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Abstract

Wood-pastures are threatened biotopes in which trees and livestock grazing maintain high conservation values. However, browsing may threaten tree regeneration, whereas abandonment leads to tree encroachment. We studied the regeneration of trees in grazed and abandoned boreal wood-pastures. In grazed sites the density of young spruces (*Picea abies*) was high, while the density of young birches (*Betula* spp.) was very low. Sprucification can be prevented only by removing spruces. The number of young birches and pines (*Pinus sylvestris*) were correlated with the number of junipers (*Juniperus communis*), probably because thorny junipers protect palatable seedlings from browsing. In abandoned sites, deciduous trees and spruces regenerated abundantly. In the long term both grazing and abandonment lead to changes in tree species compositions and low diversity wood-pastures. Landscape scale planning and disturbance dynamics are needed for the creation of new wood-pastures and the maintenance of all pasture types within the landscape.

Keywords

Browsing, forest pasture, herbivores, regeneration, silvopasture, wooded pasture

INTRODUCTION

Wood-pastures are wooded traditional rural biotopes where livestock, usually cattle, horses or sheep, are allowed to forage (Bergmeier et al. 2010). Different types of wood-pastures occur throughout Europe and they provide a variety of ecosystem goods and services (Bergmeier and Roellig 2014). Canopy cover in wood-pastures varies locally and regionally, depending on forest type, tree species composition, grazing intensity and potential selective cutting by managers. Together the trees and grazers create and maintain habitat heterogeneity and consequently high values related to biodiversity, landscape, history and culture (McAdam et al. 2009; Bergmeier et al. 2010). However, grazing may threaten the regeneration of seedlings and saplings, especially in overgrazed areas (Bergmeier et al. 2010). The failure of regeneration and the loss of old trees due to senescence and cutting threaten the long-term persistence of wood-pastures (Bergmeier et al. 2010). Such changes have been recorded, for example, in the oak-dominated wood-pastures in Spain (called *dehesas*) and Portugal (*montados*) (Costa et al. 2014). Furthermore, rural depopulation and the end of low-intensity farming have desolated vast areas of wood-pastures, in which the encroachment of shrubs, trees and dominant field layer plants have resulted in losses of biodiversity and landscape values (Bignal and McCracken 1996; Bergmeier et al. 2010; Oldén et al. 2016).

Grazers affect tree regeneration in several ways by defoliation (or grazing *sensu stricto*), browsing and trampling as well as via excrements. Grazers can improve the germination of seeds and growth of seedlings by reducing competition from grasses, increasing light availability, creating bare ground and providing nutrient-rich patches (Lampimäki 1939; Vandenberghe et al. 2006). However, large herbivores trample large numbers of small seedlings and graze them among grass (Smit et al. 2006). Later, larger seedlings or saplings of palatable tree species are browsed selectively while unpalatable seedlings are avoided (Lampimäki 1939; Vandenberghe et al. 2007). Broadleaved deciduous trees are often favored, whereas conifers are avoided. Deciduous trees, however, have a greater potential for compensatory growth (Hester et al. 2004; Vandenberghe et al. 2007). The browsing pressure on palatable seedlings may be lower if they are protected by surrounding unpalatable vegetation (Smit et al. 2006; VanUytvanck et al. 2008). Thorny or toxic shrubs may facilitate the survival of palatable trees, which in turn will grow to outshade the shrubs (Olff et al. 1999; Bakker et al. 2004). Alternatively, time gaps (of a few years) in grazing can improve the growth of trees that regenerate abundantly in the absence of grazers (VanUytvanck et al. 2008; VanUytvanck and Verheyen 2014).

In Northern Europe boreal wood-pastures are dominated by Norway spruce (*Picea abies* (L.) H. Karst.), Scots pine (*Pinus sylvestris* L.) or birches (*Betula pendula* Roth and *B. pubescens* Ehrh.) (Schulman et al. 2008), and they are often mixed with European aspens (*Populus tremula* L.), rowans (*Sorbus aucuparia* L.) or grey alders (*Alnus incana* (L.) Moench). In general, young deciduous trees are selectively browsed by livestock, hindering their regeneration in heavily grazed pastures (Lampimäki 1939). The poor regeneration of deciduous trees, especially aspen, is a conservation concern, because many other species are dependent on them (Esseen et al. 1992; Kouki et al. 2004). In addition, it is uncertain whether birch-dominated wood-pastures can be maintained in the long-term. Historically new birch-dominated wood-pastures were formed by the slash-and-burn agriculture, but since its demise the remaining sites have become remnants whose future is threatened (Heikinheimo 1915; Schulman et al. 2008). In boreal wood-pastures spruces are avoided by grazers, but the new growths of pines are often browsed in the spring, reducing their regeneration (Lampimäki 1939). As a result, spruce numbers have increased during the last centuries due to livestock grazing (Nilsson 1997), although in Finland, the increase has been historically slow, due to slash-and-burn agriculture and the use of spruces for fences and animal beddings (Pykälä 2001). Nowadays spruces are often removed from grazed pastures to enhance the growth of fodder and to maintain biodiversity (Pykälä 2001). They are also removed from some abandoned but protected wood-pastures where the aim is to retain a semi-open birch-dominated habitat for e.g. the threatened white-backed woodpecker (*Dendrocopos leucotos* Bechstein) (Laine and Heikkilä 2011). In addition, several plant species benefit from the semi-open conditions and grazer-induced disturbances in wood-pastures, and rare bryophyte species are dependent on dung piles and decaying wood (Takala et al. 2014; Oldén et al. 2016; Oldén and Halme 2016).

