



Contrasting responses of bats and macro-moths to structural complexity in forest borders

Heather Wood ^{a,b,*}, Adam Kimberley ^{a,c}, Sara A.O. Cousins ^{a,b}

^a Department of Physical Geography, Stockholm University, Stockholm, Sweden

^b Bolin Centre for Climate Research, Stockholm University, Stockholm, Sweden

^c UK Centre for Ecology & Hydrology, Lancaster, UK

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ABSTRACT

Habitat fragmentation increases the proportion of forest borders in the landscape and many forest borders lose their structural complexity due to modern forestry practices. However, remnants of structurally complex deciduous forests can remain as ecotones between plantations and agricultural fields. In this study we used terrestrial laser scanning to measure structural complexity of different forest borders, measured microclimate, and surveyed bats and macro-moths to understand how these taxa are affected. Our aim is to disentangle the main drivers, direct or indirect, that influence bat and moth assemblages. We studied 79 forest borders, and surrounding landscapes and compared them with adjacent agricultural fields and coniferous plantations. Overall, we found less bat activity and lower macro-moth diversity in simple compared to complex borders. Using structural equation modelling, we show the contrasting responses of forest-specialist bats and moths to structural complexity; with bats responding positively and moths negatively. We found similar divergent results in relation to understorey openness; with increasing forest-specialist bat activity but a lower diversity of forest-specialist moths in more open borders. Understorey vegetation also appears to regulate microclimate with more open borders being warmer and less humid. This has a potential knock-on effect for bats as they favoured borders that were warmer and more humid. Surrounding land-cover was more important than structural complexity for generalist species; with increasing generalist bat activity due to a higher proportion of local deciduous forest cover and increasing generalist moth diversity in landscapes with more forest borders. Overall, these complex relationships between forest structure, microclimate and landscape factors, coupled with divergent responses of both taxa highlight their diverse ecological needs. Therefore, we highlight the importance of managing forest borders to retain complexity and connectivity within multifunctional landscapes.

1. Introduction

Forests with complex vegetation structure are increasingly seen as important for supporting high levels of biodiversity (Ehbrecht et al., 2021; Hekkala et al., 2023). Structurally complex forests have more developed understoreys, variation in tree sizes, and high tree and shrub diversity (McElhinny et al., 2005). High complexity is often associated with old growth forests whereas modern forestry, particularly coniferous plantations, often results in monocultures of even aged tree stands with low complexity (Ishii et al., 2004). Furthermore, expansion of intensive land-use has increased forest fragmentation resulting in reduced patch size and connectivity that negatively impacts animal movements (Fischer and Lindenmayer, 2007). This fragmentation has

also resulted in increased forest borders and globally 20 % of forest is within 100 m of an edge (Haddad et al., 2015). Despite this, forest borders are increasingly considered as important habitats and represent one fifth of the total forest area (Meeussen et al., 2021). In Sweden, these forest borders are often ecotones between agricultural fields and coniferous plantations. They can either be structurally simple, hard borders dominated with coniferous trees right up to the adjacent land or, more rarely, they consist of a structurally complex band of habitat with a higher proportion of deciduous trees and shrubs than the core forest (Fig. 1). Complex borders are less prevalent with only 18 % of forest borders in Sweden considered structurally complex (Esseen et al., 2016). Complex borders in the region are often remnants of deciduous forests that were historically managed under low intensity. As such, they

* Corresponding author at: Department of Physical Geography, Stockholm University, Stockholm, Sweden.

E-mail address: heather.wood@natgeo.su.se (H. Wood).

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contain deciduous trees and shrubs with a diverse age structure and often have high plant diversity (Lindgren et al., 2018). They are also successional habitats that are dynamic in nature and can become encroached or removed because of agricultural or forestry practices (Esseen et al., 2016; Karlsson et al., 2017). Complex forest borders may be particularly ecologically important in countries like Sweden where much deciduous forest has been lost and currently 57 % of the land-use is structurally simple, commercial plantations, dominated by two coniferous species (*Picea abies* and *Pinus sylvestris*) (Statistiska centralbyrån, 2023). In addition, as few new structurally complex forest borders are created there is a risk of a net loss if they are not managed on a landscape level (Karlsson et al., 2017).

Structural complexity in forests is beneficial for bat populations. Bats have responded positively to canopy height (Jung and Kalko, 2011) and proportion of deciduous trees (Charbonnier et al., 2016; Froidevaux et al., 2021), with both positive and negative responses to tree density (Blakey et al., 2017; Boughey et al., 2011) and gaps in the canopy (Froidevaux et al., 2021; Tena et al., 2020). These contrasting responses are partly dependent on the foraging guild of bats with forest specialists responding positively to a more cluttered forest structure, with closed canopies and dense understories (Froidevaux et al., 2016). Bats can be classified into three foraging guilds based on their echolocation range: short-, mid- and long-range echolocators (Froidevaux et al., 2016; McKay et al., 2024). This classification is useful when studying structural complexity as bats' ability to navigate clutter are influenced by call type and manoeuvrability due to their ecomorphology (Froidevaux et al., 2016). In general, short-range echolocators (SRE) are adapted to fly in clutter, have short and broad wings (Norberg and Rayner, 1987) and are often forest specialists; mid-range echolocators (MRE) are often generalists associated with semi-open and interface habitats such as forest edges; whilst long-range echolocators (LRE) often fly over longer distances, have long, narrow wings for increased flight efficiency (Findley et al., 1972) and use more open habitats. Although less well studied, it is also known that moths are affected by forest structure with positive effects of tree density (Fuentes-Montemayor et al., 2022), tree basal area (Lintott et al., 2015) and canopy cover (Ober and Hayes, 2010) and negative effects of understory openness (La Cava et al., 2024) and forest age in restored deciduous woodlands (Fuentes-Montemayor et al., 2022).

In addition to influencing the habitat suitability in forests, structural complexity also has the potential to affect microclimatic conditions. Understorey vegetation has an important microclimatic buffering effect, with forests with denser understories being cooler than those with less understory vegetation (Stickleby and Fraterrigo, 2021). Typically forests are cooler than ambient free-air temperature during the day (known as a

negative offset), but the opposite is true at night (positive offset) when bats and moths are active (Haesen et al., 2021). Insectivorous bats are known to respond positively to higher air temperatures due to increased prey availability (Sherwin et al., 2013). Alternatively, bat activity has both a positive and negative relationship with humidity, possibly depending on competing needs for dry conditions for foraging or thermoregulatory benefits of reduced water loss when humid (Andreozzi et al., 2024; Froidevaux et al., 2021; Wolcott and Vulinec, 2012). Fewer studies have explicitly tested the effect of microclimate on moths but temperature has a positive effect whilst humidity a negative effect on moth abundance (Jonason et al., 2014). Although many bat and moth studies include microclimatic and structural variables (Blakey et al., 2017; Froidevaux et al., 2021, 2016), few studies have directly tested the mediating effect of forest structure on bats and moths via microclimatic processes (Andreozzi et al., 2024).

