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Kivinen, Sonja

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A keystone species, European aspen (Populus tremula L.), in boreal forests:

ecological role, knowledge needs and mapping using remote sensing

Sonja Kivinen¹,²*, Elina Koivisto³, Sarita Keski-Saari¹,⁴, Laura Poikolainen¹, Topi Tanhuaanpää¹,⁵, 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
Abstract

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

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

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

European aspen (*Populus tremula* L., hereafter ‘aspen’ or ‘European aspen’) is a keystone species and an early-succession species in boreal forests. Although it has a sparse and scattered occurrence in northern Europe, it contributes significantly to the biological diversity of boreal forest landscapes (Hynynen and Viherä-Aarnio, 1999; Kouki et al., 2004; Tikkanen et al., 2006; Whitham et al., 2006; MacKenzie, 2010; Caudullo and de Rigo, 2016). Aspen is an important host for many species. Aspen trees are inhabited by epiphytic bryophytes and lichens (Kuusinen, 1994; Gustafsson and Eriksson, 1995; Hazell, 1998; Pykäli et al., 2006), pathogens (Callan, 1998), herbivorous invertebrates (Robinson et al., 2012), mammals such as the flying squirrel (*Pteromys volans*; Hanski, 1998; Remm et al. 2017) and birds such as woodpeckers and owls (Hågvar et al., 1990; Angelstam and Mikusinski, 1994; Tikkanen et al., 2006; Hardenbol et al. 2019). Secondary hole-nesters, including many tits, flycatchers, owls, ducks and flying squirrels, are dependent on cavities excavated by woodpeckers (Martin and Eadie, 1999; Baroni et al. 2020). Aspen leaf litter is utilised by, for example, gastropods (Suominen et al., 2003), and dead and decaying aspen trunks provide a suitable habitat for myriad
polypore fungi (Kotiranta and Niemelä, 1981; Hynynen and Viherä-Aarnio, 1999; Junninen et al., 2007) and saproxylic invertebrate species (Siitonen and Martikainen, 1994; Martikainen, 2001; Dahlberg and Stokland, 2004; Halme et al., 2012). The conservation biological importance of aspen is illustrated by the fact that many of the aspen-associated species—dependent either on living or dead aspen trees—are red-listed (Jonsell et al., 1998; Hynynen and Viherä-Aarnio, 1999; Dahlberg and Stokland, 2004; Tikkanen et al., 2006).

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

A few earlier reviews examined European aspen or *Populus tremuloides* Michx. (quaking aspen, trembling aspen or American aspen) that occur in North America. A review by Landhäusser et al. (2019) focused on ecology, management and restoration of quaking aspen, and the review by MacKenzie (2010) examined ecology, conservation and management of both European aspen and quaking aspen in the northern hemisphere. Worrell (1995a, 1995b) reviewed the distribution, ecology 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 that aspens can live up to 100-200 years (Lilja et al., 2006; Latvakanjamaa 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
European Russia, birch and rowan appeared to be more common in gaps than European aspen (Gromtsev et al. 2002).

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

The occurrence, abundance and diversity of the aspen-associated species are markedly affected by the characteristics of individual aspen trees, including size and age. Many species prefer or are confined to old aspens, and large-diameter host trees are favoured, for example, by epiphytic bryophytes (Hazell et al., 1998; Gu et al., 2001). Due to this factor, large aspens with a diameter at breast height that exceeds 20 cm (Latva-Karjanmaa et al., 2007) or 25 cm (Maltamo et al., 2015) have been included as ecologically relevant individuals in studies that aimed to map the spatiotemporal variation in aspen abundance. Black-coloured and speckled bark, slow tree growth (as defined by visual inspection, e.g., the relationship between the diameter and bark texture) and tree inclination angle are also important determinants of epiphytic lichen species on aspen trees (Perhans et al., 2014). Further, the number of epiphytic bryophyte species increases with aspen bark thickness (Gustafsson and Eriksson, 1995). Tarasova et al. (2017) also found distinct epiphyte species composition at
different heights of aspen trunks and branches. These data show that disparate lichen and moss species often occupy different ecological niches (Fig. 1b).

