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Review Paper

A global view of aspen: Conservation science for widespread keystone systems

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ABSTRACT

Across the northern hemisphere, six species of aspen (*Populus spp.*) play a disproportionately important role in promoting biodiversity, sequestering carbon, limiting forest disturbances, and providing other ecosystem services. These species are illustrative of efforts to move beyond single-species conservation because they facilitate hundreds of plants and animals worldwide. This review is intended to place aspen in a global conservation context by focusing on the many scientific advances taking place in such biologically diverse systems. In this manner, aspen may serve as a model for other widespread keystone systems where science-based practice may have world implications for biodiversity conservation. In many regions, aspen can maintain canopy dominance for decades to centuries as the sole major broadleaf trees in forested landscapes otherwise dominated by conifers. Aspen ecosystems are valued for many reasons, but here we highlight their potential as key contributors to regional and global biodiversity. We present global trends in research priorities, strengths, and weaknesses based on, 1) a qualitative survey, 2) a systematic literature analysis, and 3) regional syntheses of leading research topics. These regional syntheses explore important aspen uses, threats, and research priorities with the ultimate intent of research sharing focused on sound conservation practice. In all regions, we found that aspen enhance biodiversity, facilitate rapid (re)colonization in natural and damaged settings (e.g., abandoned mines), and provide adaptability in changing

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environments. Common threats to aspen ecosystems in many, but not all, regions include effects of herbivory, land clearing, logging practices favoring conifer species, and projected climate warming. We also highlight regional research gaps that emerged from the three survey approaches above. We believe multi-scale research is needed that examines disturbance processes in the context of dynamic climates where ecological, physiological, and genetic variability will ultimately determine widespread aspen sustainability. Based on this global review of aspen research, we argue for the advancement of the “mega-conservation” strategy, centered on the idea of sustaining a set of common keystone communities (aspen) that support wide arrays of obligate species. This approach contrasts with conventional preservation which focuses limited resources on individual species residing in narrow niches.

1. Introduction

Species in the genus *Populus* known as “aspen” are of global importance due to their high capacity for supporting biodiversity and providing many other important ecosystem services, including soil carbon sequestration, livestock forage, revegetation capacity, and novel wood products that have been documented extensively (DeByle and Winokur, 1985; Peterson and Peterson, 1992; Esseen et al., 1997; MacKenzie, 2010; Boča and Van Miegroet, 2017). Because of the wide ecological amplitude of world aspens, we believe that as a group they present a prime example of multi-species (i.e., ecosystem) global conservation. Importantly, aspen are commonly designated “keystone species,” meaning their sustained existence supports an inordinate number of dependent plants and animals (Stohlgren et al., 1997; Kouki et al., 2004; Edenius et al., 2011; Berrill et al., 2017). Hundreds of obligate species are found in these systems, providing a unifying motivation for linking knowledge pools across international boundaries under a mega-conservation paradigm (Rogers and McAvoy, 2018). This concept, in brief, prioritizes spending limited resources on preserving widespread keystone species that support many obligates, rather than conventional practices focused on narrow single-species habitats. The massive global extent of aspen makes it unlikely that individual researchers or even dedicated labs could adequately address worldwide aspen systems preservation. Moreover, linking science efforts comprises only a small portion of true conservation; transfer of knowledge to managers and policymakers is an essential component in implementing sound stewardship practices. Thus, this review initiates a multi-national collaborative model of a science that seeks to highlight aspen's global importance as a first step toward more effective broad-scale conservation of this, and potentially, other widespread foundational species.

It is important to distinguish aspen within the greater array of *Populus* species. Here, we define aspen as being primarily upland *Populus* trees that commonly fulfill a pioneer role following forest disturbance. Aspens thrive in northern and high-elevation locations with cool summers. Poplars and cottonwoods, common designations for other *Populus* sub-groupings, are nearly exclusive to lowlands, riparian areas, and other seasonally watered zones. Aspens may grow in riparian corridors, sometimes alongside other *Populus*, though they are not confined to lowlands. Taxonomically, aspens are separated into the section *Populus* (syn. *Leuce*) of the genus *Populus* (Stettler and Bradshaw, 1996). Within this group, further subdivision of white poplar (*P. alba*; subsection *Albidae*) form a distinction from the more widespread aspen subsection (*Trepidae*; OECD, 2006). White poplars are functionally different from aspens and are distinguished by their highly varied leaf shape (coarsely toothed, deltoid, or even deeply lobed; Stettler and Bradshaw, 1996; Dickman, 2001).

Here we examine six aspen species worldwide, excluding hybrids used for commercial purposes. In North America *Populus tremuloides* and *P. grandidentata*; across Eurasia *P. tremula*; and in eastern Asia *P. davidiana, P. adenopoda,* and *P. sieboldii* (Fig. 1, Table 1). We focus predominately on locales where aspen temporarily (seral-dominant) or permanently (aspen-dominant) dominates the canopy cover. These ecosystems are most influenced by unique properties facilitated by long-term aspen cover, such as relatively rich soils and attendant diverse plant and animal assemblages. Aspen also occurs in a subdominant role in many stands, however, such forests are not our main consideration here even though small even minor aspen presence often carries some biodiversity benefits. To be clear, we focus on aspen *ecosystems* in this review; not merely a set of tree species. For this reason we emphasize systems that are most obviously aspen-dominant (or potentially so) forests. This approach allows us to directly address broad-scale biodiversity conservation when and where aspen are properly managed for long-term resilience.

Aspen commonly fulfill a role as a singular broadleaf among one-to-many regionally dominate conifers species. The element of even a single non-conifer species has been shown to contribute significantly to overall community diversity (Chong et al., 2001; Griffis-Kyle and Beier, 2003; Rogers and Ryel, 2008; Kuuluvainen et al., 2017). For example, addition of aspen species to otherwise exclusively conifer-dominated forests offers alternate bark texture and chemistry for epiphytes (Rogers et al., 2007), greater nutrient cycling (Boča and Van Miegroet, 2017), higher snow/water retention (LaMalfa and Ryle, 2008), and increased structural diversity facilitating avian diversity (Martin and Maron, 2012). Aesthetically, aspen's unique leaf structure (flattened petiole, perpendicular to leaf surface plain) lends visual and audial dimensions—the “quaking” or

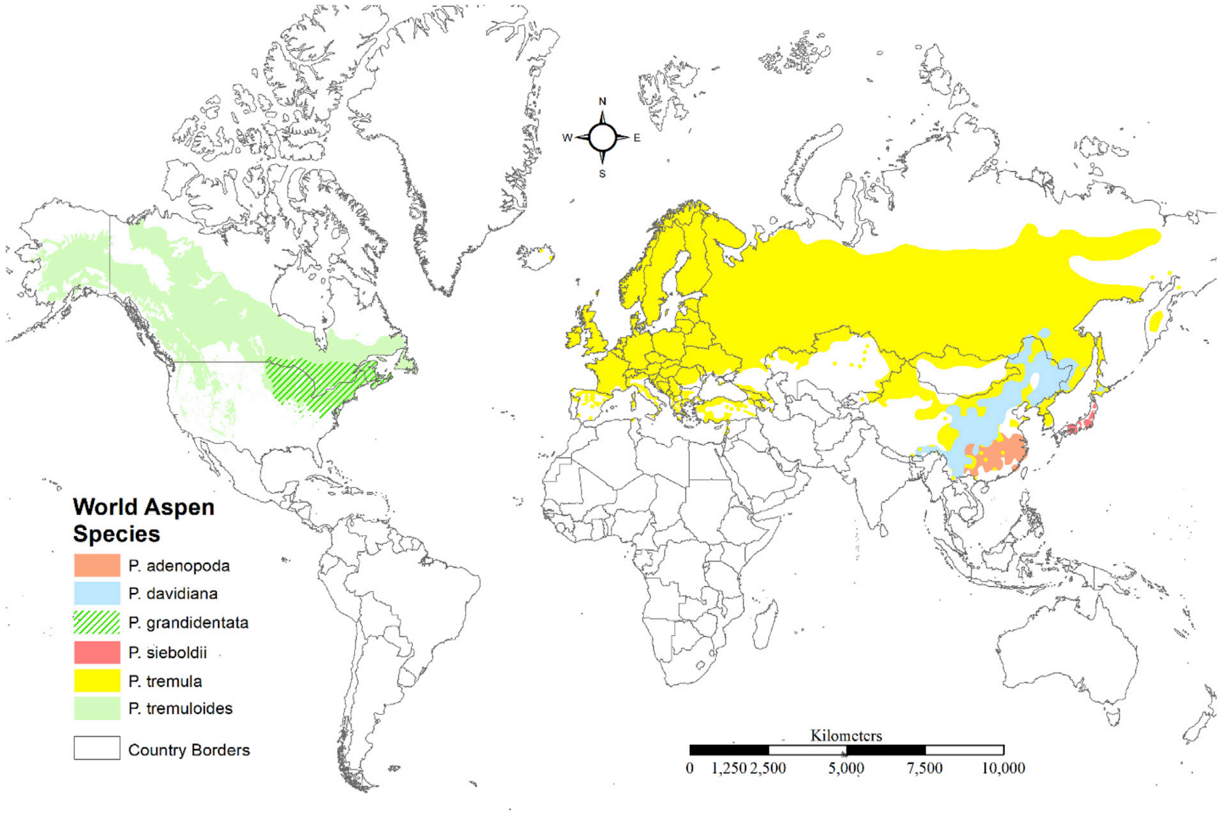

Fig. 1. Major world aspen species and ranges. Colored polygons represent range extent and should not be construed as tree species coverage densities (i.e., species may be very dense or extremely sparse within colored polygons).

