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Increase in dead wood, large living trees and tree diversity, yet decrease in understory vegetation cover: The effect of three decades of biodiversity-oriented forest policy in Swedish forests

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ABSTRACT

In Sweden, the majority of forest area has been altered by industrial forestry over the decades. Almost 30 years ago, a shift towards biodiversity-oriented forest management practices occurred. Here we took advantage of long-term data collected by the Swedish National Forest Inventory to track developmental changes in forest structural components over this time. We assessed changes in structural components that play an important role in biodiversity (dead wood, large living trees, tree species composition, and understory vegetation) in four forest types with descending tiers of biodiversity protection: protected areas, woodland key habitats, low-productivity forests and production forests. Overall, we found a positive trend in the volumes of dead wood and large living trees, as well as in tree species diversity, while there was a general decline in understory vegetation coverage. Most observed changes were consistent with the intended outcomes of the current forest policy, adapted in the early 1990s. The implementation of retention forestry is likely driving some of the observed changes in forest structural components in the south. In contrast, we observed no changes in any of the focal structural components in the north, which could be attributed to the ongoing clear-cutting of forests previously managed less intensively. Dead wood and large living trees increased not only in managed, but also in unmanaged forests, likely reflecting historical management. The increased tree species diversity can be explained through current forest management practices that encourages maintenance of additional tree species. Decreasing understory vegetation coverage in both dense managed and unmanaged forests suggests that factors other than forestry contribute to the ongoing changes in understory vegetation in Swedish forests. Overall, the observed increase in structural components has not yet been reflected in documented improvements for red-listed forest species, which may be due to delays in species responses to small improvements, as well as a lack of detailed monitoring. Similarly, the increased availability of forest structural components might still be insufficient to meet the specific habitat requirements of red-listed species.

1. Introduction

Forests ecosystems harbour an estimated 70% of global terrestrial biodiversity (IUCN, 2017). However, large-scale industrial forestry greatly influences the forest structural components on which biodiversity depends. For instance, production forests tend to be harvested before trees are old, and silvicultural advances are increasing the wood biomass produced per unit area, while concurrently reducing tree mortality during the rotation. Together, these changes result in younger and denser forests that carry less dead wood (Jonsson and Kruys, 2001). Furthermore, clear-cutting, re-planting and thinning operations lead to homogeneous and even-aged stands. Overall, these changes have negative effects on biodiversity (Sala et al., 2000; Foley et al., 2005; Nikolova et al., 2019).

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Protecting forest lands as national parks and nature reserves is a common way to preserve forest biodiversity worldwide (FAO and UNEP, 2020). However, in managed forests, additional biodiversity-oriented measures are widely applied, particularly in boreal regions (Timonen et al., 2010). Such practices include the retention of living and dead trees (Gustafsson et al., 2020) and the preservation of "woodland key habitats" (WKHs), which have high values in terms of biodiversity.

Since the Convention of Biological Diversity was signed, many national environmental policies have aimed at maintaining viable populations of all naturally existing species (CBD, 2005). Potentially in conflict with these aims, there is a demand for a higher wood production. From this perspective, Swedish forests provide a case study to evaluate the opportunity for high sustained yield wood production (Felton et al., 2020a), while also meeting other forest policy objectives such as biodiversity conservation (Lindahl et al., 2017). Over the last decades, Sweden has developed one of the most intensive forest management systems in the world (Levers et al., 2014), and the majority of its productive forest land (>85%) is subjected to forestry (Forest Statistics, 2021). Since the introduction of the 1993 Forestry Act, and the adoption of voluntary forest certification schemes (Anon, 2005; Gulbrandsen, 2005), there has been a major shift in management towards increased environmental concerns. This was mainly reflected in an increase of areas protected as nature reserves, identification and prioritized protection of WKHs, and the voluntary establishment of set aside of areas within production forest for nature conservation. Therefore, Swedish forests represent a suitable case-study to evaluate the large-scale effect of various kinds of environmental concerns on biodiversity conservation (Lindahl et al., 2017).

In this study, we investigated how the amounts of structural components of importance to biodiversity (dead wood, large living trees, tree species composition, and understory vegetation) have changed over time since the implementation of a more biodiversity-oriented forest policy. We studied four types of forests, representing descending levels of biodiversity protection: protected areas (protected by law, with no commercial wood harvest allowed), WKHs (small forest areas with high conservation value, not allowed to be harvested according to certification standards), low-productivity forests (forest lands where no conventional forest practices are allowed), and production forests (forest lands managed for commercial wood extraction).

Dead wood amounts and occurrence of large living trees were evaluated because a large proportion of forest biodiversity is associated with these structural components (Esseen et al., 1997). The tree species composition was included in the analysis since high tree species diversity increases habitat diversity and resource availability for both herbivores (Ricklefs and Marquis, 2012) and wood-dependent species (Vogel et al., 2021). Further, it generates a more heterogeneous canopy composition, which affects light and nutrient conditions, and promotes forest biodiversity (e.g. Petersson et al., 2019). Finally, we included understory vegetation since it is the most species rich and diverse component of temperate and boreal forests (Hart and Chen, 2006), and serves as an important source of food and habitat for a variety of organisms (Gilliam, 2007; Felton et al., 2010; Hedwall et al., 2019).

To account for variation in climate and major vegetation types, we examined changes at the national and regional level, using four regions covering the north-south range of the country. In Sweden, anthropogenic impacts (both temporal extent and severity) generally decline from south to north. In its natural state, the southern part was dominated by deciduous forests, which were often subsequently replaces by traditional agriculture, with large areas used for grazing and hay-making. During the last century, the change in forest cover has accelerated, largely due to the extensive use of Norway spruce for fibre production (Björse and Bradshaw, 1998; Lindbladh et al., 2014). In contrast, tree species composition has remained more constant in the conifer-dominated north, which is the part of the country that still harbours fragments of old-growth forests (Esseen et al., 1997; Svensson et al., 2018).

The Forestry act of 1993, and development of voluntary forest certification schemes from 1993 to 1998 (Angelstam et al., 2011; Johansson et al., 2013), promoted green tree retention at harvesting, the maintenance of at least a minimum proportion of deciduous trees, the setting aside of forests, and a continued exemption of forestry from low-productivity forests. We hypothesise that these changes in forest policy have resulted in an increase in (i) the amount of dead wood and large living trees and (ii) proportion of deciduous trees in all forest types, but especially in production forests. Further, we hypothesise that (iii) the coverage of understory vegetation has decreased in all studied forest types due to denser forests. We also hypothesised that (iv) the change in relative terms will be greater in the south than in the north as the development of new structural components will be faster in the more productive forests of the south. In addition, we expect that such changes will be more pronounced in the south, as southern regions (i.e. regions with a long history of management) were historically more heavily deprived in structural components, compared to the northern regions (i.e. regions with shorter management history and higher initial levels of structural components).

2. Materials and methods

2.1. Swedish forests

Almost 70% of Sweden is covered by forests (27.9 million ha), of which 23.5 million ha are productive (potential growth rate >1 m^3 ha^{-1}, yr^{-1}) while the remaining area (4.4 million ha) is low-productivity forests (Forest Statistics, 2021). Formally protected areas comprise 9% (2.3 million ha) of all forest land, of which 1.3 million ha (6%) is located within productive forests. Around 2% of all forest land has a WKHs status, although it is estimated that about 60% of the WKHs are not yet identified (Skogsstyrelsen, 2019a). In this study, we divided the forests into four types (see 2.1.1.-2.1.4.) based on descending tiers of biodiversity protection.

