

Lessons from native spruce forests in Alaska: managing Sitka spruce plantations worldwide to benefit biodiversity and ecosystem services

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There is increasing interest worldwide in managing forests to maintain or improve biodiversity, enhance ecosystem services and assure long-term sustainability of forest resources. An important goal of forest management is to increase stand diversity, provide wildlife habitat and improve forest species diversity. We synthesize results from natural spruce forests in southeast Alaska and suggest strategies for managing Sitka spruce plantations in other parts of the world to benefit biodiversity and enhance a variety of forest ecosystem services. We also discuss the roles of fungi in increasing both biological and structural diversity in Sitka spruce forests. New silvicultural systems that use partial cutting in older spruce forests could alleviate some of the problems associated with conventional even-aged management and increase both stand structural diversity and biodiversity. We found that mixed red alder-conifer stands in Alaska provided more heterogeneous structures than the pure conifer stands that typically develop after clearcutting. Well-planned silvicultural systems that include broadleaved species such as alder or birch could provide trees for timber production, improve wildlife habitat and a variety of other ecosystem services that are often compromised in young pure conifer forests.

Introduction

Worldwide, there is growing interest in devising new forest management strategies to encourage development of forests with late-successional stand characteristics including greater structural complexity and biodiversity (Franklin *et al.*, 1981; Harmon *et al.*, 1986; Franklin, 1989; Larsen, 1995; Humphrey, 2005; Deal, 2007). Such forests may provide a broader range of ecosystem services than conventional plantation forests. Several studies in the coastal Pacific Northwest region of North America (Oregon, Washington, and British Columbia) evaluated the effects of different silvicultural prescriptions designed to accelerate the development of late-successional forest characteristics (Arnott and Beese, 1997; Coates and Burton, 1997; Aubry *et al.*, 1999). This is particularly relevant for forest plantations with monocultures of exotic species or forests with simple species composition and uniform even-aged stand structures. In the Sitka spruce (*Picea sitchensis* (Bong.) Carr.) forests of southeast Alaska, native species are naturally established after timber harvest, but even-aged silvicultural systems using clearcutting have been predominantly used since the beginning of large-scale timber operations in the early 1950s (Harris and Farr, 1974; McClellan *et al.*, 2000). These even-aged forests have simple forest structures with dense, uniformly sized trees with little understorey vegetation and greatly reduced biodiversity and wildlife habitat (Alaback, 1982; Hanley, 1993; Deal, 2001).

The native range of Sitka spruce is along the Pacific coast of North America from northern California to Kodiak Island in Alaska (Peterson *et al.*, 1997). The rainforests of the North American Pacific margin have simple species composition but complex forest age and tree size structure (Alaback, 1982; Deal *et al.*, 1991). The forest ecosystem in southeast Alaska provides one of the most extensive, intact forest ecosystems in the world. These forests provide a valuable comparative example of large natural forest ecosystems to guide the management of forest plantations worldwide. The two predominant tree species, Sitka spruce and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), comprise >90 per cent of the total timber volume in designated commercial forestland (Hutchison, 1967). Proximity to the North Pacific Ocean results in cool summers and mild winters, annual precipitation is typically in excess of potential evapotranspiration, and without extended periods of drought (Farr and Hard, 1987). Much of the precipitation occurs in the autumn season along with occasional hurricane force winds. The significance of this climate for the forest is that moisture is generally not a limiting factor for tree regeneration (Harris *et al.*, 1974; Deal *et al.*, 1991; Nowacki and Kramer, 1998).

The natural disturbance regime of southeast Alaska includes high frequency, low-magnitude disturbance events (Brady and Hanley, 1984) resulting in multi-aged or uneven-aged stands (Alaback and Juday, 1989; Deal *et al.*, 1991; Lertzman *et al.*, 1996; Nowacki and Kramer, 1998). Multi-aged stands have been created by frequent but fine-scale natural disturbances such as

windthrow, landslides and endemic tree disease (Deal *et al.*, 1991; Hennon, 1995; Kramer *et al.*, 2001; Hennon and McClellan, 2003). These complex multi-aged stands contain multiple forest canopy layers, abundant and diverse understorey vegetation, large trees and snags, heartrot cavities in live trees, large woody debris and other important ecological characteristics of older, late-successional forests (Franklin *et al.*, 1981; Alaback and Juday, 1989; Franklin and Spies, 1991; Peterson *et al.*, 1997; Hennon and McClellan, 2003). The complexity induced by the gap-phase disturbance contributes habitat features that support a variety of terrestrial wildlife. The understorey vegetation that thrives in the gap-phase disturbance regime is also essential as food for herbivores and as cover for ground foraging and nesting birds and small mammals. There is general concern that many of these old-growth characteristics are lacking in even-aged young-growth forests.

Forest development in Alaska following clearcutting or other stand-replacing disturbances differs from development following natural small-scale disturbances, although western hemlock and Sitka spruce regenerate under both conditions. Conifer natural regeneration is abundant ($>10\,000$ trees ha^{-1}) following clearcutting with the development of a dense new stand of Sitka spruce and western hemlock trees. The forest canopy closes in 20–30 years on productive sites followed by a dense, long-lasting stage of stem exclusion (Alaback, 1982; Deal *et al.*, 1991). The reduction in tree density as the stand develops is mainly through mortality of small trees which die through suppression. Canopy closure eliminates most herbs and shrubs (Alaback, 1982) through shading. These dense young-growth stands have relatively uniform tree height and diameter distributions, and notably lack the multi-layered, diverse forest structures and shrub/herb layers found in old-growth or multi-aged stands (Alaback, 1984; Deal, 2001; Hennon and McClellan, 2003). Following canopy closure, densely stocked stands are recognized as having broadly negative consequences for wildlife habitat (Wallmo and Schoen, 1980; Schoen *et al.*, 1981, 1988; Thedinga *et al.*, 1989; Hanley, 1993; Dellasalla *et al.*, 1996) because many of the characteristics of old-growth forests (rich understorey, multiple canopies, snags, stem decay of live trees) are lacking.

In Great Britain and Ireland Sitka spruce forest plantations have been established over the last several decades to increase the amount of forest land and provide a future timber resource (Anon, 1996; Joyce and O'Carroll 2002; Rollinson, 2003; Macdonald *et al.*, 2010; Forestry Commission, 2012). Impressive growth rates (Farrelly *et al.*, 2011) and consistent demand for its timber have led to Sitka spruce becoming a dominant species in forestry in both Great Britain and Ireland (NFI, 2003, 2007). Sitka spruce is now planted in >16 countries worldwide and is the most common forestry species in Britain and Ireland, third most common in Denmark and a major species in Iceland, northwestern France and Norway (Hermann, 1987; Peterson *et al.*, 1997; FRA, 2010). In Denmark, Sitka spruce is a commercially important species accounting for ~ 16 per cent of Denmark's softwood timber harvest (Brauner *et al.*, 2000). Sitka spruce is particularly well adapted to the wet, cool climate and photoperiod of northern Great Britain and Ireland, and is the major tree species used in plantations in northern England, Scotland, Wales and Ireland.

