Long-term aspen cover change in the western US

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ABSTRACT

Quaking aspen (*Populus tremuloides* Michx.) is one of the most important tree species in the western United States due to its role in biodiversity, tourism, and other ecological and aesthetic values. This paper provides an overview of the drivers of long-term aspen cover change in the western US and how these drivers operate on diverse spatial and temporal scales. There has been substantial concern that aspen has been declining in the western US, but trends of aspen persistence vary both geographically and temporally. One important goal for future research is to better understand long-term and broad-scale changes in aspen cover across its range. Inferences about aspen dynamics are contingent on the spatial and temporal scales of inquiry, thus differences in scope and design among studies partly explain variation among conclusions. For example, major aspen decline has been noted when the spatial scale of inquiry is relatively small and the temporal scale of inquiry is relatively short. Thus, it is important to consider the scale of research when addressing aspen dynamics.

Successional replacement of aspen by conifer species is most pronounced in systems shaped by long fire intervals and can thus be seen as part of a normal, long-term fluctuation in forest composition. 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) appear to favor aspen and may facilitate expansion of this forest type. Thus, future aspen trends are likely to depend on the net result of the direct and indirect effects of altered climate.

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1. Introduction

Forest ecosystems are changing worldwide due to interacting effects of climate change, altered disturbance regimes, invasive species, and land use. Identifying short-term changes is informative for discerning acute impacts of these factors, but a comprehensive understanding of forest ecosystem dynamics also requires examining processes driving ecological patterns at a range of spatial and temporal scales. Quaking aspen (*Populus tremuloides* Michx.) is the most widely-distributed tree species in North America and the most widespread deciduous tree species in the United States Rocky Mountains (Little, 1971; Perala, 1990). In the Rocky Mountains and other regions, aspen forests exist in a wide variety of ecological settings (Little, 1971; Mueggler, 1988), which necessitates a nuanced perspective in examining their ecological patterns and dynamics. There has been substantial concern that aspen cover and condition have been declining over the past century in western US landscapes (e.g., Kay, 1997; Knight, 2001), but the trends of aspen decline versus persistence appear to vary both

geographically and temporally (e.g., Kulakowski et al., 2004, 2006; Kashian et al., 2007; Kurzel et al., 2007; Sankey, 2008). Inferences about trends in aspen decline are also likely to be contingent on the spatial and temporal scales of inquiry (e.g. stand vs. landscape scale and decadal vs. centennial scale) (Suzuki et al., 1999).

This paper provides an overview of the drivers of long-term aspen cover change in the western US and where possible, discusses the cumulative consequences of those drivers on overall aspen cover. The dearth of aspen studies conducted at suitable temporal and spatial scales precludes a comprehensive meta-analysis of long-term and broad-scale aspen cover trends at the time of this writing, and such studies remain a top research priority. Nevertheless, important advances have been made over the last decade that offer a glimpse into the drivers and trends of both aspen cover change and its responses to the direct (e.g. drought) and indirect (e.g. altered disturbance regimes) consequences of climate change.

More than a decade ago Knight (2001) stressed the need to understand aspen dynamics in a long-term framework, and correctly speculated that widespread disturbances in the West in the late 1800s and early 1900s may have increased the amount of aspen in the Rocky Mountains. Several studies over the last decade have affirmed Knight's speculation that aspen decline may be

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understood as one phase in a series of normal fluctuations and have provided insight into these dynamics. Likewise, more than a decade ago climate change was identified as a potential threat to aspen forests (Knight, 2001), and since then a number of studies have investigated the details of how climate is driving aspen mortality across its range.

As the extent of forest cover is ultimately a function of both tree regeneration and mortality, we review key variables that drive these two processes as well as their net result. Where possible, we also discuss the overall changes in aspen cover at different scales. Finally, we suggest potential areas of future research in aspen dynamics.

