Responses of tree-associated species to forest management

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Abstract

In forests there are many organisms that depend on trees. When forests are managed the environment for tree-associated species changes, and a lot of their habitat is lost. In boreal forests it is common with clearcutting, where almost all trees are harvested. In addition, with an increased demand for biofuel, the extraction of tree tops, branches and stumps is expanding. At the same time, some trees are retained in the open conditions after clearcutting for conservation purposes. In the boreal forests of Sweden, tree species richness is poor but the richness of flora and fauna of species associated with trees is high. I have analyzed the responses of epiphytic lichens to the environmental change on retained trees when the surrounding forest is clearcut. I have also analyzed the responses of saproxylic beetles to stump extraction in the landscape. Overall, there is a wide variety of species responses, and they can be difficult to predict. Sometimes tree traits, such as successional strategy, can help predict the responses of tree-associated species to environmental change. Sometimes the traits of the tree-associated species themselves can drive their response to environmental change. For lichens, species associated with the late-successional Norway spruce occur less on trees retained at clearcuts than on trees in closed-canopy forest. The pattern is the opposite for lichen species associated with early-successional tree species. Some lichen traits can also drive species responses to the open environment after clearcutting; characteristics that seem to increase the probability of lichens to occur on trees retained at clearcutting are a foliose or fruticose growth form, thallus sunscreen, or asexual reproduction. The responses of saproxylic beetles to landscape stump extraction varies, with predators more negatively affected than lower trophic levels. In an attempt to elucidate different aspects of the distribution of responses, I suggest ways to develop the concept of response diversity. The diverging responses of species to forest management entails different requirements for their conservation.

Keywords: Bayesian hierarchical models, biodiversity, community ecology, epiphytic lichens, forest ecology, response diversity, saproxylic beetles, species models, stump harvest, tree retention

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Skogsbrukets påverkan på trädberoende arter

Sammanfattning

Många organismer i skogar är beroende av träd. När skogar brukas förändras miljön för arterna och mycket av deras habitat går förlorat. I boreala skogar är kalhuggning vanligt och med ökad efterfrågan på biobränsle så har uttaget av trädtoppar, grenar och stubbar ökat. Samtidigt så sparas en del träd av naturvårdshänsyn i de öppna miljöer som bildas efter kalhuggning. I de svenska boreala skogarna är trädartrikedomen låg men artrikedomen av växter, djur och svampar kopplad till träden är hög. Jag har analyserat hur epifytiska lavar svarar på den miljöförändring som uppstår på kvarlämnade träd när den omgivande skogen huggs ner. Jag har också analyserat hur skalbaggar i död ved påverkas av att stubbrytning sker i det omgivande landskapet. Det är generellt stor variation i hur arter svarar på skogsbruksåtgärder och det kan därför vara svårt att förutse vilka arter som kommer att påverkas negativt. I vissa fall kan trädens egenskaper, till exempel deras successionsstrategi, bidra till att det går att förutse hur arter kopplade till träden svarar på en miljöförändring. I andra fall kan arternas egna egenskaper avgöra hur de svarar på miljöförändringen. För lavar så är arter kopplade till gran, ett sekundärträd i successionen, vanligare på träd inne i skog än träd sparade på hyggen. För lavar kopplade till pionjärträden asp, björk och tall, så är mönstret det motsatta, dvs. de är vanligare på hyggesträd än på träd i skog. En del egenskaper hos lavar kan också påverka hur de svarar på den mer öppna miljö som bildas runt träd som lämnats vid avverkning. Solskydd i lavbålen, en förmåga att reproducera sig asexuellt och ett växtsätt som blad- eller busklav verkar vara egenskaper som ökar sannolikheten att en lav förekommer på hyggesträd. Hur skalbaggar påverkas av stubbskörd i landskapet varierar också stort mellan arter men predatorer verkar påverkas mer negativt än andra arter. För att belysa fler aspekter av hur arter svarar på förändring så föreslår jag att konceptet responsdiversitet utvecklas. Arter som skiljer sig i sina svar på skogsbruk ställer olika krav på naturvårdsåtgärder.

Nyckelord: artmodeller, Bayesianska hierarkiska modeller, biodiversitet, epifytiska lavar, naturhänsyn, responsdiversitet, samhällsekologi, skalbaggar i död ved, skogsekologi, stubbskörd

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Dedication

To forests, near and far.

There's the story, then there's the real story, then there's the story of how the story came to be told. Then there's what you leave out of the story. Which is part of the story too.

Margaret Atwood

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List of publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Ranlund, Å.* and Hylander, K. Response diversity when the environment changes: examining the composition of responses (submitted)

II Ranlund, Å.*, Hylander, K., Johansson, V., and Gustafsson, L. Tree taxon association predicts epiphytic lichen responses to environmental change (submitted)

III Ranlund, Å.*, Johansson, V., Hylander, K., Gustafsson, L., and Svensson, M. Epiphyte trait distributions respond to environmental change, and interact with tree taxa and region (manuscript)

IV Ranlund, Å. and Victorsson, J.* Predatory saproxylic beetles are more negatively affected by landscape stump extraction than lower trophic levels (submitted)

* Corresponding author.

The contribution of Åsa Ranlund to the papers included in this thesis was as follows:

I Idea and writing with co-author, first author of the paper.

II Questions, hypotheses, writing, and analyses with co-authors, first author of the paper.

III Analyses. Questions, hypotheses, and writing with co-authors, first author of the paper.

IV Analyses. Writing with coauthor, first author of the paper.

1 Trees at the center of the forest

In any definition of a "forest" there will be trees. When forests are managed for production it is largely for their trees, and many organisms that live in forests do so because of the trees. Sometimes these two aspects – of forest management and forest dwellers – clash. They clash because trees ideal for forestry are not at the same time ideal for many of the organisms in forests that depend on trees.

A multitude of species from different organism groups, such as vascular plants (e.g. orchids), lichens, mosses, saproxylic insects, and fungi, are associated with trees (Alexander *et al.* 2006). When forest management alters tree species composition, light conditions or tree age demography, for example, many of those organisms are affected. Since a lot of species associated with trees are rare, or their ecology is not well-known, the effects of forestry actions on them can be difficult to assess.

Species vary widely in their abilities to cope with different environmental conditions. Within an organism group there are therefore usually different responses to the same environmental change. For species rich groups it can be challenging to predict which species that will respond positively or negatively to an environmental change, such as altered management.

Globally there are forests with high richness of trees as well as a very high richness of species associated with them. In some forests, such as in the boreal forests of northern Europe, tree species richness is low, but the flora and fauna associated with trees is high (Bernes 2011). My thesis focus is on the lichens and beetles associated with trees in these latter forests.

