

Czech University of Life Sciences Prague

Faculty of Environmental Sciences

Department of Forest Ecology



Master's Thesis

**Properties of the tree layer vegetation modulated by
environmental heterogeneity in the small forest
fragments in Český kras**

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CZECH UNIVERSITY OF LIFE SCIENCES PRAGUE

Faculty of Environmental Sciences

DIPLOMA THESIS ASSIGNMENT

Arnau Bosch Guiu

Nature Conservation

Thesis title

Properties of the tree layer vegetation modulated by environmental heterogeneity in the small forest fragments in Český kras

Objectives of thesis

This work attempts to provide description of the tree (and shrub) layer vegetation in small forest fragments in Český kras in relation to environmental conditions and their small-scale and landscape-scale heterogeneity. Conclusions will be drawn on the basis of literature review and analysis of the data from 229 plots distributed in 24 small forest fragments. Main goal of this study is to document the most important environmental variables that modulate tree species vegetation in small forest fragments. The potential changes of these factors due to climate change and their influence on the tree layer vegetation will be discussed.

Methodology

The influence of environmental conditions in small forest fragments and their spatial heterogeneity on tree layer properties will be evaluated on the basis of literature review and analyses of the data that has been previously collected in forest fragments in Český kras by colleagues and kindly provided for this thesis.

(i) An essential part of the thesis will be a comprehensive literature review concerning potentially important environmental conditions and their influence on tree layer vegetation that has been previously documented. This review includes potentially important environmental conditions at both local and landscape scales.

(ii) Analyses of the tree layer vegetation properties in relation to environmental conditions data collected in 229 plots distributed in 24 small forest fragments in Český kras. The effect of environmental conditions will be examined in relation to the main characteristic of the tree layer vegetation (mean diameter, stand basal area) and also dominant tree species.

(iii) Discussion will be focused on the effects of environmental conditions that is not enough documented or even underestimated. This part of the thesis will also include a preliminary prediction on how the effects of environmental conditions could change due to ongoing climate change.

The proposed extent of the thesis

40

Keywords

tree species, soil nutrients, light, edge effect, landscape

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Declaration

I hereby declare that I have independently elaborated the diploma/final thesis with the topic of: “Properties of the tree layer vegetation modulated by environmental heterogeneity in the small forest fragments in Český kras” and that I have cited all the information sources that I used in the thesis and that are also listed at the end of the thesis in the list of used information sources.

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In Prague on March 31, 2022

A handwritten signature in black ink, consisting of a series of loops and a long horizontal stroke extending to the right.

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Properties of the tree layer vegetation modulated by environmental heterogeneity in the small forest fragments in Český kras

Abstract

Forest fragmentation in Central Europe during the last several decades has caused 40% of the remaining forests to be located within 100 meters of the forest edge. Although responses to forest margins have been extensively studied, a consensus is still lacking. It is increasingly necessary to understand vegetation responses in fragmented ecosystems surrounded by an unfavorable matrix. This study aims to analyze how slope, edge, and soil conditions, as well as the size of forest fragments in Bohemian Karst modulate basal area of trees at different scales: (1) generalized response of individual trees, (2) response at biotope level, (3) response at species level, and (4) generalized response of stand basal area for each plot. Generalized additive models (GAM) to analyze the available data. Significant responses to various environmental properties were found for all the analyses except for stand basal area. Basal area was observed to increase near forest edges, and the influence of edges is suggested to reach further than 200 meters into forest fragments for the tree layer. In general, edges facing south (S) and southwest (SW) exhibited higher basal areas. Fragment size did not exhibit any general pattern, but biotope and species-specific patterns. The slope was negatively related to the basal area, and southeast (SE) facing slopes were associated with bigger trees. Nitrogen was a limiting factor for tree growth in general, while phosphorus was a more determinant factor at biotope level. These results contribute to a better understanding of the role of forest edges, highlighting specific responses for different biotopes and species, and emphasizing the importance of conserving large forest fragments.

Keywords: tree species, soil nutrients, slope, light, edge influence, edge effect, landscape, climate change

Vlastnosti vegetace stromového patra modulované heterogenitou prostředí v malých lesních fragmentech v Český kras

Abstrakt

Fragmentace lesů střední Evropy v posledních několika staletích způsobila, že 40 % plochy zbývajících lesů se nachází blíže než 100 m od okraje lesa. Ačkoli vliv blízkosti lesního okraje na vlastnosti lesního prostředí byl opakovaně studován, jednoznačné výsledky stále chybí. Přitom je důležité poznat změny vegetace fragmentovaných lesních stanovišť obklopených krajinou matricí s nepříznivými přírodními podmínkami. V této práci analyzuji, jak vlastnosti svahů, lesních okrajů a půdních podmínek a také velikosti lesních fragmentů v Českém krasu ovlivňují kruhové výčetní základny stromů na různých úrovních: (1) jednotlivých stromů, (2) lesních stanovišť, (3) druhů dřevin, a (4) jednotlivých výzkumných ploch. Analýzu dat jsem provedl s využitím zobecněných aditivních modelů (GAM). Pro všechny vysvětlující proměnné s výjimkou výčetní kruhové základny na úrovni ploch jsem zaznamenal statisticky významné vlivy různých proměnných prostředí. Výčetní kruhová základna vzrůstala v blízkosti lesních okrajů, jejichž vliv pravděpodobně dosahuje dále než 200 m do nitra lesních fragmentů. Jižní a jihozápadní expozice se obecně vyznačovaly vyššími výčetními kruhovými základnami. Vliv velikosti lesního fragmentu nebyl potvrzen v obecné rovině, ale jen pro některé typy lesních stanovišť a druhy dřevin. Sklon svahu byl nepřímo úměrný k výčetní kruhové základně stromů a stromy s nejvyšší kruhovou základnou se nacházely na severovýchodních svazích. Dusík pravděpodobně představuje limitující živinu pro růst stromů, zatímco fosfor více ovlivňuje výčetní kruhovou základnu jednotlivých lesních stanovišť. Tyto výsledky přispívají k lepšímu porozumění významu lesních okrajů, dokládají jejich specifický význam pro různé biotopy a druhy dřevin a dále zdůrazňují význam ochrany rozlohou velkých lesních fragmentů.

Klíčová slova: druhy dřevin, krajina, klimatické změna, okrajový efekt, půdní živiny, světlo, svah.

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1 Introduction

Fragmentation in Central and Eastern Europe started to become a large-scale impact on forest ecosystems around 5000 years ago when agriculture and grazing became more common (Argant et al., 2006). However, over the past three centuries, the increase in world population, industrialization and globalization have led to large-scale shifts in land use, increasing the anthropogenic impacts on forest ecosystems (Foley et al., 2005; Kettle & Koh, 2014). These changes in land use have caused a historically prevalent process of landscape fragmentation, with 20% of the world's remaining forests within 100 meters of a forest edge (Haddad et al., 2015). In Central Europe this percentage increases by up to 40%, where the current landscape consists of a matrix of agricultural land interrupted by fragments of temperate forest (Estreguil et al., 2013).

Riitters et al. (2000) describes that although tropical rain forests may be the forests at highest risk because of the land-use trends, Eurasian deciduous forests appear to be one of the most heavily fragmented forests in the world due to the lack of interior conditions (5%), with most of the forest being either under the edge influence or perforated. Morreale et al. (2021), subscribes to the idea that temperate forests are more heavily fragmented than tropical forest, containing 52% more edge forest area. The study also warns that considering how fragmentation has developed until now, there is a high possibility that perforations in forests will grow and coalesce, fragmenting the forest even more in the future.

As different studies have pointed out, the process of habitat fragmentation almost always leads to habitat degradation (Harrison & Bruna, 1999; Mortelliti et al., 2010). As a consequence of habitat degradation, temperate European woods are experiencing an extended biodiversity loss due to the decline of suitable habitats as a result of human land use (Curtis et al., 2018; Staude et al., 2020) and climate change (Bellard et al., 2012).

As forest ecosystems fragment, forest patches become smaller and more irregularly shaped, increasing the dominance of edge habitats. Therefore, understanding the ecologic functioning of habitat boundaries is essential for forest ecology, as well as for large-scale conservation and management decisions (Ries et al., 2004).

2 Objectives of the thesis

This work attempts to provide description of the tree layer vegetation in small deciduous forest fragments in Bohemian Karst in relation to environmental conditions and their small-scale and landscape-scale heterogeneity. The main goal of this study is to document the most important environmental variables that modulate tree species vegetation in small forest fragments. This study aims to discuss the following topics:

- (i) How forest fragment size and edge condition, including edge aspect and distance from the forest margin, modulate basal area. In addition, the study also aims to discuss the depth of edge influences on deciduous forest stands.
- (ii) How slope conditions, including slope aspect and inclination, modulate basal area.
- (iii) How soil conditions, including carbon/nitrogen (C/N) and nitrogen/phosphorus (N/P) ratios, modulate basal area.
- (iv) The potential changes of these factors due to climate change and their influence on the tree layer vegetation in the future.

This study expects to find higher basal areas at forest edges, due to the higher light availability. Similar results of higher basal areas are expected at south facing slopes and edges, as well as for less sloped sites. I also expect fragment size to have a less relevant influence on tree growth than edge influence, but still find bigger trees in large forest fragments. These responses are expected to be rather general for all biotopes and trees. Lastly, nitrogen and phosphorus should be limiting factors for tree growth in general, but have certain biotope and tree-specific responses.

3 Literature Review

3.1 Edges in ecology

Edges are generally described as boundaries between different types of patches; however, what is considered a boundary might differ depending on the scale used to define the patch (ranging from patches of different species to major biomes). Ecological boundaries are characterized by complex and multidimensional patterns, and they can have characteristics related to the patches they separate or be completely dissimilar. The gradient in the characteristics that distinguish the patches on both sides of the boundary is steeper in the boundary than in either of the neighboring patches. On the other hand, the patch width depends on the gradient of change between the patches and the characteristics used to define the boundary. (Cadenasso et al., 2003; Ries et al., 2004). In the case of forest edges, these can be defined as an interface between forested and non-forested ecosystems (Harper et al., 2005).

Clements (1907) is considered to be the first study to introduce a concept related to ecological boundaries, with the term “ecotone”. Later, Leopold (1933) described an increase in game species in patchy landscapes and used the term “edge effect” to describe this tendency. Lay (1938) and Johnston (1947) also reported an increased diversity index near edges, which contributed to the widespread belief that edges were beneficial for biodiversity, along with the recommendation of their creation for management purposes (Harris 1988; Yahner 1988). These ideas began to change with the studies that identified that an increase of bird nests towards the narrow field-forest edges could work as “ecological traps”, increasing the chances of predation and parasitism because of the high concentration of nests of birds with characteristic habitats with mixed life-form (Gates & Gysel, 1978; Chasko & Gates, 1982). Some studies even speculated that the higher predation in forest edges may contribute to the decline of songbirds with the increase in forest fragmentation, and identified differences in predation rates depending on the size of the forest patch and the surrounding matrix (Brittingham & Temple, 1983; Wilcove, 1985). This line of thought was supported by studies that related edges with decreased quality for habitat specialists, because of the lack of interior forest in fragmented areas (Mills, 1995; Burke & Nol, 1998). Therefore, these studies contributed to the present conception of

edges as undesirable landscape features, particularly anthropogenic edges (Harris, 1988; Saunders et al., 1991).

Nevertheless, recent studies suggest that forest edges can be a key feature to preserve the biodiversity that resides in the forest interior from the dominant adverse conditions in the surrounding matrix, and provide the habitat conditions for a large range of forest specialists and generalist species, even acting in some cases as local hotspots or refugia (Melin et al., 2018; Govaert et al., 2020).

Lastly, edges can be classified in two general classifications. Natural edges can exist either as smooth transitions in growing conditions (e.g., forest-grassland and forest-wetland edges) and sharp and abrupt edges (e.g., rivers, lakes, and geologic features) with different effects on forest growth. On the other hand, human-induced edges are often sharp transitions in areas that were at some point in the past forested (e.g., croplands, pastures, and infrastructures) (Morreale et al., 2021).

3.2 Edge influence

Edge influence is described as the combination of abiotic effects, which involve environmental modifications due to the interaction between structurally dissimilar matrices; biotic effects that result in a detectable difference in plant composition and habitat structure near the edge, as compared with the ecosystem on either side of the edge; and indirect biotic effects, involving alterations in species interactions, such as herbivory, competition or seed dispersal (Murcia, 1995; Harper *et al.*, 2005).

In addition, responses to forest edges can be classified into three different groups. Variables that increase near the edge are considered positive edge responses. A variable that exhibits no pattern is considered a neutral response. And lastly, a variable that decreases at forest edges is classified as a negative edge response (Ries et al., 2004).

3.3 Abiotic effects

Fragments of forest anthropogenically fragmented are frequently surrounded by croplands, pastures, or young secondary growth; these are systems characterized by low-biomass and structural complexity. These differences between forest patches and their surrounding matrix cause microclimate modifications (Murcia, 1995; Ries et al., 2004).

3.3.1 Temperature and moisture

Anthropogenic landscapes, such as crops or pastures, allowing more solar radiation to reach the ground and have higher reradiation during the night than forests, which lead to higher temperatures close to the ground during daylight hours and greater daily temperature fluctuations over the day. On the other hand, the forest canopy intercepts solar radiation, creating environments with lower temperatures and higher moisture, with more uniform daily values (Murcia, 1995; Tuff et al., 2016; Mendes, 2019; Meeussen et al., 2021a).

