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Title: High rates of short-term dynamics of forest ecosystem services

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Abstract

Currently, the main tools for assessing and managing ecosystem services at large scales are maps providing snapshots of their potential supply. However, many ecosystems change over short timescales, thus such maps soon become inaccurate. Here we show high rates of short-term dynamics of three key forest ecosystem services: wood production, bilberry production, and topsoil carbon storage. Almost 85% of the coldspots and 65% of the hotspots for these services had changed into a different state over a ten-year period. Wood production showed higher rates of short-term dynamics than bilberry production and carbon storage. The high rates of dynamics mean that static snapshot ecosystem service maps provide limited information for assessing and managing multifunctional, dynamic landscapes, such as forests. We advocate that dynamic, spatially explicit tools to assess and manage ecosystem service dynamics are further developed and applied in post-2020 biodiversity and ecosystem service policy supporting frameworks.

Assessments of ecosystem services (ES) are pivotal in policy and land-use planning for sustainable use of resources [1–7]. The main tools for assessing and managing ES are maps providing snapshots of their potential supply [8,9]. Such static maps may enable the identification of areas of high or low ES supply [10], or suggest spatial trade-offs and synergies amongst them [4]. Large resources are allocated to mapping ecosystem service supply on different spatial scales [5,11–13]. However, a major limitation in the current management of ES is our poor understanding of how their potential supply changes in space or over short timescales. ES dynamics result from dynamics of the environment, of the species underlying ES, or management actions regulating the ES levels. These dynamics further lead to constantly changing trade-offs and synergies through time. Consequently, static maps of ES may soon become inaccurate after being produced. Static snapshot quantification and mapping of ES may therefore lead managers to make erroneous inferences about ES delivery through space and time, and thus manage ecosystems inefficiently. To effectively manage ES in changing landscapes, we must account for how, and at what rates, different ES change.

There is a paucity of studies that investigate how the short-term dynamics of ES affect our ability to predict ES levels. An exception is the study of Holland et al. [14] that a decade ago inferred that freshwater ES levels vary over the short term, based on samples of freshwater biodiversity separated by five years. More recent studies have instead focused on gradual, long-term changes in ES supply, mainly based on land cover maps or chronosequences [15–19]. However, we are not aware of any previous estimations of the *rates of short-term dynamics* in the levels of single or combinations of ES based on measurements in the field. Thus, we need knowledge on these potentially complex short-term ES dynamics, and how they may change over time. Knowledge on these dynamics is needed to estimate the near future ES levels and also to understand the limitations of static mapping of ES in assessing and managing ecosystems.

In this study, we use a nationwide Swedish forest dataset and present estimates of the short-term dynamics of important boreal forest ES, including hot- and coldspots for these services. Boreal forest is the largest terrestrial biome globally [20]; it constitutes 45% of the timber stock [21], and stores one third of the forest carbon [22,23]. Moreover, the Nordic countries are large providers of wood to the continuously growing global market [24]. In addition, other forest ES hold large values, for instance, the estimated annual value of the harvested berries in Finland is 100 M€ [25]. Here, we ask if there are differences in the rates of short-term dynamics between sites with high, medium, and low levels of the ES wood production, bilberry production, and topsoil carbon storage (Supplementary

Table 1). We also examine whether there are differences in the rates of dynamics between single services, and hot- and coldspots of all three services. This includes investigating whether the short-term dynamics of ES change through succession, i.e. as the forest ages through time. Finally, we test the importance of different environmental conditions in explaining the occurrence of hot- and coldspots. We hypothesize that wood production in particular shows high rate of short-term dynamics since this ES is intensively managed. We expect to observe the highest rate of ES dynamics in young forest. Moreover, as hot- and coldspots summarize the levels of several ES, we expect them to be even more dynamic than the individual ES of which they are composed. Finally, we hypothesize that the occurrence of hot- and coldspots are explained by the most important variables explaining the ES composing them, specifically tree species richness and biomass of tree species [26].

SHORT-TERM DYNAMICS OF SINGLE ES

Wood production showed higher rates of short-term dynamics than bilberry production and topsoil carbon storage over the ten-year period, from 2000 to 2010 (Fig. 1). We categorized sites as having ‘high’, ‘medium’ and ‘low’ levels of ES (see Fig. 1 caption for definition), and found that more than half of the sites with low (63%) and medium (69%) wood production in 2000 had changed into another wood production category by 2010. For high production sites, 23% had changed. Bilberry production was the least dynamic ES with 21%, 46% and 37% of low, medium, and high sites, respectively, changing into another category by 2010 (Supplementary Results 1 and Supplementary Table 2). For carbon storage the corresponding changes were 34%, 64% and 39%. There are thus substantial changes in the levels of forest ES when comparing one snapshot to another one, separated by only ten years. For details on how these estimators were calculated, see Supplementary Result 1 and Supplementary Table 2. Additionally, we found that the mean rate of short-term dynamics of wood production was higher than that of bilberry and carbon storage dynamics, but there was no difference in mean rates between the latter (Supplementary Table 3). The mean of all ES increased at sites where the level was low in 2000 and decreased in two ES at sites where the level was high (see Supplementary Fig. 1 for further details), reflecting the dynamics of the system. Indeed, these changes in means did not result in also changes in category at more than 50% of these sites (except that 63% of sites with low wood production changed category). This is possible as the estimators of change in Fig. 1 and Supplementary Fig. 1 are different. Within and between the bubbles in Fig. 1, changes take place, and the mean and distribution of all these changes are presented in Supplementary Fig. 1.