1.1 Boreal forests

Boreal forests are one of the largest forest biomes on earth (Keenan *et al.* 2015). In them, disturbances over large areas, such as fire, storms, and pest outbreaks, are common (e.g. Bergeron *et al.* 1998). In relation to these disturbances, trees of different taxa often have typical occurrence patterns (Kneeshaw and Bergeron 1998, Bergeron 2000, Kuuluvainen 2009, Shorohova *et al.* 2009). Some dominate early after disturbance (pioneer tree taxa) in more open, irradiance-intensive, conditions, like the birches (*Betula spp.*), European aspen (*Populus tremula* L.), and Scots pine (*Pinus sylvestris* L.) do in northern Europe (Shorohova *et al.* 2009). There are also tree traits that can increase survival of forest disturbances, for example the thick bark of many old pines, which make them more resistant to fire and can allow them to dominate in the exposed conditions after disturbance (Agee 1998). Other tree taxa instead regenerate best under shaded conditions and become increasingly dominant in closed-canopy conditions (late-successional), but are sensitive to large-scale disturbances, such as Norway spruce (*Picea abies* (L.) H. Karst) (Shorohova *et al.* 2009).

In Sweden the conifers Norway spruce and Scots pine dominate boreal forests (Jansson 2011). Among deciduous trees, the birches (*Betula pendula* Roth and *B. pubescens* Ehrh.) are the most common, followed by European aspen (Swedish Forest Agency 2014). A similar set of tree species has dominated Swedish boreal forests for at least a few thousand years (Gustafsson and Ahlén 1996), though the tree composition has shifted towards more pine and spruce with forest management for industrial purposes (Östlund *et al.* 1997).

1.2 Forest management

During the last centuries, fire prevention, active regeneration, and management measures from industrial forestry, have altered tree-species composition, successional pathways and the environmental conditions in forest stands (Östlund *et al.* 1997). Today, managed forests in boreal northern Europe are characterized by even-aged, dense stands. More than 90% of the productive forest land in Sweden is used for production forestry, in which forests are used for industrial purposes and harvested with the clearcutting method (Swedish Forest Agency 2014). With forest management there has been a drastic decrease in the number of old trees, the proportion of deciduous trees, and the amount of deadwood, with adverse effects for the species that depend on these structures (Esseen *et al.* 1997, Östlund *et al.* 1997).

In forestry currently there are two opposing trends in terms of intensification. On the one hand, forest management is intensified through harvest of not only tree stems but also tree tops, branches, and sometimes tree stumps for biofuel. On the other hand, some trees are retained in managed forest stands (Figure 1).

Figure 1. Clearcut with retained trees. Photo: Lena Gustafsson.

1.2.1 Biofuel harvest

Removing tree tops and branches for bioenergy is common in Sweden and practiced on about 60% of the clearcut area (Swedish Forest Agency 2014). Extracting also tree stumps is a newer practice, which is currently performed on only 1% of the clearcut area in Sweden (Swedish Forest Agency 2014). Stump extraction has, however, been restricted in Sweden due to concerns about its environmental impacts. When stumps are extracted for biofuel, the stump wood volume in a clearcut decreases by more than half (50-80%) (Eräjää *et al.* 2010, Rabinowitsch-Jokinen and Vanha-Majamaa 2010, Victorsson and Jonsell 2013).

1.2.2 Tree retention

Tree retention on clearcuts was introduced in Sweden as a way to combine forestry and conservation in all managed forest stands (Simonsson *et al.* 2015). Tree retention is used in forestry primarily in Australia, northern Europe, and North America with retention levels ranging from 1% to 40% of harvest volumes (Gustafsson *et al.* 2012). In Sweden it has been common practice for about 25 years to retain trees, either living or dead, as single trees or in groups of trees on the clearcut, or as buffers towards adjacent habitat (Simonsson *et al.* 2015). Trees of different taxa, including shade-adapted trees like Norway spruce, are retained in similar conditions, across the study area, and over time. Tree retention has the potential to increase some of the features that have decreased with forestry, for example the number of old trees, and the amount of deadwood in managed forests (Kruys *et al.* 2013).

1.3 Trees as habitat

Throughout the life cycle of a tree there are different organisms that depend on it: from lichens and vascular plants on living trees, to beetles in deadwood, and fungi that decompose wood long after tree death. For species that live on or in trees, their environment depends on the tree they inhabit and the surroundings of that tree. Tree species differ in their characteristics, for example bark pH and bark structure (Bartels and Chen 2012, Ellis 2012). Therefore, species associated with trees often differ between tree species (e.g. for lichens (Barkman 1958, Kuusinen 1996), or beetles (Ranius *et al.* 2017)), as well as in different stages of tree life (Ellis 2012) and decomposition (Stokland *et al.* 2012). The microclimate on a tree also influences its inhabitants (mediated by both tree structure and surroundings (Leppik *et al.* 2011, Gauslaa 2014)). So, when the microclimate around a tree changes, as it does when the surrounding forest is logged (Chen *et al.* 1999), that affects species associated with the retained trees.

Forest management has decreased the amount of habitat available for the many species that depend on deadwood (Stokland *et al.* 2012). The available habitat amount is reduced further when harvesting for bioenergy (Bouget *et al.* 2012, Felton *et al.* 2016). In managed forests, tree stumps that are left after logging make up a large proportion of the deadwood (Svensson *et al.* 2016). In one particularly well-studied landscape, the bark area of clearcut stumps made up 15% of the total bark area of deadwood, and 38% for the most common tree species, Norway spruce (Jonsell and Schroeder 2014). Stumps can also be important substrate for species in several organism groups, such as for arthropods (Persson *et al.* 2013, Kataja-aho *et al.* 2016, Taylor and Victorsson 2016) and for lichens (Svensson *et al.* 2016). Notably, some beetles have more than 40% of their total population in clearcut stumps (Jonsell and Schroeder 2014). With stump extraction there could therefore be considerable loss of habitat for species that depend on deadwood.

1.3.1 Epiphytic lichens

Lichens are composite organisms with a symbiotic life-style including different fungi and photobionts[1] (Spribille *et al.* 2016). They live in a wide variety of environments, including as epiphytes[2] on trees. There seem to be large differences in lichens' ability to cope with new environmental conditions, where some lichens, for example, can acclimatize to an exposed environment through

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[1] The photosynthetic partner in the lichen, usually a green algae or cyanobacteria.