Regarding specific changes of these factors at the edges, some studies suggest that edges tend to be warmer (both soil and air temperature), have higher air vapor pressure deficit (VPD) and have lower soil and air moisture over the first 20 to 100 meters than the forest interior, due to the thermic dissimilarities between forest and the surrounding anthropogenic matrix, acting as a buffer zone to decrease the temperature variability inside the forest (Williams-Linera, 1990; Matlack, 1993; Davies-Colley et al., 2000; Schmidt et al., 2017; Hofmeister et al., 2019; Reinmann et al., 2020; Meeussen et al., 2021a). However, Wright et al. (2010) in contrast with the previous studies done in more closed forests, reported colder and moister conditions at the edges of a forest with more open conditions, suggesting that this could be a site-specific effect that depends on the type of forest.

Some studies indicate that heat stress is a substantial limitation factor to forest growth, which together with water limitation, could potentially affect forest growth on forest edges (Reinmann & Hutya, 2017; Reinmann et al., 2020). However, Morreale et al. (2021) suggested that this effect was mainly evaluated for tropical forests, but it might be not particularly significant in temperate forest edges, which unlike tropical

forests have suffered centuries of fragmentation and created permanent modifications in the microenvironment of the large areas that edges represent in temperate forests.

In addition, Reinmann et al. (2020) found a negative correlation between soil moisture and canopy light absorbance, which could explain changes in tree growth along the edge gradient.

3.3.2 Light availability

Because of the forest canopy, light availability in the forest interior is generally lower than in human-made landscapes, such as crops or pastures. Some researchers have found a light availability gradient over the first wide range of depths in forest edges (Matlack, 1993; Schmidt et al., 2017). However, at the same time, other patches from some studies show no significant differences in light availability between the edges and the forest interior or very steep gradients where values of light availability of the forest interior were reached in 5 m, indicating either site-specific responses or lack of strength of the relations caused by the sampling method or the type of forest, such as open forest stands (Matlack, 1993; Davies-Colley, 2000; Hofmeister, 2013).

Reinmann et al. (2020) describes how light availability near the edges is almost certainly related to higher growth responses, which modifies tree canopy architecture and stimulates productivity at forest edges.

3.3.3 Soil chemistry and carbon sequestration

Abiotic edge effects can also occur as a result of nutrients infiltrating edge from adjacent landscapes, altering soil conditions and nutrient availability. Chemical fertilizers from nearby croplands have been documented to reach several meters into shrublands and forests, increasing nitrate, sulfate, and herbicide concentrations in forest edge, with higher values close to the edge that gradually decreased as the distance from the forest edge increased (Hester & Hobbs, 1992; Murcia, 1995). In addition, Remy et al. (2016) indicated a close relation between nitrogen (N) and carbon (C) cycles, with increased stocks near forest edges, which can affect species distribution. Lastly, Wuyts et al. (2008) found similar results as those mentioned above, with higher chemical components that could potentially acidify the soil near the edges, but this effect was significantly greater in pine stands compared with

deciduous birch and oak stands. On the other hand, some researchers reported that forest edges register higher values of C sequestration in comparison to forest interior (Reinmann et al., 2020; Meeussen et al., 2021b). However, this increment of C sequestration is just a small fraction of the carbon stocks and future sequestration capacity lost with the forest fragmentation, therefore, does not compensate for the total loss of C sequestration (Reinmann & Hutrya, 2017).

However, Jose et al. (1996) found a completely different pattern in tropical forests in peninsular India, with higher organic carbon and total nitrogen in forest interiors, suggesting the presence of relatively more fertile soils inside the forest fragments in comparison to the forest edges.

3.3.4 Wind turbulence

Most studies suggest that larger wind turbulences of warm or cool air, depending on the time of the day and season, are associated with forest edges, creating elevated rates of wind-throw and structural damage in the forest. In addition, some researchers suggest that the direction of the wind can influence other microclimate gradients, changing the depth of temperature and VPD gradients. When the wind was directed towards the forest edge the effects of the temperature and VPD gradients penetrated further into the forest; while when the wind was directed out of the forest, these gradients stabilized at relatively short distances. (Davies-Colley et al., 2000; Schmidt et al., 2017). Nonetheless, wind turbulence seems to increase as edges age and become more closed, because of wind-tunnel models suggested by Laurance (2004).

3.4 Biotic effects

The creation of an edge in a forest ecosystem can promote certain modifications of forest abiotic and biotic conditions that can modify tree growth and change forest structure, which can be detected even several decades after the creation of the forest edge. These conditions can lead to primary responses in the forest structure at the edges of the forest (including canopy cover, tree density, downed wood, leaf area, and vegetative biomass). At the same time, these primary changes in forest structure cause secondary responses on both forest structure (e.g., sapling density, understory cover, shrub height) and species composition, and because these are a consequence of

primary responses, they could start acting later and last a longer time. With the stabilization of the habitat edge, these processes feedback and can further exacerbate responses. (Murcia, 1995; Harper et al., 2005).

3.4.1 Species richness and distribution

Alterations in species richness and occurrence along the edge-to-interior gradient have been documented for vascular plants (Gonzalez et al., 2010; Hofmeister et al., 2013; Vockenhuber et al., 2011), bryophytes (Łuczaj & Sadowska, 1997; Hofmeister et al., 2013) and some animals groups (Batáry et al., 2014; Lövei et al., 2006) in temperate European forests. As Harrison & Bruna (1999) indicate, the majority of these effects related to fragmentation are probably a consequence of edge area increment.

Plant species richness has been described to be higher near forest edges (Young & Mitchell, 1994; Davies-Colley et al., 2000). Other studies specify more, suggesting an increased abundance of exotics and shade-intolerant species and a lower abundance of shade-tolerant species. However, the responses could be species-specific, with higher growth rates and recruitment for some species and lower growth rates or higher mortality for others (Harper et al., 2005).

Regarding tree species distribution, some changes have been reported. For example, Davies-Colley et al. (2000) suggested shifts towards high light “pioneer” plant species resembling those found in forest interior gaps created by treefalls.

3.4.2 Basal area and tree (stem) density

Tree stem density is a measure of trees per unit of space (e.g., hectare). Most studies found higher values of stem density close to the forest edge, which could be a response to a higher light availability near the forest edge (Davies-Colley et al., 2000; Meeussen et al., 2020).

Basal area (BA) is considered a metric of forest structure strongly correlated with biomass, therefore it is a useful value to estimate changes in forest biomass and structure, while basal area increment (BAI) is considered a measure of forest growth. Some studies found higher BA and BAI near forest edges, probably caused by

increased light availability (Palik & Murphy, 1990; Briber et al., 2015; Meeussen et al., 2020; Reinmann et al., 2020; Morreale et al., 2021). Morreale et al. (2021) found that the pattern of higher stand basal area near forest edges is better explained by the presence of more trees than larger trees. However, other studies reported no significant changes in the basal area between forest edge and interior forest or even lower basal areas at forest edges, which could be explained by high structural damage at forest edges (Davies-Colley et al., 2000; Wright et al., 2010; Lhotka & Stringer, 2013; Harper et al., 2015; Schmidt et al., 2019).

Both BA and BAI can also be studied for individual trees, since tree species composition is affected by microclimatic gradients in forest edges, and can help to elucidate structure and growth responses to edges by species composition groups (Morreale et al., 2021).

3.4.3 Mortality

Higher mortality rates close to the forest edges were found in some areas, especially in the tropics, where it can be explained as a response to higher wind turbulence, higher development of lianas and more frequent droughts (Williams-Linera, 1990; Young & Mitchell, 1994; Laurance et al., 2011). At the same time, Laurance et al. (2011) suggests that trees specialized in growing and reproducing in dark and humid conditions, and tree species that rely exclusively on outbreeding and animal seed dispersers, seem to be vulnerable to mortality associated with forest edges. However, some researchers suggest that non-anthropogenic mortality is not significantly higher in temperate forest edges, which can indicate that temperate forest edges are less vulnerable to wind turbulence and less susceptible to the high temperatures and water stress related to forest edges. (Morreale et al., 2021).

3.4.4 Tree leaves and canopy

Generally, tree leaf production seems to be stimulated in edges where there are higher values of light availability, which suggests that is the primary mechanism promoting the higher values of forest edge growth in temperate deciduous forests edges (Reinmann et al., 2020).

On the other hand, leaf area index (LAI) has been reported to be one of the main driving forces of net primary production, water (soil moisture) and nutrient utilization, and carbon balance (Bréda, 2008). LAI and plant area index (PAI) increased with the distance from the forest edge in some studies, which might be a result of tree damage associated with edge creation (Harper et al., 2005; Meeussen et al., 2020).

Some studies report lower values of canopy height at the forest edge (Lhotka & Stringer, 2013; Ibanez et al., 2017; Schmidt et al., 2019; Meeussen et al., 2020), which could be related either, to the increased wind turbulence that can potentially result in canopy damage (Davies-Colley et al., 2000; Schmidt et al., 2017) or drier conditions with less water availability that trigger competition for this resource resulting in lower canopy heights (Hofmeister et al., 2019; Reinmann et al., 2020; Meeussen et al., 2021a).

Reinmann et al. (2020) found that forest growth and canopy light absorbance are negatively correlated in forest edges, which could be explained by the existence of a tipping point whereby large increments in air temperature can reduce the ability of trees close to the edges to profit from the increase of light availability. However, greater shading and transpiration related to edges could attenuate edge enhancements of air temperature. Herbst et al. (2007) also suggests that the microclimate conditions associated with forest edges can increase rates of canopy transpiration by more than 50% in temperate deciduous forests.

Therefore, increments in temperature together with higher leaf area and drier conditions described at forest edges may make temperate forest fragments in northeastern United States more vulnerable to heat and drought throughout the growing season (Reinmann and Hutyrá, 2017).

3.4.5 Tree seedlings

Harper et al. (2005) suggests that recruitment, as a secondary process determined by increased light availability usually reported at forest edges, tends to be higher. This is measured by higher values of seedling abundance. However, seed dispersal has not been thoughtfully studied as a response to edge distance.

Nevertheless, some researchers believe that the stress experimented under modified environmental conditions at edges might reduce germination (Bruna, 2003) and establishment (Uriarte et al., 2010) of shade-tolerant plant species, which would affect the composition and abundance of tree seedlings to a large extent. However, caution should be taken when considering these studies as they have been carried out in tropical forests and might not be applicable to other types of forests (Laurance et al., 2011).

3.5 Edge effect vs. edge influence

Edge effect (Oliveira et al., 2013) and edge influence (Dodonov et al., 2013; Harper et al., 2004) have been used as synonymous terms in much of the literature, although this study will refer to the biotic and abiotic changes on the forest edges as edge influence, as edge effect sometimes refers exclusively to the increment of diversity at edges between ecosystems (Leopold, 1933).

As Leopold (1933) initially suggested, a plausible explanation for positive edge influence, is that they allow maximal access to resources when these are spatially divided between two neighboring patches (Ries et al., 2004).

On the other hand, negative edge influence can be explained by the changes in microclimatic conditions that may hinder the performance of certain species, changing the availability of basic resources such as water and nutrients, or as a result of environmental stress (e.g., temperature and wind) (Ries et al., 2004).

Lastly, species interactions (such as predation, parasitism or herbivory) can either cause species to increase or decrease depending on the role they play in relation to the changes in distribution for other species (Ries et al., 2004).

3.6 Factors affecting edge influence

Contradictions in the studies of microclimatic gradients of forest edges indicate that edge influence could be site-specific, depending on different factors such as the surrounding matrix, slope, edge orientation or forest structure and age (Kupfer et al., 2006; Marchand & Houle, 2006; Murcia, 1995).

3.6.1 Edge orientation and slope conditions

Studies generally concur that microclimatic conditions are associated with edges and, therefore all the responses that depend on microclimatic conditions, strongly depend on the geographical orientation of the edge. Thus, edge orientation can impact the strength or expression of a variable, but it never changes the direction. This might be one of the explanations for the different microclimatic responses found at different latitudes since light availability and the effects of solar radiation change to a large extent. (Ries et al., 2004; Måren et al., 2016; Bernaschini et al., 2019).

In the case of temperate zones, north-oriented edges should display weaker edge influences, due to lower exposition to sunlight, than south-oriented edges. Moreover, changes in slope can modify light, water and nutrient availability, which would affect both microclimatic gradients and biotic responses (Young & Mitchell, 1994; Ries et al., 2004; Bernaschini et al., 2019; Hofmeister et al., 2019; Long et al., 2020).

In addition, Ries et al. (2019) suggests that orientation should have a stronger influence on microclimatic gradients than on plant patterns, and the influence should decrease as the trophic level rises.

3.6.2 Edge contrast

The differences between matrices are considered to be another factor that can alter edge influence, as stronger responses are expected near “hard” edges, where there is a high contrast between patches; than in “soft” edges, where there is low contrast between patches. Two main factors are considered to determine the contrast between patches, (a) dissimilarities in mean vegetation height near the edges, and (b) dissimilarities in vegetation density within the same edge type. These different contrasts are expected to modify the permeability of edges, leading to different rates of ecological flows (Cadenasso & Pickett, 2003; Ries et al., 2004; Morreale et al., 2021).

3.6.3 Fragment area

Isolation, landscape composition and, especially, patch size are expected to influence edge responses, although, Ries et al. (2004) suggests that the effect that these

factors can have is rather small compared with other factors (e.g., orientation, contrast, etc.). However, very little research has been carried out on the relative importance of edge influence and the effect of patch size has on the different responses. Furthermore, many “forest fragmentation” research have misunderstood different fragmentation processes and utilized “area” as the explanation, and vice versa (Didham, 1997). This highlights the importance of including the fragment area in the studies of edge influence.

