

SYNTHESIS & INTEGRATION

Transitioning western U.S. dry forests to limited committed warming with bet-hedging and natural disturbances

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Abstract. Historical evidence suggests natural disturbances could allow more forest persistence, than expected from models, over 40 yr of transition to the net-zero emissions needed to limit warming to $<2.0^{\circ}\text{C}$ (e.g., Paris Agreement). Forests must ultimately equilibrate with committed warming from accumulated emissions. Historical dry-forest landscapes were heterogeneous from large, infrequent disturbances (LIDs) that reduced tree density and basal area, followed by slow, variable tree regeneration and recovery for 1–3 centuries. These together effectively provided bet-hedging through stand- and landscape-level heterogeneity that enhanced resistance and resilience to a diversity of unpredictable subsequent disturbances. Recent disturbances have not yet exceeded historical variability in rates and patterns, but could cause mortality of $\sim 26\text{--}51\%$ of dry-forest area in the transition. This also means $1/2$ to $3/4$ of dry-forest area could escape most mortality and the mortality area could also have substantial forest persistence. Projections are unavailable for droughts or beetle outbreaks, but they recently caused about 3–4 times as much tree mortality as did moderate- to high-severity fires. Mortality could reduce forest area if new trees do not regenerate, but 24 studies showed recent regeneration after high-severity fires was slow, but indistinct from historical variability. Survival of smaller trees provided regeneration after beetle outbreaks and droughts. Regeneration in general was projected by 2060 to decline by $\sim 10\%$ in one study and increase by 50% in another. If openings from disturbances increased, some grasslands and shrublands could be restored, increasing landscape heterogeneity and resistance to disturbance spread. Given these trends and our limited ability to prevent LIDs, I suggest (1) refocusing restoration to increase bet-hedging resilience to droughts and beetle outbreaks by retaining small trees and diverse tree species, (2) expanding development of fire-safe landscapes to protect people and infrastructure from unavoidable increased fire, (3) enabling more managed fire to restore and enhance stand- and landscape-scale bet-hedging, and (4) accepting that LIDs will revise resistance, resilience, and adaptation, which enhance forest persistence, particularly if post-disturbance survivors are not logged and trees are not planted. Natural disturbance and slow recovery, if bet-hedged to increase resistance and resilience, could enable substantial forest persistence.

Key words: adaptation; beetle outbreaks; bet-hedging; climate change; disturbances; droughts; dry forests; fire; natural recovery; resilience; succession.

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INTRODUCTION

Since the 2015 Paris Agreement, the world plans to reduce emissions to limit warming to much less than 2.0°C, possibly 1.5°C, and it is worthwhile to focus on how major ecosystems may transition to this more limited level of warming that is now a global commitment. Extensive disappearing climates and ecosystem changes and the need for widespread assisted migration by the mid- to late 21st century under continuing moderate- to high emissions (e.g., Rehfeldt et al. 2014) are less likely. Understanding is now needed of impacts of more limited warming for specific ecosystems. Here, I review how bet-hedging and natural-disturbance processes (Baker and Williams 2015) could help transition current dry-forest landscapes in the western United States to limited committed warming. Bet-hedging uses small trees, large trees, and diverse trees to hedge against diverse disturbances. Committed warming occurs because once emissions are reduced so they are at net zero (emissions balanced by fixation), the long persistence of emitted CO₂ in the atmosphere and high oceanic heat capacity cause global temperatures to remain elevated for centuries near where they are at net zero (Collins et al. 2013, Mauritsen and Pincus 2017).

Dry forests are major montane ecosystems (Fig. 1), covering ~25.5 million ha of the western United States (Baker 2015). Dry forests include (1) dry pine forests most often dominated by ponderosa pine (*Pinus ponderosa*) or similar pines with relatively few associated trees, and (2) dry mixed-conifer forests with pines plus several other trees (e.g., *Abies concolor*, *Abies grandis*, *Populus tremuloides*, *Pseudotsuga menziesii*). Dry-forest landscapes historically also included grasslands and shrublands, as well as younger forests (Fig. 2), some of which were seral stages after high-severity fires in dry forests, although others were more persistent (Baker 2017a).

