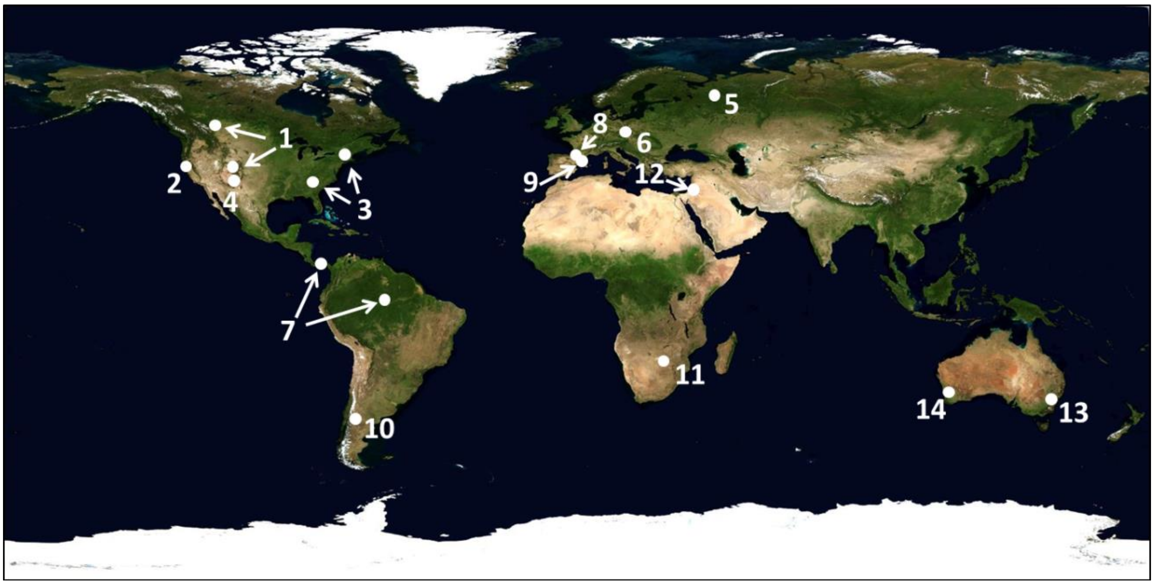
Ecosystem Dynamics and Management After Forest Die-off: A Global Synthesis with Conceptual State-and-Transition Models

Appendix S1. Consolidated case studies of global forest mortality events

Contents

Mortality Case Studies

Distribution of Case studies



Legend

Case study description	Case study Number	Transition Type	Species effected
Sudden Aspen Decline	1	Single	*Populus tremuloides* Michx.
Sudden Oak Death	2	Single	*Notholithocarpus densiflorus, Quercus agrifolia*
Hemlock woolly adelgid	3	Single	*Tsuga canadensis*
Ponderosa-Piñon-Juniper mortality	4	Cascade	*Pinus ponderosa, P. edulis, Juniperus monosperma*
Boreal spruce mortality	5	Cascade	*Picea abies* L. Karst.
Norway spruce beetle outbreaks	6	Cascade	*Picea abies* L. Karst.
Tropical forest fragmentation	7	Cascade	26 tree species impacted
Mediterranean Scots pine mortality	8	Complex	*Pinus sylvestris* L.
Holm-oak mortality	9	Complex	*Quercus ilex* L.
Northern Patagonian	10	Complex	*Nothofagus dombeyi*
African savanna woodlands	11	Complex	*Colophospermum mopane*
Yatir forest,	12	Complex	*Pinus halepensis* Mill.
Australian eucalyptus forests	13	Complex	*Eucalyptus maculata*
Eucalyptus marginata die-off	14	Complex	*Eucalyptus marginata, Corymbia calophylla*

Figure S1. Case studies of climate driven and climate-influenced regional mortality events. The legend lists individual case studies, the number corresponding to the points on the map, the ecosystem transition type, and with the dominant species impacted.

Mortality Case Studies

Single state transition shifts

1. Drought-induced aspen mortality – Bill L. Anderegg and Simon M. Landhäusser

Trembling aspen (*Populus tremuloides* Michx.) is the most widely distributed tree species in North America. Since the early 2000s, rapid decline and stem mortality has been observed in the western United States (Worrall et al., 2013) and the aspen parklands of Canada (Michaelian et al., 2011 - Figure S2). Identifying the factor(s) that drive aspen forest decline is difficult due to a multitude of inciting and predisposing stress variables including their interactions (Frey et al., 2004). However, several lines of evidence suggest that in both regions these elevated rates of stem mortality are likely due to “climate change-type” droughts – droughts accompanied by high temperatures (Anderegg et al., 2013, 2012b; Rehfeldt et al., 2009; Worrall et al., 2008; Michaelian et al., 2011). Drought damages the hydraulic system of aspen through embolism and precipitates gradual mortality over several years (Anderegg et al., 2014, 2012b) which can in turn adversely affect the viability of the clonal root system (Galvez et al. 2013; Landhäusser and Lieffers, 2012). In the U.S. a suite of six secondary biotic agents – several boring insects and one fungal pathogen – are found in dying stems and, while not the primary cause of mortality, likely exacerbate and accelerate dying stems (Marchetti et al., 2011; Worrall et al., 2008). In Canada, drought and defoliation from the tent caterpillar both impact aspen health and can compound to cause mortality (Hogg et al., 2008; Landhäusser and Lieffers, 2012).

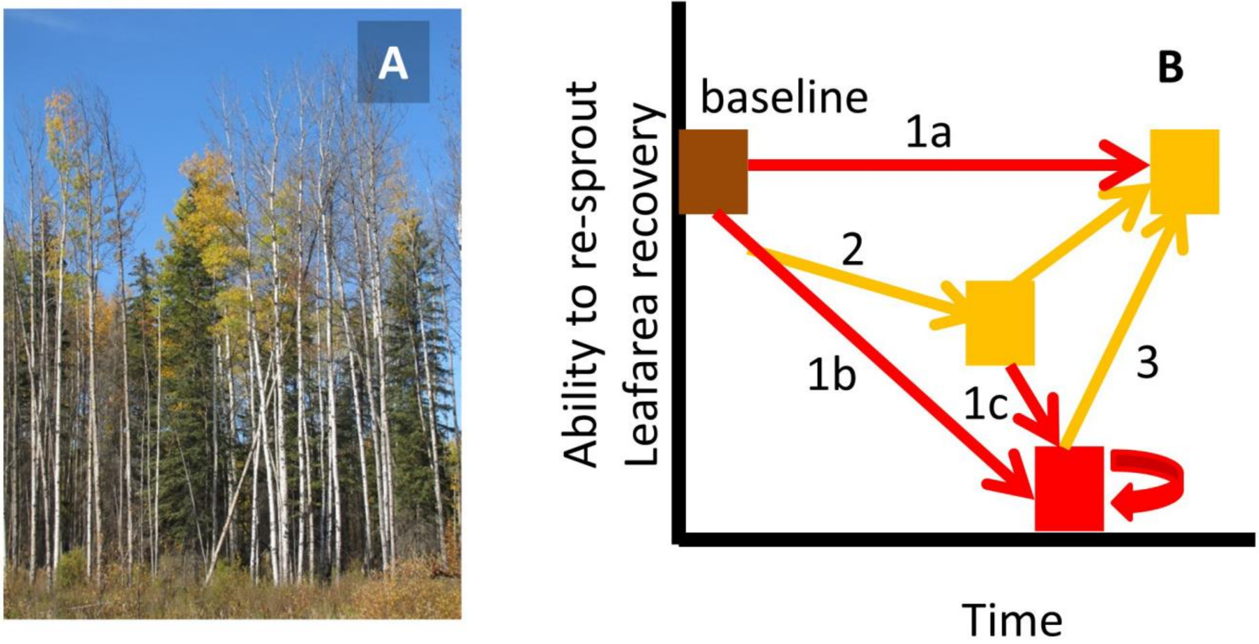


Figure S2. Aspen mortality. Inciting and predisposing factors that reduce leaf area through mortality, can degrade aspen root systems and with that its ability to re-sprout. If the disturbance is sudden (B.1a), re-sprouting of aspen can be still vigorous. If the stress has been chronic it will reduce the ability of the root system to sucker (B.1b). Early intervention after mortality can slow or prevent this loss this loss of function (B.2). If, however, factors such as herbivory reduce leaf area in the recovery stage, further mortality can occur (B.1c). Current restoration experiments focus on reforestation with planted aspen seedlings (B.3).

An important aspect of the dieback process in aspen forests is that stems are often ramets which are interconnected by a common root system. While stem mortality may not result in mortality of the individual aspen clone and its root system (DesRochers and Lieffers, 2001a), it will certainly influence ecosystem functioning and ecosystem services such as carbon sequestration. These mortality events have led to substantial decreases in carbon storage of aboveground biomass in the southern Rockies (Huang and Anderegg, 2012) and in the Canadian parklands (Michaelian et al., 2011). Mortality can alter the biophysical properties of these forests, such as surface albedo (Huang and Anderegg, 2014) and edaphic processes such as soil nutrient cycling and the associated microbial activity (Prescott, 2010). Further, changes in understory species abundances and losses in understory plant biodiversity have been observed in aspen forests following above ground mortality (Mundell et al. 2007; Anderegg et al., 2012a). In Colorado aspen forests, root mortality has been documented as extensive and regeneration rates in dying stands have been observed to be exceptionally low, likely below stand replacement levels (Worrall et al., 2010). Concomitant increases in shrub biomass are observed in these sites and more shrubs are associated with lower regeneration rates (Mundell et al. 2007; Anderegg et al., 2012a) while conifer encroachment has also been observed in many of these sites (Man and Rice 2010; Rogers et al.2014). Furthermore, ungulate browsing and grazing by cattle appear to damage and kill aspen suckers while in managed and merchantable aspen forests mechanical damage to the root system, grass encroachment, and thick slash deposits can inhibit aspen regeneration (Landhäusser and Lieffers 1998; Fraser et al., 2004; Renkema et al. 2009).

Aspen is unique in its ability to rapidly recover through sprouting from its root system. This provides several opportunities for management options to encourage aspen regrowth at sites experiencing mortality. A critical element of aspen recovery potential is the extent and health of the clonal root network (Frey et al. 2003). Suppression of suckering can result in significant root system loss in short periods of time (Desrochers and Lieffers 2001b). This fact indicates that management options must occur relatively quickly while the root network is still healthy in order to have a reasonable chance at success (Shepperd et al. 2013). Furthermore, the recovering leaf area is crucial to the maintenance of the existing root system (Landhäusser and Lieffers 2002). Treatments that reduce shrub and grass cover and prevent herbivory will likely benefit the regeneration and recovery of aspen on these sites (Fraser et al. 2003; MacIsaac et al. 2006). Furthermore, regenerating juvenile stands could also provide more resistance to future drought events by having improved root to leaf ratios. Indeed, stands with smaller stems and less evaporative load on their leaves seemed to better survive the severe droughts of the early 2000s (Worrall et al., 2010). Restoration of aspen through planting in areas where it disappeared from the landscape is another management option. While this management option is still considered rare south of the US-Canada border, aspen seedling planting has become a common practice of forest restoration surface mined areas in the Canadian boreal region (Macdonald et al. 2012).

