

Chapter 11

Biodiversity



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Abstract

- This chapter summarises biodiversity responses to continuous cover forestry (CCF). The comparator throughout this chapter is rotation forestry (RF) and its main harvesting method—clearcutting—unless otherwise stated.
- Research on the biodiversity effects of logging methods applied in CCF (mostly selection or gap cutting) mainly concerns the short-term effects of measures taken in mature, originally fairly even-aged forests, at best 10–15 years after cutting. Thus far, no surveys or chronosequences cover the whole rotation period (60–100 years).
- Continuous cover forestry is likely to benefit species that suffer when the tree cover is removed, such as bilberry and its associated species. Species requiring spatial continuity in host trees or canopy cover may also benefit.

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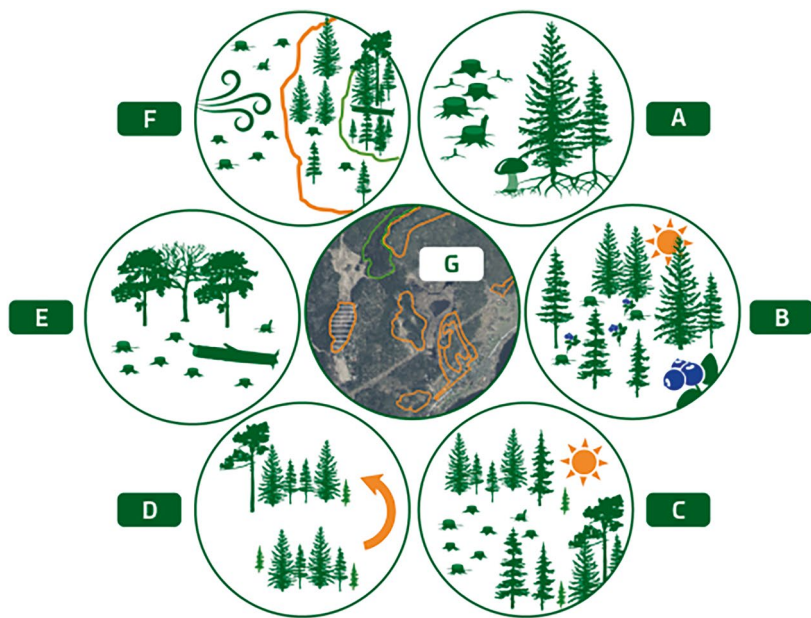
- Selection cutting may preserve the majority of species in the mature forest, but the most sensitive species may decline or even disappear. Gap cutting (diameter 20–50 m) affects forest-interior species relatively little, but species' abundances in gaps change with increasing gap size. Shelterwood cutting seems to closely resemble selection cutting in terms of species responses. In the long term, however, shelterwood cutting results in an even-aged and sparse overstorey, which does not produce the biodiversity benefits of CCF.
- Species that have declined due to forestry mostly require large living and dead trees. The preservation of these species is not ensured by CCF alone, but requires deliberately maintaining these structural features.
- A mosaic of different forest-management practices within landscapes may provide complementary ways to maintain rich biodiversity.

Keywords Forest-interior species · Red list of species · Resource continuity · Retention trees · Structural features

11.1 Recent Changes in Forest Structure and Biodiversity in Fennoscandia

In Fennoscandia, a rapid transition from continuous cover forestry (CCF), mainly in the form of diameter-limit cutting, to even-aged rotation forestry (RF) began in the 1950s (Lundmark et al. 2013). The currently dominant forest-management regime is based on clearcutting, soil preparation, and regeneration favouring conifers by planting or sowing, followed by thinning from below (Fig. 11.1). As a result, most productive forest land in Finland and Sweden is structurally simplified, even-aged and even-structured (Gustafsson et al. 2010; Kuuluvainen et al. 2012). Areas of forest with natural dynamics are greatly reduced and fragmented (Timonen et al. 2011). The conifers Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) dominate planted forests, although Fennoscandian temperate and hemi-boreal climatic zones (southern Sweden) host more tree species than boreal Fennoscandia, including European beech (*Fagus sylvatica*), pedunculate oak (*Quercus robur*), and sessile oak (*Quercus petraea*). Palaeoecological studies indicate that both beech and the two oak species have declined greatly over recent centuries in the southern region (Lindbladh and Foster 2010). Along with the increasingly conifer-dominated timber stocks, these declines emphasise the decreasing share of broadleaf trees in the southern region (Lindbladh et al. 2014).

Following all these changes, species diversity has been severely affected, and about 10% of Fennoscandian forest species are nationally red listed and often largely confined to remnant structures and habitats where forestry has been less intense (Gustafsson 2002; Puimalainen et al. 2003; Mikusiński et al. 2007; Timonen et al. 2011). The main threats to forest-dwelling species are the scarcity of old forests, large old trees, and large decaying wood, and the reduction of wildfire areas



- A** + Soil mycorrhizal fungi.
- Unknown interactions with damage agents and biodiversity.
- B** + Selection cutting supports semi-shade plants and their associates.
- Long-term effects unknown.
- C** + Gap cutting supports both shade- and sun-favoring species.
- Long-term effects unknown.
- D** + Connectivity for species dependent on large trees.
- Responses of many species groups unknown.
- E** ± Red-listed species do not benefit without separately considering deciduous and old trees, and deadwood.
- F** + Buffer to maintain conditions in key habitats or reserves.
- Responses of many species groups unknown.
- G** + Landscape mosaics of different management practices support biodiversity.
- Landscape applications unknown.

