number of species predicted by moments (n = 9).

Chapter 5

Synthesis

This study aims to contribute for a better understanding of species richness and species abundance patterns across spatial scales. We asked the following three questions:

i) how is species richness affected by the habitat amount and landscape configuration (patch size and isolation)? (chapter 2),

ii) how does beta diversity vary across scales in different land-uses? (chapter 3), and

iii) how does species abundance change across spatial scale and how can species traits shape the spatial distribution? (chapter 4).

Habitat amount, not patch size and isolation

In chapter 2, habitat amount predicts species richness better than do patch size and patch isolation, suggesting that both the patch size and isolation effects are driven by a single underlying 'sample area effect' as suggested by Fahrig (2013). Moreover, the countryside SAR is a much better tool to predict species richness than the classic SAR because countryside SAR takes into consideration information associated to the effective amount and variety of habitats used by different species groups. Previous studies had also found that the countryside SAR explains species richness patterns as a function of habitat area better than the classic SAR (in taxa plants, birds, amphibians, reptiles) (Guilherme & Pereira 2013; Proença & Pereira 2013; Martins *et al.* 2014).

We highlighted the similarities and differences between the countryside SAR and the habitat amount hypothesis, and then suggested that they should been used as complementary approach. Both methods stress the idea that each species group uses available resources in the landscape. The countryside SAR explains how the number of species in a given region changes with habitat area (i.e. gamma and beta diversity), while the habitat amount hypothesis explains the number of species in specific habitat types (i.e. alpha diversity). However, both approaches have some limitations. For example: countryside SAR ignores the influence of the landscape context on large scale, while the habitat amount hypothesis does not give any information on how biodiversity changes across scales. Both methods say nothing about individual species or about the effects of patch size and connectivity.

Although these results of both the SAR and autocovariate models provide support for the habitat amount hypothesis, it is important that other tests follow suit in order to better assess the applicability of this hypothesis. The other tests should consider comparing the responses of various taxonomic groups to habitat amount, each at their appropriate scale of effect (Ricketts *et al.* 2001; Eigenbrod *et al.* 2008), in order to determine whether habitat amount is indeed a good and sufficient predictor for species richness. Previous studies had also found that species richness increases with increasing amount of forest habitat (in taxa orthopteran and birds) (Sánchez-Zapata & Calvo 1999; Marini *et al.* 2008, 2009). In conclusion, results from our large-scale study show that species richness of both forest and meadow macro-moths respond more strongly to the total amount of habitat in the local landscape surrounding the sample site than the habitat patch configuration. As such, these results provide evidence - at least for macro-moths - supporting the habitat amount hypothesis.

Moth diversity patterns under farmland abandonment

Results from chapter 3 compared species diversity of macro-moth communities in three different habitats, representing a gradient of farmland abandonment. Both alpha and beta diversity were overall considerably higher in forest than in both shrub and meadow habitats. Nevertheless, meadow habitat showed the highest spatial turnover rate, although forest habitat was characterised by a high turnover rate too, especially for forest species.

At local and landscape scales, forest habitat displayed higher alpha and gamma diversity than both shrub and meadow habitat. In a similar vein, Beck *et al.* (2002), while studying diversity of one specific family of macro-moths (geometrids) in Borneo, showed that primary and old-grown regenerated forest sites are characterised by a much higher diversity of geometrid moths than agricultural sites. Recent studies have established that even open-biotope species can react positively to the degree of woody cover in their landscapes (Warren & Key 1991; Wagner *et al.* 2003; Kivinen *et al.* 2006). This indicates that trees and shrubs are providing essential resources, in a similar fashion to a more sheltered micro-climate (Merckx *et al.* 2008, 2010).

The analysis performed in chapter 3 showed that the differentiation between habitats in species diversity occurred for all q values. This indicates that these differences occurred for both rare and common species. However, for non-forest species the inter-habitat differentiation only occurred at low values of q, indicating that the diversity differences are due to differences in the diversity of rare species only. Results also showed that the observed beta diversity was consistently larger than the beta diversity expected by chance. This observation suggests that the size of the regional species pool for the three habitat types cannot entirely explain the geographical distribution of their beta diversity, and that macro-moth communities were additionally shaped by ecological assembly mechanisms and/or random processes (Chase 2014; Tucker *et al.* 2016).

