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Negative effects of forest edges and canopy opening on moth communities

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ABSTRACT

Forest loss and fragmentation are major threats to biodiversity and associated ecosystem services worldwide. Forest fragmentation leads to the creation of forest edges, which experience contrasting environmental conditions compared to forest interiors, inducing a strong change in biological communities. In addition, forest management interventions, such as thinning influence canopy opening, microclimate and strongly alter the structural environment of vegetation. Moths are a species-rich and functionally important taxonomic group because of their role in plant pollination and as bulk food for other species. Here we studied the effects of canopy structure and edge-to-interior gradients on macro-moth communities using light traps in Belgium and northern France. We found that forest edges had lower abundance of moths (a modeled reduction of 46 %) and lower species richness (-29 %) than forest interiors. Open stands had an overall lower abundance of moths compared to more closed stands (-17 %). Moreover, the interaction between forest structure and edge effect was significant, indicating stronger reductions of moth abundance towards the edge in open forest (-57 % vs −37 % in dense forest). Both local environmental variables and landscape variables explained the observed patterns, e.g., nighttime temperature of the plot and forest cover in the surrounding landscape both had a positive effect on moth activity density and species richness. We found limited evidence that moth species traits explained the observed edge-to-interior disparities, although species with larvae feeding on shrubs and trees tended to be more associated with forest cores than grass and herb feeders. Our results indicate the importance of functional forest interior habitat and relatively undisturbed forests with a high structural complexity for moth conservation.

1. Introduction

Forests worldwide have been heavily fragmented due to human-induced land use changes (Wade et al., 2003; Tilman et al., 2017) resulting in mosaic landscapes where forest fragments are embedded into an agricultural and urban matrix (Decocq et al., 2016). Habitat loss and fragmentation as well as land use changes are one of the major threats to biodiversity worldwide (Pereira et al., 2010). Forest fragmentation sensu stricto (i.e., no habitat loss, but equal amount of forest in smaller patches), leads to a higher proportion of forest edges compared to forest interiors, increasing the so-called forest edge effect. Forest edges have very different (a)biotic characteristics from forest

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interiors since they have, e.g., a different vegetation structure (Meeussen et al., 2020), tree growth dynamics (Reinmann and Hutyra, 2017) and plant species composition (Govaert et al., 2020) but are also warmer (Meeussen et al., 2021), drier (Chen et al., 1995), receive more light (Delgado et al., 2007; De Smedt et al., 2016) and are subjected to higher wind speeds (Wuyts et al., 2008), leading to increased convective cooling for forest ectotherms (Merckx et al., 2008). These strong gradients in environmental conditions cause forest edges to differ strongly from forest interiors, decreasing the remaining amount of intact forest interior habitat which is crucial for forest biodiversity. Riitters et al. (2016) calculated that the net loss of forest interior habitat in response to habitat fragmentation is at least two times higher compared to the net loss of forest. Haddad et al. (2015) conducted an analysis of global forest cover and revealed that 70 % of remaining forest is within 1 km of a forest edge and Estreguil et al. (2013) calculated that 40 % of forest in the European Union lies within 100 m of a forest edge and are thus subject to strong forest edge effects.

Forest edges intensely affect animal and plant species' distribution along forest edge-to-interior gradients (De Smedt et al., 2019; Ewers and Didham, 2006; Pfeifer et al., 2017). These forest edge effects are strengthened when forest fragments are embedded in a matrix of intensive agriculture compared to more extensively used agricultural landscapes (De Smedt et al., 2018a). This is most likely due to the reduced temperature and humidity buffering capacity of the surrounding intensive agricultural landscapes compared to more complex less intensively used landscapes. Additionally, the influx of herbicides and fertilizers from the adjacent agricultural fields contributes to this effect (Kleijn and Snoeijing, 1997). This results in forest edges dominated by generalists and more drought resistant species (Chabrerie et al., 2013; De Smedt et al., 2018a). Focussing on species functional traits has strongly increased our understanding on how edge effects influence species distribution across landscapes (De Smedt et al., 2018b), providing a mechanistic understanding of the nature of edge effects.

The forest edge-to-interior gradient in community composition of a diversity of taxa has been studied more intensively since the last two decades, but not much is known about how forest management interacts with edge effects on forest biodiversity. Forest management can strongly alter forest microclimate (Grayson et al., 2012), e.g., via thinning opening the forest canopy, potentially strengthening forest edge effects such as the size and depth of edge influence on forest structure and temperature (Meeussen et al., 2020; 2021). This could result in increased spill-over and deeper penetration of organisms from adjacent habitats into open *vs.* dense forest edges, further altering species composition.

Abiotic forest edge-to-interior gradients can be very strong at the spatial extent of only a few metres, especially close to the forest edge (De Smedt et al., 2016; Meeussen et al., 2021). However, scientific evidence of these effects on multiple taxa is still scarce. Moths are highly vagile species with many being forest specialists, showing strong affinity to forest habitat (Zub et al., 2019). This taxonomic group is species rich and plays an important role for ecosystem functioning as pollinators, leaf herbivores and bulk food for higher taxa such as birds and bats (Hahn and Brühl, 2016; Kolkert et al., 2020). Hence, moth research and conservation has gained attention in recent years (Macgregor et al., 2019; Blumgart et al., 2022; Duffus and Morimoto, 2022). Moth are considered a good biotic indicator for complex forest structure (Merckx et al., 2012a; De Smedt, Vangansbeke et al., 2019) and low forest management disturbance levels (Summerville et al., 2004). However, very little is known about how moth communities change along the forest edge-to-interior gradient in relation to an altered forest canopy structure due to management.

