RESEARCH ARTICLE

Ecosystem service multifunctionality of low-productivity forests and implications for conservation and management

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Abstract

1. Low-productivity forests are often the last remaining pristine forests in managed forest landscapes and typically overrepresented among protected forests. However, the provisioning of individual and multiple ecosystem services (ES-multifunctionality) by these forests remains poorly assessed, making it difficult to evaluate their importance in forest conservation and management.

2. Here, using nationwide data on ES from over 2,000 forest plots, we test whether levels of ES-multifunctionality and individual ES differ between low-productivity forested mires and rocky outcrops in relation to the levels of productive forests, and as a function of forest age, tree species richness and climate. We defined ES-multifunctionality using different threshold values of the maximum levels (low, medium and high) and weighted these according to land-use objectives (equal weight of all services, greater weight to cultural and supporting ES or greater weight to production).

3. We show that the ES-multifunctionality of forested mires is consistently lower than those of productive forests. However, the ES-multifunctionality increased with forest age in forested mires but not in productive forests. The ES-multifunctionality of forested rocky outcrops, on the other hand, was higher or equivalent to that of productive forests under equal weight and supporting land-use objectives, respectively. Our findings highlight that forested rocky outcrops can supply multiple ES, especially older forested stands with mixtures of coniferous and deciduous trees. Generally, we found no evidence for strong trade-offs between the ES studied and our results highlight the importance of forest age for increasing the ES-multifunctionality of low-productivity forests.

4. *Synthesis and applications.* Low-productivity forests should not be exempt of forestry or protected purely based on low productivity or low land-use conflict if the goal is to conserve multiple ecosystem services (ES). Inclusion grounds for protecting low-productivity forests should instead carefully consider the site type (dry vs. wet), forest age and tree species richness. To maintain higher ES-multifunctionality in low-productivity forests, older or deciduous trees should also not be harvested. This will require changes in current conservation or management policies of low-productivity forests of some countries.
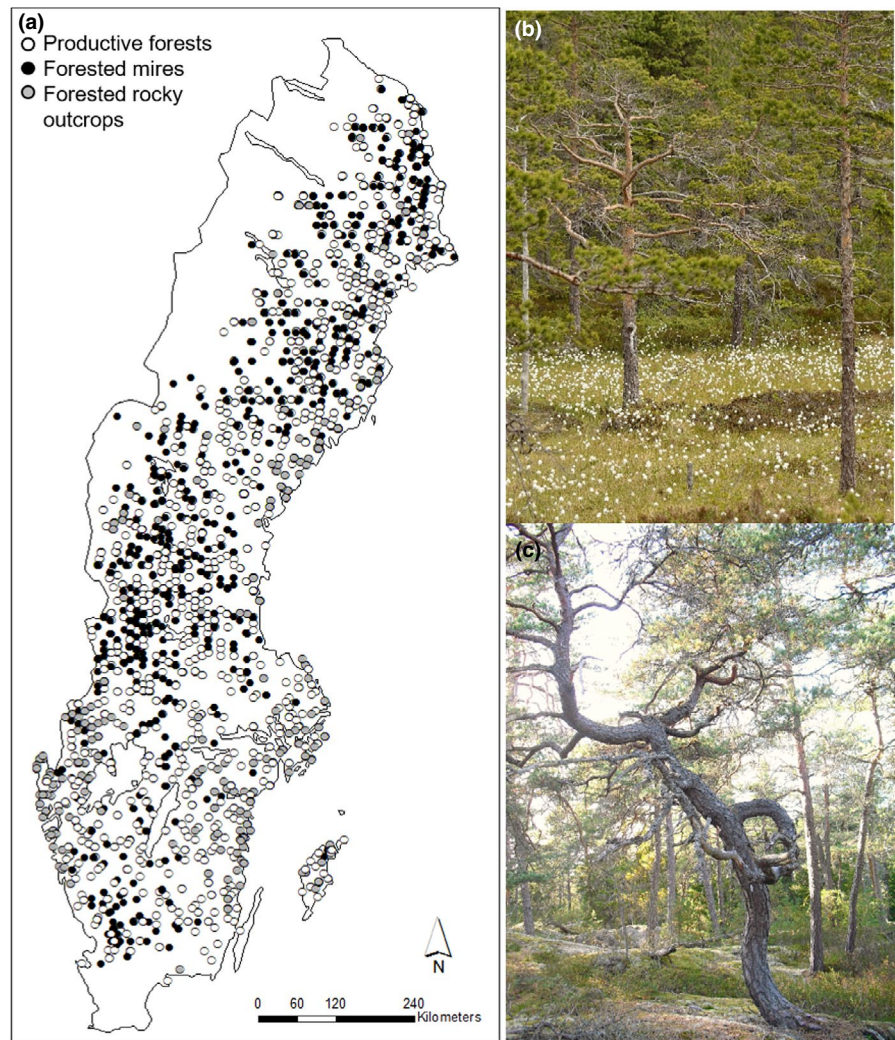
1 | INTRODUCTION

Forests provide a broad range of ecosystem services (ES) that are beneficial to human society (e.g. wood production and carbon storage) and important ecosystem functions (e.g. primary productivity and nutrient cycling). With direct and indirect impacts on human well-being, the provision of a broad range of ES from forests represents a valuable tool to be used in forest planning and management (Verkerk et al., 2014). Research on the ability of forest ecosystems to provide simultaneously multiple ecosystem functions and services (ecosystem multifunctionality) is increasing (e.g. Gamfeldt et al., 2013; van der Plas et al., 2016), as comprehensive datasets of ES and functions have become available via national monitoring programs (e.g. National Forest Inventories) and via open-access internet platforms (e.g. www.gbif.org; www.artportalen.se). Ecosystems are inherently multidimensional and multifunctionality measures, therefore provide important complements to studies investigating how individual services and functions relate to their drivers (Manning et al., 2018). To date, forest studies have mostly focused on one forest-ecosystem service (i.e. wood productivity). Furthermore, the assessment of drivers affecting the provision and interaction of multiple ES is still limited to productive forests (e.g. Gamfeldt et al., 2013; Jonsson, Bengtsson, Gamfeldt, Moen, & Snäll, 2019; van der Plas et al., 2016). Investigating what is driving ES-multifunctionality in low-productivity forests is particularly important since they are often the last remaining pristine habitats in managed forest landscapes, and are thus overrepresented among protected forests. Low-productivity forests in Sweden are regularly exempt from conventional forestry (Swedish Forestry Act, §13a 1979: 426), although not based on their conservation values. In Finland, such low-productivity forests are not regulated by law, but voluntarily set aside from forestry by the largest state-owned forest company. This results in low-productivity forests being overrepresented, as in Sweden where low-productivity forested mires (wet sites on peaty soils; Figure 1b) and rocky outcrops (dry sites on thin rocky soils; Figure 1c) comprise about half of the formally protected forest area, although they together only comprise around 17% of the total 28.1 million ha of Swedish forest land (Swedish University of Agricultural Sciences, 2015).