[2] Organism growing on another plant.

increased thallus[3] thickness, whereas others cannot and therefore go locally extinct (Jairus *et al.* 2009).

There are several traits that might influence where epiphytic lichens occur (for descriptions of some traits see Table 1), for example growth form, type of photobiont, reproductive strategy (Bässler *et al.* 2015, Matos *et al.* 2015) or thallus acting as sunscreen (Gauslaa and Solhaug 2004). Since lichens take up water passively from their surroundings, their growth form matters for how they capture water (Gauslaa 2014). The photobionts vary in which environments they occur (Hedenås *et al.* 2007) and lichen thallus substances might play an important role in coping with sun exposed environments (Rikkinen 1995, Färber *et al.* 2014, Gaya *et al.* 2015). Lichens also have different reproductive strategies and can disperse sexually using fungal spores, asexually with propagules including both fungal and photobiont partners, or combine both sexual and asexual dispersal. The reproductive strategy influences the colonization of new habitat, where asexual reproduction means larger propagules and more lichen substances, which, together with the advantage of dispersing also the photobiont, can facilitate local establishment, while sexual reproduction by spores can disperse long distances (Ellis and Coppins 2007, Ellis 2012).

1.3.2 Saproxylic beetles

There are 1300 species of saproxylic[4] beetles in Sweden, out of which about 40% are red-listed (De Jong *et al.* 2004). They utilize deadwood of different tree species, types (snags, logs, stumps), exposure, and humidity (Ols *et al.* 2013, Jonsell and Schroeder 2014). There is also succession in beetle communities with time as the deadwood decomposes. In saproxylic beetle colonization of Norway spruce wood, for example, the first successional stages are the "bark beetle stage" (0-2 years after tree death) and the "subcortical stage" (2-7 years after tree death) (Esseen *et al.* 1997, Stokland *et al.* 2012). Saproxylic beetles early in succession are believed to be good dispersers since they need to track their short-lived habitat over the landscape (Southwood 1977, Solbreck 1980, Forsse and Solbreck 1985, Travis and Dytham 1999, Jonsson *et al.* 2005). Most of these species find deadwood by using olfactory perception of chemicals released by the deadwood (Allison *et al.* 2004, Byers 2004), which makes them good at discovering suitable deadwood substrate.

Saproxylic beetles can be divided into different functional groups depending on their relation with deadwood. *Cambivores* feed directly on inner bark and outer sapwood, *predators* feed on other arthropods in the deadwood, *fungivores*

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[3] The nonreproductive body of a lichen.

[4] Living in deadwood for at least part of its life.

feed on fungal mycelium, *detritivores* feed on the remains of other species, *xylophages* or wood feeders live inside the wood proper, and *bark feeders* feed on the outer bark.

2 Aim

My aim was to investigate the consequences of forest management practices for species associated with trees. To achieve that, I aimed to explore ways of presenting, and explaining, a large variation in species responses conceptually (Paper I), and to give examples of how species-rich organism groups associated with trees respond to management practices, from different angles: a historic perspective of species pool filtering for epiphytic lichens (Paper II), a functional perspective through lichen species traits (Paper III), and a landscape view of management effects on saproxylic beetle species (Paper IV).

3 Species responses to changes in their environment

Species differ in their traits and adaptations, and so they respond differently to changes in their environment (McIntyre *et al.* 1999, Loreau and de Mazancourt 2013, Gallagher *et al.* 2015, Cavender-Bares *et al.* 2016). Often though, it is difficult to predict how species will respond, especially for organism groups that are species-rich or where the ecology of the species is not well-known. When measuring the consequences of environmental change or human management on species through measures of species richness or diversity, the differences in responses among species are hidden (Supp and Ernest 2014). Sometimes that is a problem, because behind measures of stable richness there can be species increasing and decreasing without notice (van Grunsven and Liefting 2015). A common way to approach this problem is to analyze changes in species composition and from there infer which species are promoted or disfavored. Another way is to analyze the responses of individual species, or groups of species.

Entities at different ecological levels (e.g. individuals or species) respond to environmental changes, including human-caused change (Luque *et al.* 2013, Hawkes and Keitt 2015, Oliver *et al.* 2015). The response of organisms to change in their environment can be continuous or discrete: e.g. continuous weight loss or an abrupt switch in an individual's color; continuous decline or the sudden extinction of an entire population. Responses to environmental change can also vary over time through time lags (e.g. extinction debt (Hylander and Ehrlén 2013)) and they can be direct or indirect via the responses of other species (Säterberg *et al.* 2013).

One way to predict responses of species is through their functional traits. There are two types of functional traits that are commonly recognized: traits corresponding to an effect on ecosystem function (effect traits) and traits that correspond to a response to change (response traits) (Suding *et al.* 2008). In practice, the two groups often overlap since the same trait can be related both to an ecosystem effect and a species response (e.g. Mumme *et al.* 2015). Through functional traits species can be connected to ecosystem function (e.g. Suding *et al.* 2008), but functional traits can also be used to decipher the role of specific traits in environmental filtering[5] of species (e.g. Cornwell *et al.* 2006, Mayfield *et al.* 2013).

When analyzing responses there can be many different aspects of interest. One way to start is by acknowledging the variety of responses among species. From there, depending on the question at hand, we could look for generalities or exceptions, and maybe learn something useful on the ecology of the species, and for management. Here I start with a section on response diversity[6] as a concept (Paper I), and then move on to three examples with species associated to trees, and their responses to forestry practices (Papers II-IV).

3.1 Response diversity as a concept

Elmqvist *et al.* (2003) conceptualized the idea that differences in responses among species with similar ecosystem effects are important for ecosystem resilience, by introducing the term ‘response diversity’ in ecology. In their paper Elmqvist *et al.* argue that species seen as functionally redundant under stable conditions might actually differ in their response to environmental change and therefore contribute to the stability of ecosystem functions. Since then, response diversity has been increasingly examined in relation to functional diversity, functional redundancy and resilience (Folke *et al.* 2004, Mori *et al.* 2013, Baskett *et al.* 2014, Kühsel and Blüthgen 2015, Sasaki *et al.* 2015). Response diversity can be used to examine responses at different organizational levels, both within the same species (Li *et al.* 2006, Ehlers *et al.* 2008, Braun *et al.* 2016) and among different species (Cariveau *et al.* 2013).