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

The number of species that live on dead aspen wood material is high. Thus, the occurrence of this material is of critical importance for species richness and biodiversity conservation (Martikainen et al., 2000; Kouki et al., 2004). Aspen decay is a rather fast process; most of the current dead wood will become disintegrated within about 90 years, depending on the current decay stage (Latva-Karjanmaa et al., 2007). The continued supply of dead wood depends on the regional abundance of aspen trees and the disturbances that generate fallen and dead trunks. For example, several threatened aspen-specialist polypore species require frequent emergence of new suitable host trees as old ones become unsuitable for them in approximately 10 years after colonisation (Martikainen et al., 2000).
Similarly, saproxylic insect species that utilise recently dead aspen wood are dependent on sufficiently rapid formation of new habitats (Ranius et al., 2011). Saproxylic invertebrates that live on decaying wood can often colonise several tree species and therefore are not always dependent on the occurrence of one species. However, species composition of the saprophytic fungi community may crucially impact the habitat quality for many saproxylic insects (Jonsell et al., 1998). Likewise, nematorecan (Diptera) communities of a single aspen log may markedly differ between the base and top part of the same tree, but the factors that determine this variation and the preferred microhabitat for each insect species are poorly understood (Halme et al., 2013). Økland et al. (1996), Ranius et al. (2011) and Jacobsen et al. (2015) demonstrated that species richness of aspen-associated saproxylic beetles can be related to dead wood volume within a radius of 0.1–3 km. These findings highlight the importance of habitat availability at larger scales.

Aspen has a clonal growth habit, in which several ramets can emerge from one clone as root sprouts. However, clones of European aspen often consist of a single ramet. For example, in a Finnish study, 70% of the clones comprised only one ramet (Suvanto and Latva-Karjanmaa, 2005). Genetic studies revealed that intrapopulation genetic variation of European aspen is relatively high. These data imply that the proportion of individuals that arise from seeds is higher than previously assumed (Suvanto and Latva-Karjanmaa, 2005). On the contrary, quaking aspen can form giant growth, with the largest known genet covering about 43.6 ha (DeWoody et al., 2008). Nevertheless, quaking aspen also exhibits much more genetic variation than previously presumed, with many clones encountered only once in a 50 m grid (Mock et al., 2008). In European aspen, the maximum distance between ramets in a clone can be at least 46 m (Suvanto and Latva-Karjanmaa, 2005). In Scotland, 21 clones were detected in a 4.6 ha area, when 186 aspens were sampled (Easton, 1997).
Fig. 1. a) Crowns of aspen hold-overs in a natural old-growth forest that reach above below-growing spruce trees. b) Aspen trunk with epiphytic lichens, mosses and Orthilia secunda. (Photo credits: Sarita Keski-Saari.)

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

3.1 Forest management methods

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

Recently, aspen has received more supportive consideration—based on the realisation of its keystone species role in forest biodiversity—in the management planning of commercial forests. The most important recommendations to secure aspen regeneration include restoring regeneration niches by mimicking natural disturbance processes, such as fire at various spatial scales, and retaining aspen
in clearings and pre-commercial thinnings (Kouki et al., 2004; Vanha-Majamaa et al. 2007; Edenius et al., 2011). Clear-cutting acts as a source of disturbance and promotes the regeneration of aspen. How this is realized in the number of mature aspens depends on forestry actions following the regeneration, such as thinning of seedling stands (Fraser et al. 2003). Similarly, the extent of tree retention is dependent on the forestry actions (Latva-Karjanmaa et al., 2007; Myking et al., 2011; Kuuluvainen et al. 2019). Creating dead wood by girdling aspens or leaving dead wood on clear-cuts may represent beneficial measures to preserve species that are dependent on dead aspens (Jonsell et al., 1998; Martikainen et al., 2000; Runnell et al. 2012), but could be harmful for species dependent on old living aspens.

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

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

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

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

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

3.2 Herbivores and pathogens

European aspen shoots and leaves provide valuable nutrition to several herbivore species, as reviewed by Myking et al. (2011). Browsers can suppress the regeneration of aspen and, in the long-term, reduce recruitment, delay maturation, increase mortality and ultimately cause a decline in local aspen populations. High browsing pressure is thus a major threat to species that are dependent on old aspens (Kouki et al., 2004; Komonen et al. 2020). Moose (*Alces alces*) is the primary herbivore that affects aspen recruitment (Edenius and Ericsson, 2007; Edenius et al., 2011). Fennoscandian moose populations started to grow rapidly in the 1960s, due to suitable habitats produced by clear-cutting, the low numbers of large carnivores and the use of supplementary forages, and are currently among the most productive and heavily harvested moose populations in the world (Lavsund et al., 2001). A
recent increase in the number of roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*) also causes high browsing pressure on aspens (Myking et al., 2011). Similarly, intense browsing by ungulates is harmful to the establishment and recruitment of quaking aspen in North America (Seager et al., 2013; Rhodes et al. 2017).