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Mortality Case Studies

2. Sudden oak death: climate effects on disease outbreak – Richard C. Cobb

Mortality events can be driven by factors other than drought, but which can be modified by drought in ways that can either increase or decrease the severity of impacts. Sudden oak death is a forest disease caused by the invasive pathogen *Phytophthora ramorum*, an invasive pathogen of unknown origin which has been responsible for landscape-scale tree mortality (Figure S3). Pathogen invasion is the inciting factor of these mortality events and while invasion is influenced by climate interactions, the resulting mortality occurs regardless within 2-5 years of infection (Davis et al., 2010; Cobb et al. 2012; Eyre et al., 2014). Inter annual variation in precipitation strongly influences variation in pathogen sporulation, and as a result, the spread of new infections within the landscape (Davidson et al., 2008; Filipe et al., 2012). Thus years with low precipitation levels or environments with temperature and humidity regimes nonconductive to pathogen survival have lower rates of spread and lower pathogen survival *in planta* (Davidson et al., 2008). Despite these negative climate effects on the disease, pathogen populations recover quickly following drought (Eyre et al., 2014).

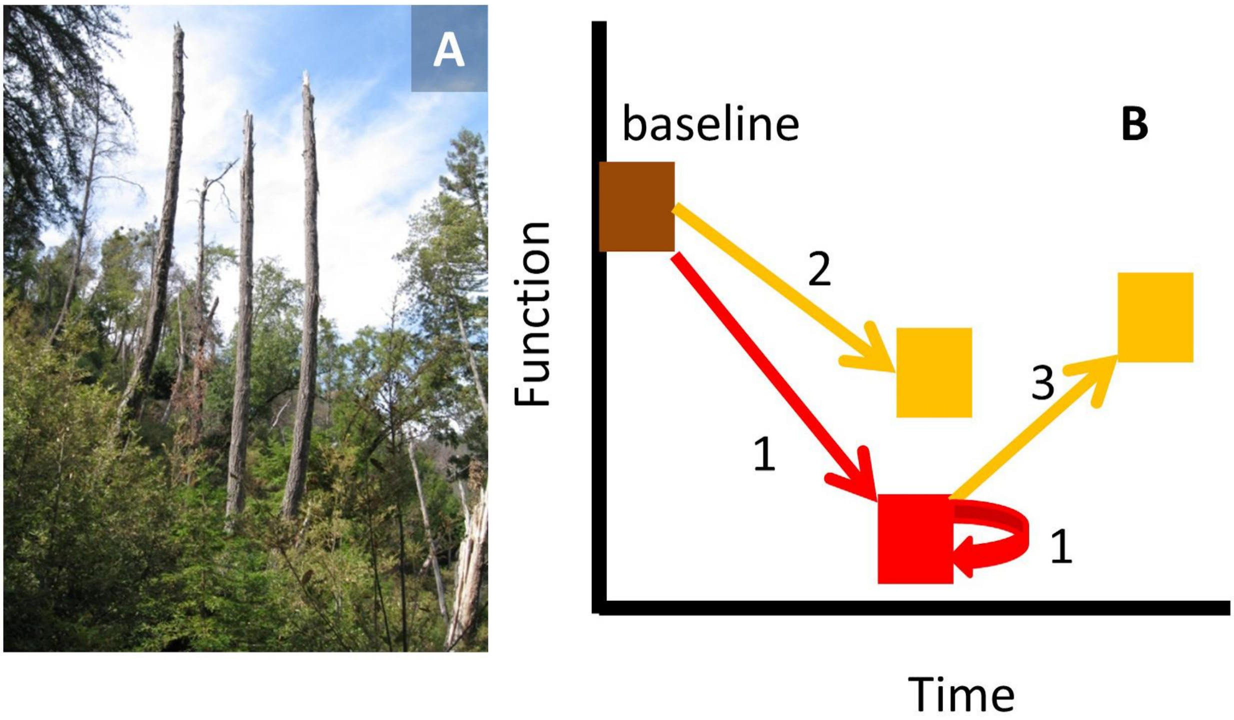

Figure S3. Sudden oak death in California forests. Disease degrades ecosystem functions including carbon sequestration and cultural resources (A, B.1). Resprouting maintains the pathogen which in turn restricts affected species (tanoak, live oaks) from reestablishing in the overstory canopy. Early intervention can slow this loss of function, but cannot prevent it (B.2). Current restoration experiments focus on reforestation with species immune to pathogen infection (B.3).

Sudden oak death causes mortality, changes forest composition, and reduces forest biomass at landscape scales (Meentemeyer et al., 2008; Metz et al., 2012). The accompanying accumulation of fuels has been show to increase wildfire severity and increase mortality of trees such as redwood which are otherwise non-susceptible to the disease and would survive a fire typical of the region (Metz et al., 2013, 2011). At stand scales, mortality alters a suite of functional processes controlling carbon and nitrogen cycling (Cobb et al., 2013a). Of great concern, the selective removal of tanoak (*Notholithocarpus densiflorus*), the species most severely impacted by the disease, threatens an important set of cultural and biological resources (Bowcutt, 2013).

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Management of sudden oak death has been variable and ineffective where eradication is the primary goal. Landscape scale interventions are unlikely to be successful (Filipe et al., 2012) despite the large required investment of management resources. More recently, management focus has shifted to protection of individual resources (stands or trees) and restoration of ecosystem function in impacted forests (Cobb et al., 2013b). For example, California Indian tribes have invested management resources into surveys of variation in susceptibility among tribal tanoak resources in advance of pathogen invasion. In highly impacted areas, organizations such as the Marin Municipal Water District (MMWD) are experimenting with techniques for restoration of overstory forest cover aimed at increasing carbon sequestration and ensuring the provisioning of water. These efforts may be aided by California state laws which mandate caps on greenhouse gas emissions and adopt carbon sequestration and sales as legitimate functions of the state's forest lands (see California state laws AB32 & AB1504). In the case of sudden oak death, and many other invasive pathogens, understanding how to maintain or restore threatened resources and ecosystem functions is a more judicious use of management resources given widespread invasion of the pathogen.

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Mortality Case Studies

3. Hemlock woolly Adelgid: drought worsens the impacts of an exotic insect – Richard C. Cobb

Exotic insects can be primary or contributing factors driving forest mortality. Insect physiology is highly influenced by ambient temperature and drought-associated plant stress can also increase the likelihood of mortality during insect outbreak implying that a combination of damaging biological agents with global-change associated stresses is a potent driver of forest mortality. This intersection of events has occurred during the region-scale outbreak of Hemlock woolly Adelgid (*Adelges tsugae*) - a damaging exotic insect - with drought to result in severe and widespread mortality of eastern hemlock (*Tsuga canadensis*). Hemlock woolly Adelgid is native to Japan, China, and the Indian subcontinent but was introduced into the native range of eastern hemlock circa 1950 and has since spread to the most southern extent of the insect's host distribution as well as north to Vermont and New Hampshire, USA (Fitzpatrick et al., 2011; Nuckolls et al., 2009; Orwig and Foster, 1998). Much of this mortality has occurred regardless of climate variability including drought, likely due to the lack of coevolutionary feedbacks which limit mortality in other insect outbreaks (c.f. Elderd et al., 2013; Régnière and Nealis, 2007). However, patterns of hemlock heath decline and mortality are constant with injection of toxic saliva and disruption of xylem function, an impact common among adelgids although never conclusively shown for *A. tsuage* (McClure, 1991). Despite an initially promising campaign to introduce natural enemies (McClure and Cheah, 1999), distribution of *A. tsuage* and associated hemlock mortality is limited by climate drivers, especially minimum winter temperature (Fitzpatrick et al., 2011).

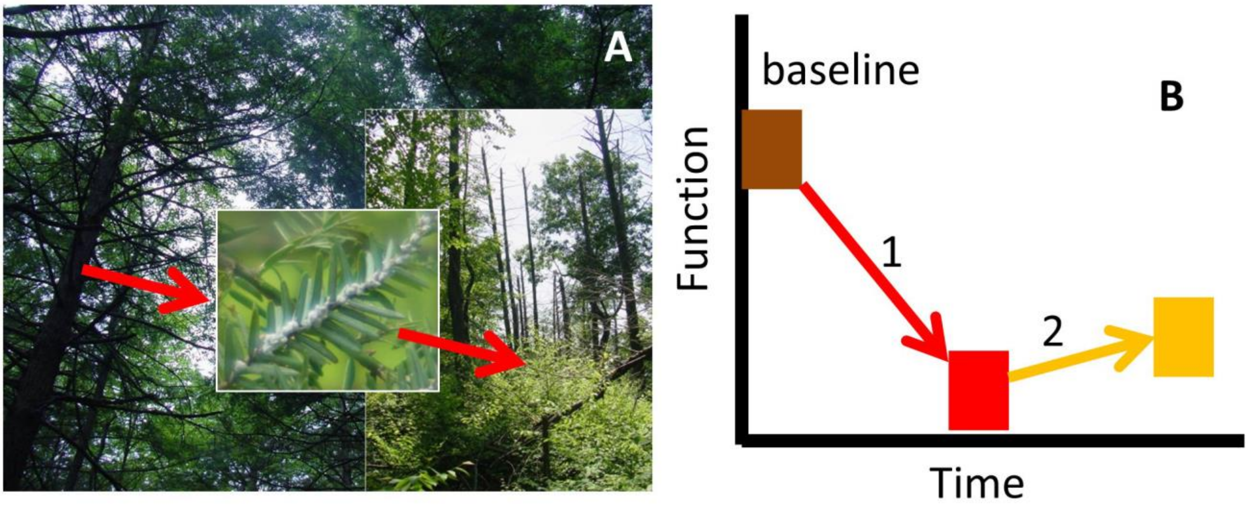

Figure S4. Hemlock woolly adelgid (*Adelges tsugae* - HWA) impacts to eastern hemlock forests. HWA, an invasive insect, causes rapid and spatially extensive mortality of eastern hemlock (*Tsuga canadensis*) throughout the tree's native range. Drought can accelerate tree mortality while mild winter temperatures increase insect survival, also increasing tree mortality (1). Dominance of shade intolerant hardwood species in impacted stands creates a long-term transformation of forest composition, structure, and function (2).

Eastern hemlock is an important source of biodiversity and stand heterogeneity at landscape and regional scales (Orwig et al., 2002). High shaped tolerance creates dense, mono-specific stands with low rates of nutrient cycling and substantial accumulations of soil organic matter (Orwig et al., 2008). Insect-caused mortality creates a series of related changes to ecosystem structure and function. Loss of canopy cover increases soil temperature and moisture, increases nutrient availability, and slows decomposition and litterfall rates (Cobb, 2010; Orwig et al., 2013). Although the host range of *A. tsuage* is limited to the two native *Tsuga* species in eastern north America, extensive mortality and greatly reduced regeneration at broad spatial scales indicate the unique ecological characteristics of hemlock will be lost from most of this area (Orwig et al., 2002; Preisser et al., 2011). The lack of effective natural enemies and biocontrol of this damaging insect indicates that restoration ecology approaches may be more useful for mitigation of damage caused by the insect. Furthermore, climate change associated increases in winter temperatures are likely to accelerate *A. tsuage* invasion into habitat which is currently protected by climatic characteristics. Identifying suitable replacement species and stand conditions that increase hemlock resilience in the face of invasion is needed to maintain the ecological conditions and biodiversity represented by this species. The unique characteristics of eastern hemlock are increasingly threatened by higher minimum winter temperatures and drought frequency in the region.