To keep committed warming below 2.0°C across dry forests of the western United States, emissions may need to be net zero by A.D. 2050 when 80% of projections show 2.0°C of warming would be reached with current emissions (Karmalkar and Bradley 2017). However, globally committed warming of well below 2.0°C that might allow 2.0°C of committed

warming across dry forests of the western United States could also be achieved if net-zero emissions are reached by A.D. 2060 after rapid near-term reductions (Sanderson et al. 2016). The 2.6 representative concentration pathway (RCP), the lowest scenario of the Fifth Assessment Report (AR5) from the Intergovernmental Panel on Climate Change, was thought to feasibly constrain warming to <2.0°C (IPCC 2015), but this now appears unlikely (Sanderson et al. 2016). The next IPCC report (AR6), with newer scenarios congruent with 1.5–2.0°C of committed warming, is not due until 2022. However, Shared Socio-Economic Pathways (SSPs) that are being developed suggest a 1.9 RCP could feasibly constrain warming to 1.5°C (Rogelj et al. 2018). Updated global carbon-emissions accounting and pathways make 1.5°C feasible (Tokarska and Gillett 2018, Van Vuuren et al. 2018). Thus, net-zero emissions by 2060 are needed and feasible to avoid rising above 1.5–2.0°C (Tanaka and O'Neill 2018). Therefore, I consider A.D. 2060, ~40 yr, as the main period for transitioning dry forests, after which further, slower adjustment to committed warming continues.

No projections yet exist for extent of climate loss (current climate moves elsewhere or is changed) or its effects on tree populations in dry forests for pathways leading to net-zero emissions by 2060, but perspective is still possible now. Projections of climate loss in dry forests, primarily from bioclimate models, were mostly for A.D. 2060–2100 and/or RCPs of medium to high emissions (Table 1). Loss of climate would likely be lower than in RCP 2.6 (Table 1), but specific projections are lacking. Nonetheless, by 2015, total human-induced global warming was 0.93°C (Millar et al. 2017), about 1/2 to 2/3 of the way to 1.5–2.0°C, suggesting that effects that will occur are well underway. Here, I synthesize what might ensue in dry forests based on recent trends in natural disturbances, tree mortality, and tree regeneration, aided by projections and scenarios to 2060 for low or modest emissions, where available. Further refinement will be needed, but substantial evidence is available now that can provide useful perspective.

Also, bioclimate models do not reveal ecological effects, since they usually lack demography, dispersal, or natural disturbance, and mostly



Fig. 1. Dry forests covered about 25.5 million ha of the western United States, including about 12.6 million ha of dry pine forests and 12.9 million ha of dry mixed-conifer forests. Data are Landfire biophysical settings, which predict historical vegetation (<http://www.landfire.gov>).

only show how the climate of an ecosystem may change, not effects (Campbell and Shinneman 2017). Climate loss is expected to move upward from lower-elevation and northward from southerly trailing edges of dry-forest ranges, and tree mortality may follow, but

unpredictably. Adult ponderosa may be most vulnerable in interior populations (var. *scopulorum*) and less in Pacific populations (var. *ponderosa*) of ponderosa pine, but vulnerability in dry forests may be heterogeneous in general (McCullough et al. 2017). These models are generally only for



Fig. 2. Historical dry-forest landscapes included forests as well as openings with grasslands and shrublands, as shown here in this Whitman Cross photograph from 1897 looking south at Mesa Verde (on the skyline), southwestern Colorado, across a ponderosa pine landscape with Gambel oak (*Quercus gambelii*) shrublands and montane grasslands. Reproduced from a scanned print of the original photograph (Cross 297) at the U.S. Geological Survey Denver Library, Photographic Collection, Denver, Colorado.

adult trees, but tree regeneration may ultimately control tree persistence and expansion (Bell et al. 2014, Dobrowski et al. 2015, Petrie et al. 2017). Natural disturbances (droughts, beetle outbreaks, wildfires, and diseases) will likely cause the tree mortality as climate is lost. Forest resilience could be exceeded and a tipping point (Reyer et al. 2015) crossed. However, inertia from long tree life spans, changing disturbances, and tree survival and regeneration might allow more forest persistence (Campbell and Shinneman 2017).