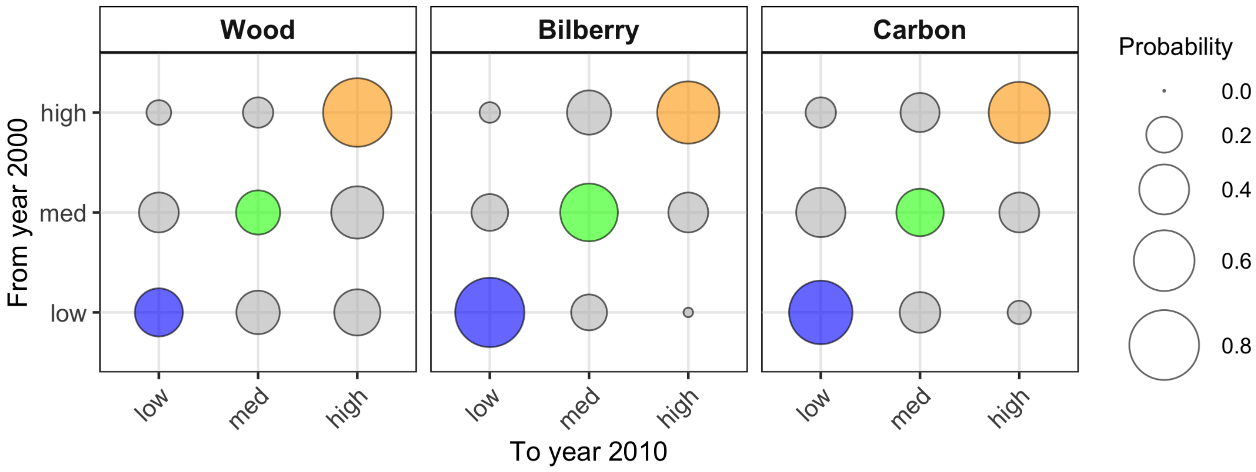

Fig. 1 | Rates of short-term dynamics of single forest ES shown as probabilities of sites changing between categories over a 10-year period. 'High' delivery is defined as the ES having a value higher than the 65th percentile of its maximum value observed, 'low' has a value lower than 35th percentile of its maximum, and 'med'(medium) is in between (35th-65th percentiles). Changes into other categories are grey, while categories staying the same (i.e. no change) along the diagonals are blue for low staying low, green for medium staying medium, and orange for high staying high.

CHANGE IN SHORT-TERM DYNAMICS AS FOREST AGES

For wood production, the rates of short-term dynamics changed as the forest became older. Thus, the change in the levels of forest ES when comparing one snapshot to another separated by ten years varied with forest age. Specifically, the probability of sites changing from one ES category into another changed with age (Fig. 2). Sites were categorized into three age classes: young (<40 years); middle-aged (40-70 years); and mature (>70 years). Sites delivering low levels of wood production were more dynamic in young forests (79% of the sites changing into another category) than in mature forests (45% changing into another category) (see Fig. 2 and Supplementary Result 2 and Supplementary Table 4a for details). In contrast, sites with high wood production were more dynamic in mature forests (41% of the high sites changed to medium or low levels) than in young forests (14% changed). There was no clear change in the rates of dynamics of bilberry production or topsoil carbon storage as the forest aged (Fig. 2 and Supplementary material Table 4a). These results can be explained by changes in the mean rate of short-term dynamics in wood production as the forest ages (Supplementary Fig. 2). For bilberry, this relationship to age was weaker and for carbon storage it was detectable only at sites with low carbon storage.