In Europe, Sitka spruce is generally established as a single species plantation and develops into dense, even-aged forests that notably lack stand structural complexity with relatively poor

plant understories and overall reduced biodiversity in some taxonomic groups compared with semi-natural woodlands (Humphrey *et al.*, 2003; Iremonger *et al.*, 2007). Recently, forest researchers have suggested ideas for improving stand structural diversity either using natural disturbances such as wind (Quine *et al.*, 1999), or silvicultural strategies to encourage greater stand structural complexity and deadwood in spruce plantations to improve biodiversity (Humphrey, 2005). In Great Britain and more recently in Ireland, there has been strong interest in the use of continuous cover forestry (CCF) for increasing stand structural complexity and improving biological diversity, thus reducing some of the negative impacts from clearfelling of forest plantations (Mason *et al.*, 1999; Gadow *et al.*, 2002; Mason and Kerr, 2004; Pommerening and Murphy, 2004; Humphrey, 2005; Ni Dhubhain, 2010). Continuous cover is defined as the use of 'silvicultural systems whereby the forest canopy is maintained at one or more levels without clearfelling' (Mason *et al.*, 1999). One of the current attractions of CCF lies in the belief that this approach may be suitable for multi-purpose forestry where environmental, recreation, aesthetic, biodiversity and other objectives are as important as timber production (Lahde *et al.*, 1999; Guldin, 2002; O'Hara, 2002; Mason, 2003).

Another ecosystem service that may be important for the long-term sustainability of forests is the presence of mushroom forming fungal communities in forest stands. In particular, there is concern that plantation forests of exotic species may not provide adequate habitat for a diverse macrofungal community (Dahlberg *et al.*, 2010), limiting the ecosystem services these fungi normally provide. Apart from the direct ecosystem functions provided by these fungi, fungal biodiversity has close links with the biodiversity of these other taxonomic groups (Bader *et al.*, 1995; Ferris and Humphrey, 1999; Norden *et al.*, 2008; Halme *et al.*, 2009). There has been some documentation of tree pathogenic fungi in Alaskan Sitka spruce forests (Tait *et al.*, 1985; Shaw, 1989; Hennon and DeMars, 1997) and extensive literature on fungi in spruce forests in the Pacific Northwest Region (Trappe, 1962, 1963; Arora, 1986; Edmonds and Lebo, 1998; Castellano *et al.*, 1999, 2003; Berch *et al.*, 2001; Bothwell *et al.*, 2001; Outerbridge, 2002; Roberts *et al.*, 2004; Trudell and Edmonds, 2004; Kroeger *et al.*, 2012.) A number of studies have investigated fungal communities of plantation Sitka spruce forests in Britain and Ireland (Humphrey *et al.*, 2003; Palfner *et al.*, 2005; O'Hanlon and Harrington, 2012a,b) and a recent analysis of their fungal communities indicated that these Sitka spruce plantations support comparable species richness to that of native Sitka spruce plantations on Vancouver Island, BC, Canada (O'Hanlon *et al.*, 2013).

The overall objective of this paper is to synthesize current knowledge on management options that improve biodiversity and structural complexity of Sitka spruce forests of Alaska, and apply this information to Sitka spruce plantations in other parts of the world, with emphasis on Great Britain and Ireland. In particular, we will use knowledge of native spruce forests of Alaska, to suggest ways of improving biodiversity of Sitka spruce forests in the British Isles and of encouraging development of stands with late-successional characteristics. We discuss the roles of fungi in increasing both biological and structural diversity in Sitka spruce forests. We summarize and assess the effects of partial cutting in older forests and their potential role in improving stand structure and maintaining forest plant communities. We also assess the ecological role of red alder in young-growth even-aged forests and

evaluate the relationship of alder with stand structure, understorey plant diversity and the potential of alder in conifer-dominated forests for improving wildlife habitat.

Lessons from native Sitka spruce forests

Studies on partially harvested older Sitka spruce forests

Tree and stand responses to partial cutting were assessed in a retrospective study where 18 partially harvested stands were sampled in 1995 and 1996 that encompassed a range of time since cutting, intensity of cutting and geographic distribution throughout southeast Alaska (Deal, 2001; Deal and Tappeiner, 2002). From this former study we selected 32 plots in 10 Sitka spruce dominated stands (Figure 1, Table 1) that were partially harvested at least 50 years ago to assess stand growth and structural changes over the initial 50-year period since cutting. In another study, the size, density (stems ha⁻¹), and form of deadwood structures were assessed from twenty 0.08 ha plots in each of 9 old-growth stands in three locations of southeast Alaska (McClellan et al., 2000). By noting the form (uprooted, broken bole or standing snag) and deterioration class, we were able to evaluate the types of tree mortality that led to dead tree structure and also to

reconstruct past mortality rates. For assessing internal wood decay of live trees, we relied on two classic cull studies on timber losses in southeast Alaska (Kimmey, 1956; Farr et al., 1976). Results from these publications provided a basis for old-growth decay levels of live trees throughout southeast Alaska. We used data from table 1 in Kimmey (1956) to evaluate the relationship of tree size structure and the amount of internal wood decay in Sitka spruce and western hemlock (Hennon and DeMars, 1997).

Stand structure, tree size distribution and dead trees of partially harvested Sitka spruce forests

In partially harvested older Sitka spruce forests in Alaska, the subsequent stand basal area and stand growth for all cutting intensities were strongly related to trees left after harvest. In this study, results indicated that small advance regeneration and larger residual trees responded with rapid and sustained growth after overstorey removal and became a major part of the current stand. Fifty years after cutting, tree size distribution of the partially harvested stands was more complex in comparison with even-aged stands. The tree frequency distribution was significantly different in stands before and after partial cutting but these stands

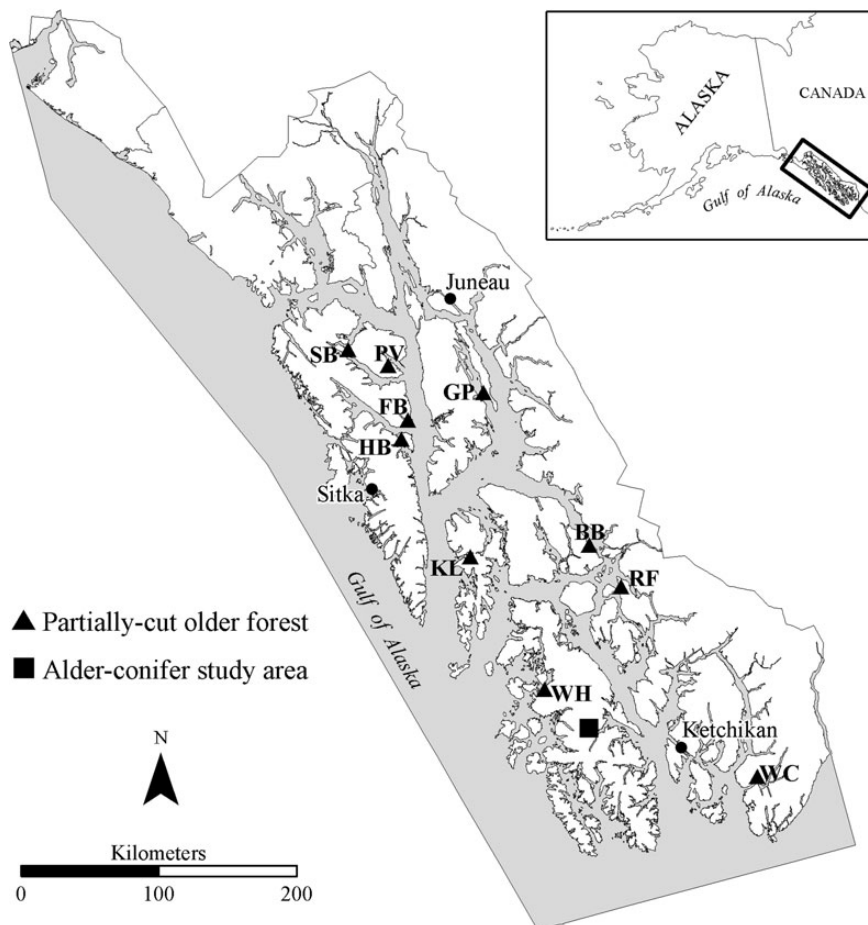


Figure 1 The research study areas in southeast Alaska. The triangles are the 10 partially cut older forest study sites; letter codes are referenced from Table 1. The square is the study area for the mixed alder–conifer younger forests.

