

ARTICLE

Forest edge effects on moss growth are amplified by drought

Irena Adia Koelemeijer^{1,2}  | Johan Ehrlén^{1,2} | Pieter De Frenne³ |
Mari Jönsson⁴ | Peter Berg⁵ | Kristoffer Hylander^{1,2} 

¹Department of Ecology, Environment and Plant Sciences, Stockholm University, SE-106 91 Stockholm, Sweden

²Bolin Centre for Climate Research, Stockholm University, SE-106 91 Stockholm, Sweden

³Forest & Nature Lab, Department of Environment, Faculty of Bioscience Engineering, Ghent University, Geraardsbergsesteenweg 267, 9090 Melle, Belgium

⁴Swedish Species Information Centre, Swedish University of Agricultural Sciences, SE-750 07 Uppsala, Sweden

⁵SMHI (Swedish Meteorological and Hydrological Institute), S-601 76 Norrköping, Sweden

Correspondence

Irena Adia Koelemeijer
Email: irena.koelemeijer@su.se

Funding information

H2020 European Research Council, Grant/Award Number: FORMICA 757833; Svenska Forskningsrådet Formas, Grant/Award Numbers: 2016-00461, 2018-02829

Handling Editor: Martin Dovciak

Abstract

Forest fragmentation increases the amount of edges in the landscape. Differences in wind, radiation, and vegetation structure create edge-to-interior gradients in forest microclimate, and these gradients are likely to be more pronounced during droughts and heatwaves. Although the effects of climate extremes on edge influences have potentially strong and long-lasting impacts on forest understory biodiversity, they are not well understood and are not often considered in management and landscape planning. Here we used a novel method of retrospectively quantifying growth to assess biologically relevant edge influences likely caused by microclimate using *Hylocomium splendens*, a moss with annual segments. We examined how spatio-temporal variation in drought across 3 years and 46 sites in central Sweden, affected the depth and magnitude of edge influences. We also investigated whether edge effects during drought were influenced by differences in forest structure. Edge effects were almost twice as strong in the drought year compared to the non-drought years, but we did not find clear evidence that they penetrated deeper into the forest in the drought year. Edge influences were also greater in areas that had fewer days with rain during the drought year. Higher levels of forest canopy cover and tree height buffered the magnitude of edge influence in times of drought. Our results demonstrate that edge effects are amplified by drought, suggesting that fragmentation effects are aggravated when droughts become more frequent and severe. Our results suggest that dense edges and buffer zones with high canopy cover can be important ways to mitigate negative drought impacts in forest edges.

KEYWORDS

biodiversity, bryophytes, climate, edge influence, forestry, fragmentation, microclimate

INTRODUCTION

Most of the earth's terrestrial biodiversity occurs in forests and this biodiversity is currently under threat

from both climate change and intensified land-use. Not only does land-use directly degrade forest habitats, it can also significantly change the vulnerability of remaining forest patches to climatic extremes, not least at

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2023 The Authors. *Ecological Applications* published by Wiley Periodicals LLC on behalf of The Ecological Society of America.

the edges (Chen et al., 1995; Schmidt et al., 2017). Clear-cut forestry, agriculture and urbanization have drastically increased the amount of forest edges, and currently more than one-fifth of forests and associated biodiversity resides within 100 m from edges (Haddad et al., 2015). Still, little is known about how increased climate variation and climate extremes, such as droughts, influences biodiversity at forest edges.

Edge habitats have biotic and abiotic conditions that differ from the forest interior and the surrounding matrix, and these differences have important consequences for biodiversity (Murcia, 1995; Schmidt et al., 2017). Solar radiation and wind penetrating at the edge result in harsh microclimates in terms of high air and soil temperatures and low humidity (Chen et al., 1995; Schmidt et al., 2017). Edge-to-interior gradients are commonly referred to as edge effects or edge influences, and can extend deep into forests (Aune et al., 2005; Hylander, 2005). Proximity to edges can therefore negatively affect the growth and survival of forest interior species that require humid and stable conditions (bryophytes: Moen & Jonsson, 2003; liverworts and lichens: Boudreault et al., 2008; Stewart & Mallik, 2006; soil fungi: Crockatt, 2012; invertebrates: Dambros et al., 2013).

Extreme droughts and heatwaves are likely to exacerbate microclimatic gradients at forest edges, as a result of increased solar radiation, higher temperatures, and desiccating winds during these events. As a result, the already existing adverse edge effects on sensitive forest understory species could be amplified, which might have long-lasting effects on biodiversity. Theoretically, both the strength and the depth of edge effects could increase. Temporal variability in microclimatic gradients at forest edges has seldom been studied in the context of climatic extremes. This is problematic since climatic extremes such as droughts and heatwaves are becoming more frequent and intense (IPCC, 2021). From a management perspective, it is important to identify means to mitigate such aggravating effects under climate change. For example, it has been shown that canopy structure can modify the amount of penetrating solar radiation and wind at edges (De Frenne et al., 2021).

Extreme climatic events are rare and unpredictable (IPCC, 2021). It is therefore difficult to study their effects on organisms and biodiversity, since pre-event data are difficult to obtain. Several methods have been used to retrospectively assess the effects of past climatic conditions. Dendroclimatology uses the width of tree rings to assess impacts of past climate and droughts on tree growth (Buras et al., 2018; Tene et al., 2011), and remote sensing techniques can be used to assess effects of past drought on vegetation browning and productivity (Buras et al., 2020). In forest understories, the growth of bryophytes can be a good indicator of variation in microclimate, since their

metabolic activity is directly related to ambient moisture levels and thus reflect local humidity and vapor pressure deficit levels, but also temperatures and soil moisture (Caners et al., 2010; Green & Lange, 1995; Hylander, 2005; Man et al., 2022).

Here we applied a novel method based on annual growth increments in the moss *Hylocomium splendens* to assess how extreme drought impacts microclimate gradients at forest edges. This species produces a distinct segment each growing season (Tamm, 1953), making it possible to assess previous years' growth. *H. splendens* is also known to be negatively affected at forest edges (Hylander, 2005), and annual moss growth can be considered a biologically meaningful indicator of the understory microclimate. We used this method to examine how spatio-temporal variation in drought intensity influenced the yearly growth of *H. splendens* along forest edge-interior transects. The summer of 2018 in Sweden was characterized by an extreme drought with significant positive temperature anomalies (Buras et al., 2020; Peters et al., 2020; Schuldts et al., 2020). Yet, drought intensity was spatially variable due to local showers in some areas (Koelemeijer et al., 2022; SMHI, 2019). We were able to pick up fine-scale spatial and temporal variation using a novel high-resolution precipitation dataset (Berg et al., 2016; van de Beek et al., n.d.). We selected 46 south-facing forest edges distributed over a spatial drought gradient in central Sweden, and at each site quantified moss growth for the drought year 2018, as well as for the two non-drought years 2016 and 2017 along forest edge-to-interior transects. This allowed us to retrospectively infer drought effects in the understory at forest edges. We quantified moss-growth edge influences in terms of magnitude (MEI, i.e., the difference in microclimate between the edge and the interior) and depth (DEI, i.e., the distance microclimatic edge effects penetrate into the interior) (e.g., Harper et al., 2015; Meeussen et al., 2021), and also assessed to what extent canopy cover and tree height buffered edge influences. We hypothesize that both the magnitude and depth of edge influence would be reinforced (i.e., greater) during the drought year compared with the non-drought years, but that vegetation structure could buffer these effects. Furthermore, we hypothesized that edge influences would be greater in sites that experienced more intense drought in 2018.

