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Effects of stand edges on the structure, functioning, and diversity of a temperate mountain forest landscape

Franziska Pöpperl[1,2,†] and Rupert Seidl[1,2,3]

[1]Institute of Silviculture, Department of Forest- and Soil Sciences, University of Natural Resources and Life Sciences (BOKU) Vienna, Peter Jordan Straße 82, Wien 1190 Austria
[2]Ecosystem Dynamics and Forest Management Group, Technical University of Munich, Hans-Carl-von-Carlowitz-Platz 2, Freising 85354 Germany
[3]Berchtesgaden National Park, Doktorberg 6, Berchtesgaden 83471 Germany

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Abstract. Human land use is fragmenting forests around the globe, increasing the edge density in forest landscapes. More frequent natural disturbances also increase the presence of edges in forest ecosystems. Studying a mountain landscape in the Eastern Alps, we contrasted 661 plots situated at varying distances from a stand edge with 615 plots sampled in forest interiors. Our objectives were (1) to analyze the strength of edge effects on forest structure, functioning, and diversity; (2) to determine the penetration depth of edge effects into the forest interior; and (3) to quantify the difference between permanent edges (i.e., to a different land cover type) and transient edges (as created e.g., by natural disturbances). Edges affected forest biomass accumulation negatively (basal area, litter depth, live tree carbon), but had positive effects on diversity (variation in tree diameter, effective plant species number, plant species richness, number of red-listed plant species). Biodiversity indicators responded most strongly to the presence of edges. The maximum distance of a significant edge effect was <50 m across all indicators. Effects on forest structure and functioning were generally stronger at transient edges compared to permanent edges. Our findings highlight that both permanent and transient edges have a considerable influence on forest ecosystems and should be considered more explicitly in the analysis and management of forest landscapes.

Key words: ecosystem functioning; edge effect; edge influence; forest structure; inventory; Kalkalpen National Park; red-listed species.

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† **E-mail:** FranziPoepperl@gmail.com

Introduction

Fragmentation is a process affecting forests at the global scale and has profound impacts on the biodiversity and functioning of forest ecosystems (Haddad et al. 2015). Land-use change is a main driver of fragmentation, creating edges between forests and non-forest ecosystem (Harper et al. 2005, Esseen et al. 2016). The global conversion from forest to non-forest land during the years 2000–2012 was estimated to 2.3 million square kilometers in total, with a gain of 0.8 million square kilometers (Hansen et al. 2013). Consequently, edges are much more prevalent in forests around the globe today compared to the edges that are occurring naturally (e.g., at the timberline, or between aquatic and terrestrial systems).

Edges have a profound effect on ecosystems. A prime reason for edge effects is the altered microclimate at the edge, influencing light availability, air and soil temperature, and wind speed (Laurance et al. 1998*a*, Marchand and Houle 2006, Heithecker and Halpern 2007, Remy et al. 2016, Thom et al. 2020). Consequently, communities are adapting to the altered climatic conditions at the edge, for example, with light-demanding species being favored by edges (Laurance et al. 2006). The presence of edges can also increase the risk of tree mortality (Laurance et al. 1998*a*, Pütz et al. 2011), affect species composition due to shifts in resource availability (Harper et al. 2005, Esseen et al. 2016), and affect forest C dynamics (Smith et al. 2018). Moreover, habitat quality for many species is directly influenced by the length and structure of edges (Esseen et al. 2016).

Natural disturbances like wildfires, windthrows, and insect outbreaks also create stand edges in forest ecosystems. In contrast to edges resulting from human-induced changes in land cover or edges between land cover types (e.g., forest and rocks, forest, and water body), disturbance-created edges are transient in nature and disappear again as disturbed forests recover (i.e., which can take several decades, e.g., Senf et al. 2019). Also, transient edges created by natural disturbances can have a strong influence on vegetation (e.g., Braithwaite and Mallik 2012, Harper et al. 2015). However, compared to the effects of edges that are permanent (on ecological time scales), the transient edges created by natural disturbances have received considerably less attention in the literature to date. Yet, as natural disturbance regimes are changing in many forest ecosystems around the globe (Seidl et al. 2014, Millar and Stephenson 2015, Thom et al. 2017*a*, McDowell et al. 2020), it can be expected that such transient edges will be an increasingly prominent feature of future forested landscapes.