Besides local conditions, bats and moths are affected by the wider landscape. In particular bats require a diverse range of habitats to meet their ecological needs e.g., foraging grounds, roosting locations and freshwater. Forest specialist bats may require large areas of old growth forest that cannot be substituted for another forest type (Dunning et al., 1992; Froidevaux et al., 2021). Both deciduous forest and water are consistently shown to be important drivers of overall bat activity at the landscape level (de Jong and Ahlén, 1991) and connectivity via hedgerows, treelines and forest edges is important for their movement in the landscape (Kalcounis-Rueppell et al., 2013). Bat activity is often higher in forest edges compared to surrounding habitats, although studies are limited to simple forest edges only (Jantzen and Fenton, 2013; Kalcounis-Rueppell et al., 2013; Morris et al., 2010). As simple forest edges are known to support high bat activity then potentially structurally complex ones could be even more valuable. Moth diversity is also known to be higher in landscapes with more deciduous forest (Kirkpatrick et al., 2018) possibly driven by presence of food plants (Waring and Townsend, 2017). Forest borders can also support higher moth diversity compared to adjacent coniferous plantations (Pinksen et al., 2021). Furthermore, managed plantation borders are known to facilitate movement of moths with moderate dispersal abilities (Mönkkönen, 1999). Overall, it's important to consider the surrounding landscape in combination with site level conditions in conservation management of forest borders, for both bats and moths.

In this study we use data on bat and moth species diversity in 79 forest ecotones in southern Sweden to assess the importance of forest borders for supporting bats relative to neighbouring coniferous plantations or agricultural land. We use structural equation modelling to quantify the relative and interacting effects of forest border structural complexity, microclimate and surrounding landscape composition on

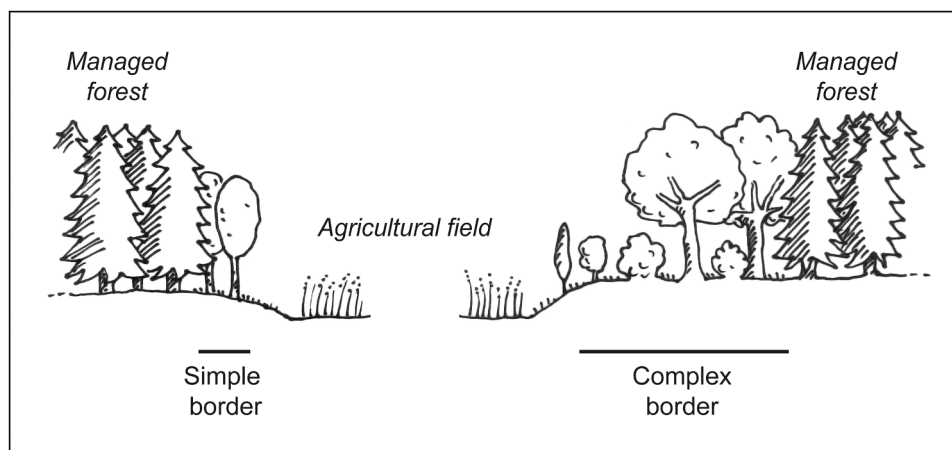


Fig. 1. Forest borders as ecotones between agricultural fields and managed forest. The simple border on the left ends abruptly with a thin line of deciduous trees. Whereas, complex borders on the right have a diverse range of deciduous trees and shrubs with gaps. From (Lindgren et al., 2018). Copyright by Jessica Lindgren. Reprinted with permission from John Wiley & Sons. License no: 5772390091340.

the presence of bats and macro-moths. Disentangling the effects of forest structure, microclimate and landscape context is key to understanding the mechanisms which determine the ecology of forest borders in managed landscapes. For instance, does forest border structural complexity affect bat species directly due to movement and echolocation specialisations, or are relationships largely due to associations between forest border structure and key microclimatic factors? Does this balance differ for species with different habitat preferences?

We hypothesise that:

1. Different assemblages of bats will occur in the forest borders, compared to the adjacent open agricultural fields and coniferous plantation.
2. Forest border structural complexity and microclimate will influence bat and macro-moth assemblages, both directly and indirectly.
3. Occurrence of bats and macro-moths will be affected by the surrounding landscape.

We predict that forest borders will support higher bat activity than the adjacent open agricultural land and coniferous plantations. Furthermore, structurally complex borders will support higher bat activity and more diverse populations of macro-moths. We anticipate that forest structure will both influence the microclimate and via microclimate have indirect effects on bats and moths. We expect short-range echolocating bats and forest specialist macro-moths to be more strongly affected by structural and microclimatic variables as these foraging guilds are ecomorphologically adapted to forests habitats and often use forest borders for commuting and as protection from predation. In terms of landscape variables, we predict that deciduous forest will have a positive effect on both bats and moths. In terms of bats, deciduous forest provides increased roosting opportunities and insect availability. Whereas for macro-moths, deciduous forest is important for shelter and increased provision of food plants. Finally, more water in the landscape benefits bats as it provides higher insect abundances and drinking water.

2. Method

2.1. Study area

We selected two study regions that have a high number of complex forest borders. The two regions are located in Stockholm and Södermanland counties in south-eastern Sweden. The northern region lies between 60.04°N and 59.71°N and the southern region lies between 59.11°N and 58.81°N. Both regions lie within the boreonemoral zone and are characterised by a mixture of agriculture, coniferous plantation (comprised of spruce (*Picea abies*) and pine (*Pinus sylvestris*), deciduous forest and lakes.

2.2. Site selection

We randomly selected 81 south-facing forest borders within nine 5000 m radius landscapes, using a combination of infrared aerial photography and site visits. We focused on south-facing borders to control for the effect of solar exposure on vegetation and microclimate (Meeussen et al., 2021). In each landscape one simple border was chosen and the remaining had some degree of complexity. A complex forest border was defined as a forest edge dominated by native deciduous trees or shrubs with herbaceous understorey, whereas simple borders were hard borders with the adjacent coniferous plantation, comprised of spruce (*P. abies*) and pine (*P. sylvestris*), with sparse or no herbaceous understorey. All borders were located between an open agricultural field and a coniferous plantation to reflect the coniferous/agricultural ecotone prevalent in this region. In Sweden plantations are typically on a 50–100 year rotation (Ahlström et al., 2022) and we avoided sampling young (approximately under 20 years) or old plantations

(approximately over 60 years) and for consistency only sampled those with little or no understorey vegetation. At each location we sub-sampled a 16 m length of forest border as per the scanning extent of the terrestrial laser scanners. Due to some moth predation in the moth traps, equipment failures and thefts only 73 borders were included in the analysis of forest border variables and 79 were included in the habitat comparison analysis.

2.3. Land-cover variables

To assess the effect of the surrounding habitat, we quantified the land-use cover at both the local-scale i.e., in a 250 m radius around each border and at the landscape scale i.e., 5000 m radius. The local-scale characterises the habitat directly surrounding the forest border, whereas the landscape-scale accounts for the nightly home ranges of bat species found in this region. They vary depending on the species, with *Eptesicus nilssonii* known to restrict its foraging to within 600 m of the colony in the maternity season (de Jong, 1994) whereas *Nyctalus noctula* is reported to forage a mean distance of 4.23 km from the roost (Mackie and Racey, 2007). Landscape analysis was carried out with QGIS version 3.4.7 (QGIS Development Team, 2024) using the Swedish National Land Cover data (Swedish: Marktäckedata (Swedish Environmental Protection Agency, 2020)). This raster landcover dataset has 25 thematic classes with a 10 m resolution and a minimum mapping area of 0.01 ha. We re-classified these into six classes: built-up, open land, coniferous forest, deciduous forest, mixed forest and water. In addition, we calculated the total length of forest borders in each landscape including all forest types bordering open land, water or built areas using ArcMap 10 (Esri, 2011).