The sustainable management of different types of wood-pastures requires that we know how grazing and browsing affect the regeneration of different tree species. We studied the numbers of small trees in 24 currently grazed wood-pastures and examined how grazing affects the regeneration of the dominant trees (birch, spruce and pine). We hypothesized that due to differences in palatability, birches regenerate poorly, spruces regenerate well and pines show an intermediate response. We also hypothesized that the regeneration of birches and pines is favored by time gaps in grazing or by high density of junipers (*Juniperus communis* L.) that protect saplings from grazers. In addition, due to the vast areas of abandoned wood-pastures, information is needed on their succession. We compared the young trees in 24 abandoned wood-pastures to the ones in currently grazed sites and examined how and how fast they change in terms of tree species and forest structure during the first decades after the abandonment. We hypothesized that birches and other deciduous trees regenerate quickly and abundantly after browsing ceases, while spruces benefit in the long-term from their ability to regenerate under shady conditions.

MATERIALS AND METHODS

Study sites

The study sites are located in Central Finland (62°14'N 25°44'E) in the southern and middle boreal zones (see Ahti et al. 1968). We studied 24 grazed (with cattle, horses, sheep or a mixture of these) wood-pastures and 24 wood-pastures that had been abandoned seven to 42 years earlier. The sites were chosen so that the abandoned ones were comparable to the grazed ones in terms of tree species and density of mature trees. The reasoning for this selection was that mature trees could not be affected by abandonment on the time scale we studied. Therefore, selecting grazed and abandoned sites with similar mature tree assemblages ensured that we studied habitats that were originally similar. All sites were classified to four types based on the dominant tree species: birch, spruce, pine, or a mixture of deciduous (birch and sometimes aspen) and coniferous trees (spruce and/or pine). Six grazed and six abandoned sites were chosen from each of the four types, totalling 48 sites in eight site types.

The sites are located on an area with non-calcareous bedrock and nutrient-poor soils. Among both grazed and abandoned sites the soils ranged from very acidic mor (pH_{CaCl2} ~3.0 to 3.5) to moderately acidic mull (pH_{CaCl2} ~4.5 to 5.0). However, the grazed sites had on average slightly higher soil pH than the abandoned ones, most likely due to management practices that have increased the pH during the last decades (Oldén et al. 2016). A more detailed description and photos of the study sites can be found in Oldén et al. (2016).

Data collection

Three study plots of 100 m^2 (ten by ten meters) were placed in each site. The plots were placed so that within each plot the species composition and density of mature trees corresponded to the dominant trees in the pasture. Within these plots, all woody plants > 130 cm tall were recorded, thus excluding seedlings that were still likely to become browsed. The tree species and the diameter at breast height (DBH, 1.3 m) were recorded. The two birch species (*Betula pendula* and *B. pubescens*) were pooled for practical reasons. Pine, spruce, aspen, rowan, grey alder and juniper were handled separately. Uncommon deciduous tree species were combined and are later called “other deciduous trees”, including willows (*Salix* spp.), bird cherries (*Prunus padus* L.), fly honeysuckles (*Lonicera xylosteum* L.), alder buckthorns (*Rhamnus frangula* L.) and Norway maples (*Acer platanoides* L.).

We measured canopy openness, which is expected to influence the regeneration of tree species. To measure canopy openness, eight fisheye-photos were taken from the center of each plot so that they covered the complete globe from the ground upwards. A fisheye-converter was used, allowing for photos with 120 degrees angle of view. For each photo, the camera was held vertically so that the lower edge of the photo was on the ground level at the edge of the plot and the upper edge was approximately upright. The proportion of sky pixels out of all pixels in the photo were calculated with ImageJ 1.45s. A more detailed description and example photos from both ends of the openness variation are given in Appendix S1. The average proportion of sky pixels in all of the 24 photos from each site was used to quantify canopy openness.