3.6.4 Edge age

If the differences between patches are maintained artificially (e.g., active agricultural lands adjacent to forest patches), a development of a “sidewall” of dense vegetation composed of canopy trees, regenerating trees and shrubs tend to fill the open space left at the edge (“seal the edge”), which can shorten the depth edge influence, weakening its effects, and make it less permeable. On the other hand, on edges left to regenerate, the contrast between patches is reduced over time as the patch adjacent to the forest starts developing, where the succession process takes place and becomes a forest again, which is especially significant for boreal forests adapted to frequent disturbances with rapid regeneration (Laurence et al., 2002; Laurence, 2004; Ries et al., 2004; Harper et al., 2015).

Tree mortality due to microclimatic stress (e.g., temperature and water deficit stress) is likely to decline over the first years of the edge creation because species that survive the edge creation probably acclimate to the microclimatic specific conditions at forest edges (Laurence et al., 2011). Therefore, Davies-Colley et al. (2000) suggests that mature and “maintained” edges are expected to have steeper and more complex microclimatic gradients than those of newly created edges.

3.6.5 Temporal effects

Daily, seasonal and year temporal changes are expected to modify edge responses, even reverse the direction of the response in some cases (Young & Mitchell, 1994; Davies-Colley et al., 2000; Ries et al., 2004). Bernaschini et al. (2019) found that edges during summer may have more elevated and fluctuating temperatures, lower water availability and stronger wind turbulence than the forest interior. Moreover,

daily temperature changes were also registered, as temperatures during daylight were colder inside the forest than on forest edges, irrespective of their orientation; while at night, both interior and south-east edges were warmer than those with north-east orientation. This effect could be explained by higher levels of re-emission of energy at forest interiors and southeast edges, compared to northeast edges (Wright et al., 2010).

3.7 Depth of edge influence (DEI)

The distance to which the edge influence extends is usually referred to as the depth of edge influence (DEI). Despite the fact that DEI values have been reported for many edge responses, these are rarely quantified in rigorous ways that would allow viable comparisons between studies and extrapolations, and statistical methodologies to allow for a rigorous calculation of DEI have just recently been proposed (Cadenasso et al., 1997; Cadenasso et al., 2003; Ries et al., 2004). Many studies use “visual examination” to identify DEI, however, these values are likely impacted by study design (i.e., size of plots, length of survey transects or the number of distance categories) (Ries et al., 2004).

Without a rigorous methodology to determine DEI, generally abiotic and plant responses have been reported to extend up to 50 m (Matlack, 1993; Meeussen et al., 2021b), invertebrate responses up to 100 m (Didham, 1997) and avian responses from 50 to 200 m (Paton, 1994). Nevertheless, Laurence (2000) indicates that DEI can be detected in some cases up to several kilometers, and together with other studies suggest that the magnitude and depth of edge influence are closely dependent on the differences in structure and composition between adjacent communities or surrounding matrix, where anthropogenic matrix tend to create deeper effects. (Haddad et al., 2015; Harper et al., 2005; Kupfer et al., 2006; Laurence et al., 2011).

More specifically, much of the literature addressing the microclimatic and biotic effects associated with the edge influence in temperate forests focuses on the first 30-50 meters into the forest interior (Lhotka & Stringer, 2013; Łuczaj & Sadowska, 1997; Reinmann & Hutyrá, 2017). However, DEI has been documented at hundreds of

meters from the forest edge (Harper et al., 2005; Tuff et al., 2016; Schmidt et al., 2017; Hofmeister *et al.*, 2019).

3.8 Forest edges, ecosystem degradation and climate change

As previously said, some studies indicate that edge influence can lead to the degradation of forest fragments (Harrison & Bruna, 1999; Laurence et al., 2002; Mortelliti et al., 2010; Haddad et al., 2015), therefore, understanding these influences could be essential to halt forest ecosystem degradation.

Furthermore, in an increasingly warmer world due to climate change (1.1°C warmer than in preindustrial times) and with predictions to reach 1.5°C of warming within just the next two decades (IPCC, 2021), is it essential to focus edge influence studies on understanding how generalized warmer temperatures will affect edge responses. Forest patches might play a key role in climate change mitigation for species associated with forest interiors, reducing temperature and its fluctuations, as well as other responses associated with temperature such as soil moisture.

The expected consequences of climate change could both intensify the influence that the edge exerts on forest patches and extend the width of edge influence, further reducing the capacity of forest fragments to attenuate temperature increases and, subsequently, humidity decrease, and to sequester carbon (Laurance & Williamson, 2001; Bellard et al., 2012; Hofmeister et al., 2019; Reinmann et al., 2020; Morreale et al., 2021). Therefore, studies on forest edges are essential to understand how ecosystems will respond to the synergic effects of the growing fragmentation process, especially in temperate forests where it has been less studied, and climate change, acknowledging the complexity of interactions between these processes (Morreale et al., 2021).

Lastly, forest edges are essential to preserve forest interior microclimates and the species associated with them, acting as buffer zones to sustain these conditions, as well as the species associated with forest edges. Therefore, forest patches and their edges should be studied in more depth and preventively protected against the advance of fragmentation (Meeussen et al., 2021a).

3.9 Importance of this study

A long history of forest anthropogenic fragmentation has resulted in a permanent alteration of microenvironmental conditions of a significant and rising proportion of the world's temperate forest. In a world where population continuously grows, expanding agricultural land and causing continued forest fragmentation, it is vital to understand fragmented forests as unique ecosystems. Any effort to predict future conditions and responses of forests must take into account edge influences, as well as their possible contribution to terrestrial carbon storage (Morreale et al., 2021).

Considering that European forest patches are surrounded mainly (60%) by intensive land uses, such as intensive agriculture (Estreguil et al., 2013), it is of great importance to study the edge influence in European forest patches in an agricultural matrix, as well as the potential importance of preserving large patches of forest in Czech landscape concerning forest productivity and diversity. Moreover, edge influences are particularly diverse since they can be modified by a diverse group of factors (e.g., orientation, edge contrast, fragment area, edge age and temporal effects), consequently it is important to gather information on how edges might influence in different ecosystems and latitudes (Meeussen et al., 2021).

In addition, although edge influence has been widely studied for decades around the globe, especially in the tropics, describing a wide range of mechanisms that try to explain the influence it has on organisms, there is still a large lack of information about the processes participating in the edge influence and the responses of vegetation. (Cadenasso et al., 1997, Harper et al., 2005; Murcia, 1995, Ries et al., 2004).

4 Methodology

4.1 Study area

The study was conducted on forests in the south-west part of Bohemian Karst (Český kras in Czech) Protected Landscape Area, Central Bohemia, Czech Republic.

Bohemian Karst historically was first populated around 180,000 years ago, due to the natural wealth of the area, which facilitated hunting and gathering for the first settlers of the area. The area became gradually more influenced by humans as societies developed, with the development came the deforestation process, which began during the Bronze and later Iron age (between 3300 BCE and 500 BCE), as humans started to construct fortresses and work with metals. As the area began to be progressively deforested, newly created non-forest patches were used to graze goats and sheep, and for establishing settlements and crops. During the first centuries of the current era, the region of Bohemian Karst was depopulated for reasons that are still unknown today. Later, the first villages and towns started to be constructed, these were mentioned for the first time in historical documents between XXI and XXII centuries. This forested and sparsely populated region also was used as one of the royal hunting forests by the aristocracy of Czech Republic. Based on the available information and general appearance of the woods, is it possible to assume relatively intense methods of landscape management in the past (pasturage, coppices with a short turn-over period, etc.). The region was used for intensive logging until approximately the time of the Second World War when the last coppicing was carried out, then the forest patches in the study area have remained relatively less influenced by timber harvesting since the middle of the XX century. Finally, Bohemian Karst was protected by the government of the Czech Republic through the designation of a Protected Landscape Area (PLA) that covers almost the whole region (132 km²), and some parts of the region are even more strictly protected with nature reserves (AOPK ČR, n.d.; Matoušek, 1993).

Bohemian Karst is located at altitudes between 268 and 497 m. It had an annual mean temperature of 10.09°C from 2012 to 2022, with a temperature increase compared to the past decade of 0.5°C; and annual mean precipitation of 518 mm, measured from 1954 to 2010 (data from the meteorological station of Crop Research Institute in

Karlštejn). The dominant geological substrate in Bohemian Karst is limestone, which forms base-rich soils; however, there are also Paleozoic schist and claystones that form acidic soils, which underlie half of the largest forest patches and many other fragments. The vegetation in the area is mostly deciduous forest, covering almost 35% of its surface.

The most present tree species in unplanted forest stands in the study area species are oaks (*Quercus petraea*, *Quercus robur*, and *Quercus pubescens*), hornbeam (*Carpinus betulus*) and beech (*Fagus sylvatica*), complemented mostly by maples (*Acer campestre*, *Acer platanoides*, and *Acer pseudoplatanus*), wild service tree (*Sorbus torminalis*), limes (*Tilia cordata* and *Tilia platyphyllos*) and ash (*Fraxinus excelsior*). On the other hand, dominant evergreen tree species in planted stands are pine (*Pinus nigra* and *Pinus sylvestris*) and spruce (*Picea abies*), and also some deciduous exotic trees such as black locust (*Robinia pseudoacacia*) can be found. Generally, over Bohemian Karst the most dominant shrubs are *Cornus mas* and *Ligustrum vulgare*, and the area has an unusually rich diversity of herbaceous species.



Figure 1 - Study area (lat 49°53'54" N, long 14°07'0.9" E).

The study area (lat 49°53'54" N, long 14°07'0.9" E) covers roughly 30 km² of rural landscape of Bohemian Karst, with 33 forest fragments mainly dominated by deciduous forest (Fig. 1.). These forest patches are generally located on slopes and near the top of hills, that range in size from 0.1 to 225 ha and represent 23% of the study area, surrounded mainly by agricultural fields (59%), meadows (9%), and five villages (6%).

4.2 Study design

The study was composed of a total of 159 square plots (Fig. 1), plots were divided into two types: 118 pairs of nested plots inside the forest fragments, to represent vegetation at the forest interior and close to the forest edge, and 41 nested plots adjacent to the forest edge, to reflect the vegetation at the same forest edge. Regarding the 179 nested plots were situated inside 23 forest fragments, their location was randomly placed, between 5 and 477 m from forest edges, in representative parts of each present forest category taking into consideration the dimension of the forest type and the variability of herb layer species composition, while excluding areas heavily influenced by anthropogenic activities (e.g., paths or sites with freshly disturbed soil surface). These nested plots consisted of a large plot (225 m²), and a smaller plot (25 m²) placed in the center of the large plot, constituting together a “pair”. The plots at the forest edge were randomly placed at the border of 15 forest fragments, accounting for the length of the edge, representation of vegetation of each forest type, geographical edge orientation, and edge shifts in the past. In these paired plots, the large plot was located with one side adjacent to the peripheral line of trees at the forest edge, while one side of the small plot was placed in the center of the side of the large plot abutting the forest boundary.

4.2.1 Vegetation

Areas with homogeneous vegetation within forest fragments in the study area were categorized according to the present vegetation in nine broadly defined categories, based on species composition, structure and age of the tree layer, accounting for diagnostic plant species in the herb layer. However, as the main objective of this research was to analyze biotic responses of trees to edge influence, I

have decided to analyze exclusively the data from forests with similar tree compositions to have similar and comparable responses. Taking this into consideration, oak stands are the most abundant type of forest in the area and more than half the plots were located in oak stands (68.56%); therefore, this research comprises exclusively a detailed analysis of edge influence on oak stands (a) thermophilic, oak-dominated stands, (b) thermophilic, oak-hornbeam stands, (c) mesophilic, oak-hornbeam stands and (d) slightly acidic, oak-hornbeam stands (Table 1).

The field sampling of the tree structure was carried out in 2007 and 2008. Diameter and basal area were measured for the tree layer (>4 m), and the sum of stem basal area of all trees, and trees and shrubs together, taller than 1 m were used to calculate the stand basal area for each plot.

Table 1 - Area of various types of forest stands (in ha), and the number of nested plots in forest stands within the study area.

Vegetation type	Area of forest (ha)	Number of plots
Thermophilic, oak-dominated stands	19.0	17
Thermophilic, oak-hornbeam stands	59.5	48
Mesophilic, oak-hornbeam stands	195.1	60
Slightly acidic, oak-hornbeam stands	56.8	32
Total	330.4	157

4.2.2 Microenvironmental conditions

As light availability conditions in the herb layer were assessed in the area by Hofmeister et al. (2013), I did not take it into account in my analyses. However, their observations on light availability will be taken into account for the discussion of the results of this study. Nevertheless, the fact that the light availability data collection was carried out from July to August 2007 will be considered, highlighting the importance that the light availability data collection was done exclusively during the summer months.

For soil chemistry separate samples of humus and topsoil were analyzed in every plot, each consisting of four composited samples gathered outside the corners of S plots during the summer of 2007. The results from S soil data were extrapolated to L plots. Samples of humus (without litter) were bulked and sieved (mesh size 3 mm). Samples of topsoil were collected at a depth of 10 cm, bulked, and sieved (mesh size 2 mm). Soil samples were air-dried before the analyses were carried out. As established by Mehlich (1984), in order to determine extractable phosphorus (P_{ex}) on soil samples digestion with Mehlich III-extract (HNO₃ + NH₄NO₃ + CH₃COOH + NH₄F + EDTA) was used, and spectrophotometric analysis at 750 nm in order to detect it. A Carlo-Erba Fisons 1108 analyzer was used to determine total C and N simultaneously.