Understanding more broadly how land-use and biodiversity influence ES can provide important insights for management and conservation strategies (Millennium Ecosystem Assessment, 2005). Biodiversity conservation and the supply of some ES rely heavily on the protection of some areas. This was highlighted in the Aichi Biodiversity Target 11, which proposed to increase the protected area to at least 17% of terrestrial areas 'of particular importance for biodiversity and ES' by 2020 (CBD, 2010). This area-based target is explicit and measurable, but it has been criticized for lack of guidance for what constitute *important*, *representative* and *effective* target areas, which influence how different countries implement the target (Watson et al., 2016). Conservation area systems often already contain a biased sample of biodiversity and ES, usually that of remote and low-productivity habitats with low land-use conflicts (e.g. Polak et al., 2016; Venter et al., 2014). Low-productivity forests are often the only land that has been left unmanaged and constitute a less expensive way to obtain large protected areas (e.g. Juutinen, Mäntymaa, Mönkkönen, & Salmi, 2004; Schröter, Rusch, Barton, Blumentrath, & Nordén, 2014). Concerns are that conservation targets may be achieved in terms of area by protecting low-productivity areas, but fail to effectively generate genuine biodiversity and ES benefits if areas are poorly located, inadequately managed, or based on unjustifiable inclusion grounds (Watson et al., 2016). For example, it has been shown that low-productivity forests may harbour lower biodiversity values than more productive forests due to lower resource availability and heterogeneity limiting population sizes (e.g. Chase, 2010; Hämäläinen, Strengbom, & Ranius, 2018; Liang et al., 2016). Comparative insights of the drivers of ES-multifunctionality of different types of low-productivity forests (i.e. site type, tree species richness, forest age) under different land-use objectives (e.g. prioritizing cultural, provisioning, regulating or supporting ES) are needed to develop efficient policies in forest conservation and management.

The overall aim of this study was to test for differences in the levels of multiple ecosystem services (individual ES and ES-multifunctionality) valued by human society in low-productivity forested mires and rocky outcrops, in relation to their levels in productive forests of comparable densities of *Pinus sylvestris*, forest age and distribution across Sweden. To do so, we used data on 12 ES from a combination of National Forest Inventory (NFI) data and Citizen Science Data (CSD) from over 2,000 forest plots. These ES covered a wide range of provisioning (tree biomass, forest berries), regulating (topsoil carbon storage), cultural and supporting services (e.g. deciduous trees, deadwood, biodiversity). First, we tested for differences in the levels of ES-multifunctionality between low-productivity and productive forests, and as a function of forest age, tree species richness and climate. We defined ES-multifunctionality using different threshold values (25%, 50% and 75% of the maximum ES level). To accommodate for different land-use objectives, we weighted the different ES values according to three scenarios (a) equal weight of all services, (b) greater weight to cultural and supporting services (hereafter called supporting)

FIGURE 1 The (a) distribution of the National Forest Inventory plots of the boreonemoral and boreal productive forests, low-productivity forested mires and rocky outcrops used in this study (points overlap). It covers 14° of latitude (55.3–69.1°N) and 28.1 million ha forest land. Photo of a (b) forested mire by Ute Bradter and (c) forested rocky outcrop by Mari Jönsson

and (c) greater weight to tree biomass production (hereafter production). Second, we tested for differences in the levels of individual ES between low-productivity and productive forests, and as a function of forest age, tree species richness and climate. We hypothesized that the overall ES-multifunctionality would be lower in low-productivity forests compared to productive forests. However, trade-offs between ES could exist which could nuance this hypothesis (e.g. Felipe-Lucia et al., 2018; Mace, Norris, & Fitter, 2012). In particular, higher levels of ES are expected in productive forests because the provision of tree biomass, forest berries, as well as forest structures important for biodiversity (e.g. deciduous trees and deadwood) are generally positively related to site productivity (Chase, 2010; Hämäläinen et al., 2018). However, low-productivity forests have been less affected by forestry and may therefore shelter higher biodiversity due to higher quantities of key forest structures such as deadwood and old trees (Fitzsimons & Michael, 2017; Hämäläinen et al., 2018). We also expected higher supplies of soil carbon storage in forested mires on more peaty soils (e.g. Clymo, Turunen, & Tolonen, 1998) compared to productive forests. In terms of the production land-use objectives, we thus generally expected a higher supply of ES in productive forests. In terms of

equal weight and supporting land-use objectives, we hypothesized that the overall ES supply in productive forests may be reduced due to trade-offs between provisioning and supporting ES.

2 | MATERIALS AND METHODS

2.1 | Study design

The principal data used in this study, characterizing forest ES and attributes, were obtained from the Swedish National Forest Inventory (NFI, www.slu.se/riksskogstaxeringen) and Forest Soil Inventory (SFSI, www.slu.se/markinventeringen). The Swedish NFI and SFSI are both carried out recurrently on the same c. 20,000 permanent circular sample plots in a randomly planned regular sampling grid in Sweden (Fridman et al., 2014). Circular plots are organized in quadratic clusters, each encompassing eight plots (four in the southwestern region), with increasing side length and distance apart towards the north. The two inventories use the same 10 m radius (314 m^2) circular plots, which are systematically surveyed in 5- (NFI) or 10-year (SFSI) intervals. From the NFI and SFSI databases,

