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Plant species loss due to forest succession in Alpine pastures depends on site conditions and observation scale

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ABSTRACT

Cessation of agricultural management and subsequent natural forest succession has been the primary land use change in the Southern Alps over the past 50 years. It is generally assumed that early stages of succession host more plant species than grazed pastures, but that this richness is partly lost as the density of woody species increases. Based on vegetation surveys on eight sites in the Italian Alps, we found the effects of forest succession on plant species richness to depend strongly on environmental conditions. The relationship between plant species richness and wood cover at the sites ranged from non-detectable over hump-shaped, to monotonically decreasing. Linear mixed-effects models indicate that high mean annual temperature is associated with a strong decrease in plant species richness and in the number of red-list species along the pasture-to-forest gradient. Sampling plant species composition at a range of scales allowed us to rule out artefacts caused by modified species–area relationships as a consequence of changes in wood cover. Multi-scale sampling also indicated that the primary loss of plant species richness by forest succession is in plant species with low abundance. Our data further allow assessment of the risk of species loss in mountain grasslands in the Southern Alps, which is highest on sites with higher mean annual temperature. These areas should receive concentrated attention and support for biodiversity conservation.

1. Introduction

In the past half a century, the Southern Alps have undergone a tremendous and arguably unprecedented change in land use. Since 1960, about 800,000 ha of grassland have been abandoned throughout the Italian Alpine Arch, which corresponds to 45% of the surface originally covered by pastures and meadows (Bovolenta, 2004; Chemini and Gianelle, 1999). As a consequence of land abandonment processes, mountain regions have been experiencing radical landscape changes, as once managed areas are reverting to forests through the process of natural succession (Conti and Fagarazzi, 2004). According to the National Statistical Bureau (ISTAT), during the second half of the 20th century, forest areas in the Italian Alps increased by 14.9%, with an increase of 7.0% in the last decade of the century alone (Piussi and Pettenella, 2000).

Studies conducted in other regions demonstrated that the reduction and abandonment of cutting or grazing favours establishment of persistent, competitive species, most of which are woody shrubs or trees. In pastures, woody species establish first in close association with the plants or vegetation patches that facilitate their establishment, for example forest edges or forest islands and individual trees within the grassland (Van Uytvanck et al., 2008). The process of forest succession is highly non-linear over time. Finegan (1984) observed that 4–11 years after the cessation of grazing activities, only few woody plants were growing in a scattered pattern. However, after 10–20 years, stable woody vegetation had established across the entire originally grazed surface (Finegan, 1984). The pace of establishment also depends on which dominant woody species are present: each woody species has a specific response to environmental factors (for example De Gasperis and Motzkin, 2007; Tasser and Tappeiner, 2002; Van Gils et al., 2008). The nutrient status of the soil is another determinant of the rate of shrub encroachment in abandoned pastures. On nutrient rich and productive sites (such as pastures), it takes 30–45 years before woody species become dominant in former open vegetation (Smit and Olff, 1998). Del Favero et al. (1998) found that *Fagus sylvatica* established at different rates on various substrates because of the competition by other shrubby and woody species. In contrast, Van Gils et al. (2008) observed that the establishment of *F. sylvatica* on abandoned farmland depended on the intensity of grazing by sheep, the distance from seed sources, the presence of protective forest or shrubby shade and the wind exposure of saplings, but not on the soil substrate. Hence, on sites where some grassland management remains, grazing increases the complexity of successional processes. Van Uytvanck et al. (2008) found that trampling

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by herbivores favor the germination of tree seeds but damages saplings not protected by established shrub or other unpalatable vegetation. Also forest management may have an important role on the succession of natural forests influencing the composition of trees, saplings and herbaceous species, and the competition between all of them (Del Favero et al., 1998).

Natural reforestation changes vegetation composition and species richness in pastures. Most studies report a decrease in the number of species with increasing forest cover (Anthelme et al., 2001; Fischer and Wipf, 2002; Kesting, 2009; Manning et al., 2006). However, there is no consensus on whether the decrease is steady over the entire investigated wood cover gradient or whether the decrease reaches a maximum at intermediate stages of forest succession. This lack of agreement arises from the fact that most studies analysed forest succession at only one site or at a number of sites covering a very limited range of environmental gradients.