The presence of an edge affects multiple processes in forest ecosystems simultaneously. Yet, most studies on edge effects have focused on a narrow set of indicators to date, assessing the influence of edges on either ecosystem structure (e.g., Laurance et al. 1998*a*, 2006, Pütz et al. 2011), functioning (e.g., Laurance et al. 2000, Reinmann and Hutyra 2017), or biodiversity (e.g., Laurance et al. 2006, Pütz et al. 2011, Harper et al. 2015, Pfeifer et al. 2017). Analyses comparing edge effects across different indicators (e.g., structure, functioning, and biodiversity) of the same forest ecosystems (e.g., with regard to differences in the prevalence of edge effects with distance from the edge) remain rare (but see e.g., Harper et al. 2015). Furthermore, recent research on forest edges has focused strongly on tropical rainforests (Didham 2006, Laurance and Peres 2006, Tabarelli et al. 2008, Pütz et al. 2011), not least motivated by the ongoing land-use changes in these ecosystems and stimulated by a fragmentation experiment in the Amazon (Laurance et al. 1998*a*, 2011). However, the insights from tropical forest fragmentation studies cannot be directly transferred to other systems that are less species-rich and governed by different ecosystem dynamics, as the responses to edges vary with biome (Smith et al. 2018). For temperate mountain forest ecosystems in Europe, only few studies on fragmentation exist (Esseen et al. 2016, Remy et al. 2016), and the effects of edges on their structure, functioning, and biodiversity remain largely unknown.

Here, we studied edge effects in a temperate mountain forest landscape of Central Europe, quantifying the strength and depth of edge effects for a range of indicators of forest structure (tree basal area, amount of standing and downed deadwood, the variation of diameter at breast height), functioning (live tree carbon, thickness of the litter layer, total cover of woody, and non-woody plants), and biodiversity (effective number of plant species, plant species richness, number of red-listed plant species). Our specific objectives were (1) to compare the strength of the edge effect among different indicators to quantify which aspects are most strongly impacted by edges, (2) to determine the penetration depth of edge effect into the interior of adjacent forest stands, and (3) to compare strength and depth between transient edges (i.e., those created by natural disturbances) and permanent edges (i.e., forest edges to other land cover types). We focused our work on Kalkalpen National Park (KA-NP), situated in the northern front range of the Alps in Austria. The complex topography and disturbance history of KA-NP offer a unique opportunity to study different types of edges in the same biogeographical setting. Based on research from the tropics (Laurance et al. 2006, 2011, Pütz et al. 2011) as well as from temperate forests (Łuczaj and Sadowska 1997), we hypothesized edge effects on plant diversity to be stronger than those on forest structure and functioning. Furthermore, we expected that transient edges have a weaker influence on ecosystems than permanent edges due to their ephemeral nature.

Materials and Methods

Study site

Kalkalpen National Park (47°46′19.074″ N, 14°23′34.9296″ E) was established in the year 1997 and is an IUCN category II protected area. It is the largest contiguous protected forest area in Austria, covering a total of 20,850 ha, whereof 81% are forested. Climatic conditions are strongly driven by topography (i.e., elevation ranging from 385 to 1963 m asl), with mean annual temperatures between 3.6° and 9.0°C and mean annual precipitation between 1205 and 1741 mm (Thom et al. 2017*b*). Low elevation forest types are dominated by *Fagus sylvatica* L., while high elevation areas are dominated by *Picea abies* (L.) Karst. and mixed forests of *P. abies*, *Abies alba* Mill., and *F. sylvatica* characterizing the montane vegetation belt. In accordance with IUCN requirements, the national park has a wilderness zone free of human interventions and a management zone (in which, e.g., bark beetle outbreaks are contained). In combination with the complex interplay between rock faces, avalanche tracks, and areas above timberline, this zoning results in a variety of different disturbances and edge types (Senf and Seidl 2018).

Data

Our analysis builds on data collected in the frame of the monitoring efforts of Kalkalpen National Park. During 1994–2006, sample plots with a size of 314.16 m^2 (radius of 10 m) were recorded in a regular grid of 300 m throughout KA-NP. In total, 2612 plots were sampled, of which we here analyze 1276 that had a complete data vector for the variables of relevance for the current study. For each sample plot, information on site and vegetation was recorded. This included a full census of the tree community as well as a quantification of the forest floor vegetation based on Adler et al. (1994). Plant lists were subsequently cross-referenced with red-listed species (Umweltbundesamt 2016). Furthermore, soil type and litter depth were assessed and local site conditions (e.g., slope, aspect, elevation) recorded for each plot. In addition, the distance from the plot center point to the nearest edge was determined in the field in six classes (i.e., <10 m, 10–24 m, 25–49 m, 50–99 m, 100–1000 m, and forest interior, no edge within 1000 m). Edges were defined as sharp boundaries in vegetation structure and were considered if they were at least 20 m long. Edge lines on the opposite side of the hillslope were not considered if the vertical difference between plot and edge was at least 30 m in elevation (Eckmüllner et al. 1993). Field teams further distinguished between permanent edges (i.e., edges to other land cover types such as alpine grasslands, rocks, or water bodies) and transient edges (i.e., edges to recently disturbed forest patches that can be assumed to disappear again with forest recovery). The complete sampling protocol can be found in Eckmüllner et al. (1993).