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

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

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

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

3.4 Spatial and temporal knowledge needs

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

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

4.1. Remote sensing techniques in vegetation mapping

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

Spectral remote sensing data consists of spatial images where every pixel contains the intensity of electromagnetic radiation reflected or emitted from the target and recorded by a sensor. Optical remote sensing is based on detecting objects at different wavelengths from visible and near-infrared range (VNIR; 400–1000 nm) and shortwave infrared range (SWIR; 1000–2500 nm) up to long-wave
infrared range (LWIR; 8000–14000 nm). Spectral resolution, i.e., the number and width of spectral bands in which information is recorded, varies between the sensors. Multispectral imagery consists of several generally non-contiguous spectral bands of varying bandwidths, whereas hyperspectral images (imaging spectroscopy) include a contiguous spectral range with hundreds of narrow bands. Temporal resolution refers to how often the remote sensing system records imagery of a particular area (revisit time; see Xie et al., 2008).

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

Rapid UAS development has mediated the development of new forestry-oriented applications (Colomina and Molina et al., 2014; Torresan et al., 2016; Franklin, 2018). The possibility of acquiring very high spatial resolution multispectral or hyperspectral UAS imagery on-demand allows estimating the structural parameters of forests at individual tree and stand level with high accuracy (Zarco-Tejada et al., 2014; Puliti et al., 2015). Recent developments in image processing software have also enabled wide-scale production of photogrammetric point clouds (PPC). PPCs have an RGB or near-infrared (NIR) value for each point, a feature that provides both colour information and the three-dimensional structure of the canopy (Hirschmuller, 2008; St-Onge et al., 2008). Airborne hyperspectral imagery (aircraft or UAS) provides new possibilities for increased accuracy of tree species mapping (Naidoo et al., 2012; Dalponte et al., 2013; Feret and Asner, 2013; Trier et al., 2018). High spatial and spectral resolution enables mapping biochemical and biophysical properties of vegetation (Alchanatis and Cohen, 2012; Roberts et al., 2012) that can be further used in species classification (Ghosh et al., 2014; Piironen et al., 2017).
Multispectral satellite imagery allows vegetation mapping from local to global scales. Satellite images generally have coarser spatial resolution compared to airborne data, and thus these data can be utilised in mapping tree groups or stands rather than individual trees. Multispectral data can be utilised to calculate spectral indices, such as normalised difference vegetation index (NDVI), to study the vegetation cover (Tucker et al., 1979). Temporal resolution of satellite imagery is typically 4-16 days, and the availability of long-time series (e.g. Landsat program) enables decadal change detection (Wulder et al., 2008, 2019; Xie et al., 2008).

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

Fig. 4 summarises the general advantages and drawbacks of different airborne and spaceborne remote sensing techniques in tree-species mapping. In the following case studies, we examine aspen detection at the tree-level and stand-level. The remote sensing studies reviewed here include mapping of European aspen, quaking aspen and a few other *Populus* species in Europe and North America.
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).
In Fennoscandia, European aspen has often been pooled with other deciduous tree species in ALS-based tree-level and stand-level studies due to the low number of aspen trees in the datasets (Packalen and Maltamo, 2007; Holmgren et al., 2008; Korpela et al., 2010; Ørka et al., 2010). However, there are some studies where aspen was classified separately from other tree species. Ørka et al. (2007) studied tree species classification by utilising ALS intensity metrics in the Østmarka natural reserve, Norway, where generally large and old aspens have a scattered occurrence in the forest landscape. Classification accuracies for aspen were relatively low (PA = 24%, UA = 56%) compared to other species (64-87% for *P. abies* L. and *Betula* ssp.). Laser metrics of aspen overlapped with those of spruce. Similar results were also reported by Korpela et al. (2010). In Canada, Li et al. (2013) classified tree species based on structure and architecture of individual tree crowns derived from high-density ALS data. Unlike in Fennoscandia, quaking aspen (*P. tremuloides* Michx.) was the dominant tree species together with sugar maple (*Acer saccharum* Marsh.), jack pine (*Pinus banksiana* Lamb.) and eastern white pine (*Pinus strobus* L.). UA and PA for quaking aspen were 74% and 76%, respectively, the highest classification error being between aspen and jack pine. The results of Li et al. (2013) highlight a positive, strong relationship between ALS point density and species classification accuracy.

