Predicted forest beetle distributions in Dalarna

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ArtDatabanken

Content

Summary

With a focus on boreal spruce dominated forests, we here examined the main factors determining species richness of beetles using extensive beetle survey data from Finland. For total species richness, richness of natural spruce forest specialists, and 3 individual species, selected models were used to predict expected species richness and occurrence probability, respectively, in Dalarna. Stand age was found to have positive effects on total beetle richness and natural spruce forest specialist species richness, as well as on the occurrence probability of the red-listed species *Tachinus elegans* and the indicator species *Xylechinus pilosus*. Connectivity to old and high volume spruce forest was important for the occurrence of *Enicmus planipennis* (assuming mean dispersal distance 5km) and *X. pilosus* (assuming mean dispersal distance 1km), and, intriguingly, also positively affected total species richness (again assuming a mean dispersal distance of 1km). The availability of high quality habitat in an area of 100–400 hectares around a focal site thus appeared to be important for high local species richness. Maps of estimated connectivity for three different assumed mean dispersal distances are provided alongside distribution maps for *T. elegans, E. planipennis* and *X. pilosus*, as well as maps of expected total species richness and the richness of natural spruce forest specialists. Since maps of old forest connectivity may be generally useful for planning in the context of green infrastructure, further connectivity maps are provided also for old pine forest.

Introduction

Beetles (order Coleoptera) are one of the world's most species-rich organism groups and constitute an important component of boreal forest ecosystems (Niemelä, 1997). Beetle assemblages in Fennoscandia have been affected by changes in forestry practices (Martikainen, Siitonen, Punttila, Kaila, & Rauh, 2000; Siitonen, 2001), and a large proportion of (especially saproxylic) forest beetle species show declining populations and are considered vulnerable in Sweden (Art-Databanken SLU, 2015). Their diversity and their sensitivity to environmental changes makes beetles a useful indicator group to assess effects of environmental management (Seibold et al., 2015).

Boreal forests are strongly structured by decades of often intensive forestry (Siitonen, Martikainen, Punttila, & Rauh, 2000). This has affected the local *quality* of forest stands (e.g. stand structure, tree species diversity and the available *amount* of dead wood), the regional amount and availability of high quality habitat as well as fragmentation and hence the distance and *connectivity* between patches of high quality habitat (Löfman & Kouki, 2001). Spruce is one of the most common tree species across Sweden, and spruce dominated forests host a high diversity of beetle species, including many natural spruce forest specialists (Hedgren, 2014).

With a focus on boreal spruce dominated forests, we here examined the main factors determining species richness of beetles using extensive beetle survey data from Finland, with the aim of developing predictive models for application in Dalarna. Both total species richness and the richness of natural spruce forest specialists were assessed. Local stand characteristics (stand age, living tree species volumes and amount of dead wood), intermediate scale connectivity based on stand characteristics in the surroundings and climatic variables were tested for. The final models were used to map expected beetle species richness across Dalarna. Further, the distribution of two red-listed species and one indicator species for "Natur-skog" (old natural forest, especially spruce) were modelled separately, and their probability of occurrence mapped for Dalarna. Additionally, maps of estimated old spruce forest connectivity for three different assumed mean dispersal distances are provided.

Sammanfattning

Med fokus på boreal, grandominerad skog har vi här undersökt de faktorer som huvudsakligen styr artmångfalden bland skalbaggar. Undersökningen grundas på omfattande finska inventeringsdata. Vi predikterade också utbredningen av det totala antalet arter, antalet specialiserade arter knutna till ursprunglig granskog respektive förekomsten av tre enskilda skalbaggsarter i Dalarna med de passade statistiska modellerna. Hög ålder hos skogsbeståndet hade en positiv effekt på såväl det totala antalet som antalet arter knutna till ursprunglig granskog. Likaså var beståndets ålder positivt korrelerad med sannolikheten för förekomst av den rödlistade arten *Tachinus elegans* och indikatorarten *Xylechinus pilosus*. Närhet till gammal, volymsrik granskog var viktig för förekomsten av *Enicmus planpennis* (om man antar att artens spridningsavstånd är i medeltal 5 km) och *X. pilosus* (om man antar ett spridningsavstånd på i medeltal 1 km). Intressant nog påverkades även den totala artrikedomen positivt av närheten till gammal, volymsrik skog (återigen med 1 km som antaget spridningsavstånd). Förekomst av högkvalitativt habitat inom ett område av 100–400 ha runt det studerade området tycks således positivt påverka den lokala artrikedomen. Vi presenterar kartor över den beräknade konnektiviteten vid tre olika värden på genomsnittligt spridningsavstånd, liksom utbredningskartor för *T. elegans*, *E. planipennis* och *X. pilosus*. Likaså visas kartor över den förväntade totala artrikedomen samt antalet arter knutna till ursprunglig granskog. Eftersom kartor över skoglig konnektivitet har ett allmänt värde vid planeringen av grön infrastruktur, presenteras även konnektivitetskartor för gammal tallskog.

Purpose/objective

Production of maps of expected forest beetle species richness and probability of occurrence of selected individual species in Dalarna.

Methods

Data

Beetle survey data (courtesy Juha Siitonen) was collated from four surveys conducted in a total of 101 sites in Finland in 1993 (material K, N = 16 sites), 1994 (material H, N = 11 sites), 2003 (material B, N = 70 sites) and 2013 (material D, N = 4 sites)[1]. Sites are distributed along a gradient from southwestern Finland to central eastern Finland, which is expected to correspond to a gradient of decreasing historical forest use intensity (Nordén, Penttilä, Siitonen, Tomppo, & Ovaskainen, 2013). In each site, five window flight traps (WT, described in (Martikainen, Siitonen, Kaila, & Punttila, 1996)) were set up hanging 1 m above the ground in randomly chosen places within the site. The sampling period was May to September, and traps were emptied 3 to 4 times during this period. All specimens were identified to species level. Taxonomy follows standards of 2017 in the Swedish taxonomy database Dyntaxa (www.dyntaxa.se), which are aligned with

the Pan-European Species directories Infrastructure (PESI, http://eu-nomen.eu). A total of 996 species (whereof 329 were saproxylic species) and 49'329 individuals were caught.

Most of the sites are spruce-dominated, mesic Myrtillus-type forests. Material B covers some more fertile, Oxalis-Myrtillus type or herb-rich forests. Stand characteristics measured for each site are stand age, volume of living trees and tree-species specific volumes (for pine, spruce, birch, aspen, and other deciduous), basal area of the living stand, and the total volume of coarse (minimum diameter 10 cm) dead wood (all volumes in m3/ha). Tree species richness was calculated for each site, including one extra species for unidentified but present "other deciduous" species. Stand age varied from recently clear-cut (3 yrs) to old-growth and overmature stands (198 yrs).

Further covariate data included climate variables with potential relevance to beetle occurrence and estimates of connectivity derived from regional forest characteristics. Climate variables used were the length of the vegetation period in degree days (i.e. number of degree days where daily mean temperature > 5ºC) and accumulated precipitation from May to November (mm). Mean annual temperature was found to be strongly collinear with the length of the vegetation period, and was therefore not included. Gridded meteorological data

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1 Detailed descriptions of study sites can be found in the following references for material **K:** (Martikainen et al., 1996), **H:** (Martikainen, Siitonen, Kaila, Punttila, & Rauh, 1999), (Martikainen et al., 2000) and (Siitonen et al., 2000), B: (Nordén et al., 2013) and (Hottola & Siitonen, 2008), and D: (Koivula et al., 2014).

