



Combining forest exploitation and heathland biodiversity: Edges structure drives microclimates quality and reptile abundance in a coniferous plantation

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ABSTRACT

In Western Europe, natural habitats such as heathlands have been converted into many commercially managed forests, with severe impacts on biodiversity. In dense planted forests, forest edges are often the only suitable areas for ectothermic organisms highly dependent on open habitats for thermoregulation. Surprisingly, the influence of forest edges structure on the thermal quality of microhabitats and reptile species distribution remains poorly understood. In this study, we examined two reptile species and thermal quality of interior forest edges of a coniferous forest in Western France (Brittany). We focused on two hypotheses (i) the vegetation structure of the forest edges drives the thermal quality of the habitat and (ii) structural complexity of the forest edges influences the abundance of two heliothermic reptiles: the common adder (*Vipera berus*) and the common lizard (*Zootoca vivipara*). We first deployed temperature sensitive data loggers to quantify thermal conditions along 16 cross-sections of inner forest margins. For each section, 4 temperature loggers were placed at 1, 3, 5 and 7 m from the driveway and we examined the relation to vegetation structure and canopy cover. Second, we carried visual encounter surveys in 55 edges in order to measure the response of two reptiles to the structure of the forest margin along exploitation driveway. Our results show that high local canopy cover decreases microhabitat quality within interior forest edges. We also found that common lizard abundance was significantly influenced by the edge orientation and increased with global canopy openness and ground level vegetation. Adder abundance only increased significantly with the driveway width, suggesting the unmodelled effect of other biotic/abiotic variables. Our study shows that thermal quality of interior edges and driveway characteristics are relevant to support heathland reptile populations. We posit that maintain strips of favourable microhabitats should be an efficient land sharing strategy to combine forestry activities and biodiversity conservation.

1. Introduction

In Western Europe, human activities have undergone an exponential growth during the last century. These major changes in practices and needs induced significant impacts on large areas of natural/semi-natural habitats and are considered as a major cause of biodiversity loss (Cafaro et al., 2022; Young et al., 2005). Thus, in highly anthropized landscapes, most habitats are directly threatened by degradation, fragmentation or destruction (Krauss et al., 2010; Newbold et al., 2016). Facing the

current growing need for resources and energy, it is now more important than ever to reconcile anthropic activities with nature conservation. Recent work in landscape ecology suggests that both land sharing and land sparing practices can be combined at small spatial scales (Grass et al., 2019). However, the spatial scale considered is largely dependent of species characteristics notably for organisms with limited dispersal and homeostatic capacities (Ekroos et al., 2016; Tews et al., 2004).

After the WWII, growing European population and needs for building materials have led to an exponential requirement for raw materials such

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as timber wood. This has resulted in a massive exploitation of natural habitats previously considered as unfavourable for wood production due to their relative humidity, soil moisture, and limited access (Ridding et al., 2020; Sargent and Bass, 1992). For instance, large areas of heathlands and moorlands have been drained and planted, mostly with mono-specific conifers, to meet the needs for wood (Donald et al., 1998; Fagúndez, 2013), thereby leading to the disappearance of 80–90% of heathlands in the European Atlantic region during the 20th century (Rosa García et al., 2013). Commercial forestry plantations on these natural habitats have strong impacts on ecosystems. Beyond the drainage of soils often necessary for forestry practice (Paavilainen and Päivänen, 1995), the growth of the thick canopy cover leads to the progressive closure of the environment and a reduction in the amount of light reaching the ground. However, the amount of solar radiation is a key factor directly influencing the growth of low vegetation (Bhattra et al., 2020). As a result, the high canopy cover leads to a decrease or even total disappearance of the specialized low shrubs (e.g., *Erica* spp., *Ulex* spp.) that are typical of open or semi-open heathland habitats previously present (Jenkins, 1986). Recent works clearly point out the importance of microclimate quality and heterogeneity, notably within forested landscapes (De Frenne et al., 2021; Pincebourde and Woods, 2020). This approach should be extended to habitat edges that can offer a diversity of thermal conditions.

Under temperate climates, many ectotherms such as reptiles are highly dependent on structurally diversified open habitats and a high degree of vegetation structural complexity that creates a wide range of abiotic (thermal and hydric) conditions available for thermoregulation and hydroregulation (Elzer et al., 2013; Guillon et al., 2014; Londe et al., 2020). For instance, habitat closure will alter the thermal quality of the habitat by limiting the access to thermal preference and therefore physiological performance (Lelièvre et al., 2011; Reading and Jofré, 2018). In turn, open and simplified habitats with vegetation height lower than 10 cm expose reptiles to potentially lethal temperatures (Worthington-Hill and Gill, 2019) or increase the desiccation risk (Rittenhouse et al., 2008). Consequently, diversified heathlands with complex matrix of microhabitats have a high conservation value for European reptiles by providing in the same area a diversity of microclimates for thermoregulation and hydroregulation (Stumpel and Van der Werf, 2012). Unfortunately, historic massive mono-specific coniferous plantations on heathlands resulted in the dominance of a thick tree structure that prevents solar radiation from reaching the ground, leading to modifications in microhabitat conditions (Chen et al., 1999). The resulting unfavourable abiotic conditions for ectotherms can generate negative impacts (Pike et al., 2011; Todd and Andrews, 2008). For instance, the increasing canopy cover in coniferous plantations resulted in a lower growth rate of smooth snakes (*Coronella austriaca*) which consequently produce fewer embryos than in heathland open habitats (Reading and Jofré, 2018). In contrast, removing the forest canopy cover can partially restore habitat quality for reptiles if low vegetation is maintained (Pike et al., 2011). In the face of worldwide decline of reptiles (Cox et al., 2022; Reading et al., 2010), it is important to conciliate economic exploitation of the commercial forestry and biodiversity.