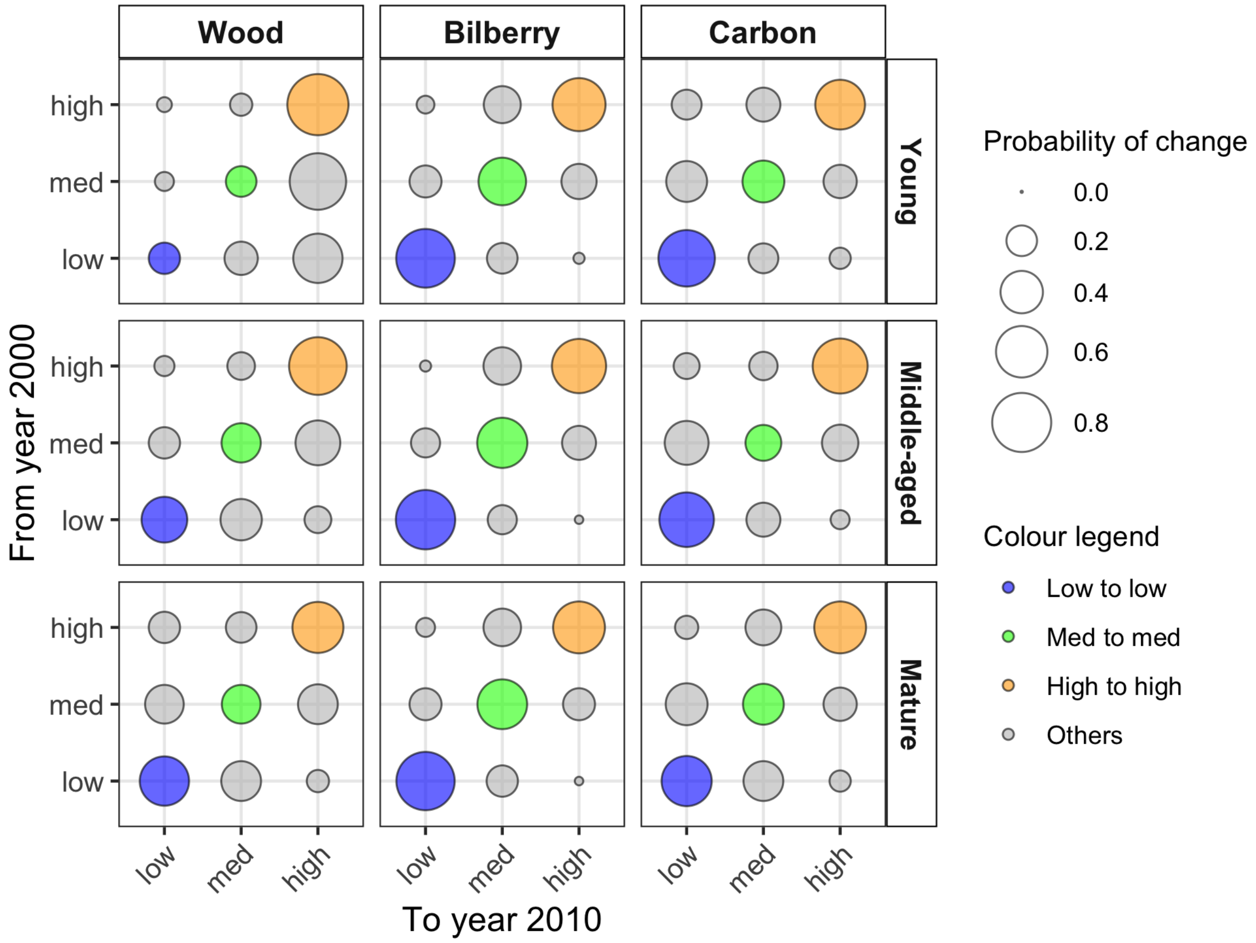

Fig. 2 | Rates of short-term dynamics of single forest ES for different forest age classes. Rates are shown as probabilities of sites changing between categories over a ten-year period. See Fig. 1 caption for definitions of high, med (medium) and low.

Changes in ES levels through succession

The levels of the individual ES changed as the forest aged (Fig. 3a and Supplementary Tables 5-7 for model details). Wood production showed a positively hump-shaped relationship with age; the level increased rapidly after clearcutting and peaked at a forest age of about 40-60 years, after which it decreased (Fig. 3a). Only for bilberry production was the change unidirectional through succession; the level increased steadily up to an age of about 120 years when there was a tendency for stabilization. Topsoil carbon storage did not change much across stand ages, the level was fairly stable up to a forest age of about 100 years, after which there was a tendency for decrease.

Sites with high or low levels for all three of the ecosystem services considered, hereafter called hotspots and coldspots, respectively, are of particular interest for ES assessments. The probability of hotspot occurrence increased as the forest reached middle-age, and then decreased when the forest became older (Fig. 3b). This decrease in old forest was driven by decrease in wood production (Fig. 3a), in this study which included three ES. In contrast, the probability of coldspot occurrence decreased with age, being highest in young forests during the first decades after clearcutting.