Legend

Finland field sites - Materials B, D, H, K
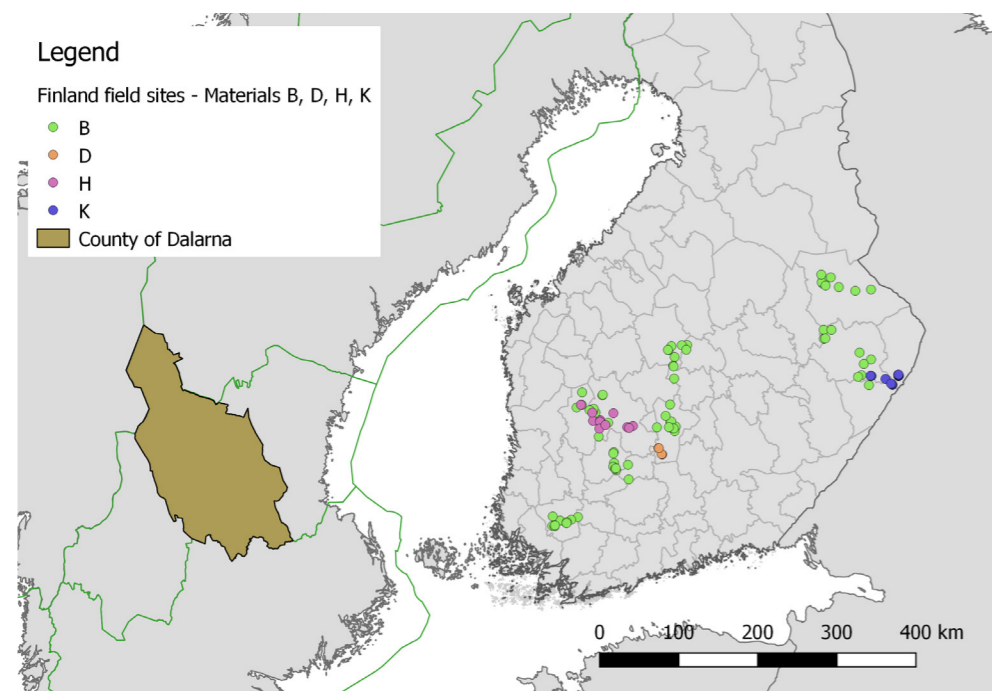
- B
- D
- H
- K
- County of Dalarna

Figure 1. Overview of the 101 field sites with survey data in Finland (color indicates datasets, i.e. "material"). Growing season length decreases towards the NE while accumulated precipitation increases. The gradient from SW to NE also corresponds to a gradient of decreasing historical forestry intensity.

were extracted from the EURO4M Mesan dataset (Landelius, Dahlgren, Gollvik, Jansson, & Olsson, 2016) for both Finland and Sweden. Estimates of connectivity were derived from forest characteristics recorded in the Finnish multisource National Forest Inventory (ms-NFI; (Tomppo, Haakana, Katila, & Peräsaari, 2008)), which combines information from satellite imagery and field inventories (source: Natural Resources Institute Finland, National Forest Inventory). For sites surveyed in 1993 and 1994 (material K and H, respectively), data from NFI8 were used. For this dataset, stand age estimates were deemed less reliable than for later datasets, and were therefore corrected by back-calculation from NFI data from 2013. To identify pixels with a stand age ≥ 100 yrs in 1993 and 1994, stands that were aged ≥ 119 and ≥ 120 yrs in 2013 were selected. Note that this approach may miss stands that were older than 100 yrs in the early 90s but subsequently logged, and could thus cause an underestimation of connectivity. For data from sites surveyed in 2003 (material B), data from NFI9 was utilized, and for sites surveyed in 2013 (material D), the NFI data for 2013 was used.

Estimates of connectivity are calculated following (Mair et al., 2017), and combine stand age and the volume of spruce to reflect potential dispersal sources in a buffer distance of 20km around each site. The approach first selects cells (resolution 25m in NFI8 and NFI9, and 16m in NFI2013) aged 100 yrs or older, aggregates these to 100×100m pixels for computational speed, and calculates the mean volume of living spruce in these aggregated 'old forest' cells (v_j). Assuming a negative exponential dispersal kernel, connectivity S_i for each site i is then calculated as

$$S_i = \sum_{j \neq i} v_j \exp(-\alpha d_{ij})$$

where α is the dispersal parameter, d_{ij} is the distance in km

from the focal cell i to cell j, and v is the average volume of spruce in cell j. Dispersal parameters of α = 5, 1, 0.2 were tested for, corresponding to mean dispersal distances of 0.2, 1 and 5 km, respectively. Some sites in eastern Finland were close to the Russian border, such that the buffer area of 20km radius extended into regions where no data was available. To avoid underestimation of connectivity due to this, S_j values were standardized by the actual buffer area over which S_j was calculated.

Data for predictions in Dalarna comprised the same climate variables (length of vegetation period and accumulated precipitation) and forest data from the latest Swedish kNN forest map (2010) (Reese et al., 2003)[2] , covering all of Sweden at a resolution of 25m. Amount of dead wood was not available for Sweden. Connectivity was calculated in Dalarna for each 100m pixel using the same approach as above (implemented using function focal{raster} in R, Version 3.3.3), including a 20km buffer around the county borders to avoid edge effects (not available for the NW part of Dalarna bordering Norway). In Dalarna, the range of some covariate variables exceeded the values recorded in Finland that were used to build the models. In order to avoid excessive extrapolation beyond the domain of the model, values in Dalarna that were higher than the model domain + 10% were therefore rounded to the maximum values + 10% for model predictions. This may result in underestimation of occurrence probabilities in some cases. For final predictions of occurrence probability and expected species richness, all raster data was aggregated to a resolution of 100m (using max values).

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2 http://www.slu.se/centrumbildningar-och-projekt/riksskogstaxeringen/statistik-om-skog/slu-skogskarta/om-slu-skogskarta/

Table 1. List of covariates.

c	Comment
Stand age (yrs)	Range from recently clear-cut (3 yrs) to overmature and old-growth stands (198 yrs)
Volume of living tree species (m³/ha)	
- Spruce	
- Pine	
- Birch	
- Deciduous trees other than birch	(e.g. *Populus, Alnus, Salix* etc.)
Volume of dead wood (m³/ha)*	Total dead wood amount of diameter >10cm
Length of vegetation period (days)	Number of days per year where mean daily temperature >5°C
Accumulated precipitation (mm)	Accumulated precipitation during vegetation period (May to Nov)
Connectivity (dimensionless)	Accumulated volume of living spruce in cells aged >100 yrs, weighted by distance for dispersal parameter α= 5, 1, 0.2

* Not available for Sweden. Tested for but not used in predictions

Species

Species red-listed in Sweden were prioritized, but the quality of the dataset for each was also considered (as minimum number of sites in which the species was recorded, out of total number of sites = 101). Species were thus selected based on i) red-list status in Sweden (red-listed 2015) and ii) occurrence in at least 10 sites in the Finland dataset. This selection procedure yielded 6 species. Two of these species are classed as regionally extinct (RE) in Dalarna and were not considered. Four species remained: *Enicmus planipennis, Epuraea oblonga, Microscydmus nanus, Tachinus elegans*. Additionally, two species classified as indicator of "Naturskog" in Sweden (Wikars 2009) were modelled: *Atrecus pilicornis* and *Xylechinus pilosus*. Models with sufficient discriminatory power to be useful for predictions could be fitted for *Enicmus planipennis, Tachinus elegans* and *Xylechinus pilosus*.