"trembling" namesake—to relatively calm needle-bearing forests. Finally, where aspen are isolated among vast conifer forests their autumn hues provide striking yellow, gold, and red colors to a contrasting dark green backdrop.

The aim of this review is to gain a comprehensive understanding of the ecological amplitude, biodiversity contributions, threats, and practices surrounding the aspen forests at the global scale. We highlight variability among partner nations in scientific prioritization of aspen research topics with some emphasis on recent research since c. 2000. The multidisciplinary nature of aspen ecology and management presents a biogeography that varies considerably in opportunities, research interests, resources, and threats. In order to structure such a wide ranging inquiry, our objectives focus on: 1) Expert and literature surveys on a country/region basis that identify key aspen issues and prominent research avenues to date; 2) Review of established research in order to better define aspens' global ecological function; 3) Attributes, threats and conservation needs for all aspen ecosystems; and 4) Regional- and global-scale aspen research gaps. By synthesizing the large body of aspen science currently available, we hope to establish a framework for advancing sustainable practices in these critical forest systems. Linking biological assets at very large scales—here, aspen forest systems around the northern hemisphere—provides a mechanism for moving beyond single-species conservation. We begin this review by identifying commonalities across the breadth of aspen species.

2. Common characteristics of world aspens

There are a variety of traits, related to their ecosystem functions, growth patterns, and autecology, that are common to all aspen species. Aspen are characterized as early successional clonal species with rapid early growth rates, intolerance to shade, and a relatively short life span of individual ramets (Børset, 1960; Lankia et al., 2012). Aspen respond rapidly and prolifically to disturbance through asexual root suckering (Frey et al., 2003; Kobayashi et al., 2007; Gradel and Mühlenberg, 2011; Caudullo and de Rigo, 2016) with roots suckers arising up to 40 m from parent trees (Jobling, 1990) and post-disturbance sucker densities as high as 250,000 stems ha^{-1} in boreal North America. Aspen are also capable of sexually regenerating via annual production of many small seeds capable of wide distribution (over several kilometers), due to the tuft of hair attached to the seed (Landhäusser et al. 2019). Though less common than sucker regeneration—likely due to exacting germination requirements—seedling regeneration is more frequent than previously thought (e.g., Larva-Karjanmaa et al., 2003) and surely plays an important long-term ecological role (Landhäusser et al. 2019). Aspens grow in a variety of habitats, are tolerant of drought

Table 1
World aspens attributes. Aspen species within the genus *Populus*, section *Populus*, subsection *Tepidae.*

Species	Region (#countries)	Estimated Range (M km^2)	Elevation (m)	Maximum Height (m)	Maximum Diameter (cm)
P. adenopoda[a]	East Asia (1)	1,522	300–2500	30	60
P. davidiana[a]	East Asia (3)	5,865	100–3800	25	60
P. grandidentata[b]	East North America (2)	4,826	0–900	24	25
P. sieboldii[c]	East Asia (1)	414	?	20	?
P. tremula[d]	Eurasia, North Africa (~70)	71,493	700–2300	35	75
P. tremuloides[b]	North America (3)	27,671	0–3500	30	40

[a] Flora of China.
[b] US Forest Service, Fire Effects Information Systems.
[c] Flora of Japan.
[d] Woody Plants of Czech Republic.

and frost, but favor fertile and well-drained soil with open light conditions, such as those created by disturbances (Worrell, 1995). Beyond responding to site conditions, aspens are known to increase soil productivity due to increased leaf litter and associated nutrient cycling (Ste-Marie and Pare, 1999) and elevated snow and water retention (LaMalfa and Ryle, 2008).

Aspens possess attributes of direct and indirect value to people. Commercial uses for aspen are similar worldwide, with aspen fiber being used in the production of pulp, strand board, solid wood, and specialty products (i.e., pencils, skis, sauna benches, coffins, furniture, matches, excelsior). People value biodiverse forests for products, animal forage, medicines, recreation, aesthetics, wildlife, and intrinsic properties. When aspen forests succeed or are converted to conifer forest types, biodiversity typically declines (McCullough et al., 2013, Rogers et al. 2008).

3. Survey approaches

We integrated known aspen research around the northern hemisphere (aspen is absent in the southern hemisphere) to gain broader understanding of the ecology, threats, values, and restoration practices to aspen forests on a global scale. As a work of review, we relied heavily on country-regional expertise to synthesize leading research themes from their respective geographic areas. This review includes a systematic survey of expert participants (authors) from the following nations: Canada, China, Czech Republic, Finland, Norway, Russia, Sweden, and United States. Input consisted of four basic parts: 1) a systematic literature search using keywords to query two common research databases, 2) author completion of the survey of activity level in 30 aspen research topic areas subdivided into three categories—basic science, applied science, and specific aspen threats, 3) summary of commonalities across all species/regions (section 2.0), and 4) written country syntheses capturing aspen ecology, prominent aspen science issues, restoration activities, and current research gaps. Literature search results for research databases are found in Appendix S1. Expert survey responses, by region and specific topic areas, are found in tabular form in Appendix S2.

A systematic search of the aspen literature since the year 2000 was undertaken based on location and region of studies within ISI Web of Science and SCOPUS. The goal of this exercise is to gain a global perspective regional variation in research themes within the aspen sciences. We queried titles, abstracts, and keywords using the basic terms *aspen*, *Populus tremuloides* or *Populus tremula*. We further used term combinations including *forestry, diversity, management, water, ecological function,* and region/geographic names. We screened out articles with similar author lists and similar topics in an effort to decrease duplication or mutliple counts of closely related publications. Additionally, we searched reference lists of retrieved articles for other relevant publications. In total, 200 articles representing 29 keywords in 9 regions were sampled (S1). Analysis based on the linear responses (present = 1/absent = 0) were chosen because the number of keywords was low and the data set was not highly heterogeneous. To better understand the data structure and heterogeneity, we projected the data set along two main axes using principal component analysis (PCA). Overlay ellipses were displayed with confidence limits of 0.70. The analysis were carried out in R v 3.0, for PCA analysis we used the “vegan” package (Oksanen et al., 2019).

In the process of retaining area experts to contribute to this aspen world review paper, we asked each national representative to rank the level of research investment and knowledge in key topic areas. Author/experts were specifically included based on their broad aspen research knowledge. We further suggested that survey participants provide seminal references to support their assessments of national research efforts. After receiving all author/expert survey responses, we grouped aspen science assessments by region in order to supplement our independent literature search and PCA analysis. By combining these two efforts—objective and subjective surveys—our hope was to gain a broader understanding of contemporary aspen exploration, as well as shortcomings, in a geographic context. We fully understand this approach is highly dependent on experts and literature selected; we consider this a first approximation of the breadth of world aspen study that will likely be improved upon in future works.

4. Summary of world aspen study

4.1. *Aspen research priorities by geographic region (literature)*

PCA analysis of topics in the aspen literature by geographic region is shown in Fig. 2. To check validity of our results, we ran PCA on a random subset of 150 articles and found no statistical difference in eigenvalues for the first two axes displayed (Fig. 2) as compared to the full 200 articles (200 runs PC1 = 0.585, PC2 = 0.415; 150 runs PC1 = 0.587, PC2 = 0.438). To better interpret the non-canonical axes the region, as an independent factor, was projected as ellipses overlays in the PCA ordination (standard deviation of point scores and correlations defines the main directional axis of the ellipse). Key aspen terms (i.e., subtopics of study) form the *data space* within the ordination, meaning regional aspen-related science endeavors group directionally towards the most explored topics for that area. While this graph shows more overlap than separation, we still gain some understanding of regional research priorities based on the recently published literature. General trends include a greater emphasis on landscape process/disturbance factors in the Western U.S., climate and growth related studies in Canada, and a focus on physiological and genetic topics in most of the remaining regions. Interestingly, as related to the present review, no regions appear to be placing greater energy toward the study of conservation and diversity as compared to other topics.