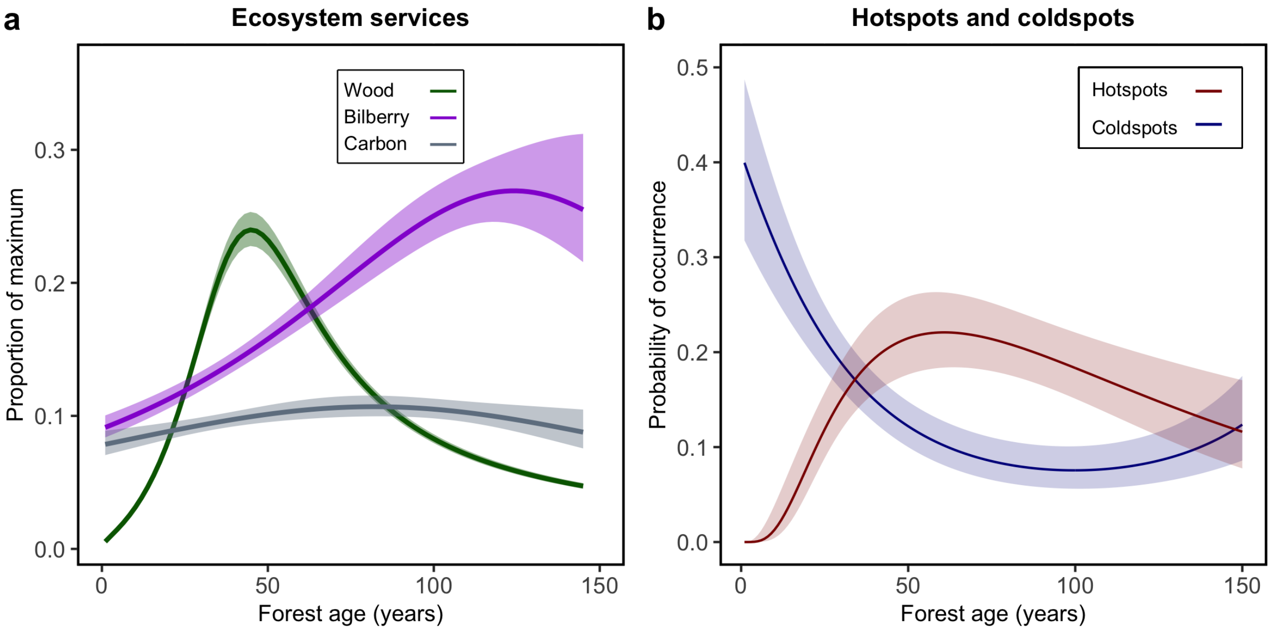

Fig. 3 | Changes in single ES and hot- and coldspots through forest succession. a,**b**, Predictions of single ES (proportion of the maximum value observed) (**a**) and probabilities of occurrence of hot- and coldspots (**b**) through forest succession based on generalized linear models (with 95% confidence bands). Hotspot is defined as at least two of the ES having a value higher than the 65th percentile of their maximum value and none having a value lower than the 35th percentile of their maximum, and coldspot as at least two of the ES having a value lower than the 35th percentile of their maximum and none having a value higher than the 65th percentile of its maximum.

The relationships between hot- and coldspots and forest age through succession were mainly driven by the development of the tree layer (Fig. 3b and Supplementary Tables 8-11 for model details), as indeed also shown earlier for single ES [26]. This is confirmed by different relationships between hot- and coldspots and forest age when jointly accounting for all other variables in models with multiple variables (Supplementary Fig. 3). Thus, the relationships in Fig. 3 are driven by increasing biomass of the different tree species and species richness rather than by the increasing forest age *per se*.

More specifically, the probability of hotspot occurrence increased with increasing tree species richness and the biomass of spruce, pine and birch (full model results in Supplementary Table 10). In addition, the probability of hotspot occurrence decreased with pH and increased with soil moisture, but was lower on peat soils. Finally, there was a non-linear relationship between hotspot occurrence and temperature. The probability of coldspot occurrence correspondingly decreased with increasing tree species richness and the biomass of trees, with an interaction effect between pine and age (Supplementary Table 11). The probability further increased with pH and decreased with soil moisture, temperature, and nitrogen deposition.

SUMMARY OF SHORT-TERM DYNAMICS OF COMBINED ES

The majority of the hotspots and coldspots changed into another category during the ten-year study period (Fig. 4), and these changes were generally higher than for individual services (Fig. 1). Specifically, 65% of the hotspots and 84% of the coldspots changed into another category (Fig 4, Supplementary Table 12), as compared to 23-69% for individual services (Supplementary Table 2). The hotspot sites were more likely to remain hotspots than the coldspot sites were to remain coldspots ($Z = 2.4$, $N = 128$, $p = 0.016$, see details on transitions in Supplementary Table 12a). The most stable category was No spot. This is not surprising as it is the biologically widest one covering a wide range of ES levels, being based on 13 categories (see Supplementary Table 14). The probability of hotspot becoming coldspot, and vice versa, was very low, whereas No spot sites could end up in any category over the 10-year period.

