The Impacts of Changing Disturbance Regimes on Serotinous Plant Populations and Communities

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Climatic change is anticipated to alter disturbance regimes for many ecosystems. Among the most important effects are changes in the frequency, size, and intensity of wildfires. Serotiny *(long-term canopy storage and the heat-induced release of seeds) is a fire-resilience mechanism found in many globally important terrestrial ecosystems. Life-history traits and physiographic differences in ecosystems lead to variation in serotiny; therefore, some systems may exhibit greater resilience to shifting disturbances than others do. We present a conceptual framework to explore the consequences of changing disturbance regimes (such as mean and variance in fire severity or return intervals) to serotinous species and ecosystems and implications of altered serotinous resilience at local and regional scales. Four case studies are presented, and areas needing further research are highlighted. These studies illustrate that, despite the reputed fire resilience of serotiny, more fire does not necessarily mean more serotinous species across all systems in which they occur.*

Keywords: serotiny, fire regime, disturbance return interval, climate change, resilience

Disturbances act to maintain and promote ecosystem structure and function across much of the biosphere. However, disturbances can also act as the proximate mechanism through which changes in climate and consequences of anthropogenic activities manifest themselves and can lead to losses in biodiversity and ecosystem services. Examples of climate-sensitive disturbances include decreased return intervals and increased severity of fire (Chapin et al. 2008), drought (Allen 2007), pathogens (Metz et al. 2012), and interacting disturbances on coral reefs (Côté and Darling 2010). Changes to disturbance regimes are anticipated in many regions with ongoing climatic warming; however, the ecological consequences of such changes remain a major question (Turner 2010). Although there is broad understanding of the singular impacts of some disturbances, possible synergistic interactions among disturbances are not well investigated, despite the recognition of the potential for ecological surprises when disturbances interact (Paine et al. 1998). In addition, not all organisms will be affected in the same way; variation in plant functional traits associated with responses to disturbance will act as ecological filters, driving future ecosystem composition and function. Functional traits allow comparisons of varying species and phylogenies to similar external forces. Here, we profile how changing disturbance regimes may interact with a prevalent disturbance-adapted trait, *serotiny*: the multiyear storage of viable seeds in the canopy (e.g., a canopy seed bank) whose release is triggered by heat.

Serotiny is a widespread mechanism for fire resilience, providing an ample *in situ* seed source immediately after a disturbance, when available resources are typically high and competition is typically low. This mechanism can lead to the sustained presence of the serotinous species on the site through multiple disturbance cycles, an indicator of a system's resilience to fire. (*Resilience* is defined as the capacity of a system to tolerate disturbance without shifting to a qualitatively different state that is controlled by a different set of processes; see Holling 1973, *www.resalliance.org.*) Nonetheless, fire characteristics matter; fire prior to the reproductive maturity or after the senescence of serotinous vegetation leads to local extirpation (Keeley et al. 1999), and high-intensity fires can reduce these species' viability (Alexander and Cruz 2012). Therefore, changes in fire regimes caused by climate change or management have the potential to lead to a loss of serotinous species, many of which are widespread, dominant members of their respective communities (e.g., black spruce [*Picea mariana*] in boreal forests, lodgepole pine [*Pinus contorta* var. *latifolia*] in western North America). Conversely, altered fire regimes may stimulate the population growth of serotinous species if the new regime better matches the life history and reproductive timing of those species. Given the global importance of

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serotinous species in many biomes (e.g., *Banksia* in Australia, *Pinus* and *Picea* in North America), understanding the resilience of serotinous systems is vital to predicting where altered disturbance regimes are likely to lead to transitions to new ecosystem states. We first describe how serotiny will likely fare as a fire-resilience strategy in the face of changing disturbance frequency, size, and intensity. After developing a broad conceptual model to evaluate the resilience of serotinous systems across ecosystems, we explore four case studies that provide relevant examples of changes in resilience observed after fire. We conclude by highlighting implications of these changes and areas for further research suggested by the conceptual model and the existing literature.

Serotiny and fire

In fire-serotinous species, seeds are retained in cones on an individual tree or shrub, with seed dispersal triggered by the heat-induced opening of cones (Lamont et al. 1991). In their review, Lamont and colleagues (1991) identified some 530 species in 40 genera that displayed some level of serotiny. Of these species, more than 99% occur in fire-prone environments. Serotiny has been hypothesized to be a fire-embracing or fire-promoting reproductive strategy, as has the production of flammable resins and the retention of dead foliage that increase combustion and heat release, which, in turn, favor the regeneration of serotinous species (Mutch 1970, Schwilk and Ackerly 2001, He et al. 2011). Factors such as poor soils, highly seasonal environments, and relatively regular fire return intervals also favor serotiny (Lamont et al. 1991), which can take advantage of postfire periods with low competition and heightened resource availability. Species can exhibit varying levels of serotiny, from cones that open with age in the absence of fire to those that remain sealed unless exposed to fire (Lotan and Perry 1983, Lamont et al. 1991). Populations can also vary; the degree of serotiny in individual populations of North American pines has been linked to their disturbance return interval and the intensity of those disturbances (Schoennagel et al. 2003), such that regions characterized by regular, severe fire (i.e., in which the majority of trees are killed) regimes often support populations with the highest levels of serotiny (Givnish 1981, Gauthier et al. 1996, Radeloff et al. 2004). Similarly, gradients in the serotiny of *Banksia* species in Western Australia correspond to gradients in fire return interval and intensity; populations exposed to frequent crown fires display more serotiny than do those in woodlands with surface fires (Cowling and Lamont 1985). Although serotiny often confers an advantage in fire-disturbed locations, it is not without cost. By storing seeds in the aerial seed bank, serotinous individuals may increase their exposure to seed predation, reduce their responsiveness to other disturbances (through the lack of a continuous seed rain), and increase their vulnerability to short- and long-interval disturbances that occur before cone bank maturity or after senescence (Enright et al. 1998). Finally, postfire seedling germination and establishment is also affected by precipitation; the amount, timing, and reliability of rainfall are important considerations when assessing postdisturbance resilience (Cowling et al. 2005). Nevertheless, the prevalence of serotinous species in many fire-prone ecosystems indicates the success of this resilience mechanism in response to fire disturbances.