Response variables

Our aim was to assess the effect of edges on different dimensions of forest ecosystems, including their structure, functioning, and diversity. Based on previous studies on edge effects in forest ecosystems, we identified three indicators for each of these dimensions: To describe effects on forest structure, we focused on tree basal area (TBA), the variation in tree diameter at breast height (DBH), and the amount of standing and downed deadwood (as an indicator of recent tree mortality) (Harper et al. 2015, Esseen et al. 2016). Our analysis of forest functioning focuses on state variables as integral proxies over ecosystem fluxes. We assessed ground vegetation cover as a variable that is particularly sensitive to changes in microclimate and light. Furthermore, recent findings indicate that ground vegetation plays an important role in the carbon cycle of the ecosystems of the Northern Alps (Dirnböck et al. 2020). We also quantified litter depth, representing the integral over the ecosystem processes litterfall and decomposition, and playing an important role in the carbon and nutrient dynamics in our study system (Mayer et al. 2017). Furthermore, live tree carbon (LTC) was quantified, capturing potential net changes in tree growth and mortality on forest carbon storage (Remy et al. 2016, Reinmann and Hutyra 2017). Finally, the biodiversity response to edges was assessed for the richness and effective number of plant species (ENS, including both canopy trees and forest floor vegetation) as well as the number of red-listed plant species (Braithwaite and Mallik 2012, Harper et al. 2015, Esseen et al. 2016). These nine response variables are described in detail in Appendix S1.

Analyses

The distance to edge information for each plot, measured from the plot center to the edge, was aggregated to four classes, <10 m, 10–24 m, 25–49 m, and 50–1000 m. A total of 457 plots were in the vicinity of transient edges, while 204 plots were situated close to permanent edges. Plots with no visible edge (n = 615) served as reference for determining edge effects (Fig. 1, Appendix S1: Fig. S1 a–i).

We used multiple linear regression to control for confounding factors and test for edge effects individually for each response variable. Specifically, we used slope, aspect, and elevation as well as sand, silt, and clay content of the soil to control for differences in environmental conditions (Appendix S1: Table S1). We analyzed permanent and transient edges separately to test for differences in edge effects between these two edge categories. Due to the large amount of zero values, we first determined the presence/absence of deadwood and litter and subsequently modeled edge effects for plots with positive values only. In order to fulfill the regression assumptions, different transformations were applied (Appendix S1: Table S2). Multicollinearity was addressed by removing variables with a correlation larger than ±0.5 (Appendix S1: Fig. S3). Akaike information criterion (AIC) was used to determine the best model from all candidate models (determined by all possible combinations of explanatory variables) (MASS package [version 7.3-51.4; Venables and Ripley 2002] in R [R Core Team 2019]).

We used an ANOVA with post hoc test (car package [version 3.0-3, Fox and Weisberg 2019] in R [R Core Team 2019]) to determine whether response variables at different distances from the

