Do nature reserves influence *Ips typographus* (Linnaeus, 1758) (Coleoptera, Curculionidae) population density?

JOSTEIN GOHLI, PAAL KROKENE & BJØRN ØKLAND

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The European spruce bark beetle *Ips typographus* (Linnaeus, 1758) is a major insect pest in European forests. It causes substantial economic losses to the forest sector and negatively influences carbon sequestration and other important forest ecosystem services. Many environmental factors, such as drought, windfelling, temperature and spruce volume, are known to influence bark beetle population density and damage risk. However, one factor is a subject of much public debate – namely the importance of spruce growing in protected forests where management interventions generally are not carried out. Here, the effect of standing spruce volume in unmanaged Norwegian forest reservations on bark beetle numbers at the landscape level was analysed, while controlling for other important factors. There was no support for spruce volume in reservations being an influencing factor on bark beetle population size. Importantly, our analysis is performed at the landscape scale, and thus cannot address the risk for spruce forests growing near reservations. At a larger spatial scale, however, the present results indicate that forest reservations are not an important factor in determining bark beetle damage risk.

Key words: Coleoptera, Curculionidae, Scolytinae, *Ips typographus*, nature reserves, population dynamics, *Picea abies*.

Jostein Gohli, Division of Biotechnology and Plant Health, Norwegian Institute of Bioeconomy Research, P.O.Box 115, NO-1431 Ås, Norway. E-mail: jostein.gohli@nibio.no

Paal Krokene, Division of Biotechnology and Plant Health, Norwegian Institute of Bioeconomy Research, P.O.Box 115, NO-1431 Ås, Norway. E-mail: paal.krokene@nibio.no

Bjørn Økland, Division of Biotechnology and Plant Health, Norwegian Institute of Bioeconomy Research, P.O.Box 115, NO-1431 Ås, Norway. E-mail: bjorn.okland@nibio.no

Introduction

The European spruce bark beetle (*Ips typographus* (Linnaeus, 1758)) is the most economically important insect in Norwegian forests. Most of the time, *I. typographus* reproduces in the inner bark of dying or severely weakened spruce trees. However, natural disturbances such as storms or severe droughts can cause the beetles to increase in number and launch coordinated attacks on healthy trees. Such outbreaks of *I. typographus* can kill thousands of trees over large areas and may last for several years (Hlásny *et al.* 2021). The last major outbreak in Norway was during the 1970s, where 5-6 million m^3 spruce was killed (Gohli *et al.* 2023).

Following the outbreak in the 1970s, national authorities initiated an extensive bark beetle monitoring program, which has collected data on bark beetle population size every year since

1979 (Gohli *et al.* 2023). Monitoring is carried out with traps baited with the beetles' aggregation pheromones and uses trap counts as a proxy for local population size. The estimated population sizes, along with other relevant factors, are used to assess the risk of bark beetle damage in Norwegian spruce forests (Gohli *et al.* 2023).

Protected forests are often suspected to be sources of bark beetle outbreaks, given the absence of active forest management and often high volumes of older trees in protected areas (Montano *et al.* 2016). However, there is little empirical support in research literature for the hypothesis that forest reserves are "breeding grounds" for bark beetles (Schlyter & Lundgren 1993, Grodzki *et al.* 2006). While the absence of management in protected forests is often suggested to be a driver of bark beetle outbreaks, evidence suggests that neither *I. typographus* numbers nor offspring production differ significantly between unmanaged and managed forests (Weslien & Schroeder 1999). In fact, one study found beetle densities in a protected forest to be only half that of densities in the surrounding managed forest (Markovic & Stojanovic 2010). Certain aspects of forest management may themselves increase beetle populations. The mature even-aged (Jakuš *et al.* 2011) spruce monocultures (Hilszczanski *et al.* 2006, Müller *et al.* 2022) that dominate in many managed forests tend to be more vulnerable to infestations, especially after abiotic disturbances, such as windstorms and drought. Furthermore, clearcutting creates hard stand edges with newly exposed trees that are weakened or killed by increased wind- and sun-exposure, and potentially mechanically damaged from the felling of adjacent trees (Lindmark *et al.* 2022). Such small-scale disturbances may, through accumulated effects, increase bark beetle populations at the landscape level (Gohli *et al.* 2024).