Fig. 11.1 Infographic summarizing biodiversity benefits of CCF. Plus (+) symbols indicate a positive response to CCF when contrasting with RF, whereas minus (-) symbols indicate a negative response or a knowledge gap

and young forests originated from natural disturbances (Hyvärinen et al. 2019). The dominance of clearcutting practices has also disadvantaged species that thrive in closed-canopy or semi-open old forests with small-scale disturbance dynamics (Kuuluvainen 2009; Kuuluvainen and Aakala 2011; Kuuluvainen et al. 2012; Brunet 2023). In present-day Nordic forests, the preservation of species requiring the aforementioned resources requires conservation actions and modifications to forest management, whereas species occupying many types of habitat, or species associated with open areas such as recent clearcuts, thrive in current landscapes of managed forest.

11.2 Opportunities for Safeguarding Forest Biodiversity

Nature-conservation efforts primarily follow two different approaches: “land sparing” and “land sharing” (also referred to as wildlife-friendly farming; Green et al. 2005). Land sparing is a segregation approach that aims for spatial separation of areas for production and conservation, where conservation efforts are restricted to protected areas. Land sharing is an integrative approach to nature conservation, relevant to multifunctional productive forests where integration of productive and conservation goals is achievable and sought within the same area.

The most effective single means of protecting species and habitats is probably land sparing, i.e., the establishment of protected areas. Nordic countries have increasingly adopted voluntary measures to conserve forest biodiversity, but these actions can be considered slow. Finland serves as a representative example here. In northern Finland, there is about 1.9 million ha of strictly-protected forest and shrublands (17% of the forest area), while in southern Finland the corresponding figure is 0.4 million ha (4%; Niinistö et al. 2021). Of this area, 0.9 million ha (8%) is forest land in the north and 0.3 million ha (3%) in the south. It has been estimated that 10–30% of the forest area needs to be protected to preserve threatened forest species (Hanski 2011). In southern Finland, where the greatest abundance of threatened species and habitats is found, a 10% protection rate could be achieved, for example, by protecting 404,000 ha of forest over 120 years old and 471,000 ha of other mature forest (Kotiaho et al. 2021). This would take more than 100 years to achieve using only the resources of the state-driven programme for voluntary protection of southern-Finnish forests (METSU; Anttila et al. 2021).

Due to the slow designation of protected areas, integrative conservation actions in managed forests—land sharing—have become important for the fate of forest species in Fennoscandia. In addition to conservation measures, expectations have been placed on CCF harvesting methods—notably selection cutting and gap cutting. Developing the management practices of production forests affects a much larger area than protection and restoration measures allow.

11.3 Theoretical Justifications for Continuous Cover Forestry

Within Fennoscandia, CCF is often advocated based on the expectation that its increased use would mitigate the negative effects of rotation forestry (RF) on forest biodiversity. Three primary justifications underlie the expected biodiversity benefits. First, over the last 30 years there has been a paradigm shift in the scientific understanding of natural disturbance dynamics in European boreal forests. It was previously thought that stand-replacing disturbances were the norm (Angelstam and Kuuluvainen 2004). This understanding, prevalent since the 1950s, favoured clearcutting and even-aged forests, as this form of silviculture was thought to most closely approximate large-scale stand-replacing disturbance events and subsequent forest regrowth (Kuuluvainen 2009; Kuuluvainen and Aakala 2011). In contrast, the most recent assessments have found that non-stand-replacing disturbances resulting in gap and cohort dynamics are more typical of natural disturbance regimes in northern-European forests (Berglund and Kuuluvainen 2021). As CCF would better approximate the finer spatio-temporal scales of natural disturbance regimes, namely via selection or gap cutting, forest species adapted to such dynamics may be expected to benefit (Felton et al. 2016).

Second, conservation of Fennoscandian forest lands is largely done by leaving uncut patches at stand felling, which are relatively small and often isolated from formally or voluntarily protected and set-aside areas (Gustafsson and Perhans 2010). Whereas such small-scale conservation actions are crucial to meet biodiversity goals, their net contributions can be dampened by the intensity of the production forest matrix surrounding them (Felton et al. 2020; Kärvelo et al. 2021). For example, if production stands are clearcut, this can reduce the diversity of signal species (i.e., species that reflect conditions favourable for red-listed species at a given site; Skogsstyrelsen 2020), such as bryophytes and lichens, in adjacent buffer zones (Hylander and Weibull 2012; Johansson et al. 2018), as well as fungi in adjacent reserve edges (Ruete et al. 2016). For this reason, applying CCF instead of clearcutting in production forests neighbouring set-aside forest patches may support the biological communities of protected forests by reducing the severity of edge effects (cf. Koelemeijer et al. 2022, 2023).

Third, CCF should enhance stand- and landscape-scale habitat availability by providing distinct resources and environments from those provided by RF. These include increased within-stand horizontal and vertical structural heterogeneity (Joelsson et al. 2017), improved landscape-scale forest connectivity (Lindenmayer and Franklin 2002), and reduced distances among mature trees and large deadwood (Atlegrim and Sjöberg 2004). Furthermore, by providing understorey microclimates more commonly associated with mature tree cover, CCF may favour species associated with mature forests that are otherwise lost and require re-establishment after clearcutting (Kuuluvainen et al. 2012; Joelsson et al. 2017). CCF can potentially buffer forest understories from the ambient climate, with future regional temperature increases likely making the environment for many species after clearcutting

even more hostile (De Frenne et al. 2021; Hylander et al. 2021). Thus, CCF may support biodiversity in production forests because of its (1) consistency with natural disturbance regimes, (2) potential capacity to buffer small-scale conservation actions surrounded by production forest, and (3) provision of specific forest habitats and resources rare in even-aged forestry.