METHODS

Study system

We conducted the study in a boreal landscape in central Sweden (13.5–17.2° longitude and 60.2–62.5° latitude, Figure 1a). Central Sweden has a long history of intensive

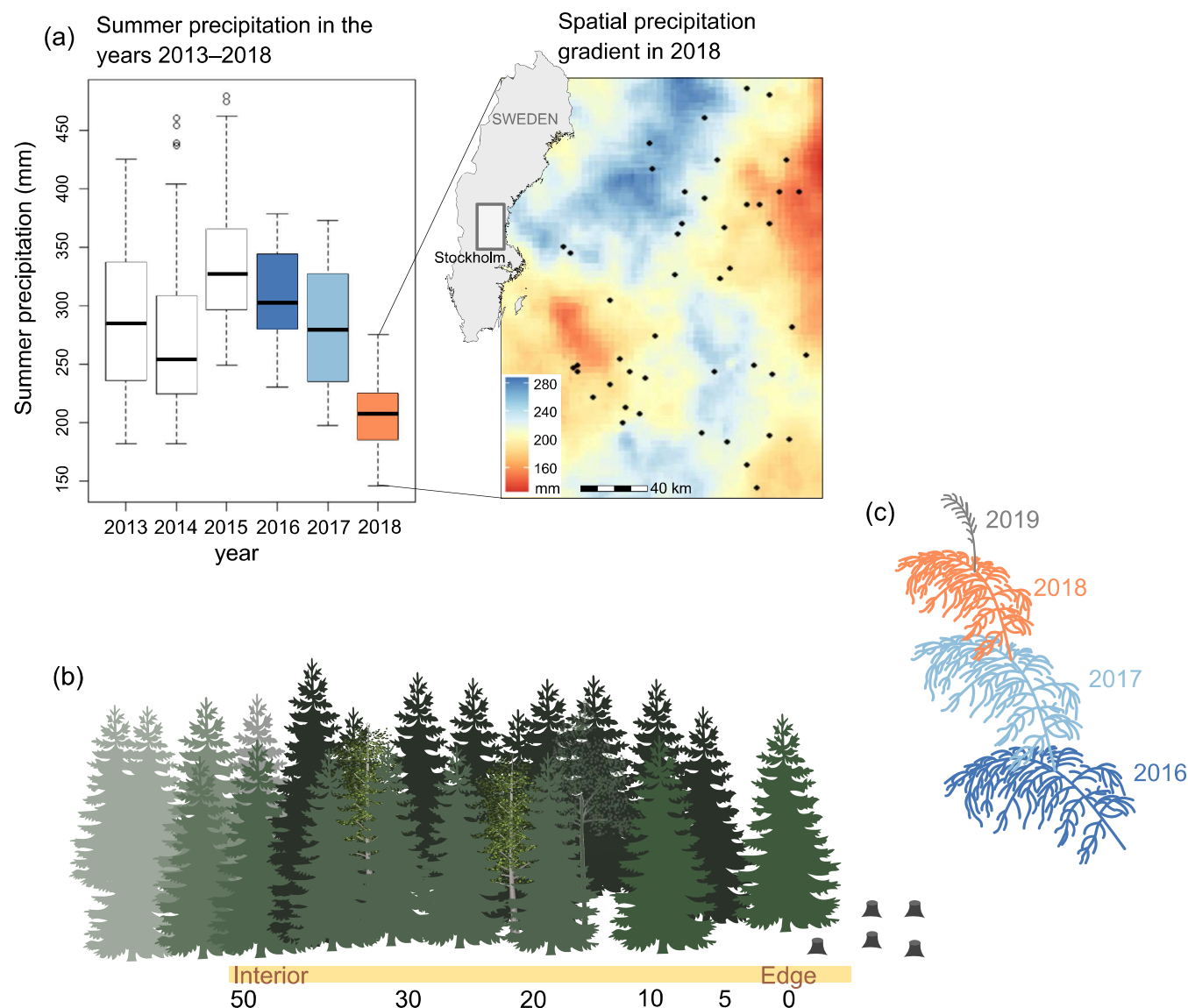


FIGURE 1 Study design and variation in precipitation. (a) Summer precipitation 2013–2018 for the 46 study sites (left), a map of Sweden showing our study area (center), and spatial variation in precipitation during 2018 with the 46 study sites marked by black dots (right). (b) A schematic forest edge, showing the inter-plot distances where we collected replicated moss samples. (c) A shoot of *Hylocomium splendens*, showing its growth pattern with yearly segments at the time of collection.

forestry (Lundmark et al., 2013), with forest stands dominated by *Picea abies* (L.) H. Karst., *Pinus sylvestris* L., and to a lesser extent *Betula* spp L. (the taxonomy follows Dyntaxa.se). The landscape is characterized by a mosaic of forest stands of different ages, clear-cuts, and some agricultural fields. The older forest patches of conservation concern are often isolated in a matrix of younger managed forest (Aune et al., 2005; Johansson & Gustafsson, 2001).

The area has a cold temperate climate with a mean annual temperature of 3°C, and a distinct seasonality with warm summers (mean temperature of June–August is 15°C) and cold winters with snowfall (mean temperature of December–February is –6°C) (SMHI, 2021).

In most years, precipitation falls mainly during the summer. However, in 2018, there was a severe summer drought (Buras et al., 2020; Peters et al., 2020; Schuldt et al., 2020) combined with positive temperature anomalies of +2–3°C (SMHI, 2019). Yet, precipitation during this summer was variable across the landscape (SMHI, 2019). For our study, we selected 46 forest edge sites distributed over a precipitation gradient, ranging from 145 to 276 mm (Figure 1a). This range corresponded to anomalies in precipitation between –47% and –82% compared to the average 2010–2017. The shortest distance from a study site to any other site ranged from 1.4 to 36 km (mean 14 km) (Figure 1a).