Table 1 Descriptions of partially cut research sites listed from the oldest to most recently cut site

Research site	Cutting intensity				Current stand ^a composition and site information							
	Time since cut (years)	Basal area			Basal area (m ² ha ⁻¹)	All				Forest type	Elev (m)	Site ^c index ₅₀ (m)
		Cut (%)	Cut (m ² ha ⁻¹)	Left (m ² ha ⁻¹)		Trees (trees ha ⁻¹)	<i>Picea</i> (%)	<i>Tsuga</i> (%)	Cedar ^b (%)			
WC – Weasel Cove	96	17–51	9–23	22–45	53–75	450–1220	0–24	67–100	0–17	<i>Picea</i>	30	24
GP – Glass Peninsula	85	23–69	15–41	17–47	60–84	147–397	11–34	28–83	0–49	<i>Picea</i>	20	29
FB – Florence Bay	82	50–57	33–38	26–38	56–83	120–360	18–75	25–82	0	<i>Picea</i>	10	32
KL – Kutlaku Lake	76	31–63	17–31	18–37	58–139	305–525	5–49	35–95	0–16	<i>Picea</i>	5	32
HB – Hanus Bay	73	49–96	24–85	3–25	56–83	413–1180	6–62	38–94	0	<i>Picea</i>	25	30
SB – Salt Lake Bay	67	48–55	28–35	29–31	63–87	158–642	17–73	27–83	0	<i>Picea</i>	10	30
WH – Winter Harbor	64	24–38	19–39	56–70	73–95	785–1311	2–33	67–98	0	<i>Picea</i>	5	29
RF – Rainbow Falls	53	34–61	15–25	16–29	44–66	348–1108	0–28	63–100	0–10	<i>Picea</i>	20	27
BB – Big Bear Creek	37	17–36	9–27	47–63	53–79	270–754	15–47	53–85	0	<i>Picea</i>	20	23
PV – Pavlov River	19	36–58	21–43	31–47	37–69	288–823	4–29	42–96	0–46	<i>Picea</i>	20	30

The cutting intensity data are the range for the partially cut plots at each site. The current stand data include the range of both uncut and cut plots at each site. The forest type is the major overstorey tree species at each site.

^aStand data for trees and basal area include all trees that are at least 2.5 cm d.b.h.

^bThe other minor species include western redcedar (*Thuja plicata* Donn ex D. Don) and yellow-cedar (*Chamaecyparis nootkatensis* (D. Don) Spach).

^cPotential site index, base age 50, height in metres.

quickly developed more variable size structures (Figure 2A). Most trees cut were large-diameter trees but usually some medium and large-diameter trees were left after cutting. The residual trees remaining after partial cutting grew rapidly and became a dominant part of the current overstorey stand. Immediately after cutting there were few trees on these plots >70 cm diameter at breast height (DBH), and these cut stands had very different tree size structures than the old-growth stands prior to cutting (Figure 2A,B). Fifty

years after cutting, however, these stands had similar numbers of large-sized (>100 cm DBH) trees compared with the old-growth stands, and these similar diameter distributions were largely a result of the growth of the smaller and medium diameter trees into the larger-diameter classes. These results are particularly important, because they highlight the long time frame required for trees in even-aged stands to reach large sizes and finally replace large-diameter trees that were cut (Figure 2C). For example, modelling tree growth in even-aged stands for comparable lower and higher site classes using a bare ground starting point (Dixon *et al.*, 1992), we found that it took 280 years for the higher sites and 350 years for lower sites for unthinned stands to reach 100 cm DBH (Deal *et al.*, 2010). In these partially cut stands, nearly half of all trees that were >100 cm DBH 50 years after cutting were 70–80 cm at the time of cutting and these medium-large trees grew rapidly following partial cutting.

The stand structures that develop after partial cutting create structurally complex, multi-layered forest canopies that are more similar to old-growth stands than to the uniform young-growth stands that develop after clearcutting. The presence of large and small residual trees left after partial cutting creates structural heterogeneity and complex overstorey–understorey interactions, and these structures were important for maintaining abundant and diverse understorey plant communities (Deal, 2001). The high species richness and abundance of understorey plants in partially cut stands is quite different from the typical plant understories found in stands that develop after clearcutting. The loss of biodiversity following clearcutting is well documented and a major management concern in southeast Alaska (Wallmo and Schoen, 1980; Schoen *et al.*, 1988; Hanley, 1993; Hanley *et al.*, 2006; Deal, 2007).

Standing dead trees (snags) are a common feature of old-growth forests in Alaska that offer valuable habitat to cavity dwelling birds and mammals. *Fomitopsis pinicola* (Sw.) P. Karst. is the principal fungus that decays and softens the wood of spruce and hemlock snags for cavity excavators, although a number of other fungi operate as wood decays of dead trees (e.g. *Laetiporus conifericola* Burds. & Banik, *Ganoderma applanatum* (Pers.) Pat.) (Holsten *et al.*, 2009). In a study that quantified dead trees in unmanaged old-growth stands with no previous history of forest management in Southeast Alaska, Hennon and McClellan (2003) reported a density of 41–55 large dead trees (d.b.h. ≥ 45 cm) ha^{-1} , with 20–35 per cent of these as standing snags. The remainder of large dead tree structures was dead trees on the forest floor in the form of broken boles or with exposed roots, indicating other forms of tree mortality. The annual mortality rate of codominant and dominant trees in these unmanaged forests that gave rise to these large woody debris structures was found to be ~ 0.4 percent through the 1900s (Hennon and McClellan, 2003). Downed dead trees are typically left along with cull logs during clearcut harvests, where they provide ecological benefit as they slowly decay on the forest floor in the young-growth stand.

Internal wood decay in live trees is generally related to tree ages (Boyce, 1961) and is an important natural feature of old forests of southeast Alaska (Hennon, 1995). Two studies reported that ~ 31 percent of the board foot volume of live trees is decayed in the old-growth forests of this region (Kimmey, 1956; Farr *et al.*, 1976). Several fungi (e.g. *Phellinus pini* (Brot.) Bondartsev & Singer and *P. hartigii*) (Allesch. & Schnabl) Pat.) are unique to old forests, but some are found as saprophytes on deadwood in young stands.