The conclusions of studies comparing the effects of silvicultural practices on species diversity, and the generalisability of the results depend on several factors. These include the structure and species composition of the study stands before treatment, cutting methods and how they are implemented, the species group studied, the length of the study period, and presumably also the wider landscape context. What matters is how well the forest-management methods are able to maintain species over the entire rotation period, both at the stand and landscape level. Unfortunately, stands or entire forest areas that have been treated with CCF for a long time are rarely available to study. Old (i.e., more than 100 years) RF stands are similarly rare. However, the long-term effects of treatments aiming at continuous tree-canopy cover can be evaluated based on how the recurrent cuttings will affect the structures of direct relevance to habitat availability and environmental conditions within the stand (Fig. 11.2).

When evaluating the effects of CCF on species diversity, the common question “Would CCF be better for biodiversity than RF?” may result in misleading answers. Instead, one should ask under which conditions, for which species, using which method, and over what timeframe, could CCF better conserve biodiversity than RF based on clearcutting—or vice versa. Here, we examine the effects of selection, gap and shelterwood cutting on stand-level forest biodiversity. We evaluate them separately because the methods differ in their spatial distribution and size of the openings and intermediate areas created during harvesting. In addition, soil preparation can be used in gap cutting, and its biodiversity effects are also discussed below. The widespread use of RF is a baseline for the potential benefits of CCF in Fennoscandia.

11.4 Impacts of CCF Logging Methods on Species Communities

11.4.1 CCF Research, and the Impact of Logging Intensity

A recent literature review found several experiments comparing the short-term (single cutting) biodiversity effects of continuous cover and even-aged cutting methods in the Nordic boreal region (Koivula and Vanha-Majamaa 2020). In most experimental designs, the treatments compared have been selection cutting and clearcutting compared with untreated reference forest. Three experiments also assessed gap cutting, whereas shelterwood cutting has rarely been examined. Monitoring periods have so far been short, usually only the first 1–5 years after harvesting and at most 10 years (Koivula and Vanha-Majamaa 2020; Savilaakso et al. 2021).



Fig. 11.2 Bilberry (*Vaccinium myrtillus*) and associated species may benefit from continuous cover forestry. (a) Hazel grouse (*Bonasa bonasia*) chicks feed on insect larvae that feed on bilberry. Finland, July 2021 © Mika Nieminen. (b) Moose (*Alces alces*) forage on tree leaves and forest-floor grasses and shrubs. Ungulate browsing affects tree regeneration (see Chap. 12 on forest damage) and, in turn, tree-species composition and associated biodiversity. © Erkki Oksanen / Luke

The studied taxa have included herbivorous insect larvae living on bilberry (Atlegrim and Sjöberg 1995, 1996a; Kvasnes and Storaas 2007), lichens and mosses (Jalonen and Vanha-Majamaa 2001; Vanha-Majamaa et al. 2017), soil organisms (Siira-Pietikäinen et al. 2001, 2003; Siira-Pietikäinen and Haimi 2009; Kim et al. 2021), spiders (Matveinen-Huju and Koivula 2008), beetles (Atlegrim et al. 1997, Koivula 2002a, 2002b, Joellsson et al. 2017, 2018; Jokela et al. 2019; Koivula et al.

2019), birds (Versluijs et al. 2020) and vascular plants (Atlegrim and Sjöberg 1996b, Jalonen and Vanha-Majamaa 2001; Vanha-Majamaa et al. 2017). Based on these studies, the species composition of mature spruce-dominated boreal forests remains almost unchanged in the short term in treatments where the proportion of removed trees is 33–50% by volume (Ekholm et al. 2023). However, the most sensitive moss and liverwort species disappear even under the most conservative logging treatments (Vanha-Majamaa et al. 2017). We discuss nuances of logging methods below.

11.4.2 Selection Cutting

Studies in boreal Sweden compared beetle faunas in spruce-dominated (1) 120–130-year-old stands that had been selectively cut 2–15 years earlier, (2) forests of similar age that had not been treated during the last 50 years, and 50–60 year-old stands that were either (3) clearcut or (4) thinned 6–7 years earlier (Joelsson et al. 2017, 2018). Thinned previously-clearcut forests in these study forests were at most 50–60 years old, so the species present in these forests reflected the longest post-clearcutting period. The results showed that fresh clearcuts clearly differed from the other forest classes in terms of species composition. However, species composition did not differ significantly between thinned stands and selectively-cut stands. The recovery of the beetle fauna therefore appears to be rapid in thinned and selectively-cut stands, whereas in clearcuts, species composition had not recovered fully 50 years after logging.

Vegetation and fungi are inconsistently affected by selection cutting. A before-after control-impact study contrasting unharvested mature forest and selection cutting 3–4 years after harvesting detected no significant differences in the community compositions of vascular plants, bryophytes or wood-inhabiting fungi (Ekholm et al. 2022). In contrast to clearcutting, recent partial harvest of 30% in uneven-aged Norway-spruce forests in mid-boreal Sweden maintained soil chemical properties and fungal communities similar to unmanaged forests (Kim et al. 2021). The composition of both fruiting-body fungal and soil-fungal communities were similar in continuous cover and unmanaged forest, but substantially different in clearcut areas (Kim et al. 2021). Similarly, Sterkenburg et al. (2019) showed that tree retention enabled the maintenance of the most frequent ectomycorrhizal fungi, whereas less abundant species were progressively lost at random with increasing harvest intensity (100%, 60%, 30% and 0% retained trees) in Scots pine forests in northern Sweden.