2. Study region

In this review we focus on quaking aspen in the western US, where it is found in all thirteen western contiguous states and Alaska and where it occurs at elevations up to 3500 m (Burns et al., 1990). In New Mexico, Colorado, Utah, and Arizona, aspen can form extensive pure stands, whereas in other regions aspen patches can be smaller, though still ecologically important. The ecological role of aspen across this region varies substantially with biophysical setting, climate, disturbance regimes, and the presence of other tree species. Although we aim to highlight some of this variability, our review is limited by existing literature, which is not equally distributed across the extent of aspen, but rather is concentrated in several key states.

3. Characteristics of studies

Studies of aspen dynamics vary substantially in the temporal and spatial scale at which they have been conducted. Given the difficulty of extrapolating across scales, it is critical to recognize this variation when comparing studies. Studies that focus on small areas or short time periods (e.g. Bartos and Campbell, 1998) are valuable, but may not be easily or accurately scaled up to provide insights into broad-scale and/or long-term patterns. Thus, studies may lead to very different conclusions about aspen dynamics even within the same study region depending on the spatial and temporal scale of observation. These differences, as well as geographic variation in aspen ecology, can explain much of the varying and at times contradictory conclusions among studies.

Compared to other forest types in the western United States, the study of long-term aspen dynamics is encumbered by several methodological limitations. Aspen ramets are relatively short-lived and prone to heart-rot, which has made long-term (i.e. >100 year) dendroecological studies difficult. Second, stand-replacing disturbances such as fires, which often re-initiate aspen stands, erase evidence of pre-disturbance stand conditions and processes (Shinneman et al. this volume). Furthermore, although most studies of aspen focus primarily on above-ground stems, the clonal habit of aspen (Barnes, 1966) makes aging ramets relatively uninformative for aging the clone itself. Additionally, studies of forest dynamics are sometimes limited to reconstructions at the scale of a stand (<c. 1000 ha), which although valuable for insights into relatively fine-scale processes, make broad-scale inferences challenging. Consequently, landscape-to-regional studies of aspen are often restricted to snapshots of aspen structure. The few long-term or broad-scale assessments of aspen change have generally been based on analyses of repeat photographs or historical maps, both of which facilitate discerning dynamics over larger extents more so than dendrocological studies, but which are hindered by the lack of available images representing most of the western landscape. Methodological limitations of studying broad-scale aspen dynamics are further complicated by the inherent

diversity of scales at which the processes that drive aspen regeneration and mortality operate (Fig. 1), which necessitates that research and management be conducted at scales appropriate to each driver. For example, browsing effects on aspen regeneration are largely limited to areas of significant ungulate populations while the impacts of high-severity fires on aspen regeneration is most prevalent in subalpine forests.

4. Regeneration

Aspen regeneration dynamics are integral to aspen cover change and have been the subject of much inquiry in the context of disturbances, climate variability, and browsing by ungulates. Adding complexity to the issue of aspen regeneration is its occasional regeneration by seed that complements the more common vegetative reproduction. Sexual regeneration of aspen is much more important to the overall genetic diversity of aspen (Mock et al. this volume) than to overall aspen dominance at broad scales, but is far less studied than asexual reproduction and thus is not as well understood.

Variation in aspen ecology, even over relatively small distances, may be partially explained by the clonal nature of aspen, in which a clone contains genetically identical ramets but may differ morphologically, physiologically, and ecologically even from adjacent clones (Barnes, 1966; Kemperman and Barnes, 1976; Mock et al. this volume). This variation may lead to different regeneration dynamics and other ecological properties. For example, Kemperman and Barnes (1976) were able to discern aspen clones in Utah in part based on their distinct timing of spring leaf flush.