2.4. Bat sampling

We recorded bats using three Audiomoth (Hill et al., 2018) sound recorders simultaneously in forest borders and adjacent agricultural fields and coniferous plantation. Six forest borders were sampled on each night during July and August 2018. Forest borders were surveyed for one night but only in optimal weather conditions for bat flight i.e., air temperature ≥ 5 °C, no heavy rainfall and wind speed < 5 m/s. Bat activity is known to vary due to weather conditions and surveying effort is often a balance between replicating at the site level to account for this variability versus sampling under strict conditions and replicating at the population level to include more sites (Fischer et al., 2009). We opted for the latter strategy to enable us to survey a larger number of forest borders with varying degrees of complexity. We only surveyed under strict weather conditions and repeated surveys on certain sites if the weather conditions did not match our protocol. We attached Audiomoth version 1.0.0 recorders to 2 m high poles or trees, using a sampling rate of 192 kHz and medium gain. The detectors were mounted at a height of 1.5 m and placed in the centre of the forest border with the microphone facing into the border, towards the coniferous plantation. The detectors in the open field and the plantation were located 20 m outwards from the open/border edge and border/plantation edge, with microphones facing away from the border. The detectors in the border and the plantation were always directed with their microphones pointing towards an area (approximately 5 m in front of the microphone) with no overhanging branches or large trees obstructing the microphone. These areas therefore provided a clear flight path for bats and optimised detection ability (Weller and Zabel, 2002). The minimum distance of 5 m accounts for the AudioMoth's optimum detection range of bats when the device is housed in waterproof casing (Rogers, 2021). This relatively small optimum detection range is explained by the normally omnidirectional microphone becoming more unidirectional when housed in waterproof casing (Rogers, 2021). The detectors recorded from 30 minutes after sunset to avoid peak emergence times for different bat species and concluded 30 minutes prior to sunrise.

Bat calls were recorded as full spectrum.wav sound files, 10 seconds

in length. These 10 second sequences were analysed using a semi-automatic approach, whereby calls were processed first in Kaleidoscope Pro 5.4.7 (Wildlife Acoustics, U.S.A; www.wildlifeacoustics.com) and then subsets of this data were manually checked. This post-processing validation is crucial as automatic identification software often miss bat passes and save them as noise files or mis-classify the species (Russo and Voigt, 2016). Files that were identified as noise were also manually checked to ensure that no bat sequences were missed. This involved checking 5 % of the noise files and if a bat sequence was identified then the 10 files preceding and following were also checked. Automatic identification was only accepted under certain conditions. If the call was assigned to *Eptesicus nilssonii*, *Pipistrellus pygmaeus* and *Nyctalus noctula* and had an accuracy of higher than 75 % the call was accepted whereas calls lower in accuracy were manually checked. All calls of *Barbastellus barbastellus*, *Eptesicus serotinus*, *Nyctalus leisleri*, *Vespertilio murinus*, *Pipistrellus pipistrellus*, *Pipistrellus nathusii*, and *Plecotus auritus* were manually checked as they can often be mis-identified in the software (Rydell et al., 2017). Additionally, social calls of many species are misidentified and when social calls for *P. auritus* and *P. pygmaeus* were identified then all *N. noctula* calls were checked as this is a common mis-identification. During some nights there was also very high cricket activity with broadband calls and this resulted in many mis-identifications of *P. pygmaeus* echolocation calls. In these cases, all *P. pygmaeus* were checked. For *Myotis* species all species were grouped in to a *Myotis* complex. Any poor quality or noisy sequences were simply identified as a faint bat. A sequence was only classified as a bat pass if it had two or more consecutive bat echolocation calls or at least one social call (Reason et al., 2016). As it is not possible to identify individual bats from their echolocation calls, we used the variable bat activity which is the total number of bats passes recorded. Bat passes were finally grouped into three foraging guilds based on their echolocation range (Froidevaux et al., 2016; McKay et al., 2024); short-range (*Myotis* spp.), mid-range (*Pipistrellus* spp.) or long-range (*Eptesicus*, *Vespertilio*, *Nyctalus* spp.) echolocators. This resulted in five bat response variables: total bat activity, activity of short-, mid- and long-range echolocators and bat species richness.

2.5. Macro-moths

To understand how moth communities respond to structural complexity, microclimate and surrounding landcover we surveyed moths within forest borders. Macro-moths were collected using portable 6 W Heath light traps on the next suitable night following the bat survey to avoid influencing bat behaviour (Froidevaux et al., 2018; Lentini et al., 2012). Moth sampling was carried out under similar weather conditions to the bat survey to minimise confounding effects. Any macro-moth species that could not be identified in the field were collected and identified under laboratory conditions. Macro-moths were identified to species level, when possible, otherwise to genus. Macro-moths were classified into either generalists, open habitat or forest specialists, based on data from ArtFakta (SLU, 2023). Then five variables were created; macro-moth species richness and total moth Shannon diversity, and Shannon diversity of each habitat specialism of moths.

2.6. Terrestrial laser scanning

Structural complexity in forest borders was investigated using terrestrial laser scanning. Measuring structural complexity can either be done using field measurements e.g., measuring diameter at breast height (DBH) or tree height and estimating shrub cover. But increasingly terrestrial laser scanning is seen as efficient alternative to manual measurements for obtaining more detailed variables that describe forest structure and complexity (Krok et al., 2020).

At each forest border we took three scans using a Trimble® TX5 3D Laser Scanner. One scanner was positioned 5 m from the field margin in

the open field, directly south of the tree/pole with the bat detector (in the centre of the forest border) and the further two scans were positioned 5 m north-east and north-west of the tree with the bat detector. Each scan covered a vertical area -60° to 90° and a horizontal area of 360° . Each scan was conducted in the pre-set preference “Outdoor ... 20 m” which scans distances to main objects of interest under 20 m from the scanner. Each scan lasted 5 minutes and produced point clouds with 28. 2 million points (MPts). The scans were merged into a single point cloud using Trimble® RealWorks 12.3. During processing of the point clouds, the forest borders were segmented into 16 m lengths of forest border i.e., 8 m east and west of the scanner position in the open field. In narrow borders the entire width of the border was segmented up until the start of the coniferous plantation, otherwise the point cloud was segmented at 8 m distance from the scanners located in the border. This 8 m length from the scanners was dictated by the scanning resolution as beyond 8 m from the scanner the resolution of the point cloud dropped off in many scenes especially those with denser trees. The segmented point clouds were then exported as.las files for further processing. This resulted in rectangular portions of the border 16 m in length but with variable widths.

Forest structure variables were extracted from the.las files using FORTLS package (Molina-Valero et al., 2022) in R (R core Team, 2022). First the.las files were normalized using the normalise function, then the trees were defined using the tree.detection.multi.scan with the following parameters: dbhmin=2 m, dbhmax=400, h.min=0.5, stem.section=c(0.5,3) breaks=c(1,1.3,1.6), slice =0.1. Finally, the forest structure variables were extracted using metrics.variables function using the following parameters plot.design= k.tree k=1000. This resulted in 131 different variables for each stand. Of these we selected variables that could be of ecological importance for bats and moths namely tree density, standing basal area, standing volume, mean tree diameter, mean tree height, the number of points below 2 m and the 20th height percentiles derived from z coordinates. This last variable is a good indicator of vegetation density close to ground level (Adhikari et al., 2023), with lower values indicating more dense understories. When the value is low e.g., 0.5 m then 20 % of the points, each representing vegetation hits, are located at a height of between 0 and 0.5 m with the remaining 80 % located from 0.5 m to the canopy. This means 1/5 of the point cloud is below 0.5 m and therefore relatively dense indicating a dense understory. Conversely, when the value is high e.g., 2 m it means that 20 % of the points fall beneath 2 m and therefore the points have a lower density and therefore a less dense understory vegetation. We also separately calculated the standard deviation of diameter at breast height (DBH) and of tree height, referred to as variation in DBH and tree height hereafter. These two variables have been shown to be useful measurements of structural complexity (McElhinny et al., 2005)