4.2. *Aspen research priorities by geographic region (Expert/Author urvey)*

Our survey of regional aspen experts was an independent attempt to get at regional research priorities. Fig. 3 displays the results of that expert/author survey in terms of 30 aspen research (basic and applied) and ecosystem threat topic areas. The graphic is most valuable for comparing regions to the overall average (black bar), rather than comparing region to region given the subjectivity of the opinion poll. In this sense, we see for example, that regions have devoted similar levels of attention to genetics/molecular and landscape assessment/mapping, but offer widely varying levels of investigation for topics such as defense chemistry or grazing practices. No regions have invested intensely in human uses and effects on aspen communities, such as social sciences, land use development, or mining/oil extraction. Overall, this modest survey of aspen research efforts, using two approaches, gives us an initial sense of strengths, weaknesses, and opportunities for technique and knowledge exchange.

4.2.1. *North America, P. tremuloides, P. grandidentata*

REGION: United States.

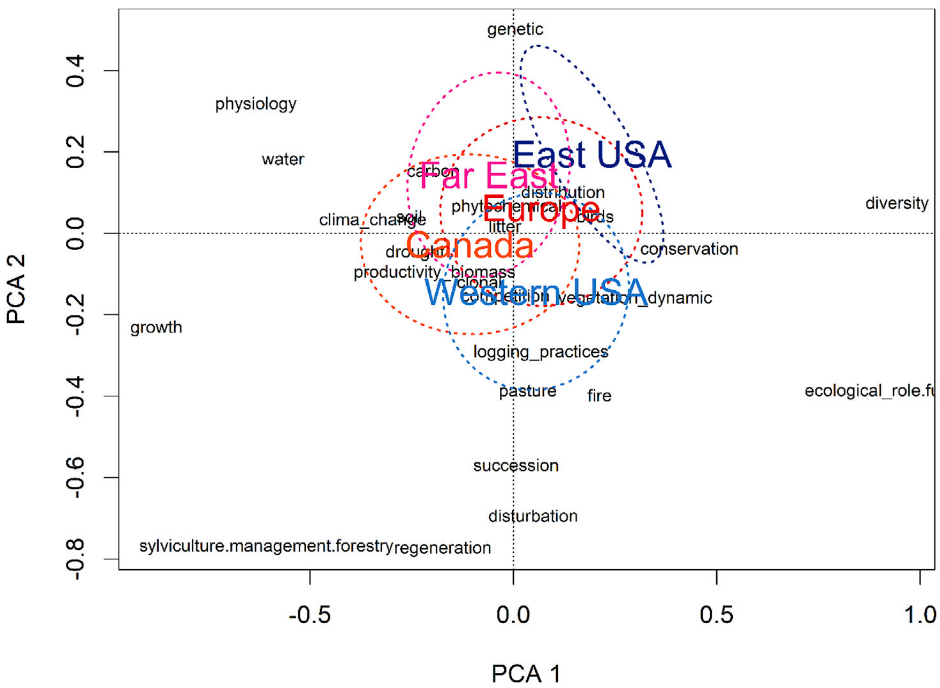

Fig. 2. Principal Component Analysis (PCA) of aspen literature for *Populus tremula* and *P. tremuloides* only. An initial search of all aspen species yielded approximately 95% of literature was centered on these two species; the remaining 5% addressed hybrid *Populus spp.* and the remaining species designated in Fig. 1.

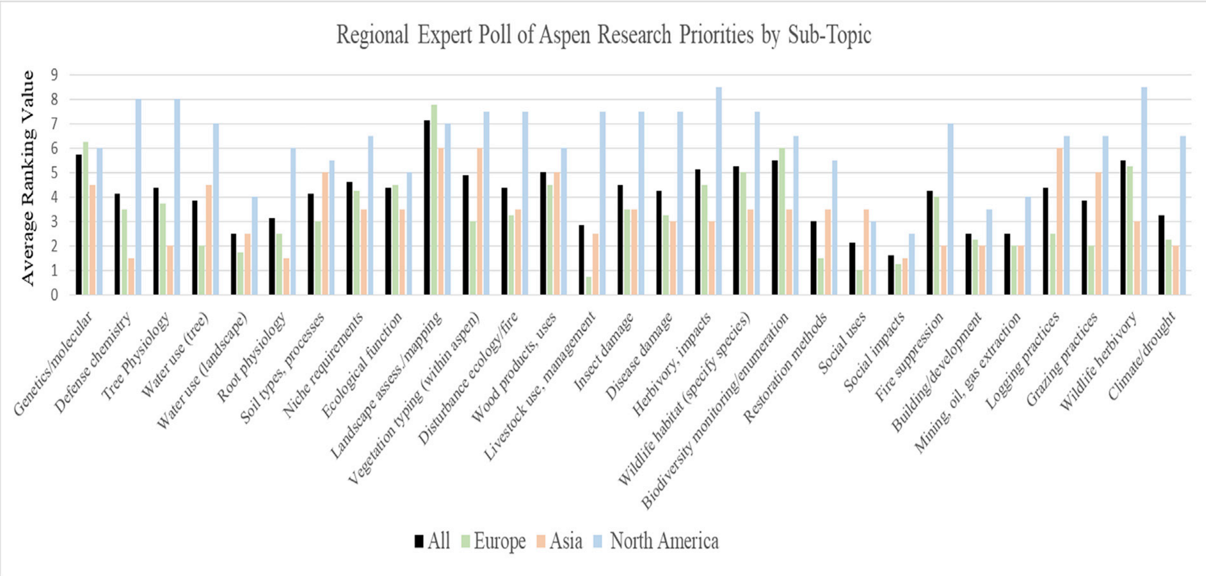

Fig. 3. Results of a qualitative opinion poll of authors of the current work gauging research energy expended on aspen sub-topics. This bar graph gives a broad indication of topics of interest and their respective regional prioritization. Numbers along the y-axis are poll rankings, as estimated by respective area experts (see author list) from low to high of regional research efforts: 1 = no investigations, 2 = poor understanding, 5 = moderate understanding, 8 = high level, 10 = complete knowledge.

FUNCTION: aspen-dominant, seral-dominant, subdominant.

THREATS: Fire suppression, browsing herbivores, past management, climate change/drought, building/development, insect/disease outbreaks, and compound effects.

RESEARCH OVERVIEW: Quaking aspen (*P. tremuloides*) forests exist in a wide variety of environmental settings, which necessitates a nuanced perspective in examining their ecological patterns and dynamics (Kashian et al., 2007; Kurzel et al., 2007; Rogers et al., 2014; Kulakowski et al., 2013a). Successional replacement of aspen by conifer species (seral-dominant; Fig. 4a) is most pronounced in systems shaped by long fire intervals (Kulakowski et al., 2004, 2006). Aspen-dominant systems are common in the region, often across broad plateaus and in specialized niches (Fig. 4b; Rogers et al., 2014). Aspen decline was initially reported primarily at the margins of aspen's distribution, but may be becoming more ubiquitous due to the direct effects of climate (e.g., drought). In contrast, the indirect effects of recent climate (e.g., forest fires, bark beetle outbreaks, and compounded disturbances) may facilitate expansion of this forest type (Kulakowski et al., 2013b; Gill et al., 2017). Thus, future aspen trends are likely to depend on the net result of the direct and indirect effects of altered climate (Kulakowski et al., 2013a; Worrall et al., 2013; Yang et al., 2015).

Successive or compound disturbances have the potential to alter post-disturbance conifer regeneration by reducing seed sources or increasing the intensity of the secondary disturbance (Kulakowski and Veblen, 2007), which in turn may influence soil and other micro-environmental conditions (Fonturbel et al., 2011). These two influences may be of minimal negative consequence for vegetative reproduction of aspen, but are more likely to inhibit regeneration of associated conifers (Gill et al., 2017). Although compounded disturbances may increase overall disturbance intensity (either additively and/or by increasing the intensity of secondary disturbances), research to date suggests that compounded disturbances favor aspen over other species (Kulakowski et al., 2013b; Gill et al., 2017).