we extracted data from 1999 to 2010 for plots that fulfilled certain criteria: (a) ≥10-year-old forests (excluding recently cut forests); (b) with tree volumes of Scots pine *Pinus sylvestris* ≥60%, since pines are abundant tree species in low-productivity forested mires and rocky outcrops (Figure 1); (c) located on managed forest land and (d) belonged to either the site types (1) low-productivity forested mires or (2) rocky outcrops, both with growth of <1 m³ ha⁻¹ year⁻¹ stem volume over bark or (3) productive forests with growth of ≥1 m³ ha⁻¹ year⁻¹, as defined in the Swedish Forestry Act. Our selection resulted in a total of 1,076 low-productivity forest plots (835 mire; 241 rocky outcrop) and 3,840 productive plots, although fewer plots (520 low-productivity [406 mire; 114 rocky outcrop] and 1,462 productive) were available for some of the ES that were based on the SFSI inventory. To obtain an equal sample size and comparable forest age and geographical distribution of low-productivity and productive forests, we paired with plot data from the nearest productive forest plot of similar forest stand age (±5 years) of each respective low-productivity plot (Figure 1). The methods for estimating forest stand age and tree species richness in 314 m² plots are presented in Appendix S1. For each centre point of the NFI and SFSI plots, the overlapping predicted habitat suitability values (hereafter referred to as habitat provisioning) for deadwood-associated biodiversity based on CSD were modelled and extracted (see Section 2.3 below).

2.2 | The studied ES

The ES considered in this study can be classified into four categories, identified in the Millennium Ecosystem Assessment (2005). *Provisioning services:* tree biomass production (kg m⁻² year⁻¹), occurrence (presence/absence) of bilberry *Vaccinium myrtillus* and cowberry *Vaccinium vitis-idaea*. *Regulating services:* soil carbon storage (g/m²) in the topsoil. *Cultural/supporting services:* the occurrence and volume of any native deciduous tree species and high conservation value deciduous tree species: aspen *Populus tremula* and goat willow *Salix caprea* with diameter at breast height ≥10 cm, and tree regeneration richness measured as the number of sapling/juvenile native tree species with diameter at breast height <10 cm, the occurrence and volume of coarse deadwood and the occurrence of coarse deadwood in at least three decay classes (from a total of five classes, representing a local diversity of deadwood) with large-end diameter ≥10 cm, habitat provisioning for saproxylic old-growth forest indicator deadwood-associated beetles, fungi and epixylic bryophytes, as predicted based on models fitted to CSD. The descriptive statistics, measurement methods for tree biomass production, soil carbon storage and further motivations for inclusion of ES are included in Appendix S1. We tested correlations between individual ES and evaluated the effect of including three positively correlated habitat provisioning services for beetles, bryophytes and fungi (we found no significant effects on model outcomes; see Appendix S2).

2.3 | Biodiversity assessment

We extracted citizen science reports of species occurrence – only data from a national species database (Swedish Species Observation System; www.artportalen.se), from 2001 to 2010 where the reporter had specified a spatial accuracy of ≤100 m (e.g. Snäll, Lehtomäki, Arponen, Elith, & Moilanen, 2016). All the studied species utilize deadwood, where the focal species of wood-living beetles (52 species) and polypore fungi (37 species) utilize dead spruce or pine and are threatened, that is, they are categorized as Vulnerable, Endangered or Critically Endangered according to IUCNs criteria (Artdatabanken, 2015). The focal bryophytes (10 species) utilize deadwood of any tree species and they are red-listed, that is, also Near Threatened species were included (Artdatabanken, 2015). Models for the relationship between citizen-generated species occurrence data (point localities) and environmental variables was used to predict the distribution of our target groups of beetles, bryophytes and fungi in 25 × 25 m² for the whole country of Sweden (excluding the alpine region) using the MaxEnt framework (e.g. Elith et al., 2006; Kearney, Wintle, & Porter, 2010). We used inductive models, where knowledge of the species–habitat relationship was inferred from the habitat where the species was recorded and the output was a quantitative habitat provisioning (0–1). The CSD in the Swedish Species Observation System have been evaluated and shown to produce reliable species distributions estimates of saproxylic species (Mair et al., 2017; Snäll, Forslund, Jeppsson, Lindhe, & O'Hara, 2014). For each NFI plot and respective forest indicator group, the habitat provisioning value of the 25 × 25 m² overlapping with the centre point of the NFI plot was extracted. Details on the statistical modelling and prediction of the forest indicator groups are provided in Appendix S3.

2.4 | ES-multifunctionality assessment

We used a threshold-based approach to quantify the ES-multifunctionality, counting the number of ES that exceed a given threshold value, where the thresholds equal a certain percentage of the maximum observed value (performance threshold value, *T*) of each service (e.g. Byrnes et al., 2014; van der Plas et al., 2016). The approach allows considering a minimum value of all ecosystem services that is considered satisfactory and is superior to an averaging-approach since it does not assume that services are substitutable (Byrnes et al., 2014). We examined several threshold values for multiple services to also understand how single service responses result in overall multifunctionality (Byrnes et al., 2014).

To facilitate comparison of all ES, values were scaled between 0 and 1. Within plots, the level of each standardized service measurement was evaluated if it exceeded a certain percentage (low = 25%, medium = 50% and high = 75%) of the performance threshold value *T*. The threshold value *T* was defined as the mean of the highest five values (to reduce the influence of single extreme values; sensu Allan

et al., 2015), measured within all plots (low-productivity and productive forests) across the country. Nine individual ES were included in the calculations of the different ES-multifunctionality values, based on plots which contained both NFI and SFSI plot data (Appendix S2). Plots with one type of forest berry were counted in low and medium thresholds values, while only plots with both berry types were counted in high threshold values. We considered separately cowberries and bilberries in our analyses as the shrubs providing these two berry types utilize different niches. Cowberry has a greater need for light and tolerance of disturbance than bilberry. Cowberry therefore peaks in abundance at an earlier stage of the forest succession, on drier soils and more open microhabitats, and also fruit later in the season, compared to bilberry. By only counting occurrences of both berries at high thresholds, we considered this as a proxy of greater microhabitat heterogeneity for all forest berries and an overall extended time period for berry production.

Finally, the scaled ES values were weighted according to three land-use scenarios and summed to quantify the ES-multifunctionality value (Allan et al., 2015; Manning et al., 2018). We defined three broad land-use objective scenarios: (a) a classic 'equal weight' with equal weighting for all services, (b) 'supporting' with an increased weighting for cultural and supporting services and (c) 'production' favouring tree biomass production (further explanations of the weightings are provided in Appendix S2).