4.2.3 Geographic and spatial attributes

Slope inclination and orientation were measured in the field. On the other hand, the location and orientation of forest edges, and forest fragment areas were evaluated from maps of the Czech Republic (2006, map scale 1:10,000).

4.3 Data analysis

Stand basal area of each plot and basal area of individual trees were related to the explanatory variables using generalized additive models (GAMs) with spline components. For stand basal area of plots analysis, I used the gaussian semiparametric GAM framework, while for the basal area of individual trees analysis I used the gamma semiparametric GAM framework with log link, considering its assumptions of continuous, positive values and flexible model form (Wood, 2006). Previous studies with similar data have made use of GAM to interpret similar data from their studies, as a support for my decision to use this kind of statistical analysis (Hofmeister et al., 2013; Lotka & Stringer, 2013). Semiparametric specification allows us to examine relations between the mean of the dependent variable and several explanatory variables whose effect is unknown beforehand. Additionally, I was able to accommodate overdispersion by using a gamma distribution.

The use of the gamma family allows us to test the goodness of fit of the possible statistical models with AIC (Akaike Information Criterion) for model selection. The selection of both parametrically and nonparametrically modeled explanatory variables

was done by comparing the values of AIC for each possible model. Nevertheless, all variables contemplated for the model selection had a reasonable explanation of why they should be included, based on a detailed literature review, and some of them were included in all models due to the nature of the study (distance from the edge and coordinates). A group of explanatory variables that summarized the possible abiotic and biotic factors affecting edge influence was selected, excluding light since it was already evaluated by Hofmeister et al. (2013), and he concluded that there was no light variation in the forest edge-to-interior gradient. Therefore, the explanatory variables selected for the first model were: slope inclination and aspect, coordinates (representing spatial context), carbon/nitrogen ratio (C/N) and nitrogen/phosphorus ratios (N/P) from mineral topsoil collected at a depth of 10 cm (representing soil conditions), biotope type and the edge of the stand (representing vegetation type and condition), forest fragment size categorized in three categories (<22 hectares, 22 – 55 hectares and >55 hectares), distance from the edge and orientation of the closest edge (representing edge conditions).

The analysis was divided into four different models: (a) the first model had a basal area of individual trees of all species as the response variable and included species as an explanatory variable to reduce the effect of interspecies variability, (b) the second model had the basal area of individual trees analyzed separately for each biotope included in this study, (c) the third model had the basal area of individual trees of the main species as three submodels, these tree species were oaks (*Quercus robur* and *Quercus petraea*), field maple (*Acer campestre*) and hornbeam (*Carpinus betulus*), and (d) the fourth model design had stand basal area of each plot as a response variable.

5 Results

5.1 Generalized response of basal area

Almost all explanatory variables considered for the GAM at the level of individual trees had a significant effect on tree basal area. Edge orientation, slope inclination and C/N ratio effects on the basal area were the most important variables explaining basal area variation, followed by distance from the edge and type of biotope and slope aspect. On the other hand, the N/P ratio and fragment area did not exhibit any significant effect on the basal area (Appendix 1).

According to the results of this study, trees close to west and southwest facing edges showed an increase in their basal area, while especially trees nearby east facing edges displayed a decrease in their basal area. Basal area exhibited an ambiguous relationship over the entire gradient of distance from the edge. A short decrease of the basal area nearby the forest border until approximately 50 meters from the edge can be observed. From 50 to roughly 200 meters from the forest edge, there was a slight increase in basal area, and a decrease of the basal area from 200 meters to the forest interior with broader confidence intervals, likely referring to the low number of plots with the distance > 200 m from the forest edge (Fig. 2).

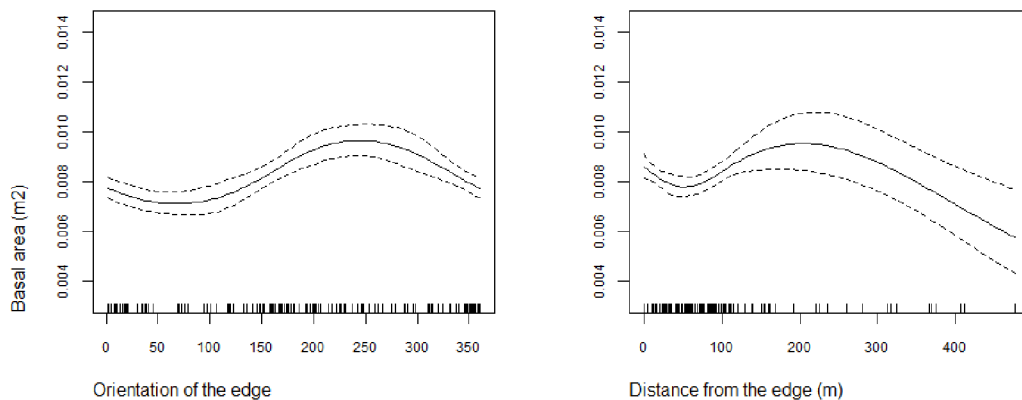


Figure 2 - Results of generalized additive model (GAM) for basal area (m²) of individual trees. The graph shows the additive effect and 95% confidence intervals (dotted lines) of edge orientation (on the left) and distance from the edge in meters (on the right) on basal area of individual trees.

Regarding slope aspect and inclination, the results of this research indicated effects of slope aspect and inclination on the basal area of trees. The slope aspect displayed an opposite tendency to the response of basal area of individual trees to edge orientation, exhibiting higher basal areas on east and southeast facing slopes, and smaller on southwest and west facing slopes. On the other hand, slope inclination was, in general negatively related to the basal area, however, this negative relation was weaker for lower inclinations (0 – 5 degrees), whereas on higher inclinations (5 – 30 degrees) these negative relation became nearly linear and stronger (Fig. 3).

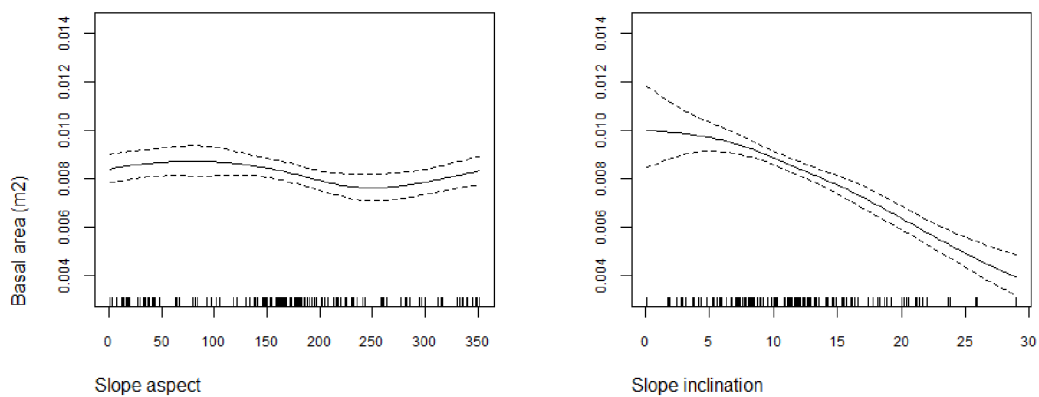


Figure 3 - Results of the generalized additive model (GAM) for the basal area (m²) of individual trees. The graph shows the additive effect and 95% confidence intervals (dotted lines) of slope aspect (on the left) and inclination (on the right) on the basal area.

The results for carbon/nitrogen ratio displayed a general positive increase in basal area is observed from the lowest observed C/N mineral ratio values to the highest observed values, materialized in an S-shape. These results exhibited an increase in the basal area concerning the C/N ratio when the C/N ratio is low (6 – 10). In contrast, for middle values of C/N ratio (10 – 14), the relation with basal area becomes negative; whereas for the highest observed values of C/N ratio (14-20), the relation becomes positive again (Fig. 4).

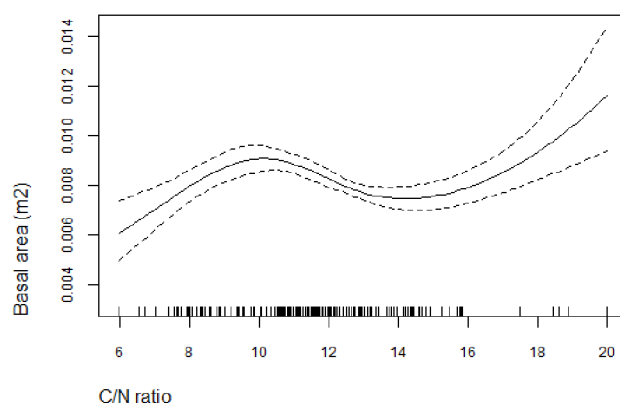


Figure 4 - Results of the generalized additive model (GAM) for the basal area (m²) of individual trees. The graph shows the additive effect and 95% confidence intervals (dotted lines) of the C/N ratio from topsoil at a depth of 10 cm on the basal area.

Finally, as regards the effect of biotope type on basal area, the only significant difference between biotopes was the higher basal area in mesophilic, oak-hornbeam stands than thermophilic, oak-dominated stands, while the other two biotopes did not show any significant differences from other biotopes in this study.

5.2 Response of basal area in different biotopes

Table 2 - Mean (\pm S.D.) values of individual basal area for each biotope and when all biotopes are included (Total).

Type of biotope	Mean (\pm SD)
Thermophilic, oak-dominated stands	0,0176 (\pm 0,0138)
Thermophilic, oak-hornbeam stands	0,0212 (\pm 0,0215)
Mesophilic, oak-hornbeam stands	0,0188 (\pm 0,0267)
Slightly acidic, oak-hornbeam stands	0,0249 (\pm 0,0251)
Total	0,0203 (\pm 0,0239)

When GAM was performed individually for each biotope included in this study (Table 2), the results disclosed a significant effect of slope and edge conditions for most of the biotopes, while soil conditions seemed to be in general less explicative for the variation of basal area in the analyzed forest biotopes. Slope inclination was significant for all biotopes, while slope orientation also affected the basal area of all biotopes except thermophilic, oak-hornbeam stands. GAM results also suggested that orientation of the closest edge was a significant effect on explaining the variability of basal areas for mesophilic and slightly acidic, oak-hornbeam stands. In addition, distance from the edge was a significant variable for all the biotope types except thermophilic, oak-hornbeam stands. Regarding soil condition, nitrogen/phosphorus

ratio seemed to be significant to explain basal area for all biotope types except thermophilic, oak-dominated stands, while carbon/nitrogen ratio was a significant variable just for slightly acidic, oak-hornbeam stands. Lastly, the results of this study showed a significant effect of forest fragment size on all biotopes except mesophilic, oak-hornbeam stands (Appendix 2).

Orientation of the closest edge, when significant, exhibited a uniform trend with generally higher values of basal area focused on slopes facing south and southwest. On the other hand, distance from the edge displayed different patterns in the biotopes where it was a significant variable. In thermophilic, oak-dominated stands basal area exhibited a clear decrease concerning distance from the edge, while in mesophilic, oak-hornbeam stands basal area peaked around 200 meters from the forest border, displaying broader confidence intervals, likely referring to the low number of plots with the distance > 200 m from the forest edge (Fig. 5).

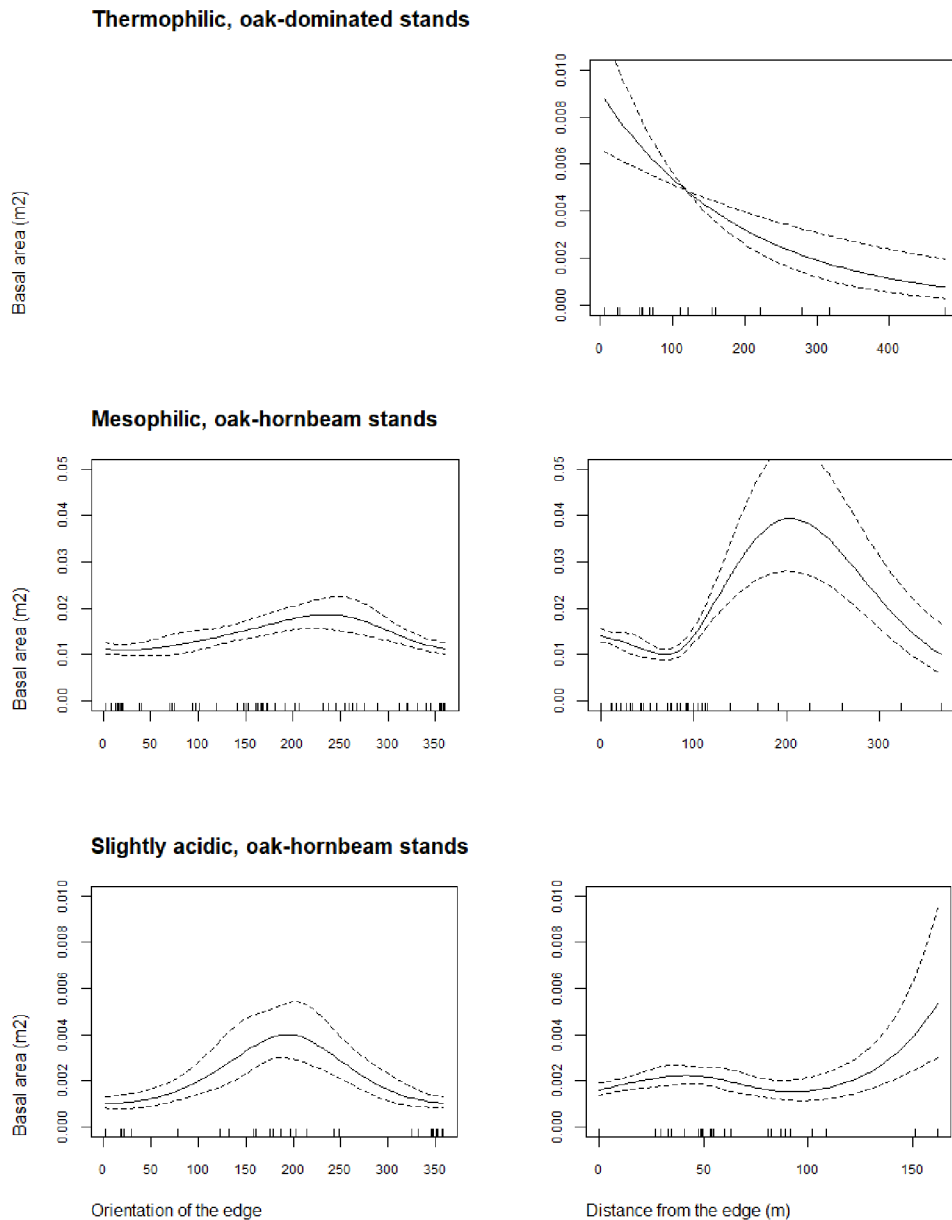


Figure 5 - Significant results regarding edge conditions of the generalized additive model (GAM) for the basal area (m²) of individual trees on different biotopes: (1) thermophilic, oak-dominated stands; (2) thermophilic, oak-hornbeam stands; (3) mesophilic, oak-hornbeam stands; and (4) slightly acidic, oak-hornbeam stands. The graph shows the additive effect and 95% confidence intervals (dotted lines) of the edge aspect (on the left) and distance from the edge (meters) (on the right) on the basal area for each biotope respectively, excluding non-significant effects.