A modern major dilemma consists in reconciling societal and economic pressures with biodiversity conservation (Grass et al., 2021). In the context of commercial forestry, forest margins and interfaces between habitats are of major importance for land sharing practices and often constitute refuge areas. It is to note that almost 20% of the world forest surfaces are within 100 m of an ecotone, demonstrating the importance of good management of these elements (Haddad et al., 2015). Edges and ecotones can be very favourable for reptiles (Graitson et al., 2020; Hansen et al., 2019) by providing appropriate abiotic conditions for foraging (Edgar et al., 2010), digestion, reproduction, thermoregulation, and hydroregulation (Blouin-Demers and Weatherhead, 2002; Lourdais et al., 2017). However, the inadequate management of these margin elements in commercial forest results in the creation of long linear abrupt margins with no intermediate height

vegetation, which leaves little room for the presence of a thermal and hydric gradient, and consequently reduces the availability of microhabitats (Meeussen et al., 2020). Given the importance of habitat edges for reptiles, it is crucial to better understand the structural factors affecting microhabitat quality and availability on the margins of exploited forests.

While intensive forestry is negative for reptiles preservation, we posit that maintaining structured internal forest edges with a linear strip of low tree density and structured vegetation is essential for the maintenance of reptiles in forest edges. We concurrently studied two reptile species and thermal quality of edges in a planted coniferous forest in Western France and address the two following hypotheses and predictions:

- (i) The vegetation structure of the forest edge drives the thermal quality of the habitat. We posit that canopy cover is a simple and reliable indicator of edge thermal conditions. Low cover within the cross-section should reflect favourable (warmer) ground level microclimatic conditions.
- (ii) Structure of the forest margin influences the abundance of two generalist reptiles: the common lizard (*Zootoca vivipara*) and the common adder (*Vipera berus*). We predict that abundance of these reptiles along the linear strips of forest edges should be positively influenced by low canopy closure of the edges.

2. Materials and methods

2.1. Study area and species

This study was carried out in 2009 in the departmental forest of Avaugour Bois-Meur (48°28'29"N, 3°02'36"W). Local climate is temperate oceanic and the forest extends from east to west along a quartz-rich linear geological structure constituting a topographic barrier culminating at 271 m. Avaugour Bois-Meur is largely dominated by mono-specific patches of coniferous forest (*Pinus* spp., *Abies* spp., *Larix decidua*, *Picea* spp.) that were planted on a heathland previously maintained by agropastoral activities. The forest was mainly planted in the seventies following a major fire and is crossed by about 20 km of forest driveways that facilitate commercial exploitation. The entire massif was classified as a sensitive natural area in 2005, resulting in the reduction but not the cessation of commercial exploitation. In 2009, four species of reptiles were present: the slow worm (*Anguis fragilis*), the grass snake (*Natrix helvetica*), the common lizard (*Zootoca vivipara*), and the common adder (*Vipera berus*). Only the latter two species were considered in this study because they are both generalist species dependent on open habitats (Edgar et al., 2010). Those two species have been extensively studied. They are active thermoregulators with high thermal preference (> 30 °C), notably during reproduction (LeGalliard et al., 2003; Lourdais et al., 2013). High quality microhabitats providing suitable thermal and hydric conditions are essential for both species. Indeed, some studies reported that hydric restriction and high temperature induce physiological stress in the common lizard which results in reduction of fitness or reproduction process (Brusch et al., 2023; Dupoué et al., 2020b, 2020a, 2019; Rozen-Rechels et al., 2018). A recent work on a congeneric species of *Vipera berus* (*Vipera aspis*) demonstrate that, during water deprivation periods, vipers can use humid microhabitats for thermoregulation and at the same time limit hydric loss (Dezetter et al., 2023). In this study we deliberately focused on the thermal ecology because humidity in a forest is high compared to open habitats (Ashcroft and Gollan, 2011; Rittenhouse et al., 2008) and notably in our study site in which ditches offer access to permanent humid environments. Consequently, we consider that the main abiotic constraint occurring in forest edges is the thermal quality related to canopy cover as reptiles can easily hydroregulate by means of behavioural hydroregulation.

2.2. Canopy cover and thermal conditions

2.2.1. Data collection

In order to describe variation in thermal conditions and their relation to canopy cover, we first selected 16 forest edge cross-sections south facing throughout the Avaugour Bois-Meur forest, with contrasting structural facies reflecting variation from abrupt forest transition to progressive vegetation variation. Each cross-section was of 10 m width, located perpendicular to the exploitation driveway, itself oriented east–west (Fig. 1) and was equipped with four temperature loggers (IButton Maxime/Dallas semi conductor® DS1922L) positioned respectively at 1, 3, 5 and 7 m from the driveway. Loggers were inserted into rubber sheaths, fixed to stakes and placed close to the ground in microhabitats potentially used by reptiles for basking (open microhabitats, top of moor-grass clumps; *Molinia caerulea*). Therefore, we targeted potential basking sites and avoided shaded microhabitats between thick grass clumps unused by reptiles for thermoregulation. Loggers were set to synchronously record temperature every 15 min between the 15th of May to the 5th of August 2009. For each data logger, we recorded the following set of variables (Table 1): the position inside the forest edge, the local distance to the closest tree trunk, and the canopy cover. To calculate canopy cover, we took a spherical picture perpendicular from the ground and facing the sky with NIKON COOLPIX (opening 45°) at 1.3 m height. GIMP 2.0 program was then used to separate vegetation pixels from sky pixels and calculate vegetation cover.