The moss *Hylocomium splendens* (Hedw.) Schimp. (family Hylocomiaceae) is a common pleurocarp moss in boreal forests. It is frequently the main ground covering species in spruce forests in Sweden, where it forms carpets on soils, litter, logs, and rocks (Hylander, 2005). *H. splendens* has key ecosystem functions in the boreal understory, by hosting nitrogen (N_2)-fixing microbial communities, as thermal insulators of the soil, and as primary producers and litter production (Lindo et al., 2013). It produces a distinct segment each year, enabling quantification of yearly growth 3–4 years back in time. Growth of new segments occurs mainly from May through September, and is minimal during winter months (Busby et al., 1978). Segments elongate slightly (~3% unpublished dataset) during the summer the next year, but mainly side branches have been recorded to grow (Busby et al., 1978; Tamm, 1953). Like all bryophytes, *H. splendens* lacks a vascular system and metabolic activity is directly related to ambient water and humidity levels. During desiccation, growth rates are reduced or halted, and growth thus reflects local climatic conditions (Busby et al., 1978; Green & Lange, 1995). Bryophytes have previously been shown to be useful indicators of variation in microclimate conditions (Caners et al., 2010; Dynesius et al., 2008; Hylander, 2005; Man et al., 2022), but they have rarely been used to retrospectively quantify growth in different years and across environmental gradients (but see Thieme et al., 2018).

Study design and data collection

The canopy in the 46 forest edges of south-facing orientation selected for the study, was dominated by *P. abies*. The understory vegetation consisted of dwarf shrubs (primarily *Vaccinium myrtillus* L. and *Vaccinium vitis-idaea* L.) and mosses (mainly *H. splendens*, but also *Pleurozium schreberi* (Brid.) Mitt. and *Ptilium crista-castrensis* (Hedw.) De Not.). Forest edges were adjacent to recent clear-cuts (up to approximately 3 years old) ($n = 28$), clear-cuts with young regenerating forest (<2 m height) ($n = 11$), or agricultural fields ($n = 7$). We did not include edges created by linear corridors, such as roads and powerlines, nor natural forest edges generated by lakes, streams, or wetlands. The forest patches differed in structure, which possibly could influence the strength of edge effects. To get a comparable measure of canopy cover and tree height at the site level, we measured these variables at five locations approximately 10 m apart along a transect parallel to the edge but located 50 m from the edge in the forest interior (Figure 1b). At each of these locations, we took hemispherical photos, from which we calculated canopy cover using the software ImageJ v. 1.53A with the plug-in *Hemispherical* 2.0.

Canopy cover levels of our sites ranged from 61% to 90% (mean 79%). Tree height was measured with a clinometer and measure-tape, and ranged from 15 to 33 m (mean 22 m) in our sites.

We collected *H. splendens* samples from June 24th to August 2nd 2019. Samples were collected along transects, at 0, 5, 10, 20, 30, and 50 m from the forest edges into the forest interiors, with 0 m located at the first tree trunks of the forest patch (Figure 1b). The locations at 50 m from the forest edge was considered as forest interior based on previous studies in similar systems (Harper et al., 2015; Hylander, 2005). Three moss samples (each with a minimum of seven shoots), approximately 1–3 m apart depending on the local terrain and vegetation, were taken perpendicular to the transect at each distance. We only selected moss patches growing on soil and avoided patches under logs, right behind large trees, or on top of rocks, which are known to have different microclimates (e.g., Hylander, 2005; Schmalholz & Hylander, 2011). Samples were air-dried after collection and rehydrated before measuring.

We retrospectively quantified yearly growth of seven randomly picked *H. splendens* shoots from each sample (Figure 1c), resulting in 21 shoots at each distance along the transect. We measured the segment length for 2016, 2017 and 2018, resulting in a total of 17,293 measurements. We measured the yearly segment length between the base of the segment to the apical tip using a ruler to the nearest 1 mm (Appendix S1: Figure S1a). Since some segments were broken and degraded, we also measured the length from the start of the segment to the start of the new years' segment (Appendix S1: Figure S1b). Based on the relationship between these two measures on each segment, we imputed values of the length for the segments that were broken (Appendix S1: Section S1).

H. splendens quite frequently produces multiple segments in 1 year. We tested and confirmed that branching was not influenced by distance from the forest edge (Appendix S1: Section S2), suggesting that including shoots with multiple segments did not influence our inferences regarding edge influences. When multiple segments were produced in 1 year ($n = 3023$), we recorded the total number of segments produced in each year and measured one of the segments per year per shoot, since shoots were mostly very similar in length, and used this in further analyses.

Spatial variation in drought intensity

We determined drought intensity across the study area based on a novel high temporal–spatial resolution dataset called HIPRAD (High-resolution Precipitation from

gauge-adjusted weather RADar, Berg et al., 2016; van de Beek et al., n.d., Figure 1b). HIPRAD is a high spatio-temporal resolution weather radar dataset (15 min; 2 km), in which non-precipitation echoes are systematically filtered out, and the data are homogenized to a gridded station-based dataset. We calculated two drought indices: First, we summed the total precipitation during the period 1 May–31 August 2018. Second, we counted the number of days with rain, assuming that the number of days when a moss is hydrated may be more important for growth than the total rainfall. We included only days with rainfall of more than 3 mm, to prevent interference of possible non-precipitation echoes left in the data despite automatic methods to remove such noise.

Statistical analyses

All statistical analyses were conducted in R version 1.2.5019 (R Core Team, 2021).

Between-year variation in drought intensity

To test whether edge effects were greater in the drought year than in the two non-drought years, we modeled moss growth as a function of distance from the forest edge in interaction with year. We used a linear mixed effect model using the *lme4* package (Bates et al., 2015) and included site, sample and individual shoot as nested random effects. We log-transformed the distance from the forest edge (e.g., Govaert et al., 2020; Meeussen et al., 2021), after adding an increment of 2.5 to be able to handle zeros in the log-transformation. We performed a post hoc test with a Tukey correction to compare slopes between years, using the *lstrends* function from the *lsmeans* package. The relationship between moss growth and distance to the forest edge is both driven by the magnitude and the depth of edge influences. To further explore which aspect of edge influences that changed during drought, we conducted separate analyses to quantify magnitude and the depth.

To test if the magnitude of edge influence was enhanced in the drought year, we calculated the relative reduction in growth at the forest edge compared to in the forest interior in all sites for the 3 years using the following formula: $\text{strength} = (i - e)/(i + e)$, where i is mean growth in the forest interior (50 m) and e is mean growth at the edge (0 m) (Harper & Macdonald, 2011). *H. splendens* was absent at 0 m in three sites. For these sites, we imputed growth at the forest edge based on moss growth at 5 m from the forest edge (Appendix S1: Section S3). We then modeled magnitude of edge influence as a function of year

and included site as a random effect. To test whether canopy structure could buffer the magnitude of edge effects during drought, we included canopy cover and tree height of the forest-patch interior in the models in interaction with year. We only tested buffering effects for the magnitude of edge influences and not for models on moss growth in order to avoid models including three-way interactions. We conducted post hoc tests with a Tukey correction to compare the magnitude of edge influence and slopes from the significant interaction terms, between years, using the *multcomp* and *lsmeans* packages, respectively. We assumed a Gaussian distribution after checking the residuals. Since we modeled only the mean magnitude value for each site, we included 1/SE as weights in the model to account for differences in standard errors of estimates, with SE being the standard error around the mean growth at the edge and in the forest interior combined.

