

<https://helda.helsinki.fi>

A keystone species, European aspen (*Populus tremula* L.), in boreal forests : Ecological role, knowledge needs and mapping using remote sensing

Kivinen, Sonja

2020-04

Kivinen , S , Koivisto , E , Keski-Saari , S , Poikolainen , L , Tanhuanpää , T , Kuzmin , A , Viinikka , A , Heikkinen , R K , Virkkala , R , Vihervaara , P & Kumpula , T 2020 , ' A keystone species, European aspen (*Populus tremula* L.), in boreal forests : Ecological role, knowledge needs and mapping using remote sensing ' , Forest Ecology and Management , vol. 462 , 118008 . <https://doi.org/10.1016/j.foreco.2020.118008>

<http://hdl.handle.net/10138/340973>

<https://doi.org/10.1016/j.foreco.2020.118008>

cc_by_nc_nd

acceptedVersion

Downloaded from Helda, University of Helsinki institutional repository.

This is an electronic reprint of the original article.

This reprint may differ from the original in pagination and typographic detail.

Please cite the original version.

**A keystone species, European aspen (*Populus tremula* L.), in boreal forests:
ecological role, knowledge needs and mapping using remote sensing**

Sonja Kivinen^{1,2*}, Elina Koivisto³, Sarita Keski-Saari^{1,4}, Laura Poikolainen¹, Topi Tanhuanpää^{1,5},
Anton Kuzmin¹, Arto Viinikka², Risto K. Heikkinen², Juha Pykälä², Raimo Virkkala², Petteri
Vihervaara² & Timo Kumpula¹

¹Department of Geographical and Historical Studies, University of Eastern Finland, P.O. Box 111,
FI-80101 Joensuu, Finland.

²Finnish Environment Institute, Latokartanonkaari 11, FI-00790 Helsinki, Finland

³University of Turku, Department of Biology, FI-20014 Turun yliopisto, Finland

⁴Department of Environmental and Biological Sciences, University of Eastern Finland, P.O. Box
111, FI-80101 Joensuu, Finland

⁵Department of Forest Sciences, University of Helsinki, FI-00014, Helsinki, Finland

*Corresponding author, E-mail: sonja.kivinen@uef.fi

26 **Abstract**

27 European aspen (*Populus tremula* L.) is a keystone species in boreal forests that are dominated by
28 coniferous tree species. Both living and dead aspen trees contribute significantly to the species
29 diversity of forest landscapes. Thus, spatial and temporal continuity of aspen is a prerequisite for the
30 long-term persistence of viable populations of numerous aspen-associated species. In this review, we
31 collate existing knowledge on the ecological role of European aspen, assess the knowledge needs for
32 aspen occurrence patterns and dynamics in boreal forests and discuss the potential of different remote
33 sensing techniques in mapping aspen at various spatiotemporal scales. The role of aspen as a key
34 ecological feature has received significant attention, and studies have recognised the negative effects
35 of modern forest management methods and heavy browsing on aspen occurrence and regeneration.
36 However, the spatial knowledge of occurrence, abundance and temporal dynamics of aspen is scarce
37 and incomprehensive. The remote sensing studies reviewed here highlight particularly the potential
38 of three-dimensional data derived from airborne laser scanning or photogrammetric point clouds and
39 airborne imaging spectroscopy in mapping European aspen, quaking aspen (*Populus tremuloides*
40 Michx.) and other *Populus* species. In addition to tree species discrimination, these methods can
41 provide information on biophysical, biochemical properties and even genetic diversity of aspen trees.
42 Major obstacles in aspen detection using remote sensing are the low proportion and scattered
43 occurrence of European aspen in boreal forests and the overlap of spectral and/or structural properties
44 of European aspen and quaking aspen with some other tree species. Furthermore, the suitability of
45 remote sensing data for aspen mapping and monitoring depends on the geographical coverage of data,
46 the availability of multitemporal data and the costs of data acquisition. Our review highlights that
47 integration of ecological knowledge with spatiotemporal information acquired by remote sensing is
48 key to understanding the current and future distribution patterns of aspen-related biodiversity.

50 **Key words:** biodiversity, boreal forests, European aspen, *Populus tremula* L., remote sensing

52 1. Introduction

53 Biodiversity loss is a global threat that deteriorates ecosystem function and thereby impacts the
54 well-being of humans (Hooper et al., 2012; IPBES, 2019). Forest biodiversity has been negatively
55 affected by modern large-scale forestry that has caused loss and fragmentation of pristine habitats
56 and reduced structural heterogeneity in managed forest stands. Boreal forests cover large areas in
57 northern Europe, but they are mostly intensively managed throughout their range. Moreover,
58 managed boreal forests tend to be monocultures of conifers (Esseen et al., 1997; Mönkkönen et al.,
59 2018; Seedre et al., 2018; Rodríguez et al., 2019). For biodiversity conservation and ecosystem
60 services, this phenomenon is a drawback because mixed-species forests can provide important
61 benefits. For example, they host greater species richness, are more resistant to pests and pathogens
62 and have a higher capacity for carbon sequestration (Gamfeldt et al., 2013; Brockerhoff et al., 2017;
63 Ampoorter et al. 2019; Rodríguez et al. 2019). Both living and dead deciduous trees play an important
64 role in diversifying the structure and species composition of boreal forests (Kouki et al. 2004).

65 European aspen (*Populus tremula* L., hereafter ‘aspen’ or ‘European aspen’) is a keystone species
66 and an early-succession species in boreal forests. Although it has a sparse and scattered occurrence
67 in northern Europe, it contributes significantly to the biological diversity of boreal forest landscapes
68 (Hynynen and Viherä-Aarnio, 1999; Kouki et al., 2004; Tikkanen et al., 2006; Whitham et al., 2006;
69 MacKenzie, 2010; Caudullo and de Rigo, 2016). Aspen is an important host for many species. Aspen
70 trees are inhabited by epiphytic bryophytes and lichens (Kuusinen, 1994; Gustafsson and Eriksson,
71 1995; Hazell, 1998; Pykälä et al., 2006), pathogens (Callan, 1998), herbivorous invertebrates
72 (Robinson et al., 2012), mammals such as the flying squirrel (*Pteromys volans*; Hanski, 1998; Remm
73 et al. 2017) and birds such as woodpeckers and owls (Hågvar et al., 1990; Angelstam and Mikusinski,
74 1994; Tikkanen et al., 2006; Hardenbol et al. 2019). Secondary hole-nesters, including many tits,
75 flycatchers, owls, ducks and flying squirrels, are dependent on cavities excavated by woodpeckers
76 (Martin and Eadie, 1999; Baroni et al. 2020). Aspen leaf litter is utilised by, for example, gastropods
77 (Suominen et al., 2003), and dead and decaying aspen trunks provide a suitable habitat for myriad

78 polypore fungi (Kotiranta and Niemelä, 1981; Hynynen and Viherä-Aarnio, 1999; Junninen et al.,
79 2007) and saproxylic invertebrate species (Siitonen and Martikainen, 1994; Martikainen, 2001;
80 Dahlberg and Stokland, 2004; Halme et al., 2012). The conservation biological importance of aspen
81 is illustrated by the fact that many of the aspen-associated species—dependent either on living of
82 dead aspen trees—are red-listed (Jonsell et al., 1998; Hynynen and Viherä-Aarnio, 1999; Dahlberg
83 and Stokland, 2004; Tikkanen et al., 2006).

84 Given this keystone role, a continuous spatial and temporal supply of aspen trees is a prerequisite
85 for maintaining viable populations of associated species in boreal forests (Kouki et al., 2004; Vehmas
86 et al., 2009). Thus, information on the occurrence, abundance and regeneration of aspen is crucial for
87 efficient planning and implementation of sustainable forest management measures and conservation
88 efforts. Knowledge on changes in aspen occurrence and distribution is also important, because aspens
89 can serve as an indicator of ecological integrity and landscape health (Kay, 1997). The widespread
90 but patchy and clustered occurrence of aspen in boreal forests poses challenges for ordinary inventory
91 and mapping methods (Maltamo et al., 2015). For example, the number of sample plots in traditional
92 forest inventories is often too low to capture patchily occurring phenomena and their variation
93 (Kangas, 2006). Recent advances in remote sensing technology hold much promise for obtaining
94 systematic and rapidly updated information on the spatiotemporal distribution and characteristics of
95 tree species over wide areas (Fassnacht et al., 2016). Thus, they can provide new opportunities to map
96 key ecological features, such as aspen, in order to create spatiotemporally comprehensive biodiversity
97 assessments (Pettorelli et al., 2014; Wang & Gamon 2019).

98 A few earlier reviews examined European aspen or *Populus tremuloides* Michx. (quaking aspen,
99 trembling aspen or American aspen) that occur in North America. A review by Landhäusser et al.
100 (2019) focused on ecology, management and restoration of quaking aspen, and the review by
101 MacKenzie (2010) examined ecology, conservation and management of both European aspen and
102 quaking aspen in the northern hemisphere. Worrell (1995a, 1995b) reviewed the distribution, ecology
103 and genetic variation—as well as values, silviculture and utilisation—of European aspen, with

particular reference to Scotland. Myking et al. (2011) reviewed life history strategies of European aspen and the browsing effects on it. Furthermore, Rogers et al. (2020) reviewed conservation of aspen in a global context. The key aims of this review are to (1) collate existing knowledge on the ecological role of European aspen in boreal forests, (2) examine knowledge needs for aspen occurrence and dynamics and (3) study the potential of different remote sensing techniques in mapping aspen trees and stands at various spatiotemporal scales. We will identify current research gaps and new methodological opportunities that can increase our understanding of aspen-related biodiversity in rapidly changing forest landscapes (Hyvärinen et al., 2019). In the remote sensing section (section 4), we examine the mapping of European aspen, quaking aspen and a few other *Populus* species to cover the current knowledge on the topic as widely as possible.

2. Aspen as a keystone species in boreal forests

Aspen is a pioneer species in boreal forests and thus needs open areas or spots to regenerate and establish. It typically grows either in sites where there are no shading trees or as hold-overs in more closed forests, and it readily colonises new open areas. Aspen has a wide ecological amplitude, and it occurs in many forest types, from dry rocky areas to water-logged sites. Aspen reproduces both by seeds and root sprouts, with the latter being the most common and most successful form of reproduction.

Long-term aspen persistence in primeval old-growth forests has only recently received attention (Fig. 1a). Studies suggest that aspens can live up to 100-200 years (Lilja et al., 2006; Latva-Karjanmaa et al., 2007; Vehmas et al., 2009), and aspen presence even in old-growth forests reaching the age of 450 years has been reported (Tarasova et al. 2017). According to Bergeron et al. (2014), gap dynamics play an important role in long-term persistence of aspen (*P. tremuloides*) in low intensity disturbance regimes (i.e., areas where stand replacing disturbances are scarce) in North America. Single blowdowns of large dominant trees or small-scale windthrow areas allow self-replacement of aspen through suckering (Groot et al. 2009, Reinikainen et al. 2012). However, in

130 European Russia, birch and rowan appeared to be more common in gaps than European aspen
131 (Gromtsev et al. 2002).

132 Aspen leaf litter has a high calcium content, which can increase the pH of the typically acidic
133 boreal forest soils. This fact has important consequences on the soil chemistry, ecosystem functioning
134 and habitat availability for accompanying species (Koivula et al., 1999; Suominen et al., 2003; Nikula
135 et al., 2010). Buck and St. Clair (2012) showed that the surface soil horizons of quaking aspen stands
136 have higher mineral nutrient availability compared to other soil types. They proposed that aspen soils
137 are biologically more active compared to other soil types. The pH of aspen bark varies widely among
138 stands as well as within stands; measured stand averages range from 4.7 to 6.3 (Kuusinen, 1994). The
139 relatively high bark pH can affect the abundance of epiphytic bryophyte and lichens that grow on
140 aspens (Kuusinen, 1994; Gustafsson and Eriksson, 1995). In addition to chemical properties, aspen
141 trees can provide unique physiological environments for associated species. For example, tree-
142 dwelling bats favour aspen as their maternity roosts because they are both warmer and safer than
143 other tree species (Michaelsen, 2016).

144 The occurrence, abundance and diversity of the aspen-associated species are markedly affected by
145 the characteristics of individual aspen trees, including size and age. Many species prefer or are
146 confined to old aspens, and large-diameter host trees are favoured, for example, by epiphytic
147 bryophytes (Hazell et al., 1998; Gu et al., 2001). Due to this factor, large aspens with a diameter at
148 breast height that exceeds 20 cm (Latva-Karjanmaa et al., 2007) or 25 cm (Maltamo et al., 2015) have
149 been included as ecologically relevant individuals in studies that aimed to map the spatiotemporal
150 variation in aspen abundance. Black-coloured and speckled bark, slow tree growth (as defined by
151 visual inspection, e.g., the relationship between the diameter and bark texture) and tree inclination
152 angle are also important determinants of epiphytic lichen species on aspen trees (Perhans et al., 2014).
153 Further, the number of epiphytic bryophyte species increases with aspen bark thickness (Gustafsson
154 and Eriksson, 1995). Tarasova et al. (2017) also found distinct epiphyte species composition at

155 different heights of aspen trunks and branches. These data show that disparate lichen and moss species
156 often occupy different ecological niches (Fig. 1b).

157 In addition to the characteristics of individual aspens, local- and landscape-level factors can impact
158 species assemblages associated with aspen trees. For example, field-layer vegetation of the forest
159 (Gustafsson and Eriksson, 1995; Hazell et al., 1998) and forest stand structure, i.e., accompanying
160 tree species (Hazell et al., 1998), affect the abundance of bryophytes on aspens. Furthermore, the
161 amount of light in a forest stand affects the number and community composition of epiphyte species
162 (Gustafsson and Eriksson, 1995). An increased density of spruce causes more shading that, in turn,
163 increases the abundance of certain bryophyte species (Hazell et al., 1998). Long-term persistence of
164 aspen in the landscape is critical for the continuance of aspen-related species. Aspen-associated
165 species, such as epiphytic lichens, may persist in the remaining small patches of host trees for some
166 time (Gu et al., 2001), but ultimately their populations become increasingly threatened as the
167 resources they need decrease in the landscape. Suominen et al. (2003) showed that the connectivity
168 of habitats and large aspen stand sizes, at least 500 m², are important determinants for abundance and
169 diversity of gastropods that live on aspen leaf litter. In general, information on aspen occurrence and
170 dynamics at the landscape level in the boreal zone is scarce. Latva-Karjanmaa et al. (2007) estimated
171 that 50% of the mature aspens of an old-growth forest in the studied nature protection area in eastern
172 Finland will die within the next 30 years, and only 10% of existing trees will survive over 90 years.