2.2.2. Thermal quality

To describe the thermal environment of the edge cross-sections, we derived five thermal indexes from the collected temperature data. These indexes were calculated for each data logger every 24-hours cycle and allowed us to evaluate the thermal quality of microhabitats within forest edges. These five indexes are: (T_{mean}) the mean temperature for the whole day, ($T_{\text{mean_Day}}$) the mean temperature of the day-time between 08 h01 and 20 h00, which is considered as the active period of reptiles, ($T_{\text{mean_Night}}$) temperature of the night-time between 20 h01 and 08 h00, which is considered as the inactive period of reptiles, (ΔT_{mean}) the difference between the mean temperature during the day and the following night and finally (Time_T_{30}) which represents the cumulative day-time in hours with a recorded temperature above 30 °C. These parameters therefore provide an estimate of how long preferred temperatures were accessible during basking activities.

Table 1

Local variables considered for the thermal characterisation of microhabitats, and variables taken into account for N-mixture modelling. Time-specific variables were meteorological variables occurring during the survey, and site-specific variables were specific to each forest edge considered in our study design.

Local variables for thermal characterisation	
Local_dist_tree	Distance from the logger to the first tree (m)
Can_cover	Local canopy cover (%) measured at 1.3 m above the ground
Position	Position of the logger inside the forest edge (1–3–5–7 m depth)
Variables for N-mixture modelling	
Time-specific	
Cloud	Cloud coverage at prospection time
Temp	Temperature (°C) at prospection time
Wind	Wind speed (km/h) at prospection time
Site-specific	
Orientation	Orientation of the forest edge (north-east-south-west)
Driveway_width	Width (m) of the forest driveway contiguous to the forest edge
Dl_subshrub	Distance (m) within the forest edge to which the last subshrub (height < 1 m) is observed
Df_shrub	Distance (m) within the forest edge to which the first shrub (height between 1 and 3 m) is observed
Df_tree	Distance (m) within the forest edge to which the first tree (height > 3 m) is observed
PC1	Principal component 1 resulting from PCA of canopy cover
PC2	Principal component 2 resulting from PCA of canopy cover

2.3. Reptile survey

2.3.1. Forest margin selection and data collection

We selected 55 sections of forest margin (50 m length) placed along forest edges parallel to the driveway. In this study, we considered that forest margins encompassed the exploitation driveway and the forest edge. These margins were distributed throughout the Avaugour Bois-Meur forest and were selected for their structure (homogenous within each linear strip but with contrasting facies among margins). We defined a survey transect as a linear strip of habitat constituted by the forest edge (7 m wide and 50 m length). The average minimum distance as the crow flies between each selected edges and the closest one was 197 ± 69 m. As reptiles tend to use the matrix of open habitat provided by forest margins for displacements (Jellinek et al., 2014), we calculated another average distance, i.e., the distance between transects using forest plot borders (230 ± 98 m). Such distance largely exceeds the dispersal capacity of the common lizard, as reported by several studies (Massot et al., 2008; Massot and Clobert, 2000, 1995). The movements and dispersal of the common adder are greater than those of the common lizard and also vary according to sex, with higher mobility for males

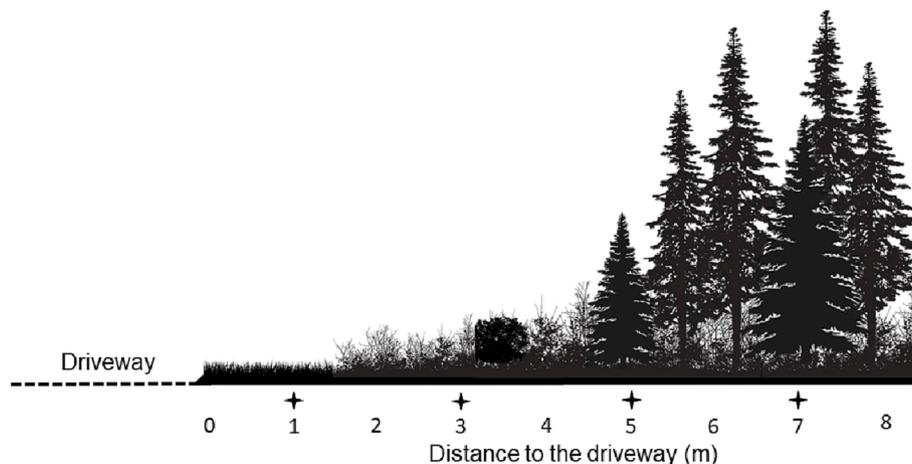


Fig. 1. Description of a forest margin cross-section that encompasses the exploitation driveway and the forest edge. The crosses represent the four positions inside forest edges where (i) thermal conditions were measured using thermosensitive loggers and (ii) local canopy cover was measured.

than females (Neumeier, 1987). However, movement capacities have to be interpreted in the landscape context and canopy cover. Indeed, survey transects were spatially selected to be separated by unsuitable habitats, hence limiting displacements of reptiles between transects. Despite the fact that individuals were not individually marked, we did not notice any clear evidence of movements between transects of phenotypically easily recognisable individuals (i.e., injuries or recognisable zigzag patterns). Consequently, while we cannot entirely ensure that no displacement has occurred between transects, we consider this bias to be limited.

We characterized transects in the margin context using a set of variables (Table 1). For each transect, we collected canopy cover (measured at 1.3 m height as described previously), respectively in the middle of the driveway and at 1, 3, 5 and 7 m depth inside the edges. We also measured: (1) the driveway width, (2) the edge orientation, (3) the distance within the forest edge to which the last heathland subshrub (height < 1 m, e.g., *Erica species*) was observed, (4) the distance within the forest edge to which the first shrub (height between 1 and 3 m) and (5) the first tree (height > 3 m) were observed. For each transect, all variables were collected at three random perpendicular sections and we used the algebraic mean of these three repetitions as transect variables for further analysis.