To summarize, understanding the effect of farmland abandonment on the diversity levels of native biodiversity is important to possibly mitigate ecological impacts on biodiversity. We showed that at a late stage of ecological succession following farmland abandonment (i.e. native woodland) is characterised by the highest diversity levels of macro-moths. But, our results also showed the importance of retaining sufficient spatial habitat heterogeneity for macro-moth diversity, especially for rare non-forest species.

Species traits shape the relationship between local and regional SADs

In chapter 4, the shape of SADs was evaluated to verify whether spatial scale and species traits would affect it, and how well Tchebichef moments and polynomials predict the regional SAD using SADs from smaller spatial scales. Our results showed that the shape of SADs changes across spatial scale as well as it depends on some species traits. Tchebichef moments predicted the number of species well in communities which follow log-normal SADs.

Body size and host-plant specialisation influenced the shape of SADs for macro-moths because they might influence the spatial structure. For instance, large species are typically more mobile (Öckinger *et al.* 2010; Sekar 2012; Slade *et al.* 2013) and some polyphagous moth species may have wider distribution ranges than oligophagous species (Quinn *et al.* 1997). This explains why the SADs for polyphagous and large species followed the log-series distribution both at the local and regional scale. On the other hand, small and oligophagous species followed the log-series at local scale and changed to the log-normal distribution at larger scales as they tend to be more aggregated, and hence more common on a local spatial scale, due to their low to intermediate mobility levels. In summary, these results highlight that some species traits interfere with the shape of SADs, and show how SADs change across spatial scales.

In conclusion, this thesis offers new insights about the effects of land-use change on biodiversity, in particular the effect of farmland abandonment. Our results show that, in order to maintain high biodiversity in a landscape it is important to take into account the habitat amount and also the surrounding matrix as previous studies has found that the quality of the landscape matrix is known to be able to influence species richness (Cook *et al.* 2004; Prevedello & Vieira 2010). Likewise, it is important to maintain a sufficient spatial heterogeneity of the habitats within a landscape (Kessler *et al.* 2009). In addition, our finding suggest that all gradients of farmland abandonment have conservation value for macro-moths, since specialist species were found in all the different habitats. Similarly, it is important to consider multiple scales and species traits for effective macro-moth conservation since each scale or trait might affect macro-moth community composition in different ways (Summerville *et al.* 2006; Merckx 2015).

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Appendix

Curriculum Vitae

Murilo Dantas de Miranda

CONTACT INFORMATION	E-mail: biomurilodantas@gmail.com	
EDUCATION	**Ph.D., Biology**	2013-present
	Martin Luther University Halle-Wittenberg (MLU)	
	Advisor: Prof. Dr. Henrique M. Pereira	
	M.S., Biometrics	2010-2012
	Department of Biostatistics, São Paulo State University, Brazil	
	B.S., Biology	2005-2009
	Depatment of Biology, Feira de Santana State University, Brazil	
PROFESSIONAL EXPERIENCE	**Training**	2012
	São Paulo Research Foundation, Brazil. I spent three months developing a package called *sads* in R.	
	Assistant Professor	2011
	Department of Biostatistics, São Paulo State University, Brazil. I taught Biomathematics for undergraduate students.	
STATISTICAL PACKAGE	*sads*: Maximum Likelihood Models for Species Abundance Distributions (2016 - version 0.3.1) in R. Paulo Inacio Prado, **Murilo Dantas de Miranda** and Andre Chalom.	