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Mortality Case Studies

Ecological Cascades

4. Successive multi-species pulses of tree establishment and mortality during 150 years of land use change and climate variability in northern New Mexico, USA – Henry Adams and David D. Breshears

Lower-elevation northern New Mexico forests and woodlands began to transition along a disturbance-related cascade of ecosystem changes following Anglo-American settlement of the southwest US in the mid-1800s (Allen 1989; Figure S5). Pre-1900 ponderosa pine (*Pinus ponderosa*) forests typically were characterized by low tree densities with highly productive grass understories (Allen et al. 2002). This forest structure was the result of frequent low-severity surface fires (stand-level composite mean fire intervals of around 5-20 years (Touchan et al. 1996) that burned the understories without killing the thick-barked mature ponderosa pine. Widespread, intense livestock grazing in the late 1800s graded into a policy of suppressing all fires by 1910, resulting in the establishment of dense young understories of fire-sensitive piñon (*Pinus edulis*) and juniper (*Juniperus monosperma*) trees amidst low-elevation stands of ponderosa pine (Allen 1989, Allen and Breshears 1998). Drought, accompanied by bark beetle outbreaks (*Dendroctonus* and *Ips*

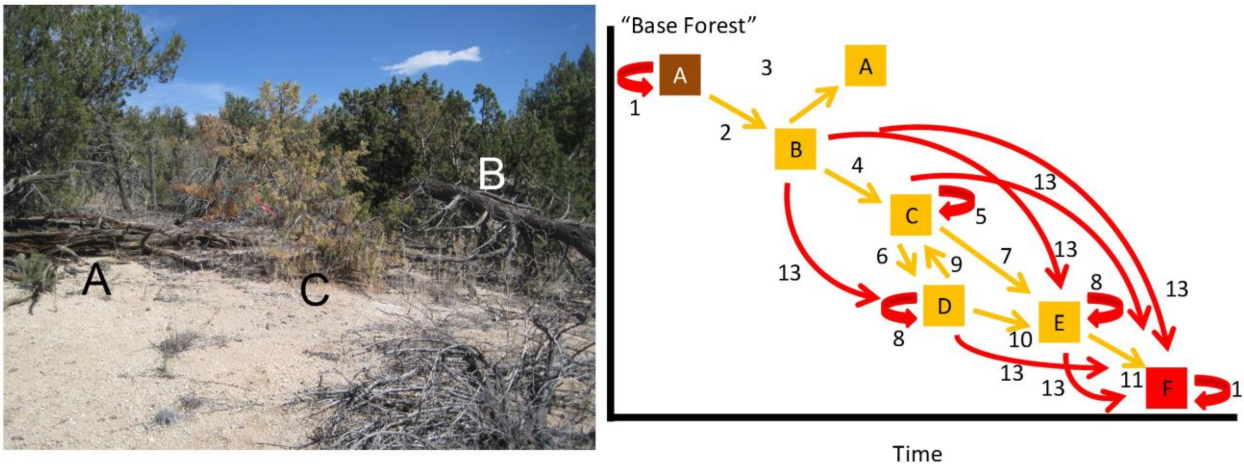

Figure S5. Three generations of tree mortality at Bandelier National Monument in northern New Mexico (left). Found near each other are ponderosa pine that died in the 1950s (A), piñon pine that died in the early 2000s (B), and recently dead juniper in 2012 (C). This site experienced a complete loss of ponderosa and piñon pine in past decades, and was recently seeing some juniper mortality (Photo: H Adams). Climate- and disturbance-related cascade of forest change in northern New Mexico (Right). Open, low density, mature ponderosa pine forest with a native grass understory (A) persisted prior to Euro-American settlement due to high-frequency, low-severity ground fires (1). With fire suppression management policies (2), a dense understory of pinon pine and juniper grew below the ponderosa pine canopy and in openings (B). This forest can be restored to A with management by thinning and removal of the pinon and juniper understory (3). Episodic drought and bark beetle outbreak causes mortality of overstory ponderosa pine (4), leaving a pinon-juniper woodland (C). With periodic low mortality followed by recruitment of piñon and juniper this ecosystem can persist (5). Further drought and bark beetle outbreak in combination with increasing temperatures cause moderate (6) or high (7) levels of mortality in piñon pine, a transition to either a less-dense, pinon-juniper savanna (D), or juniper-dominated savanna with few surviving pinon pine (E). These savanna ecosystems can persist with periodic mortality followed by recruitment, often below the canopy of mature (nurse) trees (8). Periods of high moisture availability favorable to increased seedling establishment, recruitment, and infilling of piñon pine and juniper can return D to C (9).

species) in the 1950s caused the mortality of most overstory ponderosa trees across the lower-elevation distribution of ponderosa pine, and of many old piñon trees on dry sites at low elevations (Allen 1989; Allen and Breshears 1998). Notably, juniper are not attacked by the separate bark beetle pests of either ponderosa pine of piñon (Negrón et al. 2003, Shaw et al. 2005, Negrón et al. 2009). Ponderosa pine die-off resulted in transition to a piñon-juniper woodland in what were once low-elevation ponderosa-dominated forests (Allen and Breshears 1998). A mostly wet period in the Southwest from the late 1970s to the mid-1990s fostered further recruitment and infilling of piñon-juniper woodlands (Clifford et al. 2013).

Table S1. A key to ecosystem types in the northern New Mexico forest change case study presented in Figure S5.

Code	Ecosystem
A	Open, low-density, ponderosa pine forest, with grass understory ("base" forest)
B	Ponderosa pine overstory with dense piñon pine and juniper understory
C	Piñon-juniper woodland
D	Piñon-juniper savanna
E	Juniper savanna
F	Re-sprouted oak shrubland and annual plants

In response to severe drought starting in the late 1990s, and in particular with the 2000-2003 drought that occurred during a period of elevated temperatures and was accompanied by an outbreak of the piñon Ips beetle (*Ips confusus*), varying degrees of piñon die-off affected 1.2 M hectares across the Southwest (Breshears et al. 2005, Shaw et al. 2005). Instead of effecting only the lower elevation, drier portions of the range of piñon, analogous to the 1950s drought mortality effects on both piñon and ponderosa pine (Allen 1989; Allen and Breshears 1998), mortality of piñon following the 2000-2003 drought was well-spread across elevations, including the high-distribution woodlands that had come to dominate former low ponderosa forests after the 1950s (Kleinman et al. 2012). Both experimental (Adams et al. 2009) and tree-ring research (Williams et al. 2013) has shown that elevated temperatures during 2000-2003 increased drought stress and resulted in more rapid mortality. The currently documented effects of tree density on the degree of early 2000s piñon mortality have been inconsistent around the region (Meddens et al. 2015), suggesting that thinning Southwest piñon woodlands may be ineffective for lowering mortality risk during the occurrence of a major piñon Ips beetle outbreak. The result of this pulse of drought-induced piñon mortality was a shift from relatively dense woodland to a lower canopy-cover savanna, ranging from reduced piñon-pine dominance to complete loss of mature piñon leaving only the co-occurring juniper (Breshears et al. 2005). Notably, subsequent reproduction and seedling establishment have been limited in Southwest piñon-juniper woodlands, and most observed seedlings are pre-drought advanced regeneration (Redmond et al. 2012, Redmond and Barger 2013, Allen - unpublished data).

Elevated temperatures and high variability in precipitation have continued into the 21st century, and following severe drought in 2011-2013, substantial juniper canopy dieback and whole-tree mortality were observed in northern New Mexico, including at multiple sites previously subject to piñon mortality in the early 2000s and ponderosa loss in the 1950s (H. Adams and C.D. Allen, *personal observation*, Figure S5). Morphological patterns of widespread juniper foliage dieback without apparent insect involvement implicate physiological drought stress as the primary driver, with limited evidence for a significant role of juniper borer beetles in some of the recent mortality (Norlander 2014). With projected future warming and increasingly severe episodes of drought stress (Williams et al. 2013), future juniper mortality might be expected to incrementally intensify and expand across the landscape in a manner similar to previous die-offs of ponderosa and piñon, likely resulting in further shifts toward an ecosystem dominated by increasingly drought-resistant, relatively sparse, low-statured, re-sprouting, angiosperm shrubs (e.g., *Quercus undulata, Cercocarpus montanus*, *Phalllugia paradoxa*) and diverse herbaceous plants, with more abundant bare ground. Such drought-adapted plants are fairly resistant and/or resilient to disturbance from drought and fire, and can re-sprout and grow during intermittent periods of moisture availability (Savage et al. 2013). Fire activity also has been increasing in these forests and woodlands in conjunction with more severe drought and temperature stresses (Williams et al. 2013, Allen 2106). Fire has the potential to rapidly accelerate these ecosystem transitions, and recent severe fires can convert these ecosystems from forest or woodland directly to shrublands and grasslands (Savage et al. 2013, Allen 2016), reflecting loss of ecosystem resilience and ecological legacies (memory) due to changing disturbance regimes (Johnstone et al. 2016).

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5. Boreal spruce forests in Northwest Russia:harvest, drought, and bark beetles – Tuomas Aakala

Norway spruce (*Picea abies* L. Karst.) forests cover large tracts of the European boreal forest across Fennoscandia and European Russia. On mineral soils, they commonly dominate mesic sites for which water shortage is rarely considered problematic. Accordingly, only a few studies have reported drought-related mortality (Aronsson et al. 1978).

In the Dvinsky forest in the Arkhangelsk province of NW Russia, the forests were reported to suffer from extensive tree mortality in the early 2000s (Nevolin et al. 2005). Forestry is important for the local economy and as bark beetle galleries were abundant in the dead trees and as earlier instances of increased mortality rates were associated with bark beetles (Nevolin et al. 2005), the event prompted salvage-loggings to reduce further damage. Problematically, the forest massif is also listed as one of the largest tracts of intact forests in Europe, with high conservation values (Yaroshenko et al. 2002).

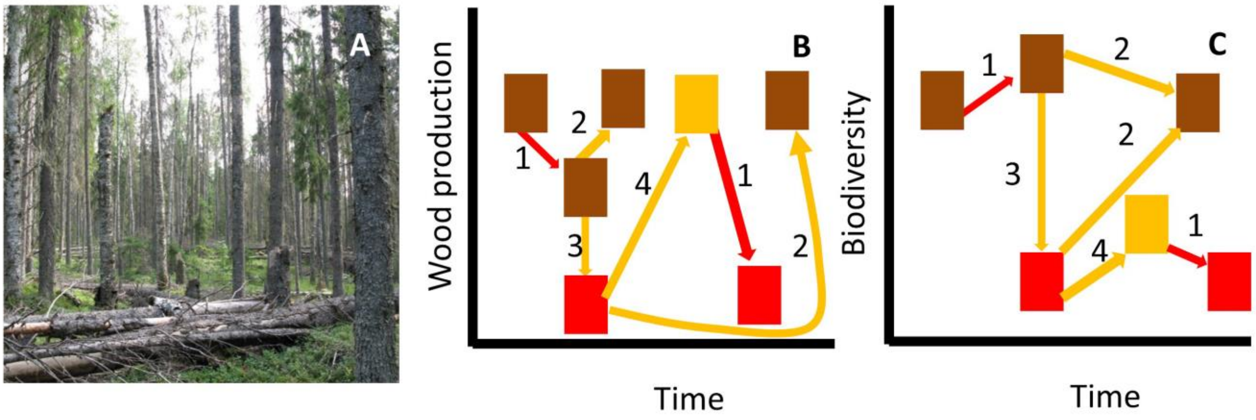

Figure S6. Patchy drought/bark beetle mortality in the Dvinsky forest, Arkhangelsk province, NW Russia (A). Patchy mortality (B-C1, red arrow) disrupts some ecosystem functions, such as wood production (B), but may promote others, such as biodiversity (C). If left uninterrupted, composition and structures are retained and functions restored to baseline after a period of recovery (B2-C2). Current management intervention is salvage logging by clear-cutting (B3-C3). If the clear-cuts are left to regenerate naturally (B2-C2), the result can be expected to follow a natural course of succession, and the forest would return to the ‘initial’ state (at centennial time-scales). If the clear-cut is followed by artificial regeneration (B4-C4) as is done in some parts of the area, spruce dominance and wood production is restored faster, but the resulting forest is otherwise structurally different from the initial state. If damage from disturbances depends on characteristics of the trees (as is the case for host-specific biotic agents such as bark beetles), such even-aged and even-sized stand can be problematic in the future, as all trees in the stands share similar vulnerability to disturbances (B1-C1).