Although there are many ways in which response diversity can be represented, studies to date have focused mainly on the spread of responses (e.g. response range or response variance). Often, however, it is equally necessary to understand the component responses. For example, whether species increase or decrease after a disturbance will be crucial for how we interpret the consequences for species conservation; how responses are distributed among species might be more important than the mere existence of different responses (Cariveau *et al.* 2013, Kühsel and Blüthgen 2015). Including information on for instance directions and magnitudes of responses (see Figure 2), and how they

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[5] Environmental limits to species distributions.

[6] The distribution of responses or any representation of that distribution.

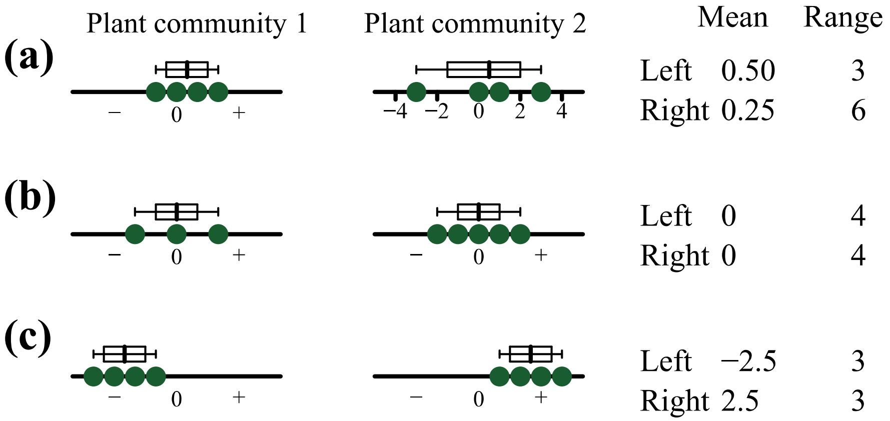

Figure 2. Response diversity illustrated for communities under environmental change. There are different ways of measuring response diversity, and the hypothetical examples here (a-c) are for abundance changes in two plant communities after a disturbance, on a scale from strong positive to strong negative responses. Each point denotes a response type (one or several species) represented in the community. Two communities that undergo change can differ in various aspects of response diversity (a-c, compare left and right panels). They can, for example, have the same number of response types but differ in their response ranges (a), have the same response range but differ in their number of response types (b), or have the same number of response types and the same response range but differ in their means (c, negative or positive means). In (a-c), two measures of response diversity are shown for each community: the mean of responses (here measured as the mean of the response types), and the range of responses (from the smallest to the largest value along an axis). The distribution of responses is also illustrated through box plots.

are distributed among species, will help to link response diversity to forecasts of ecosystem consequences (Paper I). While this might seem intuitive, the response diversity literature still largely focus on examining only the spread of responses (Paper I).

Response diversity can be used to evaluate differences among communities[7] in their responses. For example, response diversity can be driven by the environmental changes that species have evolved adaptations to, or that have been prevalent enough to filter the species pool[8] towards species that can cope with such changes. To understand the patterns of current species distribution, it becomes important to consider processes over evolutionary and historical time (Ricklefs and Schluter 1993, Pärtel *et al.* 2007, Andersson *et al.* 2014). Similarly, evolution and history likely shape how aspects of response diversity (e.g. how many positive responses there are) differ between species pools (e.g. Venable and Brown 1988, Keeley and Bond 1997). Therefore, depending on the type of

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[7] Several individuals of different species that can occur together.

[8] The species in the area that are available to colonize a site.

environmental change with which a species has had to cope, adaptations or filters over time can lead to the prevalence of different strategies.

Response diversity has been used mainly with regard to ecosystem function and then the focus has been on the different responses among species contributing to the same ecosystem function. Response diversity can also be used to evaluate potential differences between species of conservation concern and species overall, and evaluation of management for biodiversity conservation. In these applications, response diversity can be measured on organisms grouped for other reasons than their similar functional effects, which has been the most common use of the concept. The directions and magnitudes of the responses are crucial for conservation purposes (see Cariveau and Winfree 2015, Wonkka *et al.* 2016). When the distribution of responses differs between communities, which response diversity is preferable (e.g. a small or large response range) depends on the context (Nimmo *et al.* 2015, for parallel discussions on resilience, see helpful and unhelpful resilience (Standish *et al.* 2014)).

The need of studies not only on richness but also on other aspects of composition is well established in biodiversity research, commonly residing under the umbrella term of species diversity (though it is arguably also often used as a synonym for richness). The problem is similar in the response diversity context, but since it has not been conceptualized there, we explore that possibility in Paper I.

3.2 Predicting species responses from their tree taxon association

Foundation species[9] ecology might explain the responses of their associated species to environmental change either because the associated species have adapted to the environment of their foundation species, or because the pool of associated species has been filtered by the conditions where their foundation species has been prevalent over time in the region (see Cornell and Harrison 2014, Vellend 2016). One aspect of tree ecology that might influence its associated species is successional strategy, where pioneer species and late successional species are usually considered counterparts at opposite ends of a successional spectra (West *et al.* 1981).

When the microclimate around a tree changes because the surrounding trees are logged, the epiphytic lichens on the retained trees are affected. For some lichens the drastic change in environmental conditions can damage their thallus

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[9] Structurally important species (Dayton 1972), e.g. trees (Ellison *et al.* 2005).

Figure 3. Sampling design for Paper II and Paper III. Lichens were surveyed on the lower 2 m of the trunks of four tree taxa, in three forest stand types replicated in four regions.

(Jairus *et al.* 2009) and cause rapid local extinctions. Other lichens acclimatize (Jairus *et al.* 2009), and a third group colonize the exposed trees (Lõhmus and Lõhmus 2010, Lundström *et al.* 2013, Johansson *et al.* 2014).

In Paper II, we suggest that the ecology of foundation species, e.g. their successional strategy, can be used to predict responses of their associated species to environmental change. We evaluated this hypothesis in a survey of lichen species occurrences on 2400 trees in closed-canopy stands as well as in stands 3-8 years, or 15-20 years, after clearcutting (Figure 3).

In line with our hypothesis, epiphytic lichen responses varied with relation to the successional strategy of their main host tree taxon (Figure 4). Lichens associated with the late successional tree Norway spruce seemed sensitive to the exposure of a surrounding clearcut with, on average, lower probability to occur on retention trees compared to similar trees in closed-canopy forest. Lichens associated with the early successional trees European aspen, birches, or Scots pine, showed the opposite pattern with, on average, higher probability to occur on retention trees than trees in closed-canopy forest.