Natural spruce forest specialist status (23 species, see Section 7) is based on a classification by Juha Siitonen. Classification into saproxylic species (i.e. directly or indirectly dependent on dead wood at some point in their life cycle) and non-saproxylic species was also performed by Juha Siitonen based on literature and expert knowledge.

Analysis

For all analyses, data from the 5 individual traps and across all sampling periods were pooled to create a presence-absence dataset by site. Species richness is the total number of species recorded per site.

Individual species presence/absence in response to environmental factors for two red-listed species (*Enicmus planipennis, Tachinus elegans*) and one indicator species for natural forest (*Xylechinus pilosus*, Wikars 2009) was modelled using generalized linear models (GLMs) assuming a binomial distribution and logit link function. Models were specified based on ecological expectations and model selection was based on the Akaike information criterion (AIC).

Species richness of 23 natural spruce forest specialist species (see species list in Appendix 2, Section 7) was modelled using a GLM with a Poisson distribution and log link function, as no overdispersion was present. Model selection proceeded based on AIC comparison.

Total species richness was modelled with a GLM assuming Poisson distribution (log link function). Overdispersion was detected, and standard errors were therefore corrected using a quasi-GLM model where the variance is given by $\varphi \times \mu$, where μ is the mean and φ the dispersion parameter (φ estimated to be 6.44). Model selection in this case was based on analysis of deviance using the F statistic (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). A modelling approach assuming a negative binomial distribution yielded the same results (not reported).

All analyses were peformed in R, version 3.3.3 (R Core Team, 2017).

Results – individual species distributions

Enicmus planipennis

Enicmus planipennis (granbarkmögelbagge; Fam. Latridiidae, minute brown scavenger beetles) is a fungivore associated with slime molds and some polypores (e.g. *Fomitopsis pinicola, Trichaptum abietina*). Larval development occurs under spongy bark of spruce, most often on coarse woody debris (lying dead wood logs and stumps) or at the base of living trees with rough bark, often in closed stands. Occurs throughout Sweden, from the SE to the far North. The species is classified as near threatened in Sweden (ArtDatabanken SLU, 2015), and populations may decrease further owing to ongoing loss and fragmentation of suitable habitat.

Based on its known ecology, occurrence probability of this species was expected to increase with the age of the forest stand, the volume of living spruce and the amount of dead wood. Owing to its distribution throughout Sweden, climate was not expected to have a significant effect.

The initial model (R^2 = 0.19 (Nagelkerke's pseudo-R^2), AIC = 119.1) indicated a surprising significant negative effect of the amount of dead wood on occurrence probability of *E. planipennis* (β ($\pm$ SE) = -0.03 (0.01), p = 0.03) along with marginally significant positive effects of stand age (β ($\pm$ SE) = 0.02 (0.01), p = 0.07) and the volume of living spruce (β ($\pm$ SE) = 0.005 (0.003), p = 0.08).

Model selection based on AIC results in a final best fitting model with significant positive effects of the volume of living spruce and large scale connectivity assuming a mean dispersal distance of 5 km (α = 0.2) (Table 2). The volume of deciduous trees other than birch had a marginally significant positive effect. Note that connectivity, i.e. the presence of high volumes of old spruce forest in the wider surroundings, had the strongest effect on occurrence probability of *E. planipennis*.
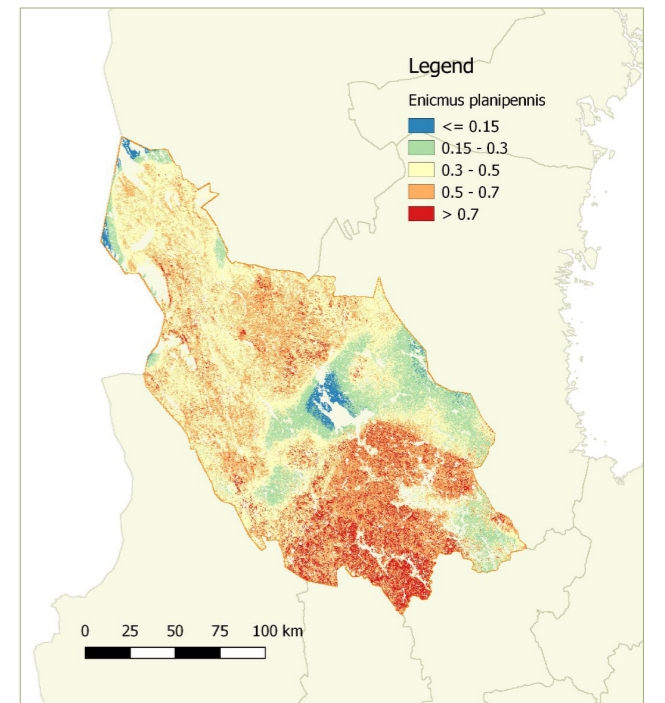

Figure 2. Predicted occurrence probability of *Enicmus planipennis* in Dalarna. The high values in the Southeast are potentially an artefact from the Swedish forest inventory data (relatively high volumes of living spruce), presumably corresponding to the outlines of a satellite image. However, this is also a region where deciduous trees other than birch show higher volumes, which according to our data increased the occurrence probability of *E. planipennis*. Low occurrence probabilities in the Northwest along the border to Norway may result from missing connectivity data beyond the border.

Table 2. Final model for *Enicmus planipennis*, used for predictions in Dalarna. R^2 = 0.28 (Nagelkerke, 1991), AIC = 111.3, AUC = 0.76.

Coefficient	Effect ± SE	z value	p
Intercept	-3.25 ± 0.74	-4.41	<0.001
Connectivity (α = 0.2)	0.051 ± 0.018	2.79	<0.01
Volume living spruce	0.0057 ± 0.0026	2.21	0.03
Volume deciduous other than birch	0.018 ± 0.010	1.91	0.06

Tachinus elegans

The ecology of *Tachinus elegans* (Fam. Staphylinidae, rove beetles) is not well understood, but presumably the species is a carnivore associated with old spruce forests, mostly humid and natural or semi-natural forest with old-growth characteristics. It may exhibit a Southern distribution limit in central Sweden. The species is classified as Near Threatened in Sweden, and feared to be negatively affected by the loss (logging or drainage) of wet old spruce forests (ArtDatabanken SLU, 2015). Coniferous forest, in particular spruce, is an important habitat and substrate. Expected effects are a positive response of occurrence probability to increasing forest age, spruce volume and dead wood volume, as well as potentially a negative effect of increasing temperatures (growing season length).