Information about time gaps in grazing history was obtained by interviewing the landowners. In six grazed sites gaps of at least five years (varied 5-12) had occurred since 1990. The owners of abandoned sites provided information regarding the year when the site was abandoned. On two abandoned sites spruce trees had been removed for conservation purposes.

Statistical analysis

We used Generalized Linear Models (GLMs) to analyze, which variables explain the numbers of small trees of the dominant species, i.e. birches, spruces and pines on a site (aspens were too scarce to be analyzed separately). For these analyses, we separated small trees (DBH <20cm) from the dominant trees (≥20cm). The number of small trees was a dependent variable, while the number of large conspecific trees was an explanatory variable (the hypothesis was that the abundance of large conspecific trees would increase the number of regenerating trees). First, we compared the number of small trees between grazed and abandoned sites, using the number of large trees as a covariate. Second, we analyzed whether the regeneration success in grazed sites was affected by four variables: the number of large conspecific trees, the occurrence of a time gap in grazing, the recorded number of junipers, and canopy openness. Third, the regeneration in abandoned sites was analyzed with four variables: the number of large conspecific trees, whether or not spruces had been removed, time since abandonment, and canopy openness. In each case, the continuous variables (number of large trees, number of junipers, openness, and time since abandonment) were standardized to zero mean and unit variance in order to make the effect sizes of different variables comparable. The full models were simplified stepwise so that the least significant variable was removed at each step until only significant ($P<0.05$) variables remained. The distributions of small trees were zero-inflated and over-dispersed so the analyses were performed with Zero Hurdle Negative Binomial GLMs. The Zero Hurdle binomial component models zero vs. larger counts, i.e. the probability that there are any small trees of the species. The zero-truncated Negative Binomial count component models the number of small trees if there are any. We used the function “hurdle” in package “pscl” (Jackman 2015) in R. An exception was made with spruces in abandoned sites where no zero-inflation occurred and we used Negative Binomial GLM with the function “glm.nb” from package ”MASS” (Venables and Ripley 2002).

Nonmetric Multidimensional Scaling (NMDS) was used to visualize the differences in tree species composition between different types of wood-pastures and between tree size classes. Wood-pastures were classified to eight types based on the dominant trees (birch, spruce, pine or mixed deciduous and coniferous) and the management situation (grazed or abandoned). Each type was represented by an arbitrary tree community that included all the trees summed from the six sites of that type. These communities were further divided to four size classes based on the tree’s diameter at breast height (DBH): 0-<10cm, 10-<20cm, 20-<30cm and ≥30cm. Using the resulting 32 arbitrary tree communities, NMDS was run with Bray-Curtis dissimilarities and the best two-dimensional solution was chosen. The size classes in each wood-pasture type were connected with lines to illustrate the difference in species composition between the size classes. The NMDS was run with all tree species included as well as including only the large-growing, dominant tree species (birch, spruce, pine and aspen). To run the NMDS we used function “metaMDS” in package “vegan” (Oksanen et al., 2013) in R version 3.2.2 (R Core Team 2015).

RESULTS

Tree regeneration in grazed wood-pastures

Birches regenerated poorly in almost all grazed wood-pastures (Figure 1A) and the chance of regeneration was not affected by the measured variables (Table 1). However, in sites where small birches were present, their numbers increased with the increasing number of large birches as well as the increasing number of junipers (Table 1, Figure 2A).

Spruces regenerated in all types of wood-pastures (Figure 1B) and the number of large spruces (DBH ≥20cm) did not have significant effects on the number of smaller spruces (<20cm), but the probability of regeneration was decreased by increasing canopy openness in the site (Table 1, Figure 2B).

Pine regeneration was successful in many pine-dominated sites, but not in the other types (Figure 1C), and the chance of regeneration was indeed positively affected by the number of large pines in the site (Table 1, Figure 2C). If regeneration occurred, the number of small pines was increased by the increasing number of junipers (Table 1, Figure 2C).

Junipers were abundant in many pine- and birch-dominated sites and in some sites with mixed trees (Figure 1E). Alders were present in some sites dominated by birches or mixed trees (Figure 1G), while small aspens, rowans and other deciduous trees were almost always absent from grazed sites (Figure 1 D,F,H).

In grazed wood-pastures dominated by birches, pines or mixed trees, the species composition of the smallest size class (DBH 0-<10cm) differed from that of larger classes due to a larger proportion of spruce (Figure 3A,B). In contrast, we observed no differences in species composition across size classes in spruce-dominated sites (Figure 3A,B).