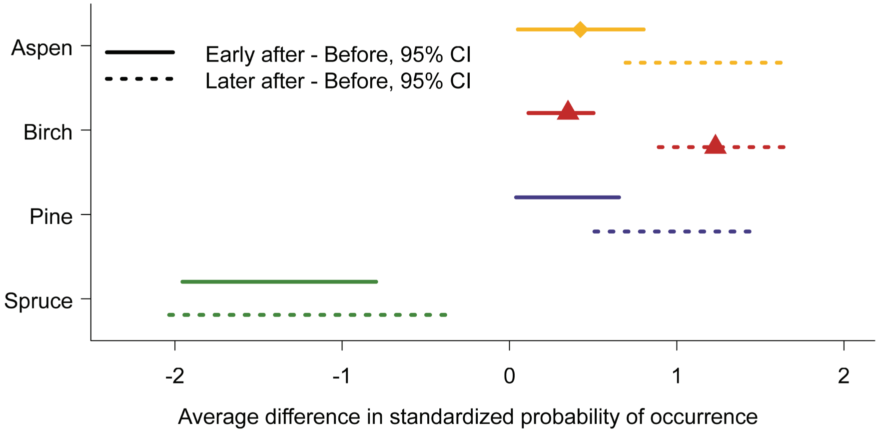

Figure 4. Lichen species differ in responses to exposure, on average, depending on the tree taxa they are associated with. Lines indicate 95% credible intervals: solid lines for differences in occurrences between trees in stands 3-8 years after clear-cutting and trees in stands that had not been clear-cut (>80 years since clear-cut); dotted lines represent differences between trees in stands 15-20 years after logging and trees in stands that had not been clear-cut (>80 years since clearcut).

The clear distinction in our results between species associated to trees with different successional strategies could be a consequence of different selection pressures for species depending on the ecology of the tree that they mostly occur on. The species pool associated with a specific tree taxa should be dominated by species that have either adapted to the most common conditions on the tree taxa or species that have high fitness in those conditions due to an exaptation[10] from former habitats. Lichen species with niche optima in environmental conditions that have been rare on its host tree taxa would, instead, be more likely to go locally extinct, since small populations are more strongly influenced by stochastic processes (ecological drift, Vellend 2016).

In our case, shaded conditions have been more common on Norway spruce compared with more varied light conditions on European aspen, birches and Scots pine, due to their successional strategies. Adaptive radiation in lichens has co-occurred in time with big changes in vegetation (Gaya *et al.* 2015). However, we do not know if lichen traits enabling life in sun-exposed or shaded conditions reflect adaptation in relation to their current tree taxa-association, or exaptation from former habitats (the two can be difficult to distinguish (Keeley *et al.* 2011)). Our approach of predicting the responses of species associated with different tree taxa could be useful also in other systems where some species are structurally important with many associated species.

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[10] An adaptation to prior conditions is used in a new role.

3.3 Responses of lichen trait distributions to environmental change

Traits can vary along environmental gradients in space, but also in the same place when the environment changes. In either case it can be difficult to decide whether differences in results among studies are due to, for example, different regional contexts, varying ecosystems, or different trait definitions, even when they concern the same organisms (Cornwell *et al.* 2006, Laliberté *et al.* 2010). A key question is therefore how environmental change alters the distribution of traits, and whether it differs among habitats or across geographical regions.

The distribution of traits across environmental gradients has been described for some well-known organism groups, such as vascular plants (e.g. Mayfield *et al.* 2013) and pollinators (e.g. Rader *et al.* 2014), but are scarce for many other organisms including lichens (Cornelissen *et al.* 2007). Recently though, there are studies at a landscape scale (along a mountain slope, Bässler *et al.* 2015, Nascimbene and Marini 2015), regional scale (across Spain, Matos *et al.* 2015), and evolutionary scale (adaptive radiation, Gaya *et al.* 2015) that relate lichen traits to environmental conditions. All of these find some correlations of traits with environment, but there is little generality in the results.

Table 1. *Descriptions of lichen traits and the different categories that we used for analyses in Paper III. For each trait, species in the data set were assigned to one category.*

Trait	Category	Description
Growth form	Crustose	Crust-like
	Foliose	Leaf-like
	Fruticose	Shrub-like
Thallus sunscreen	No sunscreen	Not dark. White – grey – green, no presence of usneic acid or atranorin.
	Sunscreen	Possible presence of yellow, orange, red, brown, or black colors in thallus, usneic acid, or atranorin.
Photobiont	Chloroccocoid	Primary photobiont a green alga of the Chloroccocoid type
	Trentepohlioid	Primary photobiont a green alga of Trenthepolioid type
	Cyanobacteria	Primary photobiont a cyanobacteria
Reproductive strategy	Asexual	Uses mainly asexual dispersal (with algae and fungus together, i.e. excluding conidia), or both asexual and sexual dispersal
	Sexual	Uses mainly sexual dispersal