173 The number of species that live on dead aspen wood material is high. Thus, the occurrence of this
174 material is of critical importance for species richness and biodiversity conservation (Martikainen et
175 al., 2000; Kouki et al., 2004). Aspen decay is a rather fast process; most of the current dead wood
176 will become disintegrated within about 90 years, depending on the current decay stage (Latva-
177 Karjanmaa et al., 2007). The continued supply of dead wood depends on the regional abundance of
178 aspen trees and the disturbances that generate fallen and dead trunks. For example, several threatened
179 aspen-specialist polypore species require frequent emergence of new suitable host trees as old ones
180 become unsuitable for them in approximately 10 years after colonisation (Martikainen et al., 2000).

181 Similarly, saproxylic insect species that utilise recently dead aspen wood are dependent on
182 sufficiently rapid formation of new habitats (Ranius et al., 2011). Saproxylic invertebrates that live
183 on decaying wood can often colonise several tree species and therefore are not always dependent on
184 the occurrence of one species. However, species composition of the saprophytic fungi community
185 may crucially impact the habitat quality for many saproxylic insects (Jonsell et al., 1998). Likewise,
186 nematodecan (Diptera) communities of a single aspen log may markedly differ between the base and
187 top part of the same tree, but the factors that determine this variation and the preferred microhabitat
188 for each insect species are poorly understood (Halme et al., 2013). Økland et al. (1996), Ranius et al.
189 (2011) and Jacobsen et al. (2015) demonstrated that species richness of aspen-associated saproxylic
190 beetles can be related to dead wood volume within a radius of 0.1–3 km. These findings highlight the
191 importance of habitat availability at larger scales.

192 Aspen has a clonal growth habit, in which several ramets can emerge from one clone as root
193 sprouts. However, clones of European aspen often consist of a single ramet. For example, in a Finnish
194 study, 70% of the clones comprised only one ramet (Suvanto and Latva-Karjanmaa, 2005). Genetic
195 studies revealed that intrapopulation genetic variation of European aspen is relatively high. These
196 data imply that the proportion of individuals that arise from seeds is higher than previously assumed
197 (Suvanto and Latva-Karjanmaa, 2005). On the contrary, quaking aspen can form giant growth, with
198 the largest known genet covering about 43.6 ha (DeWoody et al., 2008). Nevertheless, quaking aspen
199 also exhibits much more genetic variation than previously presumed, with many clones encountered
200 only once in a 50 m grid (Mock et al., 2008). In European aspen, the maximum distance between
201 ramets in a clone can be at least 46 m (Suvanto and Latva-Karjanmaa, 2005). In Scotland, 21 clones
202 were detected in a 4.6 ha area, when 186 aspens were sampled (Easton, 1997).

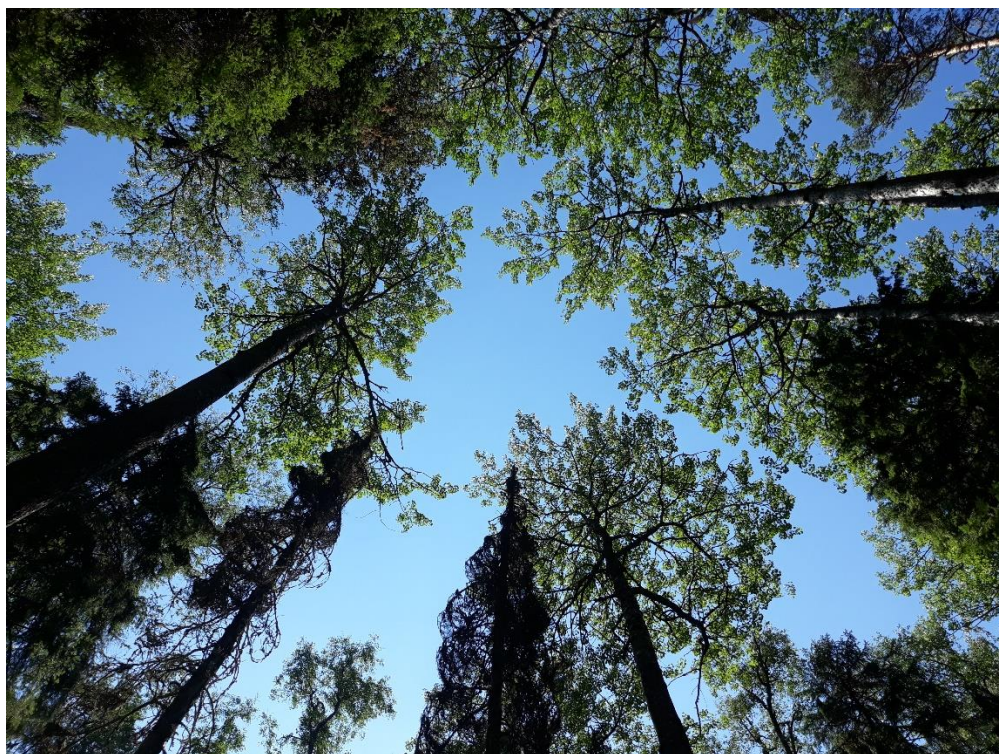
203

204

205

206

207 a)



208

209

210 b)



211

212 Fig. 1.a) Crowns of aspen hold-overs in a natural old-growth forest that reach above below-growing
213 spruce trees. b) Aspen trunk with epiphytic lichens, mosses and *Orthilia secunda*. (Photo credits:
214 Sarita Keski-Saari.)

215

216 3. Major drivers of aspen occurrence and dynamics in boreal forests

217

218 3.1 Forest management methods

219 Forest industry and management in Fennoscandia has traditionally favoured conifers (*Picea abies*,
220 *Pinus sylvestris*) over aspen. Thus, over the years aspen trees have been eradicated both mechanically
221 and via herbicides, particularly during 1950–1980 (Östlund et al., 1997; Rouvinen et al., 2005; Latva-
222 Karjanmaa et al., 2007). Such forestry actions were justified by the presumed harmful effects of
223 aspens to the more valued conifers. Aspen acts as a host for decaying fungi and rust diseases, such as
224 *Melampsora pinitorqua*, that occur in young pine stands (Östlund et al., 1997), and competition with
225 fast-growing aspen can obstruct the growth of conifers (Yang, 1991; Filipescu and Comeau, 2007).
226 Aspen regeneration and establishment are dependent on disturbances, including storms and fires. In
227 contrast, lack of natural disturbances favours coniferous species over deciduous ones. The prevailing
228 forest management practices during the last two centuries have clearly favoured conifers over
229 deciduous species; indeed, efficient fire suppression has almost eliminated fires as a rejuvenating
230 factor from the boreal forests of Sweden and Finland (Zackrisson, 1977; Kouki et al., 2004; de
231 Chantal et al., 2005; Lankia et al., 2012). Edenius et al. (2011) reported that aspen regeneration has
232 declined since the 1970s in Sweden due to the large-scale transformation of land use together with
233 mechanical clearing of deciduous trees and the use of herbicides (Fig. 2a).

234 Recently, aspen has received more supportive consideration—based on the realisation of its
235 keystone species role in forest biodiversity—in the management planning of commercial forests. The
236 most important recommendations to secure aspen regeneration include restoring regeneration niches
237 by mimicking natural disturbance processes, such as fire at various spatial scales, and retaining aspen

238 in clearings and pre-commercial thinnings (Kouki et al., 2004; Vanha-Majamaa et al. 2007; Edenius
239 et al., 2011). Clear-cutting acts as a source of disturbance and promotes the regeneration of aspen.
240 How this is realized in the number of mature aspens depends on forestry actions following the
241 regeneration, such as thinning of seedling stands (Fraser et al. 2003). Similarly, the extent of tree
242 retention is dependent on the forestry actions (Latva-Karjanmaa et al., 2007; Myking et al., 2011;
243 Kuuluvainen et al. 2019). Creating dead wood by girdling aspens or leaving dead wood on clear-cuts
244 may represent beneficial measures to preserve species that are dependent on dead aspens (Jonsell et
245 al., 1998; Martikainen et al., 2000; Runnell et al. 2012), but could be harmful for species dependent
246 on old living aspens.

247 The use of retention trees has been considered an important measure to halt forestry-related loss
248 of aspen-associated species (Martikainen, 2001; Hedenås and Hedström, 2007; Junninen et al., 2007;
249 Sahlin and Ranius, 2009; Lundström et al., 2013). In northern Europe, aspen has been widely
250 favoured as a retention tree; there are many studies that show the efficacy of retained aspens on
251 biodiversity (Rosenvald and Löhmus, 2008; Gustafsson et al., 2010; Lundström et al., 2013;
252 Fedrowitz et al., 2014; Perhans et al., 2014) (Fig. 2b). However, it is important to acknowledge that
253 there are also species that perform poorly on retention aspens (Hedenås and Hedström, 2007).
254 Furthermore, there is a need to improve the efficiency of retained aspens for biodiversity by adding
255 their numbers and using ecologically meaningful tree characteristics (e.g., black-coloured bark, slow
256 tree growth, inclined stems and speckled bark) for their selection as retention trees (Perhans et al.,
257 2014).

258 The retention trees are prone to wind disturbance (Jönsson et al., 2007). The post-harvest mortality
259 rate is high with retained aspens as well, 46 % of them reported fallen after six years of monitoring
260 (Rosenvald et al. 2008) and 52 % after 16 years of monitoring (Rosenvald et al. 2019). Hence, not
261 only it is essential to select high ecological value aspens, but they should also have qualities of high
262 survival (e.g. large tree diameter, position near forest edges, high retention density) (Rosenvald et al.,

263 2008; Hämäläinen et al., 2016). Nevertheless, the fallen retained aspens may also be valuable habitats
264 (Junninen et al., 2007; Rosenvold et al. 2019).

265 In Finland, leaving aspens standing as retention trees has had positive effect on some species
266 previously categorised as Near Threatened and even on certain species previously classified as
267 Threatened. This improvement has aided their red-listing status to be re-classified as Least Concerned
268 species (Rassi et al., 2010). Large aspens are generally the most important for biodiversity, and hence
269 they are generally favoured as retention trees (e.g., Kolström and Lumatjärvi, 2000). However, Schei
270 et al. (2013) found that, at least for lichen species, retention of young aspens may also be a beneficial
271 practice as they have a longer expected persistence compared to old aspens. Lundström et al. (2013)
272 showed that the number of aspen-dependent lichen species on retention aspens can be lower in
273 recently harvested stands compared to stands harvested 10–16 years ago. This finding may imply that
274 species that favour more interior forest conditions persisted, and in addition, new species that are
275 adapted to open environments colonised the retention trees.

276 The response of different species to retention trees appears to be species-dependent. For example,
277 cyanolichens often inhabit retention trees, whereas green algal lichens show contrasting habitat
278 preferences: they are more abundant in closed forests compared to retention trees (Hedenås and
279 Hedström, 2007). Approximately 80% of the threatened saproxylic invertebrates in Sweden occur in
280 open environments. Thus, they are likely to benefit from retention trees, while the species that require
281 shadow or semishade will not (Jonsell et al., 1998). Oldén et al. (2014) concluded that in order to be
282 as effective as possible, retention trees should be left adjacent to conservation sites, which can
283 function as sources of re-colonisation and support the populations of species that require old-growth
284 forests. Similarly, Hedenås and Ericsson (2000) and Hedenås et al. (2007) highlighted that a
285 prerequisite for new-establishment in spore dispersed lichen species is that there are old aspen stands
286 that act as source populations in the surrounding landscape. Moreover, the quantity of retention trees
287 should be substantial to prominently support, for example, the survival of accompanying forest
288 vegetation (Johnson et al., 2014). Sverdrup-Thygeson et al. (2014) highlighted that retention patches,

289 woodland key habitats and nature reserves all have important and complementary functions for wood-
290 living species in boreal forests.

291

292 a)



293

294

295

296

297

298

299

300

301

302

303

304

305 b)



306

307 Fig. 2.a) A young aspen in a clear-cut (Photo credit: Sonja Kivinen). b) A group of retention trees
308 including aspen. (Photo credit: Sarita Keski-Saari)

309

310 **3.2 *Herbivores and pathogens***

311 European aspen shoots and leaves provide valuable nutrition to several herbivore species, as
312 reviewed by Myking et al. (2011). Browsers can suppress the regeneration of aspen and, in the long-
313 term, reduce recruitment, delay maturation, increase mortality and ultimately cause a decline in local
314 aspen populations. High browsing pressure is thus a major threat to species that are dependent on old
315 aspens (Kouki et al., 2004; Komonen et al. 2020). Moose (*Alces alces*) is the primary herbivore that
316 affects aspen recruitment (Edenius and Ericsson, 2007; Edenius et al., 2011). Fennoscandian moose
317 populations started to grow rapidly in the 1960s, due to suitable habitats produced by clear-cutting,
318 the low numbers of large carnivores and the use of supplementary forages, and are currently among
319 the most productive and heavily harvested moose populations in the world (Lavsund et al., 2001). A

320 recent increase in the number of roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) also
321 causes high browsing pressure on aspens (Myking et al., 2011). Similarly, intense browsing by
322 ungulates is harmful to the establishment and recruitment of quaking aspen in North America (Seager
323 et al., 2013; Rhodes et al. 2017).

324 Edenius et al. (2007) found that heavy browsing in the absence of either human-caused or natural
325 disturbances accelerates succession towards conifer dominance. However, Myking et al. (2011)
326 emphasised that more research is needed on how browsing interacts with other factors and affects the
327 spatiotemporal variation in recruitment rates and population dynamics of aspen. Additional data are
328 also needed on ungulate densities that allow the maintenance of viable aspen populations in different
329 habitats (Edenius and Ericsson, 2015). An important management tool could be protecting established
330 aspen ramets at designated sites from browsing either by fencing or reducing ungulate numbers
331 (Kouki et al., 2004; Edenius et al., 2011). After forest fire, aggregations of dead wood can act as
332 browsing refugia for aspen seedlings (de Chantal and Granström 2007), and one option would be to
333 leave logs in a crisscross arrangement to provide dead wood and a barrier against herbivores (Latva-
334 Karjanmaa et al., 2007).