The long-term effects of old selection cutting (diameter limit cutting) on species composition have also been investigated in the Nordic countries. These studies have compared the stand structure and species composition of spruce-dominated forests selectively cut 50–100 years ago with natural old-growth forests. The results show that selection cutting, in which about 50% of the stand volume had been removed, still has negative effects on dead wood and polypore fungi many decades later (Bader et al. 1995; Lindblad 1998; Sippola et al. 2001; Josefsson et al. 2010). In old

selectively-cut forests, there were fewer large-diameter, medium-decayed trees, and both the total number of polypore species and the number of threatened species were significantly lower than in old natural forests. Similarly, selection cutting had reduced the biomass of epiphytic lichens growing on old trees with thick branches (Esseen et al. 1996), and consequently the number of invertebrates living in the lichen microhabitat (Petterson et al. 1995; Petterson 1996). It should be noted, however, that these studies did not include a comparison with 50–100-year-old even-aged forests after clearcutting. What these results mainly show is that even selection cutting of mature trees has negative long-term impacts on structural features that are important for species, and hence on species composition.

11.4.3 Gap Cutting

The main responses of species assemblages to gap cutting are increased abundance of open-habitat and generalist species, and decreased numbers of closed-forest species, especially in the cleared gaps. The species composition in retained parts of a gap-cut stand remains almost unchanged. Larger gaps show a greater change in species composition (e.g., Jokela et al. 2019). Light-demanding tree, pioneer or early-successional plant species would benefit from such gaps (Brunet 2023). Due to the relative novelty of the method, it is not yet possible to assess its long-term effects, not even by comparing the diversity of species present in different-aged gaps.

Most Nordic publications on the species effects of gap cutting are from the Finnish project “Monimuotoisuus talousmetsien uudistamisessa” (MONTA; Diversity in the regeneration of managed forests). In this project, three small gaps of about 0.16 ha (32×50 m or 40×40 m) were made in a 1-ha core of mature Norway-spruce stands, leaving the rest of the stand untreated. About 50% of the stand volume was removed, which is more than in the selection-cutting treatment in the same project (about 33%). During the first three summers following harvesting, the composition of common closed-forest species remained largely unchanged (Jalonen and Vanha-Majamaa 2001; Koivula 2002a; Koivula and Niemelä 2003; Matveinen-Huju and Koivula 2008). However, individuals of open-habitat species quickly appeared in the gaps. The soil decomposer communities in gaps and untreated parts of the stands also differed slightly (Siira-Pietikäinen et al. 2001). After 10 years, species-community structure in gaps and retained areas showed clearer differences in soil-decomposing organisms (Siira-Pietikäinen and Haimi 2009), vascular plants, mosses and lichens (Vanha-Majamaa et al. 2017) and ground beetles (Koivula et al. 2019). In gaps, common species of open, sun-exposed environments became more abundant, while species of shaded environments often decreased compared to untreated forest (ibid.).

Muurinen et al. (2019) studied understorey vegetation in a northern Finnish spruce-dominated forest area that had burned in 1919 and subsequently regenerated naturally. In 1953 (about 34 years post-fire) an experiment was set up in this area, with four 0.1-ha unlogged reference plots and four 0.1-ha gap-cut plots (about 30%

of tree volume was removed; the gaps were long, narrow strips). Vegetation was inventoried 8 years later. Compared to the reference plots, the plant and lichen community of gap-cut plots remained mostly unchanged. The contrast with the 10-year effects in the MONTA project may be due to different gap shapes, different gap origins (fire or harvesting) and/or different dominant tree ages (and associated plant communities) at the time of harvesting. Regrettably, the gap cuts reported in Muurinen et al. (2019) were thinned in 1987, so their long-term resampling is not possible.

At the beginning of the “Management models based on natural forest disturbance dynamics” (DISTDYN) experiment, established on Finnish state lands in 2009–2010, openings about 25–35 m and 40–60 m in diameter were cut in Norway spruce and Scots pine stands, with logging intensity varying between 20% and 35% of volume. During the first 3 years following logging, the amount of coarse (diameter ≥ 15 cm) deadwood in spruce stands had a greater effect on the number of saproxylic beetle species than the felling method (Jokela et al. 2019). Polypore species showed similar patterns 7 years after logging (Pasanen et al. 2019). Similar observations have also been made in a Swedish gap-cutting experiment in Norway-spruce forests (gap diameter about 20 m, logging intensity about 20%). During the first three summers after felling, gaps differed little in beetle-community composition, though some groups, including phloem-feeding beetles (e.g., bark beetles), became more abundant in the stands managed using gap cutting (Hjältén et al. 2017; Kärvelo et al. 2017). Their increase in abundance is linked to the fresh dead wood produced by logging and is therefore temporary (Jokela et al. 2019). In the Swedish study mentioned above, the stand-level bird community composition did not differ significantly between mature reference forests and gap cuts 5 years after felling (Versluijs et al. 2017). Similarly, vascular plants and mosses showed no detectable difference 8 years after felling (del Alba et al. 2021) (Fig. 11.3).

11.4.4 Shelterwood Cutting

Ecological research on CCF logging methods in the Nordic countries has so far largely focused on selection and gap cutting, but shelterwood cutting has also occasionally been studied. Based on these, the short-term effects of shelterwood cutting resemble selection cutting. Forest species communities will be additionally impacted when the shelter trees are removed, whereas selection cutting likely better maintains shade and micro-climatic conditions.