2.3.2. Survey protocol

Spring 2009 was associated to important precipitations and survey started as soon as conditions became favourable in the study site. Between the 7th of May and the 30th of July 2009, the selected linear transects were surveyed 7 times for reptiles. This period encompassed the breeding season (mating and pregnancy) which is associated to high detection rate of both species. During a visit, the field operator carefully inspected the soil and all the microhabitats present. Each survey lasted 10 min, which is a comfortable amount of time to survey a 50 m linear element. All surveys were carried out by one field operator (P-A. R.), who is experienced in reptile monitoring. Two visual surveys were separated by at least 48 h and were performed under good weather conditions (temperature < 25 °C, light wind, no rain). A special attention was paid to complete a survey session in all forest margins before starting a new one. At the end of each survey, meteorological variables occurring at survey time were recorded. Thus, cloud coverage was recorded as an ordinal class (0–20%, 21–40%, 41–60%, 61–80% and 81–100%). Temperature and wind speed have been measured using an ADC Wind (SILVA) thermometer/anemometer.

2.3.3. Abundance estimation

In order to estimate the relative abundance of our two reptiles and determine the factors affecting it, we used a hierarchical modelling technique specially developed to take into account imperfect detection: N-Mixture modelling. The N-mixture modelling is derived from the Site-occupancy modelling and uses counts of individuals and a mixing distribution (e.g., Poisson, Zero-Inflated Poisson) to estimate an individual detection probability (P_{ind}) and an index of relative abundance (λ) for each site taking into account imperfect detection (Royle, 2004). This modelling technique allows the inclusion of co-variables to explain the heterogeneity in detection and abundance between surveys and sites, respectively.

2.4. Statistical analyses and modelling approach

2.4.1. Determinants of thermal quality

In order to determine the thermal quality of microhabitats, we first examined the determinants of the canopy cover using linear mixed models (lmer). Models were built using the canopy cover as a dependant variable while distance to the first local tree, position within the forest edge, and interaction between these two variables were set as predictor variables. Forest edge identity was included in models as a random factor to account for the non-independence of data inside edges [lmer

formula; Canopy cover ~ Local_dist_tree + Position + Local_dist_tree: Position + (1|edgeID)]. A series of linear mixed models were then used to find out determinants of thermal indexes measured inside forest edges. For each thermal index, we tested the simple effect and the quadratic effect of the canopy cover, the position inside the edges, and the interaction between these variables. To account for the study design, we included edges and Ibutton identity as nested random factors and the Julian date corresponding to each thermal index as a cross random factor [lmer formula; Thermal index ~ Can_cover + Can_cover² + Position + Can_cover:Position + Can_cover²:Position + (1|edgeID/IbuttonID) + (1|JDate)]. For these linear mixed models, we developed a model selection procedure to identify the best model. Thus, starting from the most complex model and using *dredge* function (*MuMIn* package), we fitted all possible combinations of variables in lmer models with no limited number of variables. All models were then ranked by AICc and we selected the best model according to the AICc criterion. In case of multiple models within $\Delta AICc < 2$ compared to the best model, we have selected the one with the lowest degree of freedom (according to the parsimony principle). Models including the quadratic term unaccompanied by the linear term were not taken into account as recommended in interaction models (Brambor et al., 2006). We used the principle of parsimony rather than model averaging of the best models because the number of models with $\Delta AICc < 2$ was very low (maximum two) and parsimony principle does not allow any doubt on the model selection (lowest degree of freedom). Selected model validation was performed by inspection of the distribution of residuals and the respect of homoscedasticity.

2.4.2. N-Mixture Modelling

To determine the drivers of relative abundance, we used a hierarchical modelling technique: N-mixture modelling. To build models, we used time-specific variables (linear and quadratic terms) as explanatory variables of detection probability (P_{ind}). Site-specific variables were set as predictor variables of relative abundance (λ). We did not include site-specific variables for the modelling of the detection probability because we assume that these variables have little influence on detection in linear forest edges surveys. For *Zootoca vivipara* and *Vipera berus* (single species models), we fitted all possible model combinations with a maximum of 4 variables using the *dredge* function. The maximum number of variables was set to four because the number of forest edges monitored was relatively small ($N = 55$; See in Boissinot et al., 2019) and limiting the number of variables greatly reduces the risk of model overfitting. Due to this limitation, we observed numerous models with AICc close from each other with the same degree of freedom corresponding to different combinations of maximum four variables. Therefore, we applied a model averaging procedure based on the top-ranking models with $\Delta AICc < 3$. As a result of the model averaging process, only the variables with a p-value (P) < 0.1 (full model estimation) were considered as significant and were consequently further discussed. For each variable retained in our best models ranking with $\Delta AICc < 3$, we calculated the relative importance (RI) using the relative sum of AICc weights of models including the target variable.