Fire suppression (including cessation of indigenous burning) has likely played a role in decline of aspen (DeByle et al., 1987; Kay 1997, 2001; Bartos, 2001). However, fire suppression is unlikely to have changed the structure and composition of most aspen stands in the western U.S. (Shinneman et al., 2013). Instead, long intervals between natural disturbances have commonly resulted in a range of variation of forest structures; from complex structures to single cohort types (Kulakowski et al., 2004, 2006). Fire suppression would have had little impact in aspen-dominant systems (Shinneman et al., 2013).

Intense browsing by ungulates can exert a major influence on aspen dynamics, especially regeneration, by inhibiting recruitment (Bartos and Mueggler, 1981; Bartos et al., 1994; Romme et al., 1995; Baker et al. 1997; Hessl, 2002; Larsen and Ripple, 2003; Jones et al., 2009; Seager et al., 2013; Rogers and Mittanck, 2014). Such chronic herbivory can lead to vegetation type conversions, as well as deleterious effects on overall species diversity (Bailey and Whitham, 2002; Griffis-Kyle and Beier, 2003; Martin and Maron, 2012; Rogers et al., 2010).

Climatically-induced mortality of aspen could lead to long-term reduction of aspen cover in some areas. Rogers et al. (2010) reported that low mortality rates of aspen were rarely observed in drought-prone locations. Likewise, in southwestern Colorado, areas of high aspen dieback tend to be located on dry, south-facing slopes, implying that drought stress is an important mechanism driving aspen mortality (Huang and Anderegg, 2012, 2014). In the southwestern U.S., Ganey and

(a)

(b)

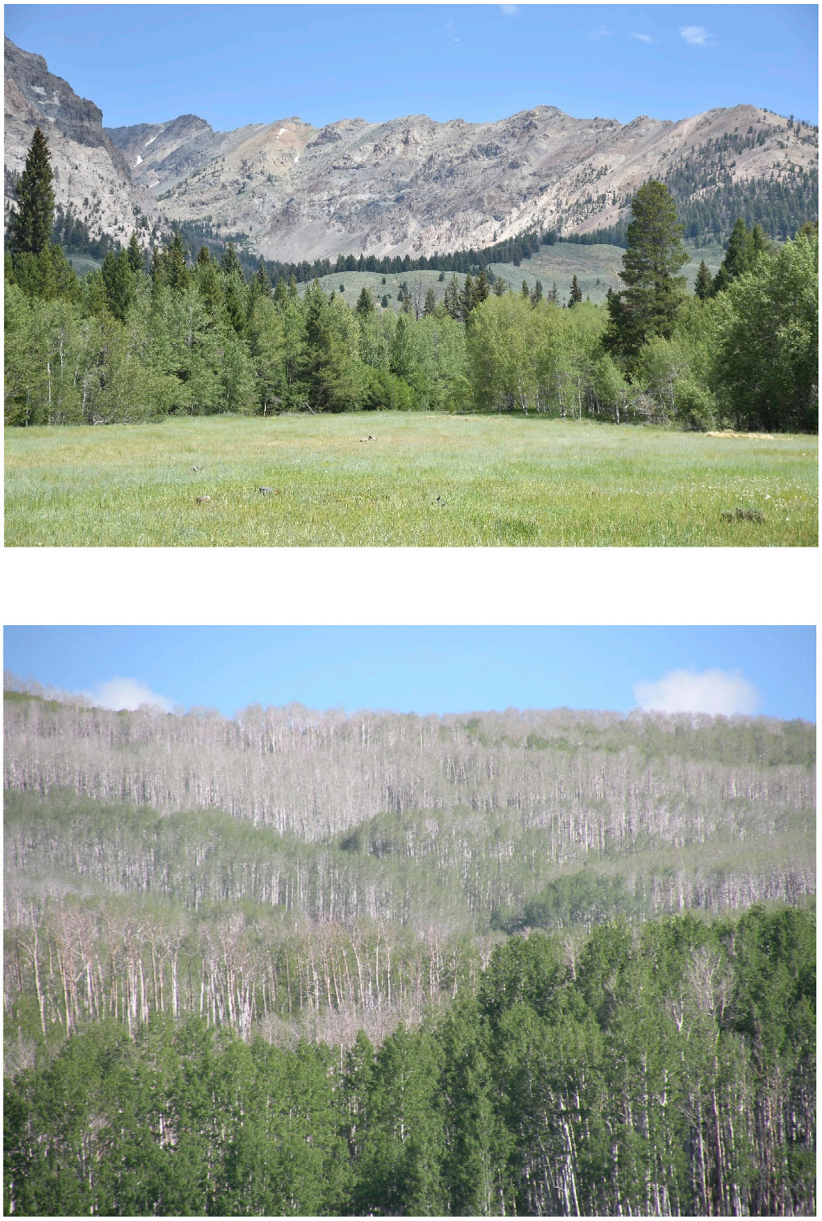

Fig. 4. Seral-dominant (a) *P. tremuloides* in Idaho. Dominant (b) *P. tremuloides* in Utah. These types occur throughout the western United States (Rogers et al., 2014).

Vojta (2011) reported that aspen mortality in mixed-conifer forests was particularly pronounced (85%) and suggested that these early trends may be indicative of future responses to climate change. At the continental scale, Worrall et al. (2013) observed that aspen on marginal sites and near ecotones are most likely to be susceptible to climatically-induced mortality. However, Hanna and Kulakowski (2012) found that growth and climatically-induced mortality of quaking aspen in Colorado and Wyoming away from transitional zones are also strongly associated with climatic trends. The interactive effects of increased drought and chronic browsing by ungulates, particularly in the absence of fire (i.e., aspen-dominant), is an increasing concern in the western U.S. (Shinneman et al., 2013; Rogers and Mittanck, 2014; Yang et al., 2015).

Other contributing factors leading to aspen decline include environmental variables or biotic agents that can aggressively act on previously stressed trees. These factors include infestation from fungi and wood boring insects (Frey et al., 2004; Kashian et al., 2007); and may be the final causes of tree mortality (Worrall et al., 2008; Marchetti et al., 2011; Steed and Burton, 2015), but are thought to be of secondary importance rather than the key drivers of change.

Bigtooth aspen (*P. grandidentata*) is commonly a subdominant component of forests in northeast U.S. and southeast Canada, although it may become temporarily dominant (<40 yr) following stand-replacing disturbance. Bigtooth aspen may co-dominate alongside quaking aspen (Fig. 1) and balsam poplar (*P. balsamifera*), though it is most commonly found as a subordinate constituent of a complex mix of some 20 species of hardwoods and softwoods (Laidly, 1990; Peterson and Peterson, 1992). Where quaking and bigtooth aspen are found in the same stands, clonal boundaries seem to remain discreet (Perala, 1981). Bigtooth aspen is shorter in stature than quaking aspen and thought to be generally less adaptable to different environments (Laidly, 1990), perhaps reflecting its' more limited range. These two species are managed similarly and are used for the same forest products (small diameter lumber, veneer, and pelletized for animal feed). Biodiversity attributes are also high among bigtooth aspen; they provide habitat and winter food for moose, beaver, and grouse (Laidly, 1990).

REGION: Canada.

FUNCTION: aspen-dominant, seral-dominant, subdominant.

THREATS: Browsing herbivores, agricultural expansion, mine reclamation, climate change/drought, insect/disease outbreaks.

RESEARCH OVERVIEW: Trembling aspen (*P. tremuloides*) is a common upland species across the boreal forest in western Canada often occurring in seral-dominant stands composed of differing amounts of white spruce (*Picea glauca*) referred to as mixedwoods (Padbury et al., 1998; Beckingham and Archibald, 1996). In the absence of a viable spruce seed source nearby or frequent disturbance, aspen-dominant stands are common across these landscapes. Boreal mixedwoods of varying composition, however, are the prevailing mesic forest type in this region.

Immediately south of the boreal forest is a transition to prairie grasslands is the region known as the aspen parkland which is characterized by a mosaic of aspen-dominant forests interspersed with grasslands (Fig. 5; Acton et al. 1998). In this region, aspen tends to be the only upland tree species although other species, including other *Populus* species, form riparian corridor forests.

Aspen is a major timber species in the boreal forest and is a major focus of forest management with numerous pulp and strand board mills. In the province of Alberta alone, the annual allowable cut for hardwoods (the vast majority of which is aspen) is currently set at over 12 M m^3/year. High levels of biodiversity, relative to the surrounding landscapes, have been recorded in both boreal seral (Macdonald and Fenniak, 2007; Berger and Puettmann, 2000; Légaré et al., 2001) and parkland stable aspen communities (Grant and Berkey, 1999). Within the context of forest management and timber harvesting, aspen is generally regenerated through root suckers (Frey et al., 2003), but in the context of mine land reclamation aspen is increasingly being planted or encouraged to regenerate via seeding as a beneficial early successional practice (Pinno and Errington, 2015; Landhausser et al., 2012; Schott et al., 2014).