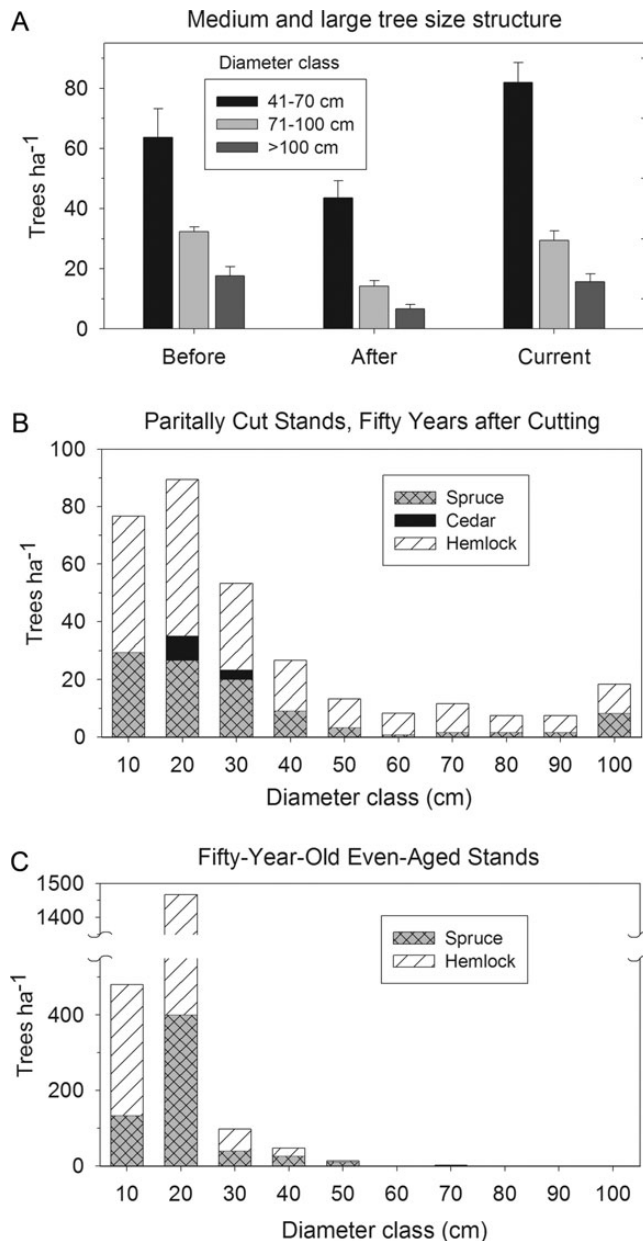


Figure 2 (A) The number of medium (41–70 cm), medium-large (71–100 cm) and large (>100 cm) sized trees ha^{-1} by d.b.h. size class in the partially cut plots immediately after and before cutting, and in the current stand 50 years after cutting (Vertical bars indicate standard errors); (B) Tree diameter distributions for partially cut stands fifty years after cutting; (C) Tree diameter distributions for 50-year-old even-aged stands.

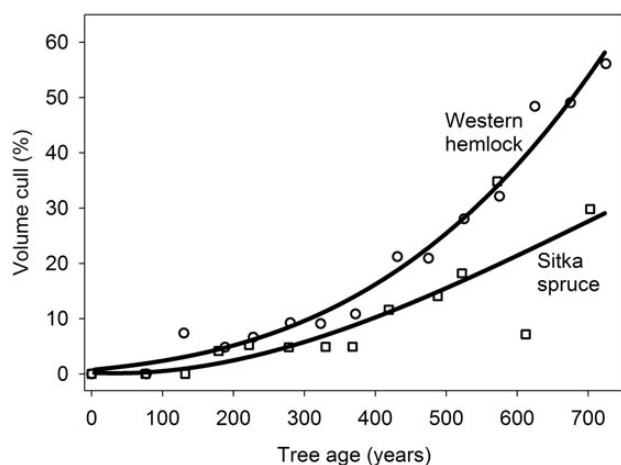


Figure 3 Influence of tree age on percentage of western hemlock and Sitka spruce wood volume that is cull with decay. Graph created from values in Table 10, Kimmey (1956) of mean gross volume cull for dissected trees grouped by 50-year age intervals. Curves were fit with three function polynomial equations.

Along with loss to the timber resource in old stands, stem decay alters carbon and nutrient cycles, provides unique wildlife habitat in the form of softened wood or hollows, and contributes to continued fine-scale disturbance through tree death by bole breakage (Hennon and McClellan, 2003). The amount of stem decay in live trees is correlated with tree age for both Sitka spruce and western hemlock in southeast Alaska (Figure 3) (Kimmey, 1956). The high level of stem decay can be attributed to the abundance of old trees that grow in these forests which are not affected by fire and infrequently experience stand-replacing disturbance. These decay–tree age relationships (Figure 3) indicate that young-growth trees managed on short rotations will contain very little stem decay.

In even-aged stands that regenerate after clearcutting in southeast Alaska, young trees typically lack internal decay as the stand develops for 100–150 years or longer (Farr *et al.*, 1976). As a management treatment to retain stem decays in managed forests, an option at the time of harvest is to conduct a green tree retention (partial) harvest, rather than a clearcut. Trees with conks, cracks, old top damage and other indicators of decay (Farr *et al.*, 1976) could be targeted for retention and even buffered by other retained trees. These alternative harvesting practices will always result in some level of top, bole and root injury to residual trees that remain, with damage (up to 30–40 percent of trees injured) related to the harvest intensity, spatial distribution and type of yarding (e.g. helicopter vs ground-based) (McClellan and Hennon, 2005). There is a clear tradeoff between timber and ecological values when encouraging stem decays in managed stands. Minimizing these injuries during harvest entries in native old-growth forests is advisable because no further injury to old residual trees is required as many will already contain the important stem decay structures for wildlife and ecological processes.

Mixed alder–conifer younger forests

Another management option for mitigating some of the issues with even-aged stands created by clearcutting is introducing

mixed broadleaved-conifer species in conifer-dominated forests. Mixed conifer-red alder (*Alnus rubra* Bong.) stands in southeast Alaska have different successional pathways following clear-cutting than the previously described development patterns of pure conifer stands (Deal *et al.*, 2004). Several mixed alder–conifer young-growth stands that developed following clear-cutting were assessed to examine the role of red alder in these stands. Study sites were located in alluvial valley sites in the Maybeso and Harris watersheds, on Prince of Wales Island in southeast Alaska (Figure 1). These mixed alder–conifer stands generally appear to have lower tree stocking and stand density than pure conifer stands of a similar age (40–50 years), with more open forest canopies and more heterogeneous stand structures (Deal, 1997; Deal *et al.*, 2004). The presence of red alder also increases invertebrate production, providing a source of food for birds, small mammals and fish, which may in turn increase their abundance (Wipfli *et al.*, 2002). Red alder is also a source of nitrogen to early successional ecosystems and provides abundant N in young-growth mixed species stands (Cole *et al.*, 1978; Bormann and DeBell, 1981; Van Miegroet *et al.*, 1990).

Stand structure, tree size distribution and dead trees of young alder–conifer forests

Diameter distributions of trees in mixed species stands differed between conifers and alders. Conifers had many more trees in the smallest size classes with decreasing numbers of trees in progressively larger sizes following a reverse J-shaped diameter distribution. These conifers were all of the same age and the stratified diameter distribution is a common stand development pattern for even-aged conifer stands in the region (Taylor, 1934; Deal *et al.*, 1991). Alders were evenly distributed with most trees in a narrow diameter (20–30 cm) and overstorey height (20–25 m) range (Figure 4). In contrast, all conifers were unevenly distributed with a few taller and larger-diameter trees and numerous smaller-diameter trees. The mixed alder–conifer stands had more variable diameter distributions than pure or conifer-dominated stands. The alder in these stands provided a different tree size cohort than the conifer-dominated stands that contained numerous small diameter trees. These mixed alder–conifer stands created a multi-layered forest canopy with a few dominant overstorey conifers, a mid-canopy level of mixed red alders and conifers and a lower canopy level dominated by small diameter conifers.