To test if the depth of edge influence was greater in the drought year, we used three different approaches out of the many different methods that have been proposed to calculate this property of edge influence (e.g., Chen et al., 1995; Harper & Macdonald, 2011; Hylander, 2005; Meeussen et al., 2021; Pohlman et al., 2009; Toms & Lesperance, 2003). First, we determined the furthest distance from the edge that was different from the interior, by contrasting the distances 0–30 to 50 m using the *emmeans* package. We did this separately for each year and included site and sample as random effects. The downside is that estimates will not be precise, since it is restricted to the distances measured in the field and is based on statistical difference rather than effect size. Second, we estimated the breaking point in a piece-wise linear regression using the package *Segmented* (Muggeo, 2017) for the 3 years separately. Third, we fitted a Michealis-Menten curve to the data for the different years and estimated where two-thirds of the asymptote was reached in each year. For this, we used the *nlme* package for non-linear mixed effect models (Pinheiro et al., 2022) with growth as a function of $d + (a \times \text{Distance})/(b + \text{Distance})$. We estimated the parameters a , b , and d for the different years, and let d change with site, sample, and shoot (in other words, this was a nested random intercept).

Among-site variation in drought intensity

To test whether edge effects were related to differences in drought intensity among sites in 2018, we modeled moss growth in 2018 as a function of distance from the forest edge (log-transformed) in interaction with either summer precipitation or the number of days with rainfall. To test if canopy cover and tree height modified edge effects in 2018, we included their interactions with distance from the forest edge in the models. We conducted a linear

mixed effect model and included site and sample as nested random effects. We added segment length of the previous years (mean of 2016 and 2017) as a covariate in order to account for differences in factors influencing growth among and within sites not included in the model.

To test whether the magnitude of edge influence was reinforced in sites that experienced more intense drought, we modeled the magnitude of edge influence values (calculated as described in section *Between-year variation in drought intensity*) in 2018 as a function of the total precipitation in one model, and the number of days with rainfall in another. To test if canopy structure buffered the magnitude of edge effects during drought, we included canopy cover and tree height in the models in interaction with the precipitation measures. We included $1/(\text{SE of the interior and edge moss growth values})$ as weights.

For all models, we standardized continuous explanatory variables (total precipitation, number of days with rainfall, canopy cover, and tree height). This was done, for each observed value, by subtracting the mean and by dividing by the standard deviation, using the `scale()` function. A correlation matrix between the explanatory variables can be found in Appendix S1: Table S1. We checked model assumptions using the *Performance* and the *DHARMA* package (Hartig, 2020; Lüdtke et al., 2021). We obtained adjusted R^2 values for the linear models from the summary output, and for the linear mixed effect models using the *MuMIN* package (Barton, 2009). We present the conditional and marginal R^2 values for the mixed effect models.

RESULTS

Between-year variation in drought intensity

We found negative edge effects, in terms of reduced moss growth toward the forest edge, in all years (Appendix S1: Table S2, Figure 2a). Moss growth in the drought year 2018 was lower at all distances from the edge compared to the two non-drought years (2016 and 2017), but the reduction in moss growth in 2018 compared with the two other years and was larger toward the forest edge than in the forest interior (Appendix S1: Table S2, Figure 2a). A post hoc test confirmed that edge-to-interior gradients in moss growth were steeper in 2018 than in the other 2 years ($p < 0.001$).

The magnitude of edge influence was greater in 2018 compared to the pre-drought years (Appendix S1: Table S3, Figure 2b left). Forest interior canopy cover

interacted with the magnitude of edge influence in 2018. In sites with relatively open canopy, the edge influence in 2018 was more than twice that in the non-drought years, whereas in sites with denser canopy cover the difference was minimal (Appendix S1: Table S3, Figure 2b right).

Estimates of the depth of edge influence ranged between 17 and 34 m. We found no consistent effect of the drought year on the depth of edge influence and the different approaches used suggested different rankings of the three different years (Figure 2c).

Among-site variation in drought intensity

Total rainfall during the summer 2018 ranged from 142 to 272 mm (mean = 201 mm) across sites and the number of days with rain more than 3 mm ranged from 12 to 27 (mean = 19). We did not find a significant main effect of drought intensity on moss growth among the sites in the drought year. However, there was an effect of the interaction between number of days with rain (but not total precipitation) and distance to the forest edge on moss growth, with stronger effects of edges at sites with high drought intensities (Appendix S1: Table S5, Figure 3a). In both models, we found negative interactive effects of distance to the forest edge and canopy structure on moss growth in 2018, indicating that dense canopy cover and high trees buffered edge effects on moss growth during the drought year (Appendix S1: Tables S4 and S5, Figure 3b,c).

We detected no effects of spatial variation in drought intensity variables on magnitude of edge influence, but the magnitude of edge effects in 2018 was reduced by tree height (Appendix S1: Tables S6 and S7).

DISCUSSION

We successfully applied a novel method that utilized the annual growth pattern of the understory moss *H. splendens* to investigate how an extreme drought affected microclimatic edge influences. We showed that edge influences were much stronger during a drought year compared to two non-drought years, while evidence of whether the effect penetrated deeper into the forest was conflicting. Similarly, across a spatial drought intensity gradient, edge effects were stronger in places that had fewer days with rainfall. Finally, we show that microclimatic edge effects during the drought year were less pronounced in forest patches with denser canopies.