2.1.1. Protected areas

Protected areas include national parks, nature reserves and biotope protection areas that are protected by law or by legally binding agreement with the forest owners (Miljöbalken, 1998). In these areas, commercial wood harvest, with some exceptions, is not allowed (Angelstam et al., 2011). For this study, the GIS layer of all protected areas in Sweden was extracted from the Swedish Forestry Agency (https://kartor.skogsstyrelsen.se/kartor/, accessed July 29, 2020). We did not include time since the protection was enforced. The protected areas category includes both productive and low-productivity forests. In total, 6484 plots (2.3%) ended up in protected forests (Supplementary Material, Fig. S8b).

2.1.2. Woodland key habitats (WKHs)

Woodland key habitats (WKHs) are most often small (median size of 6.5 ha) forest areas (Skogsstyrelsen, 2019a) with high conservation values. The concept of WKHs is based on the assumption that red-listed species are concentrated into certain sites, which can be identified based on their structural features and occurrence of indicator species (Timonen et al., 2010). In Sweden, WKHs are not legally protected, but are supposed to be left unmanaged according to Forest Stewardship Council (FSC) and Programme for the Endorsement of Forest Certification Schemes (PEFC) and are commonly included in voluntary set-asides. Similar to the protected areas category, the GIS layer of all WKHs in Sweden was extracted from the Swedish Forestry Agency (https://kartor.skogsstyrelsen.se/kartor/, accessed June 12, 2020). We did not include time since registration. The WKHs category includes both productive and low-productivity forest outside protected areas. In total, 1893 of the plots (0.7%) ended up in WKHs (Supplementary Material, Fig. S8c).

2.1.3. Low-productivity forests

Forest lands with a potential timber production less than 1 m^3 ha^{-1} $year^{-1}$ are classified as low-productivity forests. Tree covered peatlands, forests with thin soils and rocky outcrops, and transition zones between woodlands and mountains are the most common habitat types within this category (Forest Statistics, 2021). In Sweden, low-productivity forests are excluded from conventional forest practices (Swedish Forestry Act, 1979), and can thus be considered as indirectly protected from forestry. This category included only those areas that fall within international definitions of forest land e.g. areas spanning more than 0.5 ha with trees higher than 5 m and a canopy cover of more than 10% (Skogsstyrelsen, 2019b). All the NFI plots in this category were located outside WKHs and protected areas. In total, 14008 of the plots (5%) ended up in low-productivity forests (Supplementary Material, Fig. S8d).

2.1.4. Production forests

In Sweden, production forests are typically harvested by clear-cutting, followed by soil scarification and re-planting. Usually, there is one or two pre-commercial thinnings in the young plantations, followed by one to three commercial thinnings before the final clear-cutting. Rotation times vary depending on site productivity: 45–70 years in central and southern Sweden, and up to 100–120 years in the north (Simonsson, 2016). Environmental considerations in forest management, including concern for biodiversity such as retention or voluntary set-aside areas, are regulated by the Swedish Forestry Act and by forest certification standards. Currently, 63% of the forest area is certified by one or both of the two certification standards, FSC and PEFC (Skogsstyrelsen, 2020). All the NFI plots in this category were productive forests, and located outside registered WKHs and protected areas. In total, 255821 of the plots (92%) ended up in production forests (Supplementary Material, Fig. S8e).

2.2. Data set

We used data from the NFI that was collected between 1983 and 2017. The present sampling design was introduced in 1983 (Ranneby et al., 1987), and has been used consistently since then. During this time, surveys were conducted during seven separate 5-year periods, and in our analyses we compared the outcome between these. The NFI is based on systematically distributed circular sample plots in a rectangular pattern. We used both temporary (circular plots 7 m in diameter and only visited once) and permanent plots (circular plots 10 m in diameter and revisited every five years) (Fridman et al., 2014). Sampling intensity decreases toward the north of the country (Odell, 2018), and the minimum distance between plots within each tract (cluster of sample plots) varies from 600 m in the north to 200 m in the south (Hägglund, 1985). Protected areas were not inventoried before 2003 and low-productivity forest not before 1997. We reported regional data by dividing Sweden in four areas: Norra Norrland (referred as “North”), Södra Norrland (referred as “Central North”), Svealand (referred as “Central South”) and Götaland (referred as “South”) (Supplementary Material, Fig. S1).

2.3. Structural components

We analysed the development of the following structural components: volume of dead wood, volume of large living trees, tree species proportions, and understory vegetation coverage. In particular, we estimated the total volume of dead wood and large living trees, proportion of different tree species and coverage of understory vegetation in different forest types and regions over the defined study period. Dead wood (>10 cm in diameter) was also analysed separately for size categories (10–20 cm, 20–30 cm and >30 cm in diameter), tree species (conifers, deciduous) and decay stage (hard: fresh and slightly decayed (≤25% of wood decayed) and decayed: decayed to strongly decayed (>25% of wood decayed)). The detailed survey of dead wood was conducted from 1993 onwards.

We used a diameter ≥40 cm as a proxy for large trees of high conservation value, divided into conifers and deciduous trees. Data on tree species composition was surveyed in the same plot (with the same center point as vegetation plots), but with a radius of 10 m. We analysed the coverage of the dominant tree species: Scots pine (*Pinus sylvestris* L.), Norway spruce (*Picea abies* L.) and birch (*Betula* spp.) that comprise ca 90% of the growing stock (volume of living trees) as well as rare tree species: lodgepole pine (*Pinus contorta* spp. *latifolia* Engelm.), aspen (*Populus tremula* L.), alder (*Alnus glutinosa* L.), oak (*Quercus* spp.) and beech (*Fagus sylvatica* L.). The category “other species” included the following tree species: willow (*Salix* spp.), rowan (*Sorbus aucuparia* L.), hackberry (*Prunus padus* L.), Norway maple (*Acer platanoides* L.), elm (*Ulmus glabra* Huds.), ash (*Fraxinus excelsior* L.), linden (*Tilia cordata* L.), European hornbeam (*Carpinus betulus* L.), and wild cherry (*Prunus avium* L.). For assessing changes of the understory vegetation we used data for 70 forest-floor species (or combinations of species not identified individually in the field) (Odell, 2018). The understory vegetation survey was only conducted in productive forest from 1995 and onwards. The coverage of the forest-floor species was noted in 100 m^2 circular permanent plots, and is expressed as the proportion of a hectare that is covered by each species group (ha ha^{-1}) (Odell, 2018). For our analyses, we assembled the species into broader taxonomical-morphological groups (Supplementary Material, Table S1). For further information and critical evaluation on the NFI plots and survey methods, see SLU (2020) and Milberg et al. (2008).

2.4. Statistics

Although the design of the NFI is a stratified systematic cluster-sampling inventory with partial replacement of plots (Ranneby et al., 1987), we considered each tract as an independent observation and the variance was estimated assuming a simple random sampling of tracts. This is a procedure typically applied to the NFI data, and generates only a slight overestimation of variance (Fridman and Walheim, 2000).

The mean volumes per hectare of dead wood and large living trees were estimated using the ratio between the total volumes and the total forest area as described in Jonsson et al. (2016). Similarly, the mean coverage area of tree species and understory vegetation was estimated as an average of the total coverage over the total forest area. Mean values and standard error variables were calculated following the standard procedures applied in the NFI as described in Fridman and Walheim (2000) and Toet et al. (2007). Confidence intervals (95%) were obtained as the values 1.96 × standard error on either side of the mean. Non-overlapping confidence intervals were treated as significant differences in the mean value estimates.