In younger forests, mixed alder–conifer stands have more complex forest structures than is typically found in pure conifer stands of the same age. Young pure conifer stands in this coastal region are typically very densely stocked (DeMars, 2000) and have relatively uniform tree height and diameter distributions. Results suggest that alder trees can provide different tree size distributions with multiple canopy layers in mixtures with conifer stands. These multiple canopy layers may be the most important feature of mixed alder–conifer stands and may distinguish these stands from predominantly even-aged conifer stands of the same age. The presence of alder also did not significantly reduce the size of the largest spruce and hemlock trees in riparian or upland stands (Deal *et al.*, 2004; Orlikowska *et al.*, 2004). As stands age, red alder will eventually senesce and die, either through disease or overtopping by conifers. Dead red alders then represent a source of standing and downed wood debris, although this function is short-lived because its wood decomposes rapidly.

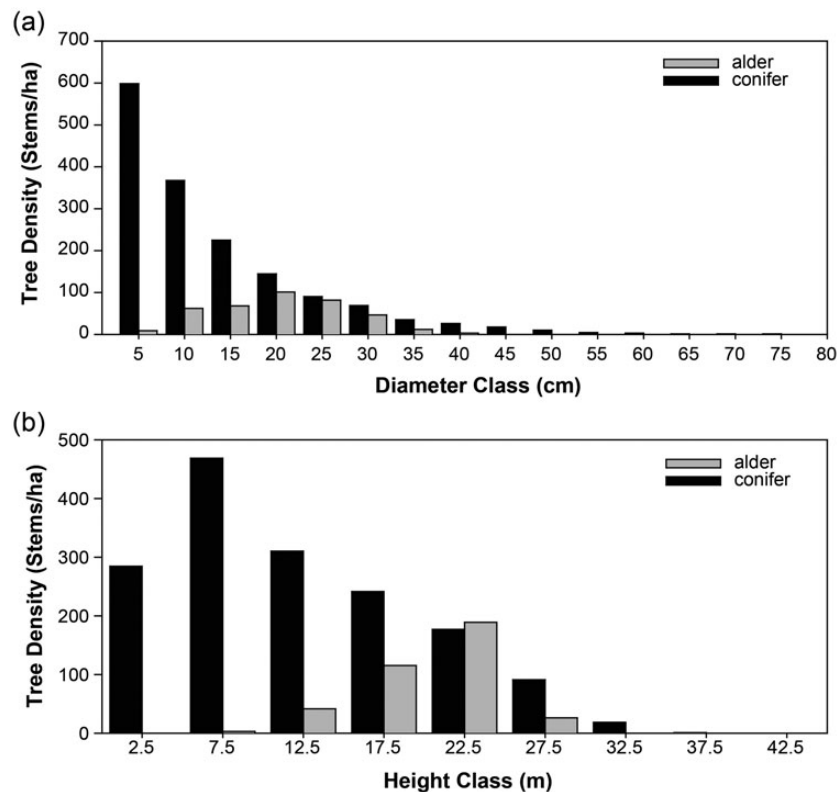


Figure 4 Average tree diameter distribution (a) and average tree height distribution (b) for all alder and conifer trees at nine sites (modified from Deal *et al.*, 2004).

Long after death, however, there will be a legacy of alder's presence, both through nitrogen in soils and vegetation and in the more open conditions in the conifer stands.

Understorey plant diversity of partially harvested Sitka spruce forests and younger alder–conifer forests

The understorey plant species richness of these partially cut older spruce stands was relatively high and comparable to levels reported for other old-growth stands in the region (Alaback, 1982; Alaback and Juday, 1989; Hanley and Hoel, 1996). Deal (2001) found no significant difference in species richness between the uncut and partially cut plots and plant community structure appeared resilient within a moderate range of cutting intensities. The high species richness and abundance of understorey plants in partially cut stands differs from the typical plant understorey found in stands that develop after clearcutting. The loss of biodiversity following clearcutting is well documented in southeast Alaska (Wallmo and Schoen, 1980; Schoen *et al.*, 1988; Hanley, 1993), and is closely associated with the rapid development of conifers (Alaback, 1982, 1984; Deal and Farr, 1994). Overall, partial cutting maintained diverse and abundant plant understoreies comparable to the plant communities typically found in old-growth stands.

Understorey plant diversity and abundance in mixed alder–conifer stands appeared to be closely related to the amount of alder in the stand, and understorey plant cover increased with increasing proportion of alder basal area. Analysis of cover for

vascular plants and non-vascular plants (bryophytes) showed different relationships. The non-vascular plant cover was similar for all of the sites and there was no significant relationship between the cover of non-vascular plants and the proportion of alder basal area (Deal, 2007). In contrast, the vascular plants showed a strong correlation between increasing vascular plant cover and increasing proportion of alder basal area. Both shrub and herbaceous biomass increased significantly with increasing percentage red alder (Hanley *et al.*, 2006).

The mixed alder–conifer younger stands had more complex stand structures and these structures have important management implications for forest wildlife resources. Recent studies documented a correlation of herbaceous biomass with increasing percentage red alder throughout the range of stands studied (Hanley *et al.*, 2006). This is important from both a biodiversity perspective and a forest management perspective, because it is the herb component that is most difficult to maintain through secondary succession of even-aged stands following clearcutting in southeast Alaska (Alaback, 1982; Doerr and Sandburg, 1986; Hanley, 1993; Deal and Farr, 1994). Summer food value for deer increased significantly with increasing percentage of alder but there was no significant increase in winter forage with red alder. Summer food value increased with more red alder because the quantity of both forbs and shrubs was greater with increasing red alder, and the nutritional quality of forbs and shrubs is high in summer (Parker *et al.*, 1999; Hanley *et al.*, 2006). However, in winter, most of these red alder-associated species are either senescent (forbs and ferns) or of very low nutritional quality (Parker

Table 2 Macrofungal species richness data from sites where Sitka spruce was the dominant tree species

Site	Species richness	Stage 1 (<i>Laccaria</i> & <i>Hebeloma</i>)	Stage 2 (<i>Inocybe</i>)	Stage 3 (<i>Cortinarius</i>)	Stage 4 (<i>Russula</i> & <i>Lactarius</i>)
Huxley island ^a	96	0	11	9	18
Kendrick point ^a	82	1	10	8	19
Sgang gwaay ^a	62	0	6	6	17
Windy bay ^a	102	2	10	14	16
Clunes ^b	159	6	11	21	21
Glentress ^b	80	1	2	9	4
Kielder ^b	52	1	1	3	4
Knapdale ^b	129	6	8	17	14
Bohatch ^c	41	4	1	7	7
Chevy Y ^c	32	4	0	6	5
Dooary ^c	32	4	0	5	2
Stanahely ^c	39	4	0	1	7

Stages refer to the stages in the Functional morphology *sensu* (Peay *et al.* 2011).
^aSites in Haida Gwaii, BC, Canada and aged 70+ years (Kroeger *et al.*, 2012).
^bSites in Britain and aged 6–69 years (Humphrey *et al.*, 2003).
^cSites in Ireland and aged 18–50 years (O’Hanlon, 2011).
Huxley Island and Sgang gwaay show signs of previously logging. All British and Irish sites are a mix of first and second rotation forests. The Haida Gwaii study conducted yearly visits to the sites and did not use permanent plots. The British study conducted three visits per year to eight permanent plots (100 m²) per site. The Irish study conducted three visits per year to a single plot (100 m²) per site.

et al., 1999). Therefore, while red alder mixed within young-growth stands might improve summer habitat for deer significantly, its potential benefits for winter habitat are somewhat limited. Other studies in mixed alder–conifer stands reported increases in plant species richness and highly productive understorey vegetation with biomass similar to that of old-growth stands of the region (Hanley and Hoel, 1996; Hanley and Barnard, 1998; Hanley *et al.*, 2006). Habitat quality for small mammals in even-aged alder-conifer stands may be equal to that of old-growth forests (Hanley and Hoel, 1996; Hanley and Barnard, 1998). The presence of red alder may increase invertebrate production, providing more food for animals such as birds, small mammals and fish, in turn affecting their abundance.