335 In addition to moose, hares (*Lepus* sp.) and voles (*Microtus* and *Myodes* sp.) have a high preference
336 for aspen (Hjältén et al., 2004). For example, in an old-growth forest in northern Finland, hare
337 browsing was as frequent for saplings as moose browsing (Latva-Karjanmaa et al., 2007). Insect
338 herbivory apparently has a limited impact on both aspen survival and growth. For example, arthropod
339 herbivore abundance and species richness co-occurred with the highest tree growth in a common
340 garden experiment in Sweden. This finding indicates that the trees preferred by insects maintained
341 the highest growth in the subsequent year (Robinson et al., 2012). On the other hand, pathogens may
342 seriously hamper aspen regeneration. The number of pathogen species that occur on aspens is notably
343 high (Callan 1998). For example, *Venturia tremulae* fungus has a high capacity to cause epidemics;
344 by attacking aspen seedlings, it can decrease growth and even cause aspen tree death (Kasanen et al.,
345 2004).

346

347 3.3 *Climate warming*

348 Climate warming results in elevated mean temperatures and changes in precipitation in northern
349 areas (IPCC, 2018). Aspen is a thermophilic species that is expected to benefit from rising
350 temperatures in boreal forests. Accordingly, elevated temperature facilitates aspen growth (Sivadasan
351 et al., 2018). On the other hand, drought can seriously hamper the growth of aspen trees, and sexual
352 reproduction and seedling establishment of aspen are strongly dependent on adequate moisture
353 (Latva-Karjanmaa et al., 2003; Singer et al., 2019). Moisture stress also negatively impacts the growth
354 of aspen seedlings (Nikula et al., 2011; Possen et al., 2011). As a general rule, increased occurrence
355 of disturbances, including storms and forest fires (IPCC 2018), may benefit aspen regeneration.
356 However, severe fires can actually be harmful because they may hamper the formation of root suckers
357 if roots are damaged by the fire. Different IPCC climate scenarios are likely to promote distinct
358 species combinations, depending on the projected outcome of the host tree species. For example,
359 saproxylic species associated with aspen may benefit from future climate characterised by an
360 intermediate rise in temperatures, whereas an extreme rise would negatively affect them (Mazziotta
361 et al., 2012).

362 Van Bogaert et al. (2010) estimated that aspen has become approximately 16 times more abundant
363 in subarctic Sweden over the past 100 years, mainly due to increased sexual regeneration. According
364 to their study, aspen colonisation at the tree line is mainly restricted by summer temperature, whereas
365 disturbances caused by moth population outbreaks in birch forests are critical for aspen establishment
366 at lower elevations. Future aspen occurrence and abundance in these areas will thus be driven by
367 complex relationships among changing disturbance regimes, future herbivore population dynamics
368 and responses of birch and pine to changing climate. Van Bogaert et al. (2009) found that moth
369 outbreaks on birch stimulate the recruitment of aspen, but aspen stand expansion can be strongly
370 restricted by moose browsing. The dynamics between aspen and birch in subarctic forest ecosystems

371 is thus likely to be dependent on the number of vertebrate browsers relative to the number of aspen
372 recruits.

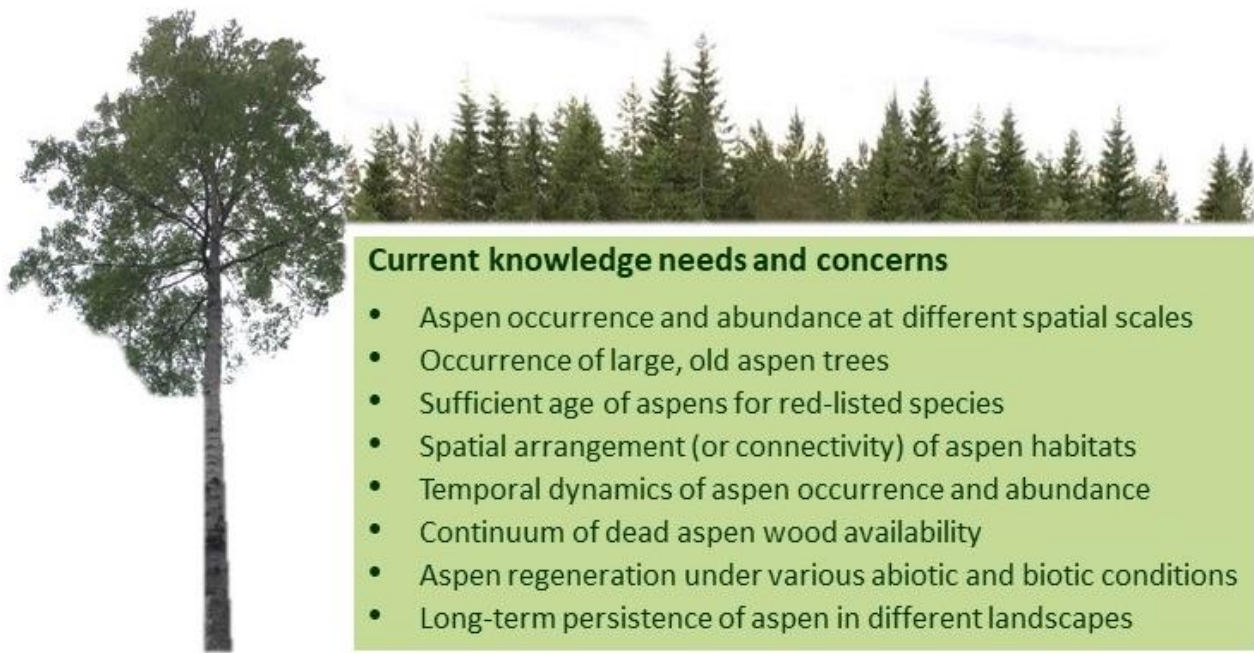
373

374 ***3.4 Spatial and temporal knowledge needs***

375 Many of the ecological studies that we reviewed highlight the significant ecological role of aspen
376 in boreal forest ecosystems in northern Europe. These studies also call for acquisition of accurate
377 spatiotemporal information on aspen occurrence and abundance, which is currently scarce and
378 incomprehensive (Fig. 3). Spatial distribution, size and age of aspen trees are highly relevant
379 information. These data will enable assessing the landscape's ability to support viable populations of
380 aspen-associated species. This information will also be of significant importance in understanding
381 the contributions of retention trees on aspen-related biodiversity.

382 A crucial ecological question is the long-term persistence of aspen in boreal forest landscapes.
383 Aspen dynamics and regeneration are driven by various anthropogenic, biotic and abiotic factors, as
384 well as the relationships among these elements. Time series analysis of aspen dynamics will increase
385 the understanding of the role of different factors on aspen persistence and enable estimates of current
386 and future status of aspen-related species. Information on the abundance of aspen trees in a landscape
387 will also provide estimates for the continuum of dead aspen wood, which is of critical importance for
388 many species. Furthermore, the ability to produce spatial and temporal information on aspen at
389 different spatial scales would facilitate more efficient planning and implementation of forest
390 management measures and conservation efforts.

391



392

393 Fig. 3. Current knowledge needs and concerns related to European aspen in boreal forest
394 landscapes.

395

396 **4. Mapping aspen occurrence and dynamics using remote sensing**

397 ***4.1. Remote sensing techniques in vegetation mapping***

398 Various remote sensing techniques enable timely and spatially explicit mapping of land cover.
399 They can provide significant opportunities in acquiring information on the occurrence and dynamics
400 of keystone species, such as aspen, in changing forest environments at various spatial and temporal
401 scales (Ghosh et al., 2014). Remote sensing data can be acquired with unmanned aerial systems (UAS,
402 also referred as drones), planes and satellite platforms. Depending on the platform and sensor, the
403 spatial resolution (pixel size) of the imagery can range from some centimetres to hundreds of metres.
404 Similarly, the geographical extent of the data can vary from local to global coverage.

405 Spectral remote sensing data consists of spatial images where every pixel contains the intensity of
406 electromagnetic radiation reflected or emitted from the target and recorded by a sensor. Optical
407 remote sensing is based on detecting objects at different wavelengths from visible and near-infrared
408 range (VNIR; 400–1000 nm) and shortwave infrared range (SWIR; 1000–2500 nm) up to long-wave

409 infrared range (LWIR; 8000–14000 nm). Spectral resolution, i.e., the number and width of spectral
410 bands in which information is recorded, varies between the sensors. Multispectral imagery consists
411 of several generally non-contiguous spectral bands of varying bandwidths, whereas hyperspectral
412 images (imaging spectroscopy) include a contiguous spectral range with hundreds of narrow bands.
413 Temporal resolution refers to how often the remote sensing system records imagery of a particular
414 area (revisit time; see Xie et al., 2008).

415 Aerial photography (panchromatic [black and white], colour [red, green, blue or RGB], or colour-
416 infrared [CIR, also referred as false-colour]) is a traditional remote sensing technique to acquire
417 information on vegetation cover. Today, digital aerial imagery acquired from aircraft provides
418 detailed information on tree species, and these data have been widely utilised in national forest
419 inventories both for direct measurements and as auxiliary information (Haara and Haarala, 2002;
420 Persson et al., 2004; McRoberts and Tomppo, 2007). Time series of aerial imagery enable tree-level
421 and stand-level detection of vegetation changes.

422 Rapid UAS development has mediated the development of new forestry-oriented applications
423 (Colomina and Molina et al., 2014; Torresan et al., 2016; Franklin, 2018). The possibility of acquiring
424 very high spatial resolution multispectral or hyperspectral UAS imagery on-demand allows
425 estimating the structural parameters of forests at individual tree and stand level with high accuracy
426 (Zarco-Tejada et al., 2014; Puliti et al., 2015). Recent developments in image processing software
427 have also enabled wide-scale production of photogrammetric point clouds (PPC). PPCs have an RGB
428 or near-infrared (NIR) value for each point, a feature that provides both colour information and the
429 three-dimensional structure of the canopy (Hirschmuller, 2008; St-Onge et al., 2008). Airborne
430 hyperspectral imagery (aircraft or UAS) provides new possibilities for increased accuracy of tree
431 species mapping (Naidoo et al., 2012; Dalponte et al., 2013; Feret and Asner, 2013; Trier et al., 2018).
432 High spatial and spectral resolution enables mapping biochemical and biophysical properties of
433 vegetation (Alchanatis and Cohen, 2012; Roberts et al., 2012) that can be further used in species
434 classification (Ghosh et al., 2014; Piironen et al., 2017).

435 Multispectral satellite imagery allows vegetation mapping from local to global scales. Satellite
436 images generally have coarser spatial resolution compared to airborne data, and thus these data can
437 be utilised in mapping tree groups or stands rather than individual trees. Multispectral data can be
438 utilised to calculate spectral indices, such as normalised difference vegetation index (NDVI), to study
439 the vegetation cover (Tucker et al., 1979). Temporal resolution of satellite imagery is typically 4-16
440 days, and the availability of long-time series (e.g. Landsat program) enables decadal change detection
441 (Wulder et al., 2008, 2019; Xie et al., 2008).

442 Airborne laser scanning (ALS), also commonly known by Light Detection And Ranging (LiDAR),
443 is a remote sensing method that provides three-dimensional information on vegetation structure
444 (Beland et al., 2019). Unlike the above mentioned (passive) remote sensing techniques, ALS is an
445 active method that is not dependent on prevailing lighting conditions. The ALS system is based on
446 measuring the time between emitting a laser pulse and receiving its backscattered echo. Once the
447 exact position and angle of the scanner are known, the time measurements can be transformed into
448 three-dimensional point clouds that depict the shape and structure of the scanned objects. The
449 accuracy of ALS metrics depends upon pulse density, i.e., the number of laser pulses that intercept
450 the surface per unit (spatial resolution). Currently, the pulse density of ALS data can be tens of
451 measurements per square metre, whereas the spectral resolution is typically restricted to a single
452 wavelength. Multispectral ALS data are available but they are rare compared to single-wavelength
453 data. Species classification using single-wavelength ALS data is based on differences in crown shape,
454 density and reflectivity (Naesset, 2007, 2009; Maltamo and Packalen, 2014; Maltamo et al., 2018),
455 whereas multispectral data enables using both spectral and structural characteristics (Budei et al.,
456 2018).

457 Fig. 4 summarises the general advantages and drawbacks of different airborne and spaceborne
458 remote sensing techniques in tree-species mapping. In the following case studies, we examine aspen
459 detection at the tree-level and stand-level. The remote sensing studies reviewed here include mapping
460 of European aspen, quaking aspen and a few other *Populus* species in Europe and North America.