Serotinous species are widely distributed across the North American continent (figure 1a) and, in many cases, represent the dominant species and strongly structure the associated community. The failure of serotinous species to regenerate, therefore, can result in regime shifts (e.g., Brown and Johnstone 2012) and novel ecosystems. Climate change is expected to alter fire return intervals across much of the globe as increased temperature, changes in precipitation, and increased evaporative demand alter the duration and extent of weather conditions suitable for fire (Flannigan et al. 2009). As fire probability (Mortiz et al. 2012) increases in many places, shortened disturbance return intervals (the time between events at a specific location) will increase the likelihood for multiple interacting disturbances, potentially posing a threat to the resilience of the system (Paine et al. 1998). North America, for example, is widely expected to become more fire prone, especially in boreal and Western forests (figure 1b,1c); other areas of the globe may see reductions in fire activity (Moritz et al. 2012). Many of the areas with predicted increases in fire probability overlap with the distribution of serotinous species. For example, Westerling and colleagues (2011) predicted drastically increased fire weather in western North America by the mid-twenty-first century on the basis of statistical climate–fire relationships. Given serotinous species' fire-stimulated regeneration strategy, one might anticipate an increase in their populations as a result of any decrease in fire return intervals. However, the resilience of serotinous tree populations under a changing climate regime may vary widely, depending on (a) local conditions, (b) specific life-history characteristics within each species or region (e.g., the time to reproductive maturity or senescence), (c) postdisturbance environmental conditions (e.g., precipitation amount and timing), and (d) the nature of changes to disturbance regimes (e.g., an increase or decrease in the mean disturbance return interval, alterations to the variance of return intervals, changes to disturbance intensity or severity, and the frequency of short-interval events).

Fire return interval changes and their impact on serotinous species

Changing disturbance regimes and fire frequencies will have a variety of effects on serotinous species and their communities, which will depend on the current disturbance context and the species' life histories. For example, a repeated disturbance before the recovery of the aerial seed bank may result in reduced resilience and potential switches to alternative ecosystems (i.e., immaturity risk; Keeley et al. 1999); these switches could occur if reproduction were limited either by absent or inadequate seed dispersal from off site or by