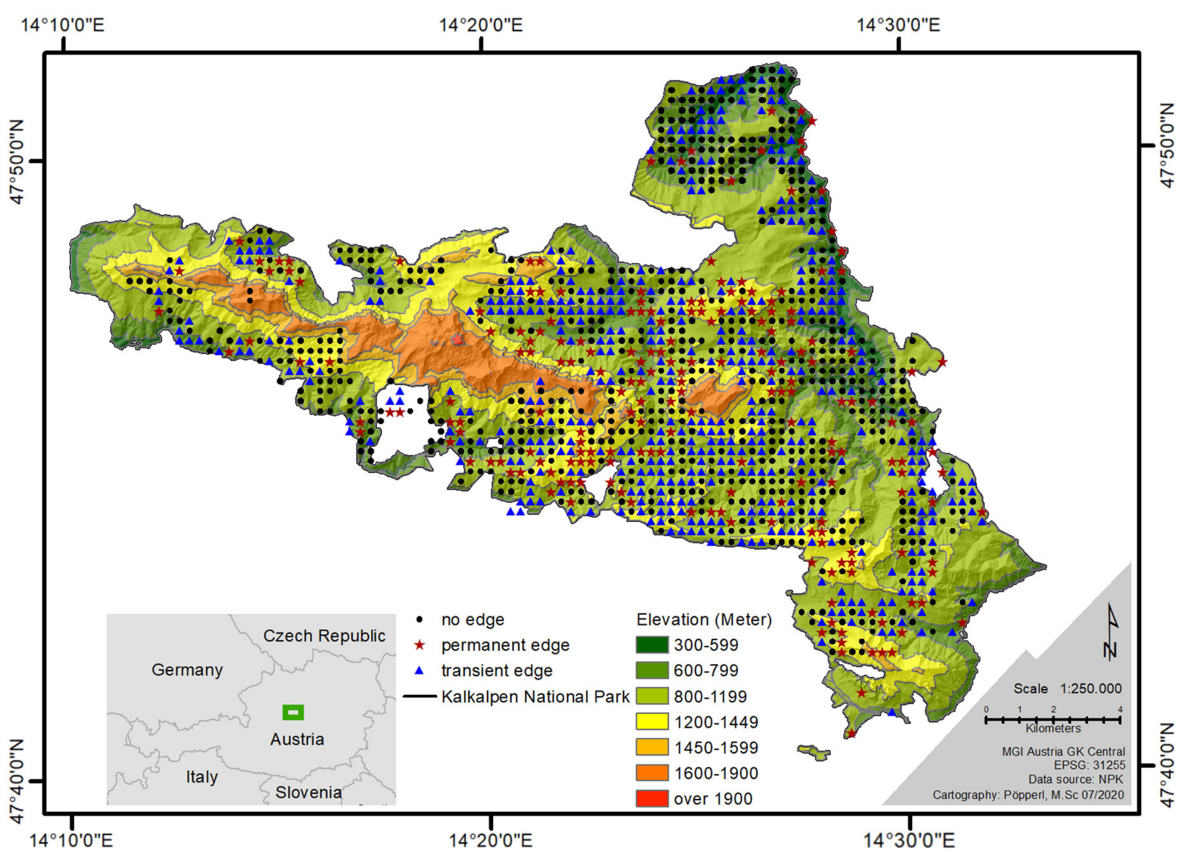

Fig. 1. Distribution of the study plots across Kalkalpen National Park. Plots are categorized as those in the vicinity of transient edges (blue triangles) and permanent edges (red stars); plots with no visible edge (forest interior) are indicated by black circles.

edge were significantly different from the reference class (no edge). The maximum distance of edge influence was determined as the last distance class with a statistically significant influence of the edge. The standardized relative effect size was calculated as the response variable at the edge (i.e., distance class <10 m) relative to the response variable in the forest interior (i.e., class no edge), with all auxiliary variables set to their landscape-level median values (using the predict function from the car package [version 3.0-3; Fox and Weisberg 2019] in R [R Core Team 2019]). A response is positive (i.e., higher values at the edge compared to a forest interior) if the relative effect size is greater than zero (Harper et al. 2015). All analyses were conducted at the landscape scale. To further elucidate potential variation of edge effects with forest type, we stratified our plots in conifer-dominated, broadleaf-dominated and mixed forests (Appendix S1: Fig. S4). We used a basal area cutoff of >67% to determine whether a plot was conifer-dominated (n = 471) or broadleaf-dominated (n = 468) (Appendix S1: Table S4). Plots on which neither conifers nor broadleaves dominated were classified as mixed forest plots (n = 255). Plots for which no basal area could be calculated because they were temporarily unstocked (n = 82) were excluded from the analysis.

Results

Tree basal area increased with distance to edge (Table 1), with lowest mean basal area at <10 m from an edge and highest mean basal area 50–1000 m from an edge. Likewise, the amount of deadwood increased with distance to edge, almost doubling over the four distance categories. Also, live tree carbon increased with distance to edge. In contrast, plant species richness and effective species number were highest at the edge and decreased distinctly with distance from edge. Species richness, for instance, decreased by 13 species on average from the edge to the forest interior, while the number of red-listed species decreased by six (Table 1).

Edge effect strength

We found strong effects of stand edges on forest structure, functioning, and diversity. With the exception of deadwood, forests at the edge (i.e., distance category <10 m) were significantly different ($P \leq 0.05$) from forest interiors with regard to all response variables when controlling for environmental covariates via regression (Fig. 2). Edge effects varied widely with indicators. The presence of edges reduced basal area, LTC, and litter depth, but increased the variation in DBH, ground vegetation cover, the ENS, species richness, and the number of red-listed species. The

Table 1. Forest structure, functioning, and biodiversity relative at stand edges at Kalkalpen National Park.