Here, I first review the historical roles of large, infrequent disturbances (LIDs), post-disturbance legacies, and slow natural recovery in dry forests. Then, I review recent natural disturbances, tree regeneration, and how persistence of tree populations in dry forests to warming could be aided by bet-hedging. Emergence of climates at higher elevations may offset losses in current ranges, if dispersal succeeds (Campbell and Shinneman 2017), but is not addressed here.

HISTORICAL VARIABILITY IN NATURAL DISTURBANCE AND RECOVERY IN DRY-FOREST LANDSCAPES

Large, infrequent disturbances historically accomplished most renewal in dry-forest landscapes

Historical dry-forest landscapes included open, low-density stands with large, old trees and a history of low-severity fires, but probabilistic landscape-scale studies found these open forests over only about 34%, on average, of dry-forest area (Baker 2017a). The other 66% historically had more diverse stand structures (examples in Table 2, reviews in Odion et al. 2014, Hanson et al. 2015). Historical forests were often younger, denser, and had been burned in fires varying in intensity and severity, as described explicitly in Hessburg et al. (2007:19): "Instead, area was dominated by forest structures that were intermediate between new and old forests, i.e., by pole to medium sized, rather than large trees. ... This observation suggested that before any extensive management had occurred, the influence of fire in the dry forest was

Table 1. Projected losses of current dry-forest climates for individual species that occur in current dry forests of the western United States, based on bioclimate and process-based (only Mathys et al. 2017) models.

Emissions level/location	Species	Change (%) [†]	Date	Emissions scenario or RCP [‡]	Author(s)
Low					
Arizona–New Mexico Plateau	<i>Pinus ponderosa</i>	–58.0	2075–2100	2.6	Mathys et al. (2017)
North America	<i>Pseudotsuga menziesii</i>	–22.0	2075–2100	2.6	Mathys et al. (2017)
Idaho Batholith	<i>Pseudotsuga menziesii</i>	–19.0	2075–2100	2.6	Mathys et al. (2017)
Wyoming Basin	<i>Pseudotsuga menziesii</i>	–1.0	2075–2100	2.6	Mathys et al. (2017)
Medium–high					
North America	<i>Abies concolor</i>	–13.4§	2071–2100	A2/B2 mean	McKenney et al. (2007)
North America	<i>Abies grandis</i>	–49.6§	2071–2100	A2/B2 mean	McKenney et al. (2007)
North America	<i>Picea pungens</i>	–51.2§	2071–2100	A2/B2 mean	McKenney et al. (2007)
North America	<i>Pinus jeffreyi</i>	–68.6§	2071–2100	A2/B2 mean	McKenney et al. (2007)
North America	<i>Pinus ponderosa</i>	–40.4§	2071–2100	A2/B2 mean	McKenney et al. (2007)
North America	<i>Pinus ponderosa</i> var. <i>ponderosa</i>	–45.0	2060	6.0	Rehfeldt et al. (2014)
North America	<i>Pinus ponderosa</i> var. <i>scopulorum</i>	–77.0	2060	6.0	Rehfeldt et al. (2014)
North America	<i>Populus tremuloides</i>	–24.7§	2071–2100	A2/B2 mean	McKenney et al. (2007)
North America	<i>Pseudotsuga menziesii</i>	–31.5§	2071–2100	A2/B2 mean	McKenney et al. (2007)
North America	<i>Pseudotsuga menziesii</i> var. <i>glauca</i>	–35.0	2060	6.0	Rehfeldt et al. (2014)
North America	<i>Pseudotsuga menziesii</i> var. <i>menziesii</i>	–18.0	2060	6.0	Rehfeldt et al. (2014)
High					
Southwestern USA	<i>Picea pungens</i>	–81.0	2070–2099	A2	Notaro et al. (2012)
Southwestern USA	<i>Pinus ponderosa</i>	–47.0	2070–2099	A2	Notaro et al. (2012)
Southwestern Colorado	<i>Populus tremuloides</i>	–52.0	2060	6.0/8.5 mean	Rehfeldt et al. (2015)
Southwestern USA	<i>Pseudotsuga menziesii</i>	–50.0	2070–2099	A2	Notaro et al. (2012)
North America	<i>Pseudotsuga menziesii</i>	–59.0	2075–2100	8.5	Mathys et al. (2017)
Southwestern USA	All needleleaf evergreen trees	–100.0	2099	A2	Jiang et al. (2013)

Note: Area outside current climates may also emerge with some new area of suitable dry-forest climates, not shown here.