3. Results

3.1. Dead wood

At the national level, the volume of dead wood increased significantly in all forest types, except in protected areas, but note that we lack data for protected areas for the first period (Fig. 1a). WKHs and production forests had higher relative increase in dead wood volumes (31% and 30% increase, respectively) in comparison to low-productivity forests (20% increase) (Supplementary Material, Table S2). The volume of dead wood increased across all regions, except for the north, where the values remained stable (Fig. 1b–e; Supplementary Material, Table S2).

The volume of dead wood increased across all diameter classes (Fig. 2a). Large dead wood volume (>30 cm in diameter) increased by 43%, whereas the other two classes increased by 27%. The volume of hard dead wood increased consistently, while there were only small changes in the volume of decayed dead wood (Fig. 2b). The volumes of both coniferous and deciduous dead wood increased with time (Fig. 2c; Supplementary Material, Table S3).

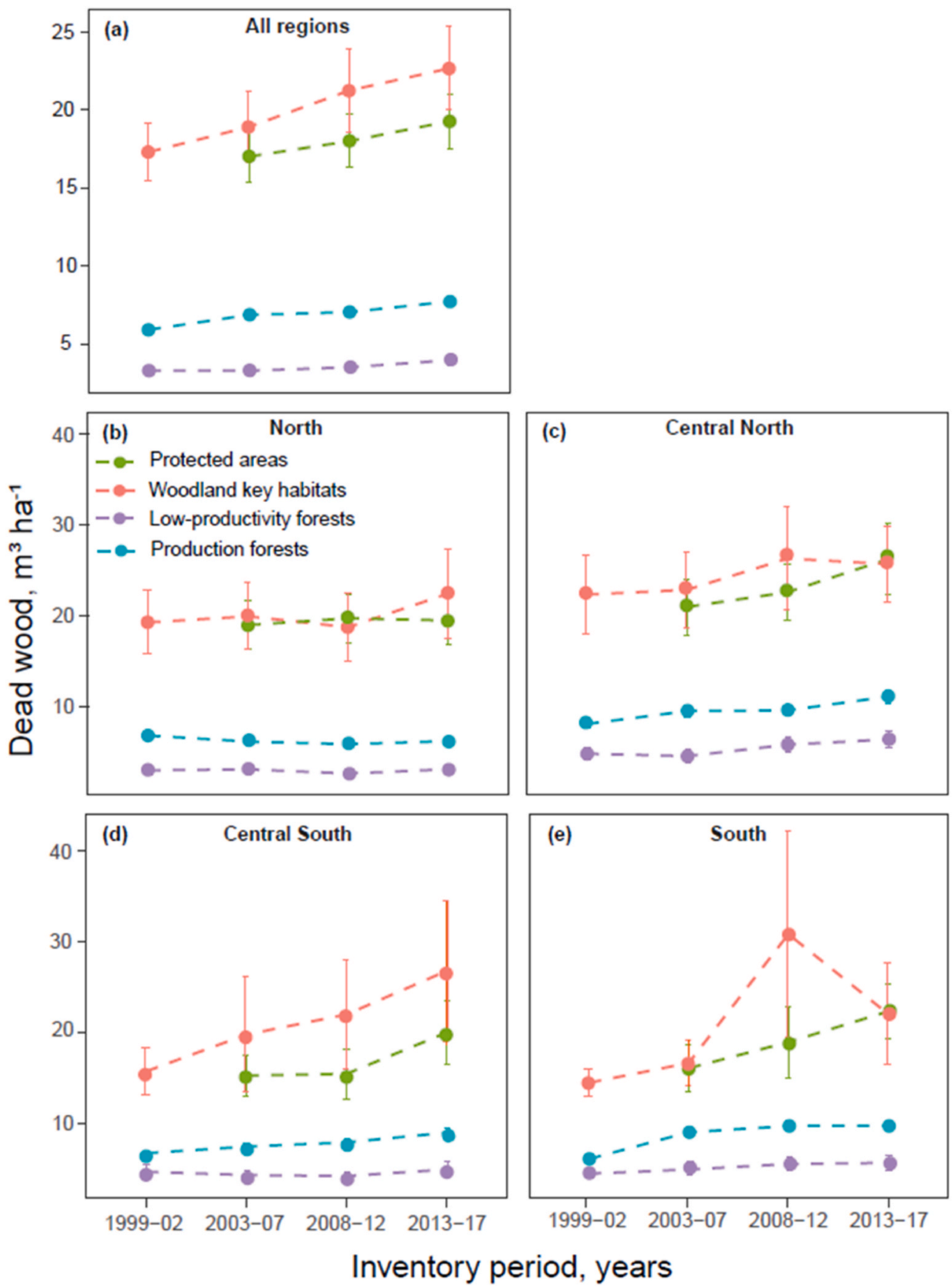

Fig. 1. Development of the volume of dead wood (diameter >10 cm; mean values ± 95% confidence interval) in four different forest types in Sweden during the period 1999–2017, as analysed in total (a) across the country, and separately (b–e) for four regions. Protected areas (in green) represent forest lands that are protected by law or by legally binding agreement with the forest owners; woodland key habitats (in red) represent small forest areas with high conservation values that are not formally protected but are supposed to be left unmanaged according to certification standards; low-productivity forests (in purple) represent forest lands with a potential timber production less than 1 m^3 ha^{-1} $year^{-1}$; production forests (in blue) represent forest lands managed for commercial wood extraction. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.2. Large living trees

The volume of large living trees (diameter ≥40 cm) tended to increase in all forest types, but the increase was statistically significant only in production forests (Fig. 3a). In production forests, the total volume of large living trees more than doubled during the study period, with the largest increase in the south (Fig. 3b–e; Supplementary Material, Table S4).

The volumes of both coniferous and deciduous large living trees tended to increase over time (Fig. 4). The deciduous trees increased more than the coniferous, and thus, the proportion of large living deciduous trees increased over time. This proportion increased most in WKHs (by 73%), followed by low-productivity forest (by 56%) and production forest (by 53%), while there was only a minor change in protected areas (Supplementary Material, Table S5).

3.3. Tree species composition

The proportion of the dominant tree species changed over time. In production forest, the change was statistically significant, with an increase in birch and a decrease in Norway spruce. For other forest types, there were no such clear trends, which could be due to shorter time series and smaller sample sizes (Fig. 5a; Supplementary Material, Fig. S8). In production forests, the proportion of Norway spruce declined by 8% at a national level, but the decline was only significant in the north and central north. The proportion of Scots pine in production forests declined by 14% in the south while no clear decline was observed in other regions (Supplementary Material, Fig. S6; Table S6). The proportion of birch increased by 26% in production forests. The increase was consistent across all regions, except for the northernmost region, where the proportion remained stable over time (Supplementary