	Distance to edge									
	<10 m (n = 220)		10–24 m (n = 253)		25–49 m (n = 139)		50–1000 m (n = 49)		Forest interior (no edge) (n = 615)	
Indicator	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Structure										
Tree basal area (m² ha^{-1})	21.95	18.60	26.36	22.11	30.20	20.78	34.03	22.35	29.61	19.48
Deadwood (m³ ha^{-1})	14.01	32.61	16.92	37.67	23.67	34.32	30.04	46.74	16.69	30.91
DBH var. (%)	0.30	0.39	0.37	0.30	0.45	0.27	0.35	0.22	0.40	0.22
Functioning										
Live tree carbon (tons ha^{-1})	110.44	110.07	138.57	121.07	156.05	129.86	182.01	127.65	147.71	116.81
Litter depth (cm)	2.52	4.42	2.71	4.76	2.94	2.97	2.38	2.97	3.56	4.43
Ground veg. cover (%)	0.54	0.26	0.53	0.32	0.46	0.33	0.42	0.32	0.45	0.32
Biodiversity										
ENS (effective number)	49.80	18.40	45.24	16.62	40.61	16.56	39.04	20.05	39.24	15.99
Species richness (no. species)	54.11	20.17	47.51	17.46	42.98	17.10	41.20	21.70	41.45	16.62
Red-listed (no. species)	18.13	10.23	13.75	7.51	11.71	7.09	10.90	7.97	12.44	7.24

Note: SD = standard deviation. n = number of 314 m² plots per category.

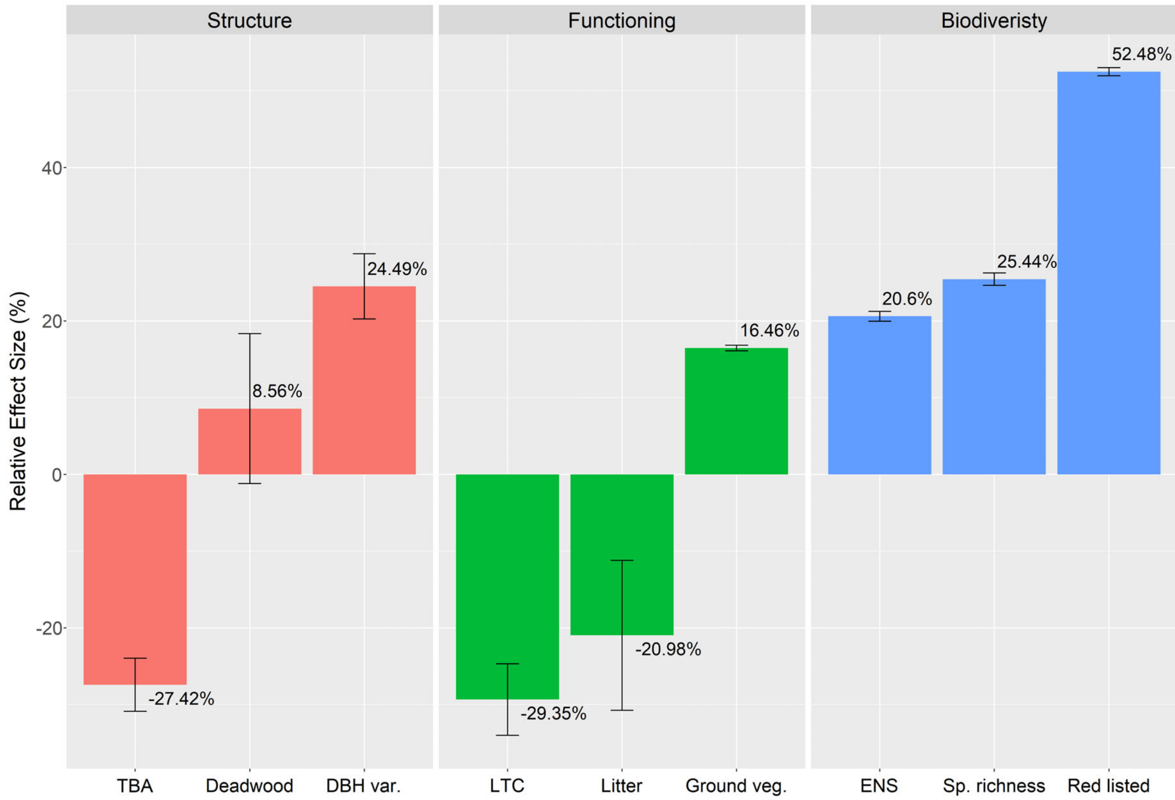

Fig. 2. Relative edge effects for variables of forest structure, functioning, and biodiversity. Relative effect size is expressed by relating the value at the edge to the corresponding value of the forest interior while controlling for variation in confounding environmental factors. Error bars show 95% confidence intervals. TBA = tree basal area, deadwood = amount of standing and downed deadwood, DBH var. = the variation in tree diameters at breast height, LTC = live tree carbon, litter = the thickness of the litter layer, ground veg. = the total cover of woody and non-woody plants, ENS = effective number of plant species, Sp.richness = plant species richness, red-listed = number of red-listed plant species.

highest positive influence was found for the number of red-listed species (+52.48%), while LTC responded most strongly negatively (−29.35%) (Fig. 2, Appendix S1: Table S3).