All variables included in models were scaled (subtracted by the mean and divided by the standard deviation) and wind speed was log scaled to best achieve the normality assumption. To avoid including autocorrelated variables in N-mixture models, and to reduce the complexity of models, we performed a principal component analysis (PCA) on margin canopy cover measures (5 variables taken from the driveway to 7 m depth inside the forest edge). Then, we extracted the two first principal components (PC) and included them in our dataset as two distinct site-specific variables for N-mixture modelling (Table 1). We used correlation coefficient between PC and original variables to interpret these two new variables. No other autocorrelations issues were detected within variables ($|r| < 0.7$). To select the best fit distribution for N-Mixture modelling, we calculated the AIC of the null model using Poisson “P” and Zero-Inflated Poisson “ZIP” distributions for the two studied species. The

distribution leading to the lowest AIC has been retained for further analysis. Accordingly, we selected “P” distribution for *Zootoca vivipara* ($\Delta\text{AIC} = 2$) and “ZIP” distribution for *Vipera berus* ($\Delta\text{AIC} = 10.94$). Negative binomial distribution “NB” were excluded from analysis due to the well documented possibility of unrealistic estimations using this distribution although it is often selected by the AIC (Joseph et al., 2009; Kéry, 2018). All analysis were carried out in R 4.2.1 using *lme4*, *MuMIn*, *Unmarked*, *AICcmodavg*, *factoextra*, and *FactoMineR* packages.

3. Results

3.1. Determinants of canopy cover and thermal quality

When analysing the 16 forest edge sections fitted with temperature loggers, we found that the best model for local canopy cover only included the local distance to the first tree (effect = -0.06 ± 0.01 , t-value = 4.786), excluded the position within the cross-section and the interaction term between these two variables (see Supplementary Table S1 for all combinations of models tested). The greater the distance to the nearest tree, the lower the local canopy cover, and so independently of the position in the edge cross-section. Global canopy cover of each cross-section (average of values collected at 1, 3, 5 and 7 m in depth) was closely related to the average distance to the nearest trees (Pearson correlation test, $r = -0.77$, p-value < 0.001).

All best models selected for thermal indexes retained local canopy cover while they excluded the position variable and interactions terms (Table 2; see Supplementary Table S2 to S6 for all combinations of models). The best model selected for $T_{\text{mean_night}}$ and $\text{Time}_{T_{30}}$ only included linear term of canopy cover. However, T_{mean} , $T_{\text{mean_Day}}$ and ΔT_{mean} included a quadratic effect of canopy cover. According to these models, increasing local canopy cover led to a decrease in mean temperature of the whole day (T_{mean} ; Fig. 2a), the mean temperature of the day-time ($T_{\text{mean_Day}}$; Fig. 2b), the difference between mean temperature of the day-time and the night-time (ΔT_{mean}) and the time during which the temperature was higher than 30 °C ($\text{Time}_{T_{30}}$; Fig. 2c). However, a similar increase in local canopy cover led to an increase in the average temperature during the night-time ($T_{\text{mean_night}}$).

3.2. Variation in edges structure

Important variations in canopy structure were observed among the 55 linear transects selected for reptile monitoring. The two first principal components of the PCA for the canopy cover from the driveway to 7 m depth inside the forest edge explained 86.99% of the variance. PC1 (68.12% of the variance) was positively related to canopy cover at every position. Therefore, PC1 reflected the overall degree of canopy closure and a high value on PC1 corresponded to a global high canopy cover at every position of the forest edge. On the other side, PC2 (18.87% of the variance) was positively related to canopy cover 5 and 7 m away from the driveway but negatively related to canopy cover at 1 m and 3 m depth as well as in the middle of the driveway. Consequently, PC2 can be interpreted as a structuring variable of the canopy cover according to the position inside the forest edge.

Table 2

Lmer results of the best selected model for each thermal index. For each model, the nature of the relation (linear or quadratic) is specified and coefficient estimates with standard error are reported.

Best model selected	Effect	Can_cover (estimates \pm SE)	Can_cover ² (estimates \pm SE)
$T_{\text{mean}} \sim \text{Can_cover} + \text{Can_cover}^2 + (1 \text{edgeID})$	Quadratic	0.27 ± 0.67	-2.57 ± 0.67
$T_{\text{mean_Day}} \sim \text{Can_cover} + \text{Can_cover}^2 + (1 \text{edgeID})$	Quadratic	-1.64 ± 1.36	-4.02 ± 1.36
$T_{\text{mean_Night}} \sim \text{Can_cover} + (1 \text{edgeID})$	Linear	1.09 ± 0.21	
$\Delta T_{\text{mean}} \sim \text{Can_cover} + \text{Can_cover}^2 + (1 \text{edgeID})$	Quadratic	-4.16 ± 1.89	-2.58 ± 1.89
$\text{Time}_{T_{30}} \sim \text{Can_cover} + (1 \text{edgeID})$	Linear	-1.56 ± 0.13	

3.3. Determinants of detection and abundance of *Zootoca vivipara*

Zootoca vivipara was detected at least once in 48 out of 55 transects (87,3%). The selection procedure and model averaging for N-Mixture modelling highlighted no significant time-specific variables strongly influencing detection probability of *Zootoca vivipara*. Indeed, even if the quadratic term of temperature was included in the averaging procedure, this time-specific variable had a relative low importance (0.72) and p-value ≥ 0.10 (Table 3). On the other side, common lizard abundance (λ) was significantly associated with $\text{DI}_{\text{subshrub}}$, PC1 and the orientation variables. These three variables were found in all models included in $\Delta\text{AICc} < 3$ rank and their relative importance was consequently equal to one. According to model averaging, the abundance of common lizards was higher in south facing edges compared to north facing ones (Fig. 3a). East and west facing edges had an intermediate abundance. Moreover, common lizard abundance was negatively influenced by PC1 (Fig. 3b) and positively related to the distance within the forest edge to which the last heathland subshrub was observed (Fig. 3c). The last abundance variable retained by the $\Delta\text{AICc} < 3$ top ranking models had a lower relative importance and p-value ≥ 0.10 (Table 3).