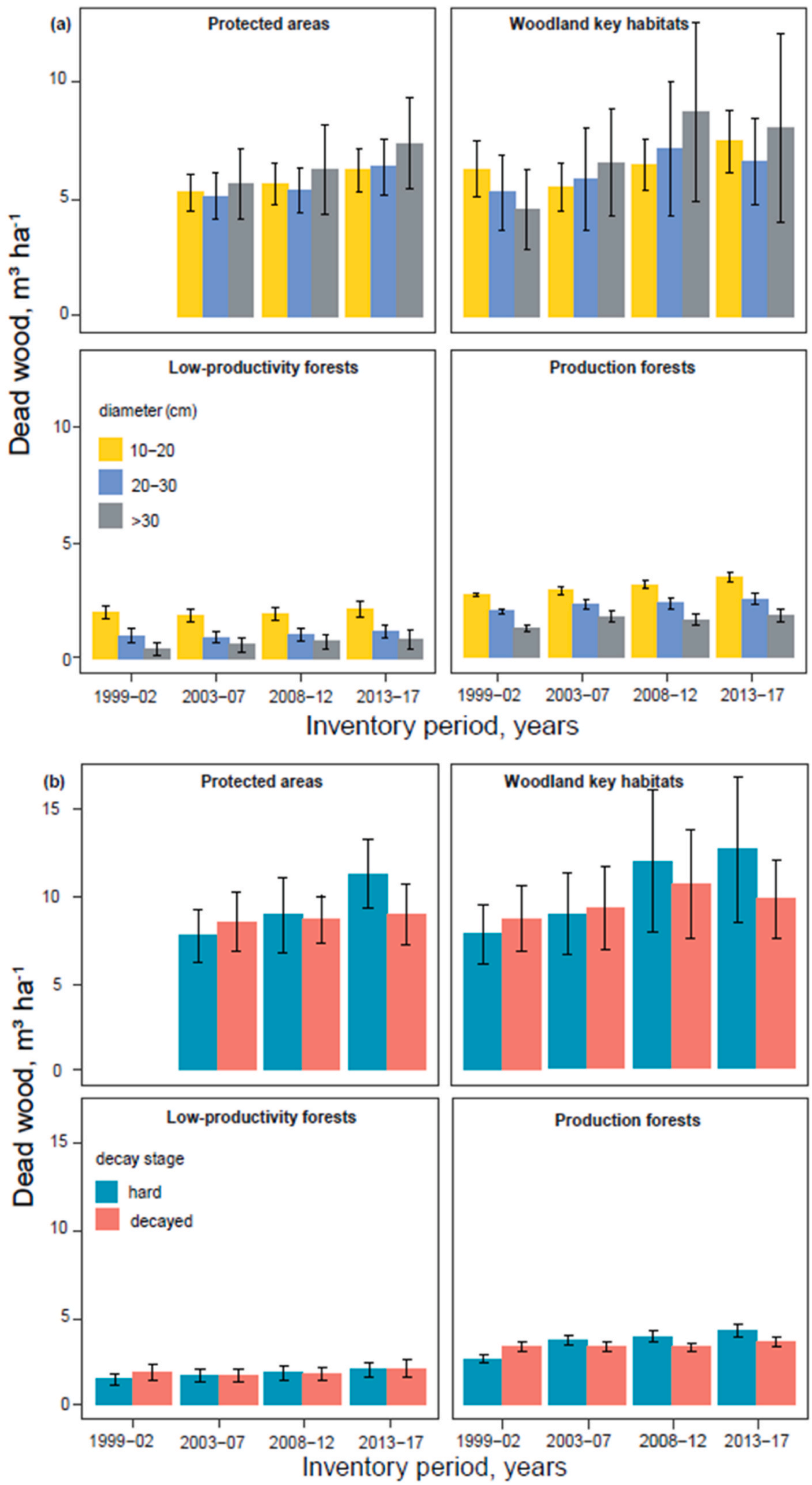

Fig. 2. Development of the volume of dead wood (diameter >10 cm; mean values ± 95% confidence interval) in four forest types in Sweden categorized according to size (a), decay stage (b), and tree species (c) during the period 1999–2017. Protected areas represent forest lands that are protected by law or by legally binding agreement with the forest owners; woodland key habitats represent small forest areas with high conservation values that are not formally protected but are supposed to be left unmanaged according to certification standards; low-productivity forests represent forest lands with a potential timber production less than 1 m^3 ha^{-1} $year^{-1}$; production forests represent forest lands managed for commercial wood extraction.

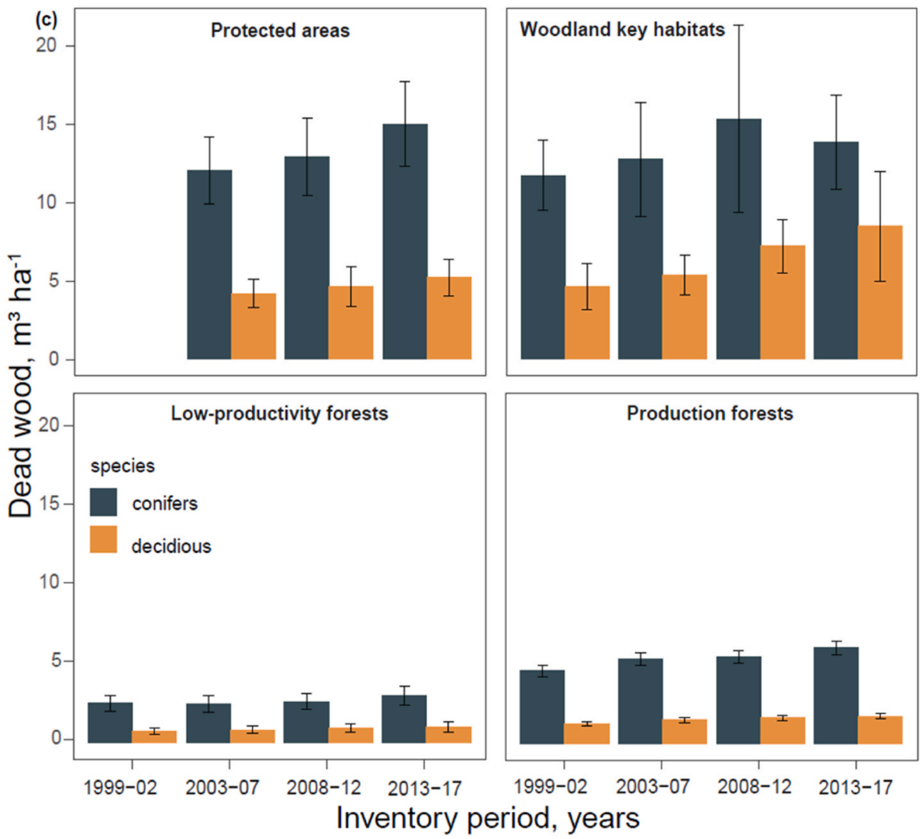

Fig. 2. (*continued*).

Material, Fig. S6).

Similarly, the total proportion of rare tree species only changed significantly in production forests (Fig. 5b). In these forests, the proportion of lodgepole pine increased from 1% to 2% in the north and central north, while this species was not observed in the south (Supplementary Material, Fig. S6; Table S6). The proportion of alder and oak increased significantly in the south, and the category "other species" increased in central north and south. Overall, no significant changes were detected for aspen and beech proportions, neither across forest types nor regions (Supplementary Material, Fig. S6; Table S6).

3.4. *Understory vegetation composition*

Understory vegetation coverage tended to decrease for all species groups and forest types. In production forest, vegetation coverage of all species groups declined significantly during the study period (Fig. 6). In these forests, the decreases were the largest for lichens and forbs (by a half during the last 20 years), intermediate for ferns and grasses (by 31% and 25%, respectively) and the smallest for mosses and dwarf shrubs (by 14% and 18%, respectively) (Supplementary Material, Table S7).

4. Discussion

By using long-term inventory data, we identified a variety of changes in the amount of structural components important for forest biodiversity. In line with our hypotheses, we found an overall increase in the volumes of dead wood and large living trees. Likewise, our hypothesis that the coverage of understory vegetation would decrease, was also supported by the data. Tree species diversity increased, primarily due to the increase in deciduous tree species, while the proportion of the two dominant conifers decreased, or remained constant.

Within woodland key habitats (WKHs) and protected areas there was a positive trend in both dead wood and large living trees volumes, suggesting that these areas usually have a legacy of management and a potential to harbour more of these structural components in the long run. In WKHs, the volume of dead wood increased more rapidly than in other forest types, and, together with a strong positive trend for large living trees, our results indicate that WKHs are important for maintaining conservation values, and that their conservation values are improving over time.