The most significant threat to aspen is generally considered to be prolonged severe droughts (Hogg et al., 2013) which can result in widespread aspen dieback and regeneration failures (Michaelian et al., 2011; Anderegg et al., 2013). This is particularly true further south in the aspen parkland with its drier climate which is unable to support consistent forest cover. With anticipated increased future drought, this phenomenon may become more extreme; even moving to the boreal forest. Current projections indicate that the area of boreal forest in western Canada is likely to have a future climate similar to today's aspen parkland (Hogg and Hurdle, 1995), perhaps seriously limiting aspen's future extent throughout the mixedwood zone.

Fig. 5. The aspen dominant forest in west-central Canada is known as the “parkland.” These forests are bordered by prairie to the south and boreal (aspen seral-dominant) mixedwoods to the north.

Beyond drought and climate change, insects (in particular forest tent caterpillar [*Malacosoma disstria*] and aspen tortrix [*Choristoneura conflictana*]) are a significant contributing threat to aspen. Although generally insect outbreaks do not result in widespread tree death, when they are followed by drought years, mortality may be significant (Hogg et al., 2002).

4.2.2. Europe, P. tremula

REGION: Northern Europe.

FUNCTION: seral-dominant, subdominant.

THREATS: Browsing herbivores, insect/disease outbreaks, climate change/drought, management favoring conifer production.

RESEARCH OVERVIEW: Eurasian aspen (*P. tremula)* grows across Eurasia from Iceland to far eastern Russia, and from northern Scandinavia to outposts along the Mediterranean coast of Africa. In northern Europe it is the only native *Populus* species. Aspen is considered both a pioneer and keystone species, but together with other broadleaved trees, it had been actively reduced during the mid-20th century to promote conifer growth (e.g., Esseen et al., 1997; Axelsson et al., 2002). In forestry, aspen was mainly thought to be harmful due to its role as a host species for *Melampsora pinitorqua* rust fungus which may threaten young Scots pine (*Pinus sylvestris*) plantations. This lead to its systematic removal from many managed forests. Remnant aspen trees and small groves are scattered in old-growth forests regionally, and aspen populations are slowly rebounding from this earlier period (Fig. 6). Similar conditions have historically been created by forest fires or land clearing. Today aspen often colonizes former disturbed habitats, such as abandoned arable land, slowly invading from the field edges by means of root suckers (Frivold, 1998). Overall, aspen occurs on the landscape as scattered subdominant individuals and small seral-dominant stands largely as a legacy of intensive conifer-oriented management, rust fungus treatment, and fire suppression (Kouki et al., 2004; Lankia et al., 2012).

European aspen is usually found growing in small groups or stands in spruce (*Picea abies*) forest types, and only rarely in early seral pure stands. Aspen is highly sensitive to several type of biotic threats like insects (*Sarperda carcharias, Chrysomela populi*) and mammal herbivory by moose, deer, and hares. Even though local aspen populations are multiplying via suckering, climate change may be threatening aspen because of a hardening and dormancy of aspen that is largely controlled by temperature and photoperiod (Pulkkinen pers. comm.). Likewise photoperiod, bud set, stomatal conductance, and chlorophyll content index (CCI) relate to photosynthetic rates and follow latitudinal clines in *Populus tremula* (Soolanayakanahally et al., 2015).

Fig. 6. A boreal seral-dominant *P. tremula* forest in northern Sweden. A lone mature aspen exists in a forest where this species at one time was more dominant, but due to historical logging practices has been nearly eliminated.

In terms of cover, early seral aspen forest constitutes a small percentage of overall forest area (e.g., 8% in Norway; Kucera and Næss, 1999), though this limited presence caries great ecological value. Aspen's fundamental importance in Scandinavia is in harbouring biodiversity (Barstow et al., 2017). In fact, the number of red-listed (threatened status) host-tree dependent species is higher for aspen than for spruce (Jonsell et al., 2007). In Finland more than 200 species use dead or living aspen trees as a source of nutrition or as a habitat (Kouki et al., 2004; Vehmas et al., 2009). Ecological consequences of the forest praxis led to detailed examinations of resulting declines of aspen cover as related to lichens (Kouki et al. 2004; Hedenås and Ericson, 2003; Gjerde et al., 2012), insects (Siitonen and Martikainen, 1994; Jonsell et al., 2007), birds (Edenius et al., 2011; Gjerde et al. 2005), and mammals (e.g., Danell et al., 1991; Edenius et al., 2011).

Broad spatial impacts on aspen-associated species via forest fragmentation have been described (Harber et al., 2005). For instance, aspen is a highly preferred winter forage for large herbivores (Bergström and Hjeljord, 1987). Abundance of large trees, being very important for biodiversity, has increased in recent decades (Myking et al., 2011). These older trees possess specific structural properties important for species diversity, such as having hollow interiors for cavity nesting birds and rough bark of low acidity that facilitates prime lichen habitat. However, Norwegian forest inventory data indicate reduced recruitment rates of young aspen trees (60–79 mm diameter) during the last 25 years (Myking at al. 2011) leading to an imbalance in demographic structure; ample mature trees with little recruitment and intermediate aspen stems. This pattern is indicative of chronic sucker browsing by large ungulates (Edenius et al., 2011). Regeneration in general may also be hampered by lack of suitable stand initiating disturbance events, such as a lack of fire resulting, in part, from active suppression.

Previously discarded aspen in northern Europe is now favored as a retention species because of its high biodiversity value. Accordingly, aspen volumes have increased, much of this being due to young trees in agricultural landscapes. Aspen in northern Europe does not carry high commercial value, however some small-market uses prevail in the region. Aspen is rarely planted, with the exception of hybrid aspen, because of limited economic use.

Although the commercial value of aspen is underappreciated in northern Europe, research interest has increased considerably after the genome of black poplar (*Populus trichocarpa)* was sequenced (Tuskan et al., 2006). This facilitated genetic and molecular studies of closely related aspen trees (Mukherjee et al., 2015). For example, the Swedish Aspen (SwAsp) collection consists of a selection of 116 *P. tremula* genotypes that originated from 12 sites located east and west, at every second degree of latitude up through Sweden (from 56.818N, 12.854E to 66.812N, 22.812E) and thus represent a naturally varying population of aspen trees (Robinson et al., 2012; Bernhardsson et al., 2013). In 2004, four root-propagated replicates of each clone were planted into each of two common gardens: Ekebo (55.854N, 13.806E) and Sävar (63.854N, 20.836E). These gardens have since been surveyed for growth and damage and their genetics and physiology related to the reciprocal garden set-up and thus studies of genotype-environment (G-E) effects. A rich research output has resulted from SwAsp garden studies across Sweden. SwAsp genotypes are kept in tissue culture at Umeå University, which allows for propagation of genets of *P. tremula* with particular properties (Robinson et al., 2012).

REGION: Central Europe.

FUNCTION: seral-dominant, subdominant.

THREATS: Insect/disease outbreaks, climate change/drought, management favoring conifer production.

RESEARCH OVERVIEW: Eurasian aspen (*P. tremula*) co-exists with many other hardwood and softwood trees across central Europe to the Mediterranean where it mostly maintains a sub-dominant position. Limited exceptions of seral-dominant aspen include sites originally established for commercial or research purposes and on former agricultural lands, quarry sites, and mines. In southern Europe, subdominant aspen are found along the Mediterranean through Spain, Italy, Greece, Turkey and Algeria (Caudullo and de Rigo, 2016). In central Europe, aspen is not commonly dominant in many stands but it typically fulfills a pioneering role. In the Czech Republic, for instance, aspen rapidly increased as a result of introductions following acid rain die-off of conifer forests and planting for match production (A. Kusbach, pers. comm.). These large plantations are up to 40–50 years old and often remain unmanaged due to unclear ownership or because of unprofitability.

Occurrence in ecologically varied habitats demonstrates a broad amplitude in central European aspen. For instance, we find aspen in extreme habitats, such as dry pine forests with shallow soils and in wet floodplains. Aspen is assumed to be mostly seral-dominant following disturbances (fire, wind-throw, pasturing), although examples of long-term dominance are limited. Most aspen stands in central Europe are quite small (<0.5 ha). Aspen has proven robust in revegetation schemes following acid rain. Aspen is used to mechanically stabilize soils as dense root networks expand and aid erosion control (Caudullo and de Rigo, 2016). We expect that aspen contributes to forest biodiversity (as elsewhere), although region-specific corroboration has not yet been conducted. Aspen forests provide forage for ungulates, as well as aesthetic enjoyment for people as fall foliage adds forest hues of gold and purple among conifers and other hardwoods. To improve tolerance and quality of wood and increase productivity, a number of hybrids have been cultivated (Caudullo and de Rigo, 2016). In fact, wood cultivation has been a primary research objective fueled by studies of genetic diversity as it relates to fiber quality for specialty products.