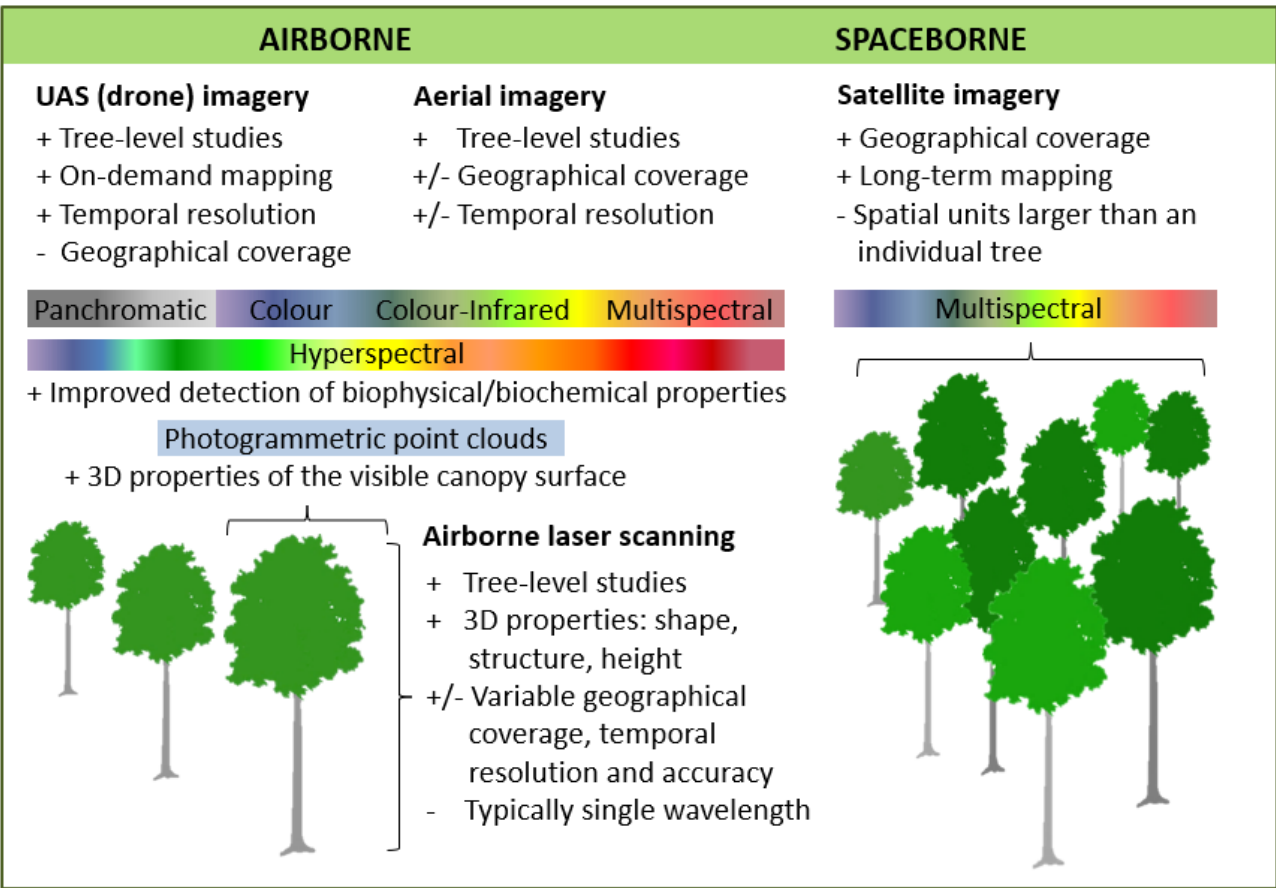


Fig. 4. Advances and drawbacks of different remote sensing techniques in tree-species mapping.

4.2. Tree-level studies

Aspen has been mapped at the tree-level using ALS, airborne photogrammetry and multispectral and hyperspectral imaging or the combination of different datasets. Table 1 provides detailed information on the case studies examined here. In many of these studies, the accuracy of tree species classifications is often evaluated based on the user's and producer's accuracy. User's accuracy (UA) reflects the reliability of classification for the class under consideration. It is calculated by dividing the number of correctly classified objects (e.g., segments or pixels) in a class by the total number of objects assigned to that class. The producer's accuracy (PA) relates to the probability that a ground reference object is correctly classified (i.e., it measures how well the class has been identified). It is obtained by dividing the number of objects correctly classified in a given class by the number of reference objects in that class (Prisley and Smith, 1987).

475 In Fennoscandia, European aspen has often been pooled with other deciduous tree species in ALS-
476 based tree-level and stand-level studies due to the low number of aspen trees in the datasets (Packalen
477 and Maltamo, 2007; Holmgren et al., 2008; Korpela et al., 2010; Ørka et al., 2010). However, there
478 are some studies where aspen was classified separately from other tree species. Ørka et al. (2007)
479 studied tree species classification by utilising ALS intensity metrics in the Østmarka natural reserve,
480 Norway, where generally large and old aspens have a scattered occurrence in the forest landscape.
481 Classification accuracies for aspen were relatively low (PA = 24%, UA = 56%) compared to other
482 species (64-87% for *P. abies* L. and *Betula* spp.). Laser metrics of aspen overlapped with those of
483 spruce. Similar results were also reported by Korpela et al. (2010). In Canada, Li et al. (2013)
484 classified tree species based on structure and architecture of individual tree crowns derived from high-
485 density ALS data. Unlike in Fennoscandia, quaking aspen (*P. tremuloides* Michx.) was the dominant
486 tree species together with sugar maple (*Acer saccharum* Marsh.), jack pine (*Pinus banksiana* Lamb.)
487 and eastern white pine (*Pinus strobus* L.). UA and PA for quaking aspen were 74% and 76%,
488 respectively, the highest classification error being between aspen and jack pine. The results of Li et
489 al. (2013) highlight a positive, strong relationship between ALS point density and species
490 classification accuracy.

491 Combining ALS data with aerial images can improve discrimination of tree species. Säynäjoki et
492 al. (2008) used ALS data and aerial images to discriminate aspen from other deciduous trees in the
493 Koli National Park in Eastern Finland, where abundance of European aspen is generally higher
494 compared to typical managed boreal forests. Deciduous trees were first separated from coniferous
495 trees using aerial images. Segments that belonged to aspen and those that belonged to other deciduous
496 trees were then classified using ALS data with 79% accuracy. Large aspen trees with diameter at
497 breast height of > 25 cm were detected with greater success compared to smaller trees. Breidenbach
498 et al. (2010) utilised the semi-individual tree crown approach based on ALS and multispectral aerial
499 images to predict species-specific forest inventory attributes for different tree species. The study was
500 conducted in a forest area in southern Norway, where the European aspen proportion was

501 approximately 2%. Relative root mean square error (RMSE) for aspen volume was significantly
502 higher (222%) compared to the relative RMSE for volume of pine, spruce and birch (38, 40 and
503 101%, respectively). These data indicated that the predictions calculated for aspen were considerably
504 less accurate compared to other tree species.

505 Aspen has also been classified using only aerial imagery or UAS imagery. Erikson (2004) utilised
506 high-spatial resolution colour infrared aerial images to automatically classify segmented tree crowns
507 of the four most common tree species (*Picea abies* Karst., *Pinus sylvestris* L., *Betula pubescens* Ehrh.
508 or *Populus tremula* L.) in boreal forest landscape in Sweden. In that study, the proportion of aspen of
509 all trees was approximately 3%, and the UA and PA were 63% and 71% respectively. Franklin and
510 Ahmed (2017) studied deciduous forest species classification in a Canadian hardwood forest using
511 multispectral UAS imagery. Crowns of quaking aspen were represented by bright and distinctive
512 tones on colour and near-infrared images, and no classification errors were reported. However, it
513 should be noted that validation of classification was based on relatively small sample of trees. Alonzo
514 et al. (2018) utilised UAS-based RGB point cloud to classify trees species in interior Alaska. The
515 dominant species in the studied boreal forest area were black spruce (*Picea mariana* Mill.), white
516 spruce (*Picea glauca* (Moench) Voss), birch (*Betula papyrifera* Marshall) and quaking aspen. The
517 UA and PA for quaking aspen were 83% and 74%, respectively. The results showed that the inclusion
518 of spectral information is critical to supplement structural information in tree species classification.

519 Imaging spectroscopy (hyperspectral data) can improve tree species classifications by providing
520 adequate information to discriminate among spectrally similar targets. Jones et al. (2010) used a
521 combination of ALS and imaging spectroscopy for tree species classification in Canada. Several
522 broad-leaved tree species, including quaking aspen and black cottonwood (*Populus trichocarpa*),
523 occurred commonly in the studied forest area dominated by Douglas fir (*Pseudotsuga menziesii*).
524 Although the methodology enabled species mapping with more detail and accuracy than is possible
525 using conventional approaches (i.e., interpretation of aerial images), or either technology on its own,
526 classification accuracies were markedly lower for quaking aspen (UA and PA < 34%) due to

527 similarity with red alder (*Alnus rubra*). However, another *Populus* species, black cottonwood, was
 528 accurately classified (UA of 82% and PA of 98%, respectively). Dalponte et al. (2009) used airborne
 529 imaging spectroscopy to image two Italian forest areas; one of them had a dense forest with 19
 530 different tree species. Two *Populus* species, *Populus canescens* and *Populus hybrida*, were identified
 531 with UAs of approximately 80-90%, depending on the applied differentiation classifier. Similarly,
 532 Roth et al. (2015b) utilised airborne imaging spectroscopy to differentiate a large number of tree
 533 species in different regions in the USA and studied the impact of spatial resolution of data on
 534 classification accuracy. For black cottonwood, UAs and PAs were 82–100% for up to 40 m resolution
 535 and 71–83% at 60 m resolution. These data highlight the fact that future spaceborne imaging
 536 spectroscopy has high potential in tree species mapping. In another study, Roth et al. (2015a)
 537 compared the accuracy of imaging spectroscopy in species detection across different ecosystems and
 538 classified *P. trichocarpa* with a UA of 87% and PA of 84%. Tuominen et al. (2018) examined tree
 539 species recognition for 26 species and 14 genera in a Finnish arboretum using UAS-based
 540 hyperspectral imagery in combination with a three-dimensional photogrammetric canopy surface
 541 model. The UA and PA for aspen were 86% and 63%, respectively. Saarinen et al. (2018) assessed
 542 plot-level biodiversity indicators using imaging spectroscopy and photogrammetric point clouds
 543 acquired from a UAS in Finland. The number of aspens was low in the study region that contained
 544 both managed and natural boreal forests. The largest errors occurred in predictions of the amount as
 545 well as the volume of deciduous trees, such as aspen.

546

547 **4.3. Stand-level studies**

548 The majority of scientific studies on aspen mapping at the stand level were performed in North
 549 America, where quaking aspen forms extensive pure stands. In particular, a recent phenomenon,
 550 referred to as sudden aspen decline, characterised by rapid overstory mortality with little to no
 551 understory regeneration (e.g., Singer et al., 2019), has resulted in numerous efforts to map aspen
 552 ecosystems in western parts of North America. Despite few studies related to European aspen, the

553 examples presented here can provide a general view on the possibilities and constraints of different
554 remote sensing methods in mapping aspen occurrence and dynamics at spatial scales coarser than
555 individual tree-level (Table 1).

556 ALS- and UAS-based methods can provide estimates of tree density, basal area and aboveground
557 biomass. In addition to individual tree detection, Alonzo et al. (2018) collected forest inventory
558 variables at the plot-level using a UAS-based approach (see section 4.2). The accuracy of tree density,
559 basal area and above-ground biomass estimates was somewhat variable. For example, quaking aspen
560 basal area was accurately estimated, whereas the aboveground biomass of quaking aspen and other
561 broadleaf species was frequently overestimated at the expense of white spruce (*P. glauca* (Moench)
562 Voss). In Finland, Pippuri et al. (2013) predicted species-specific basal areas in urban forest for seven
563 dominant species, including European aspen, using ALS data and aerial images. Their results showed
564 that separation of different deciduous tree species based on aerial images and ALS metrics is difficult.
565 The accuracy of basal area estimates for European aspen was considerably lower compared to those
566 for dominant coniferous species.

567 Aerial images can provide detailed information on forest stands at local and landscape scales. For
568 example, Strand et al. (2012) mapped local dynamics of quaking aspen in Idaho over nearly four
569 decades using aerial images. Stand structure was visible in the colour and infrared aerial images, but
570 stands were difficult to delineate in older black and white images, a factor that complicated
571 comparisons from one time period to another. They could also detect quaking aspen regeneration on
572 the edges of stands, whereas regeneration in the understory was more difficult to assess. Di Orio et
573 al. (2004) used historic and recent aerial images to study the density and fragmentation of quaking
574 aspen in California over the past 50 years. The accuracy of aerial image interpretation was 85%,
575 which is partly related to the fact that quaking aspen was the only commonly found deciduous tree in
576 the study area. Heyman et al. (2003) mapped quaking aspen in central Oregon from colour-infrared
577 aerial images using a segmentation approach into three general classes (no aspen, minor,
578 predominant) with 88% overall accuracy. Due to the possibility to fly low-cost and on-demand, UAS

579 systems are particularly useful in acquiring data from areas affected by natural or anthropogenic
580 disturbances. Aicardi et al. (2016) performed UAS-based change detection of vegetation after a stand-
581 replacing forest fire in northern Italy. Multitemporal high-resolution digital surface models derived
582 from ALS data and RGB imagery provided efficient detection of agamic regeneration of European
583 aspen in the disturbed areas with no aboveground canopy layer.

584 Advances in imaging spectroscopy have allowed even examination of species genetic variation.
585 Madritch et al. (2014) combined airborne AVIRIS imaging spectroscopy data with genetic,
586 phytochemical, microbial and biogeochemical data to study how genetic variation of quaking aspen
587 influences below-ground processes at landscape-level. Aspen genotypes were discriminated with
588 nearly 80% accuracy, and the authors suggested that imaging spectroscopy provides a useful tool for
589 mapping aspen genotypes and identifying areas of high or low genetic and chemical diversity in
590 natural forests.

591 Satellite images enable mapping vegetation dynamics over wide geographical extents. Sankey
592 (2009) detected changes in regional cover of quaking aspen using multispectral Landsat TM5 imagery
593 in a coniferous forest area interspersed with aspen patches in Idaho. The classification was based on
594 summer and fall images and took advantage of aspen phenology compared to the coniferous trees.
595 The overall accuracy of aspen presence/absence classifications was 92-93%. Using similar satellite
596 data, Sankey (2012) reported that fusing ALS data with the NDVI-based classification improved the
597 overall classification accuracies from 92% to 96%. Similarly, Bergen and Dronova (2007) identified
598 the extent of aspen-dominated cover type including quaking aspen and bigtooth aspen (*Populus*
599 *grandidentata* Michx.) in upper Great Lakes region using Landsat ETM+ leaf-on and leaf-off data
600 with UA and PA of 86-93%. Chubey et al. (2006) utilised high-resolution panchromatic and
601 multispectral IKONOS imagery in mapping forest stands in Alberta, Canada. Quaking aspen occurred
602 in the region in pure stands and mixed with conifers, and UA and PA for aspen class were 89-100%.

603 Satellite images were also utilised for mapping vegetation health. Oukrop et al. (2011) studied
604 healthy, damaged and seral stand types of quaking aspen to determine the extent of aspen decline in

605 Utah. The areas with aspen cover were defined from aerial images, and Landsat 5 TM images were
606 utilised to map different aspen classes with an overall accuracy of 81%. Hall et al. (2014) studied
607 changes in leaf area index (LAI) that resulted from insect defoliation in boreal aspen stands in
608 northern Alberta using Landsat ETM+ images and field data. There was a strong relationship between
609 LAI and the satellite image, and they observed defoliation for the study sites that included relatively
610 pure stands of quaking aspen and balsam poplar (*Populus balsamifera* L.). Further, Boyd et al. (2019)
611 examined the impact of climate and damage by the aspen epidermal leaf miner (*Phyllocnistis*
612 *populiella*) on aspen productivity and physiology in Alaska using remote sensing indices of
613 vegetation productivity (NDVI) acquired from GIMMS3g, MODIS Aqua, MODIS Terra and Landsat
614 5, 7 and 8.

