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RESEARCH PAPER

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

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Abstract

Aim: Our aim was to test whether species richness patterns are best explained by the effect of the total amount of habitat within the landscape, or instead by a combination of patch size and patch isolation effects. To this end, we jointly contrast the habitat amount hypothesis and countryside biogeography with patch size and isolation concepts from island biogeography.

Location: Three multi-habitat landscapes in Peneda-Gerês National Park, NW Portugal.

Taxon: Macro-moths (Lepidoptera).

Methods: Light-trapping using a semi-nested design at 84 fixed sites which were each repeatedly sampled six times.

Results: Autocovariate models show that sampling sites with a higher number of forest and meadow macro-moth species (alpha diversity) were surrounded by a higher amount of forest and meadow habitat, respectively within a 160 and 320 m radius (scale of effect). These top-ranked models, containing only habitat amount as a significant variable, had lower Akaike's information criteria (AIC) than models (only) containing patch size and/or isolation. Complementary to this, the countryside species–area relationship (SAR) model outperforms the classic SAR model, so that the effective area of habitat explains landscape species richness (gamma diversity) across spatial scales (beta diversity) better than the classic SAR. Specifically, we show that forest macro-moths have a higher spatial turnover than meadow macro-moths and that, on average, there are more species in forest than in meadow habitat.

Main conclusions: The habitat amount hypothesis predicts alpha species richness in multi-habitat landscapes better than do patch size and isolation while the countryside SAR predicts beta and gamma diversity better than the classic SAR. We suggest that evidence is mounting to revise the application of the classical approaches of island biogeography and metapopulation theory to conservation biogeography.

KEYWORDS

countryside SAR, farmland abandonment, habitat amount hypothesis, habitat fragmentation, habitat patch concept, Lepidoptera, moths, multi-habitat landscape, multi-scale approach, natural succession

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Thomas Merckx and Murilo Dantas de Miranda should be considered joint first author.

1 | 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 used as an inspiration by Levins (1969), Hanski (1982) and others to develop metapopulation theory based on an analogy between habitat fragments and islands (Haila, 2002), where patch size and isolation correspond to island size and isolation. 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 underlying "sample area effect", and she suggested instead that the sum of the amount of habitat in the landscape surrounding a sample site—at relevant spatial scales—would be a better indicator for predicting sample site species richness than the size and isolation of the patch containing the sample site (i.e. the habitat amount hypothesis).

The "sample area effect" is indeed one of the mechanisms behind the widely known 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, Russell, Gittleman, & Brooks, 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, Mylonas, Lika, & Vardinoyannis, 2003). Pereira and Daily (2006) proposed a method for studying patterns of species richness in multi-habitat landscapes: the "countryside" SAR (cSAR). 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 habitat types 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 cSAR model provides an interesting complement for the habitat amount hypothesis. While the habitat amount hypothesis looks at how patterns of point or alpha diversity (or species density [Phillips, Halley, Urbina-Cardona, & Purvis, 2018]) are influenced by the surrounding landscape, the cSAR looks instead at the patterns of gamma diversity in any portion or the totality of the landscape and how they depend on the habitat composition of that part of the landscape (Figure 1). The cSAR assumes that what drives species richness of a group of species in a part of the landscape is the amount of resources available in that area, ignoring the effects of larger spatial scales. But in both approaches, there is the key idea that each group of species perceives a landscape in a different way, depending on its habitat affinities, and that the area of habitat has a dominant effect on species richness.

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, Bert, & Fahrig, 2004; Jackson & Fahrig, 2012, 2015). This is important, as the use of an inappropriate spatial scale may make it impossible to capture the relationship between species richness and the amount of habitat, which would lead to erroneous conclusions (Holland, Fahrig, & Cappuccino, 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, Huertas, Basset, & Thomas, 2013). Macro-moths were collected using a semi-nested sampling design in three countryside landscapes with variable habitat composition, comprising a total of 84 equally sized sites. Our aim was to test whether point species richness of local communities is best explained by the effect of the total amount of habitat within the surrounding 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 (a) species richness will be more strongly related to habitat amount than to patch size and isolation and (b) when habitat amount in the local landscape is taken into consideration, patch size and isolation should no longer be important to explain the variance in richness among patches. Complementary to this, we test whether the countryside

FIGURE 1 Habitat amount hypothesis versus countryside species–area relationship (cSAR). A landscape with three land cover types is represented (white, grey and black). In the habitat amount hypothesis, the number of species in a site (red dot), i.e. the alpha or point diversity of a patch, depends on the amount of habitat surrounding that site (red circle). In the cSAR, the number of species in any sampling window (small and large blue squares) depends on the composition and the size of that landscape window. This gamma diversity can be sampled by combining the species from the sites within a window (blue dots). Therefore, the cSAR estimates gamma diversity across scales, from the entire landscape all the way down to local alpha diversity (corresponding to a window of the size of a blue dot), accounting for beta diversity but assuming no effect of habitat outside a given sampling window

SAR explains landscape species richness (gamma diversity) across spatial scales (beta diversity) better than the classic SAR. We expect that the effective area of habitat, consisting of the summed area of different habitats weighted by resource density, is a better predictor of species richness than the total sampled area used in the classic SAR. Summarized, our study empirically tests whether and to what extent the habitat amount hypothesis and countryside biogeography perform better than the classical approach.