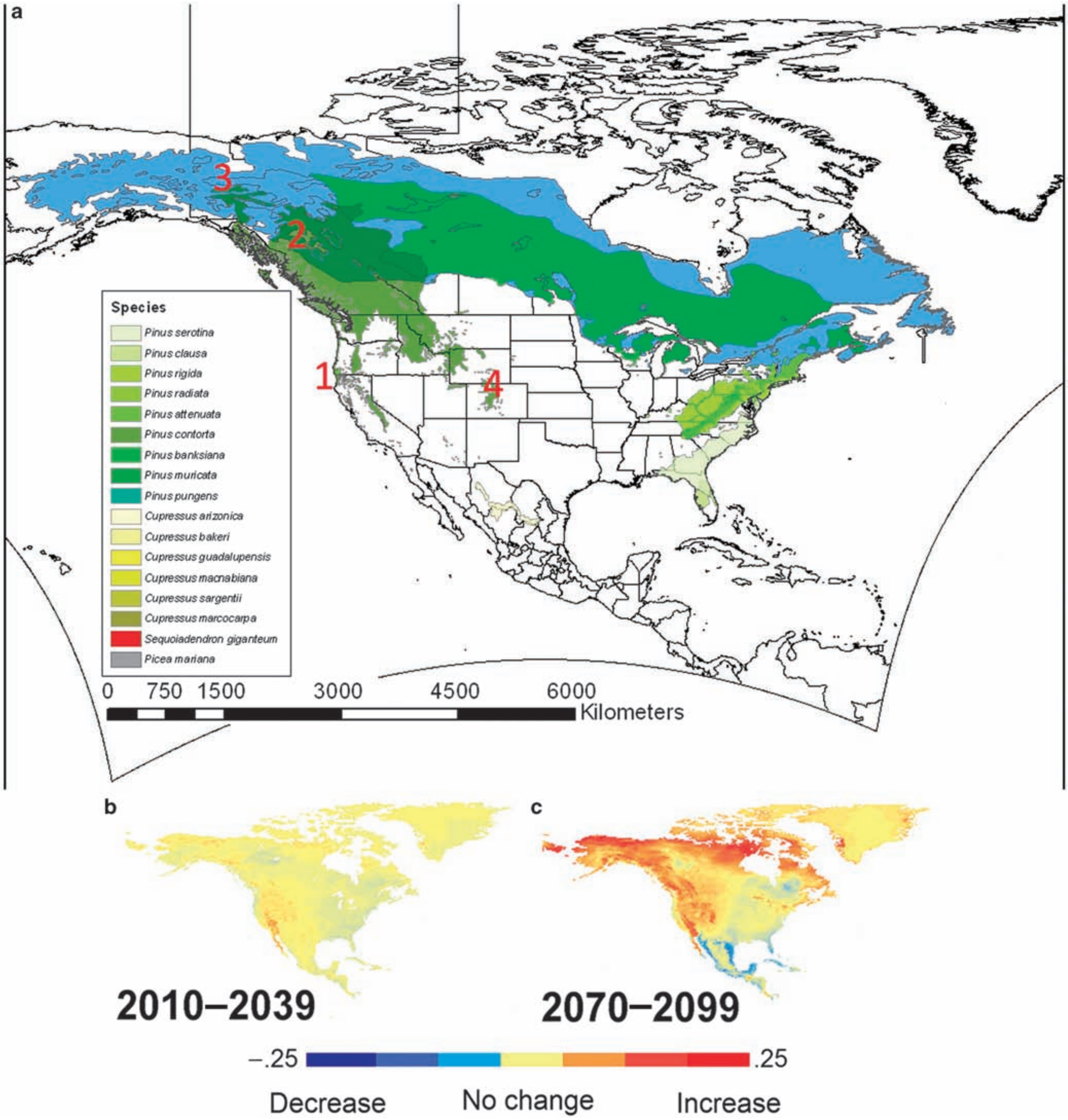

Figure 1. A comparison of the location of serotinous species and the expected changes in fire regime over the next century, to highlight areas of serotinous presence that are also expected to see significant changes in fire regime. (a) Distribution of North American tree species that exhibit serotiny over at least part of their range. The percentage serotiny may be variable even at fine scales. The red numbers refer to the locations of the case studies (see the "Case studies" section of the text). The bottom panels depict the projected relative increases in fire probability across a series of model ensembles for (b) the beginning and (c) the end of the century, relative to baseline probabilities from between 1971 and 2000. Source: Reprinted with permission from Moritz and colleagues (2012). The range maps (top) are from http://esp.cr.usgs.gov/data/atlas/little; *a zoomable file is available in the supplemental material, available online at* http://dx.doi.org/10.1525/bio.2013.63.11.5.

competition from other dispersers or on-site resprouters (see the "Case studies" section). Lengthened disturbance intervals may exceed the life span of serotinous species and may result in reproductive failure, as well (Noble and Slatyer 1980, Lamont et al. 1991). A conceptual model of these processes is presented in figure 2, in which, following the tradition of Noble and Slatyer (1980), ecosystems are plotted along a time axis that is scaled to the life-history stages of the serotinous population in a particular system. The points marked in the figure are the initial postdisturbance time; the beginnings of a mature aerial seed bank; the full development of the aerial seed bank, followed by the initial onset of senescence in serotinous individuals; and the final loss of serotinous individuals and any residual aerial seed bank due to decay, seed predation, or another mechanism. A qualitative measure of resilience is then scaled on the *y*-axis. Resilience is low immediately postdisturbance, rises with the development of the aerial seed bank, and declines as that seed bank disappears.

This conceptual framework accounts for the variation in intervals for disturbance regimes, some of which are quite large, and the variation in the degree of serotiny for any one population. For example, if the mean fire return interval in a forest stand is longer than the time required for aerial seed bank development (m_f in figure 2) and less than the time at which shade-tolerant species begin to succeed and shade out the seral serotinous species (l_i), we would expect that system to be fire resilient, because the seed bank should be of sufficient size to ensure postdisturbance recruitment. Conversely, if fire returns before maturity of the aerial seed bank (before m_i), we would expect low resilience of on-site serotinous species, and any recruitment would need to come from off-site sources. Variation in disturbance return intervals, represented by the horizontal bars around each point in figure 2, gives some expectation of the heterogeneity of resilience across landscapes. In addition to the disturbance interval, other factors associated with site history (contingent factors) can also influence resilience (the vertical bars in figure 2). For example, prior disturbances that alter forest structure and, therefore, the position of the canopy seed bank may reduce resilience, which may lead to varying levels of postfire recruitment (Buma and Wessman 2011). Variable levels of serotiny may alter any single population's relative resilience as well, which may lead to different levels of postfire regeneration within serotinous populations (e.g., lodgepole pine; Schoennagel et al. 2003) and presumably will select for more serotinous individuals over time (e.g., Gauthier et al. 1996). Little information on the variance or spatial distribution of serotiny within populations exists, despite the large influence of serotiny on fire resilience.