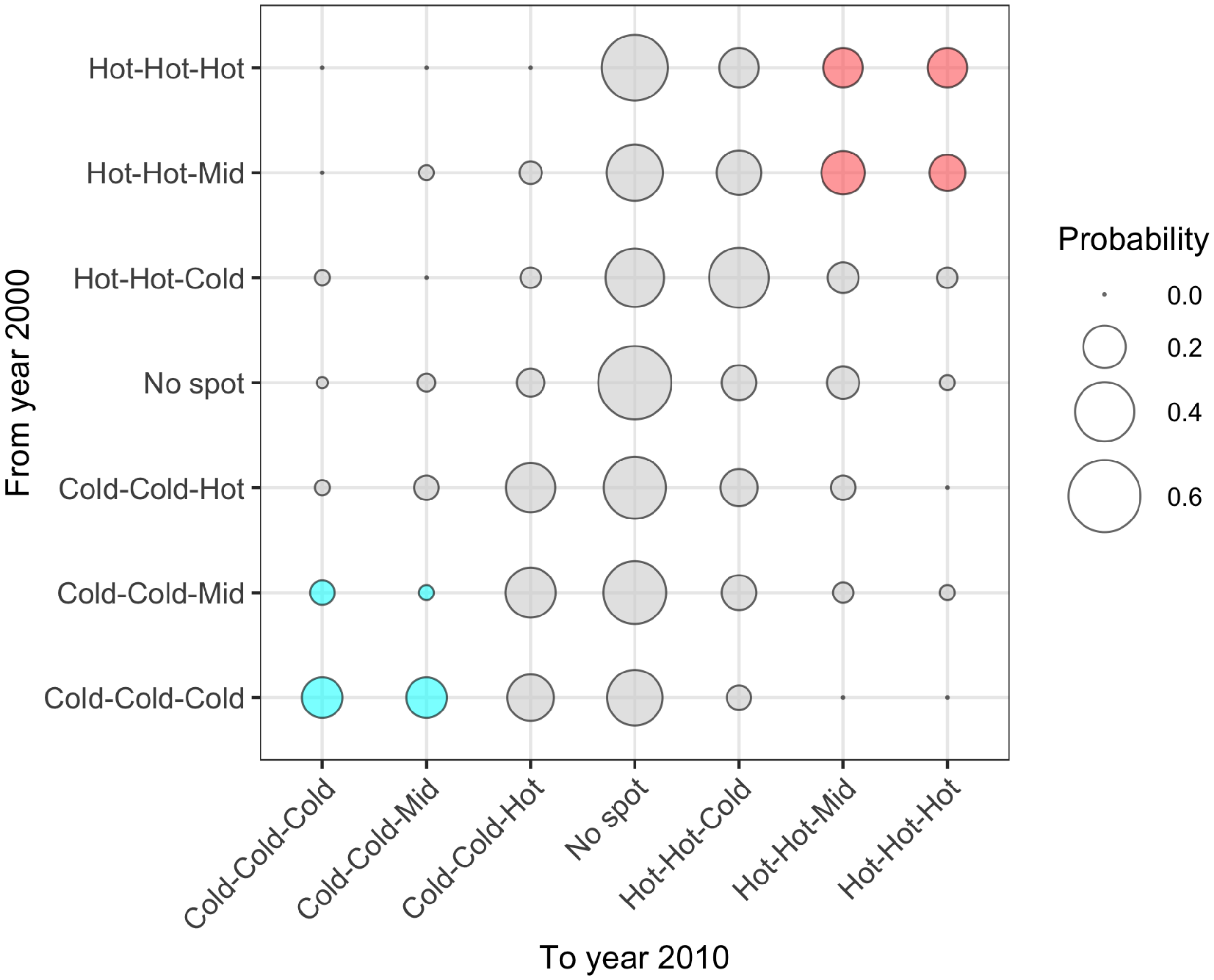

Fig. 4 | Joint short-term dynamics of combined ES quantified as the probabilities of sites changing to another category over a ten-year period. The seven categories are based on the 27 possible combinations of the three levels ‘high’, ‘medium’ and ‘low’ for the three ecosystem services. These ranged from category Cold-Cold-Cold becoming increasingly warmer via No spot to category Hot-Hot-Hot. The levels concern any ES, so that in e.g. Hot-Hot-Cold, Cold represents low supply of any of the services. Hotspots are represented by red bubbles and coldspots by blue bubbles. See Methods and Supplementary Table 14 for a full description.

Discussion

This study is the first to provide clear evidence for high rates of short-term dynamics in the supply of both single ecosystem services, and of hot- and coldspots of multiple ES, in a production ecosystem of large-scale societal importance. We used direct measures of the short-term dynamics of the ES from field data from a whole country. Previous studies have instead inferred such dynamics from biodiversity measures [14] or presented gradual long-term changes using indicators of ES [18,19]. Observing such high rates of dynamics means that static maps of ES, as are used in present ES assessments (e.g. in the European Union) [5,27–31], do not provide adequate information to make well-informed management decisions [30–32]. Static maps are snapshots and do not account for the complex short-term dynamics of ecosystems. They may therefore lead managers to make erroneous inferences about potential ES delivery through time, and consequently manage ecosystems inefficiently. In addition to the forests studied here, this is also likely to be the case for other production ecosystems in which dynamic ecosystem functions, natural conditions, or management practices cause short-term dynamics in ecosystem service levels.

HOT- AND COLDSPOTS ARE MORE DYNAMIC THAN SINGLE ES

The reliance on static maps is particularly inappropriate for managing multifunctional landscapes, i.e. for multiple ecosystem services instead of single services. This conclusion is supported by our finding that combinations of high or low levels of several ES simultaneously, i.e. hotspots and coldspots, showed high rates of short-term dynamics (Fig. 4), and somewhat higher rates than sites delivering high or low levels of single services (Fig. 1). Almost 85% of the coldspots and 65% of the hotspots changed over a 10-year period, and for single ES, 23-69% of the sites changed from having high, medium, or low levels. The most likely explanation for the higher rates of dynamics of hot- and coldspots compared to single services is that different individual services have different spatio-temporal dynamics. The level of an ES is determined by a wide range of management actions and environmental conditions, not least tree species richness and their biomass [26]. Moreover, the occurrence of hot- and coldspots were also largely determined by tree species richness and their biomass (Supplementary Tables 10 and 11), in combination with soil moisture and chemistry, and regional variation in temperature and nitrogen deposition. These actions and conditions also manifest in different trajectories of ES levels through time, with our three example services showing increasing, stable, or positively humped-shaped trajectories (Fig. 3). However, the relationships are largely determined by the tree layer (see Gamfeldt et al. [26] for individual services), which is further determined by forest management.

Wood production showed the highest rate of short-term dynamics of our study services (Fig. 1). There was a high probability of change for sites with high, medium and low levels over a 10-year period. These dynamics differed between young and mature forests (Fig. 2). Likely explanations for these dynamics are that wood production depends on a wide range of environmental conditions [26,33,34] and that management efforts usually focus on this service, which is harvested approximately when the ES is at a high level from an economic perspective. In contrast, bilberry production showed the lowest rate of dynamics (Fig. 1-2). This is likely explained by its stability and dominance in mature stands [35]. On the other hand, this is a proxy and actual berry counts may vary between years [36]. Topsoil carbon storage showed intermediate rates of dynamics (Fig. 1) and remained quite stable as the forest aged (Fig. 2). A likely reason is that its level and dynamics are largely determined by the slow rates of litter and root decomposition related to mean temperature and soil moisture [37].