Here we studied edge-to-interior gradients in large forest fragments embedded in an agricultural matrix in western Europe (Belgium and northern France). In four regions, we selected an open and dense forest stand (as a result from forest management-driven canopy opening) and sampled the moth communities in terms of abundance and species richness during four sampling events with light traps placed at increasing distance from the forest edge. We specifically addressed the following three research questions: (I) How does moth abundance and species richness change along a forest edge-to-interior gradient in forests with contrasting forest structure? (II) Which environmental variables drive these changes? and (III) Can the observed distribution patterns be explained by functional traits of the moths?

2. Material & methods

2.1. Study design

In each of four regions, located in Belgium and northern France, (Fig. 1), we selected two contrasting forest stands dominated by oak species (*Quercus robur* and *Q. petraea*): one recently thinned, open forest stand and one unthinned, dense forest stand. In recently thinned stands, trees were harvested during the last 7 years before the survey, resulting in a higher canopy openness and a lower tree basal area than in the unthinned stands, where no trees were harvested for the last 17 years, at least (Meeussen et al., 2020). All stands were ancient forest stands in the sense that they were continuously forested since the first available land-use maps (+-1775) and thus never converted to another land-use type for hundreds of years. All soils had an intermediate soil moisture (mesic). Each of the forest stands had a minimal area of 4 ha and a south-facing edge bordering agricultural land (grassland or arable land).

Perpendicular to the south-facing edge of the forest, we installed four plots at an increasing distance from the forest edge: at 1.5 m, at 12.5 m, at 35.5 m and at 99.5 m. The plot at 99.5 m from the south-facing edge was considered to represent forest interior conditions and was also located at least 100 m from any other forest edge. In total, this resulted in 32 plots (4 regions × 2 forest types × 4 plots) with varying forest structure and distance to the forest edge (Fig. 1, Fig. S1, Table S2). For more information on the design of the plot network, see Govaert et al. (2020).

2.2. Moth sampling

Between June 28 and October 12, 2020, we organised four sampling periods in which we visited each plot, resulting in 128 trapping events (32 plots × 4 sampling periods) (Table S3). During each trapping event, the macro-moth communities were sampled with battery powered light traps using a funnel principle. The term macro-moths is a not scientifically assigned group, that consists of families with generally larger adults (as opposed to micro-moths). For our study we follow Waring and Townsend (2017) and include the following 17 families occurring in Belgium and northern France as macro-moths: Hepialidae, Cossidae, Zygaenidae, Thyrididae, Limacodidae, Sesiidae, Lasiocampidae, Brahmaeidae, Saturniidae, Endromidae, Drepanidae, Geometridae, Sphingidae, Notodontidae, Erebidae, Nolidae and Noctuidae. We used low intensity Kendo light 8 Watt fluorescent lamps in the traps, with an attraction radius below 10 m (Fig. S1) (Truxa and Fiedler, 2012) to sample moth communities as local as possible and to avoid interference between different traps as much as possible (Merckx and Slade, 2014). All four plots in one stand were always sampled during the same night, and the two forest stands within one region on consecutive nights to minimize variation in weather circumstances. Overall, we tried to sample all stands as quickly as possible one after the other within one sampling period, but we excluded nights with unfavourable weather conditions (heavy wind or rain) (Table S3). Traps were installed on a white wooden plate of 1 m^2, lamps were lit one hour before sunset and all individuals in every trap and on the wooden plate were collected 30 minutes before sunrise, starting at the edge working towards the interior (because light appears first at the edge). All individuals were immediately identified to the species level (Waring and Townsend, 2017) and released, except for specimens from species that can only be reliably identified based on genital structures. A list of species

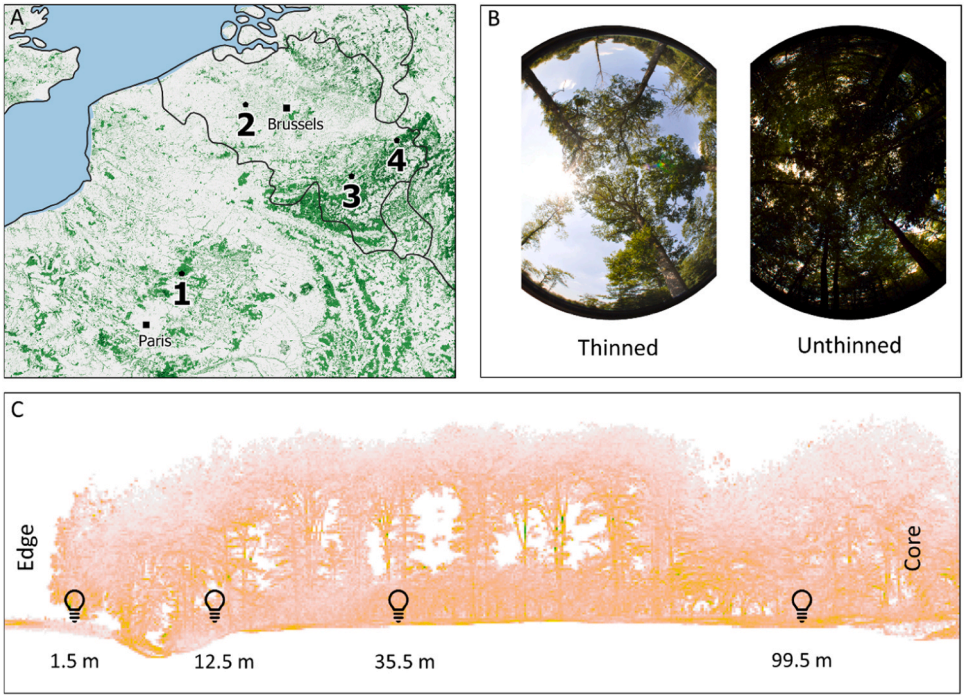

Fig. 1. A. Map of the study area with the four sampling regions and the forest cover in green (European Union, 2020). B. In every region we selected forest stand with an open (recently thinned) and a dense canopy (unthinned); example of hemispherical pictures in open and dense stands in region 3. C. In every stand, we installed four plots at an increasing distance from the forest edge. In every plot, moths were sampled on four occasions between June and October 2020, with skinner traps equipped with low intensity fluorescent lamps (Fig. S1). The picture shows a point cloud of terrestrial laser scanning in the unthinned stand of region 4 after Verhelst et al. (2023).