In central Europe, aspen has been understudied due to relatively minor coverage and a subsequent low interest in ecology of the species. Two exceptions spurred some interest in the species: First, a former interest in aspen was instigated by an ecological disaster (air pollution a site degradation) leaving tens of thousands hectares of forest mortality. Second, demands of the match industry within a communist market oriented to the former Soviet Union, alongside a shortage of aspen fiber, promoted aspen silviculture research. Future aspen interest may take advantage of this legacy, by highlighting its use as a mechanism for reforestation and site quality improvement, a source of hybrid and wood fiber research, and as refugia for central European biodiversity under changing climates.

4.2.3. Trans-Siberian and Eastern Asia, P. tremula, P. davidiana, P. adenopoda, P. sieboldii

REGION: Russian Federation.

FUNCTION: aspen-dominant, seral-dominant, subdominant.

THREATS: Stem pathogens, management favoring conifer production, climate change/drought, industrial pollution.

RESEARCH OVERVIEW: Eurasian aspen (*P. tremula*) is a widespread forest type in Russia. In the Oligocene and Miocene all Kazakhstan and Western Siberia were covered with deciduous forests. Aspen was a common tree species in these ancient forests (Khotinsky, 1977). Currently, this species occurs along forest-tundra ecotones in both forest and forest-steppe zones. The greatest distribution of aspen forests in Russia is observed between 53° N and 60° N (Vorobyev, 1986). Small areas of Eurasian aspen can be found in the steppe zone. Overall, aspen forests cover 2.7% of the total forests of the former Soviet Union (Smilga, 1986).

Aspen in Russia appears well adapted to different edaphic conditions. It commonly forms seral-dominant stands with coniferous (pine, larch, spruce) or broadleaf (birch, alder, oak) in the Ural Mountains, for example (Fig. 7). In these indigenous coniferous forests, aspen is usually present in small amounts. It is an obligatory component of the dark coniferous taiga (boreal). Secondary aspen forests are formed after harvesting or on abandoned hayfields where aspen was part of the original forest (Smilga, 1986; Danilin, 1989; Ivanova, 2014; Maiti et al., 2016). Otherwise, aspen stands are formed without conifers in subordinate tiers, even if individual spruce and fir are present in the stand (Ivanova and Andreev, 2008). Aspen-dominant forests are often found on abandoned hayfields with moist soils (Frivold, 1998). Riparian aspen may be characterized as both dominant- and seral-dominant forests depending on specific locales (*sensu* Rogers et al., 2014). These are the most productive aspen forests and yield high quality wood (Smilga, 1986).

Aspen timber is highly valued in Russia for specialty products (Smilga, 1986; Danilin, 1989). For instance, recent research in Russia has focused on developing aspen for anti-inflammatory medicines (Turetskova et al., 2011; Karomatov and Rasulova, 2017). A limitation, however, is that large healthy trees required for medicinal extraction occur infrequently, due to common stem pathogens and overtopping by conifers. As a timber species, aspen is classified as relatively low-value species and production forestry is focused almost entirely on conifer species.

A large number of studies are devoted to the polymorphism of this woody plant (e.g., Danilin, 1989; Politov et al., 2016). An overview of this area of research was conducted by Smilga (1986). Extensive work has been conducted on the biomass and productivity of aspen in different habitats (Usoltsev, 2001, 2003). This work incorporated biogeographic assessments of biomass limits and distribution for aspen of northern Eurasia based on the condition of stand self-thinning using a standardized biomass equations. Dependence of forest biomass limits upon the climate (continentality) index and the sum of effective temperatures were first suggested by Usoltsev (2003). This important tie to climate adaptation may be threatened by anticipated warming climates and increased drought. Additionally, photosynthesis studies helped determine the growth and

Fig. 7. A recent forest treatment that was intended to favor *P. tremula* in the Ural Mountain region, Russian Federation. Competing conifers quickly recolonize the site and will overtop aspen without repeated disturbance.

productivity of these forests for different locales within the country (Obydenni, 1965), as well as optimizing growth potential for production forestry (Petrova, 2011; Vays, 2013). Extensive work has documented differences in aspen structure, biodiversity, and condition in different regions of the Russian Federation (Degteva et al., 2001; Lashchinskiy, 2010; Popov, 2017).

REGION: Mongolia.

FUNCTION: aspen-dominant(?), seral-dominant, subdominant.

THREATS: Browsing herbivores, management favoring conifer production.

RESEARCH OVERVIEW: In Mongolian forests, Eurasian aspen (*P. tremula*) is a ubiquitous, widespread species but it is absent in the Altai region (Altrell and Erdenejav, 2016). Aspen occurs in modest stands (<2 ha) or mixed with other tree species such as Scots pine (*Pinus sylvestris*) and white birch (*Betula platyphylla*; Dulamsuren et al., 2005). In most native mature coniferous forests, aspen is present only in minor amounts (subdominant). Covering a relatively small portion of Mongolia's forests, the total estimate of aspen's national volume is 3.5 M m^3 (MET 2016). Aspen is a frequent component of the forest-steppe transitional zone, complementing Siberian larch (*Larix sibirica*) and white birch (Savin et al., 1988; Ermakov et al., 2002). Here, aspen stands form sub-taiga forests on upper portions of south-facing slopes in the lower montane belt (Tsedendash, 1995; Dulamsuren et al., 2005). Analogous semi-arid montane aspen forests (*P. tremuloides*) in North America are often cited as those most vulnerable to combined forces of herbivory and climate warming-induced drought (Worrall et al., 2008; Rogers and Mittanck, 2014), thus we may consider similar risks to this type in central Asia. Aspen is a minority component of the dark taiga in the upper montane belt (Müehlenberg et al., 2011; Kusbach et al., 2019). It also forms detached clones in lower areas (<1000 m elev.) at the edge of the steppe zone in the forest-steppe/lower montane vegetation zone (Kusbach et al., 2019). Following extensive logging (legal and illegal) c. 1960−1990, in which predominantly commercial conifer species were harvested, the percentage birch and aspen has increased (Tsogtbaatar, 2007). Currently, residual broadleaves form large monospecific, often diseased, stands that commonly inhibit conifer regeneration.

Mongolia's strongly continental climate is thought to be largely responsible for great genotypic and phenotypic heterogeneity across aspen's broad ecological range (Hamrick, 2004). Fire, snow, and ice are important disturbance factors which often drive regeneration and cover change in Mongolian forests (Altrell and Erdenejav, 2016). Recent research suggests that aspen dominance may persist for centuries (perhaps millennia?) based on a pedoanthracology (aging and identifying plants in ancient charcoal) study in the Khaan Khentii Mountains, central Mongolia (Novák et al., in preparation). Thus, it is yet undetermined if viable aspen-dominant stands will persist alongside the more common seral-dominant type in this region.

REGION: China.

FUNCTION: seral-dominant, subdominant.

THREATS: Land conversion, browsing herbivores, climate change/prolonged drought, management favoring conifer production.

RESEARCH OVERVIEW: David's aspen (*P. davidiana*) is found throughout eastern Asia (i.e., northeast China, Korean peninsula). Here we discuss the species mostly in the context of China. David's aspen is a tree species with wide ecological amplitude from warm to cold temperate zones (Zhang and Dai, 1984). David's aspen are generally seral-dominant, transitioning over decades to conifer (spruce-fir) or conifer mixed-broadleaf (oak, pine, spruce, fir) forests via succession (Fig. 8; Zhu and Huang, 1991; Wang et al., 2000; Guo and Li, 2012)). This aspen community is generally a mixed tree system that initiates when the original forest is altered by human activity or fire.

Fig. 8. In northern China *P. davidiana* dominates the current forest cover though this species is predominantly seral-dominant throughout its range.

In the past, due to deforestation and overconsumption, much of the aspen forest was converted into cropland or grassland. Since the Natural Forest Protection Program in China (1998), tree harvesting in these forests has been prohibited. According to the Chinese vegetation map (ECVAC, 2001), David's aspen forest covers about 21,600 km^2 in China which is substantially less than the potential/historical extent as shown in Fig. 1, Table 1. Past land clearing, agriculture, and grazing/browsing practices may impede the sustainability of aspen in China. However, recent research suggests that high-intensity fire will promote the species' expansion and moderate thinning is better for maintenance of plant diversity than clearfelling (Tian et al., 2014). New work also indicates advantages from a warming climate; moderate drought may favor aspen's quick regeneration response over competing species, but aspen in poor condition may react adversely to prolonged drought, thus threatening community stability (Zhao et al., 2018).