[†] The change (%) is relative to the present.

[‡] Emissions scenarios are A2 (High emissions), B1 (Low), and B2 (Low–Medium); RCP = representative concentration pathway, which is the change in radiative forcing (W/m²) in 2100 relative to pre-industrial conditions, as defined for emissions scenarios by the Intergovernmental Panel on Climate Change (IPCC). RCP 2.6 is Low, 4.5 is Medium, 6.0 is Medium–High, and 8.5 is High emissions.

§ This is the “no dispersal” projection result.

of a frequency and severity that intermittently regenerated rather than maintained large areas of old, fire tolerant forest.” The intermittent regeneration likely followed LIDs which varied in intensity, but were at least partly intense enough to kill substantial woody plants. Large, infrequent disturbances included fires, insect outbreaks, diseases, droughts, and blowdowns (Foster et al. 1998).

Many historical LIDs in dry-forest landscapes occurred in periodic climatic episodes. Large fires were often during droughts, as in 1848 when 41 of 63 fire-history sites across southwestern dry forests recorded this fire year (Swetnam and Baisan 1996), and in 1910 when 1.2 million ha burned in the northern Rocky Mountains (Odion et al. 2014). About 10 bark beetles had large outbreaks in dry forests (Bentz et al. 2010) when tree

defenses were weakened by drought or other events, weather favored beetle reproduction, and mass attack could overcome tree resistance (Bentz et al. 2010, Negrón and Fettig 2014). An example is the 200,000- to 300,000-ha 1895–1909 mountain pine beetle (MPB; *Dendroctonus ponderosae*) outbreak in the Black Hills, South Dakota (Graham et al. 2016). Historical droughts, such as the A.D. 1574–1594 drought in the Southwest, also likely led to extensive tree mortality in dry forests (Swetnam and Betancourt 1998, Williams et al. 2013).

Large disturbances were likely infrequent in historical fire regimes and in other disturbance regimes. Modern fire regimes globally nearly all have log-normal fire-size distributions in which large fires are exponentially less frequent than small fires (Hantson et al. 2016). Historical fire-

Table 2. Examples of probabilistic studies and ancillary supporting sources that showed evidence of historical mixed-severity fire regimes, with substantial area of high-severity fire, that fostered heterogeneous historical dry-forest landscapes in the western United States.

Data source	Author(s)	Location(s)
Probabilistic		
Early aerial photographs	Hessburg et al. (2007)	WA, OR
Forest Inventory and Analysis data	Odion et al. (2014)	W USA
Early forest-reserve reports	Baker et al. (2007), Baker (2012, 2014), Williams and Baker (2014)	AZ, CA, OR, Rocky Mountains
Reconstructions–General Land Office surveys	Williams and Baker (2012a, b)	AZ, CO, OR
Reconstructions–Tree-rings at landscape scale	Sherriff et al. (2014)	CO
Ancillary supporting sources		
Early historical accounts	Baker (2012, 2014)	CA, OR
Early photographs	Baker (2009)	Rocky Mountains
Reconstructions–Paleo-charcoal	Compilation in Baker (2015)	W USA

Note: AZ, Arizona; CA, California; CO, Colorado; OR, Oregon; WA, Washington; W USA, western USA.

size and patch-size distributions in dry forests also had inverse-J shapes suggesting log-normal distributions (Williams and Baker 2012a, Baker 2017a). While rare, LIDs could be concentrated in episodes across large land areas, as were severe fires in the late 1800s in the southern Rocky Mountains (Veblen et al. 2000, Schoennagel et al. 2011, Baker 2017b), and large MPB outbreaks across the western United States and Canada (Jarvis and Kulakowski 2015).