2 | MATERIALS AND METHODS

2.1 | Study sites

The study was conducted in the Castro Laboreiro area (*c.* 42°2′N, 8°10′W) within the Peneda-Gerês National Park, NW Portugal (Figure 2). Within our study area (50 km^2), scrub (78.4%) is the dominant land cover, followed by forest (10.5%), agricultural land (9.8%) and urban area (1.3%). The mountainous region of the National Park (altitude: 300–1,340 m a.s.l.) lies at a transitional zone between the Atlantic and Mediterranean biogeographic zones.

2.2 | Sampling design

Macro-moths were light-trapped in two consecutive years (2011–2012), across three landscapes (altitude: 750–1,155 m a.s.l.) representing a natural succession gradient, from an agricultural landscape (i.e. meadow-dominated), over a mid-successional landscape (i.e. scrub-dominated) to a landscape with climax vegetation (i.e. forest-dominated) (Figure 2). For each landscape, 28 fixed circular

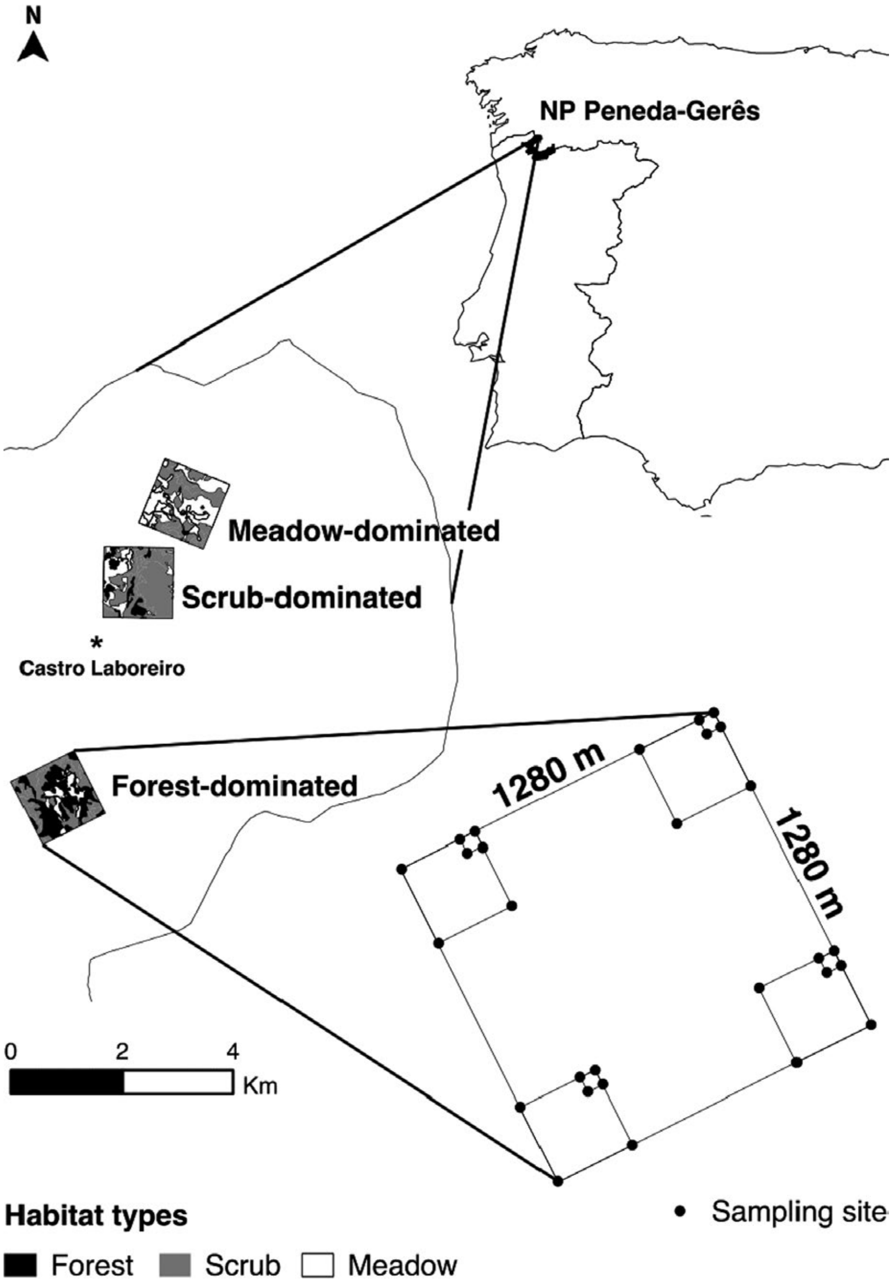

FIGURE 2 Study area and sampling design. Map of study area and macro-moth sampling sites near the town of Castro Laboreiro in Peneda-Gerês National Park, NW Portugal. Eighty-four fixed light-trap sampling sites were part of a semi-nested sampling design covering three study landscapes that represented a natural succession gradient

