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Scale-specific responses of saproxylic beetles: combining dead wood surveys with data from satellite imagery

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Abstract We investigate relevant scales and cost-efficient methods for measurements of habitat for saproxylic, aspen-associated beetles, in two boreal forest landscapes in south-eastern Norway. We sampled saproxylic beetles with window traps on fresh aspen dead wood and conducted field surveys of dead wood in the surroundings (1, 2 and 3 km radius). In addition, we used maps derived from satellite imagery to extract data on forest age and volume for the same surroundings. We found that species richness of saproxylic beetles was related to dead wood volume estimated by field survey within 1 or 2 km radius from the trapping points. However, the map-derived variable describing area of forest with high levels of deciduous wood volume was the overall best predictor of species richness. The scale of response to this variable differed; species richness of all saproxylic beetles was best predicted by estimates for the 2 km radius whereas richness of species more strongly associated with aspen was best predicted by estimates for the 3 km radius. This might indicate that aspen-associated beetles disperse over larger distances than many other beetles; possibly an adaptation to the scattered distribution and ephemeral nature of aspen dead wood in boreal forests. Our results show that substrate variables must be measured at the scale that is ecologically relevant for the study organism to elicit a response. We also show that remote sensing data -often easy to obtain for large scales—can be used to complement studies of scale-specific responses and thus improve conservation measures for saproxylic beetle species.

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Introduction

Most of the threatened species in Fennoscandia are found in the forest (Gärdenfors 2010; Kålås et al. 2010; Rassi et al. 2010) and several of these species seem to be negatively influenced by forest management (Kålås et al. 2010). Timber harvest by clear-cutting and thinning significantly reduces the volume of dead wood in the forest (Gibb et al. 2005; Siitonen 2001) and correspondingly reduces the diversity of saproxylic species (Lassauce et al. 2011), since these species are dependent on dead wood (Speight 1989). Several attempts have been made at determining threshold values for the dead wood volume required by saproxylic species (Müller and Bütler 2010), but these analyses have frequently been restricted to a single spatial scale (Lindenmayer and Luck 2005). Studies of the relationship between saproxylic species richness and dead wood abundance can get very different results depending on the scale of the dead wood survey (Sverdrup-Thygeson et al. 2014b).

While some saproxylic insects seem to be mainly affected by habitat amount in the forest stand they live in (Hedin et al. 2008), other species might depend on dead wood availability within the surrounding landscape or region (Götmark et al. 2011). Presumably, scale-specific responses reflect the dispersal capacity of the study organism (Holland et al. 2005). However, we only have

estimates of dispersal capacity for a few saproxylic insect species (Ranius 2006). Furthermore, distribution of resources can influence dispersal and thus relevant scale for the species in a specific landscape (Dennis et al. 2006; Dover 1996). When studying little known species or species richness one should ideally obtain measures of dead wood volume at a range of spatial scales and fit these against the response variable to determine the scale where their correlation is strongest (Fahrig 2013; Holland et al. 2004). However, since dead wood surveys require time-consuming field work, they are rarely conducted at multiple or large scales (Müller and Bütler 2010). Furthermore, when dead wood surveys are conducted at multiple scales, survey method often changes with increasing scale, which complicates interpretation (Sverdrup-Thygeson et al. 2014b).

In contrast to field surveys, remote sensing data, e.g. from satellite imagery, can provide variables such as forest volume for multiple and large spatial scales without much effort and these variables can be used to study the scale-specific response of saproxylic species (Holland et al. 2004). If remote sensing variables such as forest volume can reflect dead wood volume, they might complement or in some cases even replace dead wood surveys. This would allow for studies of the response of saproxylic species to habitat abundance at a wide range of scales, which could contribute to ecologically sound conservation guidelines for this important species group.

In the present study we used data for multiple and large scales from a dead wood field survey and from maps based on remote sensing data from satellite imagery to explain the species richness of saproxylic beetles. Beetles were sampled from fresh aspen (Populus tremula L.) dead wood, a keystone resource in boreal forests (Tikkanen et al. 2006). The responses of all saproxylic species and the subgroup aspen-associated saproxylic species were analysed separately.

The main questions asked were:

(1) For saproxylic beetles in aspen, what is the most relevant ecological scale for measurements of surrounding habitat?

(2) Can data on forest volume derived from satellite imagery complement field studies of dead wood, and how can this benefit future conservation of saproxylic beetles?