Modes of aspen regeneration can vary even within a relatively restricted area. Kurzel et al. (2007) found that in the majority (seven of eight) of seral stands (both aspen dominated and mixed aspen-conifer) in northwestern Colorado, regeneration of the stand was associated with coarse-scale, severe disturbance by fire. However, in the same study area, most aspen-dominated stands showed signs of aspen self replacement despite presence of conifers. Furthermore, in persistent aspen stands showing no conifer
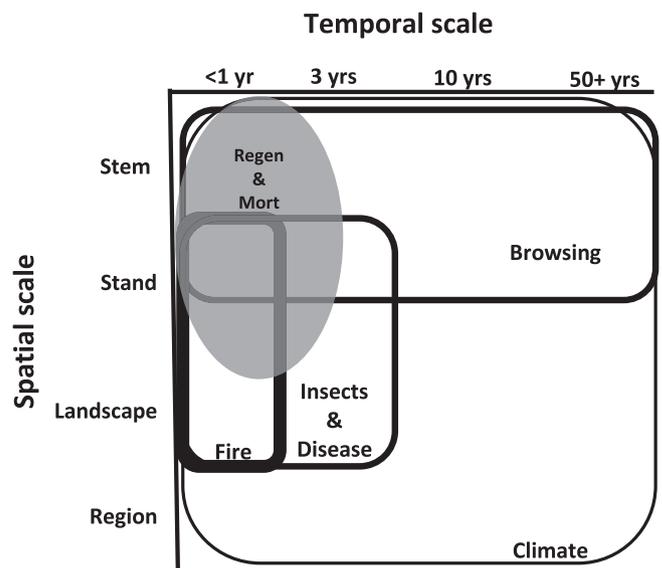
Fig. 1. Diversity of spatial and temporal scales for processes (white boxes) that drive that aspen regeneration and mortality (grey oval) in the western US. Each polygon represents the extent of a given process and thickness of the black border represents the intensity of impact on aspen, such that thicker lines represent more acute impacts. Processes range in influence from short scale and acute (e.g. fire), to broad scale and moderate (e.g. climate). When possible, research should occur at spatial and temporal scales that reflect the scale of influence of that process.

invasion, aspen were able to regenerate without severe disturbance. In fact, over 70% of the persistent aspen stands sampled did not require coarse-scale disturbance to regenerate.

4.1. Fire and regeneration

Aspen regeneration is commonly described as prolific clonal resprouting following stand-replacing disturbances, of which fire is probably the most important (Bartos and Mueggler, 1981; Brown and DeByle, 1987). Fire regimes in aspen forests are discussed in detail in Shinneman et al. (this volume). In the context of understanding drivers of aspen cover, we emphasize that fire regimes in forests of the Rocky Mountains vary substantially in size, severity, and frequency with elevation and latitude. Furthermore, variation among aspen clones as well as biophysical setting within the perimeter of a given fire can contribute to fine-scale variation in regeneration in areas affected by large and severe disturbances.

Stand-replacing fires kill both conifer and aspen canopy trees, which creates favorable post-fire conditions for the successful resprouting and initial dominance of the relatively shade-intolerant aspen (Schier et al., 1985). As mentioned above, initiation of aspen stands normally requires stand-replacing disturbances to eliminate competition from conifers or other species (Kashian et al., 2007; Kurzel et al., 2007). In post-disturbance stands, especially on favorable sites, aspen age structure will typically have a uni-modal rather than a negative exponential distribution, the latter being more often associated with continuous regeneration that is not contingent on disturbances. Thus unimodal or bimodal age structures can be indicative of typical post-disturbance stand structure rather than a failure to regenerate (e.g. Smith and Smith, 2005).

Because aspen regeneration and initial dominance are generally favored by fires, fire suppression (including cessation of burning by Native Americans) has been among the major reasons proposed for the decline of aspen (DeByle et al., 1987; Kay, 1997, 2001; Bartos, 2001). For example, Pierce and Taylor (2010) reported that in the northern Sierra Nevada Mountains in California, fires promoted aspen persistence and reduced competition from encroaching conifers, and that fire suppression has made current forests more suitable for shade-tolerant conifer species. Similar conclusions have been reached in other systems as well (e.g. Strand et al., 2009a, 2009b). Though fire suppression has had a tangible effect on forest structure and dynamics in various regions, the ecological effects of fire suppression vary widely across ecosystems (Schoennagel et al., 2004). Indeed, long intervals between natural disturbances in some forests of the Rocky Mountains have resulted in a historically broad range of variation of forest structures, including stand dominance by particular tree species (Kulakowski et al., 2004, 2006). However, while fire frequency decreased during the 20th century in forests and woodlands at xeric sites, lower elevations, and/or lower latitudes (Schoennagel et al. 2004), it is not clear that fire suppression has had a significant effect at more mesic sites, higher elevations, and/or higher latitudes. These cooler and wetter forests have historically been shaped primarily by a history of large, infrequent, and severe fires. The long intervals between fires in these systems make it unlikely that the past 50–90 years of fire suppression has substantially changed the natural fire regime of the majority of the landscape. Rather, limited fire occurrence during the 20th century may be within the range of variation of the past several centuries (e.g., Sibold et al., 2006).