Tree regeneration in abandoned wood-pastures

Birch regeneration was significantly higher in abandoned sites than in grazed sites (Table 1, Figure 2A). The numbers of small birches were high in almost all abandoned sites (Figure 2A) and none of the variables in our GLM-model affected them (Table 1).

Small spruces were abundant in all kinds of abandoned wood-pastures (Figure 1B) and their numbers were not dependent on the number of large spruces (Figure 2B). The numbers of small spruces were reduced by spruce removal and increasing canopy openness (Table 1).

Small pines were somewhat less abundant in abandoned than in grazed sites (Figure 2C), but the difference was not statistically significant. The number of small pines was not significantly affected by any of the measured variables in abandoned sites (Table 1).

Aspens regenerated in some sites dominated by birches or pines (Figure 1D). Large numbers of rowans were observed in all types of abandoned wood-pastures (Figure 1F), while alders and other deciduous trees regenerated in more modest numbers and mostly in sites dominated by birches or mixed trees (Figure 1 G,H).

In all types of abandoned wood-pastures, the tree community structure in the smallest size class of trees (DBH 0-<10cm) differed from that in the three larger size classes due to the abundant regeneration of deciduous trees (Figure 3A,B).

DISCUSSION

Tree regeneration in grazed wood-pastures

Spruces regenerated well in all types of grazed wood-pastures, except in some sites with very open canopies. Thus, it seems that most boreal wood-pastures are suitable for successful spruce regeneration, and the numbers of small spruces are hardly decreased by grazers due to their low interest towards spruce. Based on our results sprucification is a major problem in wood-pastures, because it tends to homogenize the landscape by turning most wood-pastures to spruce dominated. Cutting spruce trees seems to be the only effective way of reducing their proportion in the future canopy. This is already recommended in the Finnish guidelines for wood-pasture managers (Jääskeläinen 2003b), but based on our results this is not done sufficiently in all wood-pastures at the moment. However, some managers are removing spruces, which is also visible in our data as the low number of small spruces in some sites, and especially of those that are 10-<20cm in diameter. Spruce removal may also increase canopy openness in the future, which in turn reduces the regeneration of spruces. This is likely to benefit many rare plant and invertebrate species that dwell in semi-open woodlands (Pykälä 2001).

Birch and aspen regenerated in low numbers or not at all in the presence of grazers, while the numbers of young pines varied between sites. On the positive side, the regeneration of both birch and pine was more successful in sites where the same tree species was abundant in the dominant size classes, indicating that in many sites it may be possible to retain the dominant tree species in the future. However, this requires proper management practices, including both spruce removal and encouraging the regeneration of the targeted tree species. Based on our results, the most promising approach to increasing the regeneration of palatable species is to allow for large numbers of thorny or unpalatable nurse shrubs (Bakker et al. 2004; Smit and Ruifrok 2011), in this case junipers: Small birches and pines were more abundant in sites with numerous junipers. The most likely reason for this is that junipers facilitate the survival of palatable tree seedlings by acting as nurse shrubs, i.e. providing shelter from grazers (Lampimäki 1939; Olff et al. 1999; Bakker et al. 2004). While junipers can regenerate too intensively in hemiboreal pastures, this does not seem to be a problem in boreal wood-pastures, probably because the regenerating trees can later outcompete the junipers. Therefore we recommend that junipers are retained in boreal wood-pastures, unless they become very abundant and threaten targeted biodiversity values. However, Finnish management guidelines do not seem to take this geographic variation into account and are rather vague in their recommendations regarding junipers (Jääskeläinen 2003a,b; Priha 2003). Due to the benefits of junipers and other unattractive nurse shrubs for tree regeneration (Olff et al. 1999; Bakker et al. 2004), maintaining them in wood-pastures should be emphasized.

Contrary to our expectations, historic time gaps in grazing did not have significant effects on the regeneration of any of the dominant tree species, although the effect of time gaps can be partly masked by the possible removal of young trees by landowners during the relaunch of grazing. Interestingly, the highest observed numbers of small birches, pines and aspens were from sites that had recently experienced a ten-year gap in grazing, indicating that in some cases time gaps may indeed secure tree regeneration. However, if the gap is long enough to ensure tree regeneration, it can decrease the survival of many rare species dependent on grazing (Oldén et al. 2016). In addition, some tree species such as spruce, rowan, alder and willows may regenerate so abundantly that they have to be removed. We recommend that time gaps in grazing are avoided and they are employed to ensure tree regeneration only if regeneration of the target tree species seems to fail completely. Alternatively and preferably, the poor regeneration could be accepted as an inevitable phenomenon and wood-pastures may be allowed to evolve into open pastures in the long-term. However, because wood-pastures are becoming increasingly rare, the creation of new wood-pastures dominated by birches, for example, should be ensured within the landscape by using traditional disturbance-intensive land-use methods, such as slash-and-burn agriculture followed by grazing (Wallenius et al. 2007; Eriksson et al. 2010).