2.7. Microclimate data

Temperature and relative humidity were measured every minute during both the bat and moth surveys using Lascar EL-USB-2 data loggers. The loggers were mounted on the same tree as the bat detector but not directly touching it to avoid affecting the measurements. We recognise that these two microclimatic variables are often correlated but for comparability with previous microclimate studies (Blakey et al., 2017; De Frenne et al., 2021; Froidevaux et al., 2023) we retain these two variables. From this data the max, min, mean and standard deviation of temperature and relative humidity were calculated for each bat and moth survey period. To quantify the potential microclimatic buffering of the forest borders we used hourly recorded data from the nearest weather station to the survey location to calculate an offset value between microclimatic (i.e. under canopy) and macroclimatic (i.e. ambient free-air) (Haesen et al., 2021). Four weather stations were used: Tove-torp Research Station (Stockholm University) and three managed by the Swedish Meteorological Institute (SMHI, 2022). This weather station data is considered suitable for this comparison as they were on average

within 5 km from our sites (Greiser et al., 2024), at similar elevations and the temperature sensors are mounted at the same height as our loggers (1.5 m from the ground). From this data max, min, mean and standard deviation offset of temperature were calculated and resulted in either positive or negative offsets depending on whether the forest border was warmer or colder than the ambient free-air temperature. As bat and moth surveys were carried out on different nights, the relevant microclimate data collected during each survey period were used respectively in the bat and moth models.

2.8. Statistics

To compare the bat activity and richness across the three habitats (agricultural fields, forest borders and coniferous plantations) we used four response variables: the number of bat passes in each of three foraging guilds (short-, mid- and long-range echolocators; SRE, MRE, LRE) and bat species richness. Pairwise comparisons of the site border level explanatory variables revealed high correlation between some of the variables (Shannons rho > 0.5) and therefore some were removed (Supplementary 1) and resulted in six explanatory variables: variation in DBH, variation in tree height, tree density, 20th percentile of z values as a measure of understorey openness, mean humidity, maximum temperature offset. Similarly, the landscape level explanatory variables were reduced to proportion of deciduous forest, proportion of water and length of forest border at two different scales: local (250 m) and landscape scale (5000 m). The land-cover variables at the two different scales were also highly correlated and so separate models were run at each scale. In each model we used landscape ID as a random effect and included a categorical variable to show if the border was a simple or complex border. All explanatory variables were rescaled and centred using rescale function in R (R core Team, 2022).

Generalised Linear Mixed Effects models were used to analyse the differences in bat activity and richness between the three habitats and a categorical variable of border type (simple or complex) was included. Generalised linear mixed models are robust to unequal sample sizes and therefore appropriate for the unequal numbers of simple and complex border types in this analysis (Pinheiro, 2014). As the bat activity response variables were Poisson distributed and over-dispersed we used a negative binomial distribution with the function `glmer.nb` in R. Whereas for species richness with a Gaussian distribution we used `lme` in R. All models were run as full models using all chosen explanatory variables. Models were then validated using the DHARMA package in R. The full models were run for each of the four bat response variables resulting in 4 full models.

To investigate the effect of the structural, microclimatic and landscape variables on bat and moth diversity we used Structural Equation Modelling (SEM) with `piecewiseSEM` package in R (Lefcheck, 2016). Four bat SEMs were run, one for each bat response variable (bat activity of short-, mid- and long-range echolocators and bat species richness). The first mixed model in a SEM included the target bat response variable and the four structural, two microclimate, three land-cover variables, and macro-moth species richness as explanatory variables. We used a negative binomial distribution for bat activity in each foraging guild and a Gaussian distribution for species richness. The three remaining mixed effect models in the SEM investigated the impacts of explanatory variables on microclimate conditions and moth diversity. Specifically, to investigate if structural complexity influenced microclimatic conditions, we had two models with maximum temperature offset and mean humidity as response variables and the four structural explanatory variables (tree density, variation in DBH and height and 20 percentile of height) as explanatory variables. The final model had macro-moth species richness as a response and the same explanatory variables as the bat model. In all bat landscape models tests of directed separation revealed a weak correlation between maximum temperature offset and border length. However, we have no valid ecological reason to expect these variables to be correlated. Therefore, we ran separate SEMs

excluding either maximum temperature offset or border length and SEMs with border length were retained as they had lower AIC values. Separate bat SEMs were run at each of the two landscape scales and resulted in eight SEMs in total (see Supplementary 2 for the details of the regression models used in each SEM). We also used ANOVA to compare differences in structural complexity variables between simple and complex borders.

Separate SEMs were run on the Shannon diversity of generalist, open and forest specialist macro-moths. These SEMs contained three mixed models. One with the macro-moth diversity as a response variable and the same two microclimate models as per the bat SEMs. We also ran macro-moth SEMs including bat activity as an explanatory variable but these models had higher AIC values than the ones without bat activity and so bat activity was excluded from the final models. Separate moth SEMs were run at each of the two landscape scales and resulted in 6 SEMs in total (see Supplementary 2 for the details of the regression models used in each SEM). To interpret the results of these models we describe p values by their approximate degree of evidence rather than whether they are significant (Muff et al., 2021).

3. Results

We recorded 35202 bat passes (border = 11793, plantation = 5593, open = 17816) with 83 % identified to species, 14 % to two species complexes (*Eptesicus/Vespertilio/Nyctalus* or *Myotis spp.*) and 3 % to family (*Vespertilionidae*). Within forest borders we recorded 33 % of all bat passes, of which 8 % were short range echolocators, 16 % were medium range echolocators and 70 % long range echolocators. In total six species and two species complexes were identified and except for *Pipistrellus pipistrellus* all species and complexes were found in all habitat types; *P. pipistrellus* was only recorded sporadically in open and border habitats. The mean species richness in forest borders was 4.9 ± 1.4 , in open habitats 5.3 ± 1.3 and in coniferous plantations was 3.7 ± 1.5 (mean \pm SD). For a summary of bat passes per foraging guild see Supplementary 3.

In total 1766 macro-moths were recorded in the forest borders with 82 % identified to species level and the remaining 19 % identified to genus, resulting in 88 unique species and 18 additional genera. The most abundant species were two open specialists: *Cerapteryx graminis* (n=212) and *Triodia sylvina* (n=126) and two generalist species: *Noctua pronuba* (n=158) and *Xestia xanthographa* (n=107); occurring in 59 %, 59 %, 67 %, and 42 % of all borders, respectively. Of the species and genera identified, 39 % were classified as forest specialists, 38 % as generalists and the remaining 23 % were classified as open habitat specialists.

3.1. Variability in structure and microclimate

The structural variables measured in the borders varied between simple and complex borders with strong evidence that tree density was higher in simple borders ($F = 9.23, p < 0.01$), and moderate evidence that understorey vegetation was denser in complex borders ($F = 6.01, p = 0.02$). There was no evidence that variation in DBH and tree height were different between simple and complex borders ($F = 2.9226, p > 0.05$). There was no evidence of differences in microclimatic variables between simple and complex borders (Maximum temperature offset: $F = 0.0019, p > 0.05$; mean humidity: $F = 0.0236, p > 0.05$). In general forest borders regardless of their structural complexity tended to have positive temperature offsets compared to the ambient temperature in open areas; with 92 % of complex borders and 89 % of simple borders having positive offsets. This means that forest borders are warmer than the ambient air at night time.

3.2. Comparison of bat activity between habitats

Total bat activity was lower in coniferous plantations compared to all

forest borders, with very strong evidence (Estimate = -0.868 $z = -4.974$, $p < 0.001$) (Table 1). Even when the data was split and simple borders were compared to the adjacent coniferous plantations, bat activity was also lower in plantations compared to adjacent simple borders (Estimate = -1.457 , $z = -3.638$ $p < 0.001$). However, total activity was still higher in complex borders versus simple ones (Estimate = -0.466 , $z = -2.037$, $p = 0.042$). The highest total bat activity was recorded in open habitats (Estimate = 0.403 , $z = 2.338$, $p = 0.019$).