In production forests, especially in the south, the amounts of dead wood and large living trees have increased considerably. To some extent, this increase could be due to low initial levels of these structural components. However, the fact that the increase was more often statistically significant in comparison to other forest types can also be due to the much larger sample size for the production forests category compared to other forest types.

The smallest change in dead wood and large living trees volumes was observed in low-productivity forests. This can be explained by the fact that the capacity for harbouring structural components important for biodiversity is lower in these habitats, and also because management regimes in those forests have not changed substantially over time.

The increase in both dead wood and large living trees volumes was most prominent in the south and least in the north. These observations suggest that the net effect of altered management is decreasing towards the northern regions where the incorporation of a more biodiversity-oriented policies is counteracted by the introduction of intensive forestry to lands previously less affected by such forestry practices.

4.1. *Dead wood*

For all forest types, the volume of dead wood was far below the range of 80–120 m^3 ha^{-1} dead wood found in old natural forests (Nilsson et al., 2002; Ranius et al., 2004), indicating that all forest types, even protected areas and WKHs, are deprived in dead wood, mainly as a result of the past and current human impact like fire deprivation, forest

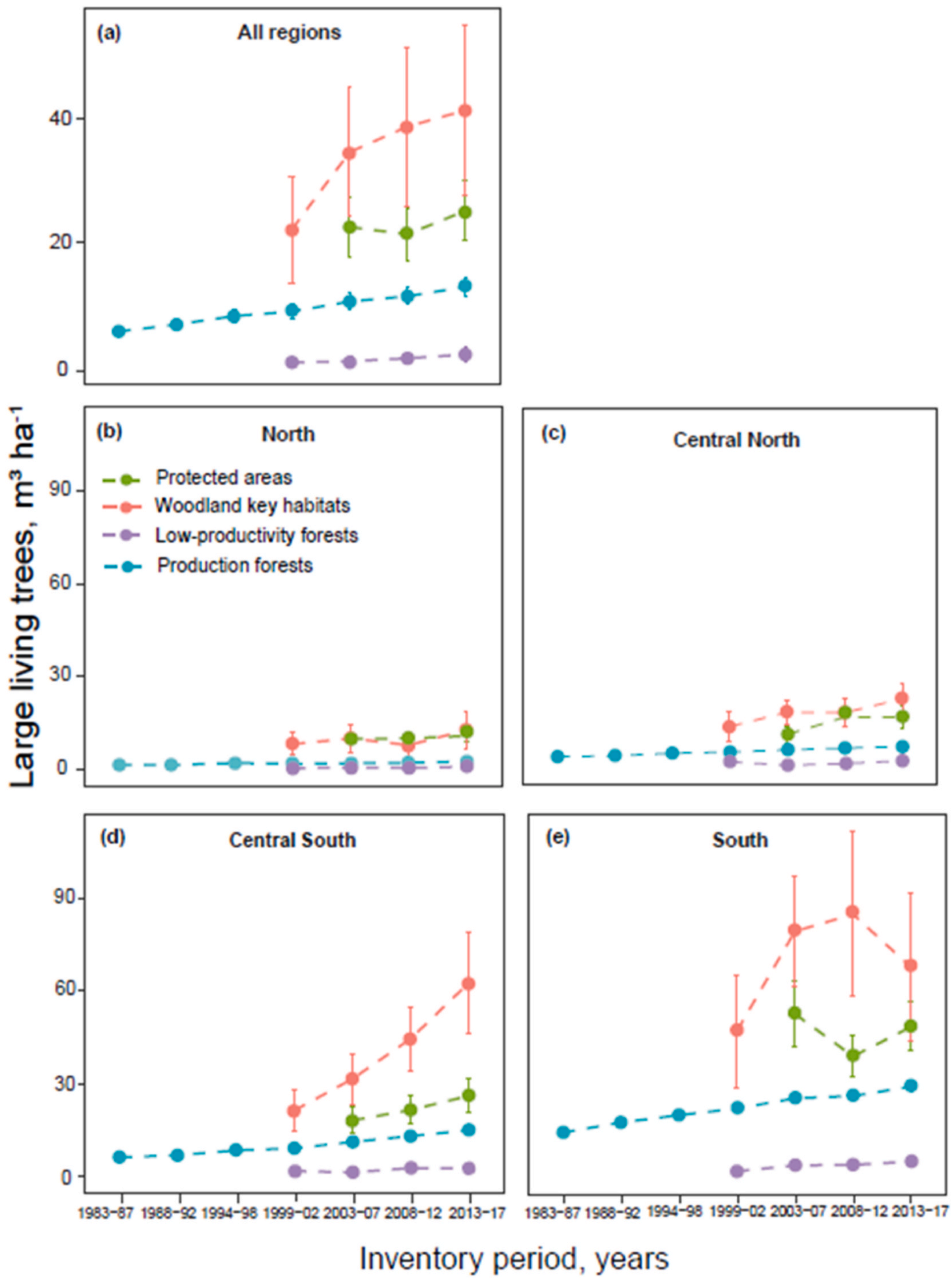

Fig. 3. Development of the volume of large living trees (diameter ≥40 cm; mean values ± 95% confidence interval) in four forest types in Sweden during the period 1983–2017, as analysed in total (a) across the country, and separately (b–e) for four regions. Protected areas represent forest lands that are protected by law or by legally binding agreement with the forest owners; woodland key habitats represent small forest areas with high conservation values that are not formally protected but are supposed to be left unmanaged according to certification standards; low-productivity forests represent forest lands with a potential timber production less than 1 m^3 ha^{-1} $year^{-1}$; production forests represent forest lands managed for commercial wood extraction.

management, and other historical land-use practices. In protected areas and WKHs, the observed dead wood volumes were still at the lower end of the threshold intervals of 20–50 m^3 ha^{-1} needed for long-term conservation of forest biodiversity (Müller and Bütler, 2010). Furthermore, current values of dead wood volumes in low-productivity forest and production forests were well below such thresholds. This means that despite 30 years of new policy implementation, an average Swedish forest still falls well under the threshold levels suggested to preserve dead-wood dependent species communities.

In line with our first hypothesis, we found that the volume of dead wood increased during the study period in all forest types. The increase in production forests is in accordance with predictions from simulations of dead wood dynamics in forests after the additional conservation measures are included in the management regime (Ranius and Kindvall, 2004). The increase may be due to the introduction of retention practices in production forests (Gustafsson et al., 2010), implemented under