Ectomycorrhizal fungi of old (157–174 years), and shelterwood and clearcut (both logged 50 years earlier) Scots pine forests were studied in central Sweden (Varenius et al. 2016). This study showed that the fungal communities differed between old and harvested forests, but sites harvested using the two methods hosted similar communities, with only occasional species-level differences. In hemiboreal forests of mainland Estonia, shelterwood logging was examined in dry pine- and mesic spruce-dominated forests (Tullus et al. 2018). These authors inventoried



Fig. 11.3 Some specialised species may benefit from continuous cover forestry. (a) Pale-footed horsehair (*Bryoria fuscescens*), an epiphytic lichen. Finland, September 2020 © Taru Rikkonen. (b) Chanterelle (*Cantharellus cibarius*), a mycorrhizal fungus. Norway, September 2023 © Frida Høistad Schei

liverworts, mosses and vascular plants in 2-ha plots in each of 30 stands: ten each of mature managed stands, stands where shelterwood logging had been done 5–9 years earlier (about 42% of tree volume was harvested), and stands where shelterwood logging had been done and the shelter trees removed 4–14 years later (in total about 95% was harvested). Generally, the richness of mosses and liverworts dropped following logging. Spruce and pine forests showed similar drops, although richness was consistently higher in spruce forests (Tullus et al. 2018). Harvesting reduced the richness of species of conservation concern by half in spruce-dominated forests,

but less so in pine-dominated forests. Differences between the two shelterwood treatments were small, but liverworts showed a significant additional decline after shelter tree removal (Tullus et al. 2018). These shelterwood studies suggest that (1) before shelter trees are removed, shelterwood cutting better maintains the forest-species community than clearcutting, whereas (2) species of conservation concern may decline, and (3) the removal of shelter trees causes an additional negative impact on sensitive forest species.

Shelterwood management has been employed in southern-Swedish beech forests since the 1840s (Brunet and Berlin 2005), largely replacing semi-open pasture beechwoods with dense even-aged beech stands ready for harvest after approximately 100–140 years (Brunet et al. 2012). This involves canopy thinning after a mast year to favour dense natural regeneration, after which the remaining seed trees are cut (Brunet et al. 2010). In their comparative review of management of European beech forests, Brunet et al. (2010) contrasted shelterwood with selection or gap cutting and concluded that selection cutting resulting in an uneven-aged stand structure is likely to benefit forest biodiversity. This is due to its resultant higher contribution of (1) multiple canopy layers, (2) variable tree sizes, (3) spatial heterogeneity, and (4) advance regeneration (Brunet et al. 2010). The general sensitivity of different species groups to shelterwood forestry in broadleaf forests roughly increases in the following order: herbaceous plants < soil macrofungi < ground-dwelling arthropods < land snails < saproxylic fungi < cavity-nesting birds and saproxylic insects < epiphytic lichens and bryophytes < epixylic bryophytes (Brunet et al. 2010).

11.4.5 Comparison of CCF Logging Methods

One important question concerning biodiversity is whether closed-forest species are equally well preserved in forests harvested with selection, gap or shelterwood cutting. We are not aware of any experiments where these treatments differ only in the spatial distribution of unharvested crop trees but not in the number of trees removed, but a cautious comparison can be made using data from the Finnish DISTDYN and MONTA projects. In the DISTDYN project, gap size appeared to have a larger (positive) effect on beetle-species abundance than the proportion of removed trees (Jokela et al. 2019). Beetle-species composition was affected in the same direction by both variables. Koivula (2012) compared logging methods using published MONTA-project data (Koivula 2002a, 2002b) and a model with stand volume (m^3/ha) as a covariate and logging method and year (1995–1998) as factors. In the analysis, the logging method did not affect the ground-beetle species, but the variation in stand volume—which changes in concert with logging method—had a strong effect, mainly by increasing the abundance of open-habitat species with decreasing stand volume. If the spatial distribution of the stand has a large effect, this should have been reflected in the significance of the logging method. It is important to note that this was a short-term result, covering only the first three post-harvest summers; in gap-cut stands seven summers later (2006), the gaps hosted beetle assemblages

distinctive from unharvested areas (Koivula et al. 2019). On the other hand, in the same stands, moss assemblages 10 years after harvesting had lost more species in selection than in gap cutting, even though more trees had been left in the selection-cut stands (Vanha-Majamaa et al. 2017). This result suggests that, when applied once in a mature forest, gap cutting is better at conserving moss species than selection cutting, but it is not yet possible to assess the effect of gap cutting on the whole logging cycle.

Unlike selection cutting, gap cutting allows the soil to be mechanically prepared to aid seedling establishment. Therefore, we briefly discuss experimental results on the biodiversity effects of soil preparation. The impact of soil preparation on common plant and ground-beetle species in a forest is primarily reflected in the variation in abundance within the stand, with pioneer species found mostly in prepared microsites and shade-demanding species in unprepared areas (Koivula 2002a, Pihlaja et al. 2006; Vanha-Majamaa et al. 2017). On the other hand, soil preparation negatively affects several plant and insect groups associated with closed forests (Hautala et al. 2011; Vanha-Majamaa et al. 2017; Tullus et al. 2018). All soil-preparation methods are particularly destructive to downed dead wood (Hautala et al. 2004; Rabinowitsch-Jokinen and Vanha-Majamaa 2010). Even patch scalping, which is lighter than ploughing, may reduce the species richness of epiphytic lichens and epixylic mosses by more than 50% (Rabinowitsch-Jokinen et al. 2012). It can also reduce the amount of advanced-decay-state deadwood—a necessary substrate for these species—by more than 50% (Rabinowitsch-Jokinen and Vanha-Majamaa 2010; Hautala et al. 2011).