The initial model (R^2 = 0.44 (Nagelkerke), AIC = 85.0) showed significant positive effects of the volume of living spruce (ß (± SE) = 0.009 (0.004), p = 0.03) and the amount of dead wood on occurrence probability of *T. elegans* (ß (± SE) = 0.03 (0.01), p = 0.03), while stand age was not significant. Length of the growing season had a strong negative effect (ß (± SE) = -0.16 (0.05), p < 0.01). This may indicate a reduced occurrence probability towards the south due to direct or indirect (e.g. via forest characteristics) climatic effects, but note that this could also be due to higher historical forestry intensity in Finland's southwestern regions. The amount of dead wood could not be used for predictions, as data on this was not available for Sweden.

The final model (R^2 = 0.39 (Nagelkerke), AIC = 88.6, AUC = 0.84) retained spruce volume (albeit only marginally significant) as well as stand age (potentially indicative of dead wood volume), and the negative effect of increasing temperatures (growing season length) (Table 3).
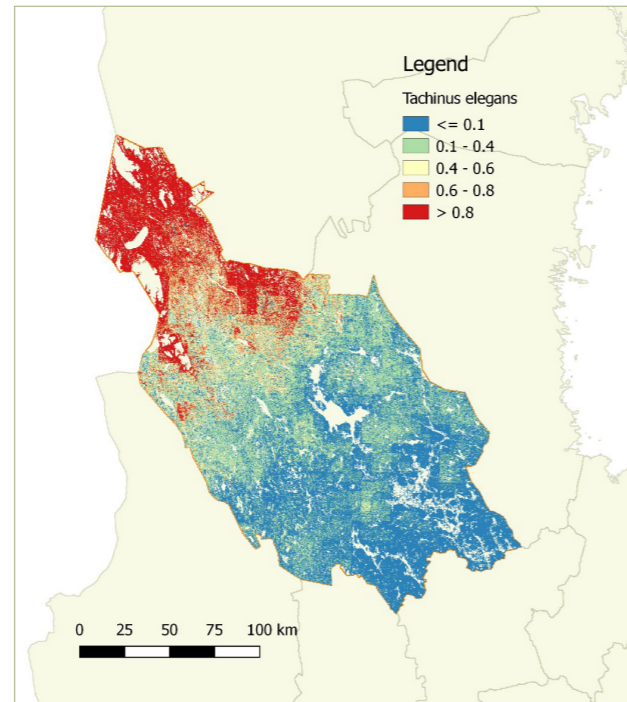

Figure 3. Predicted occurrence probability of *Tachinus elegans* in Dalarna. The distribution reflects decreasing temperatures and higher stand age towards the North.

Table 3. Final model for *Tachinus elegans*, used for predictions in Dalarna. R^2 = 0.39 (Nagelkerke), AIC = 88.6, AUC = 0.84.

Coefficient	Effect ± SE	z value	p
Intercept	19.2 ± 7.08	2.71	<0.001
Stand age	0.035 ± 0.010	3.47	<0.001
Growing season length	-0.15 ± 0.05	-3.19	<0.01
Volume living spruce	0.0064 ± 0.0036	1.79	0.0

Xylechinus pilosus

The herbivorous bark beetle *Xylechinus pilosus* (randig granbastborre; Subfam. Scolytinae, bark or ambrosia beetles) is classified as indicator species for natural forests in Sweden (Wikars 2009). Little appears to be known about its ecology. Since classed as indicator species for natural forest, stand age, spruce volume and dead wood volume may have an effect.

The initial model (R^2 = 0.39, AIC = 108.4) showed no effect of dead wood at all (ß (± SE) = 0.027 (0.022), p = 0.20), whereas the volume of living spruce had a significant positive effect (ß (± SE) = 0.007 (0.003), p = 0.03) and stand age a marginally significant positive effect (ß (± SE) = 0.019 (0.011), p = 0.08).

The final model retained significant positive effects of both stand age and volume of living spruce, as well as a marginally significant positive effect of intermediate connectivity (assuming a mean dispersal distance of 1 km) (Table 4).
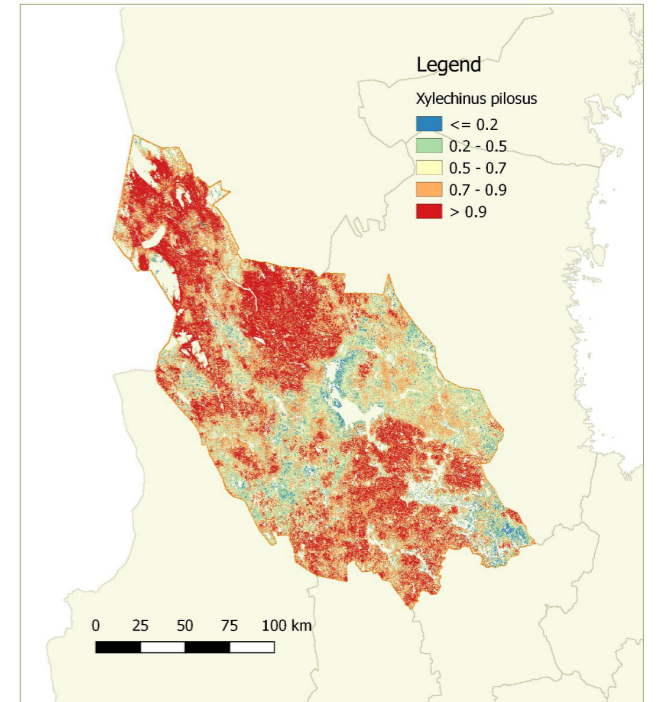

Figure 4. Predicted occurrence probability of *Xylechinus pilosus* in Dalarna.

Table 4. Final model for *Xylechinus pilosus*, used for predictions in Dalarna. R^2 = 0.40 (Nagelkerke), AIC = 107.5, AUC = 0.80.

Coefficient	Effect ± SE	z value	p
Intercept	-3.23 ± 0.86	-3.75	<0.001
Stand age	0.024 ± 0.010	2.56	0.01
Volume living spruce	0.0057 ± 0.0029	1.93	0.05
Connectivity (α = 1)	0.58 ± 0.35	1.65	0.09

Results – species richness

Total species richness

Total species richness was expected to increase with stand age, potentially levelling off in late successional stages where species turnover of specialists predominates. A quick visual inspection showed that this was indeed a pattern observed (Figure 5), although there was a lot of variation at intermediate stand age. Most striking, however, was the massive peak richness in stands that have recently (3 yrs earlier) been clear-cut.

To assess whether the species composition in recent clear-cuts was different from other communities, non-metric multidimensional scaling (NMDS) was employed, using Bray-Curtis dissimilarities in terms of species composition between sites grouped into four different development classes (1 = recently clear-cut, 2 = young sapling stand, 3 = thinning stand, 4 = mature or overmature and old-growth stand). The clear-cut stands (red points and left hand cluster in Figure 5) clearly separated in ordination space from older stands. Also young sapling stands tended to cluster away from the two later development classes, with only some overlap with stands grown up to thinning stage. The latter and mature and old-growth forests appeared fairly similar in terms of species composition. An analysis of similarity (ANOSIM) found significant, but overall not very strong differences between development classes in terms of species composition (R = 0.32, $p = 0.001$), presumably due to the fairly strong overlap of later development classes.