sampling sites of 0.03 ha were set up using a semi-nested design (Proença & Pereira, 2013) (Figure 2): sampling sites were aggregated in two groups of four, with each site placed on a corner of either a 80 × 80 m square (0.64 ha) or a 320 × 320 m square (10.24 ha). These 320 × 320 m squares were similarly aggregated in groups of four to form the 1,280 × 1,280 m landscapes (163.84 ha). Species–area relationships were fitted using species–area data at five spatial scales: 0.03, 0.64, 10.24, 163.84 and 491.52 ha, the latter scale being the sum of the three individual landscapes. Fitted curves were similar to a type IIIA curve (*sensu* Scheiner, 2003) as we used semi-nested data (0.03–163.84 ha) from spaced sampling plots, while we assumed that each scale was well sampled by the 0.03 ha sampling sites (e.g. the 0.64 ha scale was sampled as the union of the species occurring at the four 0.03 ha sites at the square corners). After the superposition of the fixed semi-nested configuration of sampling sites on each of the three landscapes, the on-site habitat type of all sampling sites (i.e. 10 m radius circles; 0.03 ha) was ground-truthed and sampling sites were classified into three classes according to the dominant habitat type: (a) meadow: low, grassy vegetation, regularly grazed or mown as part of extensive agricultural practices ($n_{meadow} = 24$), (b) scrub: low to medium-high shrubby vegetation, including heather (Ericaceae), gorse (*Ulex* sp.), *Genista tridentata* and broom (*Cytisus* sp.) vegetation ($n_{scrub} = 39$) and forest: high woodland vegetation including oaks (*Quercus* sp.) ($n_{forest} = 21$). 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 farther away (Merckx & Slade, 2014). This attraction radius hence translates to a local sampling area of *c.* 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. Nevertheless, we cannot exclude that there may be some differences in trap detectability among habitat types, but given the remarkably local sampling ranges of weak light traps (Merckx & Slade, 2014), we believe they are unlikely to influence results much.

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 that 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, scrub or meadow species according to the habitat in which they displayed the highest relative abundance, corrected for the different numbers of sites sampled in the different habitat types. Nonetheless, for species with low observed abundances ($N \le 5$), 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 scrub species and 66 as meadow species (Appendix S1).

2.3 | Scale of habitat amount 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, scrub and meadow within concentric circles around each sampling site. Land use covers were obtained by manually digitising aerial photographs (Beilin et al., 2014; IGP, 2010; Rodrigues, 2010) (minimum mapping unit: *c.* 1,000 m^2) into the following classes: forest, short scrub, tall scrub, meadow and urban. Because the most appropriate spatial scale for the local landscape was unknown, we tested multiple circles (i.e. 20, 40, 80, 160 and 320 m radii). We avoided opting for even larger scales in order to prevent substantial overlap of the circles at those scales, although, in retrospect, it would have been appropriate being able to test larger scales too.

For each radius, Pearson's correlation coefficients were calculated between the amount of habitat type (forest, scrub and meadow) and species richness of (forest, scrub and meadow) macro-moths. Then, Pearson's correlation coefficients were plotted against their respective radii (Eigenbrod, Hecnar, & Fahrig, 2008; Horner-Devine, Daily, Ehrlich, & Boggs, 2003; Ricketts, Daily, Ehrlich, & Fay, 2001). 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).

For each sampling site, the configuration of the surrounding landscape was also taken into account: we quantified both the patch size into which the sampling site was inserted as well as the distance from the sample site to the nearest neighbouring patch of the same habitat type.

2.4 | Model selection based on habitat amount, patch size and isolation

In order to evaluate the effect of (a) habitat amount (forest, scrub and meadow), (b) patch size (see Appendix S3) and (c) distance to the nearest patch on three sets of macro-moth species richness (forest, scrub and meadow species), we used autocovariate models in order to account for potential spatial autocorrelation (Bolker et al., 2009; Dormann et al., 2007). Models 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. After that, we ranked the models using Akaike's information criteria (AIC) to select the best model. We used differences in AIC as well as Akaike weights for assessing relative support of models (Burnham & Anderson, 2002).

We applied this approach separately for species groups associated with different habitat types, both with and without taking possible spatial autocorrelation into account.

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

2.5 | 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, species richness is estimated by:

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

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 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 carried out using minimum least square errors, using the sampling points clustered at different nested scales to estimate parameters c_i, h_{ij} and z_i. Model fit was evaluated using corrected Akaike's information criteria (AICc). In order to test the explanatory power of the models, we performed linear regression of the data and calculated the R^2, after log-transforming both the species richness and the sampling areas. For the countryside SAR, we used the "effective area" for each species group i in each sampling area, $Ai = \sum_j h_{ij} A_j$, using the h_{ij} estimated from the minimum least square errors fit. Note that this formula also allows for a simple interpretation of habitat affinities: when a species group i has affinity one for the preferred habitat type (h_{ii} = 1), then an affinity h_{ij} for an alternate habitat type j is the proportion of the area of habitat type j usable by species group i (e.g. forest species are able to use 20% of meadow habitat when $h_{\text{forest,meadow}}$ = 0.2).