complexes was prepared beforehand, allowing individuals from these complexes to be taken to the lab for identification via genital organs. These complexes were found in the following genera: Acronicta, Aplocera, Epirrita, Horisme, Mesapamea, Noctua, Oligia, Scotopterix, and Thera. We calculated both the abundance of moth individuals (as a metric for ecosystem functioning, such as the amount of herbivory and prey availability) and the richness of moth species (as a metric of biodiversity) per plot. We also estimated the asymptotic species richness of each sample, using the Chao Richness estimator, an abundance-based integration of rarefaction curves (Hsieh et al., 2016) that is calculated based on the number of singletons and doubletons in the sample. The asymptotic species richness gives an intuitive value of the total expected species richness independent of activity-density.

2.3. Environmental variables

Every plot was equipped with a temperature logger (Lascar EasyLog EL-USB-1) that recorded the forest microclimatic air temperature at hourly intervals throughout the sampling period. The loggers were attached to a wooden pole at 1 m above the forest floor and protected by a white PVC radiation shield to avoid direct solar radiation (see Meeussen et al. 2021). The mean, minimum and maximum temperatures of every sample night (between sunset and sunrise) were calculated as a measure of the weather conditions and the average growing season temperature of the sampling period (June-October 2020) for every plot was calculated to represent differences in climate between plots, transects and regions. In the summer of 2018, vegetation surveys were recorded at each of the 32 studied plots (see Govaert et al. 2020); all vascular plants were identified up to species level in a 3 × 3 m plot and the plant species richness was determined, as well as the number of forest specialist plant species (after Heinken et al. 2022). Also in the summer of 2018, we used single scan position terrestrial laser scanning to further quantify the complex three-dimensional structure of the forest (Calders et al., 2020), using a RIEGL VZ400 laser scanner (RIEGL Laser Measurement Systems GmbH, Horn, Austria). More information on the data acquisition parameters and setup can be found in Meeussen et al. (2020). Three important structural metrics were determined for every plot: the canopy openness (i.e., the average percentage of gap fraction across the angle 5–70°); the plant area index (PAI) (i.e., a metric for plant material density integrated over the canopy height); and the foliage height diversity (FHD) (i.e., a metric for the vertical heterogeneity, calculated as the Shannon-Wiener index of the proportion of plant material in 1 m vertical bands over the canopy height). To assess the impact of surrounding land use, we used the ESA WorldCover map (10 m resolution, 11 land use classes) (Zanaga et al., 2021). We calculated the proportion of land area classified as grassland, arable land and forest area, using circular buffers with a 400 m and an 800 m radius around each plot.

2.4. Functional traits of moths

For the 50 most common macro-moth species in our dataset (with > 20 occurrences), we gathered functional trait values to explain potential edge-to-interior patterns. First, we looked at three traits related to mobility: we determined forewing length as the mean of minimal and maximal forewing length, forewing length variation as the range (maximal – minimal length) divided by the mean forewing length and forewing shape (pointed vs broad), all according to Waring and Townsend (2017). In general, species with larger, pointed wings are more mobile than species with shorter, round wings (Slade et al., 2013). We expect forest interior specialists to be less mobile, because forest interiors represent a more stable habitat than forest edges. Second, we investigated three traits related to foraging: adult feeding behaviour (feeding vs non-feeding), larval feeding guild (grass/herb feeders vs shrub/tree feeders vs lichen/moss feeders vs detritus feeders) and larval feeding guild breadth (monophagous (i.e., feeding on one plant species), oligophagous (i.e., feeding on a limited amount of plant species within one genus/family) and polyphagous (i.e., feeding on a wide range of

plant species)) (all data from Maes et al. 2024). We hypothesize that forest edge species will also forage in adjacent open habitat and thus will be more often polyphagous and grass feeding as a caterpillar and feeding as an adult. Third, we also looked at two classifications of habitat preference: the forest affinity (weak, medium, strong) (data from Waring and Townsend 2017 after Slade et al. 2013) and habitat preference from Zub et al. (2019), which classifies moths in different categories: "w" (strong affinity to forest habitats), "wl" (mainly found in forests, with strong affinity to open forests, forest edges, or glades), "mm" (occurring equally in open landscapes and forest habitats) and "mo" (strong affinity to open landscapes, but also regularly occurring in forests, at forest edges, or in glades). Obviously, we expect species from forest interiors to have a higher forest affinity and a habitat preference of "w". Fourth, we calculated the realized thermal niche as a measure of the species temperature index (STI), based on the distributions according to Leraut (2019) and following the methodology of Vangansbeke et al. (2021). In short, we sampled 1000 random values of the mean temperature in the warmest quarter (BIO10) from WorldClim v.2 (Fick and Hijmans, 2017) across the distributions of the focal species and used the median of these 1000 values as the thermal niche optimum for the focal species, with warm-adapted species having a higher thermal niche optimum than cold adapted species (see Vangansbeke et al. 2021 for details). We expect forest interior species to have a higher thermal niche optimum, because minimum temperatures in forest interiors at night are generally higher than in open habitats (Meeussen et al., 2021). Finally, we also extracted the family from Waring and Townsend (2017), to investigate a potential relationship between phylogeny and forest interior preference. In total we extracted 10 functional traits for each of the 50 most common species (Table S4).