DYNAMICS CHANGE THROUGH FOREST SUCCESSION

Hotspots were most frequent in middle-aged forests, whereas coldspots were most frequent in young forests during the first decades after clearcutting (Fig. 3). These findings reflect the changes in the supply of high and low levels of these particular three services through succession. The decrease in hotspots in older forest was driven by decreasing wood production, while bilberry and many other ecosystem services increase in old forests [38]. The changes through succession are not driven by age *per se*, but by the developing tree layer (tree species richness, composition and tree biomass, see Supplementary Tables 10-11, Supplementary Fig. 3). Wood production changed unimodally with age. After clearcutting (the most common harvesting method in northern European forests), wood production was low during the first 20 years, but then increased quickly and peaked in middle-aged forest. Thereafter, wood production decreased in these production forests. However, recent work has showed it to be stable 50-100 years beyond the recommended harvesting age [39], which in Sweden is around 70-100 years. Bilberry production showed a linear increase as the forest aged, reaching its maximum in mature and old-growth forests of over 100 years old (Fig. 3). Previous studies show that bilberry yields are highest in mature stands and decrease drastically after clear-cutting as they are sensitive to soil disturbance and scarification [35]. Finally, topsoil carbon storage remained quite stable as the forest aged (Fig. 3). This seemingly contrasts earlier studies showing increasing carbon storage through time. However, most previous research has focused on other organic matter components than topsoil carbon, such as above or belowground biomass [40,41].

The fact that different ES follow different paths through succession implies that if we increase the number of ES under study, we may find even more types of dynamics. These findings imply that it will be increasingly difficult to provide high levels of multiple ecosystem services at the stand level, as the demand for different forest ES from various societal actors increases. This suggests that innovative landscape level solutions that increase forest diversity in space and time may have to be developed for future forests to provide multiple ES to society. These solutions could involve landscape-scale optimization approaches.

FUTURE DIRECTIONS

In a time of intensive resource exploitation and climate change, the capacity of ecosystems to sustain many services and goods to society is uncertain. The ultimate goal of managing ecosystems should be to assure and maintain the supply of *multiple* ES across space and through time [34,42]. However, the high rate of short-term dynamics of the hotspots (Fig. 4) and single services (Fig. 1) challenges this joint maximization. Earlier work has focused on explaining service levels at certain sites or in the landscape, e.g. [26,33], but has not accounted for their short-term dynamics. The provisioning of ES is spatially heterogeneous and few areas provide high levels for multiple services through time [28,43]. Structural heterogeneity of the forest may promote the supply of multiple ES [44], and some of the ES develop in a predictable way as the tree layer develops. In fact, the optimization approach used by the industry and research on forest is suitable to identify management that provides high levels of multiple ES at the landscape scale, e.g. [42,45]. The approach starts with formulating objectives to be fulfilled for the study landscape over a specified time horizon (objectives that actors and stakeholders ideally agree on). Next, a large number of management alternatives for each stand and each time step into the future is simulated. Finally, mathematical optimization is used to select, for each stand, the management that jointly fulfils the objectives initially agreed upon for the landscape, e.g. [42,46]. The ES of interest can be included in the form of predictive regression models that are becoming increasingly available, e.g. [35].

Short-term dynamics of ES are likely to be important in other production ecosystems as well. For example, in agricultural landscapes, short-term dynamics are inevitable consequences of various crop rotation systems [47,48]. Rotations may range from simple ones with one or two species to complex rotations with 6-7 species of crops over a rotation [49]. More complex rotations have the potential to replace the current dominance of a few crops over large areas, which require management using fertilizers and pesticides [47,49]. Understanding ES delivery from crop rotation systems thus requires a more dynamic perspective where different crop species, sequences and their distribution in the landscape interact with ecosystem services, e.g., biological control, pollination, or carbon sequestration having joint but partly independent dynamics. The optimization approach to assess multiple ecosystem services over time discussed for forests above may also be useful here, again assuming that farm economy and other societal goals are compatible. In marine systems, the fish resource itself moves around on different spatiotemporal scales and the short-term population dynamics of fish have formed the basis for jointly managing this and other ES [50]. Nevertheless, Gissi et al. [30] recently proposed to incorporate temporal change in the spatial planning of marine areas, and Maxwell et al. [31] now criticize the developing agreement of the United Nations Convention on the Law of the Sea for lack of focus on the fact that both catches and fisheries are highly mobile. For certain ecosystems, such as forests, there is a fairly long tradition of planning management using dynamic, spatially explicit decision support systems, e.g. [51]. Some of these already include ES and incorporate optimization tools [45,46].

A limiting factor to adopting more dynamic and spatial approaches for ES management can be the lack of predictive models for how ES of interest respond to changes in abiotic and biotic conditions and management, e.g. [35]. We therefore advocate allocating more resources to research on the processes driving both the short-term and long-term dynamics of ES, where long-term in forestry may be 30 years or more, and in agriculture at least one or several crop rotations, i.e. 7-15 years. Moreover, we look forward to a transition from the current dominant use of static maps into more frequent use of dynamic tools and perspectives in the EU and global post-2020 biodiversity and ES policy supporting frameworks, such as the EU Biodiversity Strategy for 2030.