Edge effect depth

While edge effects were pronounced for the large majority of indicators, they generally did not extend far into the forest interior (Fig. 3). For the number red-listed species, basal area, and LTC, a significant influence could only be detected <10 m from the edge. Effects were significant for up to 24 m from the edge for species richness, ENS, ground vegetation cover, and litter depth. Only the variation in DBH was still significantly different from interior forest plots at a distance of up to 49 m from the edge.

Permanent vs. transient edges

Permanent edges had a stronger positive effect on biodiversity indicators than transient edges (Table 2, Appendix S1: Fig. S2c). The maximum distance from the edge that biodiversity benefited did, however, not differ between permanent and transient edges. In contrast, the effect of edges on litter depth, basal area, LTC, and variation in DBH was stronger at transient edges compared to permanent edges, and also, the maximum depth of the edge effect was higher at transient edges for three out of these four

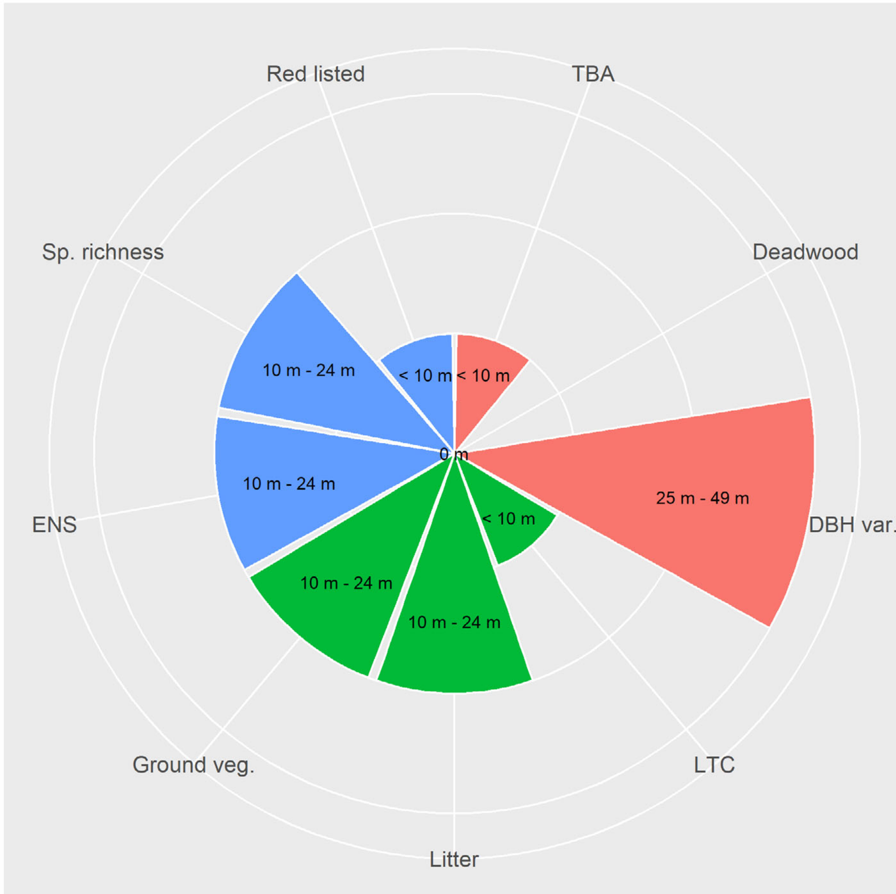

Fig. 3. Maximum distance of significant edge effects for variables of forest structure (red), functioning (green), and biodiversity (blue). TBA = tree basal area, deadwood = amount of standing and downed deadwood, DBH var. = the variation of diameter at breast height, LTC = live tree carbon, litter = the thickness of the litter layer, ground veg. = the total cover of woody and non-woody plants, ENS = effective number of plant species, Sp.richness = plant species richness, red-listed = number of red-listed plant species.

variables. The amount of deadwood did not differ significantly from interior forests at both transient and permanent edges.

