Conservation of epiphytes: Single large or several small host trees?

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ABSTRACT

Retention of selected trees in clear-felling areas has become an important conservation measure in managed forests. Trees with large size or high age are usually preferred as retention trees. In this paper we investigated whether a single large or several small trees should be left in clear-felling areas to serve as life boats and future habitat for epiphytic species. The focal species were 25 Lobarion epiphytic lichens hosted by aspen (*Populus tremula*). We analyzed the relationships between: (1) proportion of trees colonized and tree size, (2) number of lichen thalli (lichen bodies) and aspen area, and (3) number of lichen species and aspen area, for 38 forest sites. Mixed effect models and rarefaction analyzes showed that large and small host trees had the same proportion of trees colonized, the same number of thalli, and the same species richness for the same area of aspen bark. This indicates that larger aspens do not have qualities, beyond size, that make them more suitable for Lobarion lichens than smaller sized aspen trees. None of the species, not even the red-listed, showed any tendencies of being dependent on larger aspens, and our results therefore did not support a strategy of retaining only large and old trees for conservation of epiphytic Lobarion lichens. Additionally, young aspens have a longer expected persistence than old aspens. However, old retention trees might be important for other species groups. We therefore recommend a conservational strategy of retaining a mixed selection of small/young and large/old aspens.

1. Introduction

Inspired by the theory of island biogeography (MacArthur and Wilson, 1967), Diamond (1975) presented a set of design principles for nature reserves with the aim of minimizing the extinction rate. One of the principles was the preference of a single large reserve instead of several small. The response by Simberloff and Abele (1976) started a long and still on-going debate known by the acronym SLOSS, whether a single large (SL) or (O) several small (SS) reserves, with the same combined habitat area, are preferable as conservational units. Recent studies have shown that the optimal solution depends on factors varying with study design and species group (Ovaskainen, 2002; Tjørve, 2010). In situations where the aim is to maximize the number of currently occurring species, SS is in general found to be the best approach (Ovaskainen, 2002). This is because SS patches can be spread out in space, and therefore may be able to embrace a higher environmental heterogeneity and higher species richness than SL. If however, the objective is to maximize time to extinction, SL is generally found to be the better approach (Ovaskainen, 2002).

In the present study, we investigated the SLOSS problem on a fine spatial scale. We focused on epiphytic lichens on individual trees within forest stands, where each tree could be viewed as a habitat patch or island surrounded by non-suitable environmental conditions. Trees are dynamic habitat patches changing with time. As a tree grows and increases in size, new and empty habitat becomes available for colonization. As a tree ages, the number of colonisations is expected to increase, simply because the habitat has been available for colonization for a longer time period. Additionally, structural and chemical habitat qualities may change with tree age (e.g. changes in bark pH and increased bark crevice depth, bark thickness, and bark roughness), which can enhance successful establishment of epiphytic propagules and provide increased habitat heterogeneity and consequently more species (Gustafsson and Eriksson, 1995; Ranius et al., 2008). Thus, three different factors, all dependent on the tree age, may influence the density of epiphytic individuals and species on a tree; (1) tree size, (2) time window for colonization, and (3) habitat quality. These factors lead to the expectation that epiphytic species will show a higher density on large and old trees (Edman et al., 2008; Hazell et al., 1998). Large and old trees are structural elements that take a long time to develop, and are generally rare in intensively managed forests.

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To preserve late-successional epiphytic lichens it has been argued that large and old trees should be retained (Boch et al., 2013; Edman et al., 2008; Fedrowitz et al., 2012).

Retention forestry (green-tree retention, structural retention, and variable retention) started in North America more than 25 years ago (Franklin, 1989; Franklin et al., 1997), and has become a common management technique used in large parts of the world and with great variation in application (Gustafsson et al., 2012). In boreal forests, the usual retention technique is to leave single trees or groups of trees within the clear-felling area, and the retention trees are typically selected among the largest and oldest deciduous trees (Anon, 2006; Gustafsson and Perhans, 2010; Hazell and Gustafsson, 1999; Timonen et al., 2010). Here, we investigate if the retention of large aspen trees is the best strategy for a group of epiphytic lichens called Lobarion lichens.

Several Lobarion lichens experienced a rapid decrease in abundance in European countries during the 20th century (Rose, 1988), and concerns have been expressed for the future survival of species in this group (Edman et al., 2008; Hedenås and Ericson, 2004; Zoller et al., 1999). In Fennoscandia, aspen (*Populus tremula* L.) is one of the main host species of Lobarion lichens (Schei et al., 2012) and frequently used as a retention tree (Hazell and Gustafsson, 1999). Our main aim is to assess whether the retention of SL or SS host trees will maximize the number of Lobarion thalli (lichen bodies) and species, i.e. the highest number of lichen thalli and species per m^2 of bark. If SS aspens host the same or a higher density of thalli and species compared to SL aspens it could be preferable to retain SS aspens instead of a SL, because small trees have a longer life expectancy and are therefore expected to better promote the long-term survival of lichens (Snäll et al., 2003). In contrast, if a SL aspen hosts a higher density of thalli and species than SS, retention of SS aspens would not compensate for retention of a larger aspen. We analyze the individuals-area and species–area relationships for Lobarion lichens on aspen trees in several forest stands to determine if these relationships are changing with (1) tree sizes and (2) forest stand age. Further, we discuss our results in the context of a long-term strategy of tree retention.