Age structures of aspen forests and long-term dynamics are likely to reflect differences in fire regimes where fire is an important driver of aspen regeneration. For example, Kashian et al. (2007) documented substantial aspen decline at lower elevations where frequent, low-severity fires were historically more easily suppressed, compared to seral stands at higher elevations where fire intervals are long and fires are high-severity and are less easily suppressed.

Recent increases in fires in the western US (e.g. Miller et al., 2009) have favored vegetative regeneration of aspen and studies across this region consistently report abundant aspen regeneration following fire. For example, seven years following a 2002 fire in southern Utah, resprouting aspen were abundant throughout the burned area, although pre-fire abundance of conifers was negatively correlated with post-fire aspen stem density (Smith et al., 2011). Stand-replacing fires over the past three decades in Glacier National Park, MT have promoted aspen resprouting and an increase in relative density of aspen from pre- to post-fire forests (McKenzie and Tinker, 2012). Likewise, in southwestern Colorado, prescribed fire following forest thinning resulted in significant increases in aspen stem density (Korb et al., 2012). The stimulation of aspen regeneration by recent fires both supports assumptions about historical relationships between fire and aspen and also suggests a positive trajectory for aspen in post-fire landscapes (Landhäusser et al., 2010).

4.2. Browsing and regeneration

Browsing by ungulates can exert a major influence on aspen dynamics because intense browsing by elk on regenerating aspen, particularly in elk winter ranges, can inhibit aspen recruitment (Bartos and Mueggler, 1981; Bartos et al., 1994; Romme et al., 1995; Baker et al., 1997; Suzuki et al., 1999; Ripple and Larsen, 2000; Hessl, 2002; Larsen and Ripple, 2003; Jones et al., 2009; Seager and Eisenberg this volume). For example, Kimble et al. (2011) reported that winter ungulate browsing, conifer establishment, and cattle (Bos spp.) grazing were the most important factors contributing to the decline in density of overstory stems. Similarly, Binkley (2008) found that expected cohorts of aspen were missing from Rocky Mountain National Park, perhaps due to browsing. Kaye et al. (2005) found that elk browsing and conifer infilling negatively affected aspen regeneration, while aspen growth and mortality were more resilient to these two influences. Likewise, existing aspen stems in areas of widespread elk browsing seem to be resilient to browsing (Kaye et al., 2003), suggesting that elk browsing is most influential on aspen regeneration rather than on the growth and survival of aspen that is already established.

The magnitude of browsing damage on aspen varies regionally and locally with several key factors that affect elk populations. Low snowpack in the Rocky Mountains leads to greater elk visitations and higher browse impacts on aspen stems (Brodie et al., 2012). Conversely, areas inaccessible to elk (refugia) such as steep, rocky slopes are free of the potentially detrimental effect of browsing on aspen regeneration (Kashian et al., 2007). Finally, as wolves can affect elk populations, trophic cascades involving wolves, elk, and aspen regeneration have been suggested (Ripple et al., 2001; Kauffman et al., 2010), though these relationships can be complex and time-lagged (e.g. Kimble et al., 2011). Although it is clear that effects of browsing are most pronounced in elk winter ranges and where predator pressure is low, limited spatial data on elk populations and the spatio-temporal variability in those populations makes it challenging to generalize and predict the effects of browsing on aspen dynamics across broad regions.