2.5 | Statistical modelling of ES-multifunctionality

We analysed the relationship between ES-multifunctionality and site type, forest age, tree species richness and climate, using separate generalized linear regression models for each threshold-based ES-multifunctionality value and land-use scenario. Each ES-multifunctionality value was analysed as a function of forest site type (factor: low-productivity mire/rocky outcrop = 1 and productive forest = 0), tree species richness (number of tree species with diameter at breast height ≥10 cm per plot), forest age (years), mean annual temperature averaged over 1999–2010 and summed precipitation May–November (mm) averaged over 1999–2010 (see Appendix S4). Squared terms were included to account for nonlinear relationships (intermediate optima) in ES-multifunctionality. Two-way interactions between site type and tree species richness, site type and forest age, as well as interactions between temperature and precipitation were also modelled. We fitted separate models for forested mires and rocky outcrops, respectively, pairing with different nearest neighbour productive forest plots for each type of low-productivity forest plot (see above). To facilitate assessment of the relative importance of explanatory variables, all continuous variables were scaled prior to the modelling. The effect sizes of the explanatory variables were estimated using multi-model inference and the likelihood framework (Burnham & Anderson, 2002). The final minimal adequate models were selected to include explanatory variables and interactions with strong support (Akaike's information criterion ΔAIC ≤2; Burnham & Anderson, 2002).

2.6 | Statistical modelling of individual ES

In all, 12 ES were individually modelled as a function of forest site type, simple and squared terms for forest age, tree species richness, mean annual temperature 1999–2010 and summed precipitation May–November 1999–2010 using regression models with varying statistical distributions (see Appendix S1). The same three interactions as for ES-multifunctionality were modelled. In models of ES based on SFSI plot data, we included an additional explanatory variable on the extent (m^2) of non-fertile ground conditions within plots, for example, extent of stones and boulders. Stone and boulder content influences many soil processes and is thus an important factor to take into account when estimating element pools such as soil carbon (Stendahl, Lundin, & Nilsson, 2009). Tree species richness was not included as an explanatory variable in models for the occurrence of deciduous trees and sapling tree species richness, since they were not independent (trees additional to *Pinus sylvestris* and *Picea abies* are mainly deciduous tree species). As described for ES-multifunctionality models, continuous variables were scaled, and the final minimal adequate models were selected to include explanatory variables and interactions with strong support (ΔAIC ≤2; Burnham & Anderson, 2002).

All statistical analyses and diagnostics testing were done in R version 3.5.1 (R Core Team, 2018). Spatial correlograms (Moran's *I*) and Mantel tests were conducted with the package NCF to examine and ascertain no significant spatial autocorrelation in ES-multifunctionality and individual ES. The model coefficients were plotted with the package COEFPLOT and regression lines with package VISREG.

3 | RESULTS

3.1 | The ES-multifunctionality of low-productivity forests

All ES-multifunctionality values of forested mires were consistently lower than those of productive forests, but increased with forest age and tree species richness (medium thresholds shown in Figure 2, all thresholds shown in Appendix S5). In contrast to forested mires, the ES-multifunctionality of productive forests decreased or remained stable with forest age (Figure 2b) and increased unimodally or less strongly with tree species richness independently of the land-use objective scenario considered (Figure 2c).

The ES-multifunctionality of forested rocky outcrops was higher or equivalent to productive forests, for equal weight and supporting land-use objectives, respectively (Figure 3a; see Appendix S6). Considering production objectives, the ES-multifunctionality values of forested rocky outcrops were lower than those of productive forests (Figure 3a). The ES-multifunctionality of forested rocky outcrops and productive forests increased with forest age under supporting objectives while under production objectives the two site types had opposing relationships with forest age (Figure 3b). All ES-multifunctionality values increased with tree
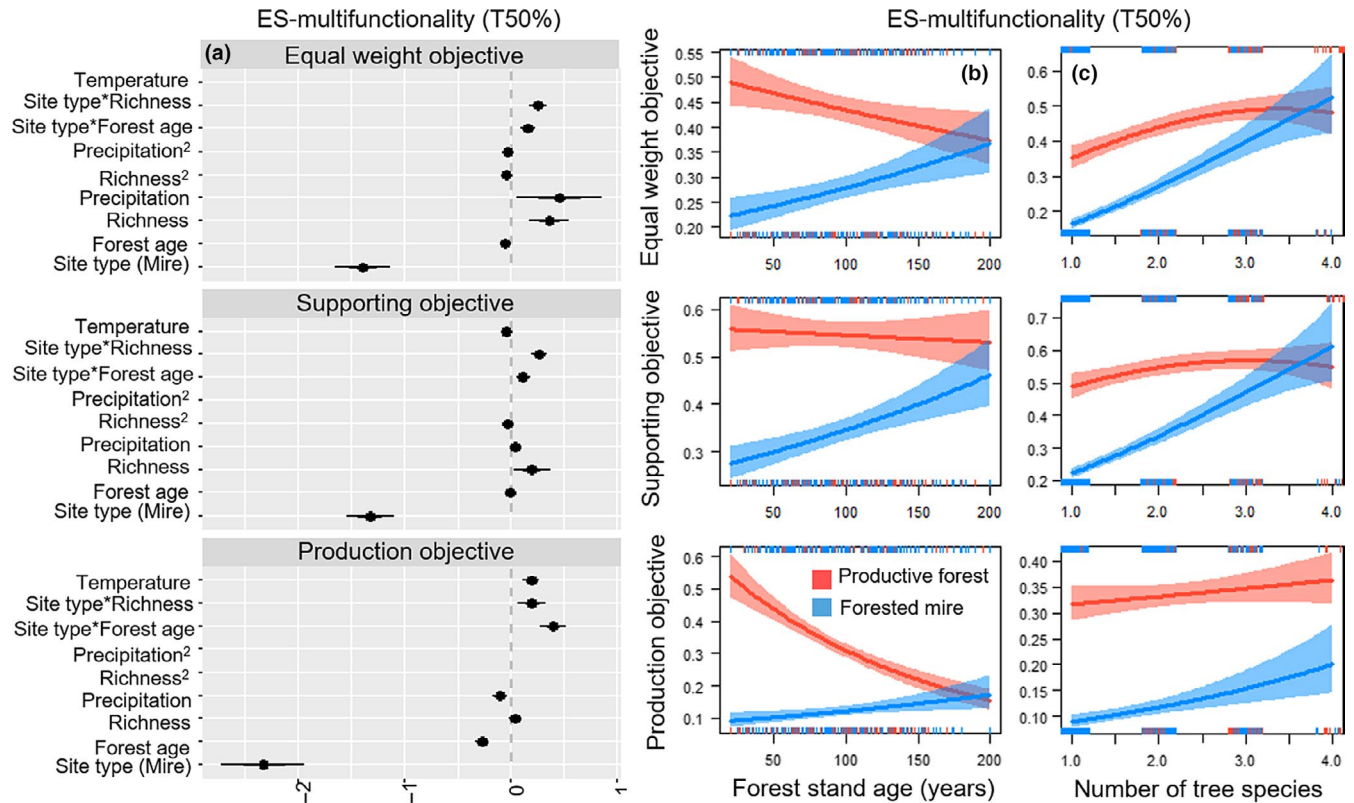
FIGURE 2 (a) Standardized coefficient estimates and 95% CIs (horizontal lines) in models of medium threshold-based (50% threshold) ecosystem services (ES)-multifunctionality values at three land-use objectives in forested mires in relation to productive forests (reference) and as a function of simple and squared terms for tree species richness (Richness), forest age, mean annual temperature (Temperature) and summed seasonal precipitation (Precipitation), as well as their interactions. Mean relationships and 95% confidence intervals between medium ES-multifunctionality values and (b) forest stand age and (c) tree species richness in productive forests and forested mires, conditional of holding all other explanatory variables constant at the median level. The rug at the top (positive residuals) and bottom (negative residuals) show the location of data points. The regression lines are plotted on the scale of the original response