Lower activity of short-range echolocators (SRE) were recorded in coniferous plantations compared to borders (Estimate = -0.537 , $z = -2.613$, $p < 0.01$) and there was lower activity of SRE bats in open habitats (Estimate = -0.421 , $z = -2.115$, $p = 0.034$). We found no evidence for different activity levels of SRE bats between simple and complex borders. As for mid-range echolocators (MRE) we found no differences in activity between the three habitat types or between simple and complex borders. There was strong evidence that more long-range echolocators (LRE) are found in open habitats, (estimate = 0.632 , $z = 3.226$, $p < 0.01$) and less in plantations compared to borders (Estimate = -1.063 , $z = -5.233$, $p < 0.001$). There was also less LRE activity in simple compared to complex borders (Estimate = -0.523 , $z = -1.998$ $p = 0.046$). Bat species richness showed similar trends to activity with very strong evidence that less species are encountered in plantations (Estimate = -0.284 , $z = -3.726$, $p < 0.001$). We found no evidence for differences in bat species richness in open habitats compared to borders or between simple or complex borders.

3.3. Drivers of bat activity and species richness within forest borders

Short-range echolocating (SRE) bats were positively affected by variation in tree height (Standardised Effect Size = 0.22 , $p = 0.010$, $R_c^2 = 0.37$) and understorey openness in the landscape model (Standardised Effect Size = 0.21 , $p = 0.029$, $p = 0.020$, $R_c^2 = 0.37$). There was very strong evidence that mean humidity has a positive effect on SRE bats in both the local (Standardised Effect Size = 0.52 , $p < 0.001$, $R_c^2 = 0.42$) and landscape models (Standardised Effect Size = 0.27 , $p < 0.01$, $R_c^2 = 0.37$) (Fig. 2). Border length had a positive effect on SRE bats at the local scale (Standardised Effect Size = 0.24 , $p = 0.041$, $R_c^2 = 0.37$).

There was weak evidence of a positive effect of tree density on mid-range echolocators (MRE) in the local model (Standardised Effect Size = 0.16 , $p = 0.070$, $R_c^2 = 0.50$) and mean humidity had a positive effect in both local (Standardised Effect Size = 0.35 , $p = 0.035$, $R_c^2 = 0.50$) and landscape models (Standardised Effect Size = 0.10 , $p = 0.047$, $R_c^2 = 0.32$) (Fig. 3). Deciduous forest had a positive effect with very strong evidence at the local level (Standardised Effect Size = 0.36 , $p < 0.001$, $R_c^2 = 0.41$) whereas total border length had a negative effect with weak evidence at the local scale (Standardised Effect Size = -0.17 , $p = 0.070$, $R_c^2 = 0.50$) and very strong evidence at the landscape level (Standardised Effect Size = -0.18 , $p < 0.001$, $R_c^2 = 0.32$).

In comparison, there was no evidence of forest structure or land-

cover variables affecting activity of long-range echolocating bats. However, similar to the other foraging guilds there was very strong evidence of a positive effect of mean humidity in the local model (Standardised Effect Size = 0.45 , $p < 0.001$, $R_c^2 = 0.27$) and moderate evidence in the landscape model (Standardised Effect Size = 0.18 , $p = 0.037$, $R_c^2 = 0.13$). Additionally, there was very strong evidence for a positive effect of maximum temperature offset in the local model (Standardised Effect Size = 0.42 , $p < 0.001$, $R_c^2 = 0.27$). (Supplementary 2)

In the landscape model, variation in DBH had a weak positive effect on bat species richness (Standardised Effect Size = 0.19 , $p = 0.055$, $R_c^2 = 0.42$). Similar to the bat activity models, mean humidity had a positive effect with moderate evidence in both local and landscape models (Standardised Effect Size = 0.39 & 0.27 , $p = 0.011$ & 0.018 , $R_c^2 = 0.46$ & 0.42). There was no evidence that local or large -scale landscape factors were important (Supplementary 2).

In all local bat models, there was weak evidence of understorey openness increasing maximum temperature offset in the border (Standardised Effect Size = 0.22 , $p = 0.065$, $R_c^2 = 0.15$) and very strong evidence that maximum temperature offset has a negative effect on mean humidity (Standardised effect size = -0.67 , $p < 0.001$, $R_c^2 = 0.36$). In all landscape models there was weak evidence of a positive effect of length of forest borders on macro-moth species richness (Standardised Effect Size = 0.29 , $p = 0.067$, $R_c^2 = 0.38$). We also found no correlation between bat activity and moth species richness in any of our models.

3.4. Drivers of macro-moth diversity within forest borders

Similar to overall bat activity, macro-moth diversity was lowest in simple forest borders (Estimate = -0.270 , $t = -2.013$, $p = 0.480$). However, in contrast to short- and mid-range echolocating bats, forest specialist macro-moths were negatively affected by forest structural variation with strong evidence that variation in DBH had a negative effect in the local model (Fig. 4) and moderate evidence in the landscape model (Standardised Effect Size = -0.30 & -0.23 $p < 0.01$ & $p = 0.047$, $R_c^2 = 0.29$ & 0.26). There was also moderate evidence of a negative effect of understorey openness on forest specialist moths in the local model (Standardised Effect Size = -0.28 $p = 0.021$, $R_c^2 = 0.29$) and weak evidence in the landscape model (Standardised Effect Size = -0.21 $p = 0.086$, $R_c^2 = 0.26$). There was also strong evidence that the amount of water at the local-scale had a negative effect on forest specialist macro-moths (Standardised Effect Size = -0.31 $p < 0.01$, $R_c^2 = 0.29$).

As for generalist macro-moths, there was no evidence that forest structure or microclimate affected diversity but total forest border length at the landscape scale had a strong positive effect on generalist moths (Standardised Effect Size = 0.42 , $p < 0.01$, $R_c^2 = 0.25$) (Fig. 5; see Supplementary 2 for the results from all other moth SEMs). No evidence was found that any of the structural, microclimatic or land-cover variables affected open specialist macro-moths.

Table 1

Generalised linear mixed model estimates of differences in bat activity (bat passes) and species richness within three habitat types: forest borders, forest and open habitats, based on 79 habitat triplets located in Southern Sweden. Estimates shown are from the full models; using either glmer.nb or lme (species richness). A comparison of activity and richness between simple and complex borders is shown by the variable simple. Estimates for bat passes are also shown by echolocation type (short-range echolocator, mid-range echolocator, long-range echolocator).

Variable	Bat Activity				Bat species richness ^b					
	Total bat passes ^a	Short-range echolocators ^a	Mid-range echolocators ^a	Long-range echolocators ^a						
Habitat Type:										
Border (intercept)	4.941	***	2.341	***	2.783	***	4.553	***	1.581	***
Forest	-0.868	***	-0.537	**	ns		-1.063	***	-0.284	***
Open	0.403	*	-0.421	*	ns		0.632	***	ns	
Border type:										
Simple	-0.466	*	ns		ns		-0.626	*	ns	

Significance levels given: *** <0.001 , ** <0.01 , * <0.05 , <0.1 , ns = not significant.

^aNegative binomial distributions.

^bGaussian distributions.