4.3. Compounded disturbances and regeneration

A potentially important element affecting aspen regeneration, and possibly broader landscape patterns, is the effect of compounded disturbances – i.e. disturbances that occur in relatively short succession, such that a second disturbance occurs while the ecosystem is still responding by establishment or reorganization to a previous disturbance. It is generally recognized that post-fire

aspen regeneration is strongly correlated with pre-fire stand age and composition (Smith et al., 2011; Kulakowski et al., 2013). However, recent research has highlighted the fact that pre-fire disturbance history also affects post-fire regeneration such that regeneration following single disturbances is different from regeneration following compounded disturbances in both overall abundance and species composition (Buma and Wessman, 2011; D'Amato et al., 2011; Kulakowski et al., 2013).

In principle, compounded disturbances have the potential to alter post-disturbance 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 the vegetative reproduction of aspen but are more likely to inhibit regeneration of conifers within the same stands. Although compounded disturbances may increase overall disturbance intensity (either additively and/or by increasing the intensity of secondary disturbances) to the point that below-ground aspen roots are killed and re-sprouting is impeded (e.g. Parker and Parker, 1983), research to date suggests that compounded disturbances favor aspen over other species. For example, a combination of wind blowdown followed by fire in northwestern Colorado (Kulakowski et al., 2013) and a combination of blowdown, logging, then fire in northern Minnesota (D'Amato et al., 2011) reduced the regeneration of conifers, which regenerate exclusively from seed, and favored initial dominance by aspen, which regenerates both sexually and asexually.

Ecological disturbances are increasing in extent, severity, and frequency in many systems worldwide, including in the western US, and are predicted to continue increasing as climate continues to change (Dutzik and Willcox, 2010). It is therefore likely that forests will be affected by more than one disturbance and/or more than one type of disturbance in short succession. In this context, and given aspen's relatively high resilience to compounded disturbances as well as its ability to exploit early-successional environments, future disturbance regimes may lead to increased regeneration of aspen relative to other species and ultimately to increased cover of aspen forests at broad scales, if climate remains favorable for the future regeneration and growth of aspen. However, as few studies have directly considered the effect of compounded disturbances on aspen ecology, this is a fruitful area for future research.

5. Causes of mortality

5.1. Competition with conifers

Successional replacement of aspen by shade-tolerant conifers is an important driver of compositional change in some aspen forests and numerous studies have reported aspen replacement by conifers that establish in the understory of aspen-dominated stands (e.g., Rogers, 2002; Vankat, 2011). The transition from aspen to conifer dominance may occur over the lifespan of aspen stems that established following a disturbance, but may also take much longer (Crawford et al., 1998; Kaye et al., 2005). Competitive effects of conifers may decrease aspen regeneration (Kaye et al., 2005; Calder et al., 2011; Calder and St. Clair, 2012) and/or increase overstory aspen mortality (Calder and St. Clair, 2012), and thereby contribute to changes in forest composition (Smith and Smith, 2005).

Given aspen's propensity to gain dominance after stand-replacing disturbances and then be gradually replaced by conifers on some sites, disturbance regimes clearly affect successional outcomes and cover changes in aspen forests that are often described as "seral". The extent of seral, aspen-dominated stands on a landscape is therefore partly a function of the disturbance regime on that landscape. Several studies have suggested that succession to conifers results from fire exclusion on some sites (Brown and DeByle, 1987; Bartos et al., 1991), but others have emphasized that aspen replacement by conifers is within the natural range of variability where fire intervals are long and aspen dominance re-establishes following stand-replacing fires (e.g., Kaye et al., 2005; Kashian et al., 2007). Understanding aspen dynamics within the context of the local disturbance regime and at the appropriate temporal scale is therefore critical for interpreting successional trends, aspen mortality, and the future of aspen persistence across the West (Kulakowski et al., 2004, 2006). Although succession is an important driver of aspen cover in the West, its importance may be overstated if the role of infrequent, severe disturbances in contributing to broad fluctuations in forest composition is underappreciated.

5.2. Climate and mortality

Understanding the links between climate variability and tree mortality is an important goal of current ecological research. Species near ecotones are traditionally thought to be most susceptible to climatically-induced stress associated with extreme temperatures or precipitation (Neilson, 1993). However, recent examples of tree mortality associated with prolonged high temperatures and/or low moisture availability suggest that forest susceptibility to climatic variation may be more widespread than previously expected, even outside of transitional zones (Allen et al., 2010). Furthermore, climate models predict continued increases in drought and heat stress that could fundamentally alter the structure and function of forests in many regions (IPCC, 2007). Climate operates at broad spatial scales, and aspen responds to that climatic variability from the sub-continental scale (e.g. Kaye, 2011) to local scales (Fig. 1).