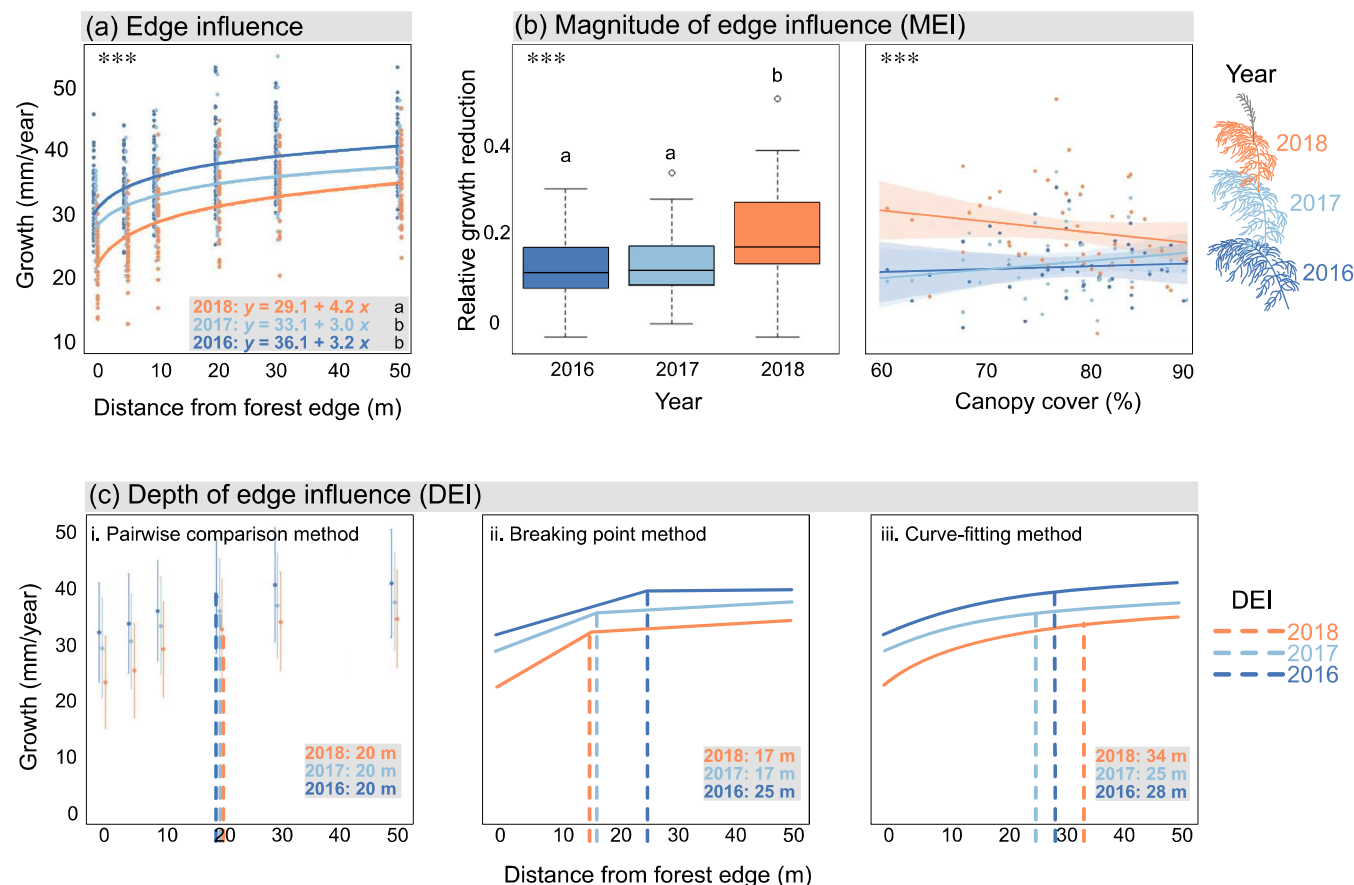


FIGURE 2 Edge influence on moss growth in the three different years. (a) Showing the predicted relationships between growth and distance from the forest edge from our models and the raw datapoints (the mean growth for each site at each measured distance). Significance is indicated top left in the plot as $***p < 0.001$. See Appendix S1: Table S2 for further statistical inference. (b) The magnitude of the edge influence (MEI) in (left) different years and (right) related to forest canopy cover. MEI was calculated as the relative growth reduction at the forest edge (0 m) compared to the forest interior (50 m). Significance is indicated top left, and further statistical inference, such as slope estimates, can be found in Appendix S1: Table S3. (c) Estimates of the depth of edge influence (DEI) for the different years using the different methods: (left) the pairwise comparison, (middle) the breaking point in a piece-wise regression, (right) the curve fitting method where DEI is estimated as 2/3th of the asymptote. The dashed vertical lines indicate the estimated depth and the exact estimates are shown in the gray boxes. $N = 46$.

Between-year variation in drought intensity

Our results show that extreme climatic events can reinforce edge effects in the forest understory. Sunny, warm, and windy days have previously been shown to increase the magnitude of microclimatic edge effects (e.g., Chen et al., 1995; Gignac & Dale, 2005; Schmidt et al., 2017), as have air humidity (e.g., dry season vs. wet season, Pohlman et al., 2009), and the contrast between open habitat and the forest edge (the offset) is larger when temperatures are higher (Meeussen et al., 2021). However, between-year variability in edge effects and the impact of extreme events remains unknown. The edge gradients in moss growth, assumed to reflect microclimate gradients, in our study were steeper in the drought

year compared to the regular years, and the magnitude of edge influence was almost twice as large. This is likely due to the enhanced cumulative solar radiation, warmer temperatures, and desiccating winds penetrating at forest edges during episodes with unusually dry and sunny conditions (Chen et al., 1995; Gignac & Dale, 2005; Schmidt et al., 2017). The reinforcing effect of the drought year on the magnitude of edge effects was particularly profound in forests with low canopy cover, and less so in forests with denser canopies. The reason behind that pattern is likely to be that higher canopy cover buffers effects of drought due to shielding of incoming solar radiation (De Frenne et al., 2021). Unfortunately, we did not have estimates of how canopy cover changed from edge to interior in each site. Such data could have further helped in explaining variation in edge-effects between sites, and

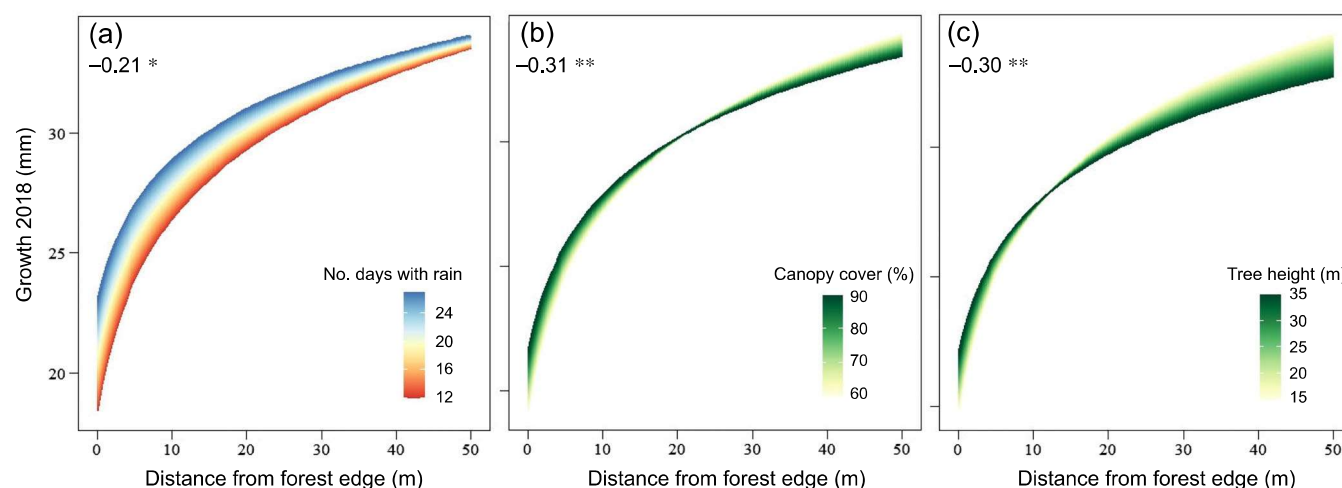


FIGURE 3 Interactive effects of distance from the forest edge and drought intensity, as well as canopy structure, on annual moss growth during the drought year 2018. (a) The interaction with the number of days with rain in 2018. (b) The interaction with canopy cover. (c) The interaction with tree height. Estimates for the interaction terms are shown top left in each plot and significance is indicated as ** $p < 0.01$, * $p < 0.05$. For further statistical inference, see Appendix S1: Table S5. $N = 46$.

the lack of these data may have caused some noise and unexplained variation in our models.