Combining ALS data with aerial images can improve discrimination of tree species. Säynäjoki et al. (2008) used ALS data and aerial images to discriminate aspen from other deciduous trees in the Koli National Park in Eastern Finland, where abundance of European aspen is generally higher compared to typical managed boreal forests. Deciduous trees were first separated from coniferous trees using aerial images. Segments that belonged to aspen and those that belonged to other deciduous trees were then classified using ALS data with 79% accuracy. Large aspen trees with diameter at breast height of > 25 cm were detected with greater success compared to smaller trees. Breidenbach et al. (2010) utilised the semi-individual tree crown approach based on ALS and multispectral aerial images to predict species-specific forest inventory attributes for different tree species. The study was conducted in a forest area in southern Norway, where the European aspen proportion was
approximately 2%. Relative root mean square error (RMSE) for aspen volume was significantly higher (222%) compared to the relative RMSE for volume of pine, spruce and birch (38, 40 and 101%, respectively). These data indicated that the predictions calculated for aspen were considerably less accurate compared to other tree species.

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

Imaging spectroscopy (hyperspectral data) can improve tree species classifications by providing adequate information to discriminate among spectrally similar targets. Jones et al. (2010) used a combination of ALS and imaging spectroscopy for tree species classification in Canada. Several broad-leaved tree species, including quaking aspen and black cottonwood (*Populus trichocarpa*), occurred commonly in the studied forest area dominated by Douglas fir (*Pseudotsuga menziesii*). Although the methodology enabled species mapping with more detail and accuracy than is possible using conventional approaches (i.e., interpretation of aerial images), or either technology on its own, classification accuracies were markedly lower for quaking aspen (UA and PA < 34%) due to
similarity with red alder (*Alnus rubra*). However, another *Populus* species, black cottonwood, was accurately classified (UA of 82% and PA of 98%, respectively). Dalponte et al. (2009) used airborne imaging spectroscopy to image two Italian forest areas; one of them had a dense forest with 19 different tree species. Two *Populus* species, *Populus canescens* and *Populus hybrida*, were identified with UAs of approximately 80-90%, depending on the applied differentiation classifier. Similarly, Roth et al. (2015b) utilised airborne imaging spectroscopy to differentiate a large number of tree species in different regions in the USA and studied the impact of spatial resolution of data on classification accuracy. For black cottonwood, UAs and PAs were 82–100% for up to 40 m resolution and 71–83% at 60 m resolution. These data highlight the fact that future spaceborne imaging spectroscopy has high potential in tree species mapping. In another study, Roth et al. (2015a) compared the accuracy of imaging spectroscopy in species detection across different ecosystems and classified *P. trichocarpa* with a UA of 87% and PA of 84%. Tuominen et al. (2018) examined tree species recognition for 26 species and 14 genera in a Finnish arboretum using UAS-based hyperspectral imagery in combination with a three-dimensional photogrammetric canopy surface model. The UA and PA for aspen were 86% and 63%, respectively. Saarinen et al. (2018) assessed plot-level biodiversity indicators using imaging spectroscopy and photogrammetric point clouds acquired from a UAS in Finland. The number of aspens was low in the study region that contained both managed and natural boreal forests. The largest errors occurred in predictions of the amount as well as the volume of deciduous trees, such as aspen.

**4.3. Stand-level studies**

The majority of scientific studies on aspen mapping at the stand level were performed in North America, where quaking aspen forms extensive pure stands. In particular, a recent phenomenon, referred to as sudden aspen decline, characterised by rapid overstory mortality with little to no understory regeneration (e.g., Singer et al., 2019), has resulted in numerous efforts to map aspen ecosystems in western parts of North America. Despite few studies related to European aspen, the
examples presented here can provide a general view on the possibilities and constraints of different remote sensing methods in mapping aspen occurrence and dynamics at spatial scales coarser than individual tree-level (Table 1).