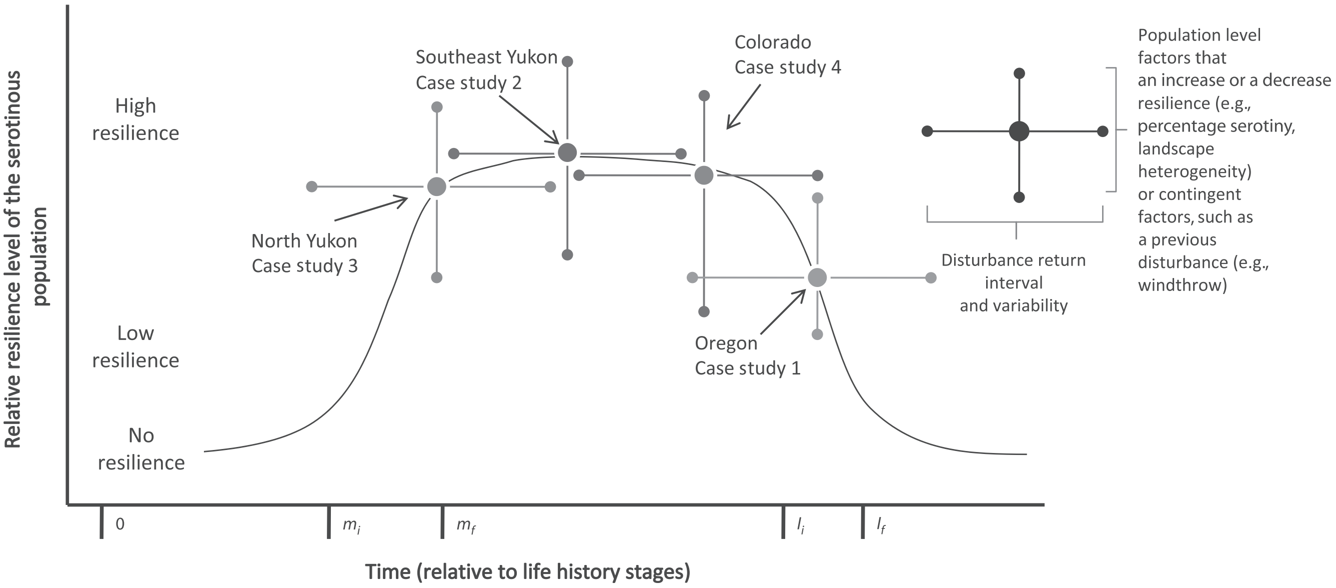

Figure 2. Resilience diagram with plots of the case studies. The plotted points represent the mean disturbance return interval scaled to the life-history stage of the dominant serotinous species. The horizontal bars represent the range of variability in that return interval; the vertical bars represent other factors that may increase or decrease a specific population's resilience, such as spatial heterogeneity; varying degrees of serotiny; or other disturbances that alter forest structure and, therefore, the position and size of the seed bank (e.g., wind throw, insect outbreaks). Shifts in the mean disturbance return interval would therefore be expected to increase or decrease resilience according to the ecosystems' current place on the line. Zero (0) on the x-axis represents the immediate time postdisturbance; m_i is when the serotinous seed bank begins to accumulate; m_f is the final maturation of aerial seed bank; l_i is the initial loss of the seed bank, due to senescence, decay, seed predation, or another factor; and l_f is the final loss of the aerial seed bank (i.e., local extirpation).

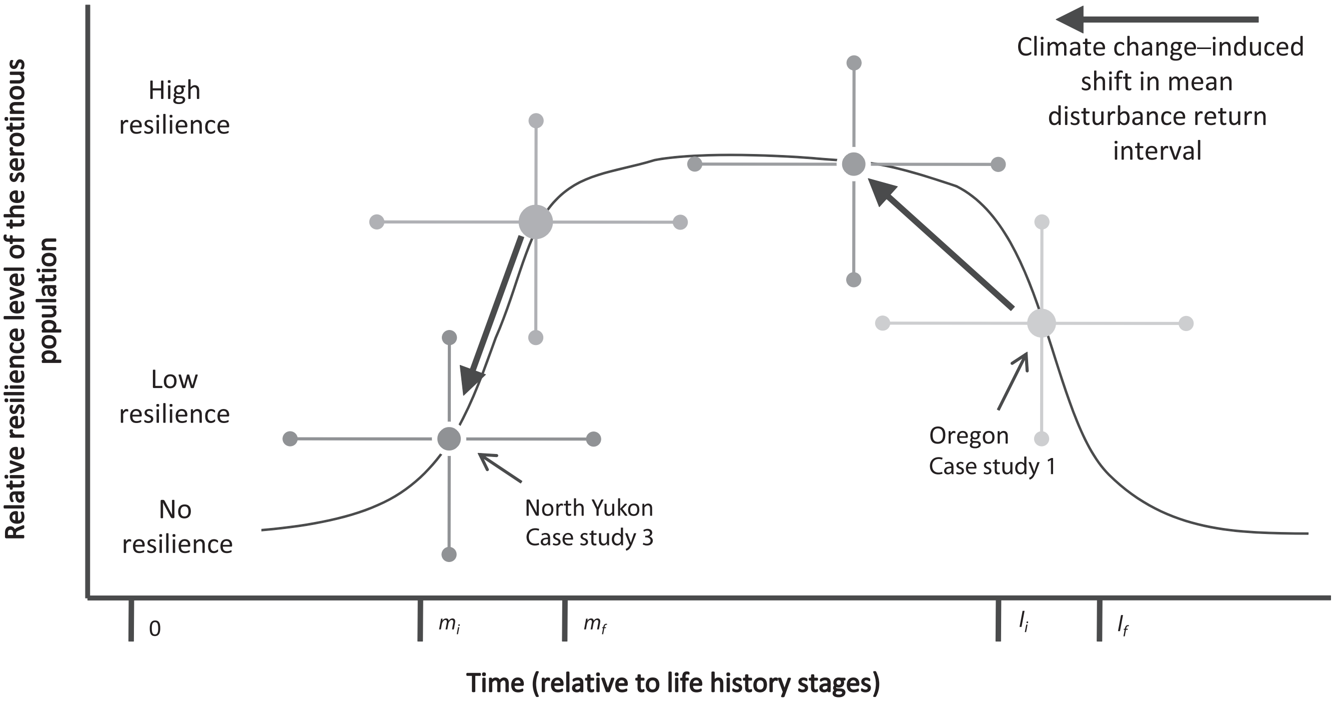

Figure 3. Shifts in expected serotinous resilience in two of the case studies presented in the text (case studies 1 and 3). Even if the mean (the points amid the crossed bars) is still within the resilient portion of the graph, the inherent variance may increase the likelihood of multiple deleterious disturbance events, such as in case study 3, whereas other systems may become more resilient with decreases in the fire return interval, as in case study 1. The need to understand changes in means and variances is apparent. On the x*-axis, zero (0) represents the immediate time postdisturbance;* m_i *is the initial maturity of serotinous seeds;* m_f *is the final maturation of aerial seed bank;* l_i *is the initial loss of seed bank, due to senescence, decay, seed predation, or another factor; and* l_f *is the final loss of the aerial seed bank.*

In addition, there are scant data exploring how quickly populations expressing varying percentages of serotiny can adapt to more frequent fires by expressing a higher proportion of serotiny at the landscape scale. Whether this level of expression can adapt as fast as the fire regime is expected to change remains an open and important question.