3 | RESULTS

3.1 | Scale of habitat amount 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) (Figures 3a and 4a). The species richness of scrub macro-moths was not significantly correlated with the amount of scrub habitat (Figure 3b). Meadow macro-moth species richness 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

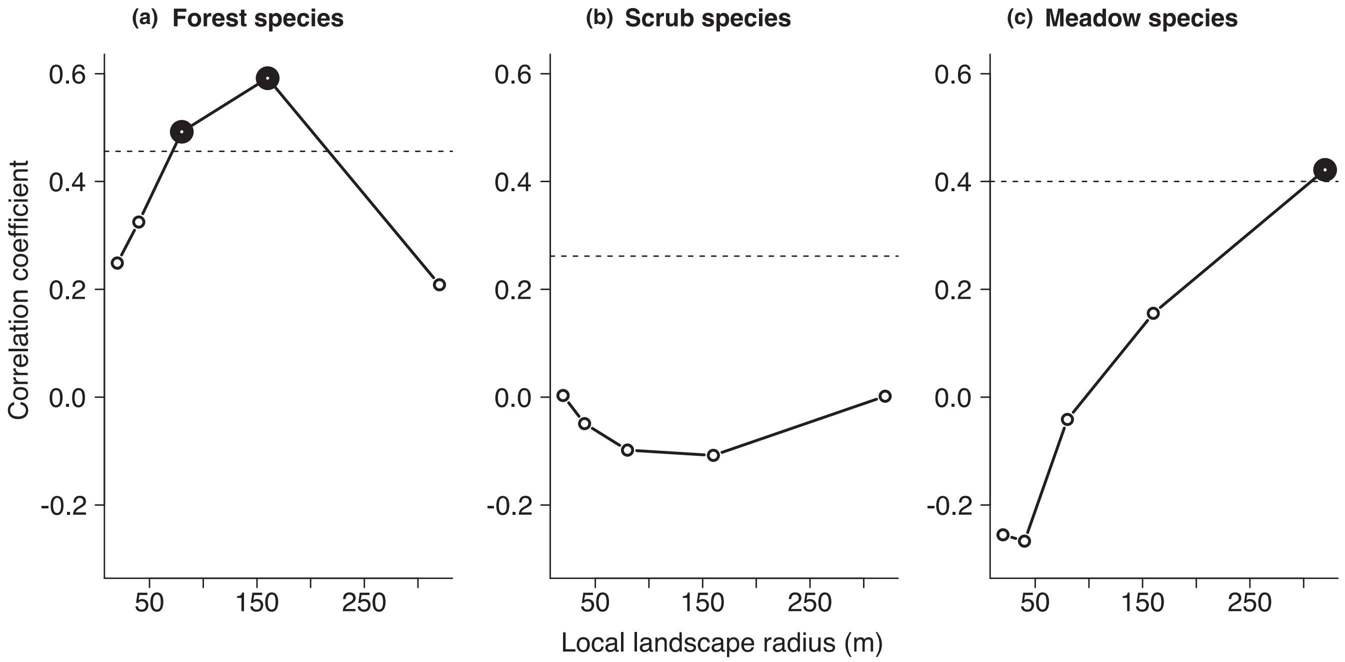
(a) Forest species (b) Scrub species (c) Meadow species

FIGURE 3 Multi-scale richness–habitat amount relationships. Correlation between habitat amount and species richness of (a) forest, (b) scrub and (c) meadow macro-moth 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. A significant relationship is indicated by a large black dot, which for forest habitat was strongest at the 160 m scale, while for meadow habitat it was strongest at the 320 m scale. These radii were used for further analyses

(Figures 3c and 4b). We identified the 160 m radius as the scale which maximizes the relationship between forest moth species richness and forest habitat amount, and 320 m for meadow moth species richness and meadow habitat amount. Although it remains a possibility that the best scale of effect for meadow species is larger than the current 320 m radius scale (e.g. 640 m), our semi-nested sampling design puts limits to the spatial independence of data at such larger scales. Still, the 320 m radius scale appears to be large enough relative to the large majority of typical, routine inter-patch movements for common macro-moth species in agricultural landscapes with (semi-)natural habitat patches (Merckx et al., 2009, 2010; Slade et al., 2013). Also, the 320 m radius scale for meadow species is double the most significant spatial scale for the forest moths. Already, this is a big difference between both species groups and we judge it unlikely that their spatial scales of effect would eventually show a fourfold difference. The more generalist group of scrub macro-moths—showing high affinity for meadow habitat as well as some affinity towards forest habitat—was unsuitable to compare the habitat amount hypothesis and the habitat island hypothesis, as the latter assumes habitat specialization, and therefore this group was not retained for further analyses. The lack of a clear scale of effect for the scrub species, and their higher level of habitat generalism, are probably due to the way we categorized scrub habitat, as it actually entails various (sub)habitat types, differing in plant species composition and vegetation height.