2.5. Data analysis

All data analyses were performed in R version 4.2.1 (R Core Team, 2022). To answer the first research question, we built generalized linear mixed-effects models with moth abundance (activity-density), species richness and asymptotic species richness of the 128 (32 ×4) trapping events as response variables and with forest type (open vs dense), the log-transformed distance to the forest edge and their interaction as fixed effects. To account for the nested study design, we included transect nested within region, nested within the sampling time period as a random intercept term in the model formulas. We used the lme4 package (Bates et al., 2015) and a Poisson distribution for the response variables, since both moth species richness and abundance are count data.

To answer the second research question, we started from full models with moth abundance and species richness as response variables and eight fixed effects in the model formulas and with the same random effect as above. Because some predictor variables were highly correlated, we selected, in each of the full models, only two fixed effects related to microclimate, two fixed-effects related to forest structure, two fixed-effects related to land use and two fixed-effects related to understorey vegetation composition. For microclimate, we selected either the minimum, maximum or mean temperature of the sampling night as first fixed effect, and then added the mean sampling temperature across the entire period (June-October 2020) as second fixed effect for the full models (3 different possible microclimate fixed effects). For land use, we only included land use categories of one spatial scale in the full models (2 possible land use fixed effects). For forest structure, we included the FHD and either the canopy openness or the PAI in the full models (2 possible forest structure fixed effects). For vegetation, we only had 1 possible fixed effect, including the two non-correlated vegetation variables, i.e., plant species richness and number of forest specialist plants. Combining all potential fixed effects, resulted in 12 full models with 8 predictors (i.e., 3 possible fixed effects for microclimate x 2 land use x 2 forest structure x 1 vegetation). All full models that were finally tested showed no indications of multicollinearity (all VIF's < 5). We then used the dredge function in the MuMIn package to select the most parsimonious model based on AICc criterion, i.e., based on goodness of fit and simplicity (Symonds and Moussalli, 2011), starting from the 12 potential full models. We did not test any interactions, due to limits of model complexity (only including all two-way interactions already results in an overcomplex full model with 36 predictors). All predictors were z-transformed prior to the analysis, to better compare the effect of the different environmental variables.

To answer the third research question, we first designed a simple Forest Core Affinity score (FCA-score) for each of the 50 most common species in our database (again with > 20 occurrences). This FCA-score was calculated as the number of occurrences in the forest interior plot to which we added 0.5 times the number of occurrences at 35 m from the edge. From this sum, we subtracted 0.5 times the number of occurrences at 12.5 m from the edge as well as the number of occurrences in the forest edge plots which we then divided by the total number of occurrences. This resulted in a very intuitive FCA-score with a value of $+1$ for species that only occur in the forest interior plot across all four locations and -1 for species that only occur in the forest edge plot across all four locations. For example, if a species was sampled 50 times and occurred 30 times in the forest interior plot, 15 times at 35 m from the edge and 5 times at 12.5 m from the edge, this resulted in an FCA score of 0.7 (i.e., $[(30 * 1) + (15 * 0.5) - (5 * 0.5)]/50$). The relationship between the FCA-score and different literature-derived traits of these moth species was then evaluated based on simple linear models (thermal niche optimum, forewing length and forewing length variation) and generalized linear models (family, wing shape, larval feeding guild, larval feeding guild breadth, adult feeding behaviour, forest affinity and habitat preference).

3. Results

3.1. Negative effects of forest edges and management

In total we sampled 4743 individuals of 264 macro-moth species, with relatively large differences between sampling periods: we found higher numbers of individuals and species in June and July but lower numbers in later sampling periods (Table S3, Vangansbeke et al., 2024). We found a significant interaction effect between the edge-to-interior gradient and forest structure ($p < 0.01$) on the activity-density of moths ($R^2m = 0.04$, $R^2c = 0.98$), such that the activity-density of moths is greater in dense forest interiors and lower at the edge in open forests. We found reduced numbers of moths in forest edges (modelled reduction of 46 % compared to forest cores) and in open forests (reduction of 17 %) and the difference between edge and interior was larger in open forests than in dense forests (modelled reduction of 57 % vs 37 %) (Fig. 2a). For species richness, we found no interaction effect between forest management and the edge-to-interior gradient. Nonetheless, we found a significant positive effect of the distance to the forest edge on moth species richness, leading to a modelled decrease of 17 % from edge to core ($p < 0.01$) ($R^2m = 0.02$, $R^2c = 0.88$) (Fig. 2b). Forest structure had no significant effect on moth species richness. We tested the same model formula for asymptotic species richness and found a similar result: only a negative effect of proximity to the forest edge ($p < 0.01$) ($R^2m = 0.03$, $R^2c = 0.97$) (Fig. S5).

3.2. Effects of the environmental variables

For all response variables, models including mean sampling night temperature generally had lower AICc values than models including minimum or maximum temperature of the sampling night; canopy openness performed better than PAI; and for land use we found the lowest AICc values for models including forest and grassland cover in a 400 m radius and we thus omitted arable land and the 800 m radius metrics. In the most parsimonious model for activity-density (based on AICc), we found significant positive effects of the forest cover in a 400 m radius around the plot, the mean sampling night temperature, the