From a forest management perspective, it is important to determine whether spruce in protected forests influence *I. typographus* population size, and hence damage risk, in production forests. Management interventions in protected forests are problematic and generally not permitted, given the role such forests play in harbouring biodiversity. If protected forests turn out to have little effect on the risk of *I. typographus* damage in managed forests, there is little need for management interventions in protected areas. In this study, we use data from the Norwegian bark beetle monitoring program to test whether the volume of spruce in protected forests is associated with the population size of *I. typographus* at the landscape level.

Materials and methods

Here, trap counts from the Norwegian bark beetle monitoring program, which is treated as a proxy for local population size, was analysed. Data from 1731 bark beetle traps (Figure 1), collected during the period 2004-2021, were included in the study. The volume of mature spruce (m^3/ha) inside nature reservations or national parks (hereafter referred to collectively as 'nature reservations'), was obtained from the Norwegian forest resources map (SR16; Astrup *et al.* 2019). Spruce volume was masked (i.e., removed) in non-reservation areas (Figure 1), before extracting spruce volume – inside reservations only – in a 5 km radius around each trap site.

To control for other important predictors of bark beetle population density, spruce volume in reservations was included as a predictor in an existing model (Gohli *et al.* 2024). This model is a negative binomial regression analysis of untransformed bark beetle trap counts and includes the following predictor variables of bark beetle trap counts: (1) spruce volume in non-reservation areas, (2) the total length of new clearcut edges, (3) temperature, precipitation, and soil moisture, (4) vegetation zone ['boreonemoral', 'boreal < 61.7 N°', and 'boreal > 62.8 N°'], (5) sampling year, and (6) latitude, longitude, and altitude. For predictor variables (1) and (2) we used values representing a 5 km radius around each trap site. For more detailed information on the methodology, and the effects of the aforementioned factors on bark beetle population density, we refer to Gohli *et al.* (2024).

The chosen predictor 'volume mature spruce inside nature reservations' was added to the Gohli *et al.* model. Spruce volume inside nature reservations was *ln*-transformed due to a

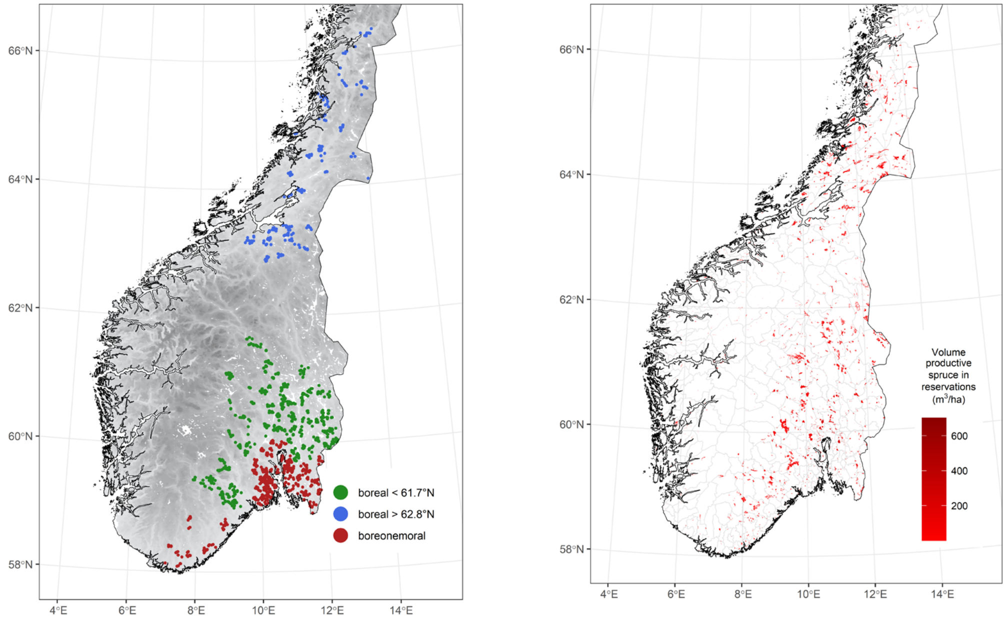

FIGURE 1. Left: Trapping localities included in the study (N = 1731) colour coded by vegetation zone. Right: Volume of mature Norway spruce (from the Norwegian forest resources map; SR16; m3/ha) in nature reservations and national parks in Norway.