Effect of forest type

Edge effect strength and penetration depth were largely consistent across forest types (Appendix S1: Table S5). However, the variation in DBH responded both stronger and penetrated deeper into forest interiors in broadleaved-dominated forests compared to conifer-dominated forests. Likewise, the litter layer was more sensitive to edges in broadleaved forests. In contrast, all indicators of plant species diversity responded more strongly to the presence of an edge in conifer-dominated forests. For species richness and the effective number of species, conifer-dominated forests had an effect size that was more than double that of broadleaved-dominated forests, yet the maximum penetration depth of a significant edge effect did not differ between forest types (Appendix S1: Table S5).

Discussion

Here we present, to our knowledge, the first assessment of permanent vs. transient edge effects across multiple indicators of temperate

Table 2. Difference in relative effect size and maximum depth of edge effects between permanent and transient edges (Appendix S1: Fig. S2 a–c).

Indicator	Permanent		Transient		Maximum depth of significant edge effect (m)	
	Relative effect size (%)	95% CI	Relative effect size (%)	95% CI	Permanent	Transient
Structure						
Tree basal area	−17.06	±8.4	−28.71	±4.63	<10	<10
Deadwood	−16.00	±34.99	+14.41	±16.28	ns	ns
DBH var.	+19.52	±12.87	+27.33	±4.28	<10	25–49
Functioning						
Live tree carbon	−13.03	±9.17	−34.32	±6.29	<10	<10
Litter depth	−7.42	±26.82	−24.84	±10.62	ns	10–24
Ground veg. cover	+20.14	±3.86	+11.92	±2.13	<10	10–24
Biodiversity						
ENS	+30.58	±3.88	+14.57	±1.51	10–24	10–24
Species richness	+34.93	±5.48	+18.00	±0.22	10–24	10–24
Red-listed	+82.68	±1.01	+43.88	±0.98	10–24	10–24

Notes: Relative effect sizes were derived from regression modeling and are calculated as the response variable at the edge relative to the response variable in the forest interior (i.e., no edge), controlling for variation in the environment by setting all auxiliary variables to their landscape-level median values, ns = not significant.

mountain forest ecosystems. We show that the presence of edges has a profound effect on forest ecosystems, altering their structure, functioning, and diversity. Our results highlight that edges affect biomass accumulation negatively. This suggests that the increased exposure to extremes at the edge (e.g., strong winds, drought, Buras et al. 2018) overcompensates the effect of elevated resource availability (e.g., light) for plant growth.

For litter depth, for instance, these findings are congruent with findings of increased decomposition and litter loss in disturbed ecosystems of the Northern Alps (Mayer et al. 2017). Also, reduced leaf area at the edge and the resultant lower litter input could contribute to lower litter layer depth. More broadly, our findings regarding biomass accumulation are in line with previous studies on edge effects in boreal and tropical ecosystems (Laurance 1997, Laurance et al. 1998*b*, Braithwaite and Mallik 2012, Harper et al. 2015). Other work, however, report positive effects of edges on biomass accumulation in temperate broadleaved forests (Reinmann and Hutyra 2017, Meeussen et al. 2021). Interestingly, in our analysis, both live tree carbon and the litter layer responded more strongly negatively in broadleaved forests compared to coniferous forests (Appendix S1: Table S5). This highlights that further research on what tips the balance of the underlying processes at the edge is needed. Measuring the specific microclimatic conditions at the edge (e.g., Thom et al. 2020, Zellweger et al. 2020) could, for instance, provide an important means toward understanding the processes driving the patterns identified here.

In contrast to biomass accumulation, we found positive effects on indicators quantifying the diversity and complexity of forest vegetation, that is, all assessed biodiversity indicators as well as variation in DBH and ground vegetation cover responded positively to the presence of an edge. This finding is in line with studies on edge effects in boreal and tropical forests (Nascimento and Laurance 2004, Braithwaite and Mallik 2012, Harper et al. 2015). Furthermore, it is congruent with findings that disturbance generally increase diversity in temperate forest ecosystems (Thom et al. 2017*b*, Hilmers et al. 2018). Overall, we found support for our hypothesis that biodiversity responds more strongly to the presence of edges than forest structure and functioning (Fig. 2).

The maximum distance of a significant edge effect was limited and generally remained below 25 m (i.e., approximately the average tree height in our study system). These maximum distances are considerably lower than those reported in previous studies, for example, for tropical forests, where the edge influence extends up to 335 m into adjacent forests (Laurance et al. 1998*a*). While studies on boreal and temperate forests generally report lower values more in line with our findings (e.g., Reinmann and Hutyra 2017), they still document a maximum influence of edges of up to 137 m (Chen et al. 1992, Harper et al. 2015). However, Chen et al. (1992) studied temperate rainforest with dominant tree heights of 50–60 m, which is more than twice the average tree height in our study system. The lower effect depth in our study is thus in line with the notion that the distance over which an edge exerts an influence depends on forest type (Chen et al. 1992).