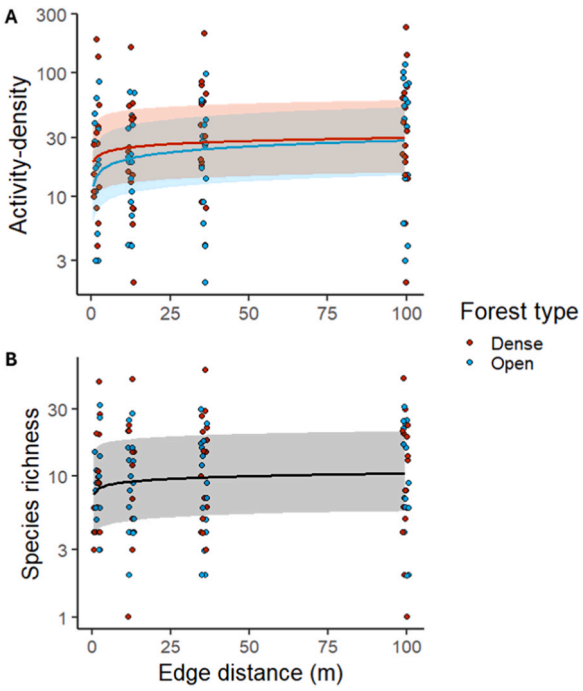

Fig. 2. A. Open forest edges had a lower activity density than dense forest cores. Each dot represents one trapping event in an open (blue) or dense (red) forest, the lines represent the modelled activity-density for open (blue) and dense (red) forests and the hull the 95 % confidence interval. Note that the y-axis uses a logarithmic scale. B. The species richness of moth communities increases towards the forest interior, indicating a negative effect of forest edges on species richness. Each dot represents one trapping event in an open (blue) or dense (red) forest, the line represents the modelled species richness and the hull the 95 % confidence interval. Note that the y-axis uses a logarithmic scale.

grassland cover in a 400 m radius, the foliage height diversity and the number of forest specialist plant species, while we found a negative effect of overall plant species richness (all p-values < 0.01; $R^2m = 0.56$, $R^2c = 0.98$) (Fig. 3). For species richness, we also found positive effects of mean sampling night temperature, the forest and grassland cover in a 400 m radius around the plot and the foliage height diversity (all p-values < 0.01) ($R^2m = 0.36$, $R^2c = 0.86$). For the asymptotic species richness, we found a positive effect of the mean sampling temperature, the FHD, the canopy openness and a negative effect of the growing season temperature ($R^2m = 0.32$, $R^2c = 0.97$) (Fig. S6).

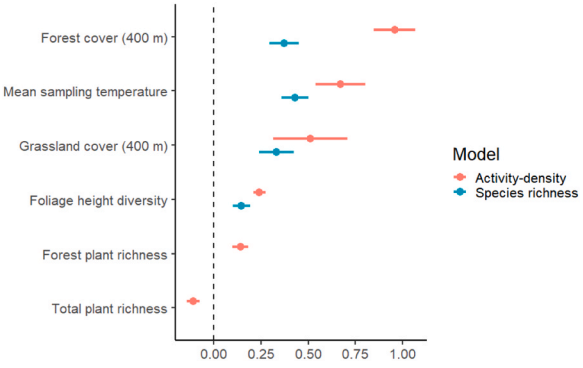

Fig. 3. Coefficient estimates (error bars denote standard deviations) of the environmental predictors in the most parsimonious model based on AICc on moth activity-density (red) and number of moth species (blue). When the symbol for a predictor variable is not shown, this predictor was not retained in the optimal model.

3.3. Life history traits of forest interior moths

The 50 most common species in our data set represented in total 80.52 % of the sampled individuals and thus represent a very important part of the activity-density of the investigated moth communities. We found no significant correlation between the Forest Core Affinity score (FCA-score) on the one hand and the thermal niche and forewing length of moth species on the other hand, although there appeared to be a tendency towards more warm adapted species with longer wings in species from the forest interior compared with species that preferred forest edges (Fig. 4A and B). We found, however, a significant effect of larval feeding guild, with moth species from forest interiors having mostly caterpillars that feed on shrubs and trees, while larvae of moth species from the forest edge tend to feed more often on grasses and herbs ($p = 0.03$; Fig. 4C). There was also a slight phylogenetic effect, with *Erebidae* occurring more in the forest interior plots than *Noctuidae* ($p = 0.08$, Fig. 4D). We found no correlation between the FCA-score and the forewing length variation, wing shape, larval feeding guild breadth or adult feeding behaviour. Both the forest affinity according to Waring and Townsend (2017) and the habitat preference after Zub et al. (2019) showed high similarities to the FCA-score from this study. In general, species with high FCA-scores had a strong forest affinity according to Waring and Townsend (2017) and belonged to the "mm" group (occurring equally in open landscapes and forest habitats) and the "w" group (strong affinity to forest habitats) of Zub et al. (2019), as expected. However, there were some species with a diverging pattern for which the classification could be reconsidered based on the current study (indicated in Fig. S7).

4. Discussion

4.1. Macro-moths along forest edge-to-interior gradients

Despite the huge variation between sampling sites and across seasons in moth abundances, our results show that forest edges harbor lower activity-density of macro-moths than forest interiors, a trend that is even more pronounced in forests with an open canopy. In addition, forest edges show a reduced species richness irrespective of the forest structure or management type. Forest edges strongly alter invertebrate communities but, hitherto, limited evidence was available for moth communities in temperate forest edges. Our study, specifically designed to assess the effect of increasing distances from the forest edge, can not only contrast forest edges with forest interiors but it also allows to study the entire continuum of the edge-to-interior gradient. We indeed found a strong increase in moth abundance and species richness from the forest edge up to 12.5 m inside the forest, slowly increasing asymptotically further away from the edge inside the forest. Slade et al. (2013) used a comparable design by sampling forest edges and forest interiors of different forest patches in one landscape; they also found the strongest decrease in abundance and species richness close to the forest edge. Summerville et al. (2004) sampled forests in eastern north America by setting up moth traps at 0, 50 and 100 m from the forest edge. Although they did not find significant differences between the plots there was a tendency for some families to be more abundant in the forest interior. These results are somewhat contrasting to other forest biomes. For instance, Mönkkönen and Mutanen (2003) did not find a difference in moth abundance or species richness between forest edges and interior in boreal forests and Jaimes-Nino et al. (2019) found higher or lower numbers of moths in forest edges compared to forest interiors depending on the family in the Amazonian rainforest. In addition, the proximity to urban areas appears to be crucial in shaping moth communities (Uhl et al., 2021) and might influence the above-stated patterns. Therefore, we suppose that patterns are biome dependent but that in our climate (temperate), and forest type (oak dominated forests), moths are likely more abundant and species rich in the forest interior compared to the edge. Our study was limited to the period between June and October and