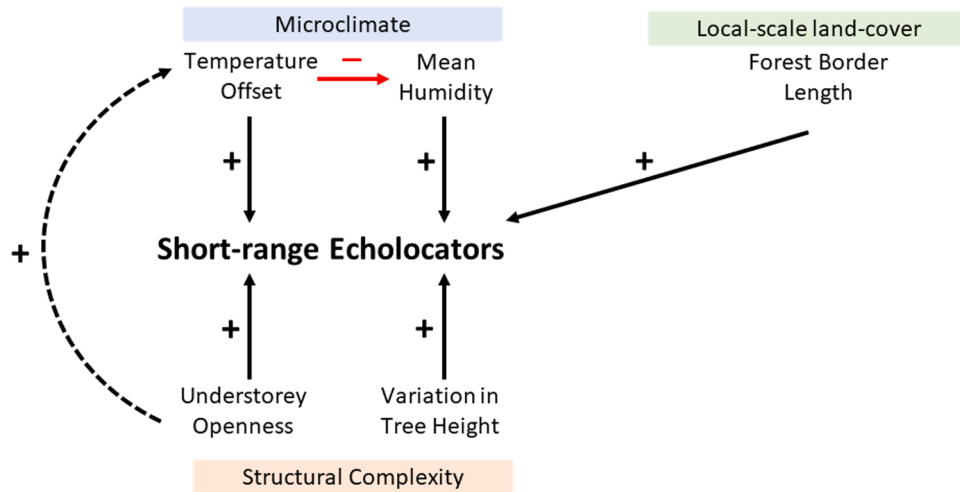


Fig. 2. Structural Equation Model diagram showing the relationship between forest structural complexity, microclimate and land-cover variables on the activity of short-range echolocating (SRE) bats in forest borders (n= 73) in Southern Sweden. Local-scale variables are measured within a 250 m radius of the border whilst landscape land-cover variables are measured within a 5000 m radius of the forest border. Macro-moth richness was included both as response and predictor variables but is not included in the figure as no relationship between bats was found. Positive effects are shown with black arrows and negative with red and hatched lines show relationships with $p < 0.1$. See Supplementary 2 for full statistical output.

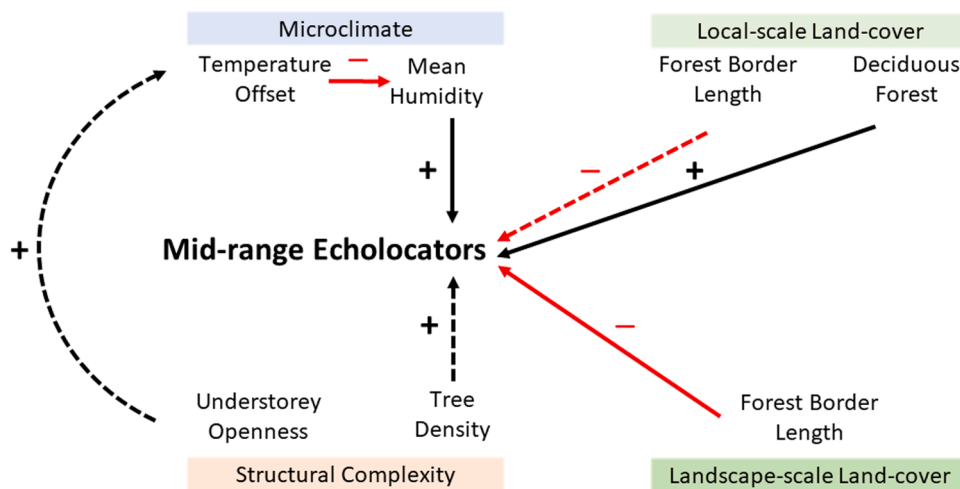


Fig. 3. Structural Equation Model diagram showing the relationship between forest structural complexity, microclimate and land-cover variables on the activity of mid-range echolocating (MRE) bats in forest borders (n= 73) in Southern Sweden. Local-scale variables are measured within a 250 m radius of the border whilst landscape land-cover variables are measured within a 5000 m radius of the forest border. Macro-moth richness was included both as response and predictor variable but is not included in the figure as no relationship between bats was found. Positive effects are shown with black arrows and negative with red and hatched lines show relationships with $p < 0.1$. See Supplementary 2 for full statistical output.

In all moth models there was a positive effect of understorey openness on maximum temperature offset in the borders (Standardised Effect Size= 0.21 $p = 0.048$, $R_c^2 = 0.36$) and weak evidence of a negative effect on mean humidity (Standardised Effect Size= -0.18 $p = 0.093$, $R_c^2 = 0.36$). In other words, forest borders with more open understories were warmer than the ambient temperature outside the borders and had a tendency to be less humid. There was also very strong evidence of a negative effect of maximum temperature offset on mean humidity (Standardised Effect Size= -0.48 $p < 0.001$, $R_c^2 = 0.36$) and therefore warmer borders were less humid.

4. Discussion

Forest borders are an important habitat in managed landscapes often with more varied and complex vegetation structure compared to adjacent coniferous plantations. In Sweden, where forests are dominated by

coniferous plantations, complex forest borders with high proportions of deciduous trees are important ecotones (Lindgren et al., 2018). Here we show that forest borders are also important habitats for bats and macro-moths. Specifically, we found higher activity of short-range echolocating (SRE) bats in forest borders compared to surrounding coniferous plantations and open habitats. We also found that bat activity and moth diversity were higher in complex forest borders compared to structurally simple ones. Importantly, bats and moths showed contrasting responses to structural complexity, with bats responding positively to variation in tree height whereas moths responded negatively to variation in DBH. As for understorey openness, bats responded positively and moths negatively. Regarding microclimate, warmer and more humid borders supported higher bat activity but had no effect on macro-moths. Contrasting responses of bats and moths were also observed in relation to land-cover variables, with total length of forest borders having a negative effect on bats and a positive effect on

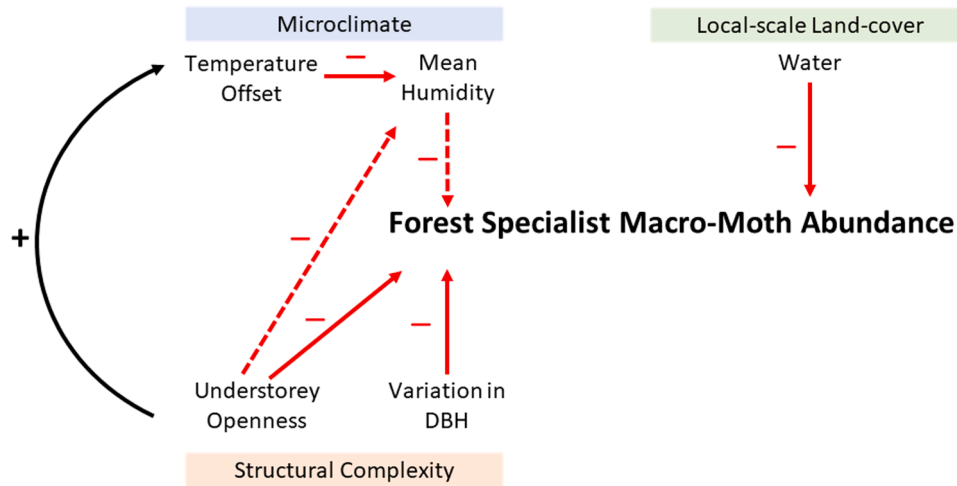


Fig. 4. Structural Equation Model diagram showing the relationship between forest structural complexity, microclimate and land-cover variables on the abundance of forest specialist macro-moths in forest borders (n= 73) in Southern Sweden. Local-scale variables are measured within a 250 m radius of the border. Positive effects are shown with black arrows and negative with red and hatched lines show relationships with $p < 0.1$. See Supplementary 2 for full statistical output.