Methods

This study is part of a larger study aiming to compare the assemblages of insects and fungi in different conservation set-asides in forest (Birkemoe and Sverdrup-Thygeson

2015; Sverdrup-Thygeson et al. 2014a). Therefore, our insect data comes from flight interception traps (with windows 20 cm × 40 cm, a funnel and a container underneath filled with ethylene glycol and detergent) on experimentally added aspen wood units (1 m long, 20 cm diameter) at eight sites within nature reserves (NAT), eight sites within woodland key habitats (WKH) and eight sites within retention patches (RET) in two different landscapes, i.e. 48 sites in total. Each woodland key habitat covered on average 1 ha of forest, while retention patches consisted of smaller clusters of trees retained after clear-cutting covering on average less than 0.1 ha. Whereas the sites in WKH and RET were geographically dispersed in the two landscapes, there was only one NAT in each landscape. The insect sampling sites within this set-aside were placed with a minimum distance to each other of 200 m to avoid window traps interfering with each other. The wood units were positioned as standing dead wood in pairs separated by 1.5 m at each of the sites. A flight interception trap was attached to each wood unit in 2007, 2008 and 2009, all years from mid-May to mid-August. Data from the two traps at each site for all 3 years was combined in the analysis. All beetles were identified to species, and saproxylic species and the subgroup aspen-associated saproxylic species were defined based on the database of Dahlberg and Stokland (2004).

Study areas

The two study areas, both covering approximately 100 km^2, were in the southern or middle boreal vegetation zone (Moen 1998) and consisted mainly of mixed coniferous managed forest. Norway spruce (Picea abies (L.) H.Karst.) was the dominant tree species, with Scots pine (Pinus sylvestris L.), birch (Betula pubescens Ehrh.) and aspen (Populus tremula L.) as subdominants. The first area was Losby Bruk in Lørenskog municipality (Lat.59.89, Long.10.97, 150–300 masl). It included Østmarka nature reserve which covers 17.8 km^2. The second area was Selvik Bruk in Drammen municipality (Lat.59.68, Long.10.12, 130–200 masl), including Presteseter nature reserve which covers 3.2 km^2. The managed forest in both areas was certified by PEFC (the Programme for the Endorsement of Forest Certification schemes, Norway, pefcnorway.org, accessed 16.12.2014) and the Norwegian standard for sustainable forestry, "Living Forests" (Anon 2006).

Dead wood field survey

The dead wood (DW) survey was conducted during the summer of 2012. A grid of dead wood survey plots (0.04 ha) within at least 3 km radius of each insect sampling site was established (Fig. 1). The survey plots were