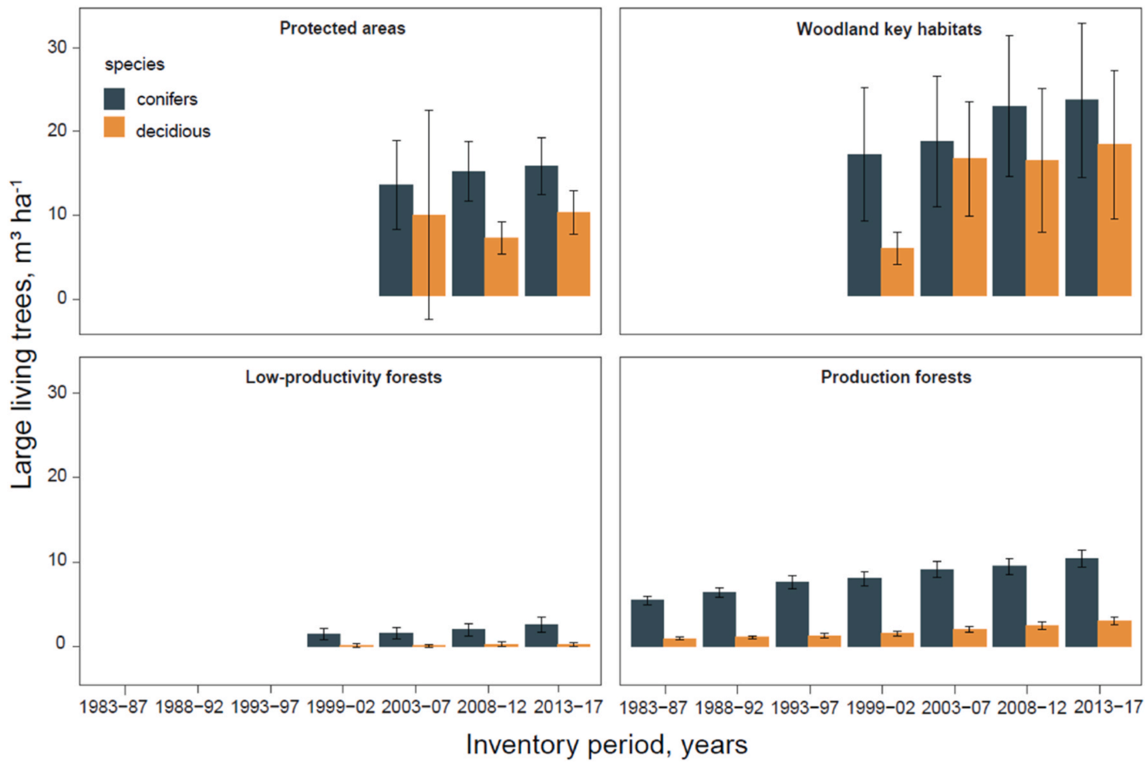

Fig. 4. Development of the volume of large living trees (diameter ≥40 cm; mean values ± 95% confidence interval) in Swedish forests categorized according to tree species (conifers or deciduous) during the period 1983–2017. Protected areas represent forest lands that are protected by law or by legally binding agreement with the forest owners; woodland key habitats represent small forest areas with high conservation values that are not formally protected but are supposed to be left unmanaged according to certification standards; low-productivity forests represent forest lands with a potential timber production less than 1 m^3 ha^{-1} $year^{-1}$; production forests represent forest lands managed for commercial wood extraction.

the new Swedish Forestry Act in 1993, and due to the adoption of a national FSC certification standard launched in 1998. This is supported by the fact that the amount of dead wood in young (0–10 years) Swedish forests has increased during the period 1997–2007 (Kruys et al., 2013). Thus, the observed increase in dead wood was expected, especially in young forests, and the full consequences of biodiversity-oriented forest management practices will be seen once all production forests have undergone a harvesting cycle.

Although the observed increase in dead wood in production forests could be linked to conservation measures, it is difficult to exclude other explanations – disturbances like droughts, fires, storms and insect outbreaks can also increase volumes of dead wood (Mazziotta et al., 2014; Jonsson et al., 2016). Indeed, Jonsson et al. (2016) suggested that recent increases in dead wood volume can be attributed to storm events during the early 2000's, although the evidence for storms as a driver is likewise circumstantial. Hence, various factors could be affecting the amounts of dead wood in forests, but it is difficult to disentangle these other factors from the effects of conservation measures and forest management practices using the NFI data.

We found that dead wood volumes are increasing in WKHs and protected areas, which are generally left unmanaged. This could be to the legacy effects from past logging activitiesthat have deprived parts of the dead wood in these forests (Ericsson et al., 2005). Simulation studies support this explanation, since they indicate that restoring dead wood volumes may take many decades (Ranius et al., 2003; Ranius and Kindvall, 2004). In addition, WKHs and protected areas are generally not salvage-logged after disturbances, and it is, thus, more likely that pulse increases in dead wood after disturbances will lead to detectable changes of dead wood volumes in these forest types in comparison to production forest.

Low-productivity forests had the lowest starting volumes and the slowest accumulation of dead wood. The low amounts of dead wood were anticipated, since these forests, due to their lower productivity, produce less dead wood than more productive forests (cf. Ranius et al., 2004). Although wood extraction from these forests historically has been small, they have been utilized (Rydin and Jeglum, 2013), and our result may reflect the slow recovery of dead wood that can be expected in low productivity forests.

Not only the volumes but also the quality of dead wood matters for biodiversity. Although, the NFI data only allows analyses of rough categories of dead wood, our analyses showed that several different types of dead wood have increased. Nevertheless, there may still be unaccounted decreases in the availability of certain substrates that cannot be detected by the NFI data. Furthermore, we found an increase in hard (less decayed) wood, but not in decayed wood (in later decay stages), in line with simulations of dead wood dynamics suggesting that the increase in hard dead wood comes earlier compared to decayed wood (Ranius and Kindvall, 2004). Consequently, we may expect a delayed positive effect of changed forest management in the future with respect to decayed dead wood. Alternatively, the lack of an increase in decayed dead wood could result from management related activities such as soil scarification that mechanically destroy dead wood (cf. Hautala et al., 2004). Since the 1990s, the proportion of clear-cuts that are scarified has increased (Bernes, 2011), which may counteract the actions that tend to increase the amount of dead wood. The increased level of scarification differs from the assumption made by Ranius and Kindvall (2004), suggesting that their predicted increase in decayed dead wood in the long term is too optimistic. Finally, the discrepancy between trends in hard dead wood and decayed dead wood can also be partly attributed to salvage logging, whereby hard dead wood produced by natural disturbances is removed.

As hypothesised, our regional based analysis showed that the increase in dead wood volumes was the highest in the south, whereas no or only minor changes were observed in the north. There are at least two