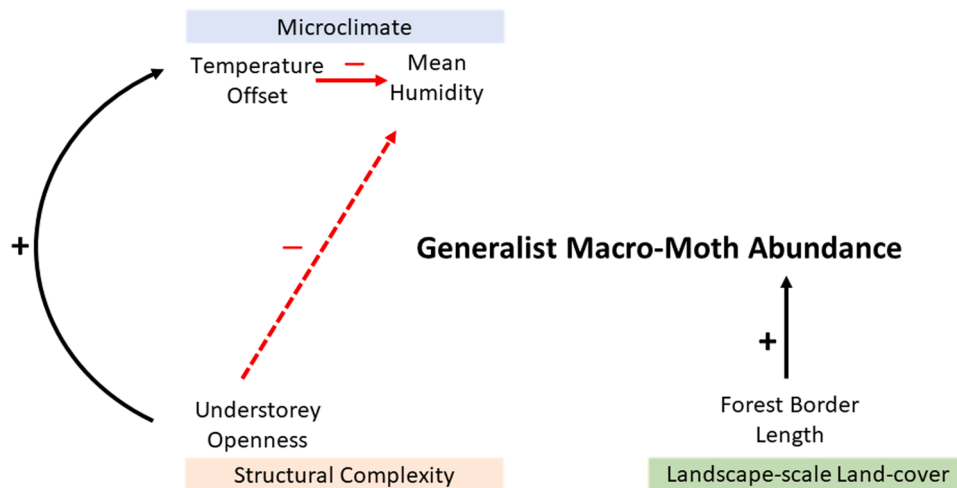


Fig. 5. Structural Equation Model diagram showing the relationship between forest structural complexity, microclimate and land-cover variables on the abundance of generalist macro-moths in forest borders (n= 73) in Southern Sweden. Local-scale variables are measured within a 250 m radius of the border. Positive effects are shown with black arrows and negative with red and hatched lines show relationships with $p < 0.1$. See Supplementary 2 for full statistical output.

macro-moths. Surprisingly we only find weak evidence of an indirect effect of forest structure on bats via microclimatic processes, whereby borders with more open understorey tend to be warmer and warmer borders support higher activity of SRE bats. Overall, site level structural and microclimatic variables were most important for forest bat specialists and surrounding land-cover was more important for generalists.

4.1. Importance of forest border habitats

We show that forest borders support higher bat activity and species richness compared to coniferous plantations. This trend was more pronounced for our forest specialist short-range echolocating (SRE) bats, with more activity in borders compared to both plantations and open agricultural fields and echoes the findings of Jantzen and Fenton (2013) and Morris et al., (2010). This is probably driven by a combination of bat ecomorphology, prey availability and predator avoidance. Forest specialist bats are adapted in terms of ecomorphology to fly in cluttered vegetation (Norberg and Rayner, 1987) and will avoid more open habitat (Entwistle et al., 1996). They also require protection from predators when commuting and foraging (Moussy, 2011). Forest borders

are known to offer good foraging habitat as insect prey (e.g. Diptera and Lepidoptera consumed by bat species in this region) also concentrate along borders (Morris et al., 2010). Otherwise, open fields had more activity of the other foraging guilds compared to borders and could be partly explained by detectability whereby its easiest to detect bats in open environments without trees or shrubs blocking signals to the microphone. Though we believe we partially mitigated for this by only placing detectors in openings within borders and forests to maximise detection ability in these more cluttered habitats. This is also potential that we recorded more cricket noise due to the low height of detectors and this may have obscured some calls. Furthermore, long-range echolocators dominated the activity in open fields and their calls are louder and detectable at longer distances from the microphone, increasing the chance of recording their calls (Russ, 2021). Our findings show, that forest borders are valuable ecotones between coniferous plantations and open agricultural fields and provide a mixture of semi-open and forested habitat providing diverse conditions for semi-open and forest specialists bats. Our results mirror previous research that shows that semi-open ecotones such as wood pastures (Wood, Lindborg and Jakobsson, 2017) support high levels of bat activity compared to surrounding

habitat types. Hence, forest border ecotones are valuable habitats within otherwise highly managed species poor landscapes and should be prioritised in management plans.

4.2. Effects of tree structural complexity

To understand the processes that govern higher bat activity and moth abundance in forest borders it is important to investigate the specific responses to structural complexity variables. We found a positive effect of the variation of tree height on forest specialist short-range echolocating (SRE) bats. Forest stands with more variable tree height will have more gaps and therefore SRE bats were more active in these semi-open borders. This is in contrast to previous work where variation in tree height was shown to be negatively correlated with bat activity because more open forests are less suitable for certain bat species (Jung et al., 2012). This could partly be explained by increased detectability of SRE bats in more open borders where there is increased likelihood of their short-range calls reaching the microphone. Although if detectability of SRE bats was affected by clutter in our study we would expect to see a negative correlation between tree density and activity of SRE bats. Mid-storey tree stem density is known to negatively affect detectability of high frequency bats (O'Keefe et al., 2014), such as the SRE bats in our study, although our results show that tree density had no effect on SRE activity and therefore we assume clutter had a marginal effect on detectability. Similar positive effects of forest gaps have been found and this may be due to increased insect availability in these openings (Blakey et al., 2017; Tena et al., 2020). This could be true in our forest borders as borders with more variable vegetation height would have more shrubs and small trees that may be beneficial for SRE bats that typically glean insect prey from vegetation (Law et al., 2015).

Short-range echolocating bats with high manoeuvrability should also be better adapted for flight in more structurally complex borders. The combination of their short, broad wings and broadband echolocation calls (Norberg and Rayner, 1987) means they can navigate the variable vegetation heights. Furthermore, in our study region these borders are situated in landscapes dominated by coniferous plantations. They can be densely planted with few natural forest gaps or glades. Dense plantations are known to be avoided by most bat species including forest specialists and possibly they are too dense even for bats adapted to flying in clutter (Kirkpatrick et al., 2017b). Furthermore, plantations often lack tree features required for roosting such as cavities and dead wood that are particularly important for forest specialist bat species (Russo et al., 2010). So perhaps these forest borders with diverse tree heights are providing a range of habitats that are largely absent from the surrounding landscape. Tree density in the borders was also important for mid-range echolocating bats similar to previous findings (Kalda et al., 2014; Wood et al., 2017) and is likely linked to their wing morphology and their manoeuvrability in cluttered environments. Finally, we found no effect of structural variables on long-range echolocators and this may be related to their flight mode; often flying above the canopy. Previously, activity of long-range echolocating bats has been shown to have a positive relationship with canopy ruggedness (Froidevaux et al., 2016), a variable measured using airborne LiDAR rather than the terrestrial LiDAR used in our study.

We also found higher overall diversity of macro-moths in complex borders but they showed the opposite response to bats in terms of structural complexity variables. Forest specialist macro-moth abundance decreased in borders with more variable DBH. As DBH and canopy cover are known to be correlated (Gill et al., 2000), variation in DBH could translate to variation in canopy cover, possibly with more gaps. Moths have been shown to favour closed canopies possibly due to increased food plant abundance (Ober and Hayes, 2010) and lower predation (La Cava et al., 2024). Therefore, it is possible that borders with more variation in tree size are less suitable for them. Younger woodlands, which are less structurally diverse, have also been shown to support higher abundance of generalists macro-moth species

(Fuentes-Montemayor et al., 2022). Clearly tree structural complexity influences bat and moth-moth assemblages and heterogenous forest borders are required to fulfil the contrasting ecological requirements of both taxa.