The strong compositional difference of species richness in clear-cuts indicates the potential presence of transient species and of species potentially adapted to more open habitat. The data was therefore split into recently clear-cut sites (with high species richness but differing species composition) and forest species assemblages.

Total species richness in recently clear-cut sites (n=4) ranged from 217 to 250 species, with an average of 229 species (±15 SD). Figure 6 indicates the location of such sites in Dalarna. Due to the low number of such sites, no additional covariates were tested for. Even if these beetle assemblages are different from typical forest communities, the high value of recently clear-cut, relatively open sites for species richness should be noted. Maintaining a mosaic of stands of different successional stage in the landscape should be beneficial for the regional diversity of beetle species.

Total species richness in the remaining sites (ranging from stand age 16 to 198) was found to increase with stand age, the volume of deciduous trees other than birch, and connectivity assuming a mean dispersal distance of 1 km (Table 5). The amount of dead wood had no noticeable effect. The importance of deciduous tree volume indicates that a considerable proportion of species in this dataset are not spruce specialists, but species preferring a variety of deciduous trees. That connectivity had an effect was surprising to some degree, as species are expected to differ widely in their dispersal capacity. Nonetheless, the availability and amount of old, high volume spruce stands at an intermediate distance around each focal site had a strong positive effect on total species richness. Maintaining old growth stands thus is not only beneficial for immediate local species richness, but also for insect diversity in the surroundings. For maps of estimated connectivity assuming different dispersal abilities, see Section 6 (Appendix 1).
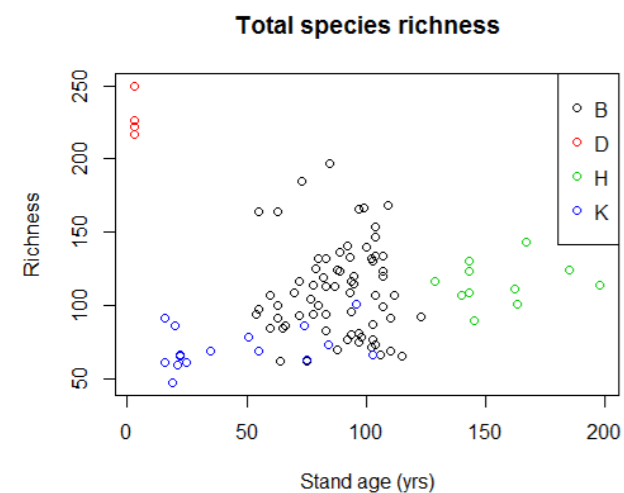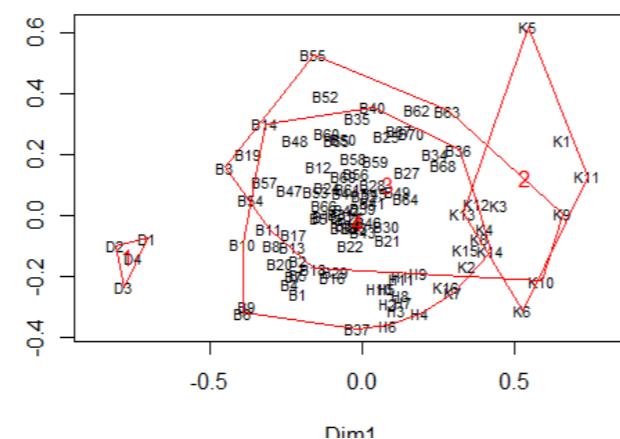

Figure 5. Left panel: Total species richness vs. stand age (yrs). Note the high total richness (>200 species) in recently cleared forest (age = 3 yrs, red points, material D). The color indicates the dataset (material B (2003); D (2013); H (1994); K (1993)).

Right panel: Results of NMDS shows clustering of sites by development classes (1–4) in terms of species composition. Recently clear-cut sites (development class 1, clustering in the lower left ordination space) show a clearly distinct species composition compared to older stands.

Natural spruce forest specialist species richness

The 23 species modelled here are classified as specialized inhabitants of natural spruce forest. Stand age, volume of living spruce and dead wood amount were tested for effects. Due to results from total richness models that indicated a substantially different assemblage in recently clear-cut sites, these sites were excluded before model fitting. But note that even in clear-cut sites, 2 to 3 (on average 2.5) of these species were encountered. These records, however, may be due to transient presence of species not reproducing there, i.e. spillover effects from adjacent habitat.

The initial model (R² = 0.39 (Nagelkerke), AIC = 285.5) confirmed a positive effect of the total amount of dead wood on specialist richness (ß (± SE) = 0.009 (0.003), $p < 0.01$) and a marginally significant positive effect of the volume of living spruce (ß (± SE) = 0.002 (0.009), $p = 0.06$), while stand age was not significant. Connectivity had no effect on specialist richness, probably due to variation in dispersal capacities amongst these species.

Upon removal of dead wood (which was unavailable for predictions), however, stand age alone remained in the model with a significant positive effect on spruce forest specialist richness (Table 5). Stand age here appeared to capture the positive effect of dead wood as well as increasing volumes of living spruce.
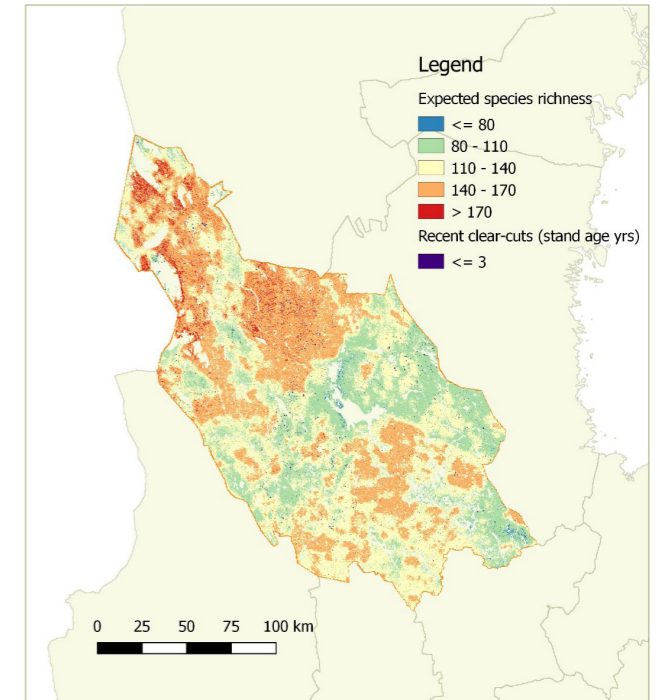

Figure 6. Expected total beetle species richness in Dalarna, modelled as a function of stand age, volume of deciduous trees other than birch and connectivity assuming a mean dispersal distance of 1km. The distribution of stands of age 3yrs or less is shown in dark purple (expected beetle species richness (mean ± SD) 214 ± 15 species).

Table 5. Summary of the final model used for predictions of total species richness in Dalarna.