The severely disturbed extent of LIDs had historical rotations (the expected time to affect the area of a landscape once) of one or more centuries. High-severity fires that killed >70% of basal area in dry forests historically had rotations of about 2–8 centuries (Baker 2015); moderate- to high-severity fires that killed 20% or more of basal area had rotations of 235–319 yr (Odion et al. 2014). Tree age distributions and early observations suggest large insect outbreaks and droughts were also infrequent events in dry forests (Blackman 1931, Swetnam and Betancourt 1998). The historical rotation for outbreaks of MPB, the main outbreak beetle in the western United States (Meddens et al. 2012), might be somewhat longer in ponderosa pine than lodgepole pine (*Pinus contorta*) forests, since ponderosa pine forests are more heterogeneous (Chapman et al. 2012). Jarvis and Kulakowski (2015) reconstructed MPB outbreaks in lodgepole pine at 10 sites in 200,000 ha of western Colorado and found four episodes from 1742 to 1910 that affected 0.5, 0.7, 0.5, and 0.4 of the 10 sites, a rotation of about 80 yr (168 yr/2.1). The rotation for drought-caused mortality in dry

forests is unknown as there are no historical reconstructions. Pan-continental droughts that affected several U.S. regions occurred historically in ~12% of the last 1000 yr, but megadroughts of a decade or more, mainly in the Southwest and Central Plains, were rare in the last 500 yr (Cook et al. 2014). The 1574–1594 event, mentioned earlier, is the only historical one known to have caused extensive mortality in dry forests.

In the case of fires, the few percent that are large typically account for most of the total burned area (Strauss et al. 1989) and are often more intense (Swetnam and Baisan 1996). This importance of only a few percent of fires, the largest fires, to total burned area is evident in modern dry forests (Farris et al. 2010) and other forests (Baker 2009). Larger fires often have a mix of intensities and higher intensity, since fires become large because of rapid spread, driven by wind and drier fuels that allow more fuel consumption, increasing fire intensity (Alexander 1982). Large beetle outbreaks and lengthy droughts also appear to cause most tree mortality (Allen et al. 2010, Baker and Williams 2015, Graham et al. 2016), likely because resistance thresholds in trees are difficult to cross with smaller, less severe events (Romme et al. 1998).

Large, infrequent disturbances updated resistance, resilience, and legacies that facilitated recovery and bet-hedging

Large, infrequent disturbances with varying severities historically provided episodic adjustment across dry-forest landscapes, reducing area,

density, and basal area of less disturbance-resistant trees, while increasing more disturbance-resistant trees, although current trees simply regenerate at times. Competition was lessened and the canopy was opened (Fig. 3a, b), often reducing vulnerability to subsequent disturbances for decades or longer (Parks et al. 2016).

Large, infrequent disturbances episodically tested and updated resistance, resilience, and bet-hedging across changing landscapes. Large, infrequent disturbances fostered diverse surviving tree species, sizes, and regeneration strategies that provided resistance and resilience to subsequent diverse disturbances (Table 3). This diverse stand and landscape structure and composition after LIDs could effectively provide stand- and landscape-level bet-hedging against an uncertain array of subsequent disturbances (Baker and Williams 2015). At the stand scale, bet-hedging was provided by combinations of large, old trees with thick bark that resisted mortality in fires and some beetle outbreaks (Graham et al. 2016, Welch et al. 2016), abundant small trees that resisted mortality in beetle outbreaks and droughts (Baker and Williams 2015), and diverse tree species so that some trees were not vulnerable to particular insects or diseases. At the landscape scale, areas of large trees, other fire-resistant trees, and low tree density provided landscape resistance to severe fires. Low-to-moderate fuel continuity allowed fires to spread, but with patchiness. Openings reduced ignitions, slowed disturbance spread, and reduced severity, while natural breaks could slow or terminate fires. Low-moderate contiguity of large trees and diverse patches may have reduced beetle spread and limited the size of patches of tree mortality (Graham et al. 2016). Young, recovering forests had high tree survival in beetle outbreaks (Graham et al. 2016) and droughts (Allen et al. 2010).

Natural recovery exemplifies resilience: "...the capacity of a system to absorb disturbance and reorganize while undergoing change so as to retain essentially the same function, structure, identity and feedbacks" (Walker et al. 2004:2). Large, infrequent disturbances in dry forests left behind complex effects from variable disturbance types and severities (Fig. 3), and these legacies (Foster et al.