Retrospective studies combining field observations with tree ring data showed that although the event had resulted in considerable and widespread mortality (Kuuluvainen et al. 2014, Khakimulina et al. 2015), mortality was elevated for approximately five years, and had since returned to pre-episode levels (Aakala et al. 2011). Consistent with earlier reports (Nevolin et al. 2005, Ogibin and Demidova 2009), most of the dead trees were influenced by the spruce bark beetle (*Ips typographus*). However, based on spruce radial growth-climate relationships (Aakala and Kuuluvainen 2011), and the occurrence of exceptionally dry years from 1999 to 2001, Aakala et al. (2011) suggested that these episodes may be triggered by drought, and exacerbated by the bark beetles. Along these lines, Khakimulina et al. (2015) found drier sites being more damaged compared to wetter sites. Earlier, widespread partial disturbances were detected in growth-release analysis and tree age-structures (Aakala et al. 2011), but the detailed analysis of past disturbances by Khakimulina et al. (2015) suggested that the recent disturbance episode may have been the most severe at least in the past 200 years.

How the forests develop in the future is partially dependent on the management solution (Figure S6). The solution advocated by conservationists is to leave the forest untouched. Based on the longer-term disturbance histories and age structures, spruce mostly retains its dominance following these partial disturbances (Aakala et al. 2011, Khakimulina et al. 2015). In the current conditions the species composition and uneven-age structure would be retained. The second strategy, salvage logging by clear-cutting leads to a birch-dominated forest that is gradually replaced by spruce over the course of succession. The third strategy aims in restoring the conifer production faster, by planting the clear cut areas with spruce. However, extensive areas of pure spruce forest can be problematic in future droughts, because in even-aged monocultures most of the trees share a similar vulnerability to disturbances. Although data is lacking, local forestry reports suggest that plantations at parts of the massif may have already suffered greater mortality in the most recent episode (Nevolin et al. 2005). Khakimulina et al. (2015) also postulate that drought stress may be enhanced in the edges of clear cut forest (Kautz et al. 2013).

Based on reconstructions of stand disturbance history, these forests are likely to retain their cover and species composition. However, in a scenario where droughts become more severe and/or frequent, sensible management strategies for retaining ecosystem services (especially wood production) are particularly difficult in the European boreal forest. This is because the number of native species suitable for a certain site is limited. Hence, biotic disturbance agents that are often host-specific (such as the spruce bark beetle) may exacerbate drought-triggered mortality. Promoting heterogeneity in stand- and landscape structure might reduce larger-scale vulnerability to disturbances, and to maintain economically viable forestry, silvicultural strategies that reduce vulnerability to drought-triggered mortality need further research (e.g., D’Amato et al. 2013).

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Mortality Case Studies

6. Temperate Norway spruce bark beetle outbreaks – Volodymyr Trotsiuk

Windstorms followed by bark beetle (*Ips typographus* L.) outbreaks are among the primary drivers of temperate Norway spruce (*Picea abies* (L.) Karst.) forest dynamics, having important impact on forest services and functioning (Figure S7). In recent years massive landscape scale outbreaks hit extensive areas of natural and managed spruce forests in Central, East and south-east Europe (Brůna et al., 2013; Čada et al., 2013; Christiansen and Bakke, 1988; Panayotov et al., 2011). The dynamics and extent of outbreaks largely depend on insect abundance, tree and stand susceptibility, climatic conditions, past land use history and current human intervention (Raffa et al., 2008; Wermelinger, 2004). Warmer and dryer climate is likely to increase severity and extent of outbreaks due to: i) a prolonged period suitable for bark beetle breading, ii) weakening trees due to drought stress (Mezei et al., 2014; Temperli et al., 2013). In addition, increased landscape level homogeneity of stand structure resulting from past and current forest management creates perfect conditions for insect outbreak. While, bark-beetle populations have always been part of these natural forest ecosystems, regional climate change can trigger insect population increases from endemic to epidemic levels.

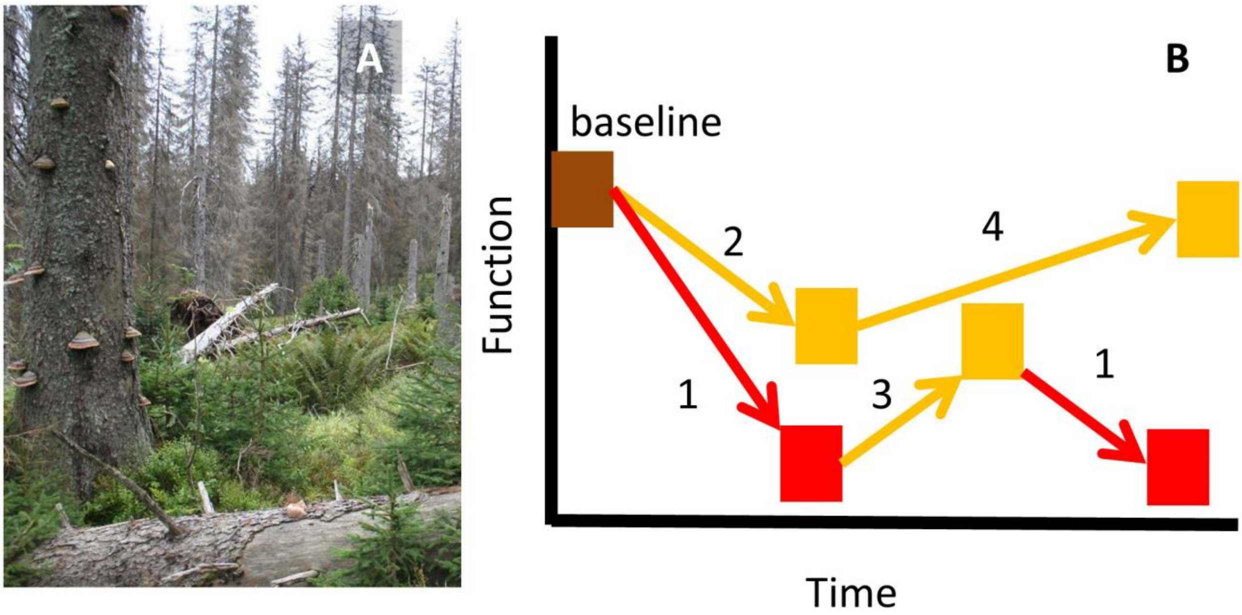

Figure S7. Spruce bark-beetle outbreaks in Central Europe. Extensive outbreaks impact forest ecosystem functioning (carbon pools, biodiversity, wood supply) (A, B.1). Salvage logged stands replanted with beetle host species create a positive feedback on outbreak dynamics and susceptibility to windstorms-associated mortality (B.1, B.3). In contrast, stands left that develop without replanting are more resilient to outbreak (B.2), however these stands require more time to reach late-seral structure and ecosystem function (B.4).

Extensive outbreaks continuously affect ecological and economical functioning of the forest (e.g. carbon pools, biodiversity, and wood supply) across stand to landscape scales (Seidl et al., 2014), leading to controversial scientific and political discussions on sources and consequences of these events. In landscapes managed for forest commodities insect outbreak can cause high economic loses. However, it has been shown that in the protected areas (natural forests, national parks), such disturbances could have beneficial effects for biodiversity by creating suitable habitat conditions for many species (Müller et al., 2008). By increasing complexity and diversity in early-successional forest stages, bark-beetle was reconsidered from pest to key-stone species (Müller et al., 2008).

Management of the affected areas differs between and within countries depending on the management goals, and often reflects political climate and forest management priorities. Management interventions in commodity-focused landscapes (but often national parks and conservation areas also) often include salvage logging operation such as complete tree removal or bark removal on the attacked trees. Such interventions are often found to have little positive effect on outbreak dynamics. Following breeding periods, insect populations quickly recover and expand to nearby stands suitable for outbreak. Natural barriers, e.g. increasing forest structural heterogeneity and species mixture, are known to be a better moderator of these explosive beetle outbreaks relative to salvage harvesting. In addition, post event salvage logging creates unfavorable conditions for natural regeneration (Jonášová and Prach, 2004) by increasing factors associated with seedling water stress. Furthermore, reforestation by planting often leads to structural homogenization of the post-disturbance sites thus decreasing forest resistance against new outbreaks while also negatively affecting biodiversity.

Forest structure and climate conditions influence initiation and development of bark-beetle within the landscape. Predicted higher frequency of windstorms in combination with prolonged warmer summer will create favorable conditions for beetle and might trigger large outbreaks in both managed and natural areas. While it is hardly possible (impossible) to control for climate change, managers can increase forest resistance by promoting forest heterogeneity which is more biologically complex with uneven-age structure. However, no clear management guidelines exist for forest management towards higher spruce forest resistance against bark-beetle outbreaks. But these guidelines are even more important in a warmer climate where higher beetle breading rates and drought-associated decreases in tree-level defenses create conditions ideal for continued or more severe outbreak.

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7. The role of species richness and forest fragmentation in climate driven tree mortality in tropical landscapes - Norbert Kunert

Tropical forests are one of the most important terrestrial carbon pools and as such, they play a very important role in the Earth's climate. Tropical forests are diverse and include a wide variety of tree functional types. Despite their relevance, tropical forests have been subject to accelerating deforestation rates due to manifold reasons. However, one of the most important drivers of deforestation is agricultural expansion which creates highly fragmented landscapes with widely scattered forest patches. Over the long term, forest fragmentation reduces species richness and shifts the forest edge to open land ratio to a non-positive relationship (Laurance et al., 2006).

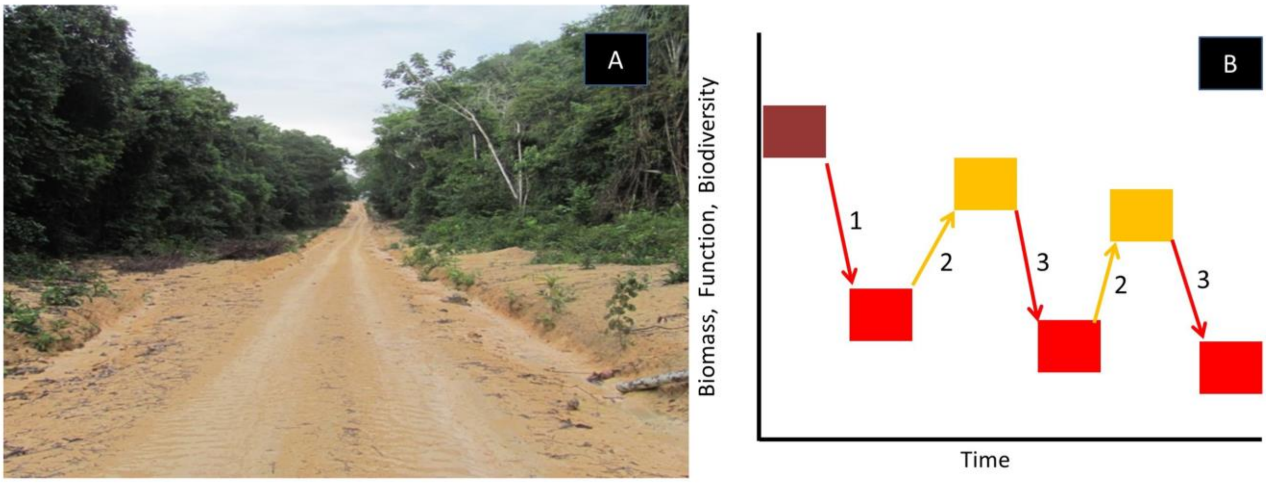

Figure S8. Forest fragmentation and the creation of new forest edges have cascading effects of forest structure and composition. Roads construction also greatly increases forest edges and effects on the remaining forest has been shown to accelerate tree mortality over time (A). Roads are thought to act as very narrow but long gaps (Laurance et al., 2009). Following edge creation (for example by road construction), the remaining forest will often experience intense tree mortality due to wind disturbance (1). Secondary growth with less functional diversity tends to colonize areas with wind-associated mortality (2). A higher boundary layer conductance within edge habitat leads to increased water use but lower functional diversity within these habitats decreases complementary soil water, which renders the forest more susceptible to drought-associated mortality. Decreased tree longevity increases stand turnover times (3) and results in a slow and steady decline of biomass and species diversity (Laurance et al., 2006).