Coefficient	Effect ± SE	t value	p
Intercept	4.27 ± 0.08	54.4	<0.001
Stand age	0.0023 ± 0.0007	3.10	<0.01
Volume living deciduous other than birch	0.0027 ± 0.0009	3.15	<0.01
Connectivity (α = 1)	0.12 ± 0.03	4.14	<0.001

Table 6. Final model used for predictions of expected natural spruce forest specialist richness. R² = 0.28 (Nagelkerke), AIC = 291.1.

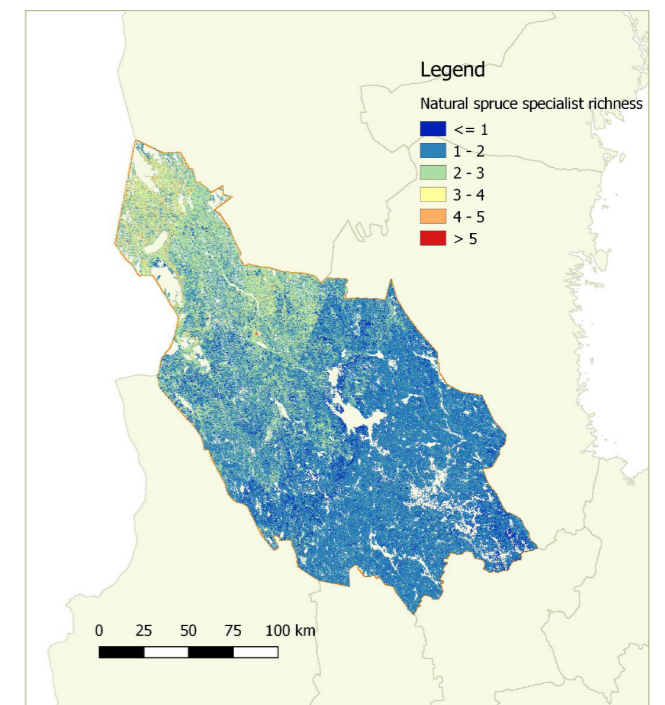| Coefficient	Effect ± SE	z value	p
Intercept	-0.59 ± 0.24	-2.45	0.01
Stand age	0.010 ± 0.002	4.81	< 0.001

Figure 7. Expected species richness of natural spruce forest specialists in Dalarna. Only towards the NW are pockets of high expected specialist species richness.

Discussion

Stand age was the most important predictor across all response variables. It was found to positively affect expected total species richness, richness of natural spruce forest specialists as well as the occurrence probability of *Tachinus elegans* and *Xylechinus pilosus*. Only for *Enicmus planipennis*, stand age was not retained in the best fitting model, where the volume of living spruce had a positive effect instead. The total volume of dead wood showed variable effects: while increasing amounts of dead wood had positive effects on the richness of natural spruce forest specialists and the occurrence probability of *T. elegans*, there were no effects on total species richness nor on the occurrence probability of *X. pilosus*. In the case of *E. planipennis*, a negative effect of increasing dead wood amount on occurrence probability was detected, which is difficult to explain and may stem from other, unmeasured covariates. Connectivity with old (stand age >100 yrs) and high volume spruce stands in the wider surroundings (assuming a mean dispersal distance of 5km), however, had a strong positive effect on occurrence probability of *E. planipennis*. Also *X. pilosus* responded positively to increasing connectivity with old-growth spruce forest, but within a narrower radius around the focal site, i.e. assuming a mean dispersal distance of 1km. The same connectivity measure had a strong positive effect on total species richness. This was somewhat surprising, as species are expected to vary considerably in their dispersal capacity. That connectivity was a significant predictor of total species richness indicates the importance of habitat quality in the forest mosaic surrounding a focal site within an area of several hundred hectares. In Dalarna, a hotspot in terms of old-growth spruce forest connectivity appears to occur in an area extending north of Mora to the county border (Figure 9). Other areas of high connectivity are noticeable along bands

of lower elevation around Långfjället, Nipfjället and Svartfjället, as well as Fulufjället and the area around Sälen in the Northwest of Dalarna, potentially reflecting less intensive forestry in these more remote and hilly regions. Smaller pockets of intermediately high connectivity occur around Borlänge and at the county borders in the west, bordering Värmland around Tyfors, and in the east, bordering Gävleborg around Horndal. For further notes on connectivity, see Appendix 1 (Section 6).

Another interesting finding was the very high species richness recorded in recently clear-cut sites. Beetle assemblage composition in such clear-cuts differed substantially from older forest stands, but nonetheless 2 to 3 species considered natural spruce forest specialists were recorded in each of them. These may be transient species that were not actually reproducing on site, but together with the high levels of richness of other species, this suggests that also recently clear-felled areas play an important role in maintaining regional species richness. A mosaic of different stand ages at the regional scale may mimic natural stand dynamics and help maintain a diversity of habitats and species.

Further analyses could draw on species classifications to study in which way clear-cuts differ from older stands, and how beetle assemblage composition varies during stand succession. In Canada, for example, beetle abundance was found to be highest in clear-cuts, but at the same time, ecological feeding group was a strong determinant of association with stand age: while in clear-cuts, predators and xylophagous species dominated, fungivorous beetles were associated with older, forest-interior habitats (Bouchard & Hébert, 2016). Insights into such patterns could greatly enhance the predictive capacity of models.

Appendix 1: Connectivity

Maps of estimated connectivity for dispersal parameter α = 5, 1, 0.2, corresponding to mean dispersal distances of 200m, 1 km and 5 km, respectively, are shown in the following for both spruce (used as covariate in the presented distribution models) and pine (not used in the present analysis). Higher values indicate higher connectivity (larger volumes of old spruce forest closer to the focal site). Values can be interpreted as weighted average volume of old spruce forest in the surroundings, but are perhaps more easily viewed as essentially dimensionless; they should at any rate not be directly compared between maps with different values for α. Since data for Norway was not available, connectivity along the Norwegian border may be underestimated.

The connectivity layers in themselves may provide useful additional information for planning in the context of green infrastructure. In a broad sense, the connectivity mapping employed here is related to the estimation of valuable core areas (värdekärnor) which underlies proposed value regions (värdetrakter) (Bovin, Elcim, & Wennberg, 2017), but may provide complementary information. There are two main differences between the two approaches.

The first difference lies in the input data: while value regions are based on high density of previously mapped habitat of high conservation value (e.g. for red-listed species (Naturvårdsverket, 2005)), the connectivity maps presented here are based on the density of all old spruce forest and its volume, without taking conservation value into account. They are thus more general, but also have lower data requirements (using only simple and publicly available maps of forest age and tree species volumes).

The second main difference lies in the calculation of connectivity, or, in other words, the distance-weighting of habitat to calculate density: in the analysis of value regions, the value of high quality habitat within a fixed radius around a focal site is simply summed and standardised to represent a percentage, and then smoothed to a continuous "density" map using the kernel tool in ArcMap (Bovin, Elcim, & Wennberg, 2017; Länsstyrelsen Västerbotten, 2016). This kernel tool uses a standard Gaussian kernel function to smooth values over distance, up to a fixed threshold radius. The connectivity calculation used here, on the other hand, uses a distance-decay function. This negative exponential kernel models the fact that animals (or seeds) tend to disperse short distances most of the time, but still occasionally dislocate far (so-called long distance dispersal events). Rather than being a simple visualisation tool, the distance-decay function here models dispersal probability based on best ecological knowledge, and the connectivity maps therefore more closely resemble habitat density or connectivity as experienced by the animal itself.