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

Aerial images can provide detailed information on forest stands at local and landscape scales. For example, Strand et al. (2012) mapped local dynamics of quaking aspen in Idaho over nearly four decades using aerial images. Stand structure was visible in the colour and infrared aerial images, but stands were difficult to delineate in older black and white images, a factor that complicated comparisons from one time period to another. They could also detect quaking aspen regeneration on the edges of stands, whereas regeneration in the understory was more difficult to assess. Di Orio et al. (2004) used historic and recent aerial images to study the density and fragmentation of quaking aspen in California over the past 50 years. The accuracy of aerial image interpretation was 85%, which is partly related to the fact that quaking aspen was the only commonly found deciduous tree in the study area. Heyman et al. (2003) mapped quaking aspen in central Oregon from colour-infrared aerial images using a segmentation approach into three general classes (no aspen, minor, predominant) with 88% overall accuracy. Due to the possibility to fly low-cost and on-demand, UAS
systems are particularly useful in acquiring data from areas affected by natural or anthropogenic disturbances. Aicardi et al. (2016) performed UAS-based change detection of vegetation after a stand-replacing forest fire in northern Italy. Multitemporal high-resolution digital surface models derived from ALS data and RGB imagery provided efficient detection of agamic regeneration of European aspen in the disturbed areas with no aboveground canopy layer.

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

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

Satellite images were also utilised for mapping vegetation health. Oukrop et al. (2011) studied healthy, damaged and seral stand types of quaking aspen to determine the extent of aspen decline in
Utah. The areas with aspen cover were defined from aerial images, and Landsat 5 TM images were utilised to map different aspen classes with an overall accuracy of 81%. Hall et al. (2014) studied changes in leaf area index (LAI) that resulted from insect defoliation in boreal aspen stands in northern Alberta using Landsat ETM+ images and field data. There was a strong relationship between LAI and the satellite image, and they observed defoliation for the study sites that included relatively pure stands of quaking aspen and balsam poplar (*Populus balsamifera* L.). Further, Boyd et al. (2019) examined the impact of climate and damage by the aspen epidermal leaf miner (*Phyllocnistis populiella*) on aspen productivity and physiology in Alaska using remote sensing indices of vegetation productivity (NDVI) acquired from GIMMS3g, MODIS Aqua, MODIS Terra and Landsat 5, 7 and 8.
Table 1. Tree-level and stand-level studies on mapping aspen (*P. tremula, P. tremuloides, Populus* spp.) using different remote sensing techniques.