3.2 | Model selection based on habitat amount, patch size and isolation

Given these different "scales of effect", we separated the models into four groups: forest habitat at the 160 m radius scale for forest species (Table 1A), and meadow habitat at the 320 m radius scale for meadow species (Table 1B), with and without a spatial autocovariate. Sampling sites surrounded by a higher amount of forest habitat within a 160 m radius were characterized by a higher number of forest species (top-ranked models with and without spatial autocovariate) (Table 1A and Figure 4a). These top-ranked models, containing only forest habitat amount as a significant variable, were strongly supported in contrast with models additionally containing patch size and patch distance or these two variables alone (ΔAICc >2) (Table 1A) (see also Appendix S2). Meadow species richness increased with increasing amount of meadow habitat surrounding the sampling site (Figure 4b), although spatial autocorrelation contended with habitat amount in the top-ranked models (Table 1B). In the model with spatial autocovariate, patch distance was almost as good a predictor of site species richness as habitat amount (ΔAICc = 0.38, Table 1B), while in the model without autocovariate, adding patch distance to habitat amount or even using patch size alone produced also good models (ΔAICc <2, Table 1B, see also Appendix S2).

In models without habitat amount, patch size had a positive effect on species richness as expected (Table 1). Patch distance had more complex dynamics: it had a negative influence on meadow species richness in models without spatial autocovariate; a non-significant positive or negative influence on meadow species richness in models with spatial autocovariate; and, surprisingly, a positive influence on forest species richness in both models with and without spatial autocovariate, although not significantly so unless in the case where it was the only predictor variable in the model.

3.3 | SAR models

The AICc value for the countryside SAR model was considerably smaller than the value for the classic SAR model (Table 2), which

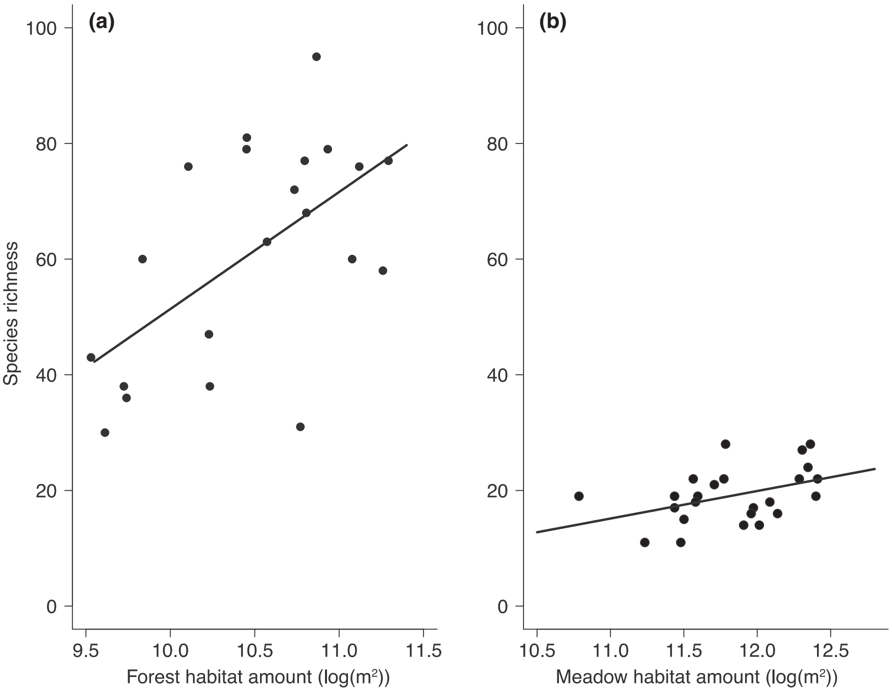

FIGURE 4 Scales of effect for forest and meadow habitat. (a) Relationship between the amount of forest habitat (m^2) within an area with a 160 m radius (see Figure 3) around the sampling sites and species richness of forest macro-moths. (b) Relationship between the amount of meadow habitat (m^2) within an area with a 320 m radius (see Figure 3) around the sampling sites and species richness of meadow macro-moths. Please note that area is log-transformed

TABLE 1 Results of model selection for explaining species richness (A) of forest macro-moth species as a function of forest habitat amount (Hab) at the 160 m radius scale, patch size (Size) and distance to nearest patch (Dist), both with (A1) and without (A2) spatial autocorrelation (AS), and (B) for meadow macro-moth species as a function of meadow habitat amount (Hab) at the 320 m radius scale, Size and Dist, both with (B1) and without (B2) AS. Values for each variable correspond to unstandardized model coefficients (i.e. parameter estimates of slopes), and values in bold indicate significant effects ($p \leq 0.05$)