Since connectivity maps per se thus may provide information complementary to value region mapping, they are provided here. Additionally to the old spruce forest connectivity used as covariate in the analyses of beetle distributions described above, connectivity for old pine forest is also provided. While it was not deemed informative for the models built here, it may have more general applicability in regional planning in the county of Dalarna. A protocol and example R script for connectivity calculations using Swedish data is available via this link.

Acknowledgements
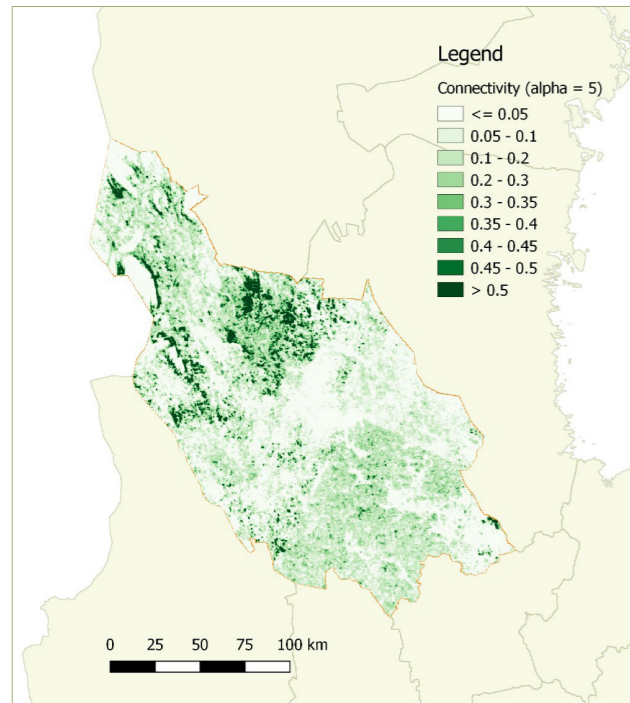
Old spruce forest connectivity (*Picea abies*)

Figure 8. Small scale connectivity based on stand age, **spruce** volume and distance, assuming a mean dispersal distance of 200m (α = 5).
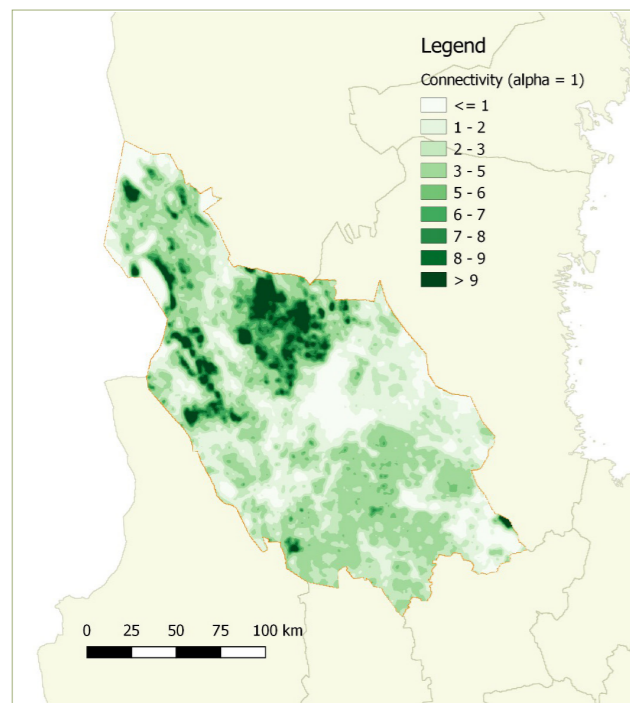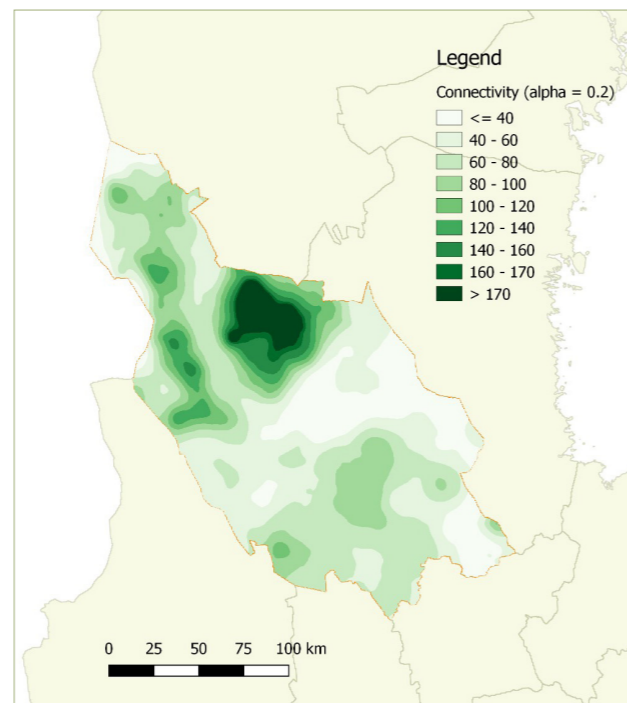
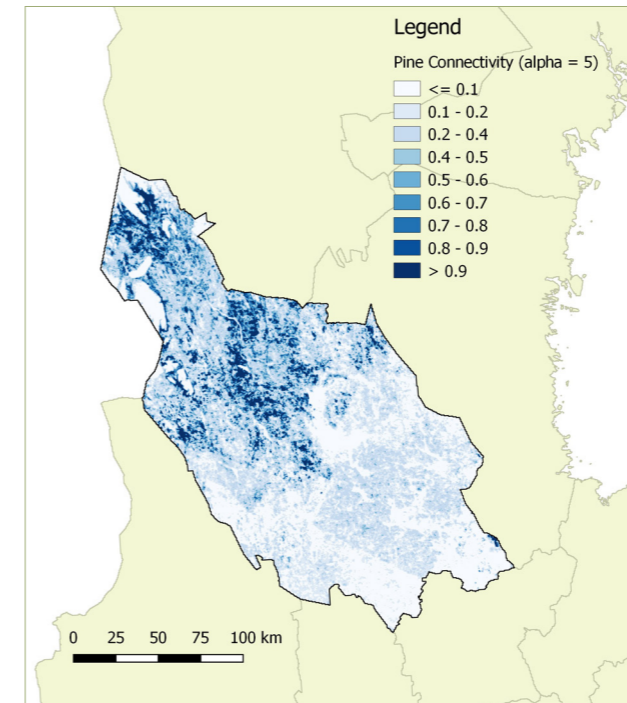## Old pine forest connectivity (*Pinus sylvestris*)