Macrofungal communities of native vs non-native Sitka spruce forests

The data used in our macrofungal communities section come from three studies of macrofungal diversity in Sitka spruce forests – (1) the recent 4-year-survey of macrofungi on the islands of Haida Gwaii (formerly known as the Queen Charlotte Islands, British Columbia) (Kroeger *et al.*, 2012) which recorded 656 species; (2) the 4-year survey of fungi in several forest types in Britain (Humphrey *et al.*, 2003) which recorded 677 species; (3) the 3-year survey of macrofungi in four Irish forests types (O’Hanlon, 2011) which recorded 409 species. Four sites from each of the three studies were used to assess macrofungal diversity in native and non-native Sitka spruce forests (Table 2).

Overall, the macrofungal communities from Haida Gwaii were different from those found in either Britain or Ireland (Figure 5). Out of a total of 202 species found in the four sites on Haida Gwaii, only 53 were also found in the British and Irish Sitka spruce sites. The five most frequent species from all three regions were entirely different. This result mirrors recent findings of

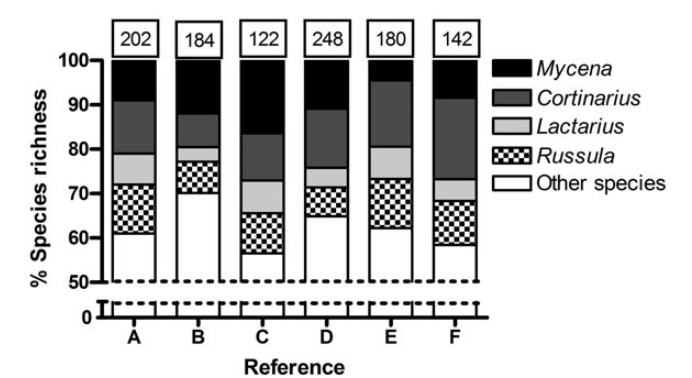


Figure 5 Species rich genera of macrofungi found in previous studies of selected forests types. Figures in text box are total species richness found in that study. Note break in Y-axis at Y = 5–50. X-axis: study references, (A) Sitka spruce (Roberts *et al.*, 2004); (B) Sitka spruce (Outerbridge, 2002); (C) Sitka spruce (O’Hanlon, 2011); (D) Sitka spruce (Humphrey *et al.*, 2003); (E): birch (Watling, 1984); (F) Scots pine (Alexander and Watling, 1987; Orton, 1987).

largely different communities in Sitka spruce plantations in Vancouver Island BC, Britain and Ireland (O’Hanlon *et al.*, 2013). Some of the wood decay/parasitic species important for creating structural heterogeneity in native Sitka spruce forests in Alaska found in the Haida Gwaii sites were *Ganoderma tsugae* Murrill, *L. conifericola* Burdsall & Banik, *Peniophora aurantiaca* (Bres.) Hoehn. & Litsch. and *Polyporus elegans* Bull. Fr.

Individual species data aside, certain trends can be identified by examining the data at the genus level. The ectomycorrhizal genera *Russula*, *Lactarius* and *Inocybe* make a higher proportion of the total species richness in Haida Gwaii (32 per cent) than in Britain (13 per cent) or Ireland (15 per cent). Furthermore, the abundance

of some 'early-stage' (Mason *et al.*, 1982), here recently termed Stage 1 (*sensu* Peay *et al.*, 2011), fungi in Irish and British sites is slightly higher than in the Haida Gwaii sites (Table 2). *Laccaria* species were some of the most frequently found species in two of the British and two of the Irish sites. Stage 1 species from the genus *Laccaria* and *Hebeloma* are known to be particularly suited to the early successional stages of the forest (O'Hanlon and Harrington, 2012b), and these early successional stages can be perpetuated by clearcutting (Jones *et al.*, 2003).

Management strategies to increase stand structural diversity and improve biodiversity in Sitka spruce plantations in other parts of the world

Maintaining old-growth stand characteristics in managed forests

With careful tree selection and control of stand density it will be possible to maintain diverse tree size structures with silvicultural systems that use partial cutting in Sitka spruce forests. If a primary goal is to maintain stand structures similar to those in native old-growth stands, it will be important to select individual or groups of trees in large or medium-large size classes to retain. In addition, maintaining some large spruce as seed trees, thinning overly dense stands to reduce stocking and planting spruce in some cases would provide larger-diameter trees for future timber production. Thus, by thoughtfully implementing normal forest management practices, new silvicultural systems could be developed to further enhance desirable tree species composition, provide productive stands for timber, and also maintain diverse stand structures similar to old-growth forests. The more complex structures left after partial harvesting may create conditions similar to natural low intensity disturbances that are common in southeast Alaska. These structures also appear important for maintaining plant and macrofungal diversity and abundance – thus providing food and habitat cover for ground nesting birds and small mammals. Retention of mature trees would also help conserve macrofungal species that rely on mature trees (Jones *et al.*, 2003; Durall *et al.*, 2006; Kranabetter *et al.*, 2013), particularly ectomycorrhizal species and the mycelia networks they create. Ensuring the persistence of the ectomycorrhizal network in commercially harvested forests has been identified as one of the challenges facing modern forestry (Simard, 2009), as these networks have a strong regulating effect on temperate forest ecosystems (Simard *et al.*, 2012).

Mixed spruce-broadleaf stands as management option

Mixed broadleaf-conifer stands (e.g. red alder-conifer or birch-conifer) stands provide more heterogeneous structures than the pure conifer stands that typically develop after clearcutting. Attempts to reestablish understorey herbs and shrubs through thinning young-growth conifer stands in Alaska have led to predominantly conifer regeneration with little new herbaceous colonization (Deal and Farr, 1994). Altering the composition of young, pure conifer forests with the inclusion of red alder may improve habitat and food resources for deer and other wildlife and thereby offset some of the negative consequences of clearcutting.

If deliberate regeneration of broadleaved species such as birch or red alder could be incorporated into present harvest plans, managers might be able to exploit the positive benefits of alder or birch and improve structure and function of young forests. Well-planned silvicultural systems that include a mixture of broadleaf-conifer compositions is another strategy that could enhance stand diversity and provide other ecosystem services earlier in stand development as compared with typical even-aged conifer plantations. This technique could provide trees for timber production and also improve other forest resources that are often compromised in young pure conifer forests.

Furthermore, including alder or birch in Sitka spruce plantations would increase the microhabitats necessary for many host restricted macrofungal species. Although, the effect of mixed vs monoculture in non-native Sitka spruce forests on macrofungal biodiversity has received little research, one study carried out in young forests (16–28 years) in Ireland found that forests of Sitka spruce mixed with either Japanese larch *Larix kaempferi* (Lamb.) Carr. or lodgepole pine *Pinus contorta* Dougl. var. *latifolia* Wats. supported more species of macrofungi ($\times 2$) and ECM morphotypes ($\times 1.2$) than monoculture Sitka spruce forests (Heslin *et al.*, 1992). Forest with more tree species often have more fungal species present (Schmit *et al.*, 2005; Dickie, 2007) and this is thought to be due to differing levels of specificity for certain hosts/substrates exhibited by fungi (Heilmann-Clausen *et al.*, 2005; Ishida *et al.*, 2007; Ludley *et al.*, 2008; O'Hanlon and Harrington, 2012b). Thus, increasing tree species diversity in Sitka spruce plantations is one possible method for fostering increased fungal biodiversity; along with the diversity of several other taxonomic groups (see O'Hanlon and Harrington, 2011).