species richness, although unimodally under production objectives (Figure 3c).

3.2 | Individual ES in forested mires

Low-productivity forested mires had lower levels of all individual ES compared to productive forests, with the exception of comparable levels of sapling tree species richness and higher levels of soil carbon storage (Figure 4). Most ES had a positive or unimodal relation to forest age, but the relationship sometimes also differed for productive and low-productivity forests (Figure 4; see Appendix S7). The habitat provisioning for saproxylic beetles and fungi increased more strongly with forest age in productive forests compared to low-productivity forested mires. Tree biomass production, however, increased more with forest age in forested mires compared to productive forests. Most ES had a positive or unimodal relation to tree species richness (Figure 4; see Appendix S8). The habitat provisioning for conifer-dependent saproxylic beetles and fungi decreased with tree species richness, likely due to the addition of tree species that produce unsuitable deciduous deadwood. Soil carbon storage

increased with tree species richness in productive forests but not in forested mires, and storage levels generally increased with temperature and precipitation.

3.3 | Individual ES in forested rocky outcrops

Low-productivity forested rocky outcrops had lower levels of forest berries, tree biomass production, soil carbon storage, deciduous trees and sapling tree species richness, compared to productive forests (Figure 5). However, the occurrence of deadwood, high conservation value deciduous trees (*P. tremula* or *S. caprea*) and the habitat provision for deadwood indicator species were comparable, or even higher in forested rocky outcrops than in productive forests. Soil carbon storage, occurrence of deadwood and habitat provisioning for beetles, bryophytes and fungi increased with forest age, whereas sapling tree species richness and the occurrence of aspen and willow decreased (see Appendix S9). The occurrence of bilberries and deadwood increased with tree species richness in both site types, whereas the habitat provisioning for indicator species decreased (see Appendix S10). Tree biomass production had a unimodal relationship with tree species
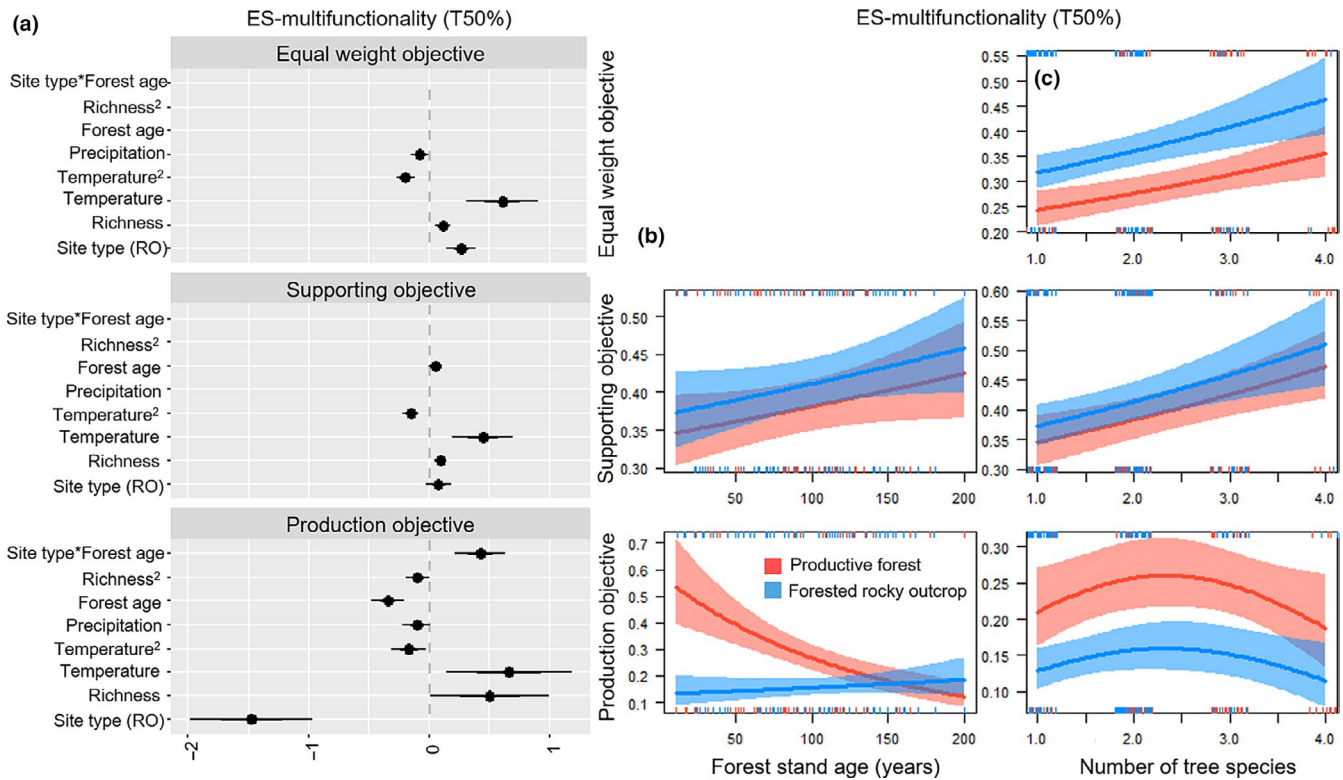
FIGURE 3 (a) Standardized coefficient estimates and 95% CIs (horizontal lines) in models of medium threshold-based (50%-threshold) ecosystem services-multifunctionality values at three land-use objectives in forested rocky outcrops (RO) in relation to productive forests (reference) and as a function of simple and squared terms for tree species richness (Richness), forest age, mean annual temperature (Temperature) and summed seasonal precipitation (Precipitation), as well as their interactions. Mean relationships and 95% confidence intervals between medium ecosystem services-multifunctionality values and (b) forest stand age and (c) tree species richness in productive forests and forested rocky outcrops, conditional of holding all other explanatory variables constant at the median level. The rug at the top (positive residuals) and bottom (negative residuals) show the location of data points. The regression lines are plotted on the scale of the original response