Figure 11. Small scale connectivity based on stand age, **pine** volume and distance, assuming a mean dispersal distance of 200m (α = 5).
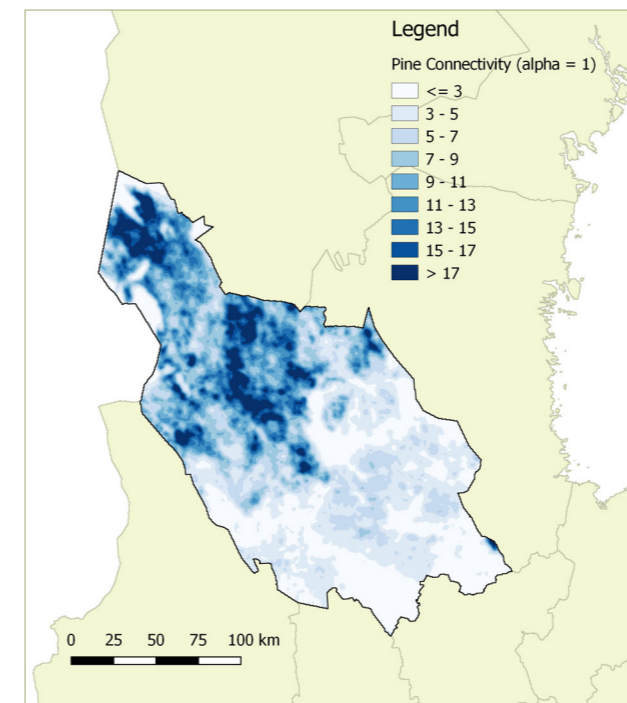

Figure 9. Intermediate scale connectivity based on stand age, **spruce** volume and distance, assuming a mean dispersal distance of 1km (α = 1).

Figure 10. Larger scale connectivity based on stand age, **spruce** volume and distance, assuming a mean dispersal distance of 5km (α = 0.2).

Figure 12. Intermediate scale connectivity based on stand age, **pine** volume and distance, assuming a mean dispersal distance of 1km (α = 1).
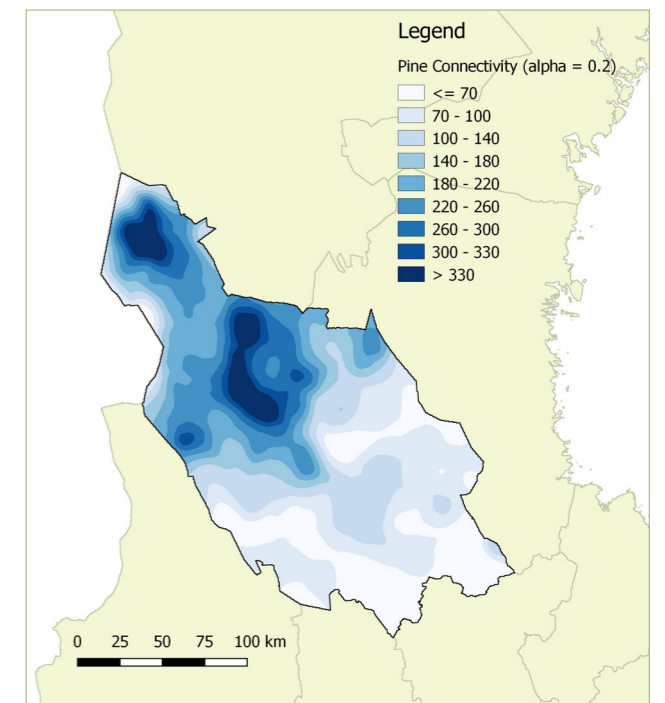

Figure 13. Larger scale connectivity based on stand age, **pine** volume and distance, assuming a mean dispersal distance of 5km (α = 0.2).

Appendix 2: Natural spruce forest specialist species list

The following table lists the species classified as natural spruce forest specialists by J. Siitonen ("JS"), used here to model specialist species richness. Also shown is the classification as indicator species for "Naturskog" following Wikars (2009) ("LW"). There is little overlap. A potential extension could be an additional model for this group.

Species (Dyntaxa)	Family	Redlist (S)	JS	LW
Corticaria interstitialis	Latrididae	NT	1	1
Corticaria polypori	Latrididae	NT	1	1
Mycetochara obscura	Tenebrionodae		1	1
Orchesia fasciata	Melandryidae	NT	1	1
Zilora ferruginea	Melandryidae	NT	1	1
Atomaria abietina	Cryptophagidae	VU	1	0
Atomaria alpina	Cryptophagidae	NT	1	0
Atomaria badia	Cryptophagidae	NT	1	0
Corticaria obsoleta	Latrididae		1	0
Cryptophagus quadrihamatus	Cryptophagidae	VU	1	0
Danosoma conspersum	Elateridae	NT	1	0
Danosoma fasciatum	Elateridae		1	0
Dolotarsus lividus	Melandryidae	RE	1	0
Enicmus apicalis	Latrididae	NT	1	0
Epuraea fussi	Nitidulidae		1	0
Epuraea laeviuscula	Nitidulidae		1	0
Epuraea oblonga	Nitidulidae	NT	1	0
Microscydmus nanus	Scydmaenidae	NT	1	0
Olisthaerus substriatus	Staphylinidae	NT	1	0
Orchesia minor	Melandryidae	NT	1	0
Pytho abieticola	Pythidae	VU	1	0
Rhizophagus grandis	Monotomidae	NT	1	0
Tachinus elegans	Staphylinidae	NT	1	0
Atrecus affinis	Staphylinidae		0	1
Atrecus pilicornis	Staphylinidae		0	1
Corticaria lateritia	Latrididae		0	1
Corticaria orbicollis	Latrididae		0	1
Dendroctonus micans	Scolytinae		0	1
Dendrophagus crenatus	Silvanidae		0	1
Epuraea deubeli	Nitidulidae		0	1
Ernobius explanatus	Anobiidae		0	1
Hallomenus binotatus	Melandryidae		0	1
Hylis procerulus	Eucnemidae		0	1
Lordithon speciosus	Staphylinidae		0	1
Lordithon trimaculatus	Staphylinidae		0	1
Microbregma emarginatum	Anobiidae		0	1
Nemozoma elongatum	Trogossitidae		0	1
Platycis minutus	Lycidae		0	1
Pteryngium crenatum	Cryptophagidae		0	1
Pyropterus nigroruber	Lycidae		0	1
Tyrus mucronatus	Staphylinidae		0	1
Xylechinus pilosus	Scolytinae		0	1

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ArtDatabanken

ArtDatabanken vid SLU är ett kunskapscentrum för Sveriges arter och naturtyper. Vår övertygelse är att större kunskap om vår natur ökar viljan och förmågan att värna den. Därför är vår strategi att ha information till hands och kommunicera den för de behov som finns. Vi stärker arbetet med svensk naturvård genom expertstöd och rådgivning, forskning och miljöanalys. En strävan är att alla som arbetar med biologisk mångfald ska tala samma språk genom att vi håller reda på artnamn, naturtyper, termer och begrepp. Här spelar rödlistan, Svenska artprojektet, Nationalnyckeln, Artportalen liksom Analysportalen en viktig roll. Vi arbetar för att den biologiska mångfalden ska bevaras så att även kommande generationer kan nyttja naturens tjänster och njuta av dess rikedom.