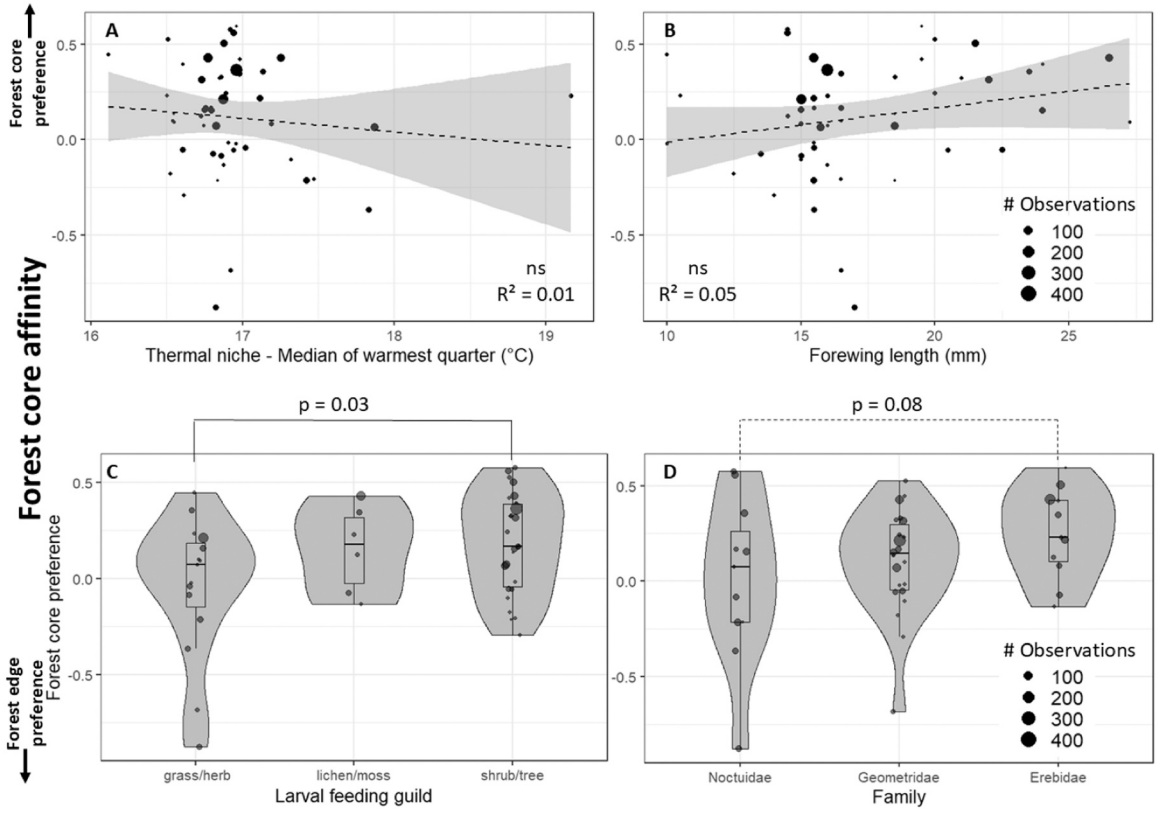

Fig. 4. Relationship between forest core affinity and (A) Thermal niche, (B) Forewing length, (C) Larval feeding guild and (D) Family of the 50 most abundant moth species in the study. Each dot represents one species and the size of the dots is scaled by the number of observations in the dataset.

thus excluded typical spring species. Sampling in spring would be an interesting avenue for further research, as nectar availability in temperate forests is typically high in spring, due to flowering of geophytic plant species (De Schuyter et al., 2024), potentially further strengthening attraction of forest cores to macro-moths in this time of the year. As mentioned earlier, our study was also characterized by a large variability in species richness and activity density between periods, regions and trapping nights, potentially further amplified by meteorological conditions and lunar phases (Yela and Holyoak, 1997), resulting in a large part of the variation explained by the random effect. Given our sampling design with plots in one transect sampled on the same night and same regions sampled on consecutive nights in each sampling period, we consider this variation to be truly random and not affecting the main patterns we found. A potential drawback of this design is the potential overlap between attraction radii of different traps, however we believe this effect was minimal, because we used low intensity lights with a very limited attraction radius (Merckx and Slade, 2014) to sample very locally, moreover, even the most nearby traps were often visually shielded from each other by shrubs and tall forbs.

For soil invertebrates (such as carabid beetles, spiders, millipedes and woodlice), we see in general a reversed pattern compared to moths with more individuals at temperate forest edges (De Smedt et al., 2019). These soil communities thrive on detritus as primary food source, of which the quality (nutritional content) is generally higher in forest edges (De Smedt et al., 2016). In addition, soil temperatures are more buffered in forest edges compared to air temperatures (Meeussen et al., 2021), creating a more stable environment for soil-associated taxa. However, other stages of the moths' life cycle could benefit from increased food quality at forest edges, as moths are more mobile compared to soil organisms and depend on aboveground vegetation for feeding and activity. van Schrojenstein Lantman et al. (2020) found higher abundance of leaf miners (mostly (micro)-Lepidoptera larva) closer to forest edges which could indicate that other patterns are expressed by adult or larval stages of moths. In addition, not only abundance but also plant functional traits can be impacted by forest edge conditions. For example, the higher nutritional content of tree leaves at the forest edge, on which caterpillars feed, results in higher pupal weight and pupal survivorship for larvae living at the forest edge (Fortin and Maufette, 2001). Therefore, potentially different drivers apply and forest edge conditions might be beneficial for moths during earlier life stages.