Recent observations have indicated a sudden onset and rapid progression of aspen dieback in the western United States that may be climatically driven (Frey et al., 2004). Climatically-driven mortality of aspen could lead to long-term reduction of aspen cover in these 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). In the southwestern US, Ganey and Vojta (2011) reported that aspen mortality in mixed-conifer forest was particularly pronounced (85%), and suggested that these early trends may be indicative of future responses to climate change. This phenomenon appears to be widespread, as in a broad-scale analysis Worrall et al. (this volume) report that aspen on marginal sites and near ecotones are most likely to be susceptible to climatically-induced mortality.

In addition to aspen near transitional zones, Hanna and Kulakowski (2012) found that growth and mortality of quaking aspen in Colorado and Wyoming away from transitional zones are also strongly associated with climatic variation. Specifically they found that in stands with substantial recent dieback of aspen, reduced growth of aspen was associated with warm temperatures, except at the highest elevations; mortality of aspen was preceded by multiple years of reduced growth; and the frequency of mortality was associated with multiple years of drought as indicated by negative Palmer drought severity index values.

5.3. Other factors affecting aspen cover

Although aspen regeneration is primarily vegetative, aspen can also establish from seed following stand-replacing disturbances if

optimal conditions for germination and establishment are met (Barnes, 1966; Romme et al., 1997; Mock et al. this volume). Sexual reproduction of aspen has not been the focus of much research and remains poorly understood. Romme et al. (2005) reported widespread aspen regeneration from seed following the 1988 Yellowstone fires, but predicted that many or most of the seedlings will die within a few decades with little lasting effect on broad-scale vegetation patterns or post-fire successional trajectories. However, at least some new genets appear likely to survive and to establish new aspen clones, with potentially important consequences for demographic and genetic structure of the Yellowstone aspen population (Romme et al., 2005). While documented cases of aspen seedlings over the past 50 years have been uncommon in the western US, infrequent episodes of sexual reproduction may accumulate in the population and diversify the genetic pool over long temporal scales (Mock et al., 2008; Mock et al. this volume). Aspen regeneration by seed is generally thought to require cool, moist conditions and exposed mineral soil soon after a stand-replacing disturbance (Barnes, 1966), a scenario that is somewhat rare in the Intermountain West (Romme et al., 1997). Future warmer, drier climate scenarios predicted by current climate models may therefore further limit the incidence of conditions necessary for aspen regeneration by seed, and the establishment of new genotypes on the landscape may be curtailed.

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

6. Cumulative trends in landscape patterns

The cumulative effects of establishment and mortality ultimately determine population size and total forest cover. In the preceding sections we have discussed key factors that drive these demographic processes and thus contribute to cumulative trends in landscape patterns. Long-term trends in aspen cover, spatiotemporal variability in those patterns, and the dispersion of sites around expected trends have yet to be quantified throughout the western US and such assessments remain a top research priority as well as challenge. In the following section we highlight apparent generalities in the studies that have been conducted to date and we discuss trends in aspen cover in the Rocky Mountains of Colorado, where a critical number of studies on long-term aspen cover have been conducted.

As discussed above, aspen's broad distribution and varying ecological roles result in substantial variation in the processes that dominate long-term cover change. Based on a review of local-scale aspen studies in Montana, Sankey (2008) drew attention to substantial regional-scale spatial variability in aspen dynamics and the fact that areas of successful aspen regeneration and recruitment are juxtaposed with areas that lack these attributes. Similarly, even over fairly short distances, the population structure of aspen in Colorado has been shown to be highly variable (Kaye et al., 2003).