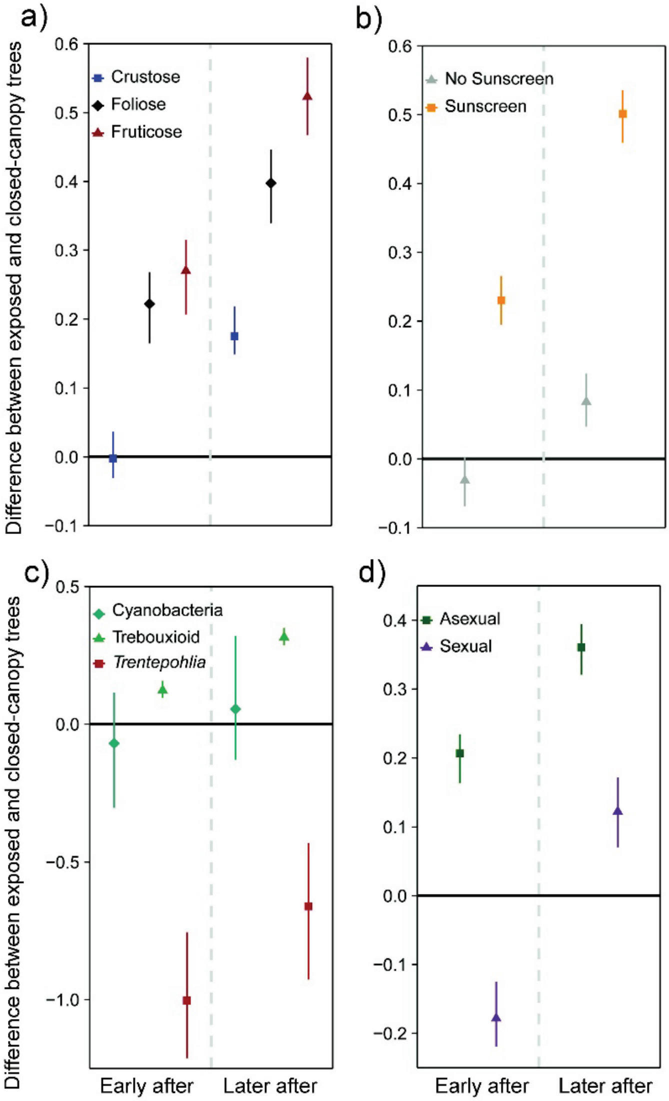

Figure 5. The distribution of lichen traits differ between trees retained after clearcut and trees in closed-canopy forest. The graphs represents the trait distributions of (a) growth forms, (b) sunscreen, (c) photobiont association, and (d) reproductive strategy. Each graph is divided into two sections, one for each stand category comparison: 3-8 years after clearcutting (‘early after’), and 15-20 years after clearcutting (‘later after’), compared with closed-canopy forest (‘old’). The estimates and 95% CI:s are for the difference between stand categories, measured in probability of occurrence standardized by the probability of occurrence in the trait category on an average tree (across tree taxa and regions). Therefore, a value of 0 represents no difference in occurrence probability between stand categories, whereas >0 means that occurrence probability is higher on retained trees than trees in closed-canopy forest, and <0 that occurrence probability is lower on retained trees than on trees in closed-canopy forest.

Our main aim in Paper III was to investigate how lichen trait distributions change when the environment of a forest stand changes at clearcutting (for trait descriptions see Table 1, for study design see Figure 3). Overall, we expected variation among the distributions of lichen traits to be driven by the large contrast in microclimate between trees in closed-canopy forest and trees in clearcut stands. We hypothesized that (1) lichens with a fruticose growth form are more favored on clearcut trees than lichens with other growth forms since they might have an advantage in water uptake from dew, (2) lichens with thallus sunscreen are more favored on trees retained at clearcutting than lichens without sunscreen due to higher tolerance to increased irradiance, (3) lichens with *Trentepohlia* algae as their photobiont decrease more on trees after the surrounding forest has been clearcut than lichens with trebouxioid algae or cyanobacteria since the niche optimum of *Trentepohlia* algae is in more shaded conditions, and (4) lichens with asexual propagules are more favored by trees exposed after clearcutting than lichens with mainly sexual propagules since asexual propagules might establish faster. We also wanted to see whether it is possible to generalize results across tree taxa and geographical regions.

Lichen trait distributions did vary among forest stand categories, in line with our hypotheses (Figure 5). Lichens with a foliose or fruticose growth form, thallus sunscreen, or asexual reproductive strategy, had higher probability of occurrence on trees retained in clearcuts, especially after some time had passed (15-20 years), than on trees in closed-canopy forest. For lichens with *Trentepohlia* algae, the pattern was the opposite, as predicted, with higher probability on trees in closed-canopy forest than on retention trees in clearcuts. For lichens in most of the trait groups, responses to logging were similar in direction across tree taxa and region, although the response strength varied. The exceptions were lichens with crustose growth form, no sunscreen, or sexual reproduction, where responses were sometimes positive (more occurrences on retained trees than closed-canopy trees) and sometimes negative (less occurrences on retained trees than closed-canopy trees), depending on tree taxa or region.

Overall, the composition of traits differed among both tree taxa and regions. In particular, lichen trait distributions on European aspen differed from that of the other tree species, as aspen had more lichens with cyanobacteria or mainly sexual reproduction than the other tree taxa did. The unique composition of traits on European aspen is consistent with its distinct species composition of lichens compared to the other tree taxa (Kuusinen 1996). Among regions the composition of traits differed, especially between the two southern and the two northern regions, with higher occurrence probability in the north than in the south for all trait-groups of lichens except for lichens associated with

Trentepohlia algae. Our result concur with the first distributional maps of lichen traits that show decreasing abundance of lichens with *Trentepohlia* algae towards the north in Europe (Rambold *et al.* 2016). The probability of occurrence for lichens with thallus sunscreen increased more towards the north than for lichens without thallus sunscreen. Dark pigmentation, which we included as sunscreen, could be an advantage for lichens in colder areas where a dark thallus elevating lichen temperature might enable better use of snow melt for carbon uptake (Kershaw 1983).

Knowing when generalization is possible, and when it is not, could help explain differences among studies. We did not consider interactions among traits, although they could be important. The distribution of algal partners, for example, could potentially influence the establishment of spore dispersed species, since they might be facilitated by the presence of already established lichens with the same algal partner (the core-fringe hypothesis (Rikkinen 2002, Belinchón *et al.* 2015), but see Svensson *et al.* (2016)). We applied a response perspective on these traits, although several of them also can have an impact on ecosystem functioning (Asplund and Wardle 2016). We conclude that several lichen traits respond similarly to the changed environment after logging, irrespective of tree taxa or region. For some lichen traits, especially crustose growth form, no sunscreen, or sexual reproduction, generalizations should be made with care; our results were not generalizable across tree taxa and region for them.

3.4 Landscape effects of stump extraction on saproxylic beetles

Although the impacts of land use intensification on organisms is often important at a landscape level (e.g. for pollinators in agricultural landscapes (Cariveau *et al*. 2013)), we still know little about landscape effects of forestry intensification on saproxylic organisms. However, theoretical simulation studies show that a landscape perspective can be important to consider (Ranius and Roberge 2011, Johansson *et al*. 2016). For the newer practice of extracting stumps, in addition to tree tops and branches, after clearcutting there is a need for empirical data since there are no previous empirical studies investigating its potential landscape effects (Ranius *et al.* 2017).