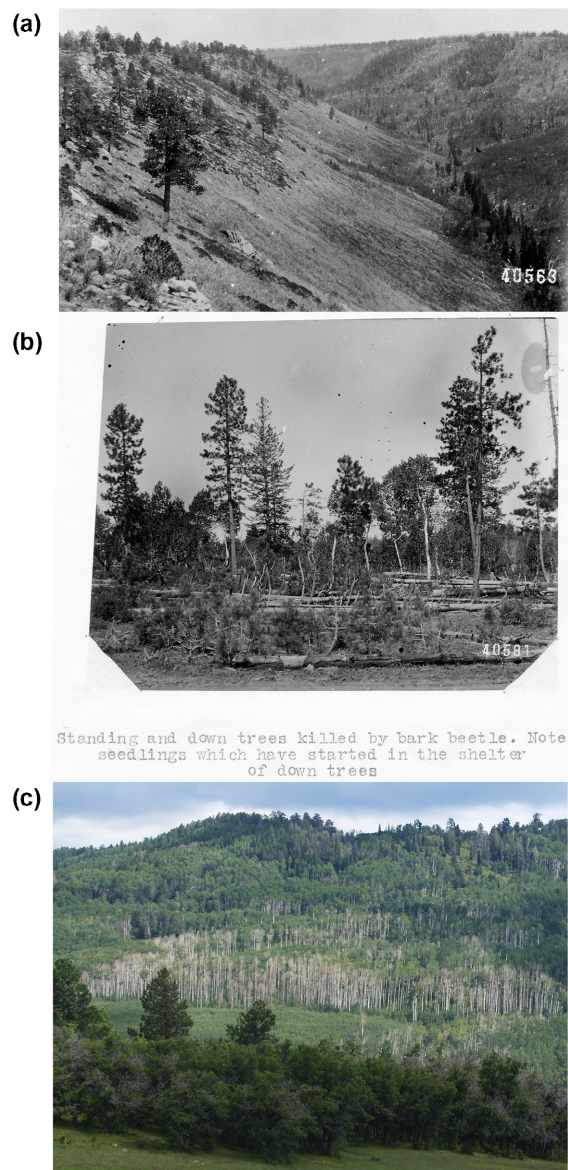


Fig. 3. Legacies after large, infrequent disturbances in dry forests: (a) a historical moderate- to high-severity fire in dry forests on the Uncompahgre Plateau, western Colorado, photograph in 1903 from Riley (1904); (b) a historical beetle outbreak in dry forests on the Uncompahgre Plateau, western Colorado, photograph in 1903 from Riley (1904); and (c) sudden aspen decline (SAD), a recent drought-linked disturbance, in southwestern Colorado, photograph by W. L. Baker, in 2006.

Table 3. Some historical structures (table entries), created by LIDs and environmental heterogeneity, that provided resistance and resilience at the stand and landscape scales to the three main types of LIDs in dry forests.

Property	Moderate- to high-severity fires	Beetle outbreaks	Droughts
Resistance–stand scale	Abundant large trees, some small trees	Abundant small trees, some large trees	Abundant small trees
	Fire-resistant trees	Diverse tree species	Diverse tree species
	Moderate fuel continuity (e.g., patches of rocks, low fuels)	Contiguous patches of small trees	Diverse topo-edaphic settings, some with more moisture
	Lower tree density/fuels, where this occurred, reducing fire severity	Lower tree density, where this occurred	Lower tree density, where this occurred
	Higher tree density/cover leading to shaded, moister fuels, where this occurred		
Resistance–landscape scale	Areas of large trees	Low–moderate contiguity of areas of large trees	Low–moderate contiguity of areas of large trees
	Areas of fire-resistant trees	Diverse patches dominated by different tree species	Diverse patches dominated by different tree species
	Areas of low tree density/fuels, where they occurred	Areas of low tree density, where they occurred	Areas of low tree density, where they occurred
	Limited areas of young, recovering forests	Large areas of young, recovering forests	Large areas of young, recovering forests
	Moderate fuel continuity	Discontinuous suitable host trees	
	Areas of higher tree density/cover leading to shaded fuels		
	Openings that slowed fire spread (e.g., grasslands, wetlands)	Openings that broke up contiguous suitable host trees	
	Natural fire breaks (e.g., rock outcrops, streams, moist stands)	Natural openings with few or no host trees	
Resilience–stand scale	Resprouting trees and shrubs	Resprouting trees and shrubs	Resprouting trees and shrubs
	Surviving large seed trees, some patches of surviving small trees	Abundant small trees, some large surviving trees for seed	Abundant small trees, some large surviving trees for seed
Resilience–landscape scale		As much diversity in tree species as possible	As much diversity in tree species as possible
	Large seed trees, likely to survive, every 50–100 m, limited patches of small trees	Large areas with abundant small trees likely to survive, some patches of large trees	Large areas with abundant small trees likely to survive, some patches of large trees
	Diverse tree densities, basal areas, and tree species composition	Diverse tree densities, basal areas, and tree species composition	Diverse tree densities, basal areas, and tree species composition
	Most severely burned area within 100–200 m of an unburned edge	Patches with a diversity of dominant tree species	Patches with a diversity of dominant tree species

Note: LIDs, large, infrequent disturbances.