Another possible factor limiting the influence of edges in our study system compared to others is the high topographic complexity (Senf and Seidl 2018), which strongly mediates the influence of abiotic drivers such as wind and radiation. Future work could thus focus on comparing edge effects between systems of different topography in order to determine how the topographic template of a landscape modulates the influence of edges. Furthermore, while we here focus on unmanaged forests developing naturally, edge effects could differ in managed forests, for example, because of a faster closure of gaps due to tree planting (Senf et al. 2019). Overall, our results show that the maximum distance of edge effects is also dependent on the indicator considered, which underlines that the area influenced by edges is context-dependent and no unifying value exists for a given ecosystem (Matlack 1993).

We here found clear differences in the effects of permanent and transient edges. The amplified edge effects for indicators of biomass accumulation suggest that adaptation of trees to the altered conditions at the edge (e.g., changed carbohydrate allocation, changed crown architecture) has not yet fully set in at transient edges. This also suggests that trees have a substantial potential to adapt to conditions at the edge and can compensate potential negative effects if these conditions persist for a longer time period. In contrast, edge effects were lower at transient edges compared to permanent edges for ground vegetation cover and all biodiversity indicators (Table 2, Appendix S1: Fig. S2 a-c). This can be explained by the fact that the species considered here (vascular plants, lichens, mosses) need time to adjust to the conditions at the edge and are only gradually able to exploit the new niches created by edges. Our second hypothesis of stronger effects of permanent edges can thus not be confirmed unequivocally.

A number of methodological limitations need to be considered when interpreting our results. Despite the fact that we here analyzed a large number of systematically sampled plots (n = 1276), we were not able to determine significant effects for highly stochastic variables such as the amount of deadwood. A further limitation of our analysis is that the presence of edges was assessed visually in the field. This could result in a decreasing probability of identifying an edge with increasing distance to edge, due to the influence of vegetation and topography on visibility. However, since a visual detection of edges in the field works with high fidelity in a ~100 m radius around a plot, and given that edge effects were constrained to the first 50 m from the edge in our analysis, we are confident that the visual detection of edges did not bias our findings. Furthermore, only the presence of an edge was recorded, but neither the magnitude of an edge (Harper et al. 2005) nor the cause of the edge or the adjacent land cover type was recorded. Land use is one of the main drivers creating forest edges (Esseen et al. 2016, Reinmann and Hutyra 2017), yet how the process creating an edge influences its effect could not be investigated based on our data. Our results thus need to be interpreted in the context of the main drivers of edge creation in our study system, that is, natural disturbances such as windthrow, bark beetle outbreaks, and avalanches as the main causes of transient edges, and permanent edges to other land cover types such as rock and scree as well as alpine flora. Future work should aim to elucidate how edge characteristics and causal agents of edge creation modulate edge effects. While we here strove to quantify edge effects comprehensively across different dimensions of forest ecosystems using multiple indicators, edge effects likely extend beyond the nine focal indicators of our current study. Other relevant indicators would, for instance, be canopy cover or the effect on species at higher trophic levels (Harper et al. 2005, Braithwaite and Mallik 2012, Harper et al. 2015, Hilmers et al. 2018).

We conclude that edge effects need broader consideration in the assessment of temperate forest dynamics. Current model-based assessments of future forest trajectories are, for instance, widely neglecting the effects of edges on forest carbon storage and biodiversity (Elkin et al. 2013, Thom et al. 2017*a*,*b*). However, edges are likely to become more prevalent in the future due to ongoing changes in land-use and natural disturbance regimes (Sala et al. 2000, Seidl et al. 2017, McDowell et al. 2020). Our analysis suggests that neglecting edge effects will likely lead to biased assessments of future forest trajectories, overestimating forest C storage potential and underestimating plant species diversity. Edge effects should therefore be considered explicitly in the management of forest landscapes. Furthermore, our findings underscore that transient edges have effects that differ distinctly from permanent edges, highlighting the need for a more nuanced quantification of the spatio-temporal dynamics at forest edges. We conclude that stand edges are an important part of forest landscape structure and have a distinct influence on the structure, functioning, and diversity of forest ecosystems.

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Data Availability

Data are not publicly available due to sensitive species data. Data can be obtained from Nationalpark Oö Kalkalpen Ges.m.b.H. Nationalpark Alle 1, 4591 Molln Austria. Homepage: https://www.kalkalpen.at/. The name of the dataset: Naturrauminventur Nationalpark Kalkalpen.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3692/full