Fig. 1 The study area Selvik with insect sampling sites in nature reserve (NAT) marked with *squares*, retention patches (RET) marked with *triangles*, woodland key habitats (WKH) marked with *circles* and dead wood (DW) survey *plots* (*black dots*). The map data shows m³ wood in living trees per ha as derived from satellite imagery ("SAT-skog", see Remote sensing data). Areas not registered as forest are *coloured white*
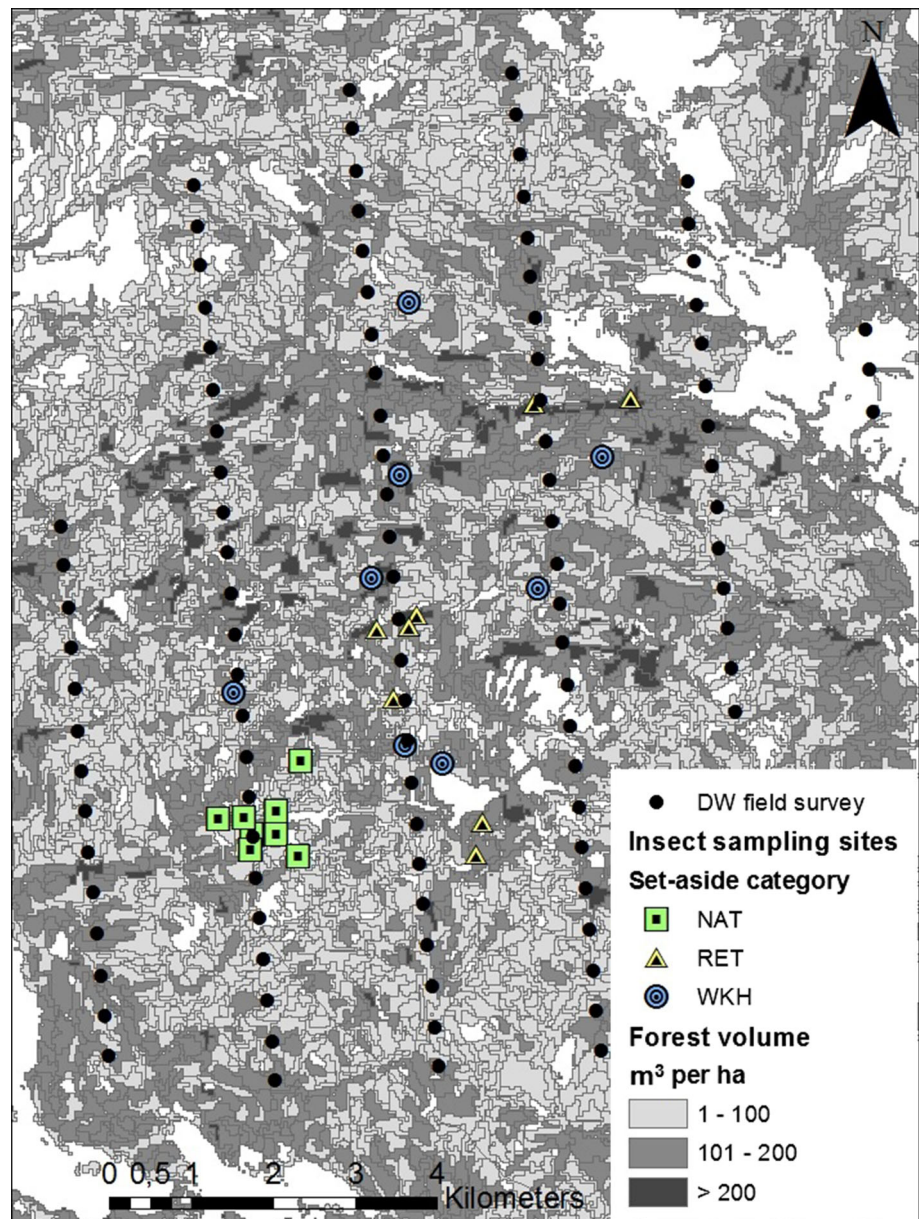
placed with 500 m intervals in the north–south direction and 2 km intervals in the east–west direction, since the terrain was easier to follow in a north–south direction. A total of 104 plots within an area of 100 km² were surveyed in Selvik and 119 plots within an area of 113 km² were surveyed in Losby. At each plot, any lying or standing dead wood longer or taller than 1 m and with a diameter of at least 10 cm was recorded. Diameter was measured at breast height (approximately 1.3 m from base) using a calliper. Length was measured using a measuring tape to the closest half meter, while height was approximated by observation to the closest meter. When logs extended outside the boundaries of the survey plot, only the part inside the plot was registered. Each log or snag was identified as spruce,

pine, aspen or none of these (the last group consisted effectively of other deciduous trees, mostly birch). Decay stage was recorded for each dead wood object as one of five decay classes, based on the classification used by Høiland and Bendiksen (1996);

1. Wood hard, bark intact, both larger and smaller branches intact.
2. Wood hard, bark beginning to break up, smaller branches beginning to break off.
3. Wood soft up to 3 cm depth, some bark lost, smaller branches rare.
4. Wood soft for more than 3 cm depth, little bark, larger branches beginning to break off.

5. Wood soft all the way through, little or no bark, few or no branches.

Volume of each dead wood object was calculated as in Fridman and Walheim (2000); $V = (\pi d^2/4)$ l, where V is volume of the dead wood object, d is diameter in meters and l is length or height in meters. Volume of all dead wood objects at each survey plot was expressed per ha. For each insect sampling site, the average DW volume per ha within a 1 km (covering 3.1 km^2), 2 km (covering 12.6 km^2) and 3 km (covering 28.3 km^2) radius was calculated. The DW volume was split into tree species (DW Spruce, DW Aspen, DW Pine, DW Other), decay stages (DW Decay 1, DW Decay 2, DW Decay 3, DW Decay 4, DW Decay 5) and trunk diameter groups (SmallDiam (10–20 cm), MidDiam (21–30 cm) and LargeDiam (31–65 cm), 65 cm being the largest diameter recorded).