skewed distribution towards smaller values. The predictor was specified with a second order term (i.e., examining non-linear associations with trap counts), and included an interaction term with vegetation zone ('boreonemoral', 'boreal < 61.7 N°', and 'boreal > 62.8 N°'; Figure 1) to examine if any effect of spruce in nature reserves differed across these zones.

After evaluating the model outcome, i.e., predicted bark beetle trap counts as a function of the covariate 'volume mature spruce inside nature reservations', an additional analysis where all zero-values for this predictor was dropped was performed. To test whether changes to the results were due to removing zero-values, and not to loss of data, data was randomly selected from our full model dataset with the same data depth as the non-zero dataset (N = 1221) and ran as 1000 model iterations. The results from these tests prompted the running of generalized linear models where significant predictors from the Gohli *et al.* (2024) model was regressed on a binary variable indicating whether 'volume mature spruce inside nature reservations' was zero for a given data point. Here, separate models for each vegetation zone was fitted.

All analyses were performed in R (v. 4.1.1, R Core Team 2024).

Results

Volume spruce inside nature reservations was significantly associated with trap counts in the first model run (first order term: *estimate* = -0.041, P = 0.0254; second order term: *estimate* = -1.880, P = 0.0154), and there were significant differences in the effect size across the three vegetation zones (P = 0.001; Figure 2A and 2C). Since the effect of spruce volume inside reservations was restricted to, and pronounced, near zero-values (Figure 2A), a new model was fitted after removing 510 zero-values for 'volume spruce inside reservations' (Figure 2C). In this new model 'volume spruce inside reservations' was not a significant predictor (second and first order P-values > 0.85; Figures 2B and 2D). Importantly, the model with no zero-values showed effectively flat prediction curves