<table>
<thead>
<tr>
<th>Tree-level</th>
<th>Species</th>
<th>Platform</th>
<th>Data type</th>
<th>Spectral range (µm (nr of bands))</th>
<th>Pixel size m</th>
<th>Pulse density pts/m²</th>
<th>Accuracy estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alonzo et al. (2018)</td>
<td>QA</td>
<td>UAS</td>
<td>PPC, RGB</td>
<td>B, G, R (3)</td>
<td>0.019–0.027</td>
<td></td>
<td>UA = 83%, PA = 74%</td>
</tr>
<tr>
<td>Breidenbach et al. (2010)</td>
<td>EA</td>
<td>AIR</td>
<td>ALS, RGB</td>
<td>G, R, NIR, PAN (4)</td>
<td>0.275 - 0.86</td>
<td>7.4</td>
<td>High RMSE</td>
</tr>
<tr>
<td>Dalponte et al. 2009</td>
<td>PO</td>
<td>AIR</td>
<td>HI</td>
<td>0.40–0.99 (126)</td>
<td>1</td>
<td></td>
<td>UA = 80–90%</td>
</tr>
<tr>
<td>Erikson (2004)</td>
<td>EA</td>
<td>AIR</td>
<td>CIR</td>
<td>0.60–0.90 (3)</td>
<td>0.03-0.1</td>
<td></td>
<td>UA = 63%, PA = 71%</td>
</tr>
<tr>
<td>Franklin and Ahmed (2017)</td>
<td>QA</td>
<td>UAS</td>
<td>MI</td>
<td>0.49–0.90 (6)</td>
<td>0.11</td>
<td></td>
<td>UA &amp; PA = 100%</td>
</tr>
<tr>
<td>Jones et al. (2010)</td>
<td>QA, PO</td>
<td>AIR</td>
<td>ALS, HI</td>
<td>0.40–2.50 (492)</td>
<td>2</td>
<td>0.4</td>
<td>UA &amp; PA &lt; 34%; UA = 82%, PA = 98%</td>
</tr>
<tr>
<td>Li et al. (2013)</td>
<td>QA</td>
<td>AIR</td>
<td>ALS</td>
<td></td>
<td></td>
<td>90</td>
<td></td>
</tr>
<tr>
<td>Ørka et al. (2007)</td>
<td>EA</td>
<td>AIR</td>
<td>ALS</td>
<td></td>
<td></td>
<td></td>
<td>UA = 56%, PA = 24%</td>
</tr>
<tr>
<td>Roth et al. (2015a)</td>
<td>PO</td>
<td>AIR</td>
<td>HI</td>
<td>0.35–2.00 (224)</td>
<td>4</td>
<td></td>
<td>UA = 84%, PA = 87%</td>
</tr>
<tr>
<td>Roth et al. (2015b)</td>
<td>PO</td>
<td>AIR</td>
<td>HI</td>
<td>0.35–2.50 (224)</td>
<td>1; 20; 40; 60</td>
<td></td>
<td>UA = 83–100%, PA = 71–96%</td>
</tr>
<tr>
<td>Saarinen et al. (2018)</td>
<td>EA</td>
<td>UAS</td>
<td>HI, PPC, RGB</td>
<td>0.50–0.90 (22)</td>
<td>0.10; 0.25</td>
<td></td>
<td>High RMSE</td>
</tr>
<tr>
<td>Säynäjoki et al. (2008)</td>
<td>EA</td>
<td>AIR</td>
<td>MLS, PAN</td>
<td>G, R, NIR, PAN (4)</td>
<td>0.25</td>
<td>3.86</td>
<td>OA = 79%</td>
</tr>
<tr>
<td>Tuominen et al. (2018)</td>
<td>EA</td>
<td>UAS</td>
<td>HI, PPC, RGB</td>
<td>0.4–1.60 (60)</td>
<td>0.015–0.20</td>
<td></td>
<td>UA = 86%, PA = 63%</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Stand-level</th>
<th>Species</th>
<th>Platform</th>
<th>Data type</th>
<th>Spectral range (µm (nr of bands))</th>
<th>Pixel size m</th>
<th>Pulse density pts/m²</th>
<th>Accuracy estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alcardi et al. (2016)</td>
<td>EA</td>
<td>UAS, AIR</td>
<td>ALS, RGB</td>
<td>R, G, B (3)</td>
<td>0.30</td>
<td>0.5-10</td>
<td>Efficient detection of vegetation dynamics</td>
</tr>
<tr>
<td>Bergen and Dronova (2007)</td>
<td>QA, PO</td>
<td>SAT</td>
<td>MI</td>
<td>0.63–0.90; 1.55–1.75 (3)</td>
<td>30</td>
<td></td>
<td>UA = 87-93%, PA= 86-91%</td>
</tr>
<tr>
<td>Boyd et al. 2019</td>
<td>QA</td>
<td>AIR</td>
<td>MI</td>
<td>0.63–0.90 (2)</td>
<td>30; 250; 0.07*</td>
<td></td>
<td>Detection of productivity/physiology changes</td>
</tr>
<tr>
<td>Chubey et al. 2006</td>
<td>QA</td>
<td>SAT</td>
<td>MI</td>
<td>0.45 -0.85 / PAN</td>
<td>1; 4</td>
<td></td>
<td>UA = 100%, PA = 89%</td>
</tr>
<tr>
<td>Di Orio et al. (2004)</td>
<td>QA</td>
<td>AIR</td>
<td>AI (n.d.)</td>
<td>n.d.</td>
<td></td>
<td></td>
<td>OA = 85%</td>
</tr>
<tr>
<td>Hall et al. (2014)</td>
<td>QA, PO</td>
<td>SAT</td>
<td>MI</td>
<td>0.77–0.90; 1.55–1.75 (2)</td>
<td>30</td>
<td></td>
<td>n.d.</td>
</tr>
<tr>
<td>Heyman et al. (2003)</td>
<td>QA</td>
<td>AIR</td>
<td>CIR</td>
<td>G, R, NIR (3)</td>
<td>1–2</td>
<td></td>
<td>OA = 88%</td>
</tr>
<tr>
<td>Madritch et al. (2014)</td>
<td>QA</td>
<td>AIR</td>
<td>HI</td>
<td>0.41–2.45 (224)</td>
<td>15–18</td>
<td></td>
<td>OA = 80%</td>
</tr>
<tr>
<td>Oukrop et al. (2011)</td>
<td>QA</td>
<td>AIR, SAT</td>
<td>CIR, MI</td>
<td>G, R, NIR (3); 0.45–0.90; 1.55–1.75; 2.08–2.35 (6)</td>
<td>30</td>
<td></td>
<td>OA = 81%</td>
</tr>
<tr>
<td>Pippuri et al. (2014)</td>
<td>EA</td>
<td>AIR</td>
<td>ALS, MI</td>
<td>B, G, R, PAN (4)</td>
<td>0.15</td>
<td>1.56</td>
<td>Low compared to dominant species</td>
</tr>
<tr>
<td>Sankey (2009)</td>
<td>QA</td>
<td>SAT</td>
<td>MI</td>
<td>0.52–0.90; 1.55–1.75 (4)</td>
<td>30</td>
<td></td>
<td>OA = 92-93%</td>
</tr>
<tr>
<td>Sankey (2012)</td>
<td>QA</td>
<td>AIR; SAT</td>
<td>ALS, MI</td>
<td>0.52–0.90; 1.55–1.75 (4)</td>
<td>30</td>
<td>5.6</td>
<td>OA = 92-96%</td>
</tr>
<tr>
<td>Strand et al. (2012)</td>
<td>QA</td>
<td>AIR</td>
<td>CIR, PAN, RGB</td>
<td>B, G, R, NIR, PAN</td>
<td>1–2</td>
<td></td>
<td>Visual interpretation</td>
</tr>
</tbody>
</table>