Shifts in disturbance return interval

Current research (e.g., Moritz et al. 2012) makes it clear that disturbance intervals will be altered as climate changes, and these increases or decreases in frequency can be incorporated into our conceptual model. Alterations to the average disturbance return interval would move the points either right or left along the expected resilience curve (figure 2). Some populations in fire-prone areas may be close to m_i (i.e., the seed bank is just beginning to mature) and may therefore be sensitive to any decrease in return interval (either natural or anthropogenic) that would shift that point to the left; this would cause a dramatic decrease in serotinous populations (figure 3). In contrast, some serotinous populations may currently be declining because of a lack of fire and the resultant competitive exclusion. These conditions are on the far right of the curve in figure 2, at which point only residual populations of serotinous species remain. Anthropogenic fire-exclusion policies may exacerbate these situations. A decrease in fire return interval (through climate change, relaxation of suppression policies, or the intentional application of fire as a management tool) would shift the points into a high-resilience portion of the curve, which would increase the population size of serotinous species (figure 3).

Shifts in variance

Increased variance in return intervals—the horizontal bars around each point in figure 2—may also alter ecosystem resilience, independent of any directional shift in return interval. A short-interval fire event (e.g., occurring before the seed bank reaches maturity in the conceptual model) that extirpates a population will leave a long-lasting legacy, even if the long-term mean disturbance return interval remains unchanged. Therefore, the minimum fire return interval, which is rarely considered in the literature, could have drastic implications for landscape resilience, functioning as a “ratchet of events” (*sensu* Jackson et al. 2009) and incrementally removing serotinous species. Therefore, increases in variance also increase the likelihood of threshold losses of serotinous species (figure 4; this figure portrays a normal distribution, which is not necessarily the

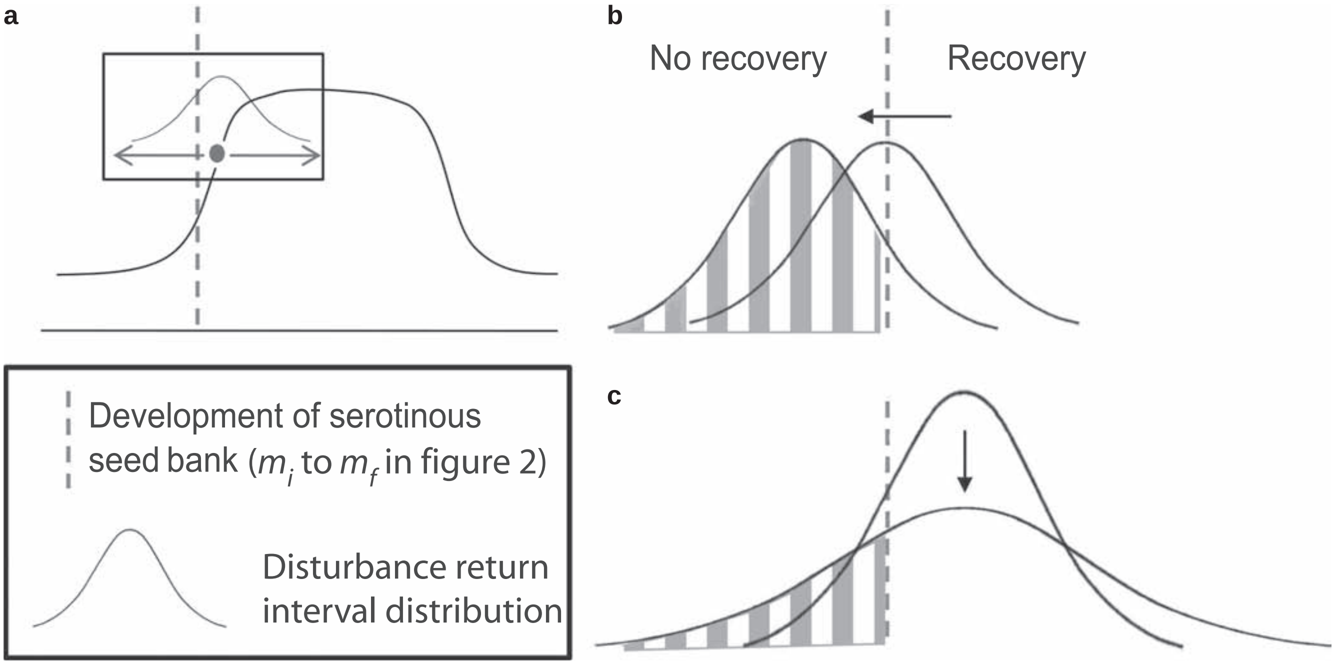

Figure 4. The impact of shifting the mean return interval and increased variance on serotinous resilience. Panel (a) is a resilience diagram similar to figure 2; the inset shows a disturbance return interval probability distribution overlaid on the variance arrows (it assumes a normal distribution); the dashed line indicates a hypothetical threshold, beyond which little resilience is expected (e.g., m_i *in figure 2). Panel (b) shows the panel (a) inset's normal distribution alongside a reduction in the return interval, which increases the likelihood of a threshold loss in serotinous species. The striped area to the left of the dashed line represents a disturbance return interval that would eliminate serotinous species, triggering potential long-lasting regime changes. Those interacting events are more likely after the shift. Panel (c) shows an increased variance without a change in the return interval, which may have an effect similar to that in panel (b).*

case; see Moritz et al. 2009 for a discussion of statistical fire frequency distributions and the difficulties inherent in defining spatially explicit return intervals). Indeed, it would take only one short-interval event to extirpate a population that had not developed a seed bank, so short-interval events are the proximate mechanism by which ecosystem changes driven by altered disturbance regimes (e.g., the mean return interval) would manifest. Altered variance in disturbances is a relatively underexplored area of ecological research (Fraterrigo and Rusak 2008) and would probably express itself at a finer spatial scale (the scale of individual events) than would fundamental changes to the disturbance return interval resulting from climate change. The probability of those short-interval events is likely to be related to the mean return interval, which is much more studied. However, changes in variance may be more important in the short term because events overlap, and high variability may exacerbate conditions brought on by shifts in mean timing.