Many significant edge effects have been described over the last decades of intensive research (Laurance, 2013; Figure S8). The strongest effect of forest edges found was on tree mortality with an increasing effect of the structural gradient between the forest and the adjacent open area (Laurance et al., 2006), but even small lateral fragmentations like roads can have significant effects (Kunert et al., 2015). Increased tree mortality has been measured up to 500 m in newly created forest edges (Laurance et al., 2002). Changes in microclimate can penetrate 100 m into the forest with a positive feedback on tree transpiration rates (Giambelluca et al., 2003; Kapos, 1989; Kunert et al., 2015). Trees adjacent to a forest edge consume up to 50% more water than trees growing in the undisturbed forest interior (Kunert et al., 2015), and even greater enhancement of tree water use within forest edges are known from temperate forest systems (Ringgaard et al., 2012). In addition to higher tree mortality due to wind disturbance in the remaining forest fragment (Laurance et al., 2002), water stress within the forest remnant appears to be increased during years with relatively intense dry seasons (Kunert et al., 2015; Laurance et al., 2001). Increased edge mortality and water stress create a feedback cycle that leads to less species rich forest patches dominated by early successional light demanding species and lower species and functional forest diversity overall.

Traits related to tree hydraulics play an important role in the water budget of secondary regrowth forests (Dierick et al., 2010). Furthermore, leaf phenology is one of the most important controls of resistance to seasonally changing water availability (Kunert et al., 2010) and probably a key variable during intensive droughts in forest fragments (Briant et al., 2010). However, forest edge tree communities with fast growing pioneering tropical trees species are known to be more severely affected by drought relative to forest interior species as these early successional species are less effective in accessing soil water sources than old growth forests with a high functional diversity. This functional diversity plays an important role in tropical forest water cycling as it tends to create tropical forests which are more resilient to drought-associated mortality (Kunert and Mercado Cardenas, 2015; Kunert et al., 2012) due to niche separation of soil water in older forests (Schwendenmann et al., 2015).

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Mortality Case Studies

Complex dynamics

8. Mediterranean Scots pine die-off at the arid edge of the species' distribution – Lucía Galiano and Francisco Lloret

Forest die-off is a complex phenomenon wherein climate anomalies may interact with a wide range of other contributing factors (Manion 1991). Scots pine (*Pinus sylvestris* L.) is one of the most widely distributed trees on Earth. Although largest populations of this species occur in boreal regions, Scots pine also occupies important areas in relatively dry regions within the Mediterranean basin, from the Iberian Peninsula to Turkey (Barbéro et al 1998). These populations, located at the lower latitudes of Scots pine distribution are likely to be particularly sensitive to the effects of the projected increased aridity (Hampe & Petit 2005). Up until the early twentieth century, European Scots pine forests, and particularly in the Mediterranean basin, had traditionally been under strong agro-pastoral pressure. More recently, both natural and artificial afforestation have taken place well within the natural distribution area of the species (Poyatos et al 2003; Pan et al 2011). These processes of forest densification have critical implications in a climate change context, as they

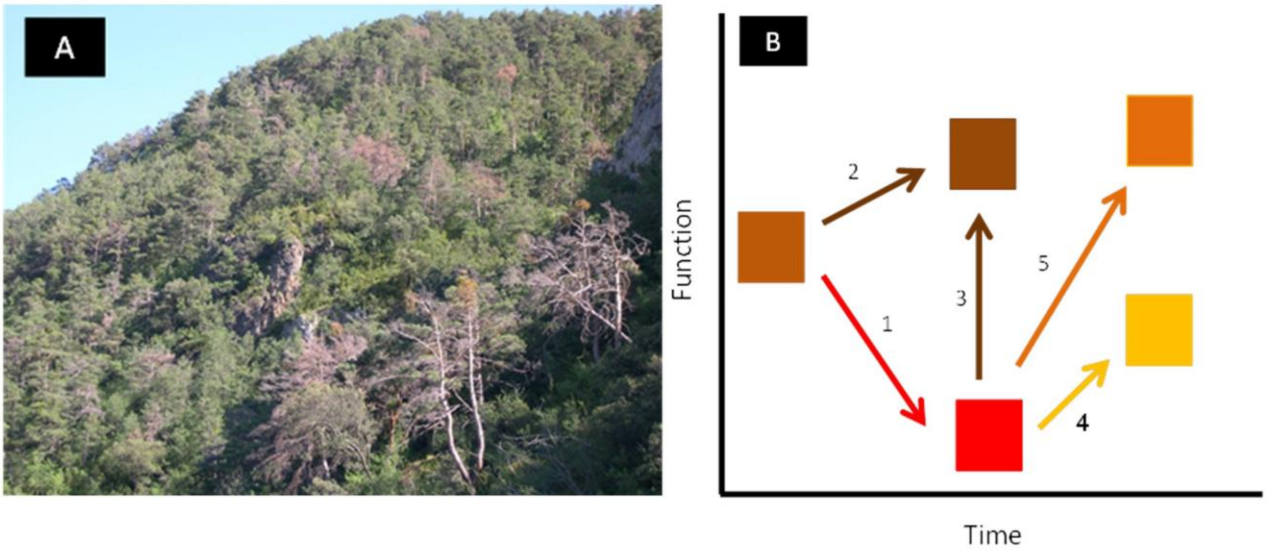

Figure S9. Scots pine die-off in the Mediterranean dry edge of its distribution. Intense drought episodes cause loss of canopy in Scots pine forests that have traditionally been under strong agro-pastoral pressure. More recently, natural and artificial afforestation has developed. Die-off compromises ecosystem functions including carbon sequestration and water cycling (A, B.1). Drought-driven impact exhibits a multifactor nature, with shallow and clayey soils, high stand densities and mistletoe infection predisposing trees to succumb to drought (B.1). Thinning treatments may mitigate effects of drought by reducing competition for water, and enhanced structural diversity may thus benefit ecosystem functioning (B.2). Natural self-thinning processes induced by drought may also reduce competition which would increase desired ecosystem functioning (B.3). By contrast, other below-canopy hardwood species, Quercus spp. mostly, may benefit from drought-induced canopy openings of the dominant Scots pine, potentially resulting in mid-term compositional changes in the community with intermediate values of ecosystem functioning (B.4). Other management strategies (eg., shading *Quercus* spp. seedlings) could help to optimally accommodate natural dynamics of succession, resulting in mid-term compositional changes in the community with maximum values of ecosystem functioning (B.5).

increase the competition for water and therefore the vulnerability of Scots pine to drought-induced forest die-off (Galiano et al 2010; Vilà-Cabrera et al 2011; Figure S9).

Scots pine is a good example of a species exhibiting isohydric stomatal control (Irvine et al 1998) that has been observed to reduce transpiration nearly to zero during periods of extreme drought and to rarely drop midday water potentials below -2.5 MPa (Poyatos et al 2013). For these species, the C starvation hypothesis (McDowell et al 2008; McDowell 2011) predicts that continued metabolic demand would eventually deplete carbon reserves when strict stomatal closure is prolonged. This scenario coupled with drought-induced leaf area reductions and their negative effects on the tree carbon balance have been associated with increased risk of mortality in Scots pine (Galiano et al 2011). At the stand level, small trees preferentially show decline-symptoms of defoliation and eventual death, probably due to their lower rooting depth, and the corresponding disadvantage for belowground water competition (Galiano et al 2010). Indeed, drought-driven Scots pine decline exhibits a multifactor nature, with shallow and less clayey soils, high stand densities and mistletoe infection predisposing trees to succumb to climate drought (Galiano et al 2010). While bark beetles have been also observed in many dead trees, outbreaks are still not acting as primary drivers of tree mortality.

Drought-induced canopy losses of Scots pine might not be compensated by natural regeneration, given that decline has been observed at the scale of the entire Iberian Peninsula (Vilà-Cabrera et al 2011) and more locally in some Scots pine populations in north-east Spain (Galiano et al 2010; Vilà-Cabrera et al 2013). Despite the shade-intolerant nature of Scots pine (Ceballos & Ruiz de la Torre 1971), pine seedlings require moderate shade to ensure critical levels of soil moisture and below-canopy ambient humidity, and openings from drought-induced dieback appear to degrade conditions needed to promote regeneration (Galiano et al 2010). By contrast, other below-canopy hardwood species, *Quercus* spp. mostly, may benefit from these drier, more open conditions compared to intact forests dominated by Scots pine (Galiano et al 2010; 2013). The shade-tolerant nature of *Quercus* spp. allows seedlings to persist in the understorey with very low growth rates until canopy opening creates new opportunities to grow into the upper canopy strata (Espelta 2004). Management aimed at promote Scots pine species over recent decades (Heres et al 2011) are presumably concomitant factors favouring the migration of hardwood forests upwards on altitude. Accordingly, drought-induced die-off is likely a main driver of recent rapid changes in the distribution of these species (Gimmi et al 2010; Galiano et al 2013; Vilà-Cabrera et al 2013).

Forest management based on the identification of the most vulnerable Scots pine populations to the different components of global change becomes crucial, and a major focus of management and research should consider extensive mortality in southern Scots pine forests, located at the edge of the species distribution (Martínez-Vilalta & Piñol 2002; Galiano et al 2010; Vilà-Cabrera et al 2013). Mitigation strategies such as thinning treatments and sustainable harvest activities enhancing structural diversity may release competition within denser stands, and probably could reduce vulnerability of Scots pine forests to drought-induced die-off (Dale et al 2001). However, these mitigation actions might not be economically reasonable under future scenarios of climate change. In this context, it seems reasonable to perform mitigation activities only on those populations which occur on sites projected to have a suitable climate, and to plan other management strategies (eg., shading young *Quercus* spp. seedlings under drought-induced canopy gaps) to accommodate unviable populations to successional dynamics (Dale et al 2001).

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9. Holm-oak die-off in evergreen Mediterranean forest – Francisco Lloret and Lucía Galiano

Environmental gradients associated with plant stress are among the most important co-drivers of forest die-off during drought. The importance of stress gradients is reinforced when a primary agent of mortality emerges. Hom-oak (*Quercus ilex* L.) is a dominant tree in evergreen forests of the western Mediterranean Basin, covering a broad range of lithological substrates and topographies. These forests have been managed over hundreds of years for coppicing and grazing, including acorn consumption. The resulting forests are impoverished in plant species – both in canopy and understory – and have developed a multi-stemmed structure thanks to the great ability of holm-oak to resprout after loss of above-ground biomass (Espelta et al 1999). Holm-oak is considered a drought-tolerant species with several physiological mechanisms to survive seasonal drought (Sala and Tenhunen 1994). Nevertheless, reduction of coppicing in recent decades due to changes in forest use has led to high-density stands experiencing strong competition and low growth rates (Gracia et al. 1999).