In Finland wood-pastures are classified to habitat types and subtypes based on the density and species of the dominant trees (Vainio et al. 2001; Schulman et al. 2008). Our results show that such types are not constant in the long term. Instead, they are successional stages and the progress towards spruce-dominated wood-pastures or alternatively open pastures cannot be halted by grazing alone. This results in problems with the evaluation of the conservation status of these biotopes. For example, the current spruce-dominated wood-pastures retain their structure while those dominated by any other tree species may slowly develop into either spruce-dominated or open habitats. We recommend that succession should be taken into account when the need for conservation actions for different biotopes is evaluated. For example, more constant site properties, such as soil fertility or moisture, could be used to classify habitat types and to evaluate their rarity since they affect the plant communities in wood-pastures (Oldén et al. 2016).

Tree regeneration in abandoned wood-pastures

In the abandoned sites, the species composition of small trees differed from that of the dominant trees, due to the abundant regeneration of deciduous trees that were rare or absent in the larger size classes. Especially rowans regenerated very well in all types of abandoned wood-pastures.

During the first decades after the abandonment the wood-pastures became quite densely filled with such pioneering deciduous trees. Among them, birches and spruces regenerated abundantly and rapidly, while pines regenerated poorly almost everywhere. The numbers of newly regenerated birches, spruces and pines were independent of the original abundances of the species in the dominant cohorts, indicating that abandonment results in biotic homogenization of the tree composition in wood-pastures. During the following decades most abandoned wood-pastures are likely to become dominated by birches and spruces. Later on, if succession is allowed to proceed, spruces will probably dominate most of the sites. The succession may be slower in more fertile and open-canopy sites where deciduous trees can resist sprucification for a longer time.

Spruces are sometimes removed from old, abandoned wood-pastures in order to retain semi-open birch dominated habitats with high conservation values, mostly as a territory of an endangered bird, the white-backed woodpecker (Laine and Heikkilä 2011). Based on our results this can indeed reduce the amount of spruces (at least temporarily), but the problem is that deciduous trees do not seem to regenerate more abundantly after spruce removal. Our data included only two abandoned sites with spruce removal, but the result is supported by another study where the regeneration of deciduous trees was observed to be equally low in spruce-removed and unaffected parts of abandoned wood-pastures (Mustonen and Saine 2013). This type of management is usually performed in remote conservation areas where elks (*Alces alces* L.) tend to be so numerous that they browse the majority of the seedlings of deciduous trees (Mustonen and Saine 2013). It should be acknowledged that a birch-dominated wood-pasture is only a temporary successional stage that probably cannot be retained for centuries. We recommend a landscape-level management plan that ensures the supply of new birch-dominated habitats, their decade-long management as wood-pastures and later on abandonment to be slowly changed into a mixed forest and later a spruce dominated old-growth forest. After this stage the cycle could be restarted or the forest retained as an old-growth site depending on the conservation priorities of that era.

To restore an abandoned wood-pasture, it is recommended that grazing is resumed and most young trees are removed (Jääskeläinen 2003a). Based on our results, the effort should be concentrated in removing most spruce and alder seedlings that the grazers avoid. Small individuals of other tree species are susceptible to, and thus controlled by, grazers. However, if the trees are growing densely and many of them are higher than about two meters, they may need to be thinned in order to regain the semi-open conditions that favor species typical to semi-open pastures. Wood-pastures can host many species that are of conservation importance and favor semi-open conditions (Bergmeier and Roellig 2014). When planning the restoration, it is crucial to keep in mind the aimed tree structure so that sufficient numbers of the preferred trees are retained. Due to the low abundance of small pines in abandoned wood-pastures it may be necessary to retain all young pines, if the aim is to restore the site to a pine-dominated pasture.

CONCLUSIONS

Our results show that the regenerating tree cohorts have different species composition than the current adult cohorts in both grazed and abandoned wood-pastures, except for sites that are dominated by spruces. While grazing can maintain pioneer species in the field and ground layers (Oldén et al. 2016), it reduces the number of deciduous pioneer trees and may even speed succession by favoring competitive species, in this case spruce. In contrast, abandonment results in a rapid increase of deciduous species, but this early successional phase is likely to be short, because also spruces increase in numbers.