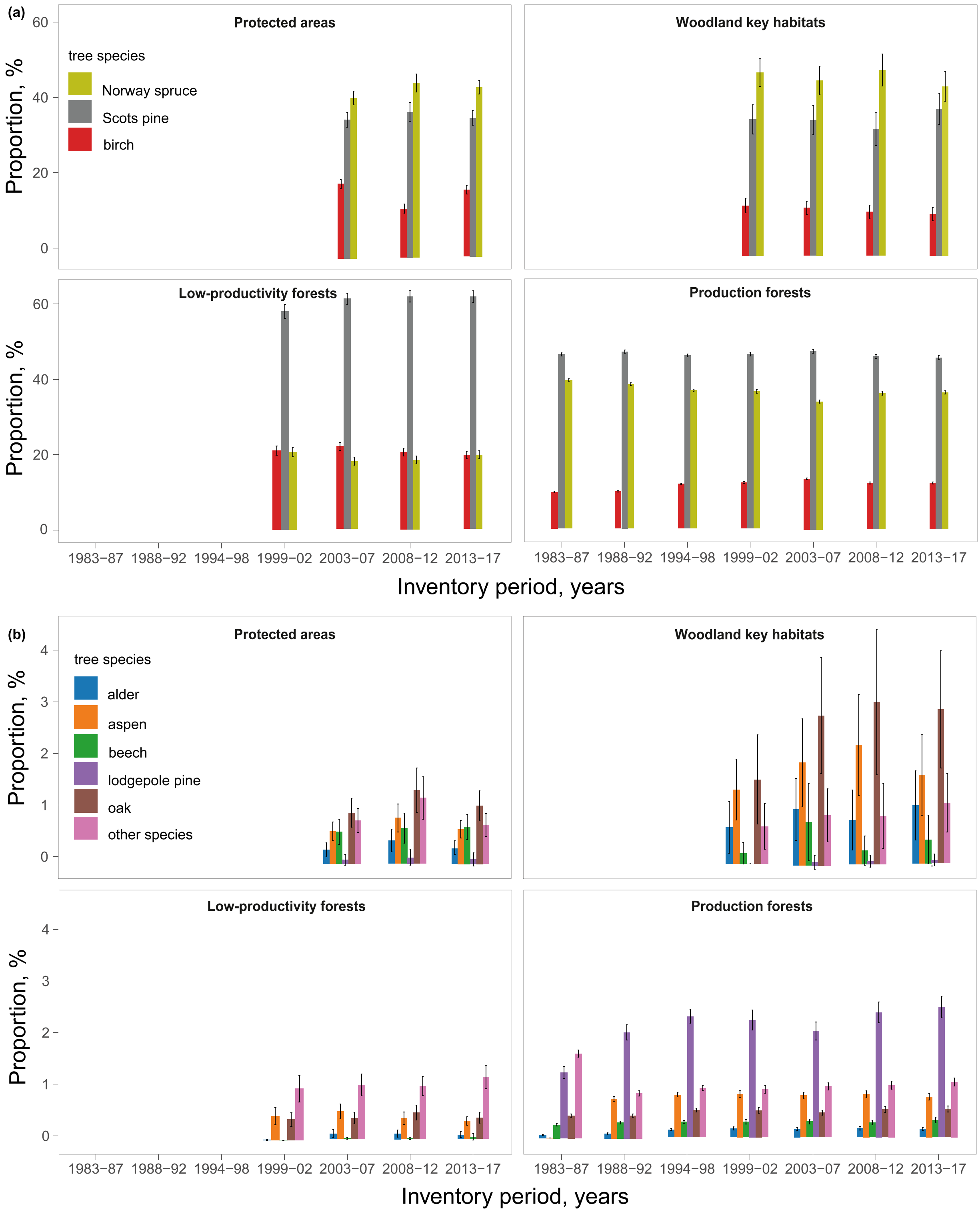

Fig. 5. Dominant (a) and rare (b) tree species composition as percentage of canopy cover (mean proportions ± 95% confidence interval) in different forest types during the period 1983–2017. Protected areas represent forest lands that are protected by law or by legally binding agreement with the forest owners; woodland key habitats represent small forest areas with high conservation values that are not formally protected but are supposed to be left unmanaged according to certification standards; low-productivity forests represent forest lands with a potential timber production less than 1 m^3 ha^{-1} $year^{-1}$; production forests represent forest lands managed for commercial wood extraction.

reasons for this difference. First, in the north, there are more forests that have not been, until recently, subjected to large-scale intensive forestry practices, including clear-cutting. Such forests often have high starting volumes of dead wood, much of which is lost after being clear-cut for the first time. Second, the higher productivity in the south implies that the increase in dead wood amounts after the introduction of a more biodiversity-oriented forestry can be more rapid (Ranius and Kindvall, 2004). Thus, in regions with intensive forest management (south of the country), biodiversity-oriented forestry will lead to a substantial improvement in dead wood volumes, while that may not be the case for

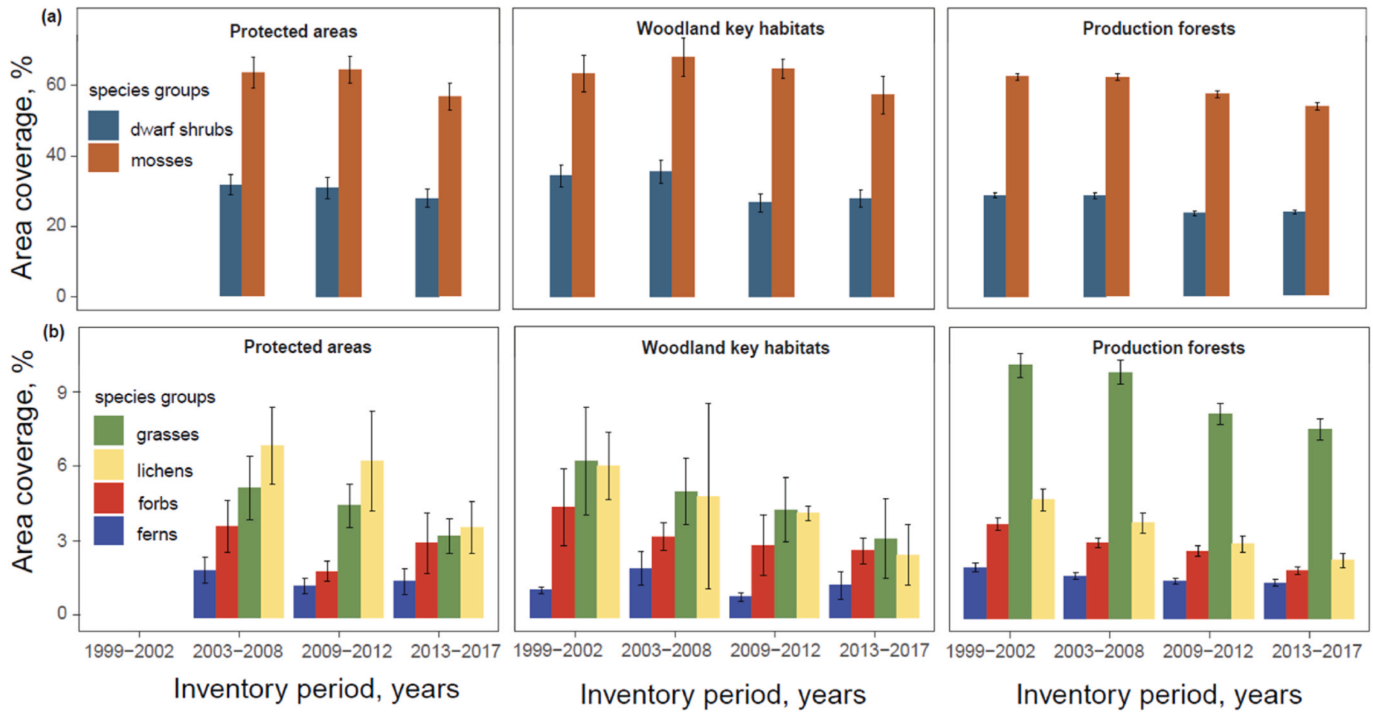

Fig. 6. Coverage area of dominant (a) and rare (b) understory vegetation groups (mean proportions ± 95% confidence interval) in different forest types during the period 1999–2017. Protected areas represent forest lands that are protected by law or by legally binding agreement with the forest owners; woodland key habitats represent small forest areas with high conservation values that are not formally protected but are supposed to be left unmanaged according to certification standards; production forests represent forest lands managed for commercial wood extraction.

regions originally having larger forest areas not yet utilized for intensive forestry (north of the country).

4.2. Large living trees

Although, the volume of large living trees tended to increase (both coniferous and deciduous trees) in all forest types (Supplementary Material, Fig. S7), this increase was only statistically significant in production forests. Possibly, this may be due to a higher statistical power (larger sample size) within this category. Nevertheless, the observed increase in large living trees volumes in production forest may at least be partly explained by the trees being temporarily or permanently, retained at final harvesting. This is supported by earlier findings indicating an increase in the amount of large living trees in young forest (Kruys et al., 2013). However, the increase could also be related to earlier changes in forestry, such as the end of diameter-limit cuttings during the 1950's (Lundmark et al., 2013). Such forestry regimes involved the selective cutting of larger trees (Nyland, 2005), often with a lower size limit of 30 cm diameter. If such forests were left uncut after 1950, they may contribute to the increase of large-diameter trees observed in our study. In neighbouring Finland, the development has been similar, with the density of large trees increasing rapidly since 1970s, attributed primarily to the introduction of the current forest management regime, including thinnings from below and abandonment of selective dimensional cuttings, slash and burn agriculture, cattle grazing, and tar production (Henttonen et al., 2020).