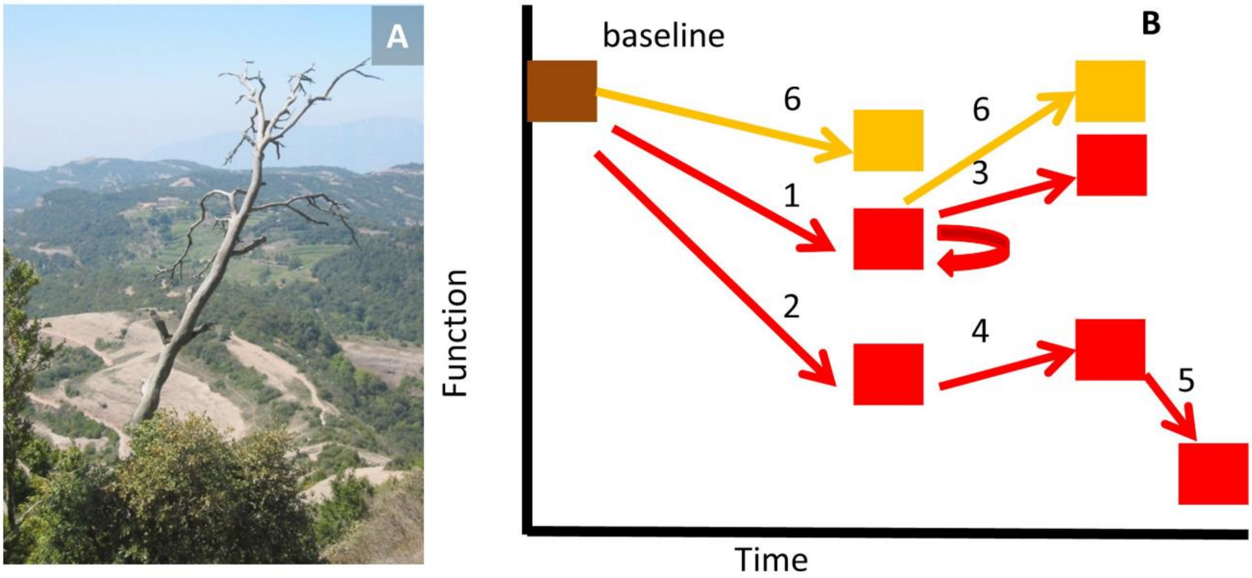

Figure S10. Sudden holm-oak die-off in western Mediterranean Basin. Intense drought periods cause loss of canopy in evergreen forests dominated by holm oak. Impacts on ecosystem functions includes carbon sequestration and soil conservation (A, B.1). Drought-induced impact is largely meditated by soil and bedrock configuration allowing roots to access to deep water table, resulting in a patchy pattern of affectation at landscape level (B.1, B.2). Holm-oak successfully resprouts when precipitation returns to average values (B.3), except in sites with shallow soils, which may become degraded by loss of vegetation cover (B.4). In these areas, recurrent drought episodes may result in a complete loss of vegetation cover and soil (B.5). Management can minimize this risk by preventing soil erosion (B.6). Also, modelling and experiments point a needed role of stand density and thinning on resistance to drought-induced die-off and later resprouting.

Recent episodes of extreme climatic drought have produced extensive canopy browning and eventual defoliation (Figure S10). A major determinant of this damage is the access of roots to deep water table which varies with lithology. Root penetration is lower and defoliation higher in plants growing over compact breccia than over fissured schist (Lloret et al. 2004). Additionally, the location in the topographical gradient has a strong effect as plants growing over shallow, fragmented soil pockets on ridge tops and steep slopes are the most vulnerable to drought related mortality (Galiano et al. 2012). Other relevant co-drivers increasing vulnerability include stand structure, such as within-tree factors such as between stem competition for light – Holm Oak is multiple stemmed – and stand density (Galiano et al. 2012).

An important feature of these die-off episodes is the great ability of holm-oak to resprout from the canopy, stem or stump (Lloret et al. 2004; Galiano et al. 2012), a feature common to other disturbances in Mediterranean environments such as wildfires or coppicing. Holm-oak defoliation initially induces a successional pathway in which some understory species can increase in the canopy, but this effect is limited because the rapid canopy growth of holm-oak (Saura-Mas et al 2014). Nevertheless, the ability of holm-oak to recover is not unlimited at the medium to long-term, due to intrinsic factors such as ability to restore carbon reserves (Galiano et al. 2012), and location on developed soils. In fact, recurrent drought episodes eventually cause significant holm-oak mortality, particularly on rocky ridges and steep slopes (Lloret et al. 2004). Thus a reinforcing feedback where canopy loss increases the likelihood of soil loss that in turn will increases die-off is likely to arise across the region.

Although the effect of die-off in holm-oak forests seems in many cases transitory, they may be relevant in terms of carbon balance and fuel accumulation which can promote increased risk of fire occurrence and intensity at the short term (Doblas-Miranda et al. 2014). Management of damaged forests often face the challenge to cut off extremely defoliated trees, which are likely to resprout at some extent, but with limited probabilities to survive over the long-term, particularly if drought episodes become more frequent in the future. In fact, several studies (Cotillas et al. 2009; Rodríguez-Calcerrada et al. 2011) suggest that a reduction of stand density –i.e. basal area- can help these forests to face increasing drought conditions. Thus, thinning in forests affected by die-off can improve survival in the face of the predicted trend to decreasing water availability, in which episodes of drought-induced die-off should be included. This practice could also be performed as a preventive tool in currently unaffected forests. Nevertheless, most holm-oak forests have private owners and the criteria for forest exploitation are more sensitive to short-term outcomes than to long-term projections. Currently, increasing wood demand for biomass electric generation is starting to favour forest coppicing, although the eventual fate of this activity is still uncertain, particularly when confronted with carbon sequestration balances. Other actions to minimize the impact of climate-oak die-off should include soil protection in sensitive areas with erodible soils, which will be likely affected by losses of canopy cover with increasing drought in the future.

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10. Drought induced *Nothofagus dombeyi* mortality in northern Patagonian forests - Maria L. Suarez and Thomas Kitzberger

Nothofagus dombeyi (Mirb.) Blume is a dominant, evergreen species growing in a wide range of environmental conditions along the northern Patagonian Andes in South America. During last decades, extreme climatic events such as droughts are directly impacting the demography and dominance of these forests, in particular in stands where *N. dombeyi* co-occurs with the southern conifer *Austrocedrus chilensis* (Bran et al. 2001; Suarez et al. 2004; Suarez and Kitzberger 2010; Figure S11). In this context, considering that recent extreme droughts had their strongest negative impact on *N. dombeyi* populations at the eastern distributional limits, a potential redistribution of this species and tree species compositional shifts are expected.

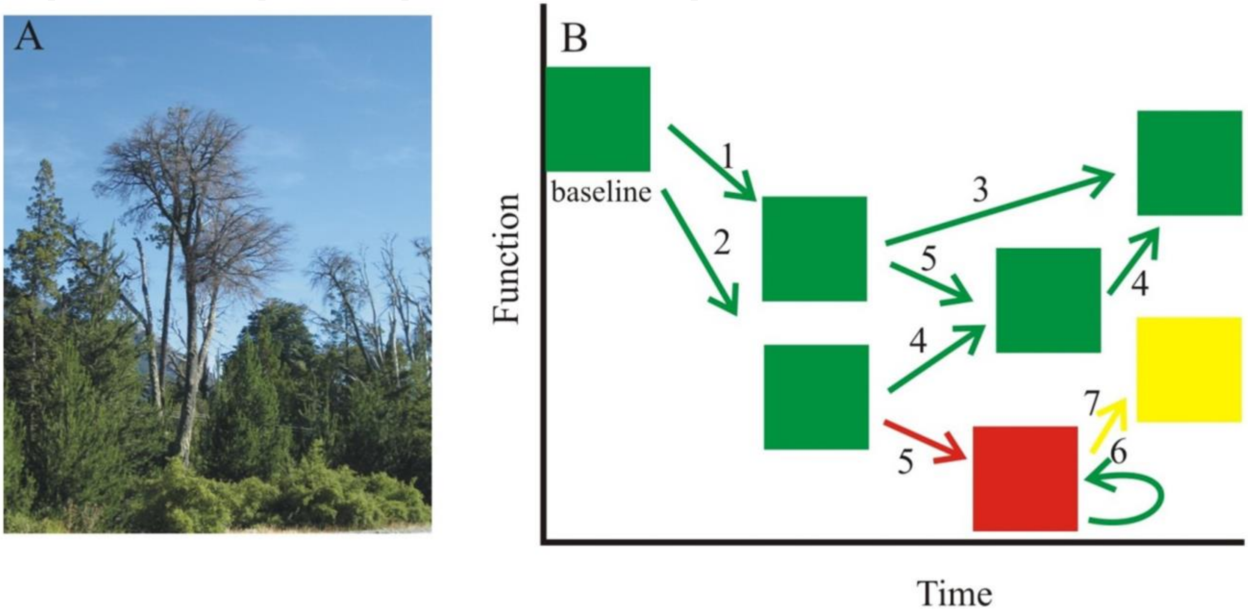

Figure S11. Drought-induced *Nothofagus dombeyi* mortality in northern Patagonia, Argentina. Punctuated warm-droughts have affected vast areas of pure *Nothofagus dombeyi* and mixed *N. dombeyi-Austrocedrus chilensis* forests (left panel), the easternmost forest trees developing along a transandean W-E gradient of decreasing rainfall. Drought impacts reduced leaf area and carbon sequestration capacity by either partial crown dieback (B1) or by killing entire trees (B2). Forests affected by partial crown dieback can rapidly recover most leaf area by lateral branch growth from neighboring *N.dombeyi* (B3). Severely killed *N.dombeyi* forests can also partially recover function by the height growth of suppressed *A. chilensis* (B4). Subsequent droughts may further reduce forest function by either advancing the crown mortality process or by killing entire trees that had previous partial mortality leading to a state in which resprouting shrub and grasses dominate the site as a matrix with sparse surviving/damaged trees (B5). This state may self perpetuate because conditions for regeneration of light demanding trees becomes difficult and because fuel loads generate conditions for more frequent fires (B6). Forest killed by drought are mostly restricted to National Parks an no post drought management has been implemented. Fire protection and enrichment of the forest with moderate shade tolerant and drought tolerant *A. chilensis* may improve ecosystem function as the conifer becomes dominant of the canopy (B7).

In particular, massive die-off occurred as a consequence of the extreme1998-99 drought event, caused an abrupt reduction in *N. dombeyi* overstory density (~ 57%) shifting the composition of overstory trees from a *N. dombeyi* dominated forests (~65%) to a nearly equally represented *N. dombeyi – A. chilensis* forest (Suarez and Kitzberger 2008). In less severely affected areas, the main consequence after drought event was the presence of partial crown mortality consisting of a reduction of tree level leaf area by shutting off of upper most radiation-exposed crown branches while retaining lower branches. Possibly related to plastic physiological responses, the presence of partial crown mortality seems to be involved in survivorship of canopy tree during the stressful event (Suarez et al. 2004). Despite this plasticity, repeated droughts could lead increasingly sparser canopies and eventually to total tree death. For instance, the moderate 2006-07 drought killed many trees that had suffered 50% partial crown dieback during the 1998-99 drought; and a new event of *N. dombeyi* mortality have been recorded recently in humid locations of the specie distribution (Lago Puelo and Pto. Blest - Suarez *personal observation*).