One tree species that has been identified as suitable for planting in mixtures with Sitka spruce in Britain is birch (*Betula pendula* or *B. pubescens*). Indeed, the results of a multi-taxon study indicated that inclusion of birch in spruce plantations in Britain would result in increases in biodiversity of ground vegetation ($\times 1.7$), lichen ($\times 1.6$), hoverfly ($\times 1.6$), rove beetles ($\times 1.5$) and moths ($\times 5$) (Humphrey *et al.*, 1998). One concern about this proposal would be that the birch competes with and possibly reduces the productivity of the spruce (Humphrey *et al.*, 1998). However, a recent trial described by Mason (2006) indicated that in cases where the spruce is in the majority it outcompetes birch after 30 years. Furthermore, it has been found that birch naturally regenerates in the gaps formed within Sitka spruce stands in Britain (Quine and Malcolm, 2007); however, the absence of a local seed source is one of the factors most restricting to birch regeneration in upland spruce plantations. There are several possible advantages to mixing birch with Sitka spruce, (1) Birch forests in Britain are known to have a particularly rich macrofungal biodiversity (Watling, 1984), sharing many species in common with Sitka spruce in Scotland (Alexander and Watling, 1987). Mixing Sitka spruce and birch in forests would accommodate more macrofungal species than forests containing just Sitka spruce, (2) The birch eventually dies either as a result of overtopping by spruce or through disease (e.g. *Piptoporus betulinus* (Bull.); Watling, 1984). The remaining woody debris creates a microhabitat for many ectomycorrhizal and wood decay macrofungi; a lack of large-diameter coarse woody debris (CWD) has been identified in Irish and British Sitka spruce plantations (Humphrey and Peace, 2003; Sweeney *et al.*, 2010a). (3) Added benefits to mixing birch with Sitka spruce may come in increased stand resistance to forest pathogens. Birch

was found to have a ‘diluting’ effect on the severity of *Armillaria* root disease in Douglas fir forests in BC (Baleshta *et al.*, 2005). This dilution effect has also been shown to reduce the mortality caused by the generalist forest pathogen *Phytophthora ramorum* Werres, de Cock & Man in’t Veld in California (Haas *et al.*, 2011). *Phytophthora ramorum* is an increasing problem in Ireland and Britain, especially since the discovery of it forming novel host–pathogen combinations with larch (Brasier and Webber, 2010), and the finding of *P. ramorum* infected Sitka spruce in the wild in Ireland (Forest Service, 2011).

Thinning and managing tree injuries and stem decays in young stands

Thinning of young stands to reduce stocking density at about age 20 is a common practice in southeast Alaska (DeMars, 2000). This form of thinning favours the largest crop trees (i.e. precommercial thinning) and typical stocking after thinning varies from ~500 to 1500 trees ha⁻¹. In Ireland, Sitka spruce is planted at a spacing of 2 × 2 m, or 2500 plants ha⁻¹. First thinning is normally carried out when trees reach a height of 10 m, using the ‘line and selection’ method. This involves the removal of every seventh line of trees along with selective thinning of the smaller trees remaining. Thinnings occur at 3–6-year cycles, depending on the Yield Class of the forest, with a final thinning carried out 3–6 years before final harvest (Horgan *et al.*, 2004). Silvicultural goals for thinning young stands include increasing light to maintain or enhance understorey plants and also favouring the growth of individual trees for future timber production. Thus, the number of benefiting ecosystem services is fairly small, mainly wildlife and timber resources being favoured, unless plans change to allow these stands to reach more advanced ages.

Commercial thinning is just now being practiced in southeast Alaska as more young-growth stands are reaching an age and tree size class to make this feasible. In this case, tree boles are removed to produce wood products and a possible revenue source to pay for the silvicultural operation. This type of thinning treatment may be a useful practice in the Sitka spruce forests in the British Isles. With careful planning, commercial thinning has the potential of accelerating the development of some structural characteristics in old-growth forests such as such as stem decays (through tree injuries) and multiple canopy layers. Other recent studies in Great Britain have suggested that commercial thinning via the use of CCF will not significantly degrade the quality of timber being produced in the UK (Macdonald *et al.*, 2010) and may improve other important ecosystem services in these forests.

Precommercial thinning generally does not lead to substantial injuries to the remaining small trees and therefore does not influence stem decay. Even if wounded, young trees need to be of an age where they are producing heartwood (at about age 14–18; Hillis, 1987) in order to develop decay in boles. Commercial thinning may have multiple benefits in managed spruce forests. Timber is produced, and stem density and canopies are reduced to favour understories and the growth of larger individual trees. Any form of harvest that involves tree removal will result in unintentional injury of some residual trees. Bole injuries will be common because Sitka spruce has thin bark. Top breakage and bole wounds are important infection courts for decay fungi in Sitka spruce and western hemlock (Bier *et al.*, 1946; Buckland *et al.*, 1949). Although these fungi will reduce future timber values,

they produce the heart rot structures that are essential characteristics of old forests. Decay development is a slow process in wounded trees in southeast Alaska (Hennon and DeMars, 1997), with several decades required for substantial decay to develop in western hemlock and even longer in Sitka spruce. Intentional mechanical wounding of selected trees offers the possibility of decay developing in an optimal location in the tree. Some wildlife species prefer decay structures far off the ground, so mechanically breaking tops in a prescribed number of trees may eventually lead to desirable placement of wood decay. Another direct approach is to inoculate stem decay fungi into live young-growth trees (Parks and Hildebrand, 2002; Filip *et al.*, 2011), but this has not yet been attempted in southeast Alaska or elsewhere in Sitka spruce. Although decay development is slow, introducing decay into young stands at the time of commercial thinning through tree injuries or direct inoculation can speed the development of stem decay by up to a century compared with waiting for it to return naturally through stand development. With enough time, live trees with heart rot can eventually die through bole breaking to produce unique, hollow woody debris structures. Decay in live and dead trees provides the stand with CWD that encompasses a number of decay stages, providing suitable habitat for decay stage restricted macrofungi (Boddy, 2001).

Management options for Sitka spruce plantations in other parts of the world

A number of recent studies have investigated the biodiversity of Sitka spruce plantations in Ireland and Britain (Table 3). In

Table 3 Management actions and the taxonomic groups that will benefit from the actions in Irish and British Sitka spruce forests

Management action	Taxonomic group benefitting from actions	
	Ireland	Britain
Increase retention of mature trees	Epiphytes ¹	Epiphytes ⁸
	Fungi ²	Fungi ⁹
	Spiders ^{2, 4}	Vascular plants ¹⁰
	Beetles ⁴	
Increase tree species diversity	Epiphytes ¹	Epiphytes ⁸
	Fungi ²	Fungi ⁹
	Vascular plants ⁵	Birds ¹¹
Increase open spaces in forests	Spiders ³	Epiphytes ⁸
	Beetles ⁴	Vascular plants ¹⁰
	Vascular plants ⁵	Birds ¹¹
	Hoverflies ⁶	Beetles ¹²
Increase deadwood retention	Birds ⁷	Hoverflies ¹²
	Fungi ²	Epiphytes ⁸
	Vascular plants ⁵	Fungi ⁹
	Hoverflies ⁶	Vascular plants ¹⁰
	Birds ⁷	Birds ¹¹

Study references: 1, Coote *et al.* (2008); 2, O’Hanlon and Harrington (2012a); 3, Oxbridge *et al.* (2006); 4, Oxbridge *et al.* (2010); 5, French *et al.* (2008); 6, Smith *et al.* (2005); 7, Sweeney *et al.* (2010b); 8, Humphrey *et al.* (2002); 9, Humphrey *et al.* (2000); 10, Ferris *et al.* (2000); 11, Fuller and Browne (2003); 12, Humphrey *et al.* (1999).

general, these non-native plantation forests do not support similar levels of species richness as native species forests in Ireland and Britain. However, all studies indicated that Sitka spruce plantations have the ability to support higher species richness if management actions that sought to increase structural diversity in these forests were carried out (Table 3). The retention of mature trees and large-diameter CWD, along with increasing tree species diversity and canopy gaps were some of the actions highlighted.