We also found a strong effect of forest structural complexity along the forest edge-to-interior gradients on the abundance of moths, where open forest had a lower moth activity-density and a stronger decline along the forest edge-to-interior gradient than dense forests. These results support earlier research by Merckx et al. (2012b) where they found higher abundance and species of moths in sheltered, dark, humid, late-successional deciduous forests. They stress the importance of these closed forests for moth conservation which we ego here. The effect of forest management is crucial in this respect. For example, Mönkkönen and Mutanen (2003) found lower numbers of moths in clear-cuts compared to forest interiors, forest edges and forest corridors. This is supported by Summerville (2021) who found different moth families to be less abundant in clear-cuts *vs.* selective logging; in turn, selective logging had lower abundance across moth families compared to unlogged forests. The open forests in our study were not as open as clear-cuts but comparable to a selective logging system. Despite the effect on moth activity-density, we found no differences in moth species richness between forest stand structures. This contrasts with the observations of Summerville (2011) in North America where the first years after partial logging resulted in lower moth species richness. Potentially, it takes some years for species from more open forest conditions to establish in recently managed stands creating only temporarily (first years after logging) lower species richness. In our study, the open stands were generally thinned in the last 7 years before the survey, which is also relatively recent in terms of forest management cycles.

4.2. Environmental drivers along forest edge-to-interior gradients

We linked the patterns of moth abundance and species richness to relevant environmental variables and found correlations with air temperature, forest cover, foliage height diversity, amount of forest specialist plants and total plant species richness. Temperature is an important driver shaping the distribution and activity of terrestrial arthropods (Logan et al., 2006; Vasseur et al., 2014). Also, moth activity depends on ambient temperatures such that higher activity-density was observed during warmer nights (Table S3). We found relatively subtle differences in forest temperatures between forest edges and forest interiors (e.g., minimum temperatures were 0.68°C +- 0.77 °C warmer in forest interior plots than in forest edges during the nights of sampling), albeit temperature showing the largest effect size for moth species richness of all measured variables. Moths are mobile organisms and can probably fly within a forest patch to suitable (i.e., warmer) temperatures within one night. De Smedt, Vangansbeke et al. (2019) studied moths along a vertical gradient in an old deciduous forest patch and found higher temperatures in forest canopies, correlating with higher catches of certain moth species. In addition, dense forests have a higher thermal buffering capacity and remain in general warmer at night compared to open forests (De Frenne et al., 2021), aiding habitat suitability for moths. This could be further supported by the positive relation of moth abundance and species richness with foliage height diversity (higher in denser forests) in our study. All stressing the importance of maintaining dense forests with stable higher minimum temperatures for moth activity-density.

Moth activity-density was positively correlated to forest specialist plant species and negatively to total plant species richness. Both patterns are well explained by their own gradients along forest edge-to-interior transects: forest specialist plants are relatively more important in forest interiors (Govaert et al., 2020), while the number of species in forest edges is probably higher because of the ecotonal nature of forest edges harboring also species from open areas next to the forest (Chabrerie et al., 2013; Govaert et al., 2020). Although not specifically measured during our study, forest interiors are likely darker at night compared to forest edges (Honnay et al., 2002; Delgado et al., 2007; De Smedt et al., 2016) and, albeit with some exceptions, adult moths are active when it is dark at night. Forest interior habitats could therefore be preferred by moths especially at dusk and dawn when forest interiors become or remain dark earlier or later (respectively) compared to forest edges. In addition, artificial light at night reaching forest edges might also have a negative effect on forest edge moth communities in the long term (van Grunsven et al., 2020; Boyes et al., 2021; Merckx et al., 2023).

The landscape context surrounding our studied forests is also important for moth abundance and species richness. The amount of surrounding forest seems to positively correlate with moth abundance and species richness, while grassland areas are linked only to higher species richness. This also means that the amount of arable land (the third major land use category round the plots) has a negative effect on moth abundance and diversity. These findings are supported by landscape-wide research by Merckx et al. (2019) who found higher numbers of forest and meadow moth species when higher amount of forest and meadow-habitat is present in a given radius around the focal location (160–320 m) that is comparable to the one we used in our study (400 m). This is especially true for rare and endangered moth species as Merckx et al. (2012b) showed that agricultural intensification lowers the species richness of severely declining species in the UK and the abundance of both moderately declining and priority species in the UK. These effects are most pronounced at relatively small spatial scales of a few hundred metres. These results underpin the important role of landscape composition for moth occurrence and distribution in fragmented forests. In addition, increased area of forest-like habitat whether in the form of solitary trees, hedgerows or small forest fragments increase connectivity for forest affiliated moths since these landscape features are used as stepping stones or migration corridors for moth dispersal (Slade et al., 2013; Uhl et al., 2020).

4.3. Moth community trait composition

We could not detect significant relations between the forest edge-to-interior gradient, as analyzed via the species-specific forest core affinity (FCA) score, and adult moth traits. However, we are confident that the calculated FCA-score is a good measure for forest interior affinity since we found strong similarities between our FCA values and the forest affinity values from both Waring and Townsend (2017) and Zub et al. (2019). The lack of correlation between FCA and thermal niche could indicate that moths are mobile enough on these small scales and the thermal niche of the species is probably a better explanatory trait at larger (e.g., national, continental) spatial extents.