While areas of aspen decline have been given considerable attention among researchers, managers, and policy makers, many studies that have examined longer-term and/or broad-scale trends have not concluded that aspen is declining. It has been estimated that only one-third of western aspen may be persistent (Mueggler, 1988), but other reviews considered it unlikely that most aspen forests will be lost in the near future (Knight, 2001). At spatial

scales of individual stands and over time periods of several years, mortality of aspen has been reported to be as high as 100% (Worrall et al., 2008). In contrast, studies that have focused on broader spatial and/or longer temporal scales have reported either lower decreases or even increases in aspen cover. Zier and Baker (2006) found an increase in extent of aspen over the past century in Colorado along boundary edges of both self-replacing stands and seral aspen stands, as well as persistence of aspen in many stands even in the presence of conifers. They concluded that forest recovery from historical large disturbances contributed substantially to this increase (Zier and Baker, 2006). Across broad spatial scales in the Greater Yellowstone Ecosystem, Brown et al. (2006) found an average of 10% aspen loss overall, much lower than that suggested by studies conducted at finer spatial scales. Likewise, Sankey (2012) reported a 69% decline in aspen cover in some areas but a 179% increase in aspen cover in other areas of the landscape and concluded that changes in aspen cover are spatially variable. It is therefore important to consider where in the landscape and to what extent aspen is declining vs. forming self-replacing persistent stands. Moreover, assessments of aspen conditions can be easily biased by subjective selection of stands where decline is known to occur, rather than by representatively sampling the condition of aspen on the larger landscape.

Variability of aspen dominance over time is likely to depend on the relative importance of the factors governing establishment and mortality in any given region. In some systems aspen abundance is likely to vary quite minimally over decades to centuries, whereas in other systems low frequency and high severity events or processes structure the ecosystem and may result in a broad range of natural conditions that oscillate over long time periods. Studies in Colorado have shown that aspen cover varies substantially over time in ecosystems shaped by infrequent, high-severity fires (Kulakowski et al., 2004, 2006; Kashian et al., 2007). In such systems any decline of aspen must be placed in the context of the major pulse of regeneration of aspen that followed the often extensive and severe fires of the late 19th century (Rogers et al., 2007). These fires promoted aspen dominance on the landscape (Kulakowski et al., 2004, 2006) and aspen decline during the 20th century in some areas may therefore represent a return to conditions that preceded the widespread burning of the 19th century. In sum, the amount of aspen on a given landscape is likely to vary at a centennial scale to the degree to which infrequent stand-replacing fires affect aspen stands in that region.

In a broad synthesis of aspen across the interior western US, Kaye (2011) recognized that the widespread late-1800s peak in aspen recruitment was driven primarily by the occurrence of the last historical fires throughout the intermountain West. However, a second peak of recruitment in the 1970s and 1980s was driven not by large disturbances, but rather was associated with improved moisture conditions brought about by a shift to a positive phase of the Pacific Decadal Oscillation and a persistent negative phase of the Atlantic Multidecadal Oscillation. Kaye (2011) concluded that the over-arching implication of large-scale synchrony in aspen dynamics is that current aspen ecosystem condition is not solely the result of local-scale histories of browsing or fire, but is also the interwoven legacy of these local factors combined with broad factors such as climate and Euro-American settlement. Similarly, while Kulakowski et al. (2004, 2006) found that much aspen establishment in Colorado in the late 19th century occurred in areas that burned in large and severe fires, they also reported establishment from that same period that could not be definitively linked to fires. A possible explanation for this recruitment is that mortality in some aspen stands was caused by drought rather than fire and then new regeneration, perhaps even by seed, was facilitated by the slightly moister conditions that followed.

Long-term and large-scale trends in aspen cover driven by aspen regeneration and mortality have yet to be quantified for much of the western US, but have been most thoroughly documented in the Rocky Mountains of Colorado. Even across Colorado, it is important to recognize that substantial variation in aspen ecology exists and thus conclusions from studies in one area do not necessarily apply to other regions within or outside of the state. Rather, existing studies of aspen in Colorado may serve as starting hypotheses for the greater Western region. Aspen cover in Colorado appears to have decreased over the past few decades (e.g. Worrall et al., 2008), especially on marginal sites, and climatically-driven mortality is continuing to reduce total aspen cover (e.g. Hanna and Kulakowski, 2012). However, longer-term studies indicate that aspen cover has actually increased over the past century (Manier and Laven, 2002; Kulakowski et al., 2004, 2006; Zier and Baker, 2006; Kashian et al., 2007), especially at higher elevations.