	Variable[a]						
Rank	Hab	Size	Dist	AS (e^{-5})	*df*	AICc	ΔAICc
(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	−0.020	5	187.1	2.96
3	**19.66**	−3.17		2.900	5	187.2	3.04
4			0.14	2.916	4	187.6	3.48
5		0.96		6.240	4	188.9	4.70
6	18.24	−2.79	0.08	1.032	6	190.8	6.60
7		1.12	0.14	2.356	5	191.1	6.92
(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			**0.20**		3	185.0	3.59
5	18.49	−2.39	0.09		5	186.8	5.42
6		2.16	0.18		4	187.8	6.41
7		5.83			3	188.3	6.87
(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		0.99		**6.778**	4	140.9	0.38
3			0.004	**6.756**	4	142.9	2.39
4	2.16	0.43		**5.809**	5	143.6	3.05
5	3.06		0.001	5.481	5	143.8	3.22
6		1.00	−0.002	**6.599**	5	144.2	3.60
7	2.16	0.43	−0.0002	5.788	6	147.2	6.66
(B2) Meadow species—without spatial autocovariate							
1	**4.76**				3	144.0	0.00
2	4.16		−0.02		4	144.2	0.15
3			−0.03		3	145.3	1.27
4	**6.29**	−0.87			4	146.1	2.12
5		1.07	**−0.03**		4	146.4	2.33
6	4.37	−0.11	−0.02		5	147.4	3.37
7		0.62			3	148.2	4.22

[a] Intercepts of the models are omitted.

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 2). 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 forest than in meadow sampling units (300 m^2) (Table 2). Forest species showed a much stronger affinity towards scrub habitat than meadow species (Table 2).

As expected, the R^2 was higher for countryside SAR compared to classic SAR models. With regard to area per se, the relationships between forest species richness and total area as well as between meadow species richness and total area were statistically significant (Figure 5). 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 ($\Delta R^2 = 0.10$) (Figure 5).

4 | DISCUSSION

Our novel perspective to synergistically analyse the habitat amount hypothesis with the countryside SAR demonstrates that habitat

TABLE 2 Model goodness-of-fit results for both classic and countryside species–area relationship (SAR) models, based on semi-nested species–area data at five spatial scales. c and z are model parameters that depend on the taxonomic group and the sampling design (equation [1] and [2]), respectively; h_f, h_s and h_m represent the affinity of the macro-moth species groups to forest, scrub and meadow habitat (equation [2]) respectively. A single countryside SAR model combines the projections for the number of forest and meadow macro-moth species

Group	c	z	h_f	h_s	h_m	AICc
$\text{cSAR}_{\text{Forest}}$	14.69	0.183	1	0.190	0.055	825.11
$\text{cSAR}_{\text{Meadow}}$	7.84	0.133	0.001	0.021	1	
SAR	17.54	0.192	–	–	–	1,072.89

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 mainly 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.

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's (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) drew attention to the need for rigorous testing of her hypothesis, before rejecting it prematurely. Until recently, only two studies had tested, and rejected, the habitat amount hypothesis. A first study explored the effects of habitat amount and isolation on host–parasitoid interactions (*in casu* solitary bees and wasps and their parasitoids) (Coudrain, Schüepp, Herzog, Albrecht, & Entling, 2014), while the other study did so for vascular plants in dry calcareous grasslands (Evju & Sverdrup-Thygeson, 2016). However, in the first study, habitat amount may have failed to explain species richness because the