Changes in fire extent and intensity

Changes in the spatial extent and intensity of fires may affect serotinous populations, independent of interval-mediated impacts. Increases in fire size and the proportion of high-intensity burns have been noted in recent years for some areas and are often linked to temperature and precipitation anomalies, which are expected to become the new normal under various climate change scenarios (e.g., Holden et al. 2007, Miller et al. 2009, Dillon et al. 2011). Increases in intensity and patch size can also result from compounded disturbances interactions, raising the required dispersal distance into large parts of the disturbed area (Kulakowski and Veblen 2007, Buma and Wessman 2011). Increases in fire size, without alterations in the fire return interval, would be expected to increase the relative resilience (by way of selective advantage) of serotinous species because of a decrease in the relative resilience of nonserotinous dispersers, which must reach the interior of larger burns from the edges (e.g., Donato et al. 2009a, Haire and McGarigal 2010). Assuming an adequate aerial seed bank for serotinous species, the resilience of serotinous species may be unaffected by increases in intensity or patch size (but see Johnstone et al. 2009 and Alexander and Cruz 2012 for discussions of extremely high intensities' leading to lower seed survival).

Decreases in fire intensity are also possible and may have the converse effect. For example, reestablishment of historical high-frequency–low-intensity fire regimes is often a restoration or management goal (e.g., certain areas under the National Cohesive Wildland Fire Management Strategy, *www.forestsandrangelands.gov*); in a warmer climate, higher-frequency–lower-severity fire regimes may also be maintained naturally. There is a temperature and duration threshold required to open cones, starting at a minimum of approximately 50 degrees Celsius to break the resin that holds the cones closed (Alexander and Cruz 2012). Even assuming the required temperatures, the higher-frequency fires may still remove serotinous species, as is predicted by our conceptual model. For example, the restoration of high-frequency–low-intensity fire in a ponderosa pine (*Pinus ponderosa)* forest removed lodgepole pine, because the fires were too frequent to allow the maturation of the aerial seed bank (Larson et al. 2013). This may be desirable in a restoration context; however, the local elimination of serotinous species may have implications in the context of a warming climate (see the "Future questions" section).

Case studies

We illustrate our general conceptual framework with four case studies. In some cases, increases in serotinous individuals are apparent (case study 1), but others are characterized by decreases due to frequent fire (case studies 2 and 3) or compounding disturbance events (case study 4). Each case study is plotted in figure 2. The relevant specifics, including seed bank development timing, seed size, dispersal distances, and alternate vegetation are in supplemental table S1, available online at *http://dx.doi.org/10.1525/bio.2013.63.11.5.*

Case study 1: Multiple fires promote serotinous species. In regions where fire has been actively suppressed and where that has resulted in longer fire intervals, increased fire frequency may increase the serotinous component of the ecosystem. The Klamath Mountains of coastal Oregon and California are characterized by a Mediterranean-type climate and are covered by highly diverse mixed-evergreen forests. The region has had a low- to mixed-severity fire regime with return intervals of approximately 25–100 years in most settings (Agee 1993). Knobcone pine (*Pinus attenuata*), a regional endemic, is a fire-dependent, strongly serotinous species that was historically common in high-severity burn patches, often cooccurring with chaparral vegetation. The species produces robust cone crops at a very early age (8–12 years) and lives for less than 80 years (Howard 1992). Knobcone pine has declined heavily since the onset of effective fire exclusion in the early twentieth century (e.g., the fire return interval in figure 2 artificially shifted to the right), with remnant populations persisting in scattered locales. However, a recent sequence of two large fires within 15 years, in 1987 and in 2002, has begun to reverse this trend, with substantial new regeneration of knobcone pine over large areas (Donato et al. 2009a, 2009b). Sequential fires favored the quick-maturing serotinous strategy, largely because of the rapid cone bank development for knobcone pine. Therefore, in the Klamath region, at the northern mesic limit of the species range, the serotinous strategy may be resilient under the predicted increases in fire activity and severity with changing climate. The degree to which this mechanism is advantageous (compared with competitors that rely on seed dispersal from outside the burned areas, such as Douglas fir [*Pseudotsuga menziesii*]) depends on whether future fires shift toward larger high-severity patches.

Case study 2: Multiple fires may cause species shifts. In other areas, decreased fire return interval may result in a decline or local extirpation of serotinous species. The boreal region of northern British Columbia and southern Yukon Territory, Canada, is dominated by a mix of serotinous tree species (lodgepole pine and black spruce) and nonserotinous species (white spruce [*Picea glauca*] and trembling aspen [*Populus tremuloides*]) that all display some adaptation to approximately 100-year-long fire cycles. Fires that recur after very short intervals (less than 25 years) disrupt the regeneration of the serotinous conifers and instead favor the trembling aspen, because it can regenerate from resprouting or seed after virtually any length of fire interval (Johnstone and Chapin 2006; fire in 1982, preceded by fires in 1965, 1959, and pre-1902). In these mixed deciduous and conifer systems, fuel feedbacks associated with the low flammability of deciduous fuels may be sufficient to stabilize fire cycles to a length that allows serotinous species to persist in the landscape (e.g., Johnstone et al. 2011), which would prevent the transformation to a completely deciduous-dominated or nonforested landscape.