richness in both site types, and increased with temperature. The levels of carbon storage in the soil increased with temperature. A greater extent of non-fertile grounds (e.g. boulders and stones) had a significant negative effect on soil carbon storage in forested rocky outcrops.

4 | DISCUSSION

4.1 | ES-multifunctionality in low-productivity forests

Few studies have considered multiple ES simultaneously in relation to forest age, tree species richness and climate in low-productivity and productive forests. The ES-multifunctionality of forested mires was consistently lower than that of productive forests, however increasing with forest age in forested mires but not in productive forests. The ES-multifunctionality generally also increased with tree species richness, but more steeply and from a lower level in forested mires compared to productive forests. Thus, if land managers protect or exempt forested mires from conventional forestry, we recommend prioritizing older forested mires with many tree species to promote the most multifunctional forests. The ES-multifunctionality

of forested rocky outcrops, on the other hand, was higher or equivalent to that of productive forests under several land-use objectives. The ES-multifunctionality of these forested rocky outcrops also increased with forest age and tree species richness. These findings highlight that forested rocky outcrops can provide multiple ES, especially as old forested stands with mixtures of coniferous and deciduous trees.

To our knowledge, this is the first study to highlight the importance of the age of the forest stand and of tree species richness in determining ES-multifunctionality in low-productivity forested mires and rocky outcrops. Our results suggest that low-productivity forests should not be protected purely based on low wood productivity or low land-use conflict if the goal is to supply multiple ES. Inclusion grounds for the protection of low-productivity forests should instead carefully consider the site type (dry vs. wet), forest age and tree species richness, similar to how productive forests are often evaluated for conservation values (e.g. Gao, Nielsen, & Hedblom, 2015; Timonen et al., 2010). To maintain higher ES-multifunctionality in low-productivity forests, older or deciduous trees should also not be selectively harvested. In many countries, this necessitates changes in current conservation and management policies concerning low-productivity forested environments
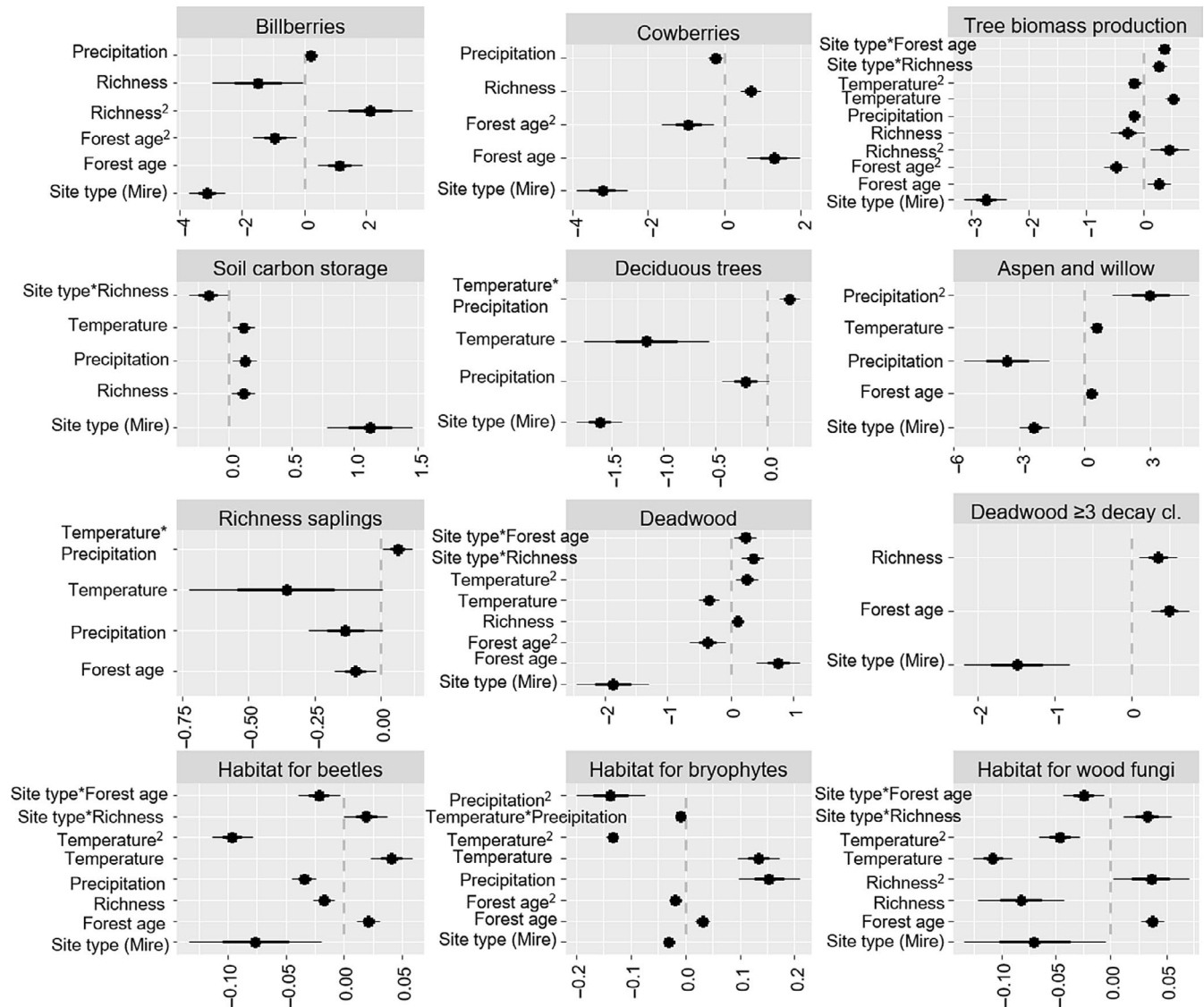
FIGURE 4 Standardized coefficient estimates and 95% (horizontal lines) CIs for 12 individual ecosystem services in low-productivity forested mires in relation to productive forests (reference), and as a function of simple and squared terms for forest age, tree species richness (Richness), mean annual temperature (Temperature) and summed precipitation (Precipitation), and their interaction terms. Note the differences in the explanatory variables and scales of the x-axes among panels