7. Consequences and future scenarios

Recent, ongoing, and future global environmental changes in forest ecosystems include an increase in tree mortality either as a direct (e.g. drought) or an indirect (e.g. insect outbreak or wildfire) result of a changing climate as well as an increased likelihood of compounded disturbances. Drought appears to impact aspen growth and vigor negatively and contribute to its dieback (e.g. Worral et al., this volume), but other aspects of an altered climate and altered disturbance regimes may favor aspen over conifer species that often co-dominate the landscape. For example, ongoing extensive outbreaks of bark beetles across western North America (Raffa et al., 2008) coupled with a shift in precipitation and temperature regimes (Dutzik and Willcox, 2010) may set the stage for a possible conversion of some forests from conifer to aspen dominance. Likewise, increased warmer and drier conditions in the West are also likely to increase wildfires (Westerling et al., 2006) that favor aspen dominance. Finally, compounded disturbances also appear to favor regeneration of aspen over conifers (Kulakowski et al., 2013) and could increase aspen dominance if compounded disturbances continue increasing with projected shifts in climate regimes.

As aspen stands are generally more mesic than adjacent conifer stands, the former are less likely to burn. Aspen stands are also less susceptible to bark beetle outbreaks that affect conifers (Kulakowski et al., 2003) and wind disturbances (Kulakowski and Veblen, 2002). Thus any change in the amount of aspen in the landscape has the potential to feedback to the overall disturbance regime at broad scales.

8. Key information gaps and uncertainties

Aspen in the western United States has received considerable research attention over the past 50 years, and important advances have been made in understanding the drivers of landscape dynamics at broad spatial scales. However, important uncertainties remain about aspen ecology and dynamics that should continue to be goals for future research. Among the most pressing needs for research are an improved understanding of broad-scale, long-term aspen dynamics across geographic and biophysical gradients to complement the research that has been conducted at finer spatial and shorter temporal scales. Eventually such research may permit a meta-analysis of cover change based on more regional studies.

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. For example, it is important to understand how aspen cover would be affected if the current trend of increasing extent, severity, and frequency of fires continues as well as if widespread drought becomes the norm across the West. Furthermore, given the likelihood that forest ecosystems will be increasingly affected by multiple disturbances over short time periods, future research should further explore how such compounded disturbances affect aspen regeneration and potential dominance.

Other fertile areas for research 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 quality, spatially-explicit modeling of aspen population dynamics, and high-resolution remote sensing of aspen distribution and condition. Shifts between vegetative and sexual reproduction will influence aspen population dynamics, and continued research on the influence of climate, disturbance, and population dynamics on regeneration mode is needed. Finally, an important knowledge gap is an integrated synthesis of regional or eco-regional trends in aspen dynamics that will better explain aspen landscape patterns.

9. Conclusions

An important theme across studies of aspen dynamics and cover is that aspen persistence, decline, regeneration dynamics, and other key processes vary across space and time. Understanding the diverse spatial and temporal scales of these factors is key to understanding the variation in aspen dynamics across its geographical range. In the western United States, successional replacement of aspen is most pronounced in settings historically shaped by long fire intervals and can thus be seen as a part of normal, long-term fluctuations in forest composition. 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) favor aspen and may facilitate expansion of this forest type. Thus, future aspen trends are likely to depend on the net results of the direct and indirect effects of altered climate.

Attempts to understand the future of aspen in the western US need to occur across a range of spatial and temporal scales. The processes driving trends in aspen cover outlined in this paper occur at scales ranging from annual and local to centennial, regional, and broader, such that the ability to scale results from individual studies to larger areas is limited by the extent of the driving process. It is critical to identify the appropriate spatial and temporal scales of observation for any given area depending on the nature of the research questions and objectives. In short, it is important to recognize that changes in aspen cover and underlying dynamics vary across space and time.

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