3.4. Determinants of detection and abundance of *Vipera berus*

Vipera berus was detected at least once in 22 out of 55 forest edges (40%). N-Mixture modelling identified a quadratic effect of cloud coverage on individual detection probability (P_{ind}). The relative importance of the cloud coverage was equal to 1 (with p-value < 0.01) for the linear and the quadratic terms (Table 3). The individual detection probability increased with cloud cover up to $\sim 60\%$ and then dropped beyond this threshold (Fig. 4a). None of the other variables relating to the probability of detection were included in the top-ranking models, thus excluding them from the model averaging procedure. On the other side, our selection procedure identified driveway width as an important variable positively related to adder abundance (λ) and which was retained in the 2 top ranking models out of 3, leading to a high relative importance equal to 0.83 (p-value < 0.1; Table 3). Thus, the greater the width of the exploitation driveway, the greater the abundance of common adder (Fig. 4b). All other abundance attributes selected for model averaging had a lower relative importance and a p-value ≥ 0.10 .

4. Discussion

4.1. Canopy cover and edges thermal quality

In accordance with our first hypothesis, this study shows that local canopy cover was (a) closely associated to forest edges structure (distance to the nearest tree) and also (b) predictive of microhabitat thermal quality within edges. Therefore, low canopy cover allows the development of thermally suitable microhabitats close to the ground and this parameter is of paramount importance to explain edges thermal properties. Notably, low canopy cover allows solar radiation to reach the ground, increasing the mean temperature of the whole day and during day-time (Fig. 2). Additionally, the greater the canopy opening, the

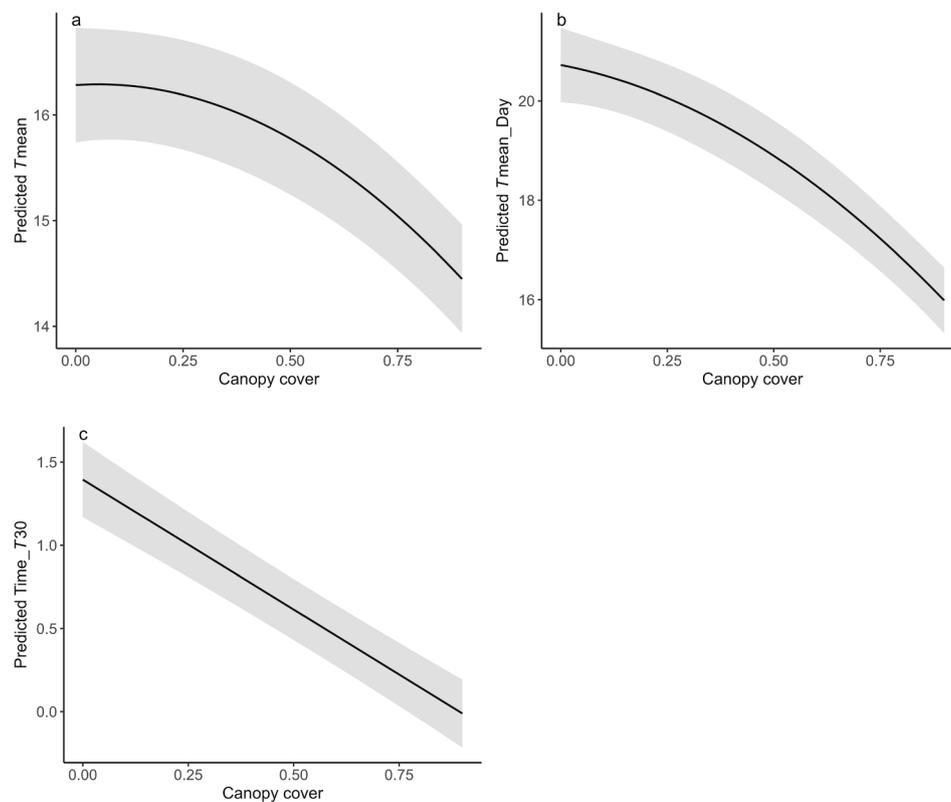


Fig. 2. Significant effect of local canopy cover on 3 thermal indexes (a) the mean temperature of the whole day (Tmean); (b) the mean temperature of the day-time (Tmean_Day); (c) the cumulative day-time in hours with a recorded temperature above 30 °C (Time_T30).

greater the commuted time with environmental temperature above 30 °C. On the other hand, during the night-time, high canopy cover positively influenced surface temperature.

Ectotherm organisms such as reptiles are highly dependent on thermal exploitation of microhabitats to reach preferred body temperature. Consistent with other studies, our results suggest that the general encroachment and development of canopy cover is associated with the degradation of microhabitat thermal quality available for reptiles (Azor et al., 2015; Greenberg et al., 2018; Jofré et al., 2016; Webb et al., 2005). By inference, global cooling of microhabitats due to high canopy cover likely impacts the activity and life history traits of reptiles. For instance, low temperatures are associated with a lowering of metabolic rate directly impacting physiological processes such as digestion (Lelièvre et al., 2011, 2010). On the other hand, sub-optimal temperatures during pregnancy can result in low-quality offspring (Lorioux et al., 2013). The high structural complexity of the lower vegetation is also a key factor directly affecting microhabitat quality. Indeed, increasing vegetation structural complexity leads to a higher range of available abiotic conditions in the local environment (Elzer et al., 2013; Guillon et al., 2014; Londe et al., 2020) and at the same time modulates the risk of predation (Duchesne et al., 2022; Worthington-Hill and Gill, 2019). It is therefore crucial to consider both canopy cover and vegetation structural complexity as important drivers of microhabitat quality for reptiles.