615

616 Table 1. Tree-level and stand-level studies on mapping aspen (*P. tremula*, *P. tremuloides*, *Populus* spp.) using different remote sensing techniques.
617

	Species	Platform	Data type	Spectral range µm (nr of bands)	Pixel size m	Pulse density pts/m ²	Accuracy estimate
Tree-level							
Alonzo et al. (2018)	QA	UAS	PPC, RGB	B, G, R (3)	0.019–0.027		UA = 83%, PA = 74%
Breidenbach et al. (2010)	EA	AIR	ALS, MI	G, R, NIR, PAN (4)	0.275 -0.86	7.4	High RMSE
Dalponte et al. 2009	PO	AIR	HI	0.40–0.99 (126)	1		UA = 80–90%
Erikson (2004)	EA	AIR	CIR	0.60–0.90 (3)	0.03–0.1		UA = 63%, PA = 71%
Franklin and Ahmed (2017)	QA	UAS	MI	0.49–0.90 (6)	0.11		UA & PA = 100%
Jones et al. (2010)	QA, PO	AIR	ALS, HI	0.40–2.50 (492)	2	0.4	UA & PA < 34%; UA = 82%, PA = 98%
Li et al. (2013)	QA	AIR	ALS			90	UA = 74%, PA = 76%
Ørka et al. (2007)	EA	AIR	ALS			5.09	UA = 56%, PA = 24%
Roth et al. (2015a)	PO	AIR	HI	0.35–2.50 (224)	4		UA = 84%, PA = 87%
Roth et al. (2015b)	PO	AIR	HI	0.35–2.50 (224)	4; 20; 40; 60		UA = 83–100%, PA = 71–96%
Saarinen et al. (2018)	EA	UAS	HI, PPC, RGB	0.50–0.90 (22)	0.10; 0.25		High RMSE
Säynäjoki et al. (2008)	EA	AIR	ALS, MI	G, R, NIR, PAN (4)	0.25	3.86	OA = 79%
Tuominen et al. (2018)	EA	UAS	HI, PPC, RGB	0.4–1.60 (60)	0.015–0.20		UA = 86%, PA = 63%
Stand-level							
Aicardi et al. (2016)	EA	UAS, AIR	ALS, RGB	R, G, B (3)	0.30	0.5–10	Efficient detection of vegetation dynamics
Bergen and Dronova (2007)	QA, PO	SAT	MI	0.63–0.90; 1.55–1.75 (3)	30		UA = 87–93%, PA= 86–91%
Boyd et al. 2019	QA	SAT	MI	0.63–0.90 (2)	30; 250; 0.07°		Detection of productivity/physiology changes
Chubey et al. 2006	QA	SAT	MI	0.45 -0.85 / PAN	1; 4		UA = 100%, PA = 89%
Di Orio et al. (2004)	QA	AIR	AI (n.d.)	n.d.	≤3		OA = 85%
Hall et al. 2014	QA, PO	SAT	MI	0.77–0.90; 1.55–1.75 (2)	30		n.d.
Heyman et al. (2003)	QA	AIR	CIR	G, R, NIR (3)	1–2		OA = 88%
Madritch et al. (2014)	QA	AIR	HI	0.41–2.45 (224)	15–18		OA = 80%
Oukrop et al. (2011)	QA	AIR, SAT	CIR, MI	G, R, NIR (3); 0.45–0.90; 1.55–1.75; 2.08–2.35 (6)	1 30		OA = 81%
Pippuri et al. (2014)	EA	AIR	ALS, MI	B, G, NIR, PAN (4)	0.15	1.56	Low compared to dominant species
Sankey (2009)	QA	SAT	MI	0.52–0.90; 1.55–1.75 (4)	30		OA = 92–93%
Sankey (2012)	QA	AIR; SAT	ALS, MI	0.52–0.90; 1.55–1.75 (4)	30	5.6	OA = 92–96%
Strand et al. (2012)	QA	AIR	CIR, PAN, RGB	B, G, R, NIR, PAN	1–2		Visual interpretation
Species: EA = European aspen, PO = other Populus species, QA = quaking aspen; Platform: AIR = aircraft, SAT = satellite, UAS = unmanned aerial system; Data type: AI = aerial imagery, ALS = airborne laser scanning, CIR = color-infrared (false-color) imagery, HI = hyperspectral imagery, MI = multispectral imagery, n.d. = no data, PAN = panchromatic imagery, PPC = photogrammetric point cloud, RGB = red-green-blue (natural color) imagery; Spectral range: B = blue, G = green, R = red, NIR = near-infrared; Accuracy estimate: OA = overall accuracy, PA = producer's accuracy, RMSE = root mean square error, UA = user's accuracy							

619 **5. Discussion and conclusions**

620 The European aspen has a high conservation value in boreal forests. This feature is due to the large
621 number of species they host compared to the predominant coniferous trees. Our review highlights
622 that the role of aspen as a keystone species in boreal ecosystems has received increasing attention.
623 Negative effects of modern forest management methods and heavy browsing on occurrence,
624 regeneration and long-term persistence of aspen in forest landscapes have been recognised (e.g.,
625 Kouki et al., 2004; Edenius et al., 2011). However, there is relatively little spatiotemporal information
626 on the occurrence and distribution of European aspen at local, landscape or regional scales. This
627 deficit can seriously hinder biodiversity assessments and planning, implementation and monitoring
628 of alternative forest management measures, and conservation efforts.

629 As highlighted by ecological studies, spatially explicit data are needed in order to study aspen
630 abundance, spatial distribution and arrangement, occurrence of large/old trees, long-term occurrence
631 dynamics and aspen regeneration. Forthcoming aspen studies that utilise these data will help us to
632 better understand the current status of different aspen-associated species and their populations and
633 predict their future state. Such information should cover both protected areas—where a great
634 proportion of aspen-related research has already been conducted—as well as managed forests, which
635 characterise the majority of boreal landscape in Europe. In the field of remote sensing, recent
636 developments have provided new opportunities for acquiring more detailed information on the
637 occurrence and distribution of tree species, and characteristics of individual trees and stands
638 (Dalponte et al., 2013; Fassnacht et al., 2018; Beland et al., 2019). This information, alone or in
639 combination with other ecological data, can provide spatially explicit indicators for biodiversity and
640 ecosystem assessments, among other information (Vihervaara et al., 2015; Mononen et al., 2018;
641 Pettorelli et al., 2018).

642 Aspen was mapped with various success by different remote sensing studies reviewed here. In the
643 case of individual tree detection, the major challenges were the low proportion of European aspen in
644 Fennoscandian forest landscapes and the overlap of spectral and/or structural properties of European

645 aspen and quaking aspen with other tree species. Due to different research methods and various tree
646 species composition, comparison of different studies is not straightforward. However, the results
647 suggest that especially three-dimensional structural information derived from high-density ALS data
648 or photogrammetric point clouds, and airborne imaging spectroscopy, hold significant potential for
649 tree species mapping (Dalponte et al., 2009; Jones et al., 2010; Li et al., 2013; Roth et al., 2015b;
650 Alonzo et al., 2018). The studies also indicate that combining spectral data with three-dimensional
651 data can noticeably improve species detection at the individual tree level and stand level. Thus, remote
652 sensing with repeated monitoring should be utilized to fulfill the current need of studies on landscape
653 dynamics considering rotation lengths, succession and persistence of key species.

654 In addition to species discrimination, remote sensing can provide information on biophysical and
655 biochemical properties of vegetation (Roberts et al., 2004). For example, knowledge about individual
656 tree properties, including tree height, crown dimensions and biomass, can help predict the potential
657 occurrence and distribution of species often associated with large/old aspen trees. Mapping aspen
658 regeneration is difficult except in post-disturbance areas without dense canopy cover (see Aicardi et
659 al., 2016). Distinct spectral signatures can identify vegetation stress (Ustin et al., 2009). These
660 observations enable detection of major disturbances on aspen populations caused by insect herbivory,
661 pathogens or drought, among others (Oukrop et al., 2011; Hall et al., 2013). Furthermore, recent
662 research indicates that imaging spectroscopy data are suitable for mapping species genotypes and for
663 identifying areas of high or low genetic diversity (Madritch et al., (2014). Yamasaki et al. (2018)
664 recommend that future research that combines genomics with remote sensing could help monitoring
665 and predicting ecosystem dynamics. These findings will be particularly interesting to better
666 understand aspen's role in boreal ecosystems.

667 Suitability of remote sensing data for biodiversity mapping and monitoring is also determined by
668 geographical coverage, availability of multitemporal data and costs of data acquisition. For example,
669 high-resolution hyperspectral and three-dimensional structural data can be acquired on-demand using
670 a UAS, but this approach is only suitable for local-scale studies. Airborne hyperspectral and ALS

671 data acquisition by plane over larger areas (landscape scale) is typically conducted by service
672 providers (Beland et al., 2019). Although hyperspectral and lidar airborne sensors have developed a
673 lot over the past years, the data prices remain relatively high compared to traditional aerial and
674 multispectral satellite images. This factor prevents more extensive exploitation of the data. Several
675 spaceborne imaging spectrometers are currently under development; they should provide for the first
676 time global coverage of hyperspectral data for vegetation mapping, although in coarser resolution
677 compared to airborne data (Lee et al., 2015; Roth et al., 2015b). An important feature of spaceborne
678 data is the continual availability of multitemporal and seasonal data. Utilising seasonal spectral data
679 enables monitoring vegetation dynamics, provides valuable information for species detection and
680 improve tree species classifications, as indicated by the reviewed studies. Furthermore, a recently
681 developed multispectral laser scanning technique, which provides a dense point cloud together with
682 spectral information, may have significant potential in tree species detection in the future (Yu et al.,
683 2017; Budei et al., 2018; Beland et al., 2019).

684 Currently, increasing spatial, spectral and temporal resolutions—and the availability of three-
685 dimensional data—have brought remote sensing research closer to the scales of ecological research.
686 Communication between experts in different research fields can foster innovations, generate new
687 research directions and accelerate the development of new remote sensing products suitable for
688 mapping different ecological features or biodiversity indicators (Pettorelli et al., 2018; Wang &
689 Gamon 2019). In the case of aspen in boreal forests, or any other key ecological feature, collaboration
690 between the disciplines of ecology, conservation science and remote sensing will improve the
691 potential for remote sensing data to support biodiversity monitoring and management. Integration of
692 ecological datasets with remote sensing data describing aspen occurrence and characteristics is a key
693 for understanding the current and future distribution patterns of aspen-related biodiversity.

694

695

696 **Acknowledgements**

697 This study was funded by the project ‘The Integrated Biodiversity Conservation and Carbon
698 Sequestration in the Changing Environment’ (IBC-Carbon, project number 312559), Strategic
699 Research Council, Academy of Finland.

700

701 **References**

702 Aicardi, I., Garbarino, M., Lingua, A., Lingua, E., Marzano, R., & Piras, M. 2016. Monitoring Post-
703 Fire Forest Recovery Using Multitemporal Digital Surface Models Generated from Different
704 Platforms. *Earsel Eproceedings*, 15, 1-8.

705 Alchanatis, V., Cohen, Y. 2012. Spectral and spatial methods of hyperspectral image analysis for
706 estimation of biophysical and biochemical properties of agricultural crops. *Hyperspectral Remote*
707 *Sensing of Vegetation* 19, 289-308.

708 Alonzo, M., Andersen, H. E., Morton, D.C. & Cook, B.D. 2018. Quantifying boreal forest structure
709 and composition using UAV structure from motion. *Forests* 9, 119.

710 Ampoorter, E., Barbaro, L., Jactel, H., Baeten, L., Boberg, J., Carnol, M., ... & Smedt, P. D. 2019.
711 Tree diversity is key for promoting the diversity and abundance of forest-associated taxa in Europe.
712 *Oikos* 129, 133-146.

713 Angelstam, P., Mikusiński, G., 1994. Woodpecker assemblages in natural and managed boreal and
714 hemiboreal forest — a review. *Annales Zoologici Fennici* 31, 157-172.
715 <http://www.jstor.org/stable/23735508>

716 Baroni, D., Korpimäki, E., Selonen, V., & Laaksonen, T. 2020. Tree cavity abundance and beyond:
717 Nesting and food storing sites of the pygmy owl in managed boreal forests. *Forest Ecology and*
718 *Management* 460, 117818.

719 Beland, M., Parker, G., Sparrow, B., Harding, D., Chasmer, L., Phinn, S., ... & Strahler, A. 2019. On
720 promoting the use of lidar systems in forest ecosystem research. *Forest Ecology and Management*
721 450, 117484.

722 Bergen, K. M., Dronova, I. 2007. Observing succession on aspen-dominated landscapes using a
723 remote sensing-ecosystem approach. *Landscape Ecology* 22, 1395-1410.

724 Bergeron, Y., Chen, H. Y., Kenkel, N. C., Leduc, A. L., & Macdonald, S. E. 2014. Boreal
725 mixedwood stand dynamics: ecological processes underlying multiple pathways. *The Forestry*
726 *Chronicle* 90, 202-213.

727 Boyd, M. A., Berner, L. T., Doak, P., Goetz, S., Rogers, B., Wagner, D., ... & Mack, M. C. 2019.
728 Impacts of climate and insect herbivory on productivity and physiology of trembling aspen
729 (*Populus tremuloides*) in Alaskan boreal forests. *Environmental Research Letters* 14, 085010.

730 Breidenbach, J., Næsset, E., Lien, V., Gobakken, T. & Solberg, S. 2010. Prediction of species specific
731 forest inventory attributes using a nonparametric semi-individual tree crown approach based on
732 fused airborne laser scanning and multispectral data. *Remote Sensing of Environment*, 114, 911-
733 924.

734 Brockerhoff, E. G., Barbaro, L., Castagneyrol, B., Forrester, D. I., Gardiner, B., González-Olabarria,
735 J. R., ... & Thompson, I. D. 2017. Forest biodiversity, ecosystem functioning and the provision of
736 ecosystem services. *Biodiversity and Conservation* 26, 3005–3035

737 Buck JR, St. Clair SB 2012. Aspen increase soil moisture, nutrients, organic matter and respiration
738 in Rocky Mountain forest communities. *PLoS ONE* 7, e52369. doi:10.1371/journal.pone.0052369

739 Budei, B. C., St-Onge, B., Hopkinson, C., Audet, F. A. 2018. Identifying the genus or species of
740 individual trees using a three-wavelength airborne lidar system. *Remote Sensing of Environment*
741 204, 632-647.