Intensified management and habitat loss do not affect all species equally. Species at higher trophic levels, such as predators and fungivores among beetles, often decrease the most (Komonen *et al.* 2000, Ryall and Fahrig 2005, Vanderwel *et al.* 2006). Two possible reasons for a higher vulnerability of species at high trophic levels are that they tend to have small population sizes,

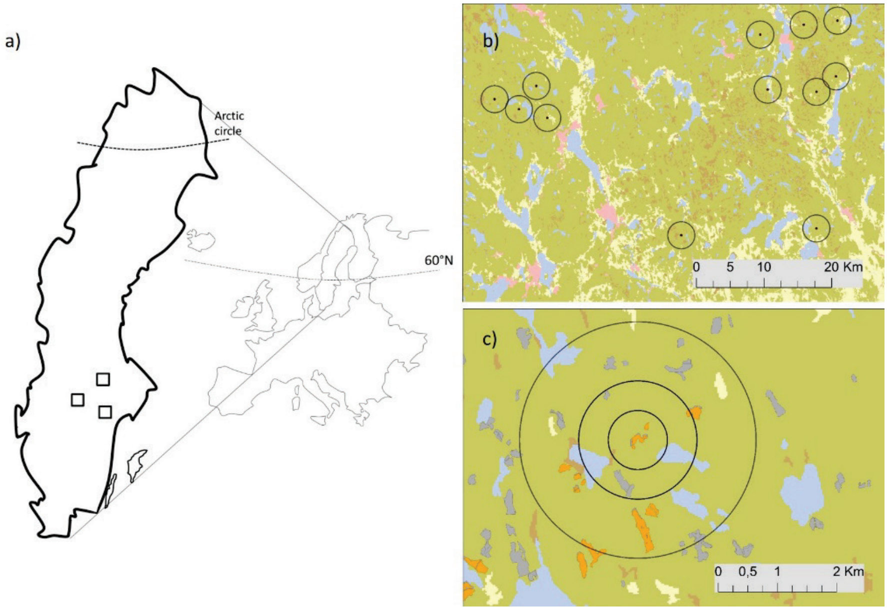

Figure 6. Sampling design for Paper IV. The three study regions were located in central Sweden (a). In each region stumps were sampled in focus clearcuts (b). Landscape variables were estimated in buffer zones of 500 m, 1000 m, and 2000 m surrounding the focus clearcut (c). Clearcuts where stumps have been extracted are shown in orange, and clearcuts without stump extraction are shown in grey.

and that they are specialized in their habitat choice (Henle *et al.* 2004), since they depend on populations at lower trophic levels.

Our aim in Paper IV was to investigate the effect of stump extraction intensity in the surrounding landscape on the abundance of individual saproxylic beetle species in stumps created at clearcutting (for study design see Figure 6). We quantified the effect of stump extraction intensity in the landscape as the percentage of clearcuts where stump extraction had been conducted, and in our landscapes we had an intensity range of 0-100%. We controlled for local factors such as clearcut age and local habitat amount (stump density in the focus clearcut). We hypothesized that species at higher trophic levels (i.e. predators, fungivores and detritivores) would be more negatively affected by stump extraction intensity in the surrounding landscape than species at low trophic levels (i.e. cambivores).

The effect of stump extraction intensity varied among species (for species examples see Figure 7), but with predators more negatively affected than cambivores or facultative predators (i.e., predators that also feed on fungi or detritus). For seven species out of the 34 (21%) there was a large probability of a decrease in species abundance per stump with increasing stump extraction in

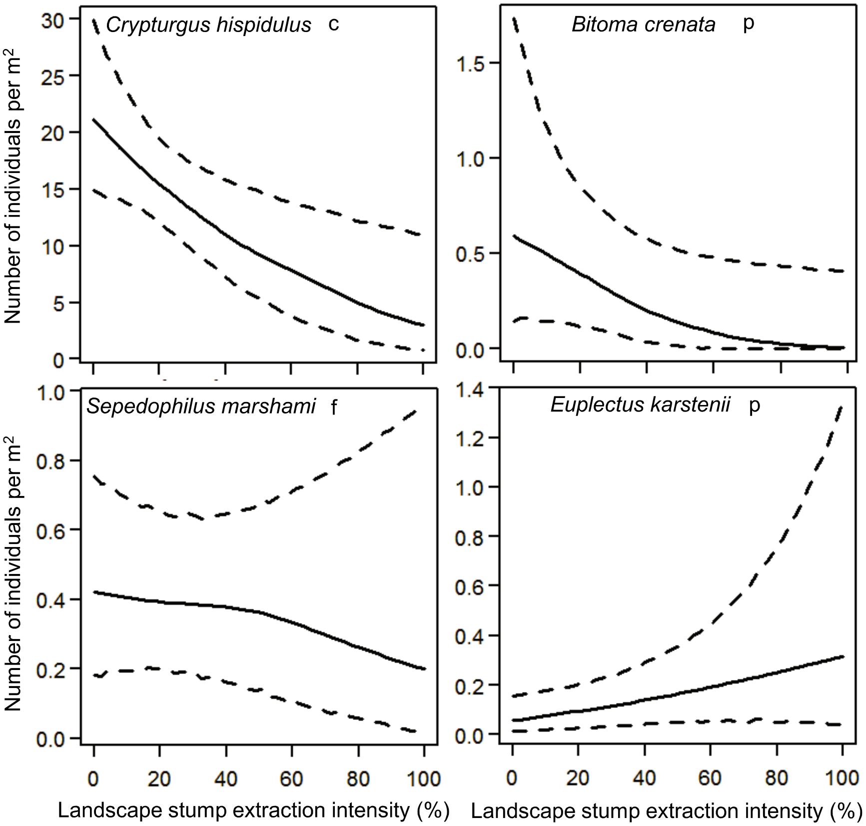

Figure 7. Predictions of species responses to stump extraction intensity in the surrounding landscape, for four example species. The predictions are based on the results for stump extraction intensity presented in Paper IV, for abundances in an average stump. Dashed lines represent 95% confidence intervals. Stump extraction intensity was calculated as the percent of extraction clearcut area in the surrounding landscape, out of the total clearcut area. The letters indicate species functional groups where c – cambivore, f – fungivore, and p – predator.

the surrounding landscape. Most species, however, showed no response. For another seven species there was a large probability of an increase in per stump abundance in landscapes with high stump extraction intensity.

Different responses for different species are common in landscape studies of saproxylic organisms (Saint-Germain and Drapeau 2011, Bergman *et al.* 2012, Sverdrup-Thygeson *et al.* 2014, Ranius *et al.* 2015). Stump extraction reduces the possible number of beetle individuals that can disperse from a clearcut out into the surrounding landscape by 70% (Victorsson and Jonsell 2013). There should therefore be lower beetle abundances in landscapes with a high stump extraction intensity. The diverging responses among species could, for example, be due to differences in their dependence on stumps as habitat, in their population sizes, or in their dispersal capacities where poor dispersers will be more affected by land-use intensification in the nearby landscape (Henle *et al.* 2004, Jackson and Fahrig 2012). The increase we see for some species in landscapes with high stump extraction intensity could be a crowding effect[11] indicating time-lag in response to habitat loss (Ewers and Didham 2006). Since stump extraction started recently in the landscapes of our study, potential time-lags in responses could influence our findings. Our results suggest that if stump extraction is widely introduced, then deadwood retention, planned for both spatial and temporal continuity, should be an integrated part of intensified forest management.