The circular areas surrounding the insect sampling sites overlapped to a varying degree. Spatial overlapping of explanatory variables is often considered problematic due to the autocorrelation it causes among the predictors (Holland et al. 2004), but it has also been argued that interdependent predictors does not necessarily mean interdependent errors which is the critical assumption for statistical modelling (Zuckerberg et al. 2012). In this study, most of the overlapping areas occurred in the nature reserves, which was an unavoidable consequence of the applied study design.

Remote sensing data

Map layers ("SAT-skog") describing the forests in the study areas were downloaded from the servers of the Norwegian Forest and Landscape Institute (skogogland-skap.no, accessed 19.10.2012). These data were ultimately derived from satellite images of the landscape (Gjertsen 2007; Gjertsen and Nilsen 2012), and we used three of the attributes from this dataset: *Forest volume* (m^3 per ha), *deciduous forest volume* (m^3 per ha) and *forest age*. These attributes only included volume of living trees, not dead wood. We categorized all attributes into three levels (Table 1), and the areas covered by each level of the three forest attributes within each radius (1, 2 and 3 km from all insect sampling sites) were used as explanatory variables in the analysis of species richness. The calculations were carried out in ArcMap version 10.1 and Microsoft Excel 2007. We also calculated the *total area of forest* ("Total Forest") for each of the three radii of the insect sampling sites.

While it might have been preferable to test more than three radii, by increasing radius with smaller increments up to the 3 km limit, this would have necessitated the use of software like Focus (Holland et al. 2004), which to our

Table 1 Variables of forest volume and age based on satellite imagery derived data calculated for 1, 2 and 3 km radius areas around the insect sampling sites

Variable	Description
Forest volume	
LowVolForest	1–100 m^3 wood per ha
MidVolForest	101–200 m^3 wood per ha
HighVolForest	>200 m^3 wood per ha
Deciduous forest volume	
LowDeciForest	0–35 m^3 deciduous wood per ha
MidDeciForest	36–75 m^3 deciduous wood per ha
HighDeciForest	>75 m^3 deciduous wood per ha
Forest age	
YoungForest	1–40 years
MidAgeForest	41–80 years
OldForest	>80 years

knowledge does not facilitate inclusion of categorical variables like landscape and set-aside category in the analysis. Furthermore, the resolution of the field survey was probably not high enough to separate radii by smaller increments.

Statistical methods

To explain the richness of saproxylic and aspen-associated saproxylic species with variables from the dead wood survey and from the satellite imagery maps, we first fitted simple linear regressions with single explanatory variables and the bivariate design variables (Dalgaard 2008) Landscape (Losby = 1, Selvik = 0) and Set-aside (NAT = 1, WKH and RET, grouped due to no difference in preliminary analysis, = 0). Variables were log-transformed or square-root transformed to achieve normality if needed. Explanatory variables with a *p* value above 0.10 in the simple linear regression were excluded from further analysis. For those variables that had a *p* value below 0.10 on several of the spatial scales (the 1, 2 and 3 km radii), the spatial scale at which the variable had the highest adjusted R^2 was chosen (only relevant for map-derived data). The remaining variables (Appendix Tables 4 and 5) were entered in an initial multiple regression model including the design variables. Variance inflation factors (VIF) were checked for the initial models, and variables with VIFs exceeding three were excluded (Zuur et al. 2013). Stepwise selection in both directions (backward and forward selection with the stepAIC-function from the MASS package) based on the Akaike information criterion (Akaike 1974) was used to select the optimal subset of the variables for the final multiple regression models. The

Table 2 Results of model selection (multiple linear regression) showing the optimal models for explaining species richness of all saproxylic beetles and the subset of aspen-associated saproxylic beetles