11.5 The Importance of Stand Structural Components in Continuous Cover Forestry

CCF poses some of the same problems for biodiversity as clearcutting-driven RF. In both cases, the trees are harvested before they have had time to develop characteristics associated with senescence. This in turn means that the amount of deadwood and old trees will be considerably smaller than in an old-growth forest, yet such features are particularly important for many threatened forest species (e.g., Hyvärinen et al. 2019). In Finland, for example, the average deadwood volume in all forests is about 6 m³/ha, whereas in natural conditions the average volume would be about 95 m³/ha (Mönkkönen et al. 2022), and the respective average densities for large (> 40 cm) trees are about 7 and 42 trees/ha (Henttonen et al. 2019). However, the average density of trees that are both large and old (> 150 years) is currently about 1 tree/ha in Finland, of which about half are in production forests (Henttonen et al. 2019). Based on the natural density of large trees (Mönkkönen et al. 2022), and assuming that the share of old trees among all large trees in the 1910s (Henttonen et al. 2019) was similar to pristine forests, the density of large and old trees in

natural conditions would be about 5–55 trees/ha, depending on geographical region and site type.

According to Nordic national legislation and certification standards (Forest Stewardship Council [FSC] and Programme for the Endorsement of Forest Certification [PEFC]), general considerations in CCF should be similar to those of clearcutting-based RF. They should thus consider rare and declining biotopes, retention of large-sized deadwood and living trees of certain minimum size and number, retaining trees of particular biodiversity value (nature value trees, very old or large trees), and creating artificial snags (“high stumps”) and buffer zones along watercourses. The effect of such conservation actions can be expected to differ between CCF stands (logged using selection, gap or shelterwood cutting) and clearcuts, for example because the retained and created substrates will be largely shaded in the former. However, while practices such as deadwood enrichment have been studied in stands harvested using CCF methods, no studies have so far compared stand structure more broadly in CCF and RF.

11.5.1 Deadwood Enrichment

The Finnish DISTDYN experiment has assessed the effects of deadwood abundance (including both deadwood of natural origin and artificial snags) in spruce-dominated, selectively- and gap-cut stands and clearcut stands, up to seven summers after harvest. Two years after logging, 10-ha clearcuts had 1.5 times higher species richness of saproxylic beetles and polypore fungi than gaps of 0.01 ha (selection cutting); selection and gap cutting did not differ significantly from each other in this respect (Jokela et al. 2019; Pasanen et al. 2019). Simultaneously, an increase in deadwood from 3.0 m³/ha to 15.0 m³/ha resulted in about a 1.3-fold increase in beetle richness (Jokela et al. 2019). Seven years after logging, a regression model for polypore richness found only the number of deadwood pieces to be a significant predictor, while cutting intensity, and pre-harvest species richness had no impact as explanatory variables (Pasanen et al. 2019). The increase in species richness in bigger gaps probably resulted from the logging-caused increased sunlight reaching the ground and the input of nutrients and organic matter from logging residue and cut stumps. The gap-size effect on richness appears ephemeral, as a Swedish study, also in Norway spruce forests, showed that 7 years after logging, the beetle richness appeared similar in selectively-cut and clearcut stands (Joelsson et al. 2017).

A Swedish deadwood-enrichment experiment assessed biodiversity responses to the addition of artificial snags and logs in clearcuts, mature managed forests and old-growth reserves (Gibb et al. 2006). The mature managed stands in this experiment had presumably not previously been clearcut, but selection cutting had occurred several decades earlier. For this reason, the results from this experiment can be considered to indicate the long-term effects of selection cutting. Results from this experiment showed that artificial snags and logs on clearcuts hosted different beetle assemblages and species of conservation concern than artificial snags and

logs in mature managed stands and reserves (Gibb et al. 2006; Johansson et al. 2006; Hjältén et al. 2010; see Pasanen et al. [2019] for a similar DISTDYN result). Moreover, deadwood in reserves and selectively-cut mature managed stands hosted similar parasitoid wasp, beetle and fungus assemblages but the reserves tended to host larger populations (Hilszczański et al. 2005; Hjältén et al. 2010; Olsson et al. 2012), apparently due to higher volumes of deadwood (Gibb et al. 2006; Stenbacka et al. 2010).

Gap cutting combined with deadwood enrichment was evaluated in a Swedish spruce-forest experiment (Hägglund et al. 2015). The results showed that the combination supports a beetle fauna similar to unharvested mature closed forest (Hjältén et al. 2017; Hägglund and Hjältén 2018). Additionally, in this experiment, artificial snags and girdled trees hosted relatively similar beetle assemblages. The two most important determinants of the beetle assemblage composition were the tree species the wood came from and whether it was standing or lying (Hägglund and Hjältén 2018). Artificial snags are also an important source of deadwood in the managed forest landscape, as they provide habitats for early-successional generalists and several red-listed beetles (Gibb et al. 2006; Johansson et al. 2006; Lindbladh et al. 2007; Lindbladh and Abrahamsson 2008). However, they rapidly become too dry for many polypore fungus species (Pasanen et al. 2019).

Deadwood enrichment efficiently promotes common polypore species, but generally fails to provide the deadwood diversity and substrates for more specialised species associated with late decay stages, at least in the short term (Olsson et al. 2012; Pasanen et al. 2014, 2018; Baber et al. 2016). Logs generally host more species than artificial snags, but the species richness increases with wood diameter (Lindhe et al. 2004; Juutilainen et al. 2014). The red-listed polypore *Fomitopsis rosea* is an example of a wood-decaying fungus that prefers larger logs (Edman et al. 2006). Some—mostly common—species also occupy fine woody debris (Kruys and Jonsson 1999; Berglund et al. 2011; Juutilainen et al. 2014). These results imply that, for wood-decaying fungi, CCF mostly only supports common generalist species because there will be a limited supply of large-diameter logs, despite the likely more continuous availability of medium-diameter logs compared to RF.