742 Callan, B.E. ,1998. *Diseases of Populus in British Columbia: a Diagnostic Manual*. Natural
743 Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, British Columbia,
744 Canada.

745 Caudullo, G., de Rigo, D. 2016. *Populus tremula* in Europe: distribution, habitat, usage and threats.
746 *European Atlas of Forest Tree Species. Publ. Off. EU, Luxembourg, pp. e01f148*.

747 Chubey, M. S., Franklin, S. E., & Wulder, M. A. 2006. Object-based analysis of Ikonos-2 imagery
748 for extraction of forest inventory parameters. *Photogrammetric Engineering & Remote Sensing*,
749 72, 383-394.

750 Clawges, R., Vierling, K., Vierling, L. & Rowell, E. 2008. The use of airborne lidar to assess avian
751 species diversity, density, and occurrence in a pine/aspen forest. *Remote Sensing of Environment*
752 112, 2064-2073.

753 Colomina, I., Molina, P. 2014. Unmanned aerial systems for photogrammetry and remote sensing: A
754 review. *ISPRS Journal of Photogrammetry and Remote Sensing*, 92, 79–97.

755 Dahlberg, A., Stokland J.N. 2004. Vedlevande arters krav på substrat - sammanställning och analys
756 av 3 600 arter. Skogsstyrelsen, Rapport 7

757 Dalponte, M., Bruzzone, L., Vescovo, L., & Gianelle, D. (2009). The role of spectral resolution and
758 classifier complexity in the analysis of hyperspectral images of forest areas. *Remote Sensing of*
759 *Environment* 113, 2345-2355.

760 Dalponte, M., Økra, H.O., Gobakken, T., Gianelle, D., & Næsset, E. 2013. Tree species classification
761 in boreal forests with hyperspectral data. *IEEE Transactions on Geoscience and Remote Sensing*
762 51, 2632–2645. doi:10.1109/TGRS.2012.2216272

763 de Chantal, M., Granström, A. 2007. Aggregations of dead wood after wildfire act as browsing refugia
764 for seedlings of *Populus tremula* and *Salix caprea*. *Forest Ecology and Management* 250, 3-8.

765 DeWoody, J., Rowe, C.A., Hipkins, V.D., Mock, K.E. 2008. "Pando" lives: molecular genetic
766 evidence of a giant aspen clone in central Utah. *Western North American Naturalist* 68, 493-497.

767 Di Orio, A.P., Callas, R., Schaefer, R. J. 2005. Forty-eight year decline and fragmentation of aspen
768 (*Populus tremuloides*) in the South Warner Mountains of California. *Forest Ecology and*
769 *Management* 206, 307-313.

770 Easton, E., 1997. Genetic variation and conservation of the native aspen (*Populus tremula* L.)
771 resource in Scotland. PhD Thesis, University of Edinburgh, UK.

772 Edenius, L., Eriksson, G. 2007. Aspen demographics in relations to spatial context and ungulate
773 browsing: Implications for conservation and forest management. *Biological Conservation* 135,
774 293-301.

775 Edenius, L., Ericsson, G., Kempe, G., Bergström, R. & Danell, K. 2011. The effects of changing land
776 use and browsing on aspen abundance and regeneration: a 50-year perspective from Sweden.
777 *Journal of Applied Ecology* 48, 301-309.

778 Edenius, L., Ericsson, G. 2015. Effects of ungulate browsing on recruitment of aspen and rowan: a
779 demographic approach. *Scandinavian Journal of Forest Research* 30, 283-288.

780 Erikson, M. 2004. Species classification of individually segmented tree crowns in high-resolution
781 aerial images using radiometric and morphologic image measures. *Remote Sensing of*
782 *Environment* 91, 469-477.

783 Esseen, P.A., Ehnström, B., Ericson, L., & Sjöberg, K. 1997. Boreal forests. *Ecological Bulletins* 46,
784 16-47.

785 Fassnacht, F. E., Latifi, H., Stereńczak, K., Modzelewska, A., Lefsky, M., Waser, L. T., ... & Ghosh,
786 A. 2016. Review of studies on tree species classification from remotely sensed data. *Remote*
787 *Sensing of Environment* 186, 64-87.

788 Féret, J-B, Asner, G.P. 2013. Tree Species Discrimination in Tropical Forests Using Airborne
789 Imaging Spectroscopy. *IEEE Transactions on Geoscience and Remote Sensing* 51, 73

790 Fedrowitz, K., Koricheva, J., Baker, S., Lindenmayer, D., Palik, B., Rosenvald, R., Beese, W.,
791 Franklin, J., Kouki, J., Macdonald, E., Messier, C., Sverdrup-Thygeson, A. & Gustafsson, L. 2014.
792 Can retention forestry help conserve biodiversity? A meta-analysis. *Journal of Applied Ecology*
793 51, 1660-1679. <http://dx.doi.org/10.1111/1365-2664.12289>

794 Filipescu, C. N., Comeau, P. G. 2007. Aspen competition affects light and white spruce growth across
795 several boreal sites in western Canada. *Canadian Journal of Forest Research* 37, 1701-1713.

796 Franklin, S. E. 2018. Pixel-and object-based multispectral classification of forest tree species from
797 small unmanned aerial vehicles. *Journal of Unmanned Vehicle Systems* 6, 195-211.

798 Franklin, S. E. & Ahmed, O. S. 2018. Deciduous tree species classification using object-based
799 analysis and machine learning with unmanned aerial vehicle multispectral data. *International*
800 *Journal of Remote Sensing* 39, 5236-5245.

801 Fraser, E. C., Landhäusser, S. M., & Lieffers, V. J. 2003. The effects of mechanical site preparation
802 and subsequent wildfire on trembling aspen (*Populus tremuloides* Michx.) regeneration in central
803 Alberta, Canada. *New Forests* 25, 49-66.

804 Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C.,
805 Fröberg, M., Stendahl, J., Philipson, C.D., Mikusiński, G., Andersson, E., Westerlund, B.,
806 Andrén, H., Moberg, F., Moen, J., Bengtsson, J., 2013. Higher levels of multiple ecosystem
807 services are found in forests with more tree species. *Nature Communications* 4, 1340.

808 Gromtsev, A. 2002. Natural disturbance dynamics in the boreal forests of European Russia: a
809 review. *Silva Fennica* 36, 41-55.

810 Groot, A., Man, R., Wood, J. 2009. Spatial and temporal patterns of *Populus tremuloides*
811 regeneration in small forest openings in northern Ontario. *The Forestry Chronicle* 85, 548-557.

812 Ghosh, A., F. E. Fassnacht, P.K. Joshi, B. Koch 2014. A framework for mapping tree species
813 combining hyperspectral and lidar data: Role of selected classifiers and sensor across three spatial
814 scales. *International Journal of Applied Earth Observation and Geoinformation* 26, 49-63.

815 Gu, W.D., Kuusinen, M., Kontinen, T., Hanski, I., 2001. Spatial pattern in the occurrence of the
816 lichen *Lobaria pulmonaria* in managed and virgin boreal forests. *Ecography* 24, 139 – 150.

817 Gustafsson, L., Eriksson, I., 1995. Factors of importance for the epiphytic vegetation of aspen
818 *Populus tremula* with special emphasis on bark chemistry and soil chemistry. *J. Appl. Ecol.* 32,
819 Gustafsson, L., Kouki, J., Sverdrup-Thygeson, A. 2010. Tree retention as a conservation measure in
820 clear-cut forests of northern Europe: a review of ecological consequences. *Scandinavian Journal*
821 *of Forest Research* 25, 295-308.

822 Haara, A., Haarala, M. 2002. Tree species classification using semi-automatic delineation of trees on
823 aerial images. *Scandinavian Journal of Forest Research* 17, 556-565.

- 824 Hågvar, S., Hågvar, G. Mønness, E. 1990. Nest site selection in Norwegian woodpeckers. *Holarctic*
825 *Ecology* 13, 156-165.
- 826 Hall, R.J., Fernandes, R.A., Hogg, E.H., Brandt, J.P., Butson, C., Case, B.S., LeBlanc, G.S. 2003.
827 Relating aspen defoliation to changes in leaf area derived from field and satellite remote sensing
828 data. *Can. J. Remote Sensing* 29, 299–313.
- 829 Halme, P., Vartiija, N., Salmela, J., Penttinen, J. Norros, V. 2013. High within- and between-trunk
830 variation in the nematoceran (Diptera) community and its physical environment in decaying aspen
831 trunks. *Insect Conservation and Diversity* 6, 502–512.
- 832 Hämäläinen, A., Hujo, M., Heikkala, O., Junninen, K., & Kouki, J. 2016. Retention tree
833 characteristics have major influence on the post-harvest tree mortality and availability of coarse
834 woody debris in clear-cut areas. *Forest Ecology and Management* 369, 66-73.
- 835 Hämäläinen, K., Junninen, K., Halme, P. & Kouki, J. 2020. Managing conservation values of
836 protected sites: How to maintain deciduous trees in white-backed woodpecker territories. *Forest*
837 *Ecology and Management* 461, 117946.
- 838 Hanski, I.K., 1998. Home ranges and habitat use in the declining flying squirrel *Pteromys volans* in
839 managed forests. *Wildlife Biology* 4, 33–46.
- 840 Hardenbol, A. A., Pakkala, T., & Kouki, J. 2019. Persistence of a keystone microhabitat in boreal
841 forests: Cavities of Eurasian Three-toed Woodpeckers (*Picoides tridactylus*). *Forest Ecology and*
842 *Management* 450, 117530.
- 843 Hazell, P., Kellner, O., Rydin, H., Gustafsson, L. 1998. Presence and abundance of four epiphytic
844 bryophytes in relation to density of aspen *Populus tremula* and other stand characteristics. *Forest*
845 *Ecology and Management* 107, 147–158.
- 846 Hedenås, H. & Ericson, L. 2000. Epiphytic macrolichens as conservation indicators: successional
847 sequence in *Populus tremula* stands. *Biol. Conserv.* 93, 43–53.
- 848 Hedenås, H., Blomberg, P., and Ericson, L., 2007. Significance of old aspen (*Populus tremula*) trees
849 for the occurrence of lichen photobionts. *Biological Conservation* 135, 380–387.

850 Hedenås, H., Hedström, P. 2007. Conservation of epiphytic lichens: Significance of remnant aspen
851 (*Populus tremula*) trees in clear-cuts. *Biological Conservation* 135, 388–395.

852 Heyman, O., Gaston, G.G., Kimerling, A.J. & Campbell, J.T. 2003. A per-segment approach to
853 improving aspen mapping from high-resolution remote sensing imagery. *Journal of Forestry*, 101,
854 29-33.

855 Hirschmuller, H., 2008. Stereo processing by semi-global matching and mutual Information. *IEEE*
856 *Transactions on Pattern Analysis and Machine Intelligence* 30, 328–341.

857 Hjältén, J., Danell, K., Ericson, L. 2004. Hare and vole browsing preferences during winter. *Acta*
858 *Theriologicala* 49, 53–62.

859 Holmgren, J., Persson, Å., Söderman, U. 2008. Species identification of individual trees by
860 combining high resolution LiDAR data with multi-spectral images. *International Journal of*
861 *Remote Sensing* 29, 1537-1552.

862 Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E., Hungate, B.A., Matulich, K.L., Gonzalez,
863 A., Duffy, J.E., Gamfeldt, L. & O'Connor, M.I., 2012. A global synthesis reveals biodiversity loss
864 as a major driver of ecosystem change. *Nature* 486, 105. doi:10.1038/nature11118

865 Hynynen, J. & Viherä-Aarnio, A. (eds.) 1999. Haapa – monimuotoisuutta metsään ja metsätalouteen.
866 *Metsäntutkimuslaitoksen tiedonantoja* 725.

867 Hyvärinen, E., Juslén, A., Kemppainen, E., Uddström, A., & Liukko, U. M. (2019). Suomen lajien
868 uhanalaisuus–Punainen kirja 2019.

869 IPBES (2019). IPBES Global Assessment Summary for Policymakers. The Intergovernmental
870 Science-Policy Platform on Biodiversity and Ecosystem Services.
871 <https://www.ipbes.net/news/ipbes-global-assessment-summary-policymakers-pdf>

872 IPCC (2018). *Global Warming of 1.5° C: An IPCC Special Report on the Impacts of Global Warming*
873 *of 1.5° C Above Pre-industrial Levels and Related Global Greenhouse Gas Emission Pathways,*
874 *in the Context of Strengthening the Global Response to the Threat of Climate Change, Sustainable*
875 *Development, and Efforts to Eradicate Poverty*. Intergovernmental Panel on Climate Change.

876 Jacobsen et al. 2015. Scale-specific responses of saproxylic beetles: combining dead wood surveys
877 with data from satellite imagery. *J Insect Conserv* 19, 1053–1062.

878 Johnson, S., Strengbom, J., Kouki, J. 2014. Low levels of tree retention do not mitigate the effects
879 of clearcutting on ground vegetation dynamics. *Forest Ecology and Management* 330, 67–74.

880 Jones, T. G., Coops, N. C. & Sharma, T. 2010. Assessing the utility of airborne hyperspectral and
881 LiDAR data for species distribution mapping in the coastal Pacific Northwest, Canada. *Remote*
882 *Sensing of Environment* 114, 2841-2852.

883 Jonsell, M., Weslien, J., Ehnström, B. 1998. Substrate requirements of red-listed saproxylic
884 invertebrates in Sweden. *Biodiversity & Conservation* 7, 749-764.

885 Jönsson, M. T., Fraver, S., Jonsson, B. G., Dynesius, M., Rydgård, M., & Esseen, P. A. 2007.
886 Eighteen years of tree mortality and structural change in an experimentally fragmented Norway
887 spruce forest. *Forest Ecology and Management* 242, 306-313.

888 Junninen, K., Penttilä, R., Martikainen, P. 2007. Fallen retention aspen trees on clear-cuts can be
889 important habitats for red-listed polypores: a case study in Finland. *Biodiversity and Conservation*
890 162, 475-490.