In contrast to our hypothesis, we did not find any conclusive evidence that the depth of edge influences differed between drought and non-drought years, but results differed between the different methods used to calculate the depth of edge influence. Previous studies found deeper edge influences during sunny and dry conditions, and in the dry season compared to wet season (Chen et al., 1995; Pohlman et al., 2009). However, windspeeds were also significantly larger in those cases, making it hard to disentangle if it was drought or windspeed that drove these patterns, since wind is a large driver of depth of edge influences by affecting evapotranspiration and enhancing conductivity for heat and gasses (Chen et al., 1995; Cienciala et al., 2002; Davies-Colley et al., 2000; Schmidt et al., 2017). On the contrary, deeper edge influence in places with a cooler climate has also been reported (Meeussen et al., 2021). The fact that results differed depending on the method used, suggests that values of depth of edge influence should be interpreted with some care when studies base their estimate on only one method. The depth of edge influence is intrinsically difficult to measure, since by definition the difference between places influenced by the edge and the true interior, and thus statistical power to detect effects, become smaller and smaller when moving from the edge (using the pairwise comparisons and the breaking point method). Curve fitting methods handle this problem better, but depend instead on assumptions, as well as choices about which model to select and which proportion of the asymptote reached to be considered

interior conditions. An important aspect of depth of microclimatic edge influence in relation to biodiversity is that the sensitivity may differ between species, microclimate variable tested, and forest type (e.g., Boucher et al., 2011; Meeussen et al., 2021; Schmidt et al., 2017). Bearing these methodological problems in mind, all our values were between 17 and 34 m, which are commonly reported depths of edge influences in similar forests (Harper et al., 2015; Hylander, 2005).

Among-site variation in drought intensity

Spatial variation in drought intensity and canopy structure among sites, influenced the strength of edge effects. In sites that experienced more days with rain during the drought, edge effects were smaller, further supporting our conclusion that drought reinforces microclimatic edge effects. Sites with denser canopy cover and higher trees displayed weaker edge effects during the summer of 2018, again highlighting the role that canopy structure can play in buffering drought effects at forest edges. However, high canopy cover seemed to negatively affect moss growth in the interior. This needs further scrutiny, but might be due to light limitations in the most shaded places, and could suggest a potential trade-off between suitable microclimates during extreme events and optimal light conditions. The number of days with rain was more important for moss growth at the forest edge than the summed summer precipitation during the drought, presumably because it determines the number of days suitable for growth. We did see clear effects of summer

precipitation in combination with forest edge exposure in another study in the same landscape on the presence of rare and sensitive understory species (Koelemeijer et al., 2022). This highlights that it is difficult to find one drought index that similarly well explains biological responses of different species.

Implications for conservation and forest management

Climatic extremes are important drivers of biodiversity patterns, and are expected to become more frequent in the coming decades (Maxwell et al., 2019). The negative effects of an increased frequency of climatic extremes on biodiversity might be exacerbated by ongoing changes in land use. One example of such potentially important, but little studied, interactive effects, is climate driven temporal variation in edge influences. Edge effects are likely to become stronger with climate change. Thus, the results of our study suggest that reducing the amount of edge habitat should be an even more important goal in conservation planning when also adapting forest biodiversity conservation to climate change (see also Hylander et al., 2022). Taking actions to protect forest patches of high conservation concern from edge influences, for example by creating buffer zones around them, is already mentioned as example of important measures (Lundström et al., 2018). In light of our results, we further recommend forest managers and conservationists to increase the microclimate buffering efficiency of buffer zones by increasing their canopy cover, tree height, and using tree species with a high shade casting ability (Garrett et al., 2021).

ACKNOWLEDGMENTS

We thank Pauline Caillault, Jonathon Winnel, Bella Siemers, Daniela Trojmar, and William Ashworth for their help in measuring moss shoots. Thanks to two anonymous reviewers for their feedback which increased the quality of this work. This project was funded by Formas with Grant no. 2018-02829 to Kristoffer Hylander and Grant no. 2016-00461 to Mari Jönsson, and by the European Research Council (ERC) under the European Union's Horizon 2020 research and innovation programme with ERC Starting Grant FORMICA 757833 to Pieter De Frenne.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data and code (Koelemeijer et al., 2023) are available in Dryad at <https://doi.org/10.5061/dryad.1g1jwsv1t>.

ORCID

Irena Adia Koelemeijer  <https://orcid.org/0000-0003-4298-5066>

Kristoffer Hylander  <https://orcid.org/0000-0002-1215-2648>

REFERENCES

- Aune, K., B. G. Jonsson, and J. Moen. 2005. "Isolation and Edge Effects among Woodland Key Habitats in Sweden: Is Forest Policy Promoting Fragmentation?" *Biological Conservation* 124: 89–95. <https://doi.org/10.1016/j.biocon.2005.01.015>.
- Barton, K. 2009. "Mu-MIn: Multi-model Inference." R Package Version 0.12.2/r18. <http://R-Forge.R-project.org/projects/mumin/>.
- Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67: 1–48. <https://doi.org/10.18637/jss.v067.i01>.
- Berg, P., L. Norin, and J. Olsson. 2016. "Creation of a High Resolution Precipitation Data Set by Merging Gridded Gauge Data and Radar Observations for Sweden. J. Hydrol." *Flash floods, hydro-geomorphic response and risk management* 541: 6–13. <https://doi.org/10.1016/j.jhydrol.2015.11.031>.
- Boucher, Y., M.-H. St-Laurent, and P. Grondin. 2011. "Logging-Induced Edge and Configuration of Old-Growth Forest Remnants in the Eastern North American Boreal Forests." *naar* 31: 300–6. <https://doi.org/10.3375/043.031.0313>.
- Boudreault, C., Y. Bergeron, P. Drapeau, and L. Mascarúa López. 2008. "Edge Effects on Epiphytic Lichens in Remnant Stands of Managed Landscapes in the Eastern Boreal Forest of Canada." *Forest Ecology and Management* 255: 1461–71. <https://doi.org/10.1016/j.foreco.2007.11.002>.
- Buras, A., A. Rammig, and C. S. Zang. 2020. "Quantifying Impacts of the 2018 Drought on European Ecosystems in Comparison to 2003." *Biogeosciences* 17: 1655–72. <https://doi.org/10.5194/bg-17-1655-2020>.
- Buras, A., C. Schunk, C. Zeiträg, C. Herrmann, L. Kaiser, H. Lemme, C. Straub, et al. 2018. "Are Scots Pine Forest Edges Particularly Prone to Drought-Induced Mortality?" *Environmental Research Letters* 13: 025001. <https://doi.org/10.1088/1748-9326/aaa0b4>.
- Busby, J. R., L. C. Bliss, and C. D. Hamilton. 1978. "Microclimate Control of Growth Rates and Habitats of the Boreal Forest Mosses, *Tomentypnum Nitens* and *Hylocomium splendens*." *Ecological Monographs* 48: 95–110. <https://doi.org/10.2307/2937294>.
- Caners, R., S. Macdonald, and R. Belland. 2010. "Responses of Boreal Epiphytic Bryophytes to Different Levels of Partial Canopy Harvest." *Botany* 88: 315–28. <https://doi.org/10.1139/B09-089>.
- Chen, J., J. F. Franklin, and T. A. Spies. 1995. "Growing-Season Microclimatic Gradients from Clearcut Edges into Old-Growth Douglas-Fir Forests." *Ecological Applications* 5: 74–86. <https://doi.org/10.2307/1942053>.
- Cienciala, E., P.-E. Mellander, J. Kučera, M. Opluštilov, M. Ottosson-Löfvenius, and K. Bishop. 2002. "The Effect of a North-Facing Forest Edge on Tree Water Use in a Boreal Scots Pine Stand." *Canadian Journal of Forest Research* 32: 693–702. <https://doi.org/10.1139/x02-013>.
- Crockatt, M. 2012. "Are there Edge Effects on Forest Fungi and if So Do they Matter?" *Fungal Biol Rev* 26: 94–101. <https://doi.org/10.1016/j.fbr.2012.08.002>.