4.2. Effect of margin structure and canopy cover on reptile abundance

Partially congruent with our second hypothesis, our results show that structural elements of margin structures influence the abundance of common lizard. On the other side, the adder abundance was only explained by the driveway width. First, orientation variable was decisive to explain lizard abundance within transects (Fig. 3a). In the Northern Hemisphere, heliothermic reptiles tend to favour sunny orientations such as south facing forest edges or hedgerows (Edgar et al., 2010). The

lizard abundance was also significantly influenced by the structure of the canopy cover within the forest edge. Indeed, lizard abundance decreased with the general encroachment of the edge (interpretation of the PC1 variable; Fig. 3b). Finally, the distance within the edges to which the last heathland subshrub (e.g., *Erica species*) was present positively influenced lizard abundance (Fig. 3c). Congruent with other studies, our results for the common lizard indicates that habitat structure is of primary importance for reptiles. For instance, canopy cover up to 25% is associated to an important reduction in the number of common lizards encountered in commercially managed forests (Jofré et al., 2016). Logically, the increase of canopy cover leads to a decrease in light reaching the ground, thereby reducing the thermal suitability of reptiles microhabitats. The low ground vegetation (i.e., subshrub) is also of paramount importance to increase the structural complexity of open habitats and accordingly to promote high diversity of microhabitats available for reptiles. Unfortunately, in commercial forests, low ground vegetation declines as tree canopy cover gradually closes over (Bhattra et al., 2020; Jofré et al., 2016). Consequently, in a commercial forest, heliothermic reptiles are restricted to high quality linear margins to achieve effective thermoregulation, foraging activities, and find shelters to avoid predation risk (Andersson et al., 2010; Blouin-Demers and Weatherhead, 2002; Edgar et al., 2010). For instance, field studies on milk snake and rat snake both indicated preference for high quality edges, where these species can find a wide range of thermic and hydric conditions in their close environment (Blouin-Demers and Weatherhead, 2002; Row and Blouin-Demers, 2006). Together, these results support the importance of maintaining high quality margins to maintain common lizards within commercial forests.

On the other hand, adder abundance was only positively influenced by the driveway width. In general, the wider the pathway, the greater the amount of light reaching the forest edges. As no other structural features were reported to significantly influence adder abundance, it is possible that adder abundance was related to other biotic or abiotic

Table 3

Results for the model averaging procedure of N-mixture modelling for *Zootoca vivipara* (ZV) and *Vipera berus* (VB). Variables are structured in 2 categories: A) Detection attributes and B) Abundance attributes. For each variable retained in top ranking models ($\Delta\text{AICc} < 3$), the relative importance (RI), the sign of the relation (S) and the p-value are provided. For the orientation categorical value, the p-value results from Chi-square Likelihood ratio test of embedded models. Significant effects resulting from model averaging are bolded.

a)		Detection attributes																							
		Cloud			Cloud ²			Wind			Wind ²			Temp			Temp ²								
		RI	S	P	RI	S	P	RI	S	P	RI	S	P	RI	S	P	RI	S	P						
N-Mixture	ZV VB	1	+	<0.01	1	-	<0.01									0.72	-	0.2							
b)		Abundance attributes (λ)																							
		Df_tree			Driveway_w			Df_shrub			Df_subshrub			PC1			PC2			Orientation					
		RI	S	P	RI	S	P	RI	S	P	RI	S	P	RI	S	P	RI	S	P	RI	S	P			
N-Mixture	ZV VB	0.71	+	0.2	0.84	+	<0.1				1	+	<0.01	1	-	<0.01	0.27	+	0.6	1	+/-	<0.01	0.44	+	0.5

variables which were not considered in this study due to inherent difficulties to estimate them. For instance, prey abundance and predation pressure might vary between edges and not taking these parameters into account might lead to unexplained heterogeneity in reptile abundance (Diaz and Carrascal, 1991; Hu et al., 2019). For future studies, we strongly recommend adapting the study design in order to include the effects of such biotic and abiotic factors.

4.3. Effect of meteorological conditions

Beside abundance, our modelling results suggest that the detection probability of adders is significantly influenced by cloud coverage. Indeed, cloud coverage between 40% and 80% maximizes the detection probability (Fig. 4a) which dovetail nicely with findings from a previous study (Graitson et al., 2022). This shows that sunny days with low cloud coverage provide enough thermal energy and there is therefore no need for adders to bask in open habitats, which leads to a decrease in detection probability. On the other hand, no meteorological variables significantly affected the detection probability of common lizards. This surprising result could be due to a limited range of weather conditions under which surveys were performed resulting in difficulties to calibrate detection models. Consequently, the detection probability of lizards was considered to be constant in this limited range of conditions. While this could potentially result in survey-specific unmodelled detection heterogeneity of individuals, simulations of assumption violations showed an existing but limited bias in abundance estimations (Kéry and Royle, 2016).

4.4. Management implications for reptile conservation

In facing the worldwide decline of reptiles (Cox et al., 2022; Reading et al., 2010), it is crucial to reconcile forestry operations with conservation efforts to achieve efficient land sharing. Ecotones and habitat margins are largely overlooked in our highly fragmented habitats and often considered as of limited economic interest (Haddad et al., 2015; Mullu, 2016). Exploited forest interior margins constitute a dense linear network that offer an opportunity to combine human activity and biodiversity conservation (*sensu* “land sharing” see Grass et al., 2021). Proper management of these forest margins can help ensure that both can co-exist (Meeussen et al., 2020). To achieve this goal, we strongly recommend promoting establishment and maintenance of several linear strips a few tens of meters long and 3 m wide of open to semi-open habitats with low tree density between driveways and forest interiors and supporting sufficient ground vegetation (> 10 cm height). These linear strips should be primarily maintained in south facing edges and secondarily in east or west facing margins. A dynamic management

(rotation) of these strips should decrease the effect of thinning disturbance by providing reptiles with a good habitat quality at proximity. Additionally, attention should be paid to the general amount of solar radiation reaching the forest margins. In this scope, sufficiently wide pathways (> 10 m) should be maintained. Highly structured edges should not be considered as a net loss of space and income for commercial forestry as they act as wind protection, limit dispersal of pests, and reduce the development of branches (Laurance and Curran, 2008; Šálek et al., 2013). Considering the global loss of reptiles (Cox et al., 2022), we strongly recommend implementing forest margin structure in forestry management plans as a land sharing strategy for reptile conservation. In a more general context, habitat structure and canopy cover in coniferous plantations have been reported to strongly influence communities of other ectotherm taxa such as Lepidoptera and Coleoptera, suggesting a combined positive effect of such management recommendations (Lin et al., 2007; van Halder et al., 2008).