Variable	Source	Scale	Estimate	Std. error	t-value	*p* value
Intercept[a]			4.04	6.12	66.05	<0.001
Landscape			−0.31	0.06	−5.32	<0.001
Set-aside			−0.28	0.07	−3.90	<0.001
MidDeciForest	Satellite imagery	2 km	2.46×10^{-7}	5.95×10^{-8}	4.14	<0.001
DW Decay 1	Field survey	2 km	0.03	0.01	2.39	0.022
DW Decay 3	Field survey	1 km	7.02×10^{-3}	3.82×10^{-3}	1.84	0.073
DW Pine	Field survey	2 km	0.02	0.01	1.69	0.099
Intercept[b]			−1.29	1.29	−1.00	0.323
Landscape			−9.56	2.07	−4.62	<0.001
HighDeciForest	Satellite imagery	3 km	1.44×10^{-4}	2.56×10^{-5}	5.63	<0.001
Total Forest	Satellite imagery	1 km	1.63×10^{-5}	4.74×10^{-6}	3.45	0.001
DW Decay 1	Field survey	2 km	1.00	0.31	3.22	0.003
DW Decay 5	Field survey	1 km	1.19	0.54	2.21	0.033

N = 47 sites in all analyses

[a] Response: log(species richness of saproxylic beetles); AIC final model: −161.48 (Initial: −157.08). Adjusted R^2: 0.66

[b] Response: species richness of aspen-associated saproxylic beetles; AIC final model: 161.22 (Initial: 165.18). Adjusted R^2: 0.64

model selection process (stepAIC) was free to exclude the design variables from the multiple regression models. R^2 of the final models was partitioned among the variables by the calc.relimp-function from the relaimpo package (Grömping 2006) using the LMG method (Lindeman et al. 1980). This function also calculates confidence intervals for relative importance by bootstrapping the data (1000 samples).

Unless otherwise stated, the significance level used was α = 0.05. All data was analyzed in R version 2.15.0.

Results

Insect sampling

The insect sampling yielded 512 different beetle species and a total of 11,159 individuals. This included 345 saproxylic species (9304 individuals), of which 138 species (5594 individuals) were considered aspen-associated.

Dead wood field survey

Spruce dead wood constituted about 72 % of the total registered dead wood volume in both landscapes, while 1.8 % in Losby and 4.5 % in Selvik was aspen dead wood. Only 5 % of the recorded DW objects had a diameter of more than 30 cm. Mean volume of dead wood per ha (±SE) was 23.1 ± 37.5 m³ in Selvik and 25.0 ± 47.1 m³ in Losby. Mean values of all dead wood and map-derived

variables surrounding the insect sampling sites can be found in Online Resource 1.

Explaining species richness of saproxylic beetles

Area of forest with medium or high volumes of deciduous wood (MidDeciForest or HighDeciForest) and dead wood in decay stage 1 significantly explained variation in species richness of all saproxylic beetles, as well as the aspen-assosiated subgroup, in the final multiple regression models (Table 2). In addition, total forest area and dead wood in decay stage 5 significantly explained variation in species richness of aspen associated species. For the aspen associated species, the high volume of deciduous wood was important at a 3 km radius, whereas the medium volume of deciduous wood was significant at a 2 km radius when all saproxylic beetles were included in the model. All other survey or map-derived variables in the models were important at a 1 or 2 km radius.

Partitioning the variation explained by the two optimal models, approximately 30 % of R^2 was explained by area of forest with medium volume of deciduous wood (2 km radius) in the model with all saproxylic species (Fig. 2). The comparable proportion explained by area of forest with high volume of deciduous wood (3 km radius) for the aspen associated species was 45 % (Fig. 3). For both species groups, the other map-derived and dead wood survey variables explained a comparatively smaller proportion than the deciduous wood volume (15–5 %). The design variables were more important in the model with total
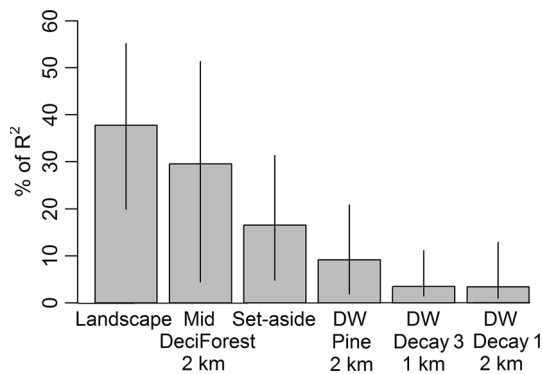
Fig. 2 Estimated proportion of R^2 explained by each predictor variable included in the optimal model explaining saproxylic beetle species richness (Table 2). $R^2 = 70.56$ % (non-adjusted). 95 % confidence intervals were made by resampling according to the bootstrapping procedure
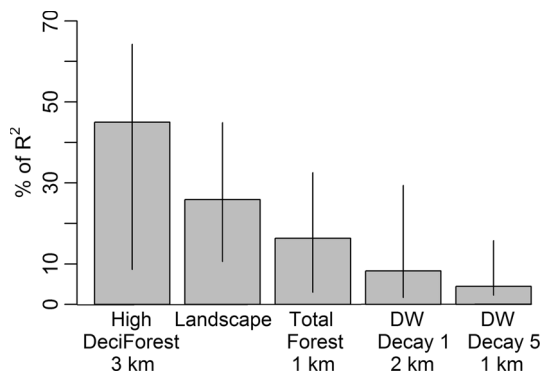