We might also expect larger moth species, characterized by a larger wingspan and higher mobility, to be more common in forest edges, as observed in the tropics (Jaimes-Nino et al., 2019). However, we did not find such a relationship in our study. We can argue that forewing length is not an optimal proxy for mobility since also the shape of the wing can determine mobility (Sekar, 2012). In addition, the phylogenetic signal in- and between moth families cannot be ignored as illustrated by our analysis of the FCA between moth families. Although only marginally significant, the less mobile Geometridae and Erebidae showed higher FCA compared to the highly mobile Noctuidae which are strong flyers. These families all occur along our forest edge-to-interior gradient but for example the less mobile Geometridae were more confined to the forest interior. This lower mobility within the Geometridae family compared to the Noctuidae family is supported by research on the vertical gradient in forests. There, geometrid moths remain close to the forest floor, where they pupate, while noctuid moths are very often found high up in the canopy where they potentially seek for more favorable temperatures (De Smedt, Vangansbeke et al., 2019). In addition, species with high mobility that are in general bound to open conditions, such as certain noctuid moths which are characteristic for grassland habitat, are found only on the ecotone in the forest edge. We also limited our study to relatively large forest fragments (>4 ha), while it has been suggested that small forest fragments can be better characterized by sessile forest specialist moth species, while larger forest fragments host both sessile and mobile forest specialists (Slade et al., 2013).

We found more moths whose larvae feed on shrubs and trees in the forest interior and more moths whose larvae feed on grasses and herbs in the forest edge. This might indicate that moths who are specialist forest species are more restricted to the forest interior. At the same time these patterns show again the ecotonal nature of forest edges. Forest edges contain more plant species from the surrounding matrix compared to forest interiors and the species therein are very often grasses and herbs (Chabrerie et al., 2013; Govaert et al., 2020). These plants can attract moth species of which the caterpillars feed on grasses and herbs for egg deposition and the light traps in the forest edge can attract more moths from neighboring grass- and herb-dominated habitat such as semi-natural grasslands bordering the forest edge. Another explanation could be that moths use forest edges to navigate through the landscape (see Merckx et al. 2010 and Slade et al. 2013). In this sense, we argue that dispersing or migrating moths from open habitat flying along the forest edge are more easily trapped by the light traps located close to the forest edge. A similar observation was done by De Smedt, Vangansbeke et al. (2019) who caught more moth individuals from open habitat with larvae feeding on grasses and herbs in the forest canopy compared to the forest floor. They argued that moths of open habitats tend to fly over the forest fragments while dispersing or migrating instead of flying through the forest, resulting in the higher catches of open-habitat species in forest canopies. The limited correlations between our observed edge-to-interior patterns and the studied moth traits likely result from the complex ecotonal habitat of these forest edges. Therefore, we recommend studying a larger set of forest edges and revising the literature traits used, as traits directly measured in the field (and including

intraspecific variation) might better indicate ongoing processes.

5. Conclusions and implications

Our findings clearly indicate a reduction in moth abundance and species richness at forest edges, with even lower numbers in open forests. This underscores the importance of large, dense forests for this diverse and functionally significant group. Therefore, we stress the ecological value of conserving large, structurally dense forest patches with intact interiors, avoiding new edge creation and further fragmentation.

We advise to keep forest edges as structurally complex as possible to strengthen the forest interior component of the forest edge-to-interior gradients and therefore extending forest interior habitat. In the light of these findings, it makes more sense for biodiversity conservation of moths to strengthen current forest patches with reforestations and afforestation connected to or in the immediate vicinity of already established and preferably ancient forest patches instead of creating new small patches by afforestation.

We advocate for thoughtful forest management that balances canopy opening through thinning and selective logging to minimize impacts on moth communities. While open forest habitats are vital for some species, including certain moths and butterflies (Gorissen et al., 2004; Merckx et al., 2012a; Dolek et al., 2018), we recommend creating zones with both closed and open habitats at forest edges and deeper within the forest (see also Merckx et al. 2012a on zonation). It is especially important to maintain sufficient areas of undisturbed core habitat.

Additionally, the surrounding landscape is crucial, as forest specialist moths may require stepping stones like hedgerows, solitary trees, and other forest patches to disperse (Slade et al., 2013). Therefore, it is crucial to consider the landscape around forest edges, including proximity of urban areas (Uhl et al., 2021), when designing conservation plans to mitigate the negative effects of fragmentation.

CRediT authorship contribution statement

De Schuyter Wim: Writing – review & editing, Methodology. **Vanneste Thomas:** Writing – review & editing, Methodology. **Perring Michael:** Writing – review & editing, Methodology. **Dhiedt Els:** Writing – review & editing, Methodology. **Meeussen Camille:** Writing – review & editing, Methodology. **Calders Kim:** Writing – review & editing, Methodology. **Van Den Berge Sanne:** Writing – review & editing, Methodology. **Bonte Dries:** Writing – review & editing, Methodology. **Sanczuk Pieter:** Writing – review & editing, Methodology. **Spicher Fabien:** Writing – review & editing, Methodology. **Lenoir Jonathan:** Writing – review & editing, Methodology. **De Frenne Pieter:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Blondeel Haben:** Writing – review & editing, Methodology. **Vangansbeke Pieter:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Ponette Quintin:** Writing – review & editing, Methodology. **De Pauw Karen:** Writing – review & editing, Methodology. **Mestdagh Cyr:** Writing – review & editing, Methodology, Data curation. **DeCock Eva:** Writing – review & editing, Methodology. **De Smedt Pallieter:** Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Govaert Sanne:** Writing – review & editing, Methodology.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.122661.

Data availability

Raw data of moth sampling has been published on GBIF and was released to the public domain under a Creative Commons Zero waiver at http://doi.org/10.15468/3sckuk

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