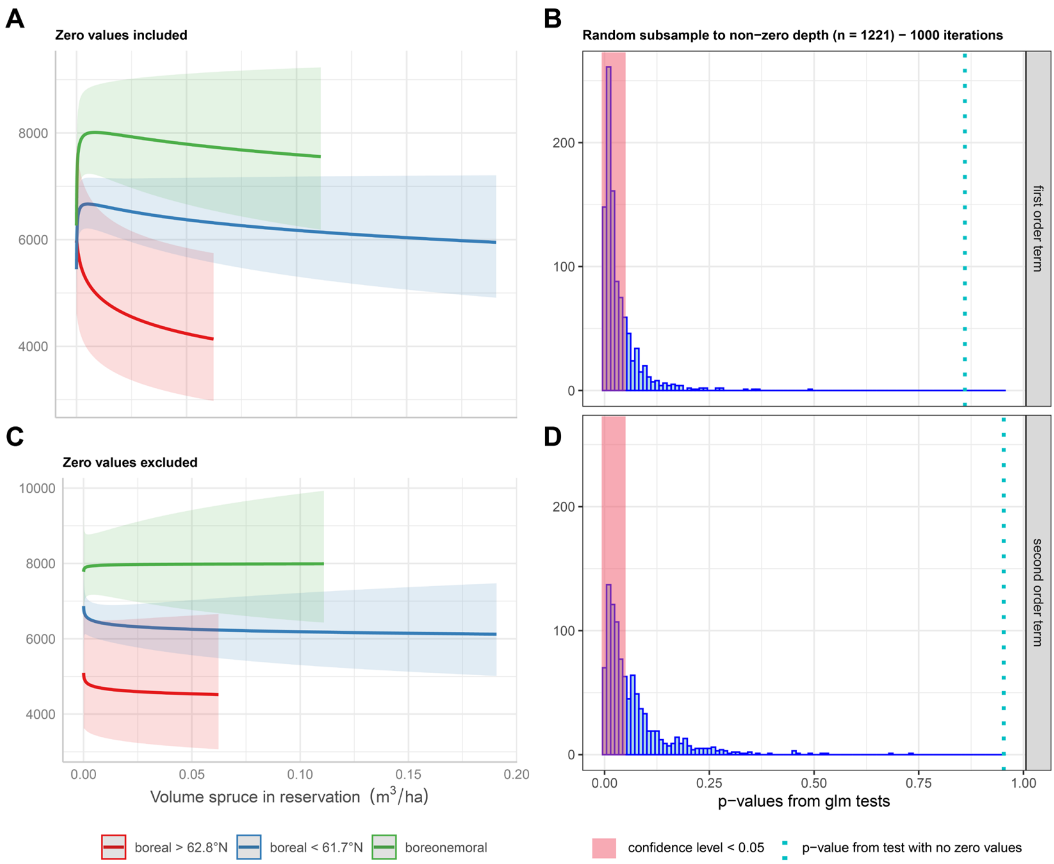

FIGURE 1. Volume of spruce inside forest reservations as a predictor of bark beetle trap counts. Panel **A** shows prediction curves for a model with the full data set (N = 1731) and panel **C** one with all zero-values removed (N = 1221). An interaction term with vegetation zone was specified, and the different coloured lines show effect sizes for the different zones. Panels on the right show the distributions of p-values for the first (**B**) and second order terms (**D**) from 1000 generalized linear model (glm) iterations with randomly subsampled data that includes zero-values (N = 1221, the number of non-zero values). Significant p-values ($p < 0.05$) are highlighted in red. Blue dotted lines show p-values from the model with all zero-values removed.

for spruce volume inside reservations in all three vegetation zones (Figure 2C).

A power test was performed to evaluate if the complete loss of significance for the new model was due to removing zero-values or to loss of data. The distribution of p-values from 1000 tests where the full dataset – with zero-values included – was randomly subsampled to non-zero depth were clustered around 0.05, with 77.4 % of the iterations being significant ($p < 0.05$) for the first order term and 55.9 % being significant for the second order term (Figure 2B and 2D).

To understand why zero and non-zero data points for ‘volume mature spruce inside nature reservations’ appeared to differ in terms of bark beetle trap counts, we regressed all the variables in the Gohli *et al.* (2024) model that significantly predicted bark beetle trap counts, on a variable which classified data points as zero/non-zero in terms of spruce volume inside reservations. The results showed that zero/non-zero values were geographically clustered and significantly associated with several landscape and/or climatic factors that are important for bark beetle population size (e.g., spruce volume, seasonal temperature, latitude, and longitude; Table 1).

TABLE 1. Generalized linear models regressing significant predictors of bark beetle trap counts (according to Gohli *et al.* 2024) on a binary variable indicating whether 'volume mature spruce inside nature reservations' was zero or not. 'Volume spruce' and 'sum new stand edge' are mean values from a 5 km radius around each trap. The analysis was performed separately for three different vegetation zones across the distribution of Norway spruce in Norway. SE = standard error; Z = z-value; p = p-value. The reference level for the response variable is 'non-zero'.

Boreal > 62.8°N	***Estimate***	***SE***	***Z***	***P***	
Intercept	46.06	22.27	2.07		
Volume spruce	0.01	0.03	0.39	0.695	
Volume spruce2	19.71	23.79	0.83	0.407	
Sum new stand edge	0.00	0.00	1.77	0.077	.
Seasonal mean temperature	-0.26	0.33	-0.81	0.418	
Seasonal mean temperature2	-25.56	11.26	-2.27	**0.023**	*
Seasonal mean soil moisture	0.08	0.03	2.29	**0.022**	*
Latitude	-0.97	0.38	-2.56	**0.011**	*
Longitude	1.15	0.31	3.65	**<0.001**	***
Boreal < 61.7°N	***Estimate***	***SE***	***Z***	***P***	
Intercept	8.18	9.79	0.84		
Volume spruce	0.01	0.00	2.41	**0.016**	*
Volume spruce2	-23.58	4.84	-4.87	**<0.001**	***
Sum new stand edge	0.00	0.00	1.83	0.067	.
Seasonal mean temperature	-0.10	0.08	-1.28	0.201	
Seasonal mean temperature2	1.62	3.73	0.43	0.664	
Seasonal mean soil moisture	0.01	0.02	0.35	0.728	
Latitude	-0.21	0.16	-1.27	0.206	
Longitude	0.31	0.09	3.60	**<0.001**	***
Boreonemoral	***Estimate***	***SE***	***Z***	***P***	
Intercept	129.00	26.02	4.96		
Volume spruce	0.00	0.01	-0.27	0.787	
Volume spruce2	-17.84	9.18	-1.94	0.052	.
Sum new stand edge	0.00	0.00	1.86	0.063	.
Seasonal mean temperature	-0.20	0.18	-1.11	0.266	
Seasonal mean temperature2	12.63	8.37	1.51	0.131	
Seasonal mean soil moisture	0.09	0.03	2.61	**0.009**	**
Latitude	-2.31	0.45	-5.11	**<0.001**	***
Longitude	0.45	0.16	2.85	**0.004**	**