The fraction of deciduous large living trees increased in all forest types. This pattern could be related to historical management practices that aimed to remove almost all deciduous trees in production forests to favour conifers, although limits on the extent and intensity of such practices have been implemented during the last few decades (Axelsson et al., 2002). This change is supported by certification standards, which require a minimum proportion of deciduous trees to be retained, and is also being encouraged by an increased demand for fibre from deciduous trees (Bernes, 2011). Furthermore, especially in southern Sweden, large deciduous trees can persist on former agricultural land that was recently converted to forest land (Hedenås and Ericsson, 2004).

4.3. Tree species composition

In line with our expectations, tree species composition changed over time, with the strongest alterations occurred in production forests prior to 2003. At that time, the dominant conifer, Norway spruce, decreased, while deciduous tree species, like birch, alder and oak increased, resulting in a trend towards increasing tree species diversity. Similarly to large trees, this pattern could be explained by a reduction in the extent to which deciduous trees are actively removed from production forests by e.g. herbicides and cutting to favour conifers (Axelsson et al., 2002). Nevertheless, especially in southern Sweden, Norway spruce continues to dominate, while deciduous trees remain far scarcer than they were historically (Nilsson, 1997). This likely stems from both the economic incentives to establish Norway spruce production forests (Felton et al., 2020b), and the tree species' lower susceptibility to browsing pressure from large herbivores compared to other tree species (Bergqvist et al., 2018). However, Norway spruce is particularly vulnerable to bark beetle outbreaks that appear to be increasing (Marini et al., 2017), potentially reducing Norway spruce prevalence in the future. Moreover, in the north, the proportion of non-native conifer lodgepole pine increased, despite the fact that the certification standards limit the use of this and other exotic tree species. However, even though this is the most abundant non-native tree species in Sweden, it is still restricted to 2% of all productive forest land (4% in Central North) (Forest Statistics, 2021).

Apart from production forest, we found no clear changes in tree species composition in the studied forest types. In boreal forests, most tree species can have a very long life spans. Without harvesting or natural disturbances, the lifespan of many tree species may extend for several hundred years (Kuuluvainen et al., 2002). Therefore, in the absence of large-scale disturbances such as fires and storms, tree species composition in unmanaged forests is expected to remain relatively stable over the time span covered in our study.

4.4. Understory vegetation composition

The coverage of all understory vegetation groups declined with time, as observed in similar studies (Hedwall and Brunet, 2016; Hedwall et al., 2019, 2021; Jonsson et al., 2021). However, in contrast to previous studies, here we investigated the development of understory vegetation composition in different forest types, and found that the pattern was consistently similar.

One important reason for the observed changes in understory vegetation could be the reduced light availability on the forest floor as caused by denser forest overstory. Denser and darker forests have negative effects on cover of understory vegetation (Petersson et al., 2019), especially for lichens (Gauslaa et al., 2007; Tonteri et al., 2016). Indeed, we observed a general increase in tree density in all studied forest types (except low-productivity forests that were never surveyed for understory vegetation; Supplementary Material, Fig. S7). Production forest management is known to increase tree density (Forest Statistics, 2021). However, in unmanaged forests the tree density and tree cover have also increased (Kulha et al., 2020), probably as a result of a decrease in surface fires (Wallenius, 2011), decreased forest cattle grazing (Henttonen et al., 2020), a warming climate (Hughes, 2000), and increased nitrogen deposition (Naaf and Kolk, 2016). As such, our results suggest that forestry is not the only important contributing factor explaining ongoing changes in understory forest vegetation in Sweden.

4.5. Consequences for biodiversity

Our results show mainly positive trends in structural components important for biodiversity in Swedish forests. It is therefore reasonable to expect that species, especially those associated with large trees and dead wood, would experience positive trends in abundance. There are currently about 2000 forest-dwelling species on the Swedish Red List (Naturvårdsverket, 2020), many of which are dependent on dead wood and large living trees. The Swedish Red List is updated every fifth year, and the proportion of red-listed species has been reported to be rather constant over the course of the last two decades. Thus, the increase in structural components has so far not resulted in any observed improvement in the overall status for red-listed species in Sweden, which could be due to several reasons. First, since the red-listing process is mainly dependent on rough, unsystematic field data and expert opinions, there may be positive trends for additional red-listed species, but due to lack of more precise monitoring, these trends are not being captured. Furthermore, time-delays in species responses to the improvements in forest quality may result in what is known as species credit (Hanski, 2000). If so, it is reasonable to expect the proportion of forest red-listed species to increase in the future, when the amount of structural components has increased over a longer time, and species populations have had more opportunity to recover. Finally, forests may simply continue to lack sufficient quantities or qualities of forest habitats or resources needed by many red-listed species, despite the increasing trend in biodiversity important structural components. The amount of dead wood and large living trees is still far below what is found under natural conditions, also in the unmanaged forest types, and although we here report a promising trend, the levels may still be too low for species dependent on these structural components. In addition, many red-listed species have specific requirements for certain types of dead wood (e.g. burned wood or very old wood from slow-growing trees) or large trees (e.g. old trees with hollows), not captured by the NFI data (e.g. Ranius et al., 2009; Santaniello et al., 2017). Therefore, it may require a larger increase in these structural components throughout much of the potential distribution areas to improve the threatened status of the dependent species. It is thus possible that the current changes in forestry and nature conservation is not enough to sustain the populations of many native species, and therefore protect biodiversity.

Each of these possible explanations may be relevant for at least some red-listed species. More systematic monitoring of certain red-listed species and specific habitats would be needed to provide information about their relative importance.

4.6. Conclusions

Changes in forest policy towards more environmentally-oriented practices have likely contributed to the observed increases in the amounts of biodiversity important structural components. However, the net outcome largely depends on how different forest categories have been affected by forestry in the past. The increase in the volumes of dead wood and large living trees in production forests suggests that by following current practices, it is reasonable to expect further increases in those structural components in Swedish managed forests, though with delayed outcomes for those structural components that develop slowly. Low-productivity forests appeared to have the lowest relative capacity for increasing structural components of importance to biodiversity. Despite a substantial increase in the amount of dead wood and large living trees observed in WKHs and protected areas, the levels of biodiversity important structural components still remains far below those found in pristine forests. Therefore, restoration measures would be useful to mitigate the effects of past forest management and to reach the full potential of structural components in these forests. The restoration efforts may include the artificial creation of dead wood, managing the forest canopy to create favourable conditions for light-demanding species, and the use of prescribed burning to mimic a natural disturbance regime.

Data availability statement

All data used in the study were obtained from the Swedish National Forest Inventory and are available upon request from the Department of Forest Resource Management, Swedish University of Agricultural Sciences, Umeå (http://www.slu.se/riksskogstaxeringen).

Credit authorship contribution statement

Julia Kyaschenko: Conceptualization, Formal analysis, Data curation, Writing – original draft, Writing – review & editing. **Joachim Strengbom:** Conceptualization, Writing – review & editing, Supervision. **Adam Felton:** Conceptualization, Writing – review & editing. **Tuomas Aakala:** Conceptualization, Writing – review & editing. **Hanna Staland:** Conceptualization, Writing – review & editing. **Thomas Ranius:** Conceptualization, Writing – review & editing, Supervision, Project administration.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2022.114993.

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