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[11] A higher concentration of organisms in remaining habitat than before, as a response to habitat loss.

4 Conclusions

Species responses to forestry practices differ, and in species rich communities this presents a challenge for predicting management consequences. Depending on the question at hand, there are different aspects of response diversity that will be of interest. Since the concept of response diversity has been used mainly to denote response spread, I suggest additional aspects of the distribution of responses that could be important to consider. It can, for example, be interesting to consider differences in the average responses among communities, or single outlier species that counter the main pattern, also within the response diversity concept.

Two ways of improving predictions of tree-associated species responses could be to use knowledge of tree species ecology to predict responses of their lesser-known associated species, and to investigate the role of the associated species' traits in their responses. The communities associated with trees in clearcuts are often species rich (e.g. beetles (Kaila *et al.* 1997), lichens and bryophytes (Lõhmus *et al.* 2006)). For lichens I show that many species occur more on trees retained in clearcuts than on similar trees in closed-canopy forest, especially for lichens associated with early-successional tree taxa. Lichens associated mostly with the late-successional Norway spruce instead occur more on trees in closed-canopy forest. One reason for these results could be that managed forests are too dark for many species associated with early successional trees. Since retained trees are few in relation to trees in closed-canopy forest, the extent to which they can fill the role of habitats for photophilic epiphytes remains an open question.

There are traits of species associated with trees that help predict their responses to environmental change. For lichens, a foliose or fruticose growth form, sunscreen in the thallus, and asexual reproduction are traits that seem to increase the probability to occur on trees retained at clearcutting. Some groups of species are more sensitive. Lichens associated with *Trentepohlia* algae decreased in occurrences on trees retained after clearcut. Among saproxylic beetles, predators were more negatively affected by landscape stump extraction than lower trophic levels.

As a consequence of forest management, selection pressures on species associated with trees might have changed, where, for example, previously common environmental conditions, or tree traits (e.g. of very old trees), might now be rare or, vice versa, where previously rare environments are now common. Forest management is affecting population dynamics and long-term persistence of tree-associated species (ArtDatabanken 2015).

My results support a management strategy of mimicking the disturbance dynamics that the species pool relies on (Kuuluvainen 2002, Bengtsson *et al.* 2003). Using information on traits of foundation species, as well as their associated species, can prove to be a valuable tool for better understanding and predicting responses to environmental change and land-use management of the associated species, especially those species for which our knowledge of responses to environmental change is poor.

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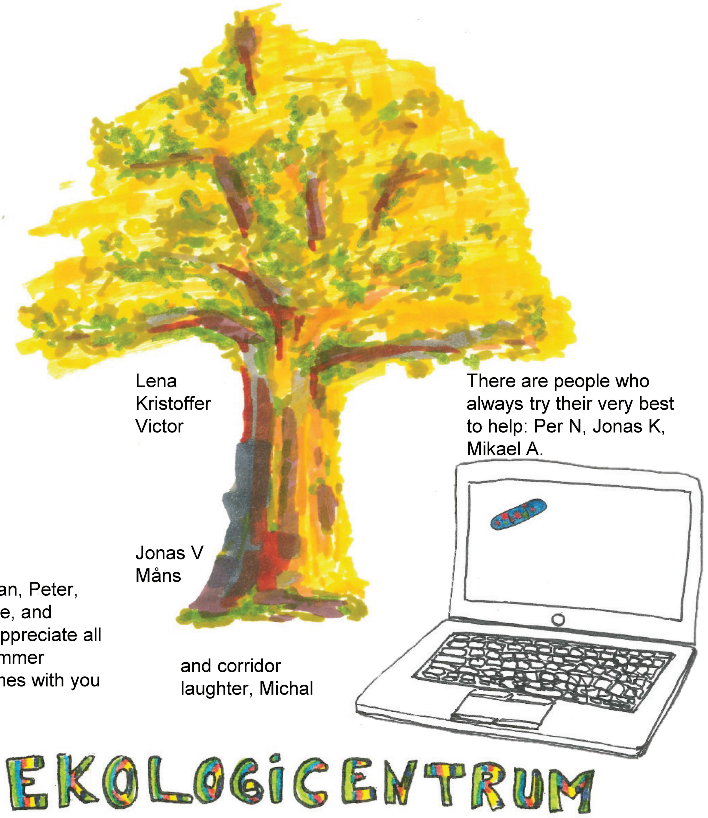
Acknowledgements



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Veera, Göran, Peter, Victor, Marie, and Samuel, I appreciate all the nice summer teaching times with you

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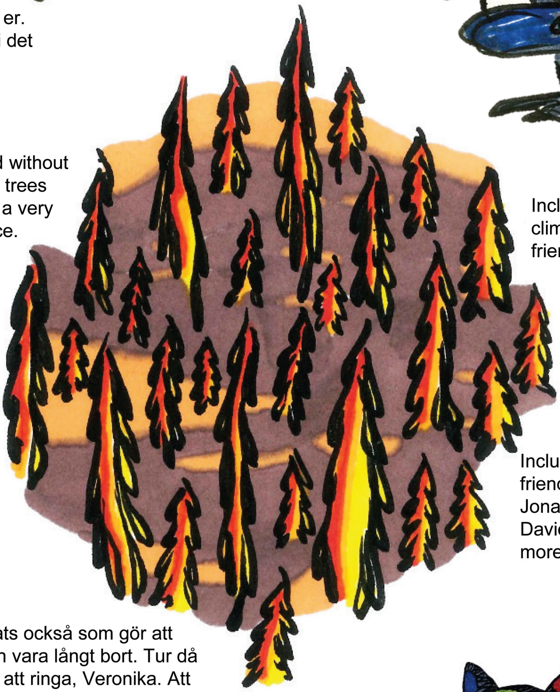
…for continuing to make each other's work day, a good day

Familjen,
en blomma till er.
Uppskattning i det
enkla.

Pernilla, det är
roligare när du
sitter där.

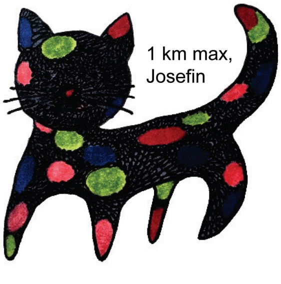


The world without
friends or trees
would be a very
sorry place.

Including
climbing
friends.

Including work
friends. Diana,
Jonas J, Veera,
David. And many
more.

En stor plats också som gör att
vänner kan vara långt bort. Tur då
att det går att ringa, Veronika. Att
du kommer hem ibland, Linda. Och
att vänskap kan bestå ändå.



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Josefin

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