- Dambros, C., V. N. V. da Silva, R. Azevedo, and J. W. de Moraes. 2013. "Road-Associated Edge Effects in Amazonia Change Termite Community Composition by Modifying Environmental Conditions." *Journal for Nature Conservation* 21: 279–85. <https://doi.org/10.1016/j.jnc.2013.02.003>.
- Davies-Colley, R. J., G. W. Payne, and M. van Elswijk. 2000. "Microclimate Gradients across a Forest Edge." *New Zealand Journal of Ecology* 24: 111–21.
- De Frenne, P., J. Lenoir, M. Luoto, B. R. Scheffers, F. Zellweger, J. Aalto, M. B. Ashcroft, et al. 2021. "Forest Microclimates and Climate Change: Importance, Drivers and Future Research Agenda." *Global Change Biology* 27: 2279–97. <https://doi.org/10.1111/gcb.15569>.
- Dynesius, M., M. Åström, and C. Nilsson. 2008. "Microclimatic Buffering by Logging Residues and Forest Edges Reduces Clear-Cutting Impacts on Forest Bryophytes." *Applied Vegetation Science* 11: 345–54. <https://doi.org/10.3170/2008-7-18457>.
- Garrett, H. E. G., S. Jose, and M. A. Gold. 2021. *North American Agroforestry*. New York: John Wiley & Sons.
- Gignac, L. D., and M. R. T. Dale. 2005. "Effects of Fragment Size and Habitat Heterogeneity on Cryptogam Diversity in the Low-Boreal Forest of Western Canada." *The Bryologist* 108: 50–66. [https://doi.org/10.1639/0007-2745\(2005\)108\[50:EOFSAH\]2.0.CO;2](https://doi.org/10.1639/0007-2745(2005)108[50:EOFSAH]2.0.CO;2).
- Govaert, S., C. Meeussen, T. Vanneste, K. Bollmann, J. Brunet, S. A. O. Cousins, M. Diekmann, et al. 2020. "Edge Influence on Understorey Plant Communities Depends on Forest Management." *Journal of Vegetation Science* 31: 281–92. <https://doi.org/10.1111/jvs.12844>.
- Green, T. G. A., and O. L. Lange. 1995. "Photosynthesis in Poikilohydric Plants: A Comparison of Lichens and Bryophytes." In *Ecophysiology of Photosynthesis*, edited by E.-D. Schulze and M. M. Caldwell, 319–41. Berlin: Springer Study Edition. Springer. https://doi.org/10.1007/978-3-642-79354-7_16.
- Haddad, N. M., L. A. Brudvig, J. Clobert, K. F. Davies, A. Gonzalez, R. D. Holt, T. E. Lovejoy, et al. 2015. "Habitat Fragmentation and its Lasting Impact on Earth's Ecosystems." *Science Advances* 1: e1500052. <https://doi.org/10.1126/sciadv.1500052>.
- Harper, K. A., and S. E. Macdonald. 2011. "Quantifying Distance of Edge Influence: A Comparison of Methods and a New Randomization Method." *Ecosphere* 2: art94. <https://doi.org/10.1890/ES11-00146.1>.
- Harper, K. A., S. E. Macdonald, M. S. Mayerhofer, S. R. Biswas, P.-A. Esseen, K. Hylander, K. J. Stewart, et al. 2015. "Edge Influence on Vegetation at Natural and Anthropogenic Edges of Boreal Forests in Canada and Fennoscandia." *Journal of Ecology* 103: 550–62. <https://doi.org/10.1111/1365-2745.12398>.
- Hartig, F. 2020. "DHARMa: Residual Diagnostics for Hierarchical (Multi-Level/Mixed) Regression Models." R Package Version 0.3.3.0. <http://florianhartig.github.io/DHARMa/>.
- Hylander, K. 2005. "Aspect Modifies the Magnitude of Edge Effects on Bryophyte Growth in Boreal Forests: North- Vs. South-Facing Edge Effects." *Journal of Applied Ecology* 42: 518–25. <https://doi.org/10.1111/j.1365-2664.2005.01033.x>.
- Hylander, K., C. Greiser, D. M. Christiansen, and I. A. Koelemeijer. 2022. "Climate Adaptation of Biodiversity Conservation in Managed Forest Landscapes." *Conservation Biology* 36: e13847. <https://doi.org/10.1111/cobi.13847>.
- IPCC. 2021. "Climate Change 2021: The Physical Science Basis." In *Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, edited by V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou. Cambridge and New York: Cambridge University Press. <https://doi.org/10.1017/9781009157896>.
- Johansson, P., and L. Gustafsson. 2001. "Red-Listed and Indicator Lichens in Woodland Key Habitats and Production Forests in Sweden." *Canadian Journal of Forest Research* 31: 1617–28. <https://doi.org/10.1139/x01-091>.
- Koelemeijer, I., J. Ehrlén, P. De Frenne, M. Jönsson, P. Berg, and K. Hylander. 2023. "Forest Edge Effects on Moss Growth Are Amplified by Drought." Dryad, Dataset. <https://doi.org/10.5061/dryad.lgljwsv1t>.
- Koelemeijer, I. A., J. Ehrlén, M. Jönsson, P. De Frenne, P. Berg, J. Andersson, H. Weibull, and K. Hylander. 2022. "Interactive Effects of Drought and Edge Exposure on Old-Growth Forest Understory Species." *Landscape Ecology* 37: 1839–53. <https://doi.org/10.1007/s10980-022-01441-9>.
- Lindo, Z., M.-C. Nilsson, and M. J. Gundale. 2013. "Bryophyte-Cyanobacteria Associations as Regulators of the Northern Latitude Carbon Balance in Response to Global Change." *Global Change Biology* 19: 222–35. <https://doi.org/10.1111/gcb.12175>.
- Lüdecke, D., M. S. Ben-Shachar, I. Patil, P. Waggoner, and D. Makowski. 2021. "Performance: An R Package for Assessment, Comparison and Testing of Statistical Models." *Journal of Open Source Software* 6: 3139. <https://doi.org/10.21105/joss.03139>.
- Lundmark, H., T. Josefsson, and L. Östlund. 2013. "The History of Clear-Cutting in Northern Sweden—Driving Forces and Myths in Boreal Silviculture." *Forest Ecology and Management* 307: 112–22. <https://doi.org/10.1016/j.foreco.2013.07.003>.
- Lundström, J., K. Öhman, and H. Laudon. 2018. "Comparing Buffer Zone Alternatives in Forest Planning Using a Decision Support System." *Scandinavian Journal of Forest Research* 33: 493–501. <https://doi.org/10.1080/02827581.2018.1441900>.
- Man, M., J. Wild, M. Macek, and M. Kopecký. 2022. "Can High-Resolution Topography and Forest Canopy Structure Substitute Microclimate Measurements? Bryophytes say no." *Science of the Total Environment* 821: 153377. <https://doi.org/10.1016/j.scitotenv.2022.153377>.
- Maxwell, S. L., N. Butt, M. Maron, C. A. McAlpine, S. Chapman, A. Ullmann, D. B. Segan, and J. E. M. Watson. 2019. "Conservation Implications of Ecological Responses to Extreme Weather and Climate Events." *Diversity and Distributions* 25: 613–25. <https://doi.org/10.1111/ddi.12878>.
- Meeussen, C., S. Govaert, T. Vanneste, K. Bollmann, J. Brunet, K. Calders, S. A. O. Cousins, et al. 2021. "Microclimatic Edge-to-Interior Gradients of European Deciduous Forests." *Agricultural and Forest Meteorology* 311: 108699. <https://doi.org/10.1016/j.agrformet.2021.108699>.
- Moen, J., and B. G. Jonsson. 2003. "Edge Effects on Liverworts and Lichens in Forest Patches in a Mosaic of Boreal Forest and Wetland." *Conservation Biology* 17: 380–8.
- Muggeo, V. M. R. 2017. "Interval Estimation for the Breakpoint in Segmented Regression: A Smoothed Score-Based Approach."