(e.g. Fitzsimons & Michael, 2017). We found limited support for strong trade-offs or synergies between the ES studied in low-productivity forests, with the exception of positive correlations (synergies) between habitat provisioning of different organisms groups dependent on deadwood (especially in forested rocky outcrops and productive forests). This illustrates that low-productivity forests can simultaneously supply multiple ecosystem services.

4.2 | Forested mires

Forested mires were likely less influenced by thinning and cutting practices than productive forests, as removal of individual trees is not allowed if it changes the characteristics of the stand (Swedish Forestry Act, §13a 1979: 426). However, such effect of less intensive

forest management did not counteract their overall lower ES values. In contrast to productive forests, however, the ES-multifunctionality of forested mires increased more sharply with forest age and tree species richness, especially in terms of supporting ES land-use objectives. The differences between forested mires and productive forests were therefore smaller for older stands with many tree species. This may result from the fact that older productive forests have been subjected to more intensive management (e.g. thinning operations) promoting coniferous monocultures, compared to forested mires. The levels of the desired ES did also influence differences between productive and low-productivity forests, and differences were generally greater at high (75%) threshold levels of maximum ES values.

While this is the first assessment of ES-multifunctionality in forested mires, our results of lower values for certain individual ES are mirrored in other studies. In agreement with our findings, forested
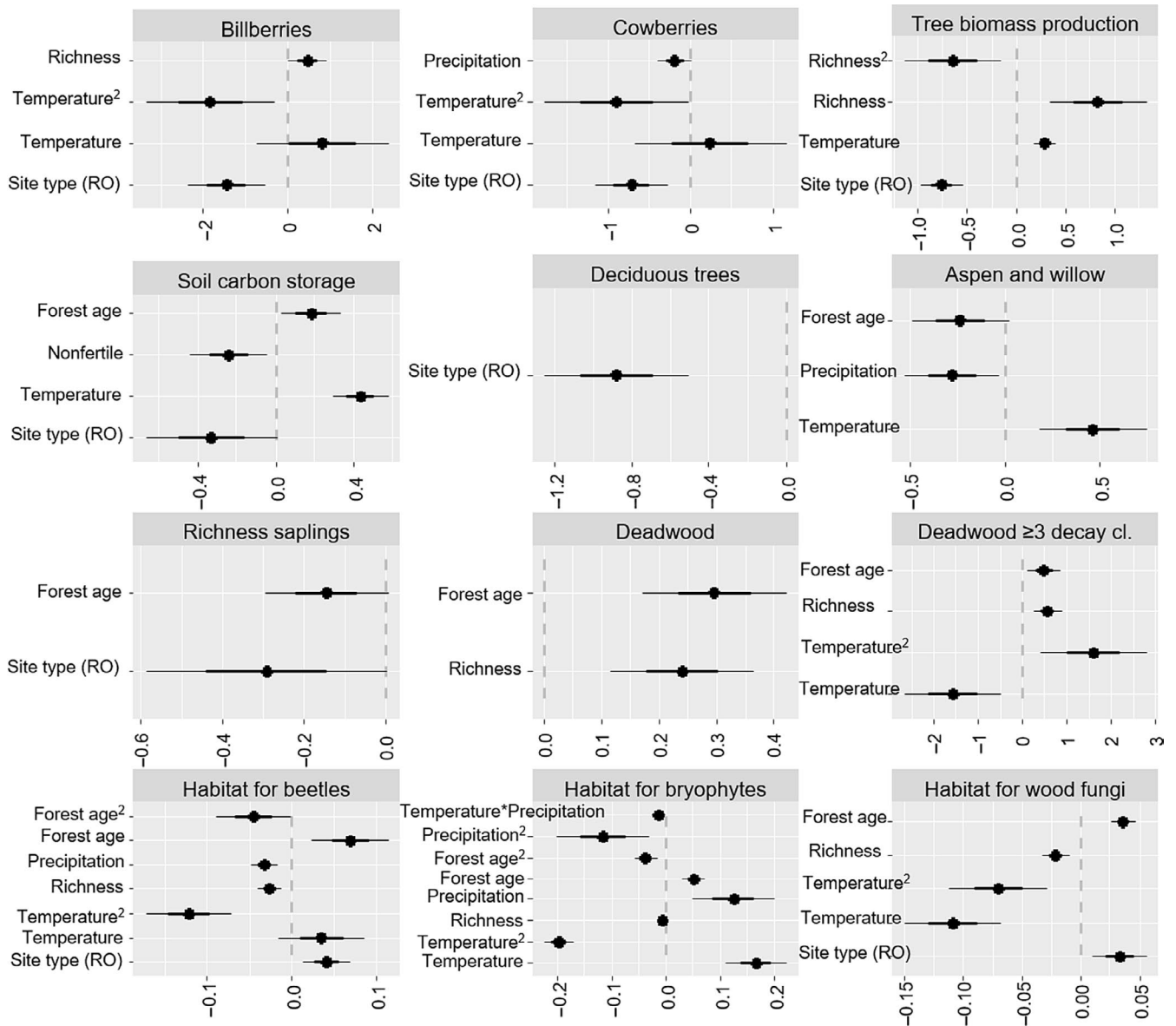
FIGURE 5 Standardized coefficient estimates and 95% (horizontal lines) CIs for 12 individual ecosystem services in low-productivity forested rocky outcrops in relation to productive forests (reference), and as a function of simple and squared terms for forest age, tree species richness (Richness), mean annual temperature (Temperature) and summed precipitation (Precipitation), and their interaction terms. In the model for soil carbon storage, non-fertile represent the amount of stones and boulders in the sample plot. Note the differences in the explanatory variables and scales of the x-axes among panels