Our analysis reveals a uniform response to slope inclination in every biotope included in this study, with a generalized decline of the basal area as slope inclination increases. However, in thermophilic and slightly acidic, oak-hornbeam stands this decline do not happen until the slope inclination reaches values of approximately 10. Slope aspect when significant, exhibited a uniform response, with generally higher values of basal area in slopes facing south, southeast and east, while basal area was lower in slopes facing southwest and west (Fig. 5), which contrast with contrary east-west responses

observed for edge aspect (Fig. 4). However, the results reveal that thermophilic stands are mostly located on southwest facing slopes (Annex 2).

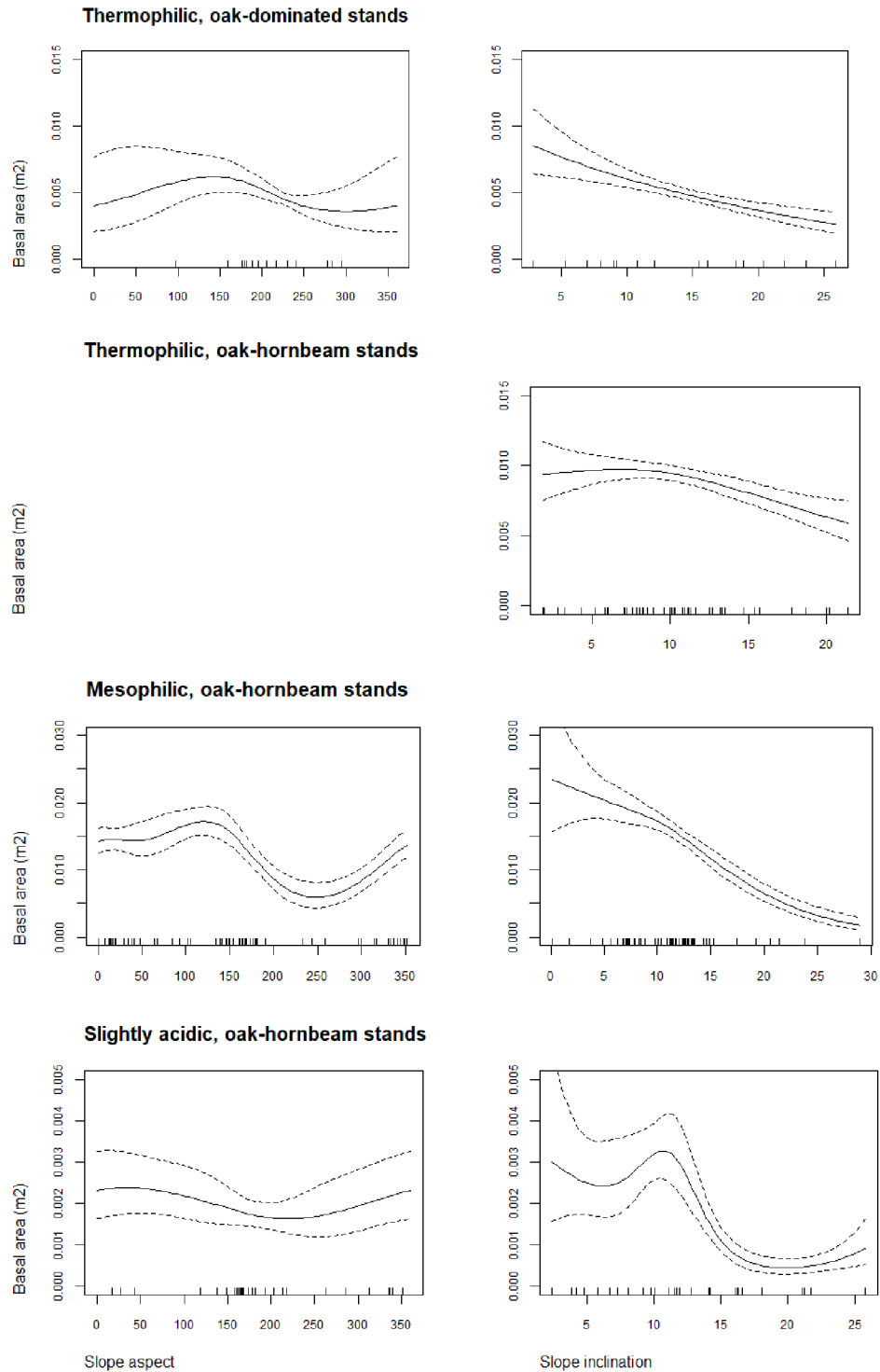


Figure 6 - Significant results regarding slope conditions of the generalized additive model (GAM) for the basal area (m²) of individual trees on different biotopes: (1) thermophilic, oak-dominated stands; (2) thermophilic, oak-hornbeam stands; (3) mesophilic, oak-hornbeam stands; and (4) slightly acidic, oak-hornbeam stands. The graph shows the additive effect and 95% confidence intervals (dotted lines) of slope aspect (on the left) and inclination (on the right) on the basal area for each biotope respectively, excluding non-significant effects.

Regarding the results on soil conditions responses, the C/N ratio just seems to be a significant variable for slightly acidic, oak-hornbeam stands. The results of this research showed a drop in basal area values on slightly acidic; oak-hornbeam stands when C/N ratio values are between 12 and 15. On the other hand, the N/P ratio was significant for all the biotopes except thermophilic, oak-dominated stands, displaying extremely different responses for each biotope type. The observed results reveal an “S” shape as a response to the N/P ratio in thermophilic, oak-hornbeam stands, with a slight decrease in basal area with low values of N/P and a peak approximately between 800 and 900 N/P ratios. Mesophilic, oak-hornbeam stands exhibited a linear increase of basal area, with broader confidence levels for high values of N/P ratio (800 – 1200), probably due to the lack of representation of these values in the study area. In contrast, slightly acidic, oak-hornbeam stands exhibited an exponential decrease in basal area when the N/P ratio increased (Fig. 7).

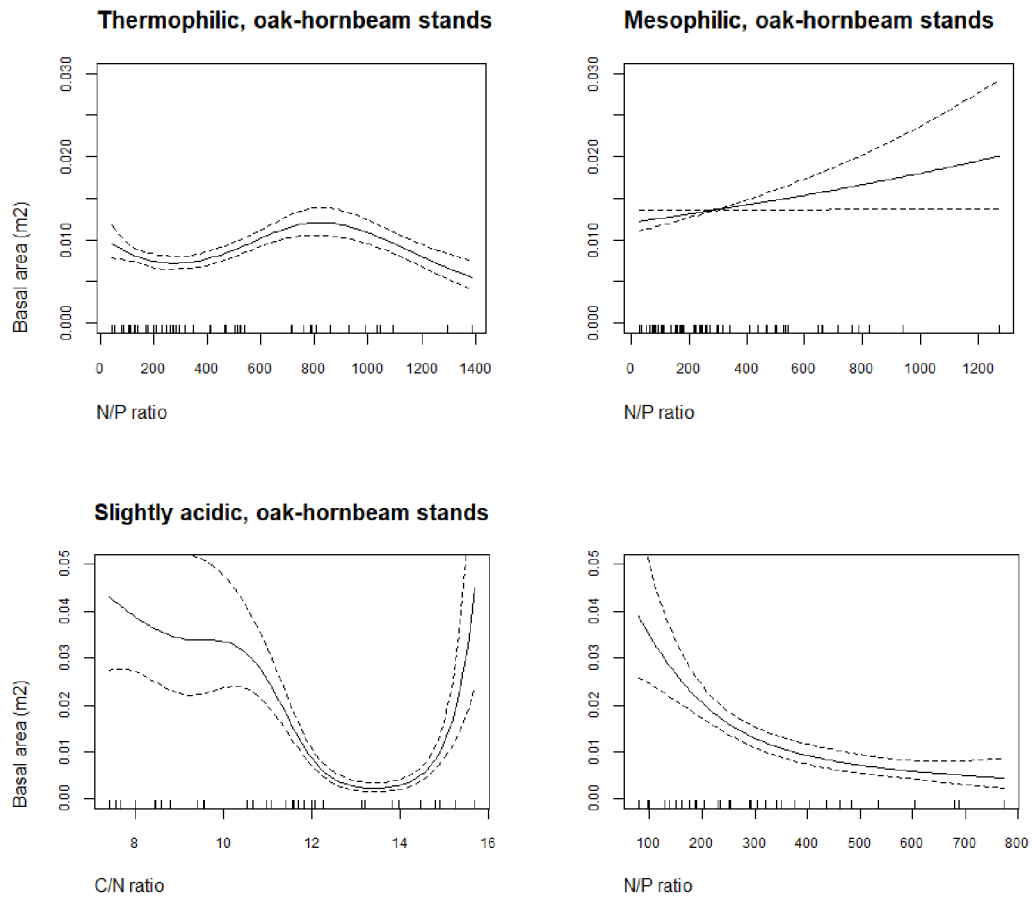


Figure 7 - Significant results regarding soil conditions of the generalized additive model (GAM) for the basal area (m²) of individual trees on different biotopes: (1) thermophilic, oak-dominated stands; (2) thermophilic, oak-hornbeam stands; (3) mesophilic, oak-hornbeam stands; and (4) slightly acidic, oak-hornbeam stands. The graph shows the additive effect and 95% confidence intervals (dotted lines) of carbon/nitrogen and nitrogen/phosphorus ratio from topsoil at a depth of 10 cm on the basal area for each biotope respectively, excluding non-significant effects.

Lastly, the size of the forest fragment where the tree is located had a significant effect on the basal area for all the biotopes except thermophilic, oak-hornbeam stands. The response of thermophilic, oak-dominated and oak-hornbeam stands had the same direction, since in both cases the biggest fragment (> 55 hectares), exhibited a higher basal area than forest fragments smaller than 22 hectares; and in oak-dominated stands, fragments between 22 and 55 hectares have the same response. In contrast, slightly acidic, oak-hornbeam stands display significantly smaller basal areas in the biggest fragment (> 55 hectares) in comparison to the smallest ones (<22 hectares).

5.3 Response of basal area for different species

The GAM analysis of basal area as a response variable on individual oaks, which included the species *Quercus robur* and *Quercus petraea*, finds significant effects of most of the explanatory variables on basal area, except for slope aspect which was non-significant. Distance from the edge, orientation of the closest edge, slope inclination and type of biotope where the tree was located, are the most important variables explaining the response of basal area for oaks, followed by C/N and N/P ratios of topsoil and size of the fragment (Annex 3).

In contrast, when the same GAM analysis is performed on the basal area of hornbeams (*Carpinus betulus*) fewer enlightening results are obtained. Based on the obtained results, the basal area of the hornbeam is only significantly affected by slope, C/N ratio and biotope type (Annex 3).

On the other hand, the results of this research showed that the basal area of field maples (*Acer campestre*) is related to all the explanatory variables except orientation of the edge, N/P ratio and size of the forest fragment. More specifically, the slope aspect, together with the C/N ratio and biotope type are the variables that best explain the variation in the basal area of field maple trees, however, distance from the edge and slope are also significant variables (Annex 3).

The results of this study, oaks that had south and southwest facing forest edges closest to their location display an increase in basal area compared to other trees. Therefore, being the only analyzed species to manifest a response in the basal area related to orientation. The effect of distance from the edge on oak basal areas has a similar pattern to that observed in the GAM including all tree species (see Chapter 5.1). The main differences are a high generalized decrease of the basal area from the forest edge to the interior and a more abrupt decline in basal area nearby the forest edge (50 meters). In contrast, basal areas of field maples seem to respond in a negative and nearly linear pattern to distance from the edge. However, these significant results for both trees had broader confidence intervals from 200 meters, likely referring to the low number of plots with a distance > 200 m from the forest edge and limiting the capacity to interpret the effects of edge distance on basal area further than 200 meters

into forest fragments. Hornbeam did not present any variation in their basal areas in response to edge orientation or distance from the edge (Fig. 8).