5. Conclusion

Forest margins can play an important role in commercially managed forests to conciliate economic exploitation of resources and biodiversity conservation. Our study reveals that local canopy cover along forest interior margins can be used as a simple predictor of microhabitats thermal quality within edges. Additionally, we found that orientation of the edge as well as global canopy openness and ground level vegetation (subshrubs) influence the abundance of common lizards showing the paramount importance of margins structure for this ectotherm species. However, adder abundance was only explained by driveway width, suggesting the influence of other biotic or abiotic variables, such as prey availability, which were not taken into account in our study design. This study provides emphasis to the importance of maintaining strips of open or semi-open habitats along forest edges to improve thermal quality of microhabitats available for reptiles. Therefore, we strongly recommend to consider the structure of forest edges when designing forestry management plans, as it is a crucial element in bridging the divide between commercial forestry and reptile conservation.

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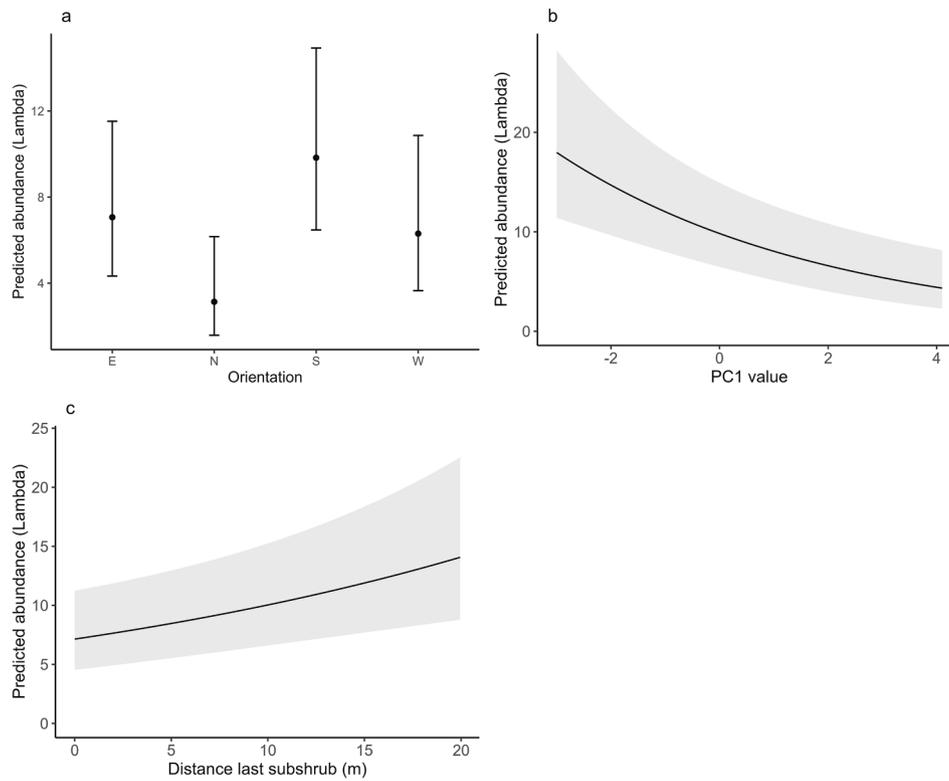


Fig. 3. Significant effect of (a) orientation, (b) principal component 1 of canopy cover PCA and (c) distance within the edges to the last subshrub on the predicted abundance of *Zootoca vivipara* in 50 m section of edges. For prediction plots (b) and (c), the orientation categorical variable was set to south.

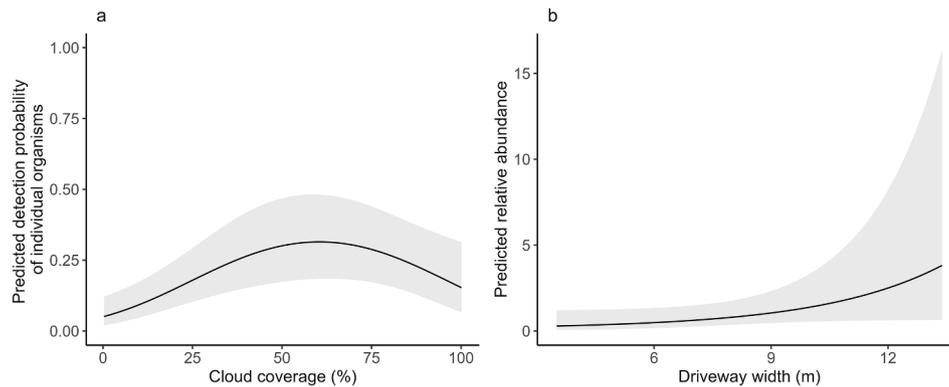


Fig. 4. (a) Effect of cloud coverage on individual detection probability of adder based on N-mixture modelling. (b) Effect of the forest driveway width on predicted relative abundance of adder based on N-mixture modelling.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.121188>.

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