Discussion

The initial finding of spruce volume inside nature reservations being a significant predictor of bark beetle trap counts appears to be an artefact. Predicted trap count values indicated that the effect of spruce inside reservations was restricted to a very narrow range between zero-values and near-zero values (Figure 2A). This pronounced effect over a minute range of the predictor variable range is not biologically meaningful; the difference between having zero vs. just a few spruce trees located inside reservations at the landscape level (i.e., within an ~80 km^2 area) is very unlikely to have any measurable effect on bark beetle populations. Based on a non-significant model when zero-values were removed (Figure 2C) and an associated power test (Figure 2B and 2D), it is concluded that the loss of significance was due to removing zero-values, not to loss of data. Further tests revealed that zero and non-zero values for this predictor were clustered geographically and associated with other significant predictors of bark beetle trap counts (Table 1). Collectively, these results thus show no support for spruce volume inside reservation being an important predictor of bark beetle population size at the landscape level. This is an important finding, particularly in light of ongoing discussions about management interventions in protected areas, such as salvation and sanitation felling (Müller *et al.* 2019). If protected areas contribute little to bark beetle numbers at the landscape scale, sanitation felling and other management interventions are not warranted from a pest management perspective. However, it must be pointed out that the present analysis is valid only at the landscape level, and that there could be local effects on beetle numbers near forest reservations.

The findings of this study may not apply to regions with large, spruce-rich reservations, which do not occur in Norway. Protected forests make up 5.3% of the total forest area in Norway, and only 4% of the productive forest area (Frivillig vern, 2024). In continental Europe, some large forest reservations contain high densities of mature spruce and deadwood, while others have mixed forests with complex structures that probably are less conducive to bark beetle mass-reproduction. It is safe to assume that any effects of forest reservations on bark beetle populations will be highly context dependent. Although the present model is not applicable to all types of protected forests, other studies conducted in continental Europe report similar findings as our study. If reservations are "breeding grounds" for bark beetles, one would expect reservations to have high levels of bark beetle damage. This prediction does not align with a recent study from Slovakia, which observed three times more forest damage in managed forests compared to strict forest reserves (Potterf *et al.* 2022). This result is corroborated by Aszalós *et al.* (2022) who observed lower cumulative disturbance rates inside strict forest reserves, leading the authors to propose that protected forest generally are more resilient to natural disturbances than production forests. In fact, nature reserves may attract more bark beetles from their surroundings than they disseminate and may thus be acting as sinks rather than sources of bark beetles at the landscape level (Montano *et al.* 2016). Furthermore, classical control measures against bark beetles, such as sanitation felling, do not appear to reduce damages in reservations, but may rather increase damages by introducing hard edges in the forest landscape (Grodzki *et al.* 2006).

In conclusion, the results presented here, as well as previously published evidence, suggest that nature reservations are not increasing bark beetle numbers or forest disturbances at the landscape scale. On the contrary, forest reservations without active management may have less, and not more, bark beetle damage than managed production forests. The present study cannot explain the mechanisms behind the apparent greater resilience of unmanaged forests, but we speculate that greater resilience is due to the higher structural and biological diversity of unmanaged forests compared to production forests.

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