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.
5. Discussion and conclusions

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

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

Aspen was mapped with various success by different remote sensing studies reviewed here. In the case of individual tree detection, the major challenges were the low proportion of European aspen in Fennoscandian forest landscapes and the overlap of spectral and/or structural properties of European
aspen and quaking aspen with other tree species. Due to different research methods and various tree species composition, comparison of different studies is not straightforward. However, the results suggest that especially three-dimensional structural information derived from high-density ALS data or photogrammetric point clouds, and airborne imaging spectroscopy, hold significant potential for tree species mapping (Dalponte et al., 2009; Jones et al., 2010; Li et al., 2013; Roth et al., 2015b; Alonzo et al., 2018). The studies also indicate that combining spectral data with three-dimensional data can noticeably improve species detection at the individual tree level and stand level. Thus, remote sensing with repeated monitoring should be utilized to fulfill the current need of studies on landscape dynamics considering rotation lengths, succession and persistence of key species.

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

Suitability of remote sensing data for biodiversity mapping and monitoring is also determined by geographical coverage, availability of multitemporal data and costs of data acquisition. For example, high-resolution hyperspectral and three-dimensional structural data can be acquired on-demand using a UAS, but this approach is only suitable for local-scale studies. Airborne hyperspectral and ALS
Data acquisition by plane over larger areas (landscape scale) is typically conducted by service providers (Beland et al., 2019). Although hyperspectral and lidar airborne sensors have developed a lot over the past years, the data prices remain relatively high compared to traditional aerial and multispectral satellite images. This factor prevents more extensive exploitation of the data. Several spaceborne imaging spectrometers are currently under development; they should provide for the first time global coverage of hyperspectral data for vegetation mapping, although in coarser resolution compared to airborne data (Lee et al., 2015; Roth et al., 2015b). An important feature of spaceborne data is the continual availability of multitemporal and seasonal data. Utilising seasonal spectral data enables monitoring vegetation dynamics, provides valuable information for species detection and improve tree species classifications, as indicated by the reviewed studies. Furthermore, a recently developed multispectral laser scanning technique, which provides a dense point cloud together with spectral information, may have significant potential in tree species detection in the future (Yu et al., 2017; Budei et al., 2018; Beland et al., 2019).

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