Regarding coarse woody debris, selection cutting and even-aged shelterwood management of beech forests result in similar levels of stem, branch and crown structures in living trees, similar amounts of fallen coarse woody debris and similar densities of snags (Brunet et al. 2010). A key determinant of achieved deadwood volumes is the extent of debris-creating conservation actions, including green-tree retention, and creation of artificial snags, among others (Fig. 11.4).



Fig. 11.4 Continuous cover forestry does not directly support most red-listed forest species, but these species can be supported in forest management through various actions. **(a)** Cut-and-downed logs to increase deadwood in a selectively-cut stand—in this case, to support the green shield-moss *Buxbaumia viridis*. Sweden, June 2023 © Mari Jönsson. **(b)** Manipulation of tree-species composition through selection cutting to increase the proportion of pine and birch in spruce-dominated forest. Finland, June 2012 © Matti Koivula

11.5.2 Other Considerations

Minimising forest-floor damage (Sect. 11.4.5), protecting riparian zones, retaining permanently trees with high habitat value, manipulating the tree-species composition, and using prescribed burning may be more challenging in CCF than in RF, yet are equally important.

Selection cutting has been suggested in forests along watercourses where completely-uncut 25–35 m wide buffer zones are not possible for some reason (e.g., Jyväsjärvi et al. 2020; Kuglerová et al. 2020, 2022). Wise application of selection cutting adjacent to such sites could help expand and improve buffer zones along waterways, for instance by promoting deciduous trees.

In selection, gap and shelterwood cutting in CCF, the largest trees will be the most attractive for harvesting in each round. This requires specific considerations to spare very large (> 40 cm) and very old (> 100 years old deciduous, > 150 years old coniferous) trees through repeated fellings. These very large and old trees have had sufficient time to develop deeply-furrowed bark upon which many rare epiphytic lichens depend (e.g., Kuusinen and Siitonen 2009; Lie et al. 2009; Fritz et al. 2009; Nascimbene et al. 2013). New techniques with individual-tree selection and clear marking of such trees might circumvent this problem. Another method is permanent retention of the most valuable within-stand patches. In beech forests, selection cutting combined with permanent retention may provide the highest habitat quality relative to either selection cutting without retention, or shelterwood cutting with or without retention (Brunet et al. 2010). These projected habitat benefits help a broad range of taxa including herbaceous plants, ground arthropods, land snails, cavity-nesting birds, epixylic bryophytes, epiphytic bryophytes and lichens, saproxylic fungi, beetles, and flies (Brunet et al. 2010).

A recently considered alternative to single-tree selection cutting in temperate deciduous forests aims to create an oak-dominated, mixed-species, uneven-aged production forest. This can involve only 13–35 production oak trees/ha, occupying 20–70% of the overstorey at harvest, around which regular thinning is used to promote the timber trees (Löf et al. 2016). In the remaining areas of the stand, regenerating trees are left for relatively free development, with understorey trees allowed to persist as long as they do not interfere with the crowns of the production stems. The denser areas of the stand could promote competition and self-thinning, resulting in more dead wood, whereas the associated free development would protect canopy gaps from wind and tree disease (Löf et al. 2016). This option would improve tree-species diversity, stand structural heterogeneity, deadwood, and trees having cavities and large dead branches (Löf et al. 2016). These features would in turn benefit a wide range of taxonomic groups, including vascular plants, birds, epiphytic lichens and bryophytes, as well as saproxylic fungi and beetles (Löf et al. 2016). However, such features can be equally easily supported in CCF and even-aged RF.

11.6 Ecological Effects of Systemic Conversion from RF to CCF

Most of the above-described studies do not examine full CCF cycles, but rather assess early phases of conversion from even-aged, mature forests toward uneven-aged and often mixed-species forests. They also usually assess stand-level, not

landscape-scale, conversion. The results generally suggest rather small ecological effects in the early phases of conversion, although some sensitive species decline. Better understanding of ecological effects of conversion would require monitoring over multiple decades, possibly a period similar to a full rotation of RF. Assessments of larger landscapes, dominated by RF or CCF (such as the set-up of DISTDYN), are crucial for understanding the ability of species to survive in forest landscapes treated in various ways.

11.7 Which Species Can Benefit from Continuous Cover Forestry?

11.7.1 *Species Requiring Shade or Spatial Continuity of Trees, and Below-Ground Biota*

Compared to current dominant, clearcut-driven forestry practices, several groups of species can benefit from CCF. Those are species requiring (1) canopy cover and shading or (2) forest stand or single-tree continuity (roots, stems and canopies), and (3) less-disturbed soils. The latter two groups include species with poor dispersal capacity and/or low establishment probability. Logging-caused changes in the abundance of common species can also have significant ecological consequences. In particular, the abundance of bilberry affects many other forest biota. Bilberry regenerates mainly vegetatively through their underground stems, and both above- and below-ground parts suffer from clearcutting and soil preparation, as well as from exposure to direct sunlight (Atlegrim and Sjöberg 1996b, Tonteri et al. 2016). The decline of bilberry after logging is often directly proportional to the intensity of logging (Bergstedt and Milberg 2001).

Bilberry is the most important plant species for herbivores in the field layer of northern coniferous forests. The quantity and quality of bilberry as a food source collapse following clearcutting. The leaves of sun-exposed bilberry shoots have less water and more phenol content than those growing in shade (Atlegrim and Sjöberg 1996b). Due to lower bilberry abundance and possibly also its lower nutritional value, the number of moth and sawfly larvae in clearcut stands is about five times lower than in old-growth stands, whereas after selection cutting the abundance of these larvae remains almost unchanged (Atlegrim and Sjöberg 1995, 1996a; Kvasnes and Storaas 2007). Herbivorous insect larvae, in turn, are an important food source for several insectivorous bird species (Atlegrim and Sjöberg 1995), so bilberry abundance may also indirectly affect the reproductive success of forest birds. During their first weeks of life, chicks of forest grouse species, notably the capercaillie (*Tetrao urogallus*), grow rapidly due to feeding mainly on protein-rich sawfly and moth larvae (Kvasnes and Storaas 2007). In addition, bilberry thickets provide the shelter needed by the chicks. Bilberry and other ericaceous shrubs are important

food resources for large herbivores hunted in boreal forests, directly contributing to cultural and provisioning services.