In addition to grazing, the maintenance of the current tree species composition requires other management practices. Young spruces need to be repeatedly removed from all sites where their regeneration is not the aim. In grazed sites the regeneration of browsing-prone species, such as birch and pine, should be facilitated by allowing the growth of numerous nurse shrubs that protect the seedlings. Time gaps in grazing may not be efficient enough in promoting the regeneration of browsing-prone target tree species. Hence, time gaps in grazing should be avoided, unless tree regeneration is failing completely, and even then the loss of grazing-dependent species should be weighed against providing a long enough gap for the establishment of palatable trees.

In the long-term it is probably most efficient to allow individual sites to change, develop and become abandoned while their habitat types are replaced by other sites within the landscape. We recommend that the management of each wood-pasture site should be planned flexibly. This means that depending on the biodiversity and landscape values as well as management resources, the site can be allowed to develop into an open pasture or a wood-pasture with variable and changing tree structures. However, at the landscape level there is a need for a long-term plan for creating and managing new wood-pastures, especially the ones dominated by deciduous trees. More generally, fighting against succession at the site scale may be doomed to fail, and more dynamic landscape planning schemes should be encouraged in wood-pastures as well as other biotopes that are dependent on active management.

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Electronic supplementary material

Appendix S1. Canopy openness measurement from photos

Figures

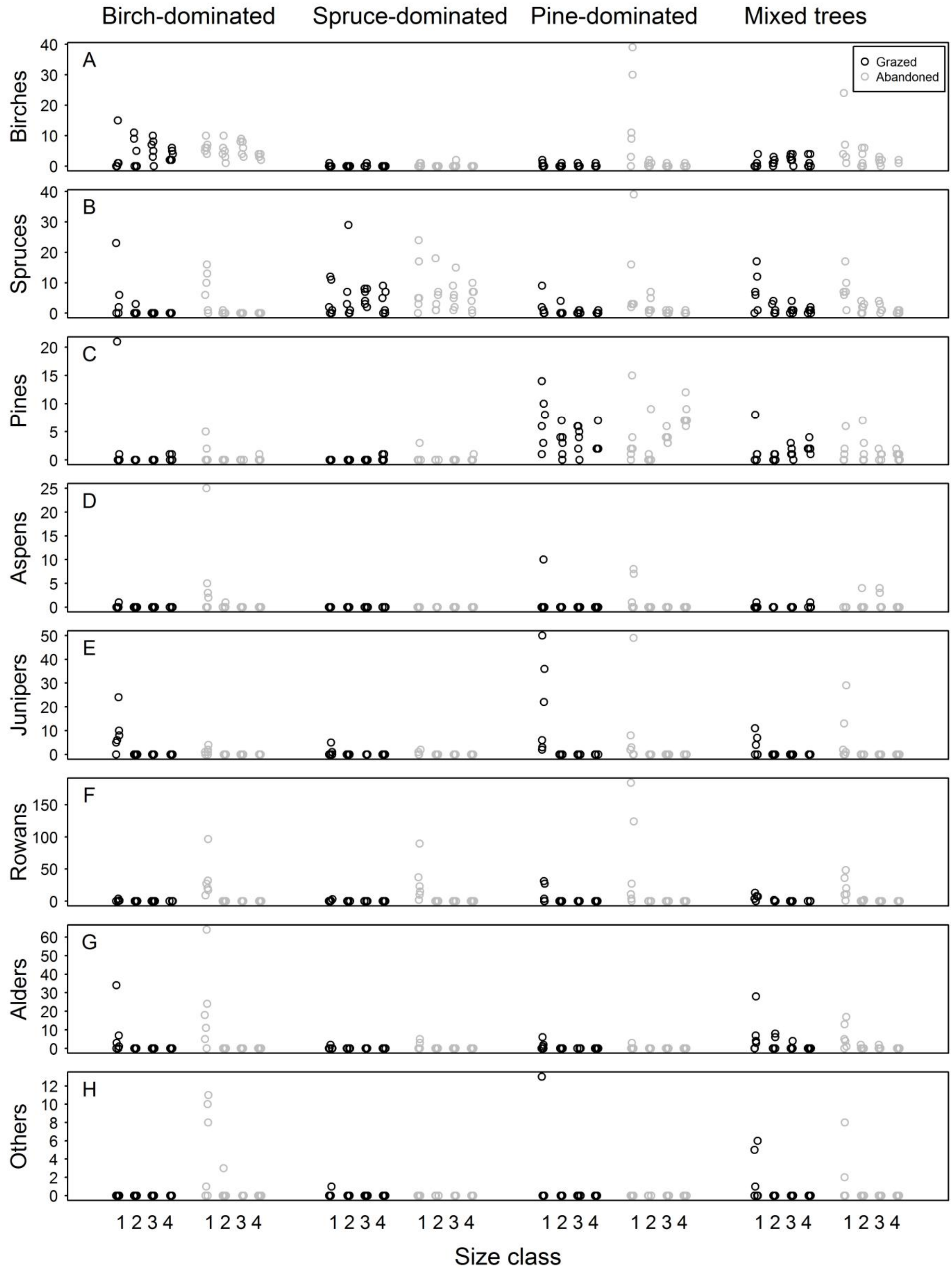

Figure 1. The recorded number of trees in grazed and abandoned wood-pastures that are dominated by birches, spruces, pines or mixed trees: A) birches, B) spruces, C) pines, D) aspens, E) junipers, F) rowans, G) alders and H) other deciduous trees. The four size classes are based on the DBH: 1) 0-<10cm, 2) 10-<20cm, 3) 20-<30cm, and 4) ≥30cm. Note that the maximum numbers of trees vary between species.

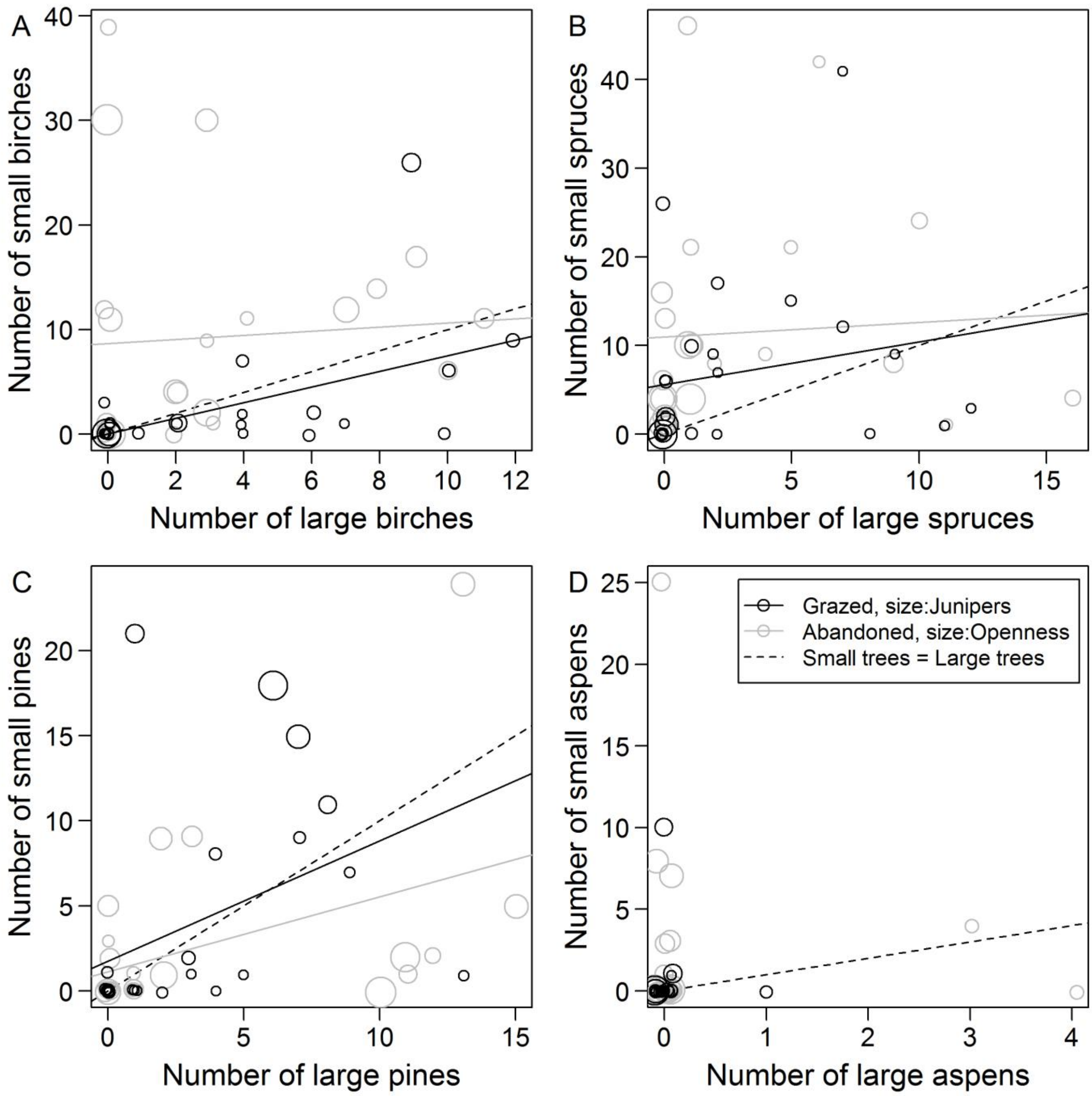

Figure 2. The recorded number of small trees (DBH <20cm) versus the number of large trees (≥20cm) on grazed and abandoned wood-pasture sites: A for birches, B for spruces, C for pines and D for aspens. Symbol size for grazed sites corresponds to the number of junipers and for abandoned sites it corresponds to the openness of the site. The dashed line indicates a hypothetical situation where small and large conspecific trees would be equally abundant.