Results from Norway spruce (*Picea abies* (L.) H. Karst.) forests in Germany have shown a direct correlation between volume of CWD and the species richness of fungi that relies on CWD as a growth substrate (Bässler *et al.*, 2010). Moreover, several studies from a variety of forest types across Europe have found that having a diversity of CWD sizes and decay stages is vital for supporting fungal biodiversity (Sippola *et al.*, 2005; Odor *et al.*, 2006; Jönsson *et al.*, 2008; Norden *et al.*, 2008; Berglund *et al.*, 2011; Abrego and Salcedo, 2013). The amounts and quality of deadwood in a forest site are useful indicators of the likely biodiversity of certain taxonomic groups in forests in Britain (Ferris and Humphrey, 1999) and Northern Finland (Juutinen *et al.*, 2006).

Previous studies in Britain and Ireland indicated that mixed tree species plantation forests can support higher biodiversity than similar monoculture forests (Humphrey *et al.*, 2003; Iremonger *et al.*, 2007). Results from Sweden show that transforming spruce monocultures into spruce–birch mixtures provide gains in the biodiversity of many taxonomic groups, and that these biodiversity gains can be amplified when modifications to other forest management techniques (e.g. rotation length and retained CWD volume) were coupled with the introduction of another species (i.e. birch) into the spruce monocultures (Felton *et al.*, 2010). Studies in Norway estimated that in a single-storey mixed Norway spruce and birch forest, productivity of the Norway spruce component is comparable to that in monoculture Norway spruce forests as long as removal of the birch component intensifies in the latter harvesting stages (Fahlvik *et al.*, 2011). Another study of mixed Norway spruce and European beech (*Fagus sylvatica* L.) reported an accelerated growth of spruce by beech admixtures on poor sites, while growth of beech can be promoted by admixture of spruce, particularly on excellent sites (Pretzsch *et al.*, 2010). These results agree with a meta-analysis of boreal and northern temperate forests, which found that mixed tree species were as productive as monoculture forests, while having increased resistance to pest damage over monoculture forests (Griess and Knoke, 2011).

Humphrey (2005) provides a comprehensive review dealing with the possibility and consequences of creating old-growth conditions in spruce plantations in Britain. Overall, he concluded that spruce plantations are an excellent candidate for such conversions, as they are widespread, somewhat lacking in biodiversity conservation abilities in their current condition, and as they develop old-growth conditions faster than many native tree species forests. Humphrey (2005) suggests that ~50 per cent of the land area could support these late-successional Sitka spruce stands; however, this area may be an overestimate as this also includes land area in Scots pine (*Pinus sylvestris* L.). It is suggested that these old-growth patches should be scattered throughout the region, situated in sheltered areas and also in close proximity to semi-natural forest. This would reduce damage caused by wind-throw while increasing the chance of native fauna and flora moving from the native forest to the plantation spruce forests.

Moreover, the management practices outlined throughout this paper (i.e. CCF, selective logging, large-diameter deadwood retention, increasing tree species diversity and increasing structural diversity) are some of the techniques proposed to aid in the development of old-growth conditions in Sitka spruce plantations in Britain. One of the largest factors that would hinder the conversion of these forests into old-growth patches would be the financial aspects of the conversion. Knoke *et al.* (2008) concluded that before admixing of broadleaves into coniferous plantations becomes a common practice, there are several unanswered questions that need to be addressed in the valuation of forests to include non-timber values, such as those of biodiversity and ecosystem services. As 65 and 43 per cent of the forests in Britain and Ireland, respectively (NFI, 2003, 2007), are privately owned, some financial incentives would be necessary to encourage private forest owners to allow their forests to develop into old-growth stands. At present, afforestation rates in Ireland do not offer any significant financial rewards for increasing the proportion of additional species planting in Sitka spruce forests over the mandatory 10 per cent (Forest Service, 2012).

A number of factors should be taken into account in selecting Sitka spruce forests that would be amenable to the management strategies we have discussed. Firstly, in public forests there may be more opportunities to put greater emphasis on the enhancement of biodiversity and ecosystem services than exists in privately owned forests. Although ownership types are governed by the same rules that act to foster biodiversity (Forest Service, 2000; UK Forestry Standard, 2011), public forests are open to public access and therefore would benefit from the increased aesthetics provided by retained CWD, mixed tree species and a large visible biodiversity component. Secondly, situating these patches of forest near existing semi-natural forests would provide a source of seed and fungal inoculum and close access by wildlife to the Sitka spruce forest. It has been shown for both ground flora (Ferris *et al.*, 2000; French *et al.*, 2008) and fungal communities (Humphrey *et al.*, 2003; Bahram *et al.*, 2012) that the closer a plantation forests is to a native forests the more similar the communities of the two. Finally, as suggested by Humphrey (2005), distributing these forests across the landscape would create a mosaic of land-use types. This diffuse, mosaic pattern would ensure a degree of connectivity or ‘habitat stepping stones’ at the landscape scale, maximizing the provision of suitable habitat patches.

Conclusions

There is increasing interest worldwide in managing forests to benefit biodiversity, enhance ecosystem services and assure long-term sustainability of forest products, wildlife and other forest resources. Simply managing forests primarily for timber may not meet the broader social values demanded by the public. Forests produce a variety of ecosystem services including important ecological services and cultural values as well as commodities such as wood products. An important goal of forest management is to increase stand structural diversity, provide fish and wildlife habitat and improve biodiversity of managed forests. In this paper we use knowledge and experience from natural spruce forests in southeast Alaska to suggest some ideas for managing Sitka spruce plantations in other parts of the world to increase biodiversity and enhance a variety of forest ecosystem services. These

perspectives indicate that new silvicultural systems that use partial cutting in older Sitka spruce stands could alleviate some of the problems associated with conventional even-aged management in southeast Alaska and increase both stand structural diversity and enhance biodiversity.

We also assessed younger mixed red alder–conifer stands to evaluate stand structure and understorey plant diversity and abundance. Altering the composition of young pure conifer forests with the inclusion of broadleaved species such as alder or birch may improve wildlife habitat and enhance biodiversity of species such as macrofungi. Increasing tree species diversity in Sitka spruce plantations may also increase fungal biodiversity and associated biodiversity of forest ecosystems. Well-planned silvicultural systems that include a mixture of broadleaved–conifer compositions could provide trees for timber production and also improve other forest ecosystem services that are often compromised in young pure conifer forests. Some of our recommendations include partial harvesting of Sitka spruce plantations and establishing mixtures of broadleaved–conifer compositions to increase structural complexity and to benefit biodiversity in Sitka spruce plantations. The ideas presented here will help guide forest managers in Great Britain, Ireland and worldwide as they consider these broad natural resource goals for their spruce forests.

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