mires have been shown to have lower volume and diversity of deadwood and species richness of deadwood-dependent beetles, especially in northern Sweden, compared to rocky outcrops and productive managed forests (Hämäläinen et al., 2018). We showed that the levels of many individual ES, such as forest berries, deciduous trees, bryophytes and fungi were also lower in forested mires compared to productive forests. On the other hand, our results showed that forested mires stored 1.6 times more soil carbon than productive forests. While the soil carbon storage increased with tree species richness in productive forests, the soil carbon storage was consistently higher in forested mires (independently of tree species richness). Increasing soil carbon storage with tree species richness in productive forests may result from different tree species having different functional traits (e.g. wood

qualities, rates of photosynthesis, respiration and decomposition) driving the increased carbon accumulation in soils (e.g. Conti & Diaz, 2013). The provision of ES was generally much lower in forested mires compared to productive forests, both in terms of production and supporting ES land-use objectives. Further investigation may be needed to see if these results hold up when considering other important ES such as landscape aesthetics or water regulation.

4.3 | Forested rocky outcrops

We showed that the ES-multifunctionality of forested rocky outcrops was greater or comparable to productive forests under equal weight

and supporting objectives. This result defies our first hypothesis that the ES-multifunctionality is higher in productive forests than in low-productivity forests. We also did not find any strong trade-offs between individual ES which could nuance this first hypothesis and offer some explanation to our results (e.g. Felipe-Lucia et al., 2018; Mace et al., 2012). These forests have likely been less intensively managed for coniferous wood production (e.g. through thinning and partial cutting practices) than productive forests of similar forest age and geographic location, and may therefore shelter more biodiversity, thus increasing our ES-multifunctionality measure. Some evidence from Northern Europe suggests that logging effects have indeed reduced the availability of biodiversity elements such as old trees and deadwood in forested rocky outcrops, although a few exceptional areas contain substantial amounts of deadwood and old-growth indicator species (Sverdrup-Thygeson & Ims, 2005). In agreement with our findings, deadwood volumes and beetle species richness of forested rocky outcrops have been shown to be similar to productive managed stands of similar age but also to host lower beetle richness and fewer red-listed species compared to older productive stands of high conservation value (Hämäläinen et al., 2018). Common for the studied forested rocky outcrops with sparse tree cover and slow tree growth is that any removal of living and dead trees will likely have a disproportionately large negative influence of certain biodiversity and ES values. This is because even when the overall amount of deadwood or deciduous trees is relatively low due to low productivity, the share of high conservation value woody elements of the total tree basal area or volume can still be high, and often of significant age and quality (Sandström, 2018).

We found that ES-multifunctionality, as well as individual ES such as soil carbon storage, deadwood and habitat provisioning for beetles and fungi, increases in forested rocky outcrop stands up to forest ages of 200 years, which is comparatively older forest stands than what have previously been studied for single ES (Hämäläinen et al., 2018). Even when prioritizing production land-use objectives, the differences in ES-multifunctionality between forested rocky outcrops and productive forests were not so large in the oldest forest stands. Forested rocky outcrops were on average older (104 years) than forested mires (89 years), which may in part also explain the higher provision of ES-multifunctionality values of these relatively more pristine forested rocky outcrops.

4.4 | Implications for conservation and management

The studied low-productivity forests represent the outer ends in an ecological gradient with respect to ground moisture, nutrients and exposition (i.e. stands are open with sparse tree cover) in forested environments. Concerns for including these habitats in forest protection targets are that they fail to generate genuine benefits if the areas are geographically biased towards low-productivity mountain and coastal regions (Svensson, Andersson, Sandström, Mikusiński, & Jonsson, 2019), inadequately managed (Fitzsimons & Michael, 2017; Swedish Forestry Act, 1979: 429), or provide low biodiversity

and ES-multifunctionality values that are already overrepresented among protected areas (this study). While low-productivity forests are often the only forests left unmanaged and the least expensive to protect (e.g. Juutinen et al., 2004; Schröter et al., 2014), our results show that older forested rocky outcrops (c. >120 years) with many tree species should be prioritized in management and conservation to maximize ES-multifunctionality. Survey methods for identifying high conservation values in productive forests commonly include information on forest age, tree species richness and availability of deadwood (e.g. Gao et al., 2015; Timonen et al., 2010), and our results suggest that such basic forest characteristics are probably also useful for identifying low-productivity forests with high ES-multifunctionality values. With lower productivity and growth, however, it may also be important to consider the occurrence or ratio of certain ES, in addition to quantitative measures of ES biomass and volume.

In this study, we focused on the forest stand level, but our findings have relevance for forest conservation and management also at the landscape scale. Low-productivity forests often represent the last remaining forests with low opportunity costs for spatial conservation planning (e.g. Polak et al., 2016; Venter et al., 2014) and improved assessment of ES may affect how different constraints in opportunity costs can change spatial priorities for conservation of low-productivity forests. Previous studies have shown that including ES in conservation planning have resulted in an increase in the size of the reserve network (Schröter et al., 2014). The optimization for a cost-effective representation of both biodiversity and ES targets selected larger areas with lower opportunity costs (Schröter et al., 2014; see also Hämäläinen et al., 2018). Low-productivity forests are clearly relevant in such spatial conservation planning but we cannot extrapolate our findings of drivers of local-scale ES-multifunctionality to larger scales, since this would require accounting for dynamics, connectivity and various interactions between forest stands (Felipe-Lucia et al., 2018; Manning et al., 2018). However, our study emphasizes the critical role of forest age and tree species richness of low-productivity forests of different site types (dry vs. wet) in driving ES-multifunctionality. Moreover, we only studied three broad scenarios for stakeholder land-use objectives. Conservation planning of low-productivity forests could also be improved with more knowledge and deeper incorporation of stakeholder preferences concerning the importance of a broader range of the ES supplied by low-productivity forests.

AUTHORS' CONTRIBUTIONS

M.J. and T.S. conceived the ideas and designed methodology; M.J. and T.S. collected the data; M.J. and T.S. analysed the data; M.J. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.vt4b8gtnp (Jönsson & Snäll, 2019).

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