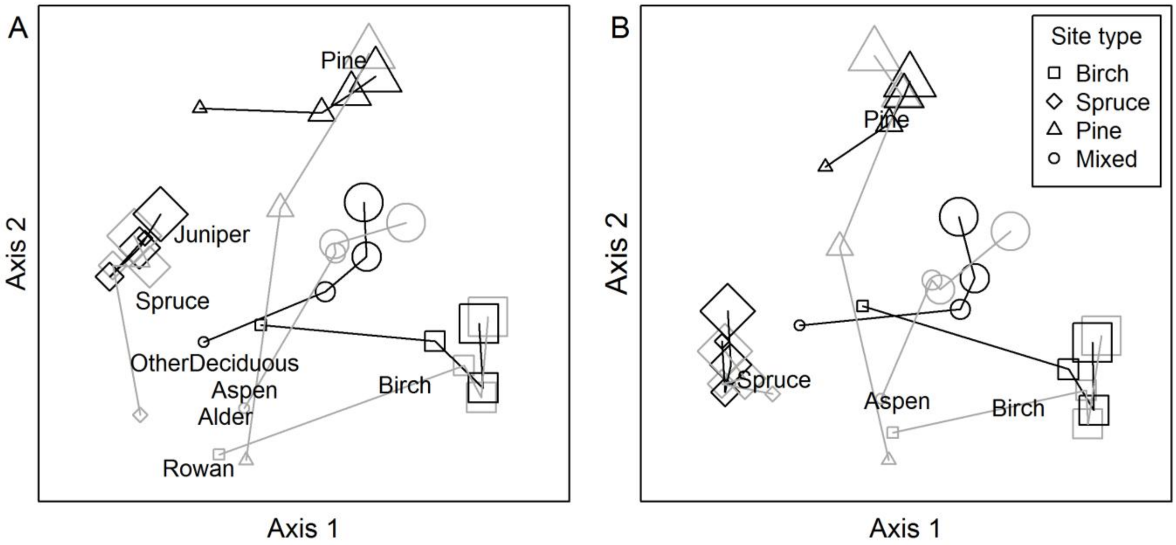

Figure 3. Non-Metric Multidimensional Scaling of the tree communities of grazed (black) and abandoned (gray) sites with different dominant trees: birch, spruce, pine or mixed deciduous and coniferous trees (see legend). Symbol size represents the size class (DBH 0-<10cm, 10-<20cm, 20-<30cm or ≥30cm) and the lines connect the symbols of different sizes in the same type of sites. A) for all tree species and B) for only the dominant tree species. The average locations of the tree species are overlaid in the figures.

Table

Table 1. Results from the Zero Hurdle Negative Binomial GLM-models explaining the numbers of small (DBH <20cm) birches, spruces and pines on all sites, grazed sites and abandoned sites: the z-value and the significance level (***=P<0.001, **=P<0.01, *=P<0.05). Results are shown only for variables with significant effects (P<0.05) except for the intercepts. The Zero Hurdle model was not run for spruces on abandoned sites due to the lack of zero inflation.

All sites	Birch		Spruce		Pine	
	Zero hurdle	Count	Zero hurdle	Count	Zero hurdle	Count
Intercept	3.11 **	3.64 ***	4.16 ***	10.64 ***	0.80	1.35
Management	-2.26 *	-2.00 *				
Large individuals	2.15 *				2.84 **	
Grazed sites	Birch		Spruce		Pine	
	Zero hurdle	Count	Zero hurdle	Count	Zero hurdle	Count
Intercept	0.41	1.47	1.61	6.92 ***	0.87	4.18 ***
Large individuals		2.26 *			2.48 *	
Gap						
Junipers		2.29 *				2.59 **
Openness			-2.11 *			
Abandoned sites	Birch		Spruce		Pine	
	Zero hurdle	Count	Zero hurdle	Count	Zero hurdle	Count
Intercept	2.94 **	7.14 ***		13.26 ***	0.00	0.57
Large individuals						
Spruce removal				-2.49 *		
Time s. abandonm.						
Openness				-2.42 *		