891 Kasanen, R., Hantula, J., Vuorinen, M., Stenlid, J., Solheim, H. Kurkela, T. 2004. Migrational
892 capacity of Fennoscandian populations of *Venturia tremulae*. *Mycol. Res.* 108, 64–70.

893 Kangas A. 2006. Sampling rare populations. In: *Forest Inventory*. Springer, Dordrecht, 2006. p. 119-
894 139.

895 Kay, C. E. 1997. Is aspen doomed? *Journal of Forestry* 95, 4-11.

896 Koivula, M., Punttila, P., Haila, Y. & Niemelä, J. 1999. Leaf litter and the small-scale distribution of
897 carabid beetles (Coleoptera, Carabidae) in the boreal forest. *Ecography* 22, 424-435.

898 Kolström, M., Lumatjärvi, J. 2000. Saproxylic beetles on aspen in commercial forests: a simulation
899 approach to species richness. *Forest Ecology and Management* 126, 113-120.

900 Komonen, A., Tuominen, L., Purhonen, J., & Halme, P. 2020. Landscape structure influences
 901 browsing on a keystone tree species in conservation areas. *Forest Ecology and Management* 457,
 902 117724.

903 Korpela, I., Ørka, H. O., Maltamo, M., Tokola, T. & Hyyppä, J. 2010. Tree species classification
 904 using airborne LiDAR—effects of stand and tree parameters, downsizing of training set, intensity
 905 normalization, and sensor type. *Silva Fennica* 44, 319-339.

906 Kotiranta, H., Niemelä, T., 1981. Composition of the polypore communities of four forest areas in
 907 southern Central Finland. *Karstenia* 21, 31–48.

908 Kouki, J., Arnold, K. & Martikainen, P. 2004. Long-term persistence of aspen—a key host for many
 909 threatened species—is endangered in old-growth conservation areas in Finland. *Journal for Nature*
 910 *Conservation* 12, 41-52.

911 Kuuluvainen, T., Lindberg, H., Vanha-Majamaa, I., Keto-Tokoi, P., & Punttila, P. 2019. Low-level
 912 retention forestry, certification, and biodiversity: case Finland. *Ecological Processes* 8, 47.

913 Kuusinen 1994. Epiphytic lichen flora and diversity on *Populus tremula* in old-growth and managed
 914 forests of southern and middle boreal Finland. *Annales Botanici Fennici* 31, 245–260.

915 Landhäusser, S.M., Pinno, B.D., Mock, K.E. 2019. Tamm Review: Seedling-based ecology,
 916 management, and restoration in aspen (*Populus tremuloides*). *Forest Ecology and Management*
 917 432, 231-245.

918 Lankia, H., Wallenius, T., Várkonyi, G., Kouki, J., Snäll, T. 2012. Forest fire history, aspen and goat
 919 willow in a Fennoscandian old-growth landscape: are current population structures a legacy of
 920 historical fires? *Journal of Vegetation Science* 23, 1159-1169.

921 Latva-Karjanmaa, T., Suvanto, L., Leinonen, K., Rita, H. 2003. Emergence and survival of *Populus*
 922 *tremula* seedlings under varying moisture conditions. *Canadian Journal of Forest Research* 33,
 923 2081–2088.

- 924 Latva-Karjanmaa, T., Penttilä, R., Siitonen, J. 2007. The demographic structure of European aspen
925 (*Populus tremula*) populations in managed and old-growth boreal forests in eastern Finland.
926 Canadian Journal of Forest Research 37, 1070-1081.
- 927 Lavsund, S., Nygrén, T. & Solberg, E. J. 2003. Status of moose populations and challenges to moose
928 management in Fennoscandia. Alces 39, 30.
- 929 Lee, C. M., Cable, M. L., Hook, S. J., Green, R. O., Ustin, S. L., Mandl, D. J., Middleton, E. M. 2015.
930 An introduction to the NASA Hyperspectral InfraRed Imager (HyspIRI) mission and preparatory
931 activities Remote Sensing of Environment 167, 6–19.
- 932 Li, J., Hu, B. & Noland, T.L. 2013. Classification of tree species based on structural features derived
933 from high density LiDAR data. Agricultural and Forest Meteorology 171, 104-114.
- 934 Lilja, S., Wallenius, T. & Kuuluvainen, T. 2006. Structure and development of old *Picea abies* forests
935 in northern boreal Fennoscandia. Ecoscience 13, 181-192.
- 936 Lundström, J., Jonsson, F., Perhans, K., Gustafsson, L. 2013. Lichen species richness on retained
937 aspens increases with time since clear-cutting. Forest Ecology and Management 293, 49-56.
- 938 MacKenzie, N.A. 2010. Ecology, conservation and management of Aspen. A literature review.
939 Scottish Native Woods, Aberfeldy.
- 940 Madritch, M.D., Kingdon, C.C., Singh, A., Mock, K.E., Lindroth, R.L. & Townsend, P.A. 2014.
941 Imaging spectroscopy links aspen genotype with below-ground processes at landscape scales.
942 Philosophical Transactions of the Royal Society of London B: Biological Sciences 369, 20130194.
- 943 Maltamo M., Packalen P. 2014. Species specific management inventory in Finland. In: Maltamo M.,
944 Naesset E., Vauhkonen J. (eds.). Forestry applications of airborne laser scanning – concepts and
945 case studies. Managing Forest Ecosystems vol. 27, Springer. p. 241–252. http://dx.doi.org/10.1007/978-94-017-8663-8_12.
946
- 947 Maltamo, M., Pesonen, A., Korhonen, L., Kouki, J., Vehmas, M. & Eerikäinen, K. 2015. Inventory
948 of aspen trees in spruce dominated stands in conservation area. Forest Ecosystems 2, 12.

949 Maltamo, M., Karjalainen, T., Repola, J. & Vauhkonen, J. 2018. Incorporating tree-and stand-level
950 information on crown base height into multivariate forest management inventories based on
951 airborne laser scanning. *Silva Fennica* 52, 10006. 10.14214/sf.10006.

952 Martikainen, P., Penttilä, R., Kotiranta, H & Miettinen, O. 2000. New records of *Funalia trogii*,
953 *Perenniporia tenuis* and *Polyporus pseudobetulinus* from Finland, with notes on their habitat
954 requirements and conservation implications. *Karstenia* 40, 79-92.

955 Martikainen, P. 2001. Conservation of threatened saproxylic beetles: significance of retained aspen
956 *Populus tremula* on clearcut areas. *Ecological Bulletins* 49, 205-218.

957 Martin, K., Eadie, J.M. 1999. Nest webs: A community-wide approach to the management and
958 conservation of cavity-nesting forest birds. *Forest Ecology and Management* 115, 243-257.

959 Mazziotta, A., Triviño, M., Tikkanen, O. P., Kouki, J., Strandman, H., & Mönkkönen, M. 2016.
960 Habitat associations drive species vulnerability to climate change in boreal forests. *Climatic*
961 *Change* 135(3-4), 585-595.

962 McRoberts, R. E., Tomppo, E. O. 2007. Remote sensing support for national forest inventories.
963 *Remote Sensing of Environment* 110(4), 412-419.

964 Michaelsen, T.C. 2016. Aspen *Populus tremula* is a key habitat for tree-dwelling bats in
965 boreonemoral and south boreal woodlands in Norway. *Scandinavian Journal of Forest Research*
966 31, 477-483.

967 Mock, K. E., Rowe, C. A., Hooten, M. B., Dewoody, J., Hipkins, V.D. 2008. Clonal dynamics in
968 western North American aspen (*Populus tremuloides*). *Molecular Ecology* 17, 4827–4844.

969 Mönkkönen, M., Burgas, D., Eyvindson, K., Le Tortorec, E., Peura, M., Pohjanmies, T., ... & Triviño,
970 M. 2018. Solving conflicts among conservation, economic, and social objectives in boreal
971 production forest landscapes: Fennoscandian perspectives. In *Ecosystem Services from Forest*
972 *Landscapes* (pp. 169-219). Springer, Cham.

973 Mononen, L., Auvinen, A.-P., Packalen, P., Virkkala, R., Valbuena, R., Bohlin, I., Valkama, J. &
974 Vihervaara, P. 2018: Usability of citizen science observations together with airborne laser

975 scanning data in determining the habitat preferences of forest birds. *Forest Ecology and*
 976 *Management* 430, 498-508.

977 Myking, T., Bøhler, F., Austrheim, G., & Solberg, E. J. 2011. Life history strategies of aspen (*Populus*
 978 *tremula* L.) and browsing effects: a literature review. *Forestry* 84, 61-71.

979 Naidoo, L., Cho, M.A., Mathieu, R., Asner, G., 2012. Classification of savanna tree species, in the
 980 Greater Kruger National Park region, by integrating hyperspectral and LiDAR data in a Random
 981 Forest data mining environment. *ISPRS J. Photogramm.*, 69, 167–179.

982 Næsset, E. 2007. Airborne laser scanning as a method in operational forest inventory: status of
 983 accuracy assessments accomplished in Scandinavia. *Scand J For Res* 22, 433–442

984 Næsset, E. 2009. Effects of different sensors, flying altitudes, and pulse repetition frequencies on
 985 forest canopy metrics and biophysical stand properties derived from small-footprint airborne laser
 986 data. *Remote Sensing of Environment* 113, 148–159.

987 Nikula, S., Vapaavuori, E., Manninen, S. 2010. Urbanization-related changes in European aspen
 988 (*Populus tremula* L.): leaf traits and litter decomposition. *Environmental Pollution* 158(6), 2132-
 989 2142.

990 Økland, B., Bakke, A., Hågvar, S., Kvamme, T., 1996. What factors influence the diversity of
 991 saproxylic beetles—a multiscaled study from a spruce forest in southern Norway. *Biodiversity*
 992 *and Conservation* 5, 75–100.

993 Oldén, A., Ovaskainen, O., Kotiaho, J. S., Laaka-Lindberg, S. & Halme, P. 2014. Bryophyte species
 994 richness on retention aspens recovers in time but community structure does not. *PloS one* 9,
 995 e93786.

996 Ørka, H. O., Næsset, E. & Bollandsås, O. M. 2007. Utilizing airborne laser intensity for tree species
 997 classification. *International Archives of the Photogrammetry, Remote Sensing and Spatial*
 998 *Information Sciences* 36, W52.

999 Ørka, H. O., Næsset, E. & Bollandsås, O. M., 2010. Effects of different sensors and leaf-on and leaf-
1000 off canopy conditions on echo distributions and individual tree properties derived from airborne
1001 laser scanning. *Remote Sensing of Environment* 114, 1445-1461.

1002 Östlund, L., Zackrisson, O., Axelsson, A. L. 1997. The history and transformation of a Scandinavian
1003 boreal forest landscape since the 19th century. *Canadian Journal of Forest Research* 27, 1198-
1004 1206.

1005 Oukrop, C.M., Evans, D.M., Bartos, D.L., Ramsey, R.D. & Ryel, R.J. 2011. Moderate-scale mapping
1006 methods of aspen stand types: a case study for Cedar Mountain in southern Utah. *Gen. Tech. Rep.*
1007 *RMRS-GTR-259. Fort Collins, CO: US Department of Agriculture, Forest Service, Rocky*
1008 *Mountain Research Station. 18 p., 259.*

1009 Packalén, P., Maltamo, M., 2007. The k-MSN method for the prediction of species-specific stand
1010 attributes using airborne laser scanning and aerial photographs. *Remote Sensing of Environment*
1011 109, 328-341.

1012 Perhans, K., Haight, R.G., Gustafsson, L. 2014. The value of information in conservation planning:
1013 selecting retention trees for lichen conservation. *Forest Ecology and Management* 318, 175-182.

1014 Persson, Å., Holmgren, J., Söderman, U., Olsson, H., 2004. Tree species classification of individual
1015 trees in sweden by combining high resolution laser data with high resolution near infrared digital
1016 images. *Proceedings of the Natscan Conference, 4-6 Oct. 2004.*

1017 Pettorelli, N., Safi, K., & Turner, W. 2014. Satellite remote sensing, biodiversity research and
1018 conservation of the future. 20130190.

1019 Piironen, R., Heiskanen, J., Maeda, E., Viinikka, A., Pellikka, P. 2017. Classification of tree species
1020 in a diverse African agroforestry landscape using imaging spectroscopy and laser scanning.
1021 *Remote Sensing* 9, 1-20.

1022 Pippuri, I., Maltamo, M., Packalen, P., Mäkitalo, J. 2013. Predicting species-specific basal areas in
1023 urban forests using airborne laser scanning data and existing stand register data. *Eur J For Res*
1024 132,999–1012.

1025 Possen, B.J.H.M., Oksanen, E., Rousi, M., Ruhanen, H., Ahonen, V., Tervahauta, A., Heinonen, J.,
 1026 Heiskanen, J., Kärenlampi, S., Vapaavuori, E. 2011. Adaptability of birch (*Betula pendula* Roth)
 1027 and aspen (*Populus tremula* L.) genotypes to different soil moisture conditions. *Forest Ecology*
 1028 *and Management* 262, 1387–1399.

1029 Prisley, S. P., Smith, J. L. 1987. Using classification error matrices to improve the accuracy of
 1030 weighted land-cover models. *Photogrammetric engineering and remote sensing* 53(9), 1259-1263

1031 Puliti, S., Ørka, H.O., Gobakken, T., Næsset, E. 2015. Inventory of small forest areas using an
 1032 unmanned aerial system. *Remote Sensing* 7, 9632–9654.

1033 Pykälä, J., Heikkinen, R. K., Toivonen, H., & Jääskeläinen, K. 2006. Importance of Forest Act
 1034 habitats for epiphytic lichens in Finnish managed forests. *Forest Ecology and Management* 223,
 1035 84-92.

1036 Ranius, T., Martikainen, P., Kouki, J. 2011. Colonisation of ephemeral forest habitats by specialized
 1037 species: beetles and bugs associated with recently dead aspen wood. *Biodivers Conserv* 20, 2903–
 1038 2915.

1039 Rassi, P., Hyvärinen, E., Juslén, A. & Mannerkoski, I. 2010. The 2010 Red List of Finnish species.
 1040 Ympäristöministeriö & Suomen ympäristökeskus, Helsinki, 685.

1041 Remm, J., Hanski, I. K., Tuominen, S., & Selonen, V. 2017. Multilevel landscape utilization of the
 1042 Siberian flying squirrel: Scale effects on species habitat use. *Ecology and evolution* 7, 8303-
 1043 8315.