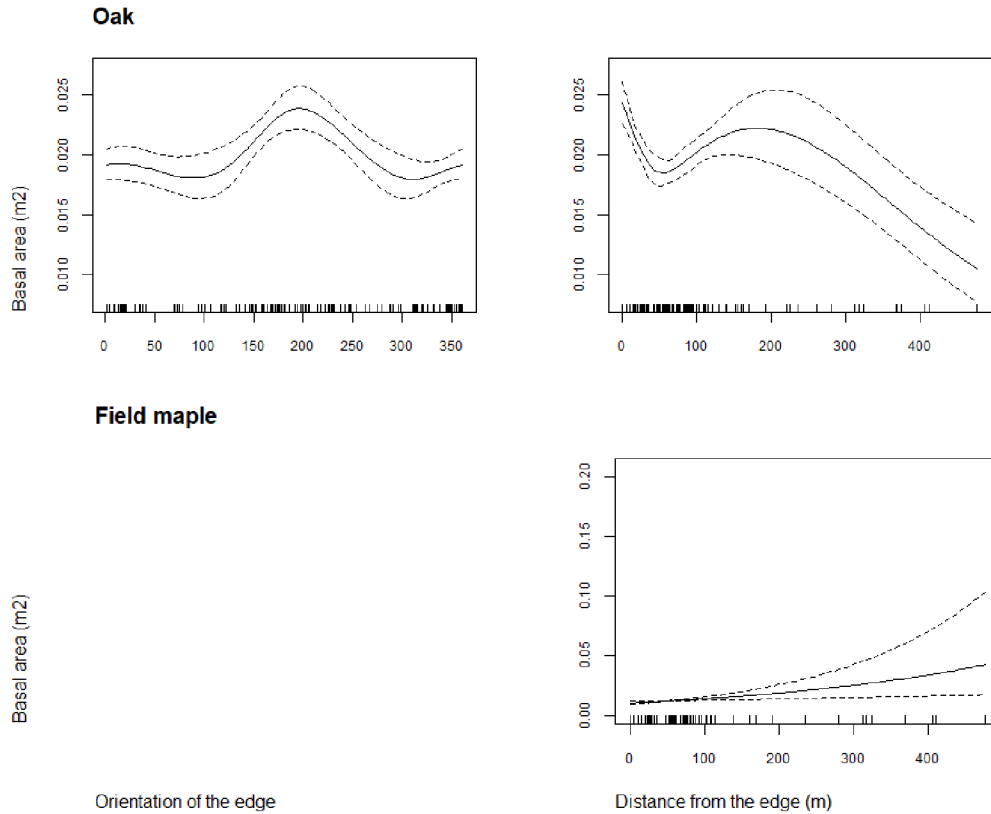


Figure 8 - Significant results of generalized additive model (GAM) for the basal area (m^2) of individual trees for the most common species: oaks (*Quercus robur* and *Quercus petraea*), hornbeam (*Carpinus betulus*) and field maple (*Acer campestre*). The graph shows the additive effect and 95% confidence intervals (dotted lines) of edge orientation (on the left) and distance from the edge (m) (on the right) on the basal area, excluding non-significant effects.

Regarding slope condition, the observed results suggest that slope aspect has no significant effect either on oak or hornbeam basal areas. However, field maple exhibits higher basal areas in trees near slopes facing north, northeast and east, than trees on southwest and west facing slopes. Conversely, slope inclination exhibits significant and similar trends for every analyzed species, the basal area of all trees generally decreases as the slope of the terrain increases. For oaks and field maples, this negative trend is linear or close to linear, while for hornbeams the results used in this research reveal a slight increase of basal area during the first values of slope inclination (5 – 10) and a nearly linear decrease after that (Fig. 9).

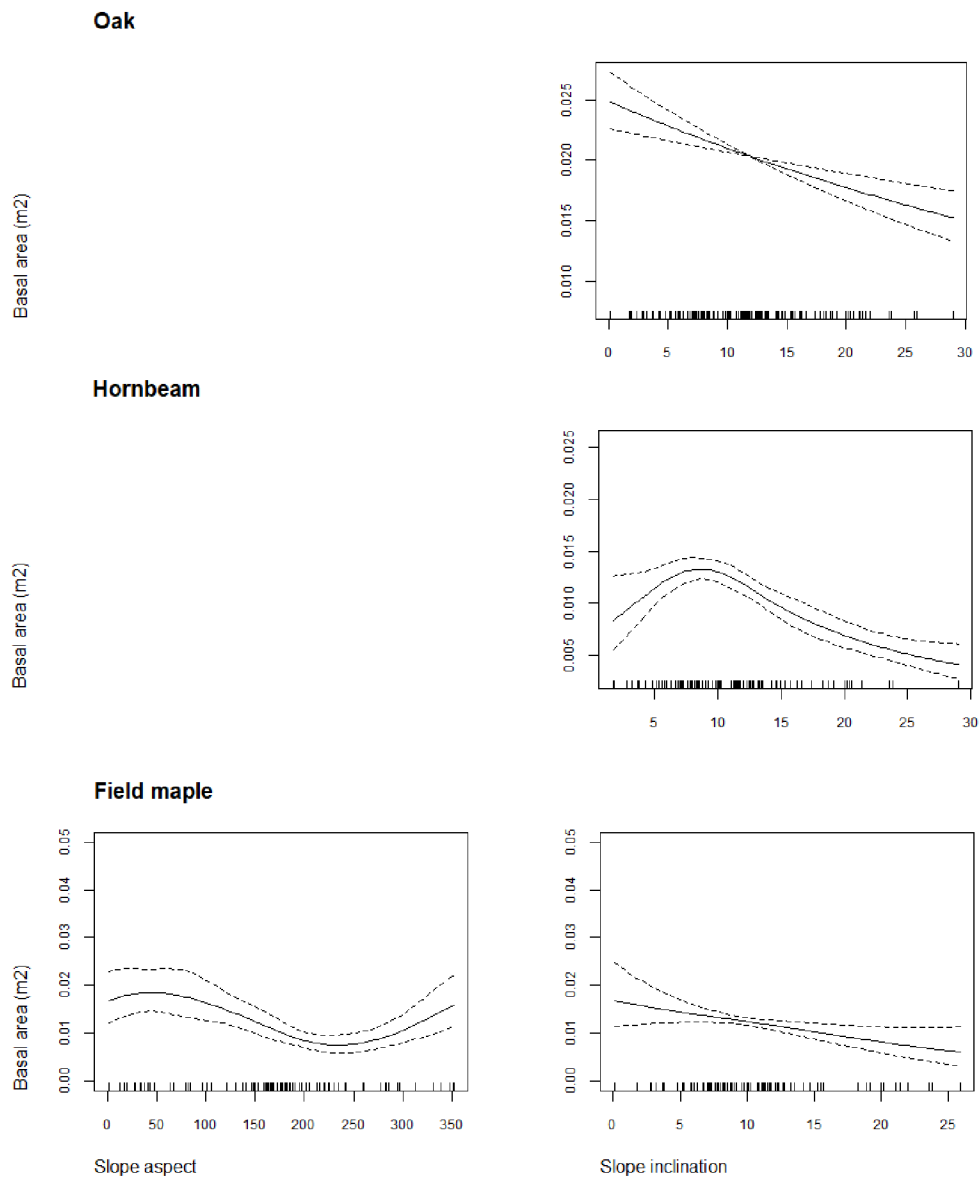


Figure 9 - Significant results of the generalized additive model (GAM) for the basal area (m^2) of individual trees for the most common species: oaks (*Quercus robur* and *Quercus petraea*), hornbeam (*Carpinus betulus*) and field maple (*Acer campestre*). The graph shows the additive effect and 95% confidence intervals (dotted lines) of slope aspect (on the left) and inclination (on the right) on the basal area, excluding non-significant effects.

Soil conditions, represented by C/N ratio had a significant effect on the basal area of all three species, while N/P had a significant effect exclusively on oaks. The basal area of oaks exhibited a negative and linear relation with C/N, while it displays a generalized increment for hornbeams and field maples with slightly higher values compared to a linear trend between 8 – 12 and 10 – 14, respectively. In contrast, N/P ratio did not have a significant effect on the basal area of hornbeams and field maples, whereas oaks exhibit a peak in their basal area between approximately 200 and 600 values of N/P ratio (Fig. 10).

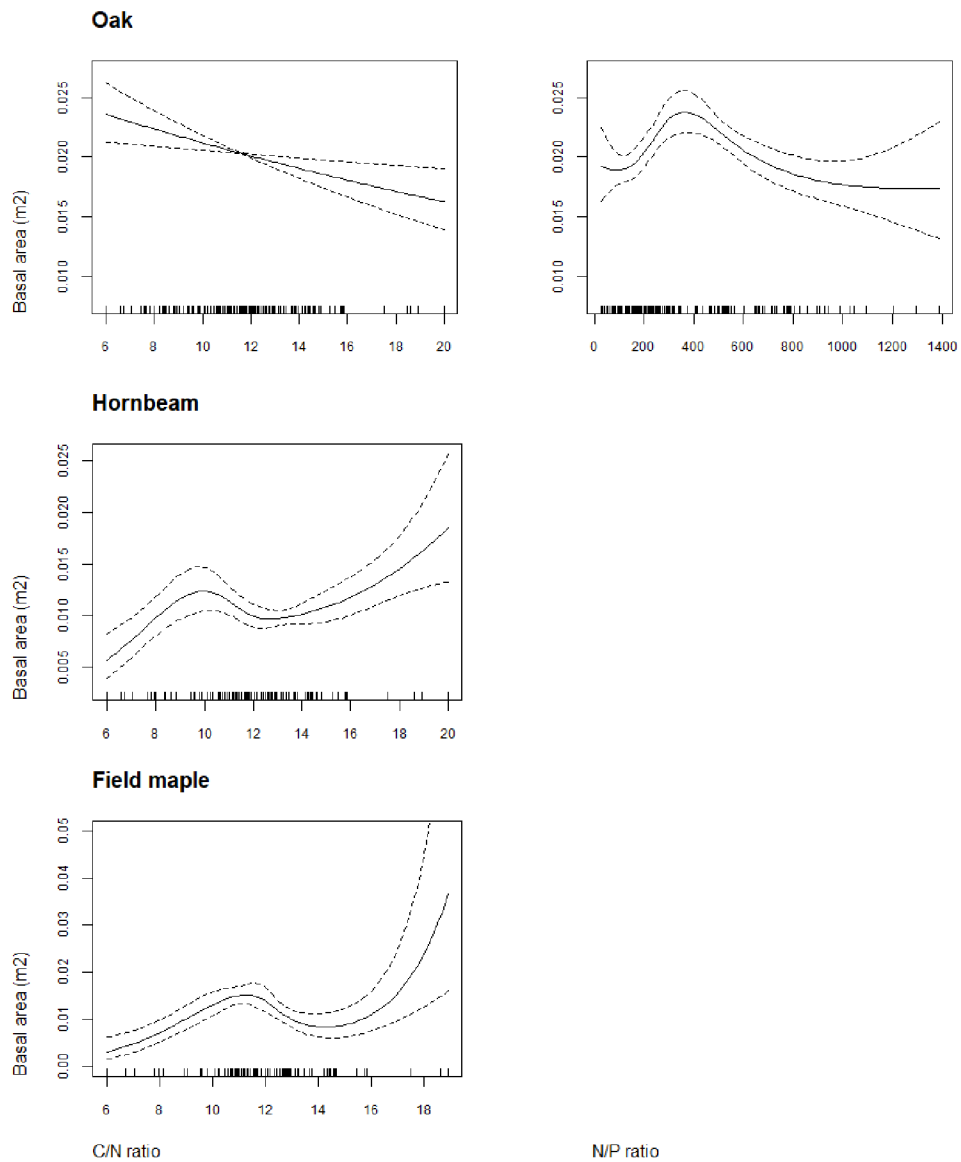


Figure 10 - Results of the generalized additive model (GAM) for the basal area (m^2) of individual trees for the most common species: oaks (*Quercus robur* and *Quercus petraea*), hornbeam (*Carpinus betulus*) and field maple (*Acer campestre*). The graph shows the additive effect and 95% confidence intervals (dotted lines) of carbon/nitrogen and nitrogen/phosphorus ratio from topsoil at a depth of 10 cm on the basal area.

Our results for oaks showed a significant difference in basal area between forest fragments smaller than 22 and between 22 and 55 hectares, while the biggest forest fragments did not exhibit any difference in basal area from small fragments. In contrast, either hornbeams or field maples had any response to forest fragment size.

On the other hand, thermophilic, oak-dominated stands exhibited significantly lower oak basal areas than all the other biotopes included in the model. Hornbeams display a lower basal area in slightly acidic, oak-hornbeam stands than in other forest types;

while field maples exhibit notably lower basal areas in slightly acidic, oak-hornbeam and relatively lower in thermophilic, oak-hornbeam stands.

5.4 Influence of environmental conditions on stand basal area

Table 3 - Mean (\pm S.D.) values of total stand basal area and stand basal area for different forest types.