4.3. Effects of understorey openness

Bats and macro-moths also responded divergently to understorey openness. Short range echolocating (SRE) bats were positively affected by openness in the understorey. SRE bats are well adapted to flying in clutter but stands with more open understoreys have been suggested to improve foraging success (i.e., in more open understoreys, prey will have fewer places to rest and avoid predation (Froidevaux et al., 2021)). This means that bats possibly do not select the habitats with the highest prey but rather habitats where prey capture is easiest (Rainho et al., 2010). This could also partly explain why we find no correlation between bat activity and macro-moth richness in any of our models. Further, the negative relationship between forest specialist macro-moths with understorey openness tallies well with the theory that moths require understorey clutter to avoid predation. A similar pattern was observed by La Cava et al. (2024), where empty space had a negative effect on moth abundance possibly driven by increased predation risk. The lack of correlation between bat activity and moth richness could also be explained by prey preferences, although the SRE bats in this study are mostly specialising in moths some such as *Myotis daubentonii* consumes mostly Diptera (Vesterinen et al., 2018) and activity of this species is unlikely to be correlated with moth abundance. Despite the negative relationship of moths to structural complexity there was still a higher overall abundance of macro-moths in complex borders compared to simple. This could suggest we are missing key site level attributes that are important for moths such as canopy cover or plant diversity. Again, the contrasting responses of moths and bats shows that it is necessary to create forest borders with a diverse range of understorey coverage to support both bats and macro-moth populations.

4.4. Effects of microclimate

Whilst there was evidence that structural variables were important for bats and moths, the most consistent and strong response was the positive effect of mean humidity on bats. Contrastingly, we found no effect of humidity on macro-moths, one of the dominant prey items of the short-range echolocating bats in our study. The effect of relative humidity on bats from previous studies shows contradictory results with some species reacting positively to relative humidity (Wolcott and Vulinec, 2012) and others reacting negatively (Andreozzi et al., 2024; Rojo Cruz et al., 2019). The positive effect of humidity that we found is contrary to the attenuation hypothesis whereby echolocation calls are absorbed by more humid atmosphere and decreases the range that calls can be detected at (Griffin, 1971). This attenuation should interfere with bat flight especially in cluttered environments. Instead, we find a positive effect of humidity that could be due to increased prey availability. There is little research on the effect of humidity on many insect groups but high humidity is known to increase mosquito abundance (Baril et al., 2023); another major component of the bat diet and particularly the mid-range echolocators in this study. Moths have shown variable effects to relative humidity with both increases in abundance (Choi, 2008) and declines, possibly due to increases in moth pathogens (Intachat et al., 2001). Humidity is also intrinsically linked to air temperatures and our models show that these two variables are also influenced by understorey openness, whereby borders with more open understoreys are warmer and less humid. Two of the bat foraging guilds (short- and long-range echolocating bats) increased in warmer and more humid borders but humidity explained the most variance. These interacting effects of structure and microclimate could suggest a play off between the benefit of having an open understorey that creates warmer borders versus more closed borders that have higher humidity.

4.5. Land-cover effects

Whilst forest specialist bat activity and moth abundance were mostly driven by site level structure and microclimate, generalist species were most affected by land-cover factors. Earlier studies have found that deciduous forest (de Jong and Ahlén, 1991; Johansson and De Jong, 1996) is an important driver of bat activity and species richness. At the local level, we found that deciduous forest was most the important factor for our generalist mid-range echolocators (MRE). Deciduous forest supports more diverse communities of invertebrates and also offers more roosting opportunities for tree-dwelling bats through provision of tree holes, crack and crevices (Johansson and De Jong, 1996). Surprisingly we did not find a positive effect of deciduous forest on moth abundance like previous studies (Froidevaux et al., 2019; Kirkpatrick et al., 2017a). This may be due to the relatively low proportion of well-connected deciduous forests in this region. Moths and particularly forest specialists are vulnerable to deciduous forest fragmentation despite their high dispersal abilities and require large patches of forest and connectivity via linear features (Slade et al., 2013).

A more striking finding is that total border length is beneficial at the local level for short-range echolocators (SRE) but strongly negative at the landscape scale for mid-range echolocating (MRE) bats. Similar positive effects of forest edge length were found for an edge specialist bat (Ethier and Fahrig, 2011) and is possibly indicative of habitat complementation providing a variety of habitats at the relevant scale. At the local scale (250 m) there is likely a higher amount of complex forest borders versus simple. We only sampled 16 m of any given complex border but this was just a small section of a longer stretch of complex border within the local landscape. Therefore, complex borders comprise a large length at the local scale. Conversely, at the larger scale complex borders will be scarcer as they are not common in the wider landscape with approximately 72 % of Swedish forest borders being narrow simple ecotones (Esseen et al., 2016). Therefore, our larger scale is dominated by simple borders between production forest and open fields and results in a negative impact on bat activity. In contrast to MRE bats, generalist moths were more abundant in landscapes with more borders. Similar to bats, it is likely that moths use linear features like forest borders as they are sheltered habitats for flight (Coulthard et al., 2019; Merckx and Macdonald, 2015). It is also likely that insects shelter more on simple forest borders versus complex ones that have more diffuse edges causing prey to scatter over the wider area (Jantzen and Fenton, 2013). Forest borders may also aid moth dispersal (Mönkkönen and Mutanen, 2003) and generalist species with moderate dispersal will likely benefit most from linear features (Mönkkönen, 1999).

Unexpectedly we also found a strong negative effect of water at the local-scale on forest specialist moths, similar results were found previously on macro-moth species richness (Lintott et al., 2014) but the mechanism behind this effect is unknown. One possibility in our study area is that forest-specialist moths are more adapted to dry coniferous forests that are the dominant forest habitat in this region. Overall, our findings show that a landscape approach to border management is required so we can maintain stable populations of generalist bat and moth species.

4.6. Conservation implications

The most striking finding in our study was the contrasting habitat and landscape level requirements for bats and moths. Despite their contrasting needs, importantly both taxa were more prevalent in structurally complex borders compared to simple borders. Specifically, to support forest specialist bats, we require structurally complex borders with diverse tree heights and a more open understorey. Simultaneously, moths require the opposite with less variation in DBH and more understorey. Understorey openness also appears to be key in microclimate regulation within forest borders, with more open borders being warmer and less humid. Humidity was a consistent, strong driver of a bat

activity and therefore a balance is required. Even though bat activity was higher in more open understoreys, some degree of denser understorey is required to maintain humidity levels that also favour bats and their prey. Our findings described here show a complex and multifaceted relationship between structural complexity, microclimatic variables and our studied taxa. However, these complex direct and indirect relationships highlight the importance of habitat heterogeneity. The very nature of complex forest borders is that they are heterogenous and can offer a multitude of micro-habitats such as gaps between trees and shrubs and patches with denser understorey. We only sampled a short distance of forest border at each location and as such our data probably represents small snapshots of different micro-habitats. If longer, continuous lengths of borders were studied it should capture this heterogeneity more completely. Site level characteristics were most important for forest specialists. However, to also ensure optimum habitats for generalists we must consider the surrounding landscape, with high connectivity of forest borders for macro-moths and patches of deciduous forest for bats. Thus, also at the landscape level it is important to maintain habitat diversity to support a diverse range of species. Overall, we highlight the importance of maintaining structurally complex forest borders that represent remnants of historical forest management, especially when they are in landscapes dominated by structurally simple managed forests.

CRedit authorship contribution statement

Adam Kimberley: Writing – review & editing, Writing – original draft, Supervision, Methodology, Formal analysis. **Heather Wood:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Sara A. O. Cousins:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization.

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.2024.122416](https://doi.org/10.1016/j.foreco.2024.122416).

Data Availability

Data will be made available on request.

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