Fig. 3 Estimated proportion of R^2 explained by each predictor variable included in the optimal model explaining aspen-associated saproxylic beetle species richness (Table 2). $R^2 = 67.50$ % (non-adjusted). 95 % confidence intervals were made by resampling according to the bootstrapping procedure

species richness, than in the model with the aspen associated subgroup.

Dead wood surveyed in field correlated with remote sensing data

Dead wood volume surveyed in the field was correlated with the volume of living trees derived from satellite imagery (Fig. 4).

As the beetles were sampled from dead aspen, aspen dead wood was of special interest. The volume of aspen dead wood as measured in the survey was positively correlated with area of forest containing medium (MidDeciForest) or much (HighDeciForest) deciduous wood, and negatively correlated with area of forest containing little deciduous wood (LowDeciForest; Table 3).
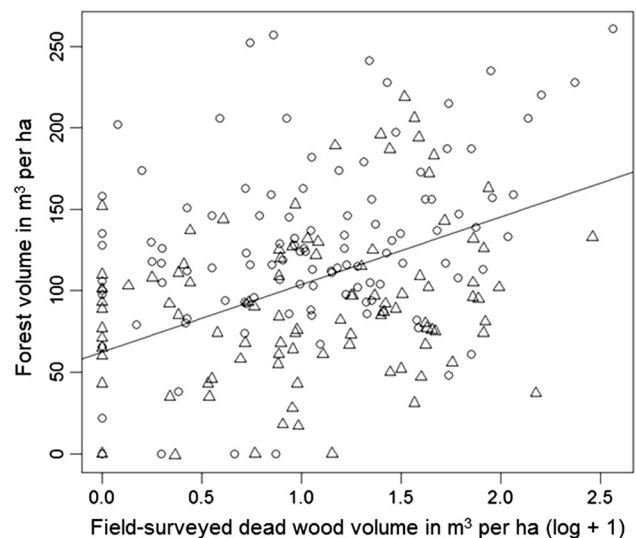

Fig. 4 Linear regression of dead wood volume in m^3 per ha surveyed in field plotted against forest volume in m^3 per ha derived from satellite imagery for each survey *plot* in Losby (*circles*) and Selvik (*triangles*). Estimate ± SE = 17.997 ± 2.353, t value = 7.649, p value = <0.001, adjusted $R^2 = 0.201$, N = 229, df = 227

Discussion

Relevant scales for saproxylic beetles in aspen

Previous studies have shown diverging patterns of scale effects for species richness of saproxylic beetles (Sverdrup-Thygeson et al. 2014b). This is not surprising as different functional groups and single species may differ in their responses to spatial resources (Holland et al. 2004; Ranius et al. 2011). In the present study, we found that aspen-associated species responded to habitat availability at larger scales than all saproxylic species including both generalists and specialists of other tree species; species richness of aspen-associated beetles was best explained by volume of deciduous wood within a 3 km radius, while saproxylic species richness responded to volume of deciduous wood within a 2 km radius.

The scale of maximum response to habitat is probably connected to both the ecology of the insect species and of the habitat itself. European aspen is a disturbance-dependent pioneer species which rarely forms stable forest stands and is usually found scattered in the landscape in low densities (Kouki et al. 2004; Latva-Karjanmaa et al. 2007). Aspen dead wood constituted 1.8–4.5 % of the dead wood surveyed in the present study, which clearly indicates the low amount of aspen within our study area. Thus, aspen-associated species probably have to disperse further in search of suitable substrate than generalist saproxylic species or spruce specialists. Furthermore, since aspen dead wood is a relatively ephemeral habitat, aspen-associated saproxylic