After die-off, substantial changes were observed in forest understory microenvironments, suggesting that in those forest ecosystems, droughts disturbance creates a new type of canopy gaps and should not be interpreted like common background canopy opening processes. Under dead canopy, undamaged understory influences the nature of resource limitation for seedling growth and survival, conditioning forest regeneration. Thus, forest trajectories in drought affected areas will ultimately increase cover of the shrub layers underneath dead canopy. While both overstory tree species are able to release their growth beneath dead canopy (Suarez and Sasal 2012), the final overstory composition will be determined by the identity of the tallest species under dead canopy; possible the main species involved in the canopy ascension process. Ongoing research on this ecological topic reveals that following fifteen years since 1998-99 drought, both canopy species are able to reach the canopy (Suarez & Lloret unpublish data). However, *A. chilensis* dominates the understory in some affected sites (because of lower mortality and/or original composition) probable reaching the canopy sooner and inhibiting the co-occurring *N. dombeyi*. Whereas main *N. dombeyi* forest affected areas are encompassed in a National Park, no management actions are planned. Thus, only speculative techniques, as enrichment with more drought tolerant specie *A. chilensis*, could be related with a recovery of forest function when consecutive drought events drive the mixed forest to shrubland as a consequence of several death episodes.

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11. Drought induced tree-death in African savanna woodlands – Shaun Levick

Strong alterations between wet and dry seasons are characteristic of the savanna biome and all its ecosystems experience water limitation for at least part of a given year (Scholes and Archer, 1997). Savanna trees are adapted to annual dry conditions, but multi-year droughts have caused high rates of tree mortality in savannas across the globe (Fensham et al., 2009; Figure S12).

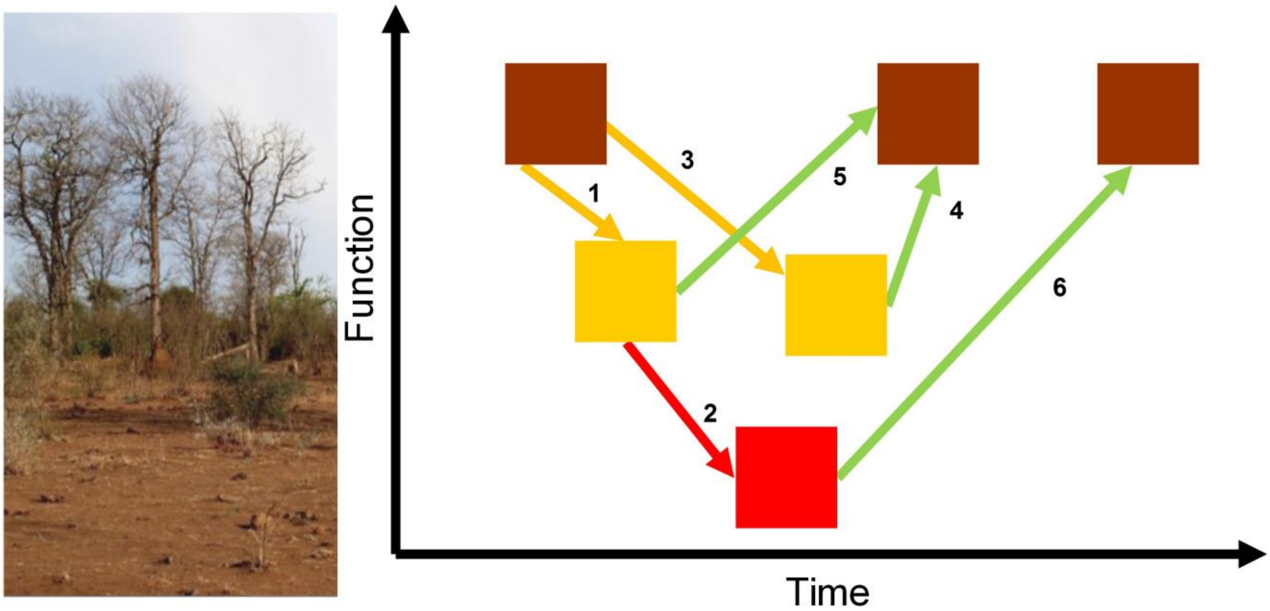

Figure S12. Drought induced tree death in savanna woodland. Prolonged periods of low soil moisture lead to die-off of established trees. Trajectory of change is dependent upon the history of land management. Areas that were subjected to overgrazing were shrub encroached – with increased stem density and decreased perennial grass cover (1). Drought conditions result in high mortality rates due to inter-tree competition for water and ecological functioning declines further (2). Similar drought conditions in non-encroached areas have lower impact on ecosystem functioning (3), and the system can return to its original state through normal successional processes over time (4). Recovery in the previously overgrazed/encroached site requires management intervention (shrub clearing, fire, anti-erosion measures) to return to its original state (5). Recovery from the combined effects of overgrazing and drought takes longer, and it is still not clear if/how restoration can best be achieved (6).

The 1988-1989 and 1991-1992 droughts in southern Africa triggered death in a number of savanna tree species. *Colophospermum mopane* dominates the savannas of northern South Africa and is considered strongly resistant to drought (Johnson et al., 1996), but high and spatially variable rates of mortality were recorded following these last major droughts of the region (MacGregor and O'Connor, 2002; Viljoen, 1995). The highest rates of loss (87% of basal area) were recorded in discrete patches in a private nature reserve in the Northern province (MacGregor and O'Connor, 2002), while 30-40% losses are estimated to have occurred in similar landscapes within the Kruger National Park (KNP) in the Limpopo province. A key distinguishing feature between these two landscapes is their management history - the private reserve was established following many years of cattle ranching while the national park has stocked only native wildlife since the 1930’s. Severe overgrazing in the private reserve led to: i) removal of perennial grass species; ii) modification of the natural fire regime; and iii) subsequent heavy encroachment of *C. mopane* shrubs by the 1980’s (O'Connor, 1998). These changes rendered the landscape ‘dysfunctional’ prior to the droughts of the late 1980’s and early 1990’s, primarily through the loss of the perennial grass cover which major implications for water and nutrient retention in semi-arid systems (Ludwig et al., 2005).

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MacGregor and O’Connor (2002) hypothesize that the increased stem density at the overgrazed site contributed to the high mortality rates during the drought periods, due to increased inter-tree competition for soil water. Patch die-back did not occur in the national park, and death was restricted to taller and isolated trees, however in the years following the drought the recovery of vegetation was impeded by the presence of numerous artificial water holes, which increased herbivore grazing and browsing in their vicinity (Thrash, 1998). Management actions following drought need to focus on the conservation of soil resources and the maintenance of eco-hydrological processes for natural vegetation succession to take place.

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Mortality Case Studies

12. Yatir forest, Israel – drought, forest thinning, and grazing interactions – José M. Grünzweig, Tamir Klein, and Yakir Preisler

Yatir forest is a 50-yr old planted, predominantly Aleppo pine (*Pinus halepensis* Mill.) forest situated in the northern Negev desert of Israel (31° 20’N 35°03’E, 550–700 m a.s.l.; Figure S13). Climate is semi-arid, with minimum, maximum and mean temperatures averaging 1.8, 36.6 and 17.7°C. Mean annual precipitation (1972-2014) is 279 (±90) mm. Potential evapotranspiration (PET) is 1600 (mm yr^{-1}) and P/PET is 0.18.

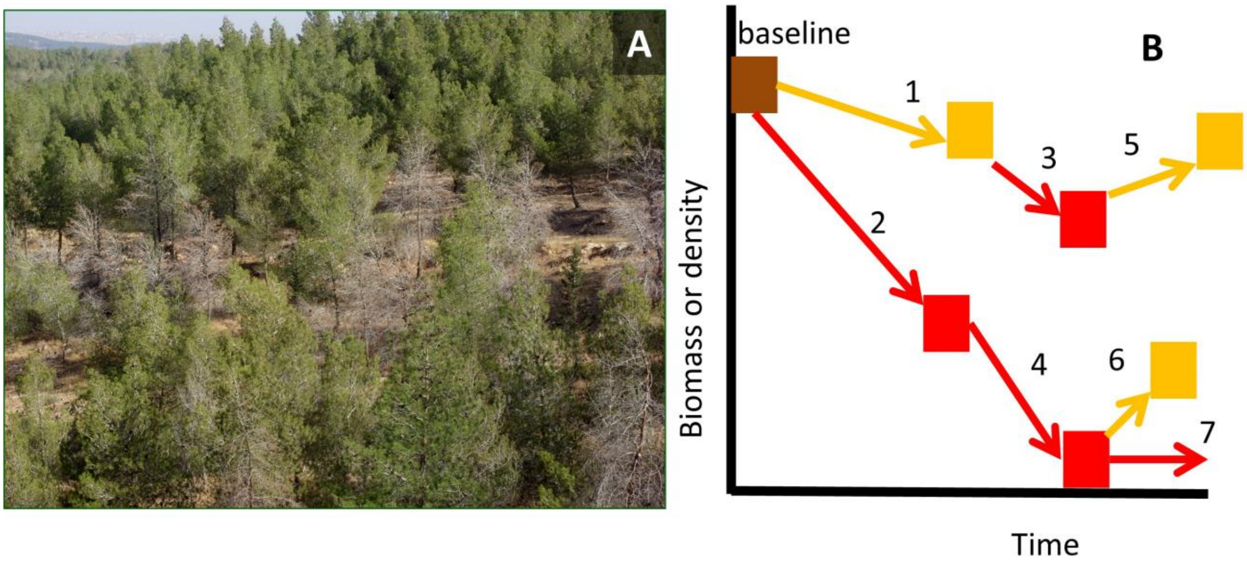

Figure S13. (A) A mature *Pinus halepensis* stand in the semi-arid Yatir forest showing dead and living trees following two consecutive drought years (2008 and 2009). (B) Suggested trajectories of aboveground tree biomass production with stand density affected by management and drought-induced mortality for a semi-arid pine forest in Yatir, Israel. Forests thinned prior to drought (1) tend to suffer lower losses of tree density and biomass than unthinned forests (2 vs. 3) during drought. Fire can greatly increase this loss of tree cover and convert forests to shrublands (4) while thinned forests can recover to pre drought levels more quickly (5). Restrictions on grazing can aid in reestablishment of canopy cover (6) while continued drought and grazing can perpetuate non-forest conditions (7).

Stand density of the base forest is around 300 trees per hectare, which is considered as near forest optimum density (Raz-Yaseef et al. 2010). Future forecasts predict a temperature rise and changes in precipitation regime, probably to drier conditions. These changes in turn will affect soil moisture and the available water for forest trees. Moderate thinning as a management tool (e.g. to 200 trees ha^{-1}) was found to increase aboveground tree biomass production at the plot level by about 50% (Figure S13; Preisler et al. *in prep*), and enables higher rates of sapling survival, while heavier thinning does not change productivity and sapling establishment as compared to the base forest. Tree mortality following two consecutive drought years in 2008 and 2009 decreased biomass production by killing 5-10% of the trees (Klein et al. 2014; Figure S13). The reduction in biomass production by mortality is assumed to be more pronounced in the base forest than in the moderately thinned forest, due to the high fractionation of the local water budget to tree water-use (Raz-Yaseef et al. 2010, Klein et al. 2014). Without forest management, severe or repeated drought and stand-replacing fire will eventually lead to a shrubland dominated by *Sarcopoterium spinosum* (L.) Spach which is about a third as productive as the base forest (Gelfand et al. 2012). Overgrazing eliminates sapling establishment, degrades the shrubland and further reduces productivity. Planting combined with proper seedling maintenance restores an optimally functioning forest, a goal that might be reached to some extent by grazing exclusion (Preisler et al. *in prep*). However, grazing exclusion can potentially increase the risk of fire through the buildup of fine fuels; tradeoffs between risk of mortality from fire vs drought are unresolved in this system.