David's aspen has a high economic and ecological value in China. Forest harvest rotations are generally short and the fast growth facilitates commercial forestry for a range of products. Concurrently, aspen has been listed as a candidate afforestation and restoration tree species in China due to its fast growth, self-renewal capacity, and adaptability to diverse environments (Hou et al., 2004). As such, it has been widely planted in northern China through encouragement of government programs targeting conversion of crop lands to forest cover. Recent research on David's aspen has focused on molecular phylogeny, water consumption characteristics, response of tree growth to soil moisture, community biodiversity and successional trends, carbon sequestration, soil erosion, and forest cutting strategies (Zhu and Huang, 1991; Zhao et al., 1994; Shen et al., 2016; Zheng et al., 2017; Hou et al., 2018).

Chinese aspen (*P. adenopoda*) is a less widespread species in China and it is distributed in the subtropical Yangtze and Huaihe River basin (Tang et al., 2011). This species possesses a robust sprouting ability facilitating rapid regeneration in clearfell-coppice treatments. In natural settings, this species coexists with *Pinus massoniana*, *Betula luminifera*, *Rhus chinensis*, and a variety of *Quercus* spp. Chinese aspen is used to make pulp and thus has important economic value. Due to cold tolerance, *P. adenopoda* has also been widely planted in the low hills region of southern China with altitude range from 800 to 1800 m. Mechanical reductions of the mid- and lower-storey associate tree species increases growth and productivity value in Chinese aspen stands (Jiang and Tan, 2009). Current research on Chinese aspen is focused on inheritance and breeding, reproduction, and growth characteristics (Tang et al., 2011; Jiang and Tan, 2009).

REGION: Japan.

FUNCTION: seral-dominant, subdominant.

THREATS: unknown.

RESEARCH OVERVIEW: Pure stands of Japanese aspen (*P. sieboldii*) are rare other than immediately following disturbance. This species, as most aspen, is a colonizer of recently disturbed sites; however, its endemism in Japan finds it revegetating volcanically impacted locations effectively, a somewhat unique mechanism for stand rejuvenation in aspen. Japanese aspen is commercially important, especially when hybridized with *P. grandidentata* (Dickmann and Kuzovkina, 2014). Overall, this species does not appear to play a major role in Japan's forests, though we speculate that there is still an important biodiversity function where it is found.

5. Synthesizing aspen regions, biodiversity, and RESEARCH needs

5.1. A global aspen perspective: biodiversity and threats

Aspen communities are widespread around the northern hemisphere and characterized by similar dynamics. Common attributes gleaned from regional summaries include high biodiversity, rapid recolonization following disturbance, and adaptability to harsh or changing environments. Additional ecosystem services common to many, but not all, regions are water retention and conservation, soil enrichment and carbon sequestration, deterrents to fire spread, and aesthetic attributes. In some regions, however, aspen are still viewed as marginal wood resources and may be actively suppressed or eradicated to facilitate commercial species. Disparities in scientific emphasis were clearly revealed in the process of this review. For example, western U.S. study places greater emphasis on landscape change is disturbance, while other regions have focused in physiological and genetic realms (Figs. 2–3, Section 4.0). Similarly, Canadian researchers appear to excel in aspen climate work, while eastern U.S. studies favor conservation (Fig. 2). Generally, qualitative self-assessments (Fig. 3) generally match research output (Fig. 2), although expert surveys attempted to take on a more specific set of research topics and thus groupings do not exactly match with literature keyword analysis. We contend that sharing science resources across international boundaries may reduce such disparities while promoting sustainable aspen management and sound conservation of aspen and a dependent array of species.

In many, though not all, locales aspen systems are biodiversity hotspots where they are often a minority species among vast conifer forests. This highlights the fact that even small stands of aspen add disproportionately to overall landscape diversity (Kouki et al., 2004; Macdonald and Fenniak, 2007; Rogers and Ryel, 2008; Hou et al., 2018). For example, where aspen stands in the southwest U.S. are in decline, avian diversity has been shown to decrease (Griffis-Kyle and Beier, 2003; Martin and Maron, 2012). In Sweden, small groves of aspen contributed significantly more than the matrix of conifers to total epiphytic lichen varieties (Hedenås and Ericson, 2003). In terms of conservation, an important implication is that the viability of some obligate species—including epiphytes, understorey plants, birds, mammals, or invertebrates—can follow the trajectory, either plus or minus, of the vitality supporting aspen communities (Chong et al., 2001; Oaten and Larsen, 2008;

Rogers and Ryel, 2008; Bailey and Whitham, 2002). Thus, though aspen are widespread, their degradation holds outsized capacity for influencing broad-scale regional and continental biodiversity.

There are numerous threats to aspen ecosystems, however. Given the functional diversity within these forests (Section 4.3), we should expect variation in the response of aspen to common stimuli (Rogers et al., 2014). Persistent drought is already occurring in some regions and is expected to increase under climate change (Gray et al., 2011; Hogg et al., 2013; Worrall et al., 2013). Intense herbivory, whether in combination with wildfire or prolonged drought, often presents acute barriers to aspen resilience (Edenius et al., 2011; Rogers and Mittanck, 2014). While land reclamation using aspen to recolonize developed or mined land has many benefits, neglect or conversion of these lands will likely still lead to overall aspen decline (Pinno and Errington, 2015). In some regions, silvicultural selection for conifers has historically, sometimes actively, degraded aspen forests. Modern realization of aspen's ecological, aesthetic, and commercial values has often reversed such trends, but legacy effects persist. Similarly, long-term fire suppression in seral-dominant aspen may allow advanced succession to overtop aspen, though this process is not thought to be widespread (Hessl, 2002; Kashian et al., 2007; Lankia et al., 2012; Kulakowski et al., 2013a). Recognition of varying aspen fire types (Shinneman et al., 2013) provides an initial step toward acknowledging benefits of fire, as well as curtailing inappropriate use of prescribed fire or silvicultural surrogates to “restore” aspen (Rogers et al., 2014). In some cases, invasive species (e.g., exotic grasses, insects, or mammalian herbivores) may suppress aspen vitality and sustainability (Chong et al., 2001; Bailey et al., 2007; Logan et al., 2007). Any combination of these threats, such as climate-herbivory or invasive species-land clearing, may exacerbate the extent and speed of aspen type conversions. Multiple combinations of impacts, therefore, should be viewed as opportunities to employ cross-disciplinary investigation as a pro-active tactic for aspen conservation.

5.2. *Research gaps in aspen sciences*

The author/expert survey of researchers around northern hemisphere countries with aspen forests (Fig. 3) reveals a number of underexplored topical areas. A few of these research gaps were common among many geographic zones. For example, there has been little systematic exploration of social or cultural uses of aspen forests and how that might affect conservation. A general need for international cross-border research will improve understanding of broad-scale, long-term, aspen dynamics across geographic and biophysical gradients to complement and connect research already conducted at finer spatial scales. Such endeavors should facilitate meta-analyses of aspen cover change based on regional studies. A prime research need is to articulate how aspen ecology differs across the range of a species (e.g., Rogers et al., 2014), as well as among ecosystems with colocation of different aspen species. Moreover, multi-scale research is needed to understand how climatic variability interacts with other predisposing factors to contribute to aspen mortality; and how ecological, physiological, and genetic variability determine successful vegetative and sexual reproduction of aspen. It is also important to understand how the cumulative effects of a changing climate and altered disturbance regimes will affect overall aspen dynamics and extent. Each of these large-scale research questions should consider comparing multiple, or single widespread, aspen species across ownership, political, and ecoregion boundaries to fully understand commonalities between aspen functional types and species. Other common themes that may be linked across species and regions include effects of herbivory, land clearing, past logging practices, and commercial uses and production. Each of these factors may have practical outcomes for large-scale biodiversity conservation given aspen's known value in this regard (Esseen et al., 1997; Chong et al., 2001; Kouki et al., 2004; Hou et al., 2018).