An ecologically important group of species that would probably benefit from switching from CCF to RF are epiphytic lichens growing on tree branches and trunks. Abundant lichens growing on large trees in turn support a diverse and abundant invertebrate fauna, which is an essential food source for many bird species such as the willow tit (*Poecile montanus*), crested tit (*Lophophanes cristatus*), Eurasian treecreeper (*Certhia familiaris*), and Siberian jay (*Perisoreus infaustus*) that forage in the canopy, especially in winter (Pettersson et al. 1995).

Several species groups can use continuous cover, uneven-aged forests as dispersal routes or habitat. Furthermore, in such forests, source populations might be frequently close by, so that distances between mature stands may not prevent the colonisation of new stands by these species. The presence and abundance of several epiphytic lichen species are limited by the ability to disperse and colonise (e.g., Dettki et al. 2000; Öcklinger et al. 2005; Fritz et al. 2008). Similarly, the movements and dispersal of the Siberian flying squirrel (*Pteromys volans*) are hampered by open clearcuts but not by tree-covered areas of sub-optimal quality for foraging or breeding (Selonen and Hanski 2003, 2004).

CCF also has implications for below-ground root-associated biodiversity and ecosystem function, notably promoting more abundant and diverse mycorrhizal communities compared to clearcutting (Sterkenburg et al. 2019; Kim et al. 2021). Mycorrhizal fungi represent a large fraction of biodiversity in boreal forests. Their mycelia form a foundation for soil food webs and play a critical symbiosis-driven role in forest production and nutrient cycling, as mediators of nutrient and water uptake by trees. The largely hidden life of mycorrhizal fungi in soils has hampered understanding of their diversity, biology and ecosystem function, as well as the consequences of forest-management practices, including CCF.

11.7.2 Threatened Species

Species that are preserved in CCF are mainly common, non-threatened forest species which also survive in even-aged managed forests. Given current conditions, no changes in forestry are required to secure the existence or population viability of common forest species and generalists, or most species requiring shade. However, if the aim is to halt and reverse the decline of European (Muys et al. 2022) or national forest biodiversity, the focus should be on declining (mostly red-listed) species. According to the Finnish Red Data, 436 (53%) vulnerable, endangered and critically endangered, primarily forest species are declining and rare due mostly to a scarcity of certain forest structural features, notably old-growth forests, very large and old trees or coarse deadwood, and natural tree-species composition (Hyvärinen et al. 2019). The numbers are quite similar in Sweden and Norway (SLU Artdatabanken 2020; Artsdatabanken 2021). These species are evolutionarily adapted to particular types, natural densities and amounts of the listed features.

Key questions are (1) whether and how quickly the species can recover from logging disturbance, and (2) whether CCF can maintain mature and old-forest species that are significantly reduced or unable to live in a commercial forest landscape based on RF. For most species that are declining and threatened by forestry, suitable structural features can be maintained and enhanced in either CCF or RF. In the case of RF, in phases of thinning and regeneration it is possible to retain individual or groups of trees that develop into old and large trees within a younger generation of trees and, when these trees die, they produce coarse deadwood. Old trees and coarse deadwood may also develop in retained forest patches outside the logging area. It is clear that CCF alone will not solve the challenges of biodiversity conservation in commercial forests. Productive and economically efficient CCF can often require repeated and intensive treatments. Management of structural features is important for biodiversity, but is neither an inherent part of RF nor CCF, so it needs to be addressed in addition to the choice of production system (cf. Gustafsson et al. 2020).

11.8 Conclusions and Research Needs

Compared to clearcutting-driven RF, CCF likely benefits species requiring shade and continuous availability of relatively big trees, such as some epiphytic lichens, including a few red-listed species. CCF also likely supports the long-distance dispersal of certain species, such as some epiphytic lichens and the Siberian flying squirrel, and provides shelter for the soil and its tree-root associated species community. Furthermore, if applied next to a protected area, it may help maintain the environmental conditions and species communities in that area by dampening edge effects. All these benefits, of course, depend on method specifics, such as gap sizes, tree structures and logging intensity. However, CCF alone does not maintain or increase structural features crucial for most red-listed forest species, particularly large and old trees and large-diameter deadwood. It is therefore unlikely to reverse negative trends of forest biodiversity, unless these features are intentionally retained and produced.

The main scientific gap in CCF concerns the cumulative biodiversity effects of decades of cutting. In CCF, the retained trees are small, so the ability of the regeneration method to maintain the microclimatic conditions of a closed forest and the species living on large trees, for example, is uncertain. On the other hand, it is not known to what extent CCF affects regional-level biodiversity, and little is known about species' responses to logging methods on soils other than heathlands; very little research has so far been carried out on peatlands. In the general forestry context, certain aspects would warrant more research, such as landscape topography, unwanted side effects of logging (e.g., wind or drought), continuities of logging intensity, and possible harvesting-associated changes in interspecific interactions (e.g., food webs) and ecosystem services such as pollination. In addition to these, several taxonomic groups (e.g., birds, mammals, slugs and snails, and soil

organisms) are under-studied and need more attention to more completely describe the effects of CCF on biodiversity.

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