In order to identify environmental drivers of the effect of forest succession on plant species richness, we investigated pasture-to-forest gradients on eight contrasting sites in the Italian Alps. All eight investigated sites are only periodically inhabited and used by livestock between May or June and September, depending on altitude and annual weather conditions. Seven sites are grazed by dairy cows, one is grazed by sheep. On all sites, grazing persisted until present, but stocking rates and labour input are not sufficient to prevent the natural succession of forests. The reasons for this are, for example, that cows are increasingly fed on concentrates instead of grass, and that farmers invest less time into the removal of saplings.

In our study we address three basic questions. The first is: how is plant species richness affected by wood cover? We hypothesize that a low percentage of wood cover outcompetes a comparatively larger number of shade-sensitive grassland species and hence species richness decreases with wood cover.

The second question is: does the effect of wood cover on plant species richness depend on environmental site conditions? We hypothesize that environmental conditions have direct effects on the grassland vegetation present before abandonment and also affects the dynamics that occur thereafter (e.g. the woody species becoming dominant). In order to test this second hypothesis, we use generalized linear mixed-effects models which allow the analysis of effects of environmental site conditions in a hierarchical manner.

The last question is: are the observed patterns of species richness an artifact of changing species–area relationship with increasing wood cover? We therefore investigate to what extent forest succession alters scale-dependent heterogeneity in species composition. Such alteration would seriously affect the interpretation of species numbers collected on equal sample sizes along the successional gradient.

2. Materials and methods

2.1. Survey sites

This study was carried out on eight sites located in the Eastern Alps of Italy, between 2006 and 2010 (Fig. 1). The sites represented typical pastures, which were formerly open grassland but are now in the process of forest succession. Pastures with an important portion of old-grown trees (i.e. traditionally wooded pastures) were not investigated. Sites were selected to assure that each of the primary establishing woody species in the region were present. Each site was dominated by a particular woody species (Table 1). In order to identify the different stages of woody species establishment, we used aerial photographs and forest settlement plans developed for forest management. These plans delineate forest, agricultural and grasslands based on surveys of past management. For the purpose of this study, we considered areas delineated as forest outside the pasture cadastral unit to be totally established woodland. Inside the area delineated as pasture land, we identified different stages of forest succession based on analysis of aerial photographs. The resulting map was used in the field to identify sampling locations with different percentage of wood cover.

All study sites are still partly communally grazed by livestock during the summer; in all sites the actual stocking rates are lower than the potential ones. Average grazing intensities are low but locally highly variable especially along the wood-cover gradient. The vegetation is heterogeneously structured, including grazed pastures without any woody species, sparse naturally established shrubland, and completely established woodland.

The climate on all sites is temperate with mean annual precipitation between 800 mm and 1550 mm and a mean annual temperature between 3.5 °C and 6.8 °C (Table 1). The rainfall shows a pronounced intra-annual pattern with May and November being the periods when most of the rainfall occurs. Four sites are situated on calcareous substrate and four sites are situated on siliceous substrate. Additional site characteristics are presented in Table 1.

2.2. Species sampling

At each study site, three different sampling methods were applied:

2.2.1. Small-area sampling (1 m^2) along transects

At each site, six transects were established perpendicular to the edge of the forest, in order to include different stages of woody species establishment. Each transect started in an area of pure grassland without woody species and finished in completely established woodland. The lengths of the transects varied between sites depending on the dominant wood species. Along the transect line, five quadrats of 1 m^2 were placed in order to represent one of five wood cover classes: 0%, 25%, 50%, 75%, and 100%. In each quadrat, the percentage of wood cover was visually estimated and all species present were recorded without their relative abundance, three times per year over 2 years.

2.2.2. Large-area sampling (100 m^2) in wood-cover strata

Thirty additional quadrats of 10 m $\times$ 10 m were established at each site in strata with particular levels of wood cover. Care was taken that the selected locations of the large area quadrats had homogenous levels of wood cover that were well distributed between 0% and 100%. Along transects, it was frequently impossible to find areas of suitable size with a homogenous wood cover. Strata of shrub and tree cover were delineated using orthophotos in which sampling locations were predetermined at random. Where the orthophoto provided insufficient information to assess the real state of reforestation, the exact locations was refined in the field. For each plot, a complete floristic survey was carried out: all herbaceous species were recorded, and their relative abundance values were visually estimated. Additionally, cover values were estimated using a 0–100% scale for each of the two vegetation layers (wood and shrub). Using these estimates, the distribution of species numbers was analysed along the entire gradient of wood cover. For every plot, the abundance of all vascular plants was recorded three times per year over 2 years. Species richness was calculated as the cumulated number of all six surveys and the abundance of each species was calculated as the mean of the estimates of all six surveys.