- Australian & New Zealand Journal of Statistics* 59: 311–22. <https://doi.org/10.1111/anzs.12200>.
- Murcia, C. 1995. “Edge Effects in Fragmented Forests: Implications for Conservation.” *Trends in Ecology & Evolution* 10: 58–62. [https://doi.org/10.1016/S0169-5347\(00\)88977-6](https://doi.org/10.1016/S0169-5347(00)88977-6).
- Peters, W., A. Bastos, P. Ciais, and A. Vermeulen. 2020. “A Historical, Geographical and Ecological Perspective on the 2018 European Summer Drought.” *Philosophical Transactions of The Royal Society B Biological Sciences* 375: 20190505. <https://doi.org/10.1098/rstb.2019.0505>.
- Pinheiro, J., D. Bates, and R Core Team. 2022. “nlme: Linear and Nonlinear Mixed Effects Models.” R Package Version 3.1-157. <https://CRAN.R-project.org/package=nlme>.
- Pohlman, C. L., S. M. Turton, and M. Goosem. 2009. “Temporal Variation in Microclimatic Edge Effects near Powerlines, Highways and Streams in Australian Tropical Rainforest.” *Agricultural and Forest Meteorology* 149: 84.
- R Core Team. 2021. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. <http://www.R-project.org/>.
- Schmalholz, M., and K. Hylander. 2011. “Microtopography Creates Small-Scale Refugia for Boreal Forest Floor Bryophytes during Clear-Cut Logging.” *Ecography* 34: 637–48. <https://doi.org/10.1111/j.1600-0587.2010.06652.x>.
- Schmidt, M., H. Jochheim, K.-C. Kersebaum, G. Lischeid, and C. Nendel. 2017. “Gradients of Microclimate, Carbon and Nitrogen in Transition Zones of Fragmented Landscapes – A Review.” *Agricultural and Forest Meteorology* 232: 659–71. <https://doi.org/10.1016/j.agrformet.2016.10.022>.
- Schuldt, B., A. Buras, M. Arend, Y. Vitasse, C. Beierkuhnlein, A. Damm, M. Gharun, et al. 2020. “A First Assessment of the Impact of the Extreme 2018 Summer Drought on Central European Forests.” *Basic and Applied Ecology* 45: 86–103. <https://doi.org/10.1016/j.baae.2020.04.003>.
- Swedish Meteorological and Hydrological Institute (SMHI). 2021. “Klimatdata. Database: Dataserier Med Normalvärden För Perioden 1991–2020.” <https://www.smhi.se/data/meteorologi/kartor/normal>.
- SMHI, E. Sjökvist, D. Abdoush, and J. Axén. 2019. “Sommaren 2018-en glimt av framtiden?” *SMHI Klimatologi*. 52.
- Stewart, K. J., and A. U. Mallik. 2006. “Bryophyte Responses to Microclimatic Edge Effects across Riparian Buffers.” *Ecological Applications* 16: 1474–86. [https://doi.org/10.1890/1051-0761\(2006\)016\[1474:BRTMEE\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[1474:BRTMEE]2.0.CO;2).
- Tamm, C. O. 1953. “Growth, Yield and Nutrition in Carpets of a Forest Moss (*Hylocomium splendens*).” Report No. 43:1. Stockholm.
- Tene, A., B. Tobin, J. Dyckmans, D. Ray, K. Black, and M. Nieuwenhuis. 2011. “Assessment of Tree Response to Drought: Validation of a Methodology to Identify and Test Proxies for Monitoring Past Environmental Changes in Trees.” *Tree Physiology* 31: 309–22. <https://doi.org/10.1093/treephys/tpq114>.
- Thiemer, K., D. M. Christiansen, N. S. Petersen, S. M. Mortensen, and K. S. Christoffersen. 2018. “Reconstruction of Annual Growth in Relation to Summer Temperatures and Translocation of Nutrients in the Aquatic Moss *Drepanocladus trifarius* from West Greenland.” *Polar Biology* 41: 2311–21. <https://doi.org/10.1007/s00300-018-2371-9>.
- Toms, J. D., and M. L. Lesperance. 2003. “Piecewise Regression: A Tool for Identifying Ecological Thresholds.” *Ecology* 84: 2034–41. <https://doi.org/10.1890/02-0472>.
- van de Beek, R. C. Z., P. Berg, J. Södling, R. Mook, and J. Olsson. n.d. “An Improved Precipitation Data Based on Radar and Merged Gridded Gauge Products for Operational Hydrology in Sweden.” In preparation.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Koelemeijer, Irena Adia, Johan Ehrlén, Pieter De Frenne, Mari Jönsson, Peter Berg, and Kristoffer Hylander. 2023. “Forest Edge Effects on Moss Growth are Amplified by Drought.” *Ecological Applications* e2851. <https://doi.org/10.1002/eap.2851>