FELLOWSHIPS	PhD fellowship from CNPq, Brazil	2012-2017
	Master scholarship from FAPESP, Brazil	2010-2012
	Undergraduate scholarship from PROBIC	2006-2009
TEACHING ASSISTANT	**Spatial Ecology and Modelling** Martin-Luther-University Halle-Wittenberg. Taught by Henrique Pereira	2014
	Nature Conservation Martin-Luther-University Halle-Wittenberg. Taught by Henrique Pereira	2014
	Introduction to Informatics São Paulo State University, Brazil. Undergraduate course for students of Animal Science.	2011
SKILLS	**Software:** Linux, Windows, R, ESRI ArcGIS, LaTeX, C Markdown.	
	Statistics: Generalized linear models, mixed effects models, multivariate statistics, data visualization, model selection, likelihood optimization, bootstrap	
	Languages: English (upper-intermediate), Portuguese (native), Spanish (intermediate)	

Halle(Saale), den 06.07.2017

Murilo Dantas de Miranda

List of publications and conference participations

Publications of the dissertation

- **Miranda, M.D.**, Merckx, T., Pereira, H.M. *in preparation.* Habitat amount, not patch size or isolation, drivers species richness of macro-moth communities in countryside landscapes.
- **Miranda, M.D.**, Corley, M, Pereira, H.M., Merckx, T. *in preparation.* Moth diversity patterns under farmland abandonment.
- **Miranda, M.D.**, Borda-de-Água, L., M, Merckx, T., Pereira, H.M. *in preparation.* Species traits shape the relationship between local and regional species abundance distributions.

Peer-reviewed journal

- Ceausu S., Borda-de-Água L., Merckx T., Sapage M., **Miranda M.**, Pereira H. M. *in preparation.* High-impact journals publish papers with high statistical significance.
- Schipper A.M., Belmaker J., **Miranda M.D.** & 17 authors (2015) Contrasting changes in the abundance and diversity of North American bird assemblages from 1971 to 2010. Global Change Biology 22: 3948-3959.
- Pereira H.M., Ziv G., **Miranda M.D.** (2014) Countryside species-area relationship as a valid alternative to the matrix-calibrated species-area model. Conservation Biology 28: 874-876.

Talks and posters in international conferences

- 2015 - **27th International Congress for Conservation Biology, 4th European Congress for Conservation Biology**, Montpellier, France - Agriculture homogenizes diversity (poster)
- 2015 - **iDiv conference**, Leipzig, Germany - Patterns of macro-moth at multiple spatial scales within a context of farmland abandonment (talk)

Authors' contributions

Chapter 2

Miranda, M.D., Merckx, T., Pereira, H.M. Habitat amount, not patch size or isolation, drivers species richness of macro-moth communities in countryside landscapes. Manuscript

Analysis: **Miranda, M.D.** (60%), Merckx, T. (30%), Pereira, H.M. (10%)

Writing: **Miranda, M.D.** (40%), Merckx, T. (40%), Pereira, H.M. (20%)

Chapter 3

Miranda, M.D., Corley, M., Pereira, H.M., Merckx, T. Moth diversity patterns under farmland abandonment. Manuscript

Analysis: **Miranda, M.D.** (75%), Merckx, T. (20%), Pereira, H.M.(5%), Corley, M. (data contributions)

Writing: **Miranda, M.D.** (50%), Merckx, T. (40%), Pereira, H.M. (10%), Corley, M. (corrections)

Chapter 4

Miranda, M.D., Borda-de-Água, L., Merckx, T., Pereira, H.M. Species traits shape the relationship between local and regional species abundance distributions. Manuscript

Analysis: **Miranda, M.D.** (55%), Borda-de-Água, L. (30%), Merckx, T. (10%), Pereira, H.M. (5%)

Writing: **Miranda, M.D.** (50%), Borda-de-Água, L. (10%), Merckx, T. (35%), Pereira, H.M. (5%)

Eigenständigkeitserklärung

Hiermit erkläre ich, dass die Arbeit mit dem Titel "Biodiversity response to land use change across scales" bisher weder bei der Naturwissenschaftlichen Fakultät I Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde. Ferner erkläre ich, dass ich die vorliegende Arbeit selbstständig und ohne fremde Hilfe verfasst sowie keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe. Die den Werken wörtlich oder inhaltlich entnommenen Stellen wurden als solche von mir kenntlich gemacht. Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe.

Halle (Saale), den 06.07.2017

Murilo Dantas de Miranda