Methods

FOREST MANAGEMENT AND FOREST DATA

We studied Swedish boreal and boreo-nemoral forest composed of approximately 40% Scots pine (*Pinus sylvestris*), 40% Norway spruce (*Picea abies*) and 20% broadleaved trees [52]. The low proportion of broadleaved trees is due to the dominant clearcutting forestry that focuses on conifers. After clear-cutting, there is often abundant natural regeneration of broadleaved trees, while conifers are mainly planted. The rotation length is 70-150 years, and is shortest in the south [53]. There are one to three thinning events per rotation. The aim of thinning is typically to reduce broadleaved trees but also to decrease competition from, and extract, naturally regenerated conifers.

We used a nation-wide forest dataset from the Swedish National Forest Inventory and the Survey of Forest Soils and Vegetation, covering an area of 400,000 km^2 of land. Hereafter the inventories are referred to as the NFI. The inventory uses a regular sampling grid with a randomly selected starting point covering the whole country [54], with each tract being surveyed once every 5 years. The tracts, which are rectangular in shape and are of different dimensions in different parts of the country, consist of 8 (in the north) to 4 (in the south) circular sample plots. The circular plots have different radii (5-20 meters) to ensure that the variables recorded characterize the short-term forest dynamics and management. We used only plots on 'productive forest' (average production of standing volume, stem volume over bark >1 m^3 ha^{-1} $year^{-1}$, 21 million hectares in Sweden). To be included in our analyses, the plots had to be located on only forested land, i.e., not including any river, road, grassland, etc. For the current study, we utilized data on the focal ES, forest age and other environmental variables (Supplementary Table 15). The NFI sampling is designed for the data to be representative of the common forest habitats, with a yearly budget for fieldwork and data maintenance of 4.7 MEuro.

ECOSYSTEM SERVICES

The three ecosystem services studied can be classified according to the Common International Classification of Ecosystem Services and Nature's Contributions to People (Supplementary Table 1). Thus, they are of high economic, cultural and/or recreational importance.

Wood production

Wood production was estimated as the yearly change in tree biomass (kg m^{-2} $year^{-1}$), calculated over a period of 5 years for all tree individuals higher than 1.3 meters. For plots where biomass was measured in 1999-2002, the baseline for wood production was thus measurements of biomass in the years 1994-1997 (hereafter referred to as '2000'), and correspondingly, we used data from 2008-2012 and 2003-2007 for what we hereafter refer to as year '2010'. We excluded plots that had been harvested, cleared, or thinned within the two periods of measuring biomass for calculating production, e.g. 2008-2012 to 2003-2007. Biomass was calculated using biomass functions [55,56] and was the sum of the biomass from the stem, twigs and branches, the stump and roots. For deciduous tree species, there is only a function for *Betula spp.*, and this function was applied to all other deciduous tree species. The *Pinus sylvestris* function was applied to *Larix decidua* and *Pinus contorta*. Even though this creates a slight tree species bias, it has minor effects on our production estimates since we calculated the difference in biomass between two points in time. This is a provisioning service. The sample size for wood production was 4,444 plots.

Bilberry production

Bilberry production was measured as the percentage of the plot covered by bilberry (*Vaccinium myrtillus*). The cover of bilberry is the main predictor of the annual bilberry production [35] and berry production further varies between years [36]. The cover of bilberry is strongly correlated with the annual bilberry production [35,57]. Bilberry is one of the most economically important wild berry species in northern Europe [35]. In addition to being a provisioning service, the recreational value of picking bilberries also makes it a cultural service. We used data from 2,187 plots inventoried 1999-2002 (hereafter '2000'), and 2009-2012 (hereafter '2010').

Topsoil carbon storage

Soil carbon storage was measured as the amount of carbon (g m^{-2}) in the topsoil of the plot, which consisted of either purely organic horizons, i.e. mor layers (63%) or peat layers (21%), or less frequently of minerogenic A-horizons (16%). This is the part of the soil most affected by the current above-ground biota. To compensate for the conceptual difference in topsoil types, mean soil carbon stocks were set equal for purely organic soils (measured in the organic horizon down to a maximum depth of 30 cm) and minerogenic topsoils (measured in the top 10 cm horizon). The soil fraction <2 mm was analysed. We used data on this regulating service from 2,001 plots inventoried 1999-2002 (hereafter '2000'), and 2009-2012 (hereafter '2010').

CATEGORIES OF ES LEVELS, HOT- AND COLDSPOTS

For each of the three ES we defined three levels: high, medium, and low. ‘High’ level was defined as plots with values higher than the 65th percentile of the maximum value observed when combining the data from both snapshot inventories (2000 and 2010), ‘low’ level was defined as plots with values lower than the 35th percentile of the maximum observed when combining both datasets, while ‘medium’ level was defined as plots in between, i.e. higher or equal than the 35th and lower or equal than the 65th percentiles of the maximum observed.

There is a wide range of methods to define hotspots and coldspots, and the most appropriate one depends on the purpose of the study [58]. We used thresholds to define them [59]. Specifically, hot- and coldspots are plots with high and low potential of ES supply. Hotspots were defined as at least two of the ES having high level and the third having high or medium level. Coldspots were defined as at least two of the ES having low level and the third having low or medium level (see Supplementary Table 14). We also conducted a sensitivity analysis of the use of different sample sizes for different ES, which did not change our conclusions, see Supplementary Fig. 4 and Supplementary Table 16 in Result 3. We further combined the levels ‘high’, ‘medium’ and ‘low’ for the three ES in 27 ways (Supplementary Table 14). To summarize the findings for this large number of combinations, we also aggregated them into seven coarser combinations according to Supplementary Table 14. These ranged from the category Cold-Cold-Cold becoming increasingly warmer via No spot into the category Hot-Hot-Hot.