2. Materials and methods

2.1. Study system and lichen inventory

This study was part of a larger project investigating the distribution of Lobarion lichens in a coastal region of Western Norway (60°N, 5°E), where patches of Lobarion habitat constitute between 0.4% and 6.4% of landscapes (Gjerde et al., 2012). The field work was conducted over a period of five seasons, and in total we investigated 118 study sites (see Gjerde et al., 2012; Schei et al., 2012). There were large differences between sites, and most young sites were not yet fully colonized by Lobarion lichens (Gjerde et al., 2012). For the present study, we selected only sites with more than 100 aspens, where at least five of the aspen trees were colonized by Lobarion lichens (Fig. 1 and Supplementary Table A.1). By selecting larger patches of aspen, with several colonized trees, we were able to estimate site-specific relationships. In total, 38 sites fulfilled our criteria and were included in the analyzes.

Within each forest site we measured the diameter of all aspen trees ⩾5 cm at breast height (DBH, 1.3 m above ground), and counted all thalli of Lobarion lichens on the three lowest meters of the tree trunk (where almost all Lobarion thalli were located during a pilot study), up to a pre-determined maximum of 100 thalli for each lichen species per tree. For *Parmeliella triptophylla* and species in the genus *Collema* we used a circle with a diameter of 3 cm to represent one typical average sized "thallus" in cases where overlapping thalli could not be separated.

The age of the younger forest sites (⩽120 years) was estimated to the nearest 5 year age class by taking core samples from the largest trees in each site and counting tree rings. The estimated age of sites ranged from 45 to 120 years. The age of forest sites older than 120 years could not be estimated by core samples because the first generation trees were fallen, dead, or heavily infected by heart rot, and the age of these sites was therefore estimated using cadastral records of firewood resources from the National Archive of Norway. The records indicated that these forest sites were between 140 and 200 years old (Gjerde et al., 2012), and they are referred to as old sites below.

To assess the relationship between aspen size (DBH) and age we randomly selected five to eleven trees within seven sites, and for each tree we measured DBH and collected a core sample. All core samples were brought back to the laboratory and tree rings were counted.

2.2. Data analysis

To investigate the relationship between DBH and tree age we estimated the expected growth-rate by using a linear mixed model (Pinheiro and Bates, 2000) with age as a fixed effect and site as a random factor allowing for a site-specific random growth-rate, and a residual variance corresponding to a power-function of the fitted values. The latter handles the obvious increase in variance as trees grow older and larger.

In our data set 83% of the trees were not colonized by Lobarion lichens. To avoid zero-inflation (e.g. Hall, 2000), we divided the analyzes in two separate parts: (1) describing the proportion of colonized trees within the different DBH classes, and (2) analyzing the individual- and species–area relationship between Lobarion lichens and the colonized trees.

2.2.1. Tree size and the proportion of colonized trees

We divided trees into DBH size classes (5–9 cm, 10–14 cm, 15–19 cm, ⋯, 70–74 cm). If only bark area was affecting the probability of a tree being colonized we would expect a simple relationship between DBH size class and proportion of occupied trees. To assess this relationship we calculated the proportion of colonized trees in the most frequent size class (DBH 10–14 cm), and used this proportion to calculate the expected proportion of other size classes colonized by at least one thallus, assuming a null model of random sampling, where area alone determines the proportion of colonized trees. By applying this null model, other effects on the frequency of colonization could be detected (see Supplementary Eq. (A.1)).

2.2.2. Thalli density

We assessed the changes in density associated with DBH in explaining the distribution of number of thalli. To accomplish this we utilized a non-linear mixed effect model (Supplementary 2.2.2; Pinheiro and Bates, 2000; Zuur et al., 2009). The model recognized a random contribution by observations of trunks being grouped within various aspen stands, as well as the uneven variance with increasing number of thalli. The density was expressed as a logarithmic function of constancy and DBH. If the effect of DBH (β_1) was significant and positive, there was an additional effect of trunk size beyond the size itself. In other words, we would expect larger trees to contain more thalli than proportional in comparison to smaller trees.

2.2.3. Species density

To evaluate if larger trees had higher species richness than smaller trees we compared sample-based species accumulation curves (see Gotelli and Colwell, 2001) for different subsets of trees. We constructed species accumulation curves based on random selection of trees, with 100 permutations, for three size classes;