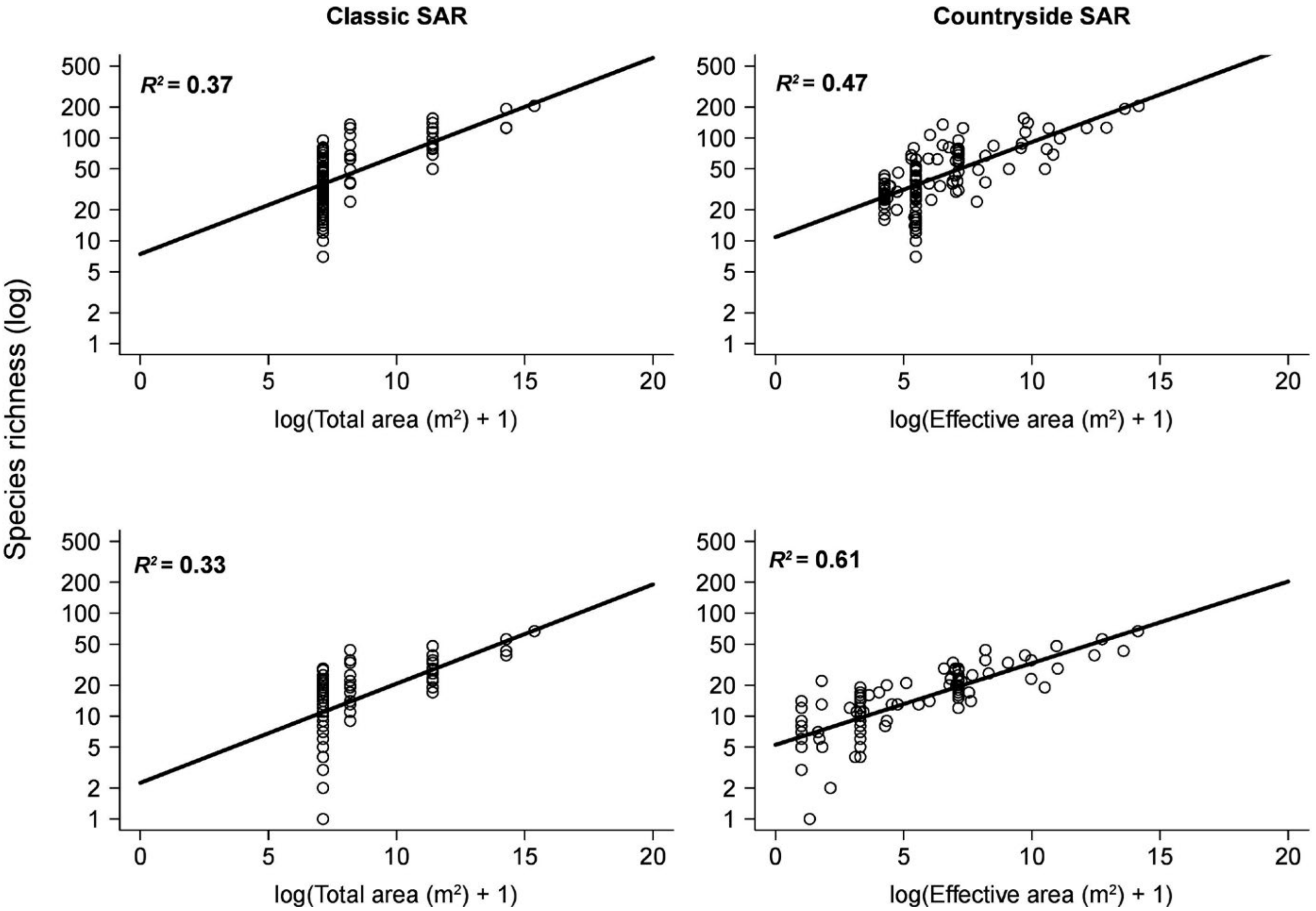

FIGURE 5 Classic and countryside species–area relationship (SAR) models. Effects of area on species richness of forest (top row) and meadow (bottom row) macro-moths following classic (left columns) versus countryside (right columns) SAR models. Countryside SAR models consistently provided a better fit than classic SAR models. R^2 values are given for each model. All four models are significant ($p < 0.05$). Please note that both area and species richness are log-transformed

authors did not verify whether 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 change in surrounding environmental conditions, given the low mobility of vascular plants. This characteristic is reflected in their considerable extinction debt (Helm, Hanski, & Pärtel, 2006; Vellend et al., 2006).

Sound empirical testing of the habitat amount hypothesis appeared only recently. Based on plant, micro-arthropod and forest bird datasets, no support for the hypothesis was shown (Haddad et al., 2017; Lindgren & Cousins, 2017; Thiele, Kellner, Buchholz, & Schirmel, 2018; Torrenta & Villard, 2017). On the other hand, eight recent studies do show empirical support for the habitat amount hypothesis. A study in the naturally heterogeneous savanna landscape of the Chapada Diamantina in Brazil did so for Euglossini bees (Moreira et al., 2017), a study within five major industrial sites in Europe did so for five out of seven tested taxa (Piano et al., 2017), while a study on fluvial islands in Amazonia did so for arboreal mammals (Rabelo, Bicca-Marques, Aragón, & Nelson, 2017). Both patch size and habitat amount in the local landscape independently affected species numbers of saproxylic beetles in German forests, without an interaction effect, hence consistent with the habitat amount hypothesis and refuting the island effect (Seibold et al., 2017). A study on woodland small mammals in the Brazilian cerrado (i.e. savanna) showed that habitat amount is the most important single predictor of species richness, while patch size and isolation generally had no effect on species richness after controlling for the effect of habitat amount (Melo, Sponchiado, Cáceres, & Fahrig, 2017). Predictions of the habitat amount hypothesis were upheld for rare reptiles and one frog species in an agricultural landscape in New South Wales, Australia (Pulsford, Lindenmayer, & Driscoll, 2017). Habitat amount, without considering spatial configuration, was already a good predictor for local species richness of plants in a Mediterranean region of France including urban habitat (Martín-Queller, Albert, Dumas, & Saatkamp, 2017). In an eighth study, avian species richness in southern Ontario, Canada, responded primarily to habitat amount and negligibly to fragmentation (De Camargo, Boucher-Lalonde, & Currie, 2018). Hence, our study gives further support to the habitat amount hypothesis, in yet another study system, namely macro-moths in extensively farmed agricultural landscapes consisting of a variety of meadow, woodland and scrub patches.

In addition, our study shows that the countryside SAR outperformed the classic SAR. This corroborates earlier findings in multi-habitat landscapes on other taxa: plants (Proença & Pereira, 2013), birds (Guilherme & Pereira, 2013) and amphibians, reptiles and passerine birds (Martins, Proença, & Pereira, 2014). While the classic SAR focuses only on the size of the habitat patch, the quality of the landscape matrix is nevertheless known to be able to influence species richness (Kupfer, Malanson, & Franklin, 2006; Prevedello & Vieira, 2010). Unlike the classic SAR, the countryside SAR aims to draw attention to the effective amount and variety of habitat types used by different species groups, facilitating the estimation of species richness in those habitat types. 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.