1044 Reinikainen, M., D’Amato, A. W., & Fraver, S. 2012. Repeated insect outbreaks promote multi-
 1045 cohort aspen mixedwood forests in northern Minnesota, USA. *Forest Ecology and Management*,
 1046 266, 148-159.

1047 Rhodes, A. C., Wan, H. Y., Clair, S. B. S. 2017. Herbivory impacts of elk, deer and cattle on aspen
 1048 forest recruitment along gradients of stand composition, topography and climate. *Forest Ecology*
 1049 *and Management* 397, 39-47.

1050 Robinson, K.M. Ingvarsson, P.K., Jansson, S., Albrechtsen, B.R. 2012. Genetic variation in functional
1051 traits influences arthropod community composition in aspen (*Populus tremula* L.) PLoS One 7,
1052 e37679.

1053 Rodríguez, A., Pohjoismäki, J. L., & Kouki, J. 2019. Diversity of forest management promotes
1054 parasitoid functional diversity in boreal forests. Biological Conservation 238, 108205.

1055 Rogers, P. C., Pinno, B. D., Šebesta, J., Albrechtsen, B. R., Li, G., Ivanova, N., ... & Myking, T. 2019.
1056 A global view of aspen: Conservation science for widespread keystone systems. Global Ecology
1057 and Conservation, e00828.

1058 Roth, K. L., Roberts, D. A., Dennison, P. E., Alonzo, M., Peterson, S. H., & Beland, M. (2015a).
1059 Differentiating plant species within and across diverse ecosystems with imaging spectroscopy.
1060 Remote Sensing of Environment 167, 135-151.

1061 Roth, K. L., Roberts, D. A., Dennison, P. E., Peterson, S. H., & Alonzo, M. (2015b). The impact of
1062 spatial resolution on the classification of plant species and functional types within imaging
1063 spectrometer data. Remote Sensing of Environment 171, 45-57.

1064 Rosenthal, R., Lohmus, A. 2008. For what, when, and where is green-tree retention better than clear-
1065 cutting? A review of the biodiversity aspects. Forest Ecology and Management 255, 1-15.

1066 Rosenthal, R., Lohmus, A., & Kiviste, A. 2008. Preadaptation and spatial effects on retention-tree
1067 survival in cut areas in Estonia. Canadian Journal of Forest Research 38, 2616-2625.

1068 Rosenthal, R., Lohmus, P., Rannap, R., Remm, L., Rosenthal, K., Runnel, K., & Lohmus, A. 2019.
1069 Assessing long-term effectiveness of green-tree retention. Forest Ecology and Management 448,
1070 543-548.

1071 Rouvinen, S., Rautiainen, A. & Kouki, J. 2005. A relation between historical forest use and current
1072 dead woody material in a boreal protected old-growth forest in Finland. Silva Fennica 39, 21–36.

1073 Runnel, K., Rosenthal, R., & Lohmus, A. 2013. The dying legacy of green-tree retention: different
1074 habitat values for polypores and wood-inhabiting lichens. Biological Conservation 159, 187-196.

1075 Saarinen, N., Vastaranta, M., Näsi, R., Rosnell, T., Hakala, T., Honkavaara, E., Wulder, M.A.,
 1076 Luoma, V., Tommaselli, A.M.G., Imai, N.N., Ribeiro, E.A.W., Guimaraes, R.B., Holopainen, M.
 1077 & Hyyppä, J. 2018. Assessing Biodiversity in Boreal Forests with UAV-Based Photogrammetric
 1078 Point Clouds and Hyperspectral Imaging. *Remote Sensing* 10, 338.

1079 Sahlin, E., Ranius, T., 2009. Habitat availability in forests and clearcuts for saproxylic beetles
 1080 associated with aspen. *Biodiversity and Conservation* 18, 621.

1081 Sankey, T.T. 2009. Regional assessment of aspen change and spatial variability on decadal time
 1082 scales. *Remote Sensing* 1, 896-914.

1083 Sankey, T.T. 2012. Decadal-scale aspen changes: evidence in remote sensing and tree ring data.
 1084 *Applied Vegetation Science* 15,

1085 Schei, F. H., Blom, H. H., Gjerde, I., Grytnes, J. A., Heegaard, E. & Sætersdal, M. 2013. Conservation
 1086 of epiphytes: Single large or several small host trees? *Biological Conservation* 168, 144-151.

1087 Seager, S.T., Eisenberg, C., St. Clair, S.B., 2013. Patterns and consequences of ungulate herbivory
 1088 on aspen in western North America. *Forest Ecology and Management* 299, 81–90.

1089 Seedre, M., Felton, A., & Lindbladh, M. 2018. What is the impact of continuous cover forestry
 1090 compared to clearcut forestry on stand-level biodiversity in boreal and temperate forests? A
 1091 systematic review protocol. *Environmental Evidence* 7, 28.

1092 Siitonen, J., Martikainen, P. 1994. Occurrence of rare and threatened insects living on decaying
 1093 *Populus tremula*: a comparison between Finnish and Russian Karelia. *Scandinavian Journal of*
 1094 *Forest Research* 9, 185-19. <https://doi.org/10.1080/02827589409382830>

1095 Singer, J. A., Turnbull, R., Foster, M., Bettigole, C., Frey, B. R., Downey, M. C., ... & Ashton, M. S.
 1096 2019. Sudden Aspen Decline: A review of pattern and process in a changing climate. *Forests* 10,
 1097 671.

1098 Sivadasan, U., Chenhao, C., Nissinen, K., Randriamanana, T., Nybakken, L., Julkunen-Tiitto, R.
 1099 Growth and defence of aspen (*Populus tremula*) after three seasons under elevated temperature
 1100 and ultraviolet-B radiation. *Can. J. For. Res.* 48, 629–641

1101 St-Onge, B., Vega, C., Fournier, R. A., Hu, Y. 2008. Mapping canopy height using a combination of
 1102 digital stereo-photogrammetry and lidar. *International Journal of Remote Sensing* 29, 3343-3364.

1103 Strand, E.K., O'Sullivan, M.T. & Bunting, S.C. 2012. Time series aerial photography can help land
 1104 owners and managers understand local aspen dynamics. *Rangelands* 34, 21-29.

1105 Suominen, O., Edenius, L., Ericsson, G. & de Dios, V.R. 2003. Gastropod diversity in aspen stands
 1106 in coastal northern Sweden. *Forest Ecology and Management* 175, 403-412.

1107 Suvanto, L.I., Latva-Karjanmaa, T.B. 2005. Clone identification and clonal structure of the European
 1108 aspen (*Populus tremula*). *Molecular Ecology* 14, 2851-2860.

1109 Sverdrup-Thygeson, A., Bendiksen, E., Birkemoe, T. & Larsson, K. H. 2014. Do conservation
 1110 measures in forest work? A comparison of three area-based conservation tools for wood-living
 1111 species in boreal forests. *Forest Ecology and Management* 330, 8-16.

1112 Säynäjoki, R., Packalén, P., Maltamo, M., Vehmas, M., Eerikäinen, K. 2008. Detection of aspens
 1113 using high resolution aerial laser scanning data and digital aerial images. *Sensors* 8, 5037–5054.

1114 Tarasova, V. N., Obabko, R. P., Himelbrant, D. E., Boychuk, M. A., Stepanchikova, I. S., &
 1115 Borovichev, E. A. 2017. Diversity and distribution of epiphytic lichens and bryophytes on aspen
 1116 (*Populus tremula*) in the middle boreal forests of Republic of Karelia (Russia). *Folia Cryptogamica*
 1117 *Estonica* 54 125-141.

1118 Thompson, I.D., Maher, S.C., Rouillard, D.P., Fryxell, J.M., Baker, J.A. 2007. Accuracy of forest
 1119 inventory mapping: some implications for boreal forest management. *For. Ecol. Manage.* 252,
 1120 208–221.

1121 Tikkanen, O.P., Martikainen, P., Hyvärinen, E., Junninen, K., Kouki, J. 2006. Red-listed boreal forest
 1122 species of Finland: associations with forest structure, tree species, and decaying wood. *Ann Zool*
 1123 *Fenn* 43, 373–383.

1124 Torresan, C., Berton, A., Carotenuto, F., Di Gennaro, S.F., Gioli, B., Matese, A., Miglietta, F.,
 1125 Vagnoli, C., Zaldei, A., Wallace, L. 2016. Forestry applications of UAVs in Europe: A review.
 1126 *Internatioanl Journal of Remote Sensing*, 1–21.

1127 Trier, Ø. D., Salberg, A. B., Kermit, M., Rudjord, Ø., Gobakken, T., Næsset, E., & Aarsten, D. 2018.
1128 Tree species classification in Norway from airborne hyperspectral and airborne laser scanning
1129 data. *European Journal of Remote Sensing* 51, 336-351.

1130 Tucker, C. J. 1979. Red and photographic infrared linear combinations for monitoring vegetation.
1131 *Remote Sensing of the Environment* 8, 127-150.

1132 Tuominen, S., Näsi, R., Honkavaara, E., Balazs, A., Hakala, T., Viljanen, N., Pölönen, I., Saari, H.,
1133 Ojanen, H. 2018. Assessment of classifiers and remote sensing features of hyperspectral imagery
1134 and stereo-photogrammetric point clouds for recognition of tree species in a forest area of high
1135 species diversity. *Remote Sensing* 10, 714.

1136 Ustin, S. L., Gitelson, A. A., Jacquemoud, S., Schaepman, M., Asner, G. P., Gamon, J. A., Zarco-
1137 Tejada, P. 2009. Retrieval of foliar information about plant pigment systems from high resolution
1138 spectroscopy. *Remote Sensing of Environment* 113, S67-S77.

1139 Van Bogaert, R., Jonasson, C., De Dapper, M. & Callaghan, T. V. 2009. Competitive interaction
1140 between aspen and birch moderated by invertebrate and vertebrate herbivores and climate
1141 warming. *Plant Ecology & Diversity* 2, 221-232.

1142 Van Bogaert, R., Jonasson, C., De Dapper, M., & Callaghan, T. V. 2010. Range expansion of
1143 thermophilic aspen (*Populus tremula* L.) in the Swedish Subarctic. *Arctic, Antarctic, and Alpine*
1144 *Research* 42, 362-375

1145 Vanha-Majamaa, I., Lilja, S., Ryömä, R., Kotiaho, J. S., Laaka-Lindberg, S., Lindberg, H., ... &
1146 Kuuluvainen, T. 2007. Rehabilitating boreal forest structure and species composition in Finland
1147 through logging, dead wood creation and fire: the EVO experiment. *Forest Ecology and*
1148 *Management* 250, 77-88.

1149 Vehmas, M., Kouki, Eerikäinen, K. 2009. Long-term spatio-temporal dynamics and historical
1150 continuity of European aspen (*Populus tremula* L.) stands in the Koli National Park, eastern
1151 Finland. *Forestry* 82, 135-148.

1152 Vihervaara, P., Mononen, L., Auvinen, A.-P., Virkkala, R., Lü, Y., Pippuri, I., Packalen P., Valbuena,
 1153 R. & Valkama, J. 2015. How to integrate remotely sensed data and biodiversity for ecosystem
 1154 assessments at landscape scale. *Landscape Ecology* 30, 501-516.

1155 Wang, R., & Gamon, J. A. 2019. Remote sensing of terrestrial plant biodiversity. *Remote Sensing of*
 1156 *Environment* 231, 111218.

1157 Whitham, T.G., Bailey, J.K., Schweitzer, J.A., Shuster, S.M., Bangert, R.K., LeRoy, C.J., ... &
 1158 Fischer, D.G. 2006. A framework for community and ecosystem genetics: from genes to
 1159 ecosystems. *Nature Reviews Genetics* 7, 510.

1160 Worrell, R., 1995a. European aspen (*Populus tremula* L.): a review with particular reference to
 1161 Scotland I. Distribution, ecology and genetic variation. *Forestry: An International Journal of Forest*
 1162 *Research* 68, 93-105.

1163 Worrell, R., 1995b. European aspen (*Populus tremula* L.): a review with particular reference to
 1164 Scotland II. Values, silviculture and utilization. *Forestry: An International Journal of Forest*
 1165 *Research* 68, 231-244.

1166 Wulder, M. A., White, J. C., Goward, S. N., Masek, J. G., Irons, J. R., Herold, M., ... & Woodcock,
 1167 C. E. (2008). Landsat continuity: Issues and opportunities for land cover monitoring. *Remote*
 1168 *Sensing of Environment* 112, 955-969.

1169 Wulder, M. A., Loveland, T. R., Roy, D. P., Crawford, C. J., Masek, J. G., Woodcock, C. E., ... &
 1170 Dwyer, J. (2019). Current status of Landsat program, science, and applications. *Remote Sensing*
 1171 *of Environment* 225, 127-147.

1172 Xie, Y., Sha, Z., & Yu, M. (2008). Remote sensing imagery in vegetation mapping: a review.
 1173 *Journal of Plant Ecology* 1, 9-23.

1174 Zakrisson, C., Ericsson, G. & Edenius, L. 2007. Effects of browsing on recruitment and mortality of
 1175 European aspen (*Populus tremula* L.). *Scandinavian Journal of Forest Research* 22, 324-332.

1176 Zarco-Tejada, P.J., Diaz-Varela, R.; Angileri, V., Loudjani, P. 2014. Tree height quantification using
 1177 very high resolution imagery acquired from an unmanned aerial vehicle (UAV) and automatic 3D
 1178 photo-reconstruction methods. *European Journal of Agronomy* 55, 89–99.

1179 Yamasaki, E., Altermatt, F., Cavender-Bares, J., Schuman, M. C., Zuppinger-Dingley, D., Garonna,
 1180 I., ... & Schmid, B. (2017). Genomics meets remote sensing in global change studies: monitoring
 1181 and predicting phenology, evolution and biodiversity. *Current Opinion in Environmental*
 1182 *Sustainability* 29, 177-186.

1183 Yang, R. C. 1991. Growth of white spruce following release from aspen competition: 35 year results.
 1184 *The Forestry Chronicle* 67, 706-711.

1185 Yu, X., Hyypä, J., Litkey, P., Kaartinen, H., Vastaranta, M., & Holopainen, M. 2017. Single-sensor
 1186 solution to tree species classification using multispectral airborne laser scanning. *Remote Sensing*
 1187 9, 108.

1188