Case study 3: Multiple fires result in a loss of forest cover. In some cases, an increased fire return interval may convert serotinous forest ecosystems entirely to nonforest, because of a lack of tree regeneration. The forests of the Eagle Plains region of the Yukon Territory, just south of the Arctic Circle, are composed of a near monoculture of black spruce, with a moss and lichen understory. Serotiny is the primary mechanism of forest resilience to fire in these northern stands. This part of the boreal forest typically has a fire return interval of 80–150 years (Viereck 1983, Larsen 1997), and postfire succession usually results in the self-replacement of black spruce stands (Johnstone et al. 2009). Those individuals that establish in the first 5–10 years after a fire are the same individuals that are burned in the next fire cycle, about 100 years later (Johnson and Fryer 1989). Therefore, these stands have typically high fire resilience and very tight age cohorts. However, repeat fires with a 15-year return interval in the Eagle Plains region were followed by a failure of black spruce to regenerate after the fires, despite the availability of high-quality seed beds (Brown and Johnstone 2012). Black spruce takes longer to reach sexual maturity in these northern forest stands than in more southerly sites, with cone production beginning after approximately 15–20 years (Burns and Honkala 1990), but more than 30 years are required for the onset of stable cone production; a lack of seed as the cause of no regeneration was experimentally confirmed in Brown and Johnstone (2012). Despite the evidence for the resilience of black spruce ecosystems to fire in this region for millennia, the short-interval fires in Eagle Plains have resulted in a grass-dominated community that shows little potential to return to a forest stand in the coming century.

Case study 4: Compound disturbances detrimentally affect serotinous species. There is evidence that compounding disturbances, such that each disturbance alters the characteristics of the following disturbance (Buma and Wessman 2011, Simard et al. 2011), also detrimentally affect serotinous species (Buma and Wessman 2012). The Colorado subalpine forest is dominated by subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and lodgepole pine, with a higher prevalence of pine at lower elevations. The fire regime is dominated by infrequent, high-severity events. Lodgepole pine exhibits variable serotiny in the region; if fire occurs before its competitive exclusion by more shade-tolerant species, regeneration can be extensive (Schoennagel et al. 2003). In the Routt National Forest of northern Colorado, a compound disturbance event (a blowdown in 1997, then a fire in 2002) nearly eliminated the serotinous lodgepole pine, probably because of the increased burn duration and temperatures resulting from the interacting disturbances, which also transferred the cone bank to the ground before the fire (Buma and Wessman 2011). In a gradient study, little postfire lodgepole pine regeneration was found, whereas the seed-dispersing species were not affected by the interaction (Buma and Wessman 2012). Similar results have been reported in multiple studies in this and other regions (Gosper et al. 2010, D'Amato et al. 2011, Fraver et al. 2011, Kulakowski et al. 2013). This illustrates another case in which the aerial seed bank had not recovered from the structural alterations caused by the initial disturbance, and a change in fire intensity (increasing as a result of the disturbance interactions) resulted in low serotinous regeneration.

Collectively, these case studies illustrate the conceptual framework presented in figure 2. Case study 1 demonstrates an ecosystem potentially shifting from a long return interval to a shorter interval, with an expected increase in the one serotinous species in the system. Case study 2 shows a way in which increases in fire frequency may cause shifts in forest type away from serotinous species to longer-dispersed deciduous species. Case study 3 exemplifies an ecosystem quite close to the limit of resilience, in which decreases in the fire return interval may severely limit tree regeneration and may result in the loss of the forest. Case study 4 shows how fires may interact with other types of disturbances to alter resilience and provides a hint of how altered disturbance rates (besides fire alone) may affect serotinous species. Many ecosystems with serotinous species are probably not on the cusp that case study 3 illustrates and will prove robust to alterations of the fire return interval. Resprouting species may also benefit. In all the case studies presented here, the seed-dispersal ability of competitors exceeds those of the serotinous species (table S1), which suggests that, if the mechanisms supporting the local resilience of serotinous species are not effective, dispersal into disturbed areas will be dominated by competitor species.

Implications of changing resilience

There are numerous changes that may be associated with increases or decreases in populations of serotinous species, especially when those species form the dominant structure of the ecosystem. Changes in serotinous species abundance have important implications at numerous scales, associated with changes in carbon stocks (Brown and Johnstone 2011, Bradford et al. 2012), wildlife habitat (Joly et al. 2012), and albedo (Jin et al. 2012), among other ecosystem functions and services. Here, we briefly discuss two implications of changing serotinous abundance for overall ecosystem resilience: the implications of local and regional control of community assembly and heterogeneity and feedbacks to future disturbances.

Local versus regional control of community assembly and landscape heterogeneity. One implication of an ecosystem dominated by serotinous individuals is the strong local control over postfire regeneration, driven by the large amount of available seed on site immediately following the fire. At the landscape scale, a diminished role of serotinous species may decrease community heterogeneity as a result of decreasing local control over regeneration. If repeated or compounding disturbances favor seed-dispersing species over more local recovery (e.g., Gosper et al. 2010, Buma and Wessman 2012), the landscape composition may shift to a more homogenized configuration dominated by long-range seed dispersers (e.g., aspen in case studies 2 and 4). Our general prediction is that in systems in which increasing disturbance frequency corresponds with decreasing resilience, the new regime will favor species adapted for colonization from off-site sources, such as long-distance-dispersing woody or weed species; increasing resilience of serotinous species will facilitate more local control over regeneration. Therefore, the relative resilience of serotinous and nonserotinous species will depend not only on life-history traits but also on the nature of future changes in disturbance regimes in a given region—altered frequency, size, and intensity. Figure 2 can be interpreted, generally, as a way to predict local and regional control over resilience, with regional control peaking on the left side of the figure. Extremely long-interval disturbance environments (e.g., old-growth forests) are more locally controlled through gap dynamics (e.g., regeneration dominated by shade-tolerant species, advanced regeneration, gap disturbances).