To support our investigation of short-term dynamics of ES, we modelled and predicted the single ES and hot- and coldspots as a function of forest age using data from 2000 (Fig. 3 and Supplementary Tables 5-9). We also tested the importance of tree species richness, their biomass and other environmental conditions in explaining the probability of hot- and coldspot occurrence (Supplementary Tables 10-11). For corresponding tests for the individual ES using these data, see the study by Gamfeldt et al. [26]. For modelling single ES (Fig. 3a), we used data from 2,001-4,444 plots (see above). Wood production was measured on all plots. Bilberry production was not measured on all plots where topsoil carbon storage was measured, but there was a proportion of plots where both were measured. In total, we had a sample of 996 plots where all three ES were measured. This constitutes the sample for modelling hot- and coldspots in 2000 (Fig 3b).

DYNAMICS OF ES AS TRANSITIONAL CHANGES

We generally quantified the rates of short-term dynamics as the percent of plots that changed into another category over a ten-year period, here 2000 to 2010. Ten years is the typical frequency of updating forest management plans. Indeed, estimates of rates of dynamics are improved with increasing number of surveys. However, our data from two nationwide surveys represent approximately 21 million hectares of forest land and include a wide range of environmental gradients. We expressed this rate as the probability (expressed as percentage) of a transition into another category. In statistical terms, these probabilities (p) are the expected values of the Bernoulli distribution, with variance p(1-p), which we also presented. For bilberry, for example, the top left bubble in Fig. 1 reflects the value 0.06 presented in Supplementary Table 2a. This value was obtained by first determining the number of plots classified as having high cover in 2000 and being resurveyed in 2010 (680) (No. plots in Supplementary Table 2a). Next, we determined which of those plots were classified as having low cover in 2010 (41). Finally, we divided these values, 41/680 = 0.06. The variance was calculated as 0.06(1-0.06) = 0.056 (Supplementary Table 2b). We calculated these rates and probabilities both for single ES, and between seven aggregations of the 27 possible combinations (Supplementary Table 14) of coldspots, No spots, hotspots, etc. (results in Fig. 4 and Supplementary Table 12). For a sensitivity analysis of these estimates of probabilities of transitions, see Supplementary Figs. 3-4 and Supplementary Tables 16-17 in Result 3. We presented these probabilities for the whole country and for three forest age classes: (i) young forests: less than 40 years, (ii) middle-aged forests: 40-70 years, and (iii) mature forests: older than 70 years, which are ready to be harvested or are old-growth (more than approximately 130 years). To test whether there was a difference in probabilities for hotspots remaining hotspots compared to coldspots remaining coldspots, we fitted a generalized linear model. As these are binary response variables, we assumed Bernoulli distributions.

To complement the estimates of short-term dynamics based on rates of transitions described above, we also investigated both mean rates of ES dynamics and changes in mean levels. Specifically, we tested whether there were differences in the mean rates of short-term dynamics of change between the ES using pairwise *t*-tests (Supplementary Table 3). We also tested whether the mean levels of each ES changed between 2000 and 2010 for sites categorized as either high, medium, or low, using paired *t*-tests assuming equal variances in ES levels in the two years (Supplementary Figure 1). Finally, we modelled the rate of short-term dynamics of each ES and forest age for sites categorized as either high, medium, or low (Supplementary Figure 2). We selected these models, specifically including (or excluding) age and age squared, based on Akaike's Information Criterion (AIC) [60].

ES THROUGH SUCCESSION AND GIVEN THE ENVIRONMENT

We investigated whether levels of single ES (proportion of maximum observed) and probabilities of occurrence of hot- and coldspots changed through forest succession. Thus, we used space for time substitution in which the contemporary spatial pattern is used to approximate the unobserved 150 years process (Fig. 3). We also tested the effect of other environmental variables on probabilities of hotspot and of coldspot occurrence (Supplementary Tables 10 and 11). Specifically, we applied generalized linear modelling with forest age and other explanatory variables (see Supplementary Table 15 for variables). We assumed gamma distributions for the single ES and Bernoulli distributions for the hot- and coldspots (see Supplementary Tables 5-11 for modelling results). We selected among models based on AIC, on parameter estimates associated with the variables and on knowledge of the biological system studied. This included testing different transformations and squared terms of the variables. We first assessed the predictive power of each explanatory variable based on AIC and on the parameter estimates. Next, we fitted a multiple model containing the retained explanatory variables. Finally, we simplified this complex model by excluding and again including earlier excluded variables in a stepwise procedure. All analyses were carried out using the R software environment [61]. We used the R packages ggpubr (v.0.3.0) and ggplot2 (v. 3.3.0) to produce figures.

Data availability

The data used for this study are archived and openly available from the University of Jyväskylä Dataverse Network (http:// dvn.jyu.fi/dvn/dv/Boreal_forest).

Code availability

The code used to analyse the data and produce the figures is available from the corresponding author upon request.

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Author contributions

T.S. conceived and obtained financial support for the study, and discussed the design with J.B., J.M. and L.M.; M.T., L.M. and T.S. analysed the data; M.T. designed and produced the figures with the input of all authors; T.S. and M.T. wrote the first draft of the manuscript. All authors interpreted the results and provided input on the manuscript.

Competing interests

The authors declare no competing interests.

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