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13. Drought-driven mortality in Australian eucalyptus forests & woodlands – Melanie J.B. Zeppel

Eucalyptus species cover many continents, are an important plantation species, and commonly grow in regions which regularly experience drought (Whitehead & Beadle, 2004; Burrows, 2013). Eucalyptus also provide an interesting biological contrast to many Northern hemisphere species which die following drought, because many resprouting *Eucalyptus* species often rapidly recover from drought stress and die-back, even following severe drought and pest attack (Zeppel *et al.*, 2015). In comparison, other non-sprouting woodlands and forests can remain in a post-drought disturbance for multiple decades (Kelley *et al.*, 2014). Many Australian Eucalyptus woodlands frequently experience drought, heat-waves and fire, and it is difficult to disentangle the effects of drought from fire and insect-attack as they often occur concurrently (Medlyn et al., 2011). The seasonality of droughts can dramatically influence the impact on water stress, on Eucalyptus woodland, as demonstrated by a case study in a *Eucalyptus maculata* forest (Pook, 1985; Pook, 1986).

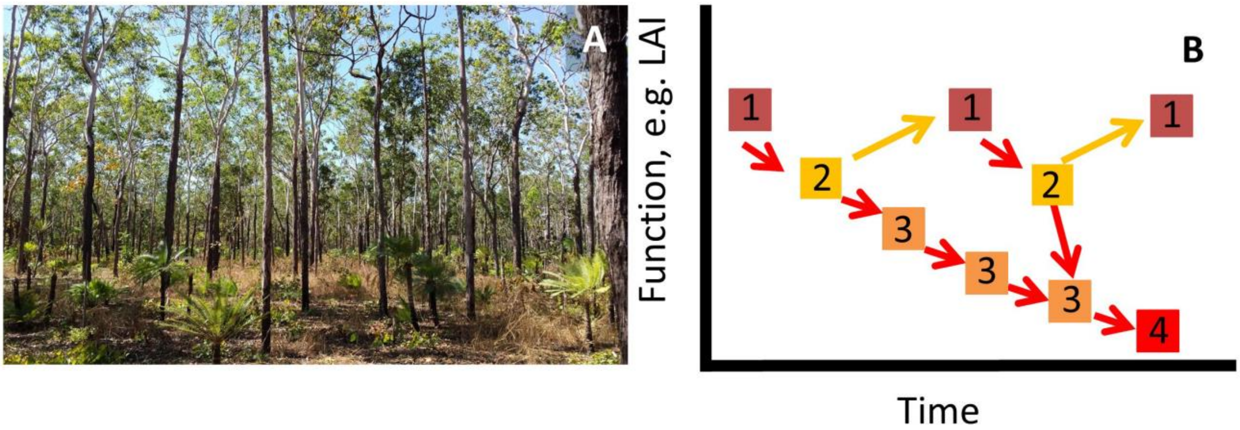

Figure S14. Eucalyptus forest/woodland (A). Cycles of drought, heat wave and fire, which influence ecosystem function including leaf area index (LAI) and water cycles. (1) shows the initial baseline function (e.g. LAI), which is then followed by (2) drought. If sufficient time occurs before the next drought (e.g. see case study, Kioloa), resprouting eucalyptus are able to recover back to the baseline LAI (Kelley et al. 2014). However if another drought rapidly follows (3), then there may be insufficient time for recovery, leading to die-back and (4) eventual mortality. (Photo credit: Rhys Whitley).

In the south coast of New South Wales, Australia, at Kioloa (Figure S14), two severe droughts occurred in 1980-1981 and 1982-1983, within a *Eucalyptus maculata* forest where dawn leaf water potential declined to -4 MPa (Pook 1986). However, the two droughts occurred in different seasons. In 1980, most rain fell in early in the year, whereas in 1982, the rain was more evenly distributed, and fell closer to the increase in evaporative demand in spring (Pook, 1986). Bole diameter shrinkage, leaf litter fall and over-storey leaf area index were more strongly influenced in the 1980, despite similar amounts of rain in both years (Pook & Forrester, 1984; Pook, 1985; Pook, 1986). Foliage retained normal appearance above pre-dawn leaf water potential of -3 MPa but became dull and obviously wilted in the range of -3 to -5 MPa, and was severely wilted and turned brown (dead) below -5 MPa (Pook, 1986). Mortality resulting from decreased water availability was also linked with increased temperatures in the comparison of two drought years. It is likely that the effect of high temperature in these studies is actually a response to higher vapour pressure deficit.

Following both drought and insect attack, there was rapid recovery following die-off in the *Eucalyptus maculata* forest (Pook *et al.*, 1998. After the 1980-81 and 1982-83 droughts, seven years later in 1989-1990, the forest was attacked by cup moth larvae (*Doratifera oxlyi* Newman (Limacodidae) which accounted for 19% of total 1990-1991 leaf loss. Recovery of the leaf area index of the *Eucalyptus maculata* 73% of the canopy returned to undamaged leaves levels after seven months (Pook *et al.*, 1998).

The consequences of die-off often differ for Eucalyptus, compared to other vegetation, potentially due to rapid recovery of leaf area from drought (Kelley et al., 2014; Zeppel et al., 2014). The *Eucalytus maculata* forest in this case study did not experience mortality, despite the severe drought, and reduction in leaf area index from 2.5-3.0 down to 0.5-0.75. Rather, within four months the over-storey leaf area index reached pre-disturbance levels (Pook *et al.*, 1998).

The consequences of drought-induced mortality on Australian forests are influenced by both the resilience (Zeppel et al., 2008) and rapid recovery after drought particularly in resprouting species (Gharun et al., 2013; Nolan et al., 2014; Zeppel et al., 2015). For example, Matusick et al. (2013) reported that in a field study of a forest characterized by resprouting Eucalyptus, half of the trees that lost leaves through drought had recovered by the next year. Similarly, Gharun et al. (2013) showed full recovery of transpiration and canopy biomass within 1-2 years in an ecosystem dominated by resprouters subjected to severe and extreme drought and heat waves. These data suggest that the consequence of drought and mortality may be smaller than research on non-sprouters would suggest, and the impact on carbon, water and nutrient cycles may differ from different vegetation types, with important implications for modeling global carbon and water cycles (Zeppel et al., 2015).

Several studies have shown that the risks of drought-induced mortality may be minimized by managing stocking density, in plantations. Horner et al. (2009) showed that drought mortality of *Eucalyptus camaldulensis* plantations in Victoria was higher in high density stands, whereas low density stands were relatively unaffected by drought. Similarly, a study on *Eucalyptus globulus* plantation in Western Australia showed similar results (Mendham et al. 2005).

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14. Jarrah (*Eucalyptus marginata*) and marri (*Corymbia calophylla*) die-off in Southwestern Australia – Katinka X. Ruthrof

In March 2011, large scale, unprecedented and sudden forest die-off and die-back occurred in a number of forest and woodland types in southwestern Australia (Matusick et al. 2012, 2013; Challis et al. 2016).. This corresponded with a prolonged heatwave lasting nine days, one of the driest years on record (2010) and a three decade downturn in precipitation (Bates et al. 2008). The most dramatic die-off occurred in the Northern Jarrah Forest, where die-off was concentrated in distinct patches and characterised by midstory and overstory crowns (of the key species *Eucalyptus marginata* and *Corymbia calophylla*) rapidly discolouring, and turning brown and whole trees dying (Matusick et al. 2013; Ruthrof et al. 2015). Die-off was associated with soil with low water holding capacity, sites that were close to rock outcrops, , on sites at high elevations, on steep slopes and in areas that were generally slightly warmer than their surroundings (Brouwers et al. 2013). Furthermore, drought-affected patches were larger, more densely clustered in xeric areas and there is evidence that these are chronic disturbance patches susceptible to recurrent drought disturbance (Andrew et al. 2016).

Drought-affected trees with lower tissue moisture were associated with an outbreak of *Phoracantha semipunctata* (Cerambycidae), however, there is minimal evidence that *P. semipunctata* can attack and kill trees that are not experiencing severe water stress and it did not spread into the healthy forest (Seaton et al., 2015).

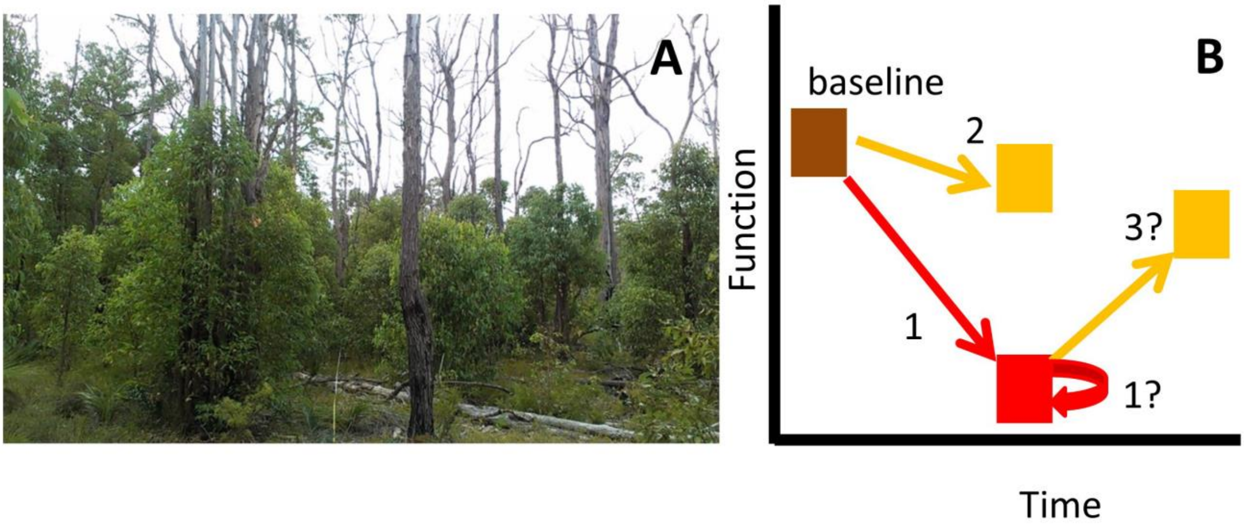

Figure S15. *Eucalyptus marginata* (Jarrah) and *Corymbia calophylla* (marri) collapse in southwestern Australia. Drought/heat have caused extensive and severe canopy and tree mortality on upper slopes and shallow soils (A, B.1), edaphic conditions which are associated with higher water stress overall. Prolific resprouting following canopy mortality maintains forest composition, but the subsequent stands have significantly different structure (B.1). Trees on lower slopes also experience some crown retraction, but not to the same extent (B.2). It is too early to tell, but resprouts may use more water and predispose themselves to further die-off (B.1), or may slowly replace the structure lost (B.3).

Forest die-off significantly increased 1-hr fuels and standing dead wood, increased visible sky, and near-ground solar radiation input. Fire spread rates were predicted to be 30% greater in die-off plots with relatively equal contributions from fuels and microclimate, highlighting need for operational consideration by fire managers (Ruthrof et al. 2016).

Recovery of the affected forest is characterised by a significant structural shift including the replacement of large, dominant stems by high densities of small resprouting stems, and a significant reduction in forest canopy height. The relative composition of the two co-dominant canopy species, however, did not change over a four year period (Matusick et al. 2016). Experimental treatments focusing on fuel reduction and thinning of basal resprouts are needed to better understand if management actions can protect against forest conversion to shrubland of resprouting trees..

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