Landscape-scale disturbance dynamics. Disturbances and their legacy of recovery interact with future disturbances. Therefore, a central question pertains to the consequences of multiple interacting disturbances on future disturbances, mediated by species resilience. Changes in plant communities can alter the drivers of disturbance regimes, through mechanisms such as increased or decreased fuel loading, continuity, flammability, and other factors. For example, decreases in serotinous postfire recovery and concurrent increases in the proportion of less-flammable deciduous species may alter future fire behavior in Alaska. This may result in an increasingly fragmented (in terms of flammability) landscape, which will act as a negative feedback to subsequent fire activity (Johnstone et al. 2011). Conversely, the replacement of less-flammable species by more-flammable species may interact with climate warming, increasing disturbance frequency. This phenomenon is well documented with grass invasions and could influence areas in which a failure of serotinous regeneration opens the canopy and allows for large amounts of graminoid or herbaceous biomass to accumulate (Brooks et al. 2004). At the northern margins of the boreal forest, where tree species richness is low, a failure of serotinous regeneration could result in a shift to a tundra community. Arctic tundra has historically been less flammable than adjacent conifer stands, exhibiting smaller and less frequent fires (Wein 1976). Although tundra fires are now occurring at an unprecedented scale, particularly in the northwest subarctic (Hu et al. 2010), differences in fuel loading and the probability of lightning ignitions (Dissing and Verbyla 2003) are likely to maintain a reduced fire frequency in tundra relative to conifer forests. Therefore, changes in the abundance of serotinous species can influence the larger-scale resilience of ecosystems to changes in climate and fire by altering the feedbacks that shape future disturbance activity.

Future questions

Changes in the relative resilience of serotinous species have implications for a variety of landscapes and scales, as do potential feedbacks among disturbances, postdisturbance regeneration, and climate. Questions surrounding these points have implications for natural and managed landscapes. For example, management strategies aimed at restoring frequent, low-severity fire regimes (for many reasons, such as increasing latent resilience; Larson et al. 2013) may be ecologically appropriate if we refer to historical fire regimes (including size, intensity, and variability), but there is some doubt that historical reference conditions are useful in the context of global change (Harris et al. 2006). Therefore, the implications for future landscape resilience under predicted fire regimes should be considered. If serotinous species are eliminated by the high-frequency–low-severity regime (as in Larson et al. 2013), the eventual increases of fire severity or intensity due to climate change may result in more dramatic landscape change because of limited tree resilience.

We highlight the following as especially promising areas of research:

Landscape heterogeneity. Will increases or decreases in serotinous resilience alter landscape structure at large scales? Will landscapes homogenize as disturbance return intervals favor or disfavor serotinous species, or will they become more heterogeneous because of alterations to local composition due to seed-dispersal differences, disturbance characteristics, or feedback loops?

Interactions with other disturbances. Where are structural interactions and compounding disturbances more or less likely? What other disturbances (e.g., wind, insects) will cause changes to the return interval, severity, or variability, and will those areas overlap with the expected changes to the fire regime?

Adaptation and recovery. In a species that is not 100% serotinous, how quickly will the degree of serotiny change from the population to regional scale? Will changes in precipitation and temperature alter the regeneration ability of those species (assuming adequate seed)? How will other fire-dependent species (e.g., resprouting, serotinous *Banksia*) respond to future compound disturbance events?

Residual populations. Where are small serotinous populations (such as those presented in case study 1) likely to increase in importance with changes in the local fire regime? In the context of a changing climate, these remnant populations may provide an unexpected functional role (Eriksson 2000): continuity in ecosystem services and habitats associated with forest cover. How common are these residual populations, and can they maintain those services?

Human action. Will restoration of frequent, low-intensity fire regimes (which may eliminate serotinous species) result in a landscape resilient to future fire conditions? What role should management seek in planning for different future fire regimes through species-level policy (e.g., maintenance of serotinous and nonserotinous species)?

Conclusions

Resilience is typically defined as the capacity of a system to recover from a disturbance (Holling 1973, *www.resalliance.org*); our conceptual model emphasizes that the resilience of forest communities adapted to disturbances must be viewed over multiple disturbance events, in the context of life-history traits and relative to potential changes in disturbance frequency, size, and severity. Serotiny, as a fire-adapted resilience mechanism, may be a help or hindrance to fire resilience if the changes in fire return intervals resulting from climate change are large or rapid. A decreased fire return interval, if it is extreme and persistent enough, can eliminate serotinous species and favor invader species that disperse from the forest edges; increased intervals might eliminate serotinous species through senescence and successional processes. Moderate increases in frequency, in areas in which serotinous populations are not near tipping points (figure 1), should result in increases in serotinous populations. In contrast, an increased size of severe fires or an increased extent of severely burned patches within fires could eliminate seed sources for invader species and effectively favor serotiny (and other resilience strategies, such as resprouting) over large areas of burn interiors, assuming no concurrent change in resilience as a result of an altered return interval. Extremely high- or extremely low-intensity fires may also have negative effects. Interactions with other disturbances are more likely if the frequency and scale of fires increase. Where both changes occur, more frequent and larger fires could eliminate most tree species, save endurers that resprout on site, or could eliminate forest cover altogether.

It will be important to address potential changes in resilience at several scales to determine local and regional policies regarding fire suppression or fire promotion, post-fire replanting, and ecosystem service goals (e.g., carbon sequestration), as well as to assess impacts on larger-scale carbon budgets, climate feedbacks, and disturbance modeling. Areas that are currently suitable for serotinous species may not be viable by the end of the century because of altered disturbance regimes (Westerling et al. 2011). The conceptual model presented here should prove useful in identifying areas where the resilience of serotinous populations may be enhanced or threatened as a result of changes in disturbance regimes or management strategies, such as restoring high-frequency–low-severity burning. Threshold-type changes mediated by disturbances will occur quickly and probably without warning. Indeed, it appears that a few fire-conducive years could be enough to extirpate serotinous species from the landscape through repeated burning (e.g., case study 3), with major implications wherever those species are foundational to the ecosystem. As a resilience mechanism, serotiny is a key ecosystem attribute that will have large impacts on population, community, and ecosystem responses to future changes in disturbance regimes. Given the wide range of ecosystems dominated by serotinous species, their large influence on the ecosystems of which they are a part, and the expected changes in disturbance return intervals, these dynamics are a pressing issue in need of further research to inform modeling, management, and ecological knowledge.

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