As we have established here, research subjects are not equally developed across regions (Figs. 2 and 3). Thus, the following represents an overview of research needs by geographic domain:

United States: Detailed knowledge is lacking in how aspen cover would be affected by current fire and climate trends; increasing extent, severity, and frequency of fires under projected widespread drought scenarios. Increasing the network of paleoecology sites may inform both historical and ancient responses of aspen to past climatic shifts (e.g., Carter et al., 2017). Furthermore, given the likelihood that forest ecosystems will be increasingly affected by multiple disturbance types over short time periods, future research should explore geographic variability in how such compounded perturbations affect aspen regeneration and potential dominance (e.g., Kulakowski et al., 2013b; Gill et al., 2017). Other fertile areas for examination may include opportunistic studies of aspen response to recent fire or bark beetle outbreaks, experimental fire and mock beetle outbreak studies to identify mechanisms underlying aspen response to disturbance, differential aspen response to climate variability on sites of varying functional types and disturbance regimes, spatially-explicit modeling of aspen population dynamics, and high-resolution remote sensing of aspen status. An important knowledge gap is an integrated synthesis of ecoregional trends in aspen dynamics that will better explain landscape patterns. Finally, exploration of social mechanisms related to aspen value, use, and change over time is a highly underexplored realm.

Canada: Over the past few decades there has been considerable research focused on aspen in western Canada, however there remains a number of critical gaps in the biology and management of this species. One of the major gaps is related to response and adaptations of aspen to drought, including physiological and morphological adaptations. For example, we know that aspen root-leaf area ratios vary with climate, but it is not known if this is genetically controlled. This is one example of how the future adaptability of the species for a warmer climate is not well understood. Another area of potential research relates to aspen regeneration. Most aspen regeneration work has focused on suckering responses to disturbance, though this response only allows aspen to remain at an established site and will not allow long-distance movement. Understanding the relationships between seed production, seedling establishment, and climatic and microsite requirements will be crucial to evaluate the response of aspen forests to future climates (Landhausser et al., 2010) either naturally or through assisted migration programs (Gray et al., 2011).

Northern Europe: In Scandinavia, there is a need to address how various ungulate densities affect recruitment rates of aspen, as well as relations between regeneration success and predation, disturbance, and national herbivore policies (Anglestam et al., 2017). This can be surveyed at a large scales by means of forest inventory data, explicitly recruitment stems (<5 cm DBH), together with monitoring of ungulate densities, but also experimentally at a smaller scales with fenced exclosures. There is also a need for thorough population dynamic studies to infer the effect of the declining recruitment on older age classes. Moreover, for the purpose of knowing the efficiency of seed dispersal, and thus the capability of migration and escape from browsers, small-scale spatial genetic studies should be undertaken in various habitats from the center to the periphery of aspen distribution. These understudied research questions are both relevant for the future conservation of aspen ecosystems (Myking et al., 2011). Active research throughout the region has been focused on biodiversity and in the breeding of hybrid stocks. The most probable knowledge gaps may be connected with aspen regeneration ecology and recruitment success, as well as cataloguing and understanding linkages of the numerous aspen obligate species reliant on self-perpetuating stands.

Central Europe: Aspen may be a promising forest species in the face of climate change. However, little is known about how this species will fare under increasing drought and, potentially, the onset of multiple forest disturbances. Elsewhere, we have seen increases in drying and disturbance-related forest replacement that favor aspen over other species (Kulakowski et al., 2013b). Additionally, aspen as a pioneer species with broad ecological amplitude holds promise for disturbed and extreme site colonization. In this regard, experimentation using aspen as a restoration agent in Central Europe is essential. Moreover, aspen and other fast-growing poplar hybrids may prove to be promising forest species for capturing carbon. Rapid colonization allows aspen to sequester large amounts of carbon within just a few years of stand-replacing events. While there are common government incentives with the European Union that support afforestation of former agricultural lands, we need further research to bolster suggested advantages of utilizing aspen as carbon stocks. Also, there are several paleoecology methods that may be used to better understand the role of past aspen clones in Europe and elsewhere. Pedoanthracology holds great promise for examining aspen's long-term role in forest development in Europe (Novák et al., 2018), but this approach is relatively new. As climates and disturbance patterns change over time it is expected that greater understanding of past developments will inform expected climate changes. We speculate that aspen will increase in prominence as European climates become drier and aspen take advantage of more intense disturbance cycles.

Russian Federation: Further investigation is needed in ecosystem-centered studies, such as biodiversity enumeration and system change associated with human- and natural-caused impacts to aspen. These areas are a priority in Russia and more attention will be paid to it in the future (Bases of State Policy, 2018). An example of such studies will be to fully understand changing climate, disturbance, and successional regimes in forests devoted to wood productions, as well as those which will remain mostly unmanaged.

Mongolia: As in Europe, aspen carries important ecological values that may be threatened by uncertain climate futures (Hessl et al. 2018). Due to their large genotypic and phenotypic variability, as well as positive feedback loops associated with shortened disturbance cycles (Kulakowski et al.), this species has the potential for great adaptability to future climatic changes (Hamrick, 2004). However, little is known about how *P. tremula* in a strongly continental environmen t will respond to climate change. Still, in plantation forestry, aspen is becoming more important for wood production, therefore hybridization research would be desired to explore broad tolerance for anticipated stresses related to rapid climate change. Understanding how central Asian aspen fits into a global and regional context (e.g., functional and species variations) will help improve both commercial and conservation practices. Further use of paleoecology techniques to understand ancient climate-disturbance adaptations could prove fruitful in developing future management strategies for resilient aspen systems.

China: In David's aspen, root development studies and basic ecology of the species, as well as additional restoration methods are lacking. Further exploration of how aspen forests provide for wildlife habitat has received little attention in China to date. The research on the ecological value and function of Chinese aspen (*P. adenopoda*) is relatively scarce and will require a concerted effort in this region. No studies have addressed threats to this species broadly, to our knowledge. We suspect that hazards faced are similar to David's aspen, mainly from past land clearing and agriculture practices, however this is largely conjecture without the support of dedicated investigations. Clearly further studies are needed to fully understand responses of both David's and Chinese aspen to common disturbances, such as fire, broad-scale cutting, and temporary land clearing. Preliminary research has been reported on pests and diseases which may attack the species, but further work is needed in this arena, too (Meng et al., 1986; Li et al., 2006).

6. Integrating an aspen conservation future

Aspens are an exemplar of systems conservation on a global scale; as foundational species they enable large numbers of dependent species around the northern hemisphere. We recognize, however, that the immensity of integrating world aspen sciences for conservation purposes is a daunting task. Here we have synthesized expertise from eight nations, plus literature reviews including several other regions (S1). A key initiative moving forward will be to expand our burgeoning Aspen Conservation Consortium to include more national experts. As we have seen here, disciplinary strengths and weaknesses abound (as would be expected) across international boundaries. However, awareness of "what is possible" through the current work, as well as an active expertise exchange program, could reduce effort spent with experimentation on initial steps that have already been addressed elsewhere. More to the point of biogeographic conservation, coordinated efforts to standardize diversity assessment methods will simplify future world syntheses and tracking of progress (or decline) in species retention. Such coordinated practices will also facilitate adaptation as likely biogeographic shifts taking place in aspen ranges accompanying warming climates, changing precipitation patterns, and land development or resource extraction (Gray et al., 2011).

Integrated practices should not be interpreted as uniform prescriptions. An overarching lesson gleaned from our review is that species and functional types (within species) perform differently under varying biophysical conditions (Kurzel et al., 2007; Shinneman et al., 2013; Rogers et al., 2014; Özel et al., 2018; Usoltsev et al., 2018). A more nuanced understanding of these differences will alleviate one-size-fits-all practices that are often counterproductive. For instance, aspen-dominant and seral-dominant forests should not be expected to react identically to cutting, fire, herbivory, or extended drought and uniform application of such practices may be considered maleficent. In order to create resilient systems, an intelligent strategy encompasses working within the bounds of ecological function as opposed to battling against evolutionary adaptations. At the community-level, this assumes some basic understanding of aspen autecology and Natural Range of Variability (Keane et al., 2009). While some have criticized this approach as we enter new climate realms (Millar, 2014), understanding aspen's response to earlier climate variation (Carter et al., 2017) retains value for informing adaptive responses to future extended droughts, for example.

Bringing these broad concepts together—shared aspen knowledge and intimate functional understanding—will greatly empower a mega-conservation strategy predicated on the idea that conserving widespread keystone ecosystems that support high biodiversity has merit as a viable approach to global species retention. We contrast this strategy with conventional species preservation which focuses vast resources on select high-profile species with (often) narrow habitat requirements. We do not advocate for replacing one tactic with another, so much as note the great potential value of mega-conservation for preserving larger overall numbers of aspen obligate species. To step forward with a shared knowledge and coordinated global strategy for aspen conservation and management holds great promise for similarly widespread species that enhance world biodiversity.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00828.

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