Table 3 Spearman's rank correlation between field-surveyed volume of aspen dead wood and different levels of deciduous wood derived from satellite images (see Table 1 for definitions)

Radius around each site	Amount of deciduous wood from satellite imagery	Correlation with field-surveyed aspen dead wood (rho-value)	*p* value
1 km	LowDeciForest	−0.101	0.499
	MidDeciForest	0.508	**<0.001**
	HighDeciForest	−0.010	0.506
2 km	LowDeciForest	−0.270	0.067
	MidDeciForest	0.467	**0.001**
	HighDeciForest	0.226	0.127
3 km	LowDeciForest	−0.344	**0.018**
	MidDeciForest	0.176	0.238
	HighDeciForest	0.500	**<0.001**

All variables were measured within 1, 2 or 3 km radius from each insect sampling site. Significant *p* values (<0.05) in bold

species would be expected to have greater dispersal capacity than species associated with more stable habitats (Nilsson and Baranowski 1997; Southwood 1977; Wikars 1997).

Økland et al. (1996) found that aspen dead wood at a 4 km^2 scale was the most important predictor for species richness of aspen-associated species, whereas dead wood at smaller scales were of less importance. Ranius et al. (2011) further found that species richness of aspen specialist beetles responded most strongly to substrate availability within 93 m radius of their insect sampling sites. The scales used by Økland et al. (1996) and Ranius et al. (2011) were much smaller than those found to be important in our study, where species richness of aspen-associated beetles was best explained by volume of deciduous wood within a 28 km^2 area (3 km radius). Their largest scales corresponded to our smallest scale, the 1 km radius covering 3 km^2. As Økland et al. found that the largest scale was most important to aspen-associated species, they might have found stronger responses to even larger scales. For Ranius et al. (2011), the difference in accuracy between the detailed survey within 100 m radius and the stand level data based on sample plots from 100 to 1000 m radius might have affected the fit of the response in this investigation and explain the discrepancy from our results. However, different distribution of the substrate in different landscapes can probably result in variable responses to scale, within the limits set by the species' dispersal capacities (Sverdrup-Thygeson et al. 2014b).

Large scales have been found to be important for saproxylic species in a previous study of oak specialists (Bergman et al. 2012). Bergman et al. (2012) conducted their study in an area where all large or hollow oaks had been registered, allowing them high accuracy at all scales (30–5284 m centred on their insect sampling sites) within this area. The species richness of oak specialist beetles was best explained by the density of hollow oaks within a radius of 2284 m. Similarly, the saproxylic beetles sampled

from fresh aspen dead wood in our study responded to dead wood in decay stage 1 within a 2 km radius.

The choice of scale in studies of saproxylic beetle richness can be crucial for the conclusions. Some studies have failed to find a relationship between saproxylic species richness and dead wood volume, but in these cases dead wood was surveyed at very small scales (100 and 500 m^2) (Gibb et al. 2006; Siitonen 1994). In our study, dead wood volume within 1 and 2 km radius around the insect sampling sites was correlated with species richness of saproxylic and aspen-associated beetles in aspen dead wood, but each dead wood variable was only significant to saproxylic species richness at one of the three scales tested. Thus, the correlation between dead wood volume and saproxylic species richness would have been missed if dead wood had been surveyed at a scale too small or too large to be relevant to the saproxylic species in question. This is important knowledge that should be taken into account when new studies are designed.

It is also important to define the relevant resources for the study organisms in question precisely, in order to provide sound data for management and conservation purposes. We found that the relationship between saproxylic species richness and dead wood volume was stronger for specific types of dead wood than for dead wood in general. For instance, dead wood in decay stage 1 was included in the optimal models for species richness of both saproxylic and aspen-associated saproxylic beetles. As these species were sampled from recently dead aspen wood, it is logical that the abundance of fresh dead wood within the surrounding area was more relevant than total abundance of dead wood, which included dead wood in decay stages that were probably not usable for many of these species.

Remote sensing data can benefit multiscale studies

The forest variables derived from satellite images proved to be good predictors for species richness of saproxylic

beetles, as has also been shown for remote sensing forest variables in previous studies (Andersson et al. 2012; Gibb et al. 2006; Holland et al. 2004; Müller et al. 2014). We confirmed that volume of deciduous wood on the maps derived from satellite images was correlated with volume of aspen dead wood surveyed in the field. Thus, although volume of aspen dead wood per se was positively correlated with species richness of aspen-associated beetles, the map-derived variable representing areas with high volumes of deciduous wood was a better predictor, probably because it described the surrounding abundance of habitat more accurately than the relatively few dead wood survey plots.