	Mean (\pm SD)
Thermophilic, oak-dominated stands	0,459 (\pm 0,156)
Thermophilic, oak-hornbeam stands	0,566 (\pm 0,188)
Mesophilic, oak-hornbeam stands	0,550 (\pm 0,191)
Slightly acidic, oak-hornbeam stands	0,491 (\pm 0,238)
Total	0,534 (\pm 0,199)

None of the explanatory variables included in the GAM model for stand basal areas at plot level are significant. Therefore, the results showed no significant effects on edge distance and orientation, slope aspect and inclination, C/N ratio and N/P ratio and type of biotope on stand basal area of trees. As observed in Table 3, differences between basal areas in the studied biotypes are not significant enough either to be taken into account.

6 Discussion

6.1 Slope conditions

Most forest fragment remnants in the study area (80%) are situated at slopes between 5 and 19 degrees, this is consistent with the study of Sandel & Svenning (2013) which revealed that agriculture, grazing, timber and construction are focused on flatter surfaces, limiting the distribution of forests to sloping terrain with more difficult access, and highlighting the implications for conservation of forests in the future. Therefore, it is of great importance to understand how slope conditions modulate tree growth on different biotopes and species. Steeper terrains are characterized by differences in light exposure, depending on their orientation, and lower water availability, which can limit tree growth either through light shortage or water deficit. In this case, slope was a significant variable determining the basal area for all the analysis and sub-analysis except stand basal area (see Chapter 5.4). In all cases, the tendency was of a generalized decrease as the slope increased, which is consistent with the results obtained by previous studies (Berrill & O'Hara, 2016; Long et al., 2020).

On the other hand, the slope aspect has been proved to be a relevant factor influencing tree growth in previous studies. Slopes facing south generally have higher diurnal temperature variability, drier conditions and higher light availability. In addition, north facing slopes have higher tree densities and smaller basal areas, while slopes facing south concentrate old and mature trees with less density and larger basal areas (Young & Mitchell, 1994; Ries et al., 2004; Bernaschini et al., 2019, Hofmeister et al., 2019; Long et al., 2020). The results of this study reveal that generally south-east facing slopes exhibit slightly higher basal areas, while north-west facing slopes generally have smaller basal areas, this is in line with previously described studies. The slight shift of the response to east could be a result of a biotope and species-specific responses that will be discussed further below.

Specific responses of biotope showed similar patterns as described for all the individual trees. However, from the results of this study, it is possible to infer that thermophilic, oak-dominated stands are distributed around southwest orientations

(with a mean aspect and standard deviation of 209 ± 45), therefore on warmer sites with more light availability. In contrast, mesophilic and slightly acidic, oak-hornbeam stands display a wider distribution along different slope aspects, with higher growth on southeast facing slopes, which most probably still have high light availability while slightly reducing the effect of solar radiation on the temperature.

Lastly, the response of field maple to slope aspect is similar. Although the general trend shows that most field maples exhibited a tendency to higher basal areas at southeast, east and northeast facing slopes, most field maples are distributed at south facing slopes, with more than 50% of the sampled field maples located on east, southeast and south facing slopes. This contrasts with the description of field maple by Jones (1945), as extremely-shade tolerant trees during their first decade, but with higher light requirements during their seed-bearing years. The results of this study showed that most of the small field maples are located between south and east facing slopes, where temperatures and light availability are higher than on slopes between east and north, where in comparison they probably have more shade and moister conditions. However, this pattern could be partially explained by their mesophilic nature.

6.2 Edge influence and fragment size

The results of all the analysis and sub-analysis, except for thermophilic, oak-hornbeam stands, found evidence for the fact that either distance from the edge or edge orientation are generally as important as other traditional factors explaining the variation of properties of tree layer vegetation such as slope conditions, soil conditions or type of biotope. Therefore, the analysis found clear support for the idea that forest edges can modulate the growth of trees, as previous studies have observed (Palik & Murphy, 1990; Meeussen et al., 2020; Reinmann et al., 2020; Morreale et al., 2021).

The generalized decline in basal area of individual trees found near the forest edge (first 50 meters into the forest) found when all species and biotopes were included in the analysis, for thermophilic and mesophilic, oak-hornbeam stands, as well as for oaks, is consistent with previous studies (Palik & Murphy, 1990; Meeussen et al., 2020; Reinmann et al., 2020; Morreale et al., 2021). This result contrast with the

narrative on tropical areas research, where the net productivity of trees is lower at the edges as a consequence of higher mortality rates associated with wind turbulence, elevated temperatures and water stress (Morreale et al., 2021), revealing that these factors less threatening or determining for forest edges of other latitudes. The decline in basal area during the first meters of forest edge (50 m) could be explained either by higher light availability conditions due to the proximity to more open areas, such as agricultural fields (Matlack, 1993; Schmidt et al., 2017); temperature, as a consequence of higher solar radiation (Murcia, 1995; Tuff et al., 2016; Mendes 2019; Meeussen et al., 2021a), or to higher nutrient availability in the soil, due to chemical fertilizers from the nearby croplands (Hester & Hobbs, 1992; Murcia, 1995) or because of higher nitrogen deposition at the edges (Schmidt et al., 2017), or a combination of all the previous variables. In addition, the response to C/N and N/P ratio supports the idea of higher basal areas for areas with high nutrient availability, as higher basal areas are observed when C/N was rather low (8 to 12), and the larger basal areas when N/P ratio was smaller. However, Hofmeister et al. (2013) found that light availability and soil nutrients in the edge of these forest fragments were comparable to those in the interior, probably due to the type of open forest stands present in the study area and spatial heterogeneity of soil nutrients. Therefore, although this variable could explain the variability at the very edge of the forest fragments, light availability alone is not able to explain the variation of the basal area along the edge-to-interior gradient during the first 50 meters into the forest interior. Nevertheless, Hofmeister et al. (2013) results should be considered with caution as they were collected only during two summer months and previous studies suggest that patterns of light availability may vary throughout the year (Young & Mitchell, 1994; Davies-Colley et al., 2000; Ries et al., 2004).

The different patterns observed in slightly acidic, oak-hornbeam stands, which exhibited a slight increase of basal area over the first meters into the forest edge might be due to the lack of data on this type of biotope over the first 25 meters into the forest edge. In addition, field maple also exhibited a slight increase over the first 100 meters into the forest edge. However, field maples were equally distributed along the first 100 meters inside the plots, therefore, the lack of data is not able to explain the increase in this case. Therefore, these results are not able to explain the increase of basal area

during the first 100 meters into the forest interior, beyond highlighting the variety of species-specific responses that can be found concerning forest edges, as other studies have suggested (Laurence et al., 2016; Morreale et al., 2021).

Results of basal area variations obtained in distances over 200 meters into the interior of the forest fragments suggest that the influence of the forest margins on trees in deciduous forests in the study area might reach further than 200 meters into the forest interior. This is supported by previous studies that found similar depths of edge influence (DEI) (Harper et al., 2005; Tuff et al., 2016; Schmidt et al., 2017; Hofmeister et al., 2019). However, these results should be interpreted carefully, since only one forest fragment larger than 55 hectares was sampled, and there is a clear concentration of plots over the first 200 meters.

The first chapter of the results (see Chapter 5.1), which analyzed the response of individual trees (including all biotopes and species), exhibited an increase of basal area from approximately 50 to 200 meters from the forest edge, which might hint at species or biotope specific patterns. The decrease in basal area from 200 meters within forest fragments is in line with previous studies that state that tree growth decreases with distance from the margin (Palik & Murphy, 1990; Meeussen et al., 2020; Reinmann et al., 2020; Morreale et al., 2021). The separate sub-analysis for biotopes and species revealed a high diversity of responses with high confidence intervals, therefore it is only possible to infer that distance from edges can show DEIs higher than 100 meters, potentially reaching 400 meters in some cases and that different biotopes and species show specific responses associated with them.

Previous studies suggest that south and/or southwest facing edges have higher solar radiation when temperature reaches its maximum during the day, shorter thermal depth into the forest fragment, especially in forest stands characterized by an open canopy layer, and forest margins with direct solar radiation (such as those adjacent to pastures or crops), as in the case of the study area. Moreover, north facing slopes seem to display weaker and steeper gradients, while slopes facing south exhibit stronger but less abrupt gradients (Matlack, 1993; Hofmeister et al., 2019). In addition to the results obtained for slope aspect, this research found evidence of a generalized response of all tree layer vegetation to edge orientation, with higher basal areas in west, southwest

and south facing edges. Basal area responses to edge aspect in this study are consistent with previous studies, as southwest facing edges had generally bigger trees probably as a response to higher light availability and thermic conditions, exhibiting a contradictory result in the axis east-west to slope aspect in most cases. Although both responses have been reported to be similar by different studies, the observed results go beyond previous reports analyzing both effects at the same time, highlighting the importance of taking into account the influence that edge orientation has on the tree layer vegetation, and revealing south oriented responses but with different patterns on the east-west axis, and suggesting potential synergies between edge and slope aspect influences on tree layer growth (Matlack, 1993; Matlack, 1994; Young & Mitchell, 1994; Ries et al., 2004; Bernaschini et al., 2019, Hofmeister et al., 2019).

Our models included fragment size, to avoid underestimating the influence of its effect, understanding it as edge influence as many previous studies have done (Didham, 1997). The results when basal areas of species and biotopes are analyzed separately, in contrast to Ries et al. (2004), suggests that the size of the fragment is positively related to tree productivity for oaks, and generally for thermophilic, oak-dominated and oak-hornbeam stands. On the other hand, the decrease observed in larger fragments for slightly acidic, oak-hornbeam stands could be a consequence of less edge influence and the concentration of nitrogen deposition and acidification found near forest borders, due to local advection, and wind turbulence (Wuyts et al., 2008; Remy et al., 2016). However, the results on the effects of soil conditions in slightly acidic, oak-hornbeam stands had no significant effect, therefore these conclusions cannot be proved by this study. These results are of special relevance, highlighting the importance of large forest fragments in agricultural landscapes, as well as the importance of not considering the results of higher basal areas near the edges in some of the models, as an argument in support of fragmentation as a forest management model for higher productivity. On the contrary, these results emphasize the species-specific and biotope-specific responses of trees, and the complexity of vegetation responses to fragmentation.

The lack of responses for the model with the sum of basal areas for each plot can be understood either by the variation in responses of different species and biotopes to edges, as a consequence of a considerable legacy of the past management, or a

combination of both. On the other hand, sites with smaller trees and sites with fewer big trees can result in the same stand basal area. Some studies have documented these contrary responses, for example for slope orientation (Måren et al., 2016; Hofmeister et al., 2019). Therefore, this effect might have contributed to dampening the responses on stand basal area for the analyzed variables.

6.3 Soil conditions

It is important to understand that areas with a history of traditional management practices such as coppicing are characterized by favoring shade-intolerant species with low nutrient requirements, as these practices tend to leave a relatively open forest and limit soil nutrient availability (primarily nitrogen) as a consequence of biomass extraction. Even so, the forest fragments in this study area have generally not been used productively for almost 70 years. Therefore, it can be assumed that the current forest has reached a stage of maturity. At the same time, the lack of nutrients in the organic matter has probably been restored (Hofmeister et al., 2004).

Regarding nutrient responses to edge conditions, previous studies report higher values of carbon and nitrogen stocks (Wuyts et al., 2008; Remy et al., 2016; Reinmann et al., 2020; Meeussen et al., 2021b). Higher nitrogen deposition and accumulation it can be caused by local advection and wind turbulence, and potentially due to chemical fertilizers from nearby croplands (such as nitrates), which have been reported to accumulate at forest edges (Hester & Hobbs, 1992; Murcia, 1995). On the other hand, phosphorus levels have been reported to be lower at forest edges in comparison to the forest interior, possibly being a limiting factor for vegetation growth at forest edges (Toledo-Aceves & García-Oliva, 2008). Nevertheless, Hofmeister et al. (2013) found no evidence to support the presence of edge-associated gradients in soil nutrients in Bohemian Karst, due to the large spatial variability of this factor. In addition, some studies suggest that although in Bohemian Karst the limiting factor is nitrogen, the availability of this nutrient tends to be higher in phosphorus-rich soils compared to phosphorus-poor soils, due to the positive influence phosphorus has on the mineralization of nitrogen in the soil (Hofmeister et al., 2002; Hofmeister et al., 2009).

Considering the results of this study, the response to the C/N ratio seems to have a generalized pattern, while N/P exhibited biotope and species-specific responses. The basal area of all tree species in all biotopes generally peaks at values approximately at 10, with most of the trees (80%) in the study area located in soils with C/N values between 8.37 and 14.6. This response is consistent with previous studies describing nitrogen as a limiting factor in Bohemian Karst (Hofmeister et al., 2002; Hofmeister et al., 2009), with better performance of trees at rather lower values of C/N ratio. Although the basal area seems to increase again for low values of C/N ratio (16-20), considering the wide confidence values observed at these values this response has to be interpreted carefully. Therefore, the increase of basal area when C/N reaches higher values can be a consequence of the lack of available samples for those values, since most trees in the plots of this study are not located in soils with those characteristics.

In contrast, biotope-specific responses seem to be generally more associated with the N/P ratio than the C/N ratio. The only response exhibited to the C/N ratio was in slightly acidic, oak-hornbeam stands, which exhibit a higher growth at the lowest and highest C/N values. The increase in basal area at C/N values could hint that nitrogen is a limiting factor for slightly acidic, oak-hornbeam stands. At the same time, similarly to the general response to C/N ratio, the increase of basal area observed at the highest values observed of C/N cannot be explained by the results obtained in this study, however, this increase could also be a consequence to the lack of sampled trees in locations with these characteristics. On the other hand, the biotope-specific responses to N/P ratio are highly diverse. Basal area in slightly acidic, oak-hornbeam stands, exhibit a logarithmic decrease over N/P ratio, suggesting that phosphorus is also a limiting factor for this biotope, possibly due to the influence phosphorus has on the mineralization of nitrogen (Hofmeister et al., 2002; Hofmeister et al., 2009). On the contrary, bigger basal areas in thermophilic, oak-hornbeam stands, seem to be peak at relatively high values of N/P ratio, this suggests that phosphorus is not a limiting factor for this type of stand. Similarly, mesophilic, oak-hornbeam stands exhibit a slight linear increase with N/P ratio, however, confidence intervals become wider at high values of N/P ratio, due to the lack of data.