However, there is a second implication of finding that both approaches are valid: none of them in isolation can explain the full patterns of alpha, beta and gamma diversity in a landscape. Much of the unexplained variation in the countryside SAR, particularly at the smallest scales, may be related to the fact that countryside SAR estimates exclude the context of the landscape surrounding the sampling windows (Figure 1). For example, both the countryside SAR and the habitat amount method provide estimates of sampling site diversity (alpha diversity), but the countryside SAR uses only information about the type of habitat in the sampling point, while the habitat amount hypothesis uses information about the amount of habitat in a surrounding landscape. This problem is repeated at each sampling scale: when four sampling sites are combined to provide the estimate of gamma diversity in an 80×80 m^2 landscape, only the habitat composition within that landscape window is taken into account, and the contribution of the surrounding habitat is ignored. This problem becomes less pronounced at larger spatial scales (i.e. in the order of hundreds of metres, following our tests of the scale of influence of surrounding habitat). In any case it suggests that the countryside SAR model could be revised to integrate the effects of surrounding habitat in the calculations of alpha diversity of a point or gamma diversity of a small landscape window. Reciprocally, the habitat amount hypothesis per se is insufficient to explain the patterns of beta and gamma diversity in landscapes and needs to be complemented by the countryside SAR.

Our results also highlight the importance of landscape heterogeneity, providing sufficient cover of forest, scrub and meadow, in order to cater for both forest and meadow macro-moths. Although forest species use scrub and meadow habitat to some degree (see also Dolman, Hinsley, Bellamy, and Watts (2007) for birds), meadow species appear more, but not fully, restricted to their preferred habitat (i.e. meadows). Nevertheless, we here show that forest species display higher spatial turnover, which suggests that they may move over shorter distances, consistent with the observed smaller scale of effect for forest than for meadow species. Also, forest species are characterized by a considerably higher species richness per sampling unit than meadow species. Consequently, a high proportion of woodland cover appears beneficial to overall moth diversity at the landscape scale. Similarly, a high proportion of woody vegetation at a landscape scale has been shown to positively affect Orthopteran species richness, whereas a high proportion of grasslands did so negatively (Marini, Fontana, Battisti, & Gaston, 2009; Marini, Fontana, Scotton, & Klimek, 2008). Recently, high forest cover has been shown to also enhance the persistence of most grassland butterflies in agricultural landscapes (Toivonen et al., 2017). 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, species richness of macro-moths in agricultural habitats strongly increased by the presence of nearby forest (Ricketts et al., 2001). Many moth species utilize both forest and agricultural habitats, and frequently move between them, 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 macro-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, by claiming that the effects of patch size and isolation are merely effects of habitat area, Fahrig (2013) predicted the total absence of fragmentation effects, and instead hypothesizes that only habitat loss is important (i.e. only the amount of habitat is important, independent of its configuration and of the total habitat amount at a larger scale). Hanski (2015) stated that this hypothesis is not corroborated by studies showing that fragmentation does have an effect on species richness, and it seems that it does so in landscapes where the originally land-covering habitat dropped below 20%–30% of the area (Andrén, 1994; Banks-Leite et al., 2014; Fahrig, 1998; Lande, 1987). Consequently, if the habitat amount hypothesis is generally true, it should be tested in landscapes with low overall habitat amount (<20%), as in our study area (49.69 km^2), where woodland cover amounts to only 10.5% or as in our three sampled landscapes (4.92 km^2), where it amounts to 18.7%, so that habitat fragmentation effects—if important—would be detectable.

In conclusion, results from our study show that species richness of both forest and meadow macro-moths responds 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 further support to the habitat amount hypothesis. Nevertheless, it is important that 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 as good a predictor of species richness as the combination of patch size and isolation. Additionally, our study presents a novel framework to integrate the habitat amount hypothesis explanation of alpha diversity patterns with the countryside SAR explanation of beta and gamma diversity patterns. This framework revises the application of island biogeography and metapopulation theory to conservation biogeography.

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA ACCESSIBILITY

The datasets analysed during the study are archived and available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.205823j .

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BIOSKETCH

Thomas Merckx is broadly interested in the landscape-scale conservation and ecology of Lepidoptera. This work represents a component of the PhD work of **Murilo Dantas de Miranda** on biodiversity response to land use change across scales. **Henrique Miguel Pereira** research interests revolve around global biodiversity change, including monitoring schemes for biodiversity, spatially explicit and species–area models for biodiversity scenarios, and empirical studies of the consequences of rewilding abandoned farmland for biodiversity and ecosystem services.

Author contributions: H.M.P. developed the methodological framework of the experiment and coordinated the study. T.M. conducted the experiment. M.D.M. analysed the data, with help from T.M. and H.M.P. All authors were involved in interpreting the results and writing the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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