The fact that forest volume and dead wood volume correlate is expected, but we are unaware of other studies that compare forest volume from satellite images with data of dead wood volume from field surveys. Dead wood field surveys are labour-intensive, so efficient direct or indirect remote sensing alternatives are valuable to research and management. At present, data from airborne laser scanning (ALS) can be used for both direct and indirect dead wood measurements, but the accessibility is low and the precision in direct measurements of dead wood is still limited (Bater et al. 2009; Blanchard et al. 2011; Maltamo et al. 2014; Pesonen et al. 2008). Variables derived from satellite imagery on the other hand are often accessible for no cost and can easily be obtained for a large range of scales.

We showed that forest volume derived from analysis of satellite imagery was correlated with field surveyed dead wood volume, and that the satellite imagery derived variables were strong predictors for saproxylic species richness

in aspen dead wood. Thus, forest volume derived from satellite imagery might be used as a proxy for dead wood volume in studies of the scale-specific response of saproxylic insects to substrate abundance at multiple and large spatial scales. Such research could both enhance our knowledge of the dispersal capacity of saproxylic insects, while also providing a basis for choosing ecologically relevant scales for dead wood field surveys.

Conclusion

This study has underlined the need to use ecologically relevant scales in research and management, and suggested the use of remote sensing data in research as an effective method to narrow down the range of relevant scales. The use of ecologically relevant spatial scales in research and management can lead to more efficient and successful conservation measures for biodiversity.

Appendix

See Tables 4 and 5.

Table 4 Linear regression models of log saproxylic beetle species richness explained with field-surveyed dead wood volume and map-derived area of forest categories

Variable	Radius around each site	Estimated β	p value
Field-surveyed volumes of dead wood (m³ per ha)			
DW Total	1 km	0.002	**0.042**
DW Aspen	2 km	0.085	0.058
DW Pine	2 km	0.026	**0.050**
DW Decay 1	2 km	0.026	**0.038**
DW Decay 3	1 km	0.009	0.058
DW MidDiam	1 km	0.005	0.064
Map-derived area of forest categories (m²)			
Total Forest	1 km	0.385×10^{-6}	0.057
YoungForest	2 km	0.109×10^{-6}	**0.031**
MidAgeForest	1 km	0.214×10^{-6}	**0.004**
OldForest	3 km	-0.029×10^{-6}	**0.012**
MidVolForest	1 km	0.333×10^{-6}	**0.005**
LowDeciForest	3 km	-0.069×10^{-6}	**0.021**
MidDeciForest	2 km	0.227×10^{-6}	**0.002**
HighDeciForest	2 km	5.850×10^{-6}	**0.002**

Design variables (landscape and set-aside category) are included in all models. Variables were measured within 1, 2 or 3 km radius from each insect sampling site, except the design variables. Significant p values (<0.05) in bold

Table 5 Linear regression models of aspen-associated saproxylic beetle species richness explained with field-surveyed dead wood volume and map-derived area of forest categories

Variable	Radius around each site	Estimated β	p value
Field-surveyed volumes of dead wood (m^3 per ha)			
DW Total	1 km	0.073	0.091
DW Aspen	2 km	4.882	**0.002**
DW Pine	2 km	0.926	0.053
DW Decay 1	2 km	0.924	**0.037**
DW Decay 5	1 km	1.643	**0.031**
Map-derived area of forest categories (m^2)			
Total Forest	1 km	17.380×10^{-6}	**0.036**
YoungForest	2 km	3.645×10^{-6}	**0.046**
MidAgeForest	1 km	7.786×10^{-6}	**0.004**
OldForest	3 km	-0.873×10^{-6}	**0.033**
MidVolForest	1 km	14.600×10^{-6}	**0.001**
LowDeciForest	3 km	-3.070×10^{-6}	**0.004**
MidDeciForest	3 km	5.709×10^{-6}	**<0.001**
HighDeciForest	3 km	133.200×10^{-6}	**<0.001**

Design variables (landscape and set-aside category) are included in all models. Variables were measured within 1, 2 or 3 km radius from each insect sampling site, except the design variables. Significant p values (<0.05) in bold

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