Regarding species-specific responses to soil nutrients, Måren et al. (2015) suggests that soil nutrients in a deciduous forest in central Germany were not a limiting factor

for either oak or hornbeam. This contrasts with the observed results, since the basal area shows significant responses to C/N for oaks and hornbeams, and to N/P exclusively for oaks. Results for C/N ratio response display a linear decrease in basal area, this suggests that nitrogen might be a limiting factor, and agrees with Easton et al. (2016) description of a preference of oaks for fertile soils. Oak response to N/P suggests that phosphorus could be a limiting factor through the role it plays in nitrogen mineralization (Hofmeister et al., 2004; Hofmeister et al., 2009) since a peak can be observed at rather low values of N/P ratio. In addition, hornbeam and field maple exhibit a peak at low values of C/N that resembles the peak exhibited by the generalized response of basal area, therefore suggesting that nitrogen could be a limiting factor for these species.

6.4 Tree layer edge response and climate change

Studies on forest responses to fragmentation and the influence of edges suggest that this can lead to the degradation of forest fragments (Harrison & Bruna, 1999; Laurence et al., 2002; Mortelliti et al., 2010; Haddad et al., 2015). This has been supported by many forestry studies in the tropics (Davies-Colley et al., 2000; Wright et al., 2010; Laurence et al., 2011), yet studies in temperate forests in the Americas and Europe have revealed that this is not always true (Palik & Murphy, 1990; Meeussen et al., 2020; Reinmann et al., 2020; Morreale et al., 2021). Temperate forests have experienced a long history of deforestation, fragmentation and abandonment of logging activities, resulting in afforestation of many previously deforested areas, probably creating more stable conditions associated with edges, where there is less mortality associated with abrupt edge formation (Meeussen et al., 2020; Morreale et al., 2021). Furthermore, some studies point out that recently created edges in temperate zones are not related to higher mortalities after the edge creation but with larger growth increases (Palik & Murphy, 1990; Briber et al., 2015; Meeussen et al., 2020; Reinmann et al., 2020; Morreale et al., 2021). Therefore, the concept of fragmented forests as degraded remnants has been questioned by some researchers (Morreale et al., 2021). However, although the results of this study agree partially with the concept of elevated growth near the forest edge, it is not possible to infer a general decrease of basal area for all trees, instead general increase can be appreciated when all the trees were included after 50 meters up to 200 meters, approximately. This is not mentioned by any previous

study and should be studied further to understand better the underlying factors modulating tree growth in Bohemian Karst forests. However, this could be a response to spatial heterogeneity of tree species/biotopes and their specific responses, since the results of this research revealed a great variety of responses from 50 meters to the interior of the forest associated with the different species and biotopes analyzed. Therefore, based on the results and highlighting the variety of responses, it is not possible to rule out the idea that fragmentation leads to the degradation of certain biotopes or is detrimental to the development of some tree species.

Moreover, results on the slope and edge conditions suggest that tree growth is related to light availability, moisture and temperature conditions associated with different slope and edge conditions in Bohemian Karst, as other studies have suggested. On the other hand, climate change is expected to increase the temperatures and reduce water availability, as well as reduce the capacity of forest fragments to attenuate temperature increases and sequester carbon (Young & Mitchell, 1994; Måren et al., 2016; Bernaschini et al., 2019; Hofmeister et al., 2019; Long et al., 2020). This context and the variability of responses make predictions on tree growth complex, but drier and warmer conditions could hinder the performance of mesophilic and slightly acidic, oak-hornbeams, according to the responses observed in this study.

Lastly, results regarding fragment size found no generalized pattern, as Ries et al. (2004) revealed in their study, however, diverse biotic and species-specific responses were found as well. Some researchers have discussed whether the conservation of plant species is better served by a few large or many small forest fragments (Lindenmayer & Fischer, 2013). The results of this research contribute to this debate in terms of the diversity of responses observed, as most biotopes, as well as oaks, show significant responses to fragment size. Thus, it is of particular importance according to the observed results to conserve large fragments as they show a higher presence of larger trees in some biotopes while highlighting that small fragments of slightly acidic, oak-hornbeam display an opposite response. In consequence, further studies should be conducted, including forest patches of different sizes, to understand the role of different size types in favoring forest growth of different species and biotopes.

7 Conclusion and contribution of the thesis

This study analyzed how spatial heterogeneity of slope, edge and soil conditions and size of forest fragments in Bohemian Karst modulate the tree layer vegetation response at different scales: (1) generalized response of basal areas of individual trees, (2) response of basal area of individual trees at each biotope, (3) response of basal area of individual trees for each of the three most present species, and (4) generalized response of stand basal area at each plot. The results of this study demonstrated a generalized, as well as at biotope and species levels, the response of basal area to distance from the edge. A reduction in growth can be observed over the first few meters of the edge, however, this reduction does not extend to the entire gradient of distance from the edge. Furthermore, the results of this study suggest that edge influence to the vegetation layer can reach further than 200 meters into the forest fragments. Nevertheless, it is important to note that this study does not suggest that forest fragmentation is an effective forest management practice for increased growth or carbon sequestration.

We found that the edge aspect generally has a positive influence on basal area at south (S) and southwest (SW) facing edges, and similar results were found for slope aspect at southeast (SE) facing slopes; these results are consistent with previous studies. Results of this research found evidence of a generalized response to slope, with larger basal areas in the less sloped sites, highlighting the importance of protecting the remaining tracts of forest in these areas. Moreover, it was not possible to infer a general pattern concerning the fragment sizes. However, the results in this study revealed responses at different scales, especially at the biotope level, which suggests the relevance large forest fragments play in avoiding the degradation of temperate forests in an agricultural matrix. The results regarding soil conditions suggest that generally Bohemian Karst vegetation is limited by nitrogen, while phosphorus is a more determinant factor at the biotope level. On the other hand, nitrogen is a relevant determinant for the growth of oaks, hornbeams and field maples, while phosphorus is only relevant for oaks. To summarize, this research aims to highlight the diversity of responses to edge effects, the importance of understanding the patterns that occur at edges to predict future responses to climate change, and the role of forest edges in mitigating its effects, as well as their potential to store carbon.

Further studies regarding edge influence on tree layer vegetation should try to plot more large fragments (>200 hectares) to better represent forest interior responses and environmental conditions. In addition, past forest management has been proved to be a key factor for explaining present structural changes in forest vegetation, as well as soil characteristics, moisture and light availability (Koerner et al., 1997; Hofmeister et al., 2009; Fedorová et al., 2016; Bricca et al., 2020). For example, Fedorová et al. (2016) suggests that thinning significantly increased the diameter increment of hornbeam (61%) and sessile oak (59%). Therefore, including factors about past forest management in the area (e.g., harvested vs. non-harvested species, previously forested vs. afforested areas) can give a better idea about how different types of management influence forest structure in the long term, giving us hints about how to better preserve the remaining forest fragments. Lastly, further studies should consider the seasonal variability of the environmental variables that can potentially affect biotic responses over the edge-to-interior gradient (e.g., light, temperature and soil conditions).

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9 Appendix

Appendix 1. Results of the generalized additive model (GAM) for the basal area (m²) of individual trees. Significance levels as obtained from ANOVA are given as * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$ and n.s. $p > 0.05$. Mean and standard deviations (SD) were included for numeric variables.

	<i>p</i>	<i>Mean (±SD)</i>
<i>Biotope type</i>		
Thermophilic, oak-dominated stands		
Thermophilic, oak-hornbeam stands	n.s.	
Mesophilic, oak-hornbeam stands	**	
Slightly acidic, oak-hornbeam stands	n.s.	
<i>Forest fragment size</i>		87.02(±103.86)
<22 hectares		
22-55 hectares	n.s.	
>55 hectares	n.s.	
<i>Edge conditions</i>		
Edge orientation	***	183(±113)
Distance from the edge	**	74.64(±93.12)
<i>Slope conditions</i>		
Slope aspect	*	166(±93)
Slope inclination	**	11.62(±5.66)
<i>Soil conditions</i>		
C/N ratio	***	11.97(±2.67)
N/P ratio	n.s.	386.67(±307.9)

Appendix 4. Results of the generalized additive models (GAM) for the basal area (m²) of individual trees, analyzed in different sub-models for each plot. Significance levels as obtained from ANOVA are given as * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$ and n.s. $p > 0.05$. Mean and standard deviations (SD) were included for numeric variables at each biotope.

	Thermophilic, oak-dominated stands		Thermophilic, oak-hornbeam stands		Mesophilic, oak-hornbeam stands		Slightly acidic, oak-hornbeam stands	
	<i>p</i>	<i>mean</i> (\pm SD)	<i>p</i>	<i>mean</i> (\pm SD)	<i>p</i>	<i>mean</i> (\pm SD)	<i>p</i>	<i>mean</i> (\pm SD)
<i>Forest fragment size (Ha)</i>		75.56(\pm 97.89)		73.47(\pm 89.02)		91.78(\pm 108.45)		109.36(\pm 117.06)
<22 hectares								
22-55 hectares	**		n.s.		n.s.		n.s.	
>55 hectares	***		**		n.s.		***	
<i>Edge conditions</i>								
Edge orientation	n.s.	200(\pm 90)	n.s.	207(\pm 106)	***	157(\pm 116)	***	197(\pm 118)
Distance from the edge	***	118.43(\pm 115.91)	n.s.	87.75(\pm 108.93)	***	65,73(\pm 81,33)	***	42,25(\pm 42,26)
<i>Slope conditions</i>								
Slope aspect	*	209 \pm 47)	n.s.	175(\pm 75)	***	139(\pm 106)	*	194(\pm 89)
Slope inclination	***	14,09 \pm 7,27)	**	10,49(\pm 4,81)	***	11,87(\pm 5,61)	***	11,34(\pm 5,43)
<i>Soil conditions</i>								
C/N ratio	n.s.	11,62(\pm 1,8)	n.s.	11,32(\pm 2.04)	n.s.	12,62(\pm 3,13)	***	11,63(\pm 2,41)
N/P ratio	n.s.	571.56(\pm 337.97)	***	489.48(\pm 355.24)	*	288.3(\pm 248)	***	331.81(\pm 195.49)

Appendix 3. Results of the generalized additive model (GAM) for the basal area (m²) of individual trees, analyzed in different submodels for the most common trees: oaks (*Quercus robur* and *Quercus petraea*), hornbeam (*Caripuns betulus*) and field maple (*Acer campestre*). Significance levels as obtained from ANOVA are given as * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$ and n.s. $p > 0.05$. Mean and standard deviations (SD) were included for numeric variables for each tree species.

		Oaks		Hornbeam		Field maple
	<i>p</i>	mean (±SD)	<i>p</i>	mean (±SD)	<i>p</i>	mean (±SD)
<i>Biotope type</i>						
Thermophilic, oak-dominated						
Thermophilic, oak-hornbeam	***		n.s.		*	
Mesophilic, oak-hornbeam	***		n.s.		n.s.	
Slightly acidic, oak-hornbeam	**		***		*	
<i>Forest fragment size</i>						
<22 hectares		92.26(±105.59)		82.82(±101.97)		70.08(±94.93)
22-55 hectares	*		n.s.		n.s.	
>55 hectares	n.s.		n.s.		n.s.	
<i>Edge conditions</i>						
Edge orientation	***	199(±110)	n.s.	145(±111)	n.s.	149(±103)
Distance from the edge	***	76.07(±88.76)	n.s.	77.88(±95.33)	**	51.14(±80.47)
<i>Slope conditions</i>						
Slope aspect	n.s.	177(±85)	n.s.	140(±99)	***	152(±90)
Slope inclination	***	11.94(±5.72)	***	11.65(±6.03)	*	10.09(±4.81)
<i>Soil conditions</i>						
C/N ratio	**	11.59(±2.37)	***	12.77(±3.17)	***	11.68(±2.37)
N/P ratio	**	418.6(±302.67)	n.s.	309.73(±281.64)	n.s.	329.58(±271.32)

Appendix 4. Results of generalized additive model (GAM) for stand basal areas (m²) of each plot. Significance levels as obtained from ANOVA are given as * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$ and n.s. $p > 0.05$. Mean and standard deviations (SD) were included for numeric variables for each tree species.

	<i>p</i>	<i>mean (±SD)</i>
<i>Biotope type</i>		
Thermophilic, oak-dominated stands		
Thermophilic, oak-hornbeam stands	n.s.	
Mesophilic, oak-hornbeam stands	n.s.	
Slightly acidic, oak-hornbeam stands	n.s.	
<i>Forest fragment size</i>		98.89(±109.53)
<22 hectares		
22-55 hectares	n.s.	
>55 hectares	n.s.	
<i>Edge conditions</i>		
Edge orientation	n.s.	76.51(±94)
Distance from the edge	n.s.	197(±114)
<i>Slope conditions</i>		
Slope aspect	n.s.	174(±93)
Slope inclination	n.s.	11.33(±5.36)
<i>Soil conditions</i>		
C/N ratio	n.s.	11.64(±2.48)
N/P ratio	n.s.	385.94(±298.56)