1998) or ecological memory (Johnstone et al. 2016) facilitated natural recovery. Resilience was enhanced by resprouting trees and shrubs, large old trees that provided post-disturbance seed, and variable tree densities and basal areas that provided diverse post-disturbance recovery (Table 3).

Highly variable historical tree regeneration, particularly in the Southwest

Successful ponderosa pine regeneration was limited by a required coincidence of favorable

processes from seed formation to seedling survival (Pearson 1923, Feddema et al. 2013, Savage et al. 2013). However, land-survey records from 22,206 km of transects across 1.7 million ha of dry forests in the late 1800s showed that seedlings and/or saplings were present over 35–57% and dense over 20–30% of dry-forest area in Oregon, California, and part of northern Arizona (Baker and Williams 2015). Pulses of regeneration seen in some age structures were favored by canopy-reducing disturbances, particularly fire

that created mineral seedbeds and reduced competition by grass, followed by fire-free periods or pluvials, that sustained regeneration (Dugan and Baker 2015). Moderate- to high-severity fires led to more regeneration than did low-severity fires (Wu 1999, Ehle and Baker 2003, Schoennagel et al. 2011, Baker and Williams 2015).

About 14% of dry-forest area, mostly in the Southwest, had sufficiently frequent low-severity fire (Baker 2017a) and drier climate to potentially limit regeneration to exceptional pluvials and fire-free periods (Covington and Moore 1994, Savage et al. 1996, 2013). Land-survey records document that seedlings and/or saplings were present over only 4–13% of two large landscapes in Arizona and one in Colorado (Baker and Williams 2015). However, forest age structure in two cases showed more continuous regeneration not limited to wet or fire-free periods, with broad peaks evident in one case (Mast et al. 1999). Broad episodes bring into question whether regeneration was rare and confined to unusual climatic episodes (Savage and Mast 2005).

Contrasting regeneration findings in the Southwest are also documented in early forest-reserve reports. Leiberg et al. (1904:28) said of the 329,000-ha San Francisco Peaks forest-reserve area on the western part of the Mogollon Plateau in northern Arizona:

Reproduction of the yellow pine is, generally, extremely deficient as regards seedling and young sapling growth, except in an area lying east of Stoneman Lake and south of Mormon Lake. Apparently there has been an almost complete cessation of reproduction over very large areas during the past twenty or twenty-five years, and there is no evidence that previous to that time it was at any period very exuberant.

What happened to favor regeneration near the lakes is unexplained, but a nearby landscape also had abundant regeneration. Stabler (1906:7) said of the eastern extension of the Mogollon Plateau onto Black Mesa and into the White Mountains:

The reproduction of the yellow pine portion of the commercial forest type is wonderfully good. This in spite of the fact that the pine bunchgrass is as a rule very thick and vigorous and but little of it kept down by grazing. The fact that the grass is not grazed makes the numerous ground fires more serious than they otherwise would have been, but in spite of these fires...the reproduction is good and occurs in all ages.

A compelling explanation is lacking for contrasts in historical regeneration over large land areas.

Historically slow and incomplete natural recovery after LIDs in dry forests

Severely disturbed dry forests historically regenerated variably, but often slowly, and could remain unforested or sparsely forested for ≥ 100 yr (Table 4). Post-fire regeneration was at times very dense over extensive area in the Southwest (Fig. 4a, b). High-severity fires could be followed by extended tree regeneration lasting 20–60 yr, which could also be lagged by 15–20 yr and even have >50-yr lags with little or no tree regeneration (Table 4). Openings (grasslands, shrublands) created or maintained by high-severity fires could persist for 130–150 yr or more (Tables 4, 5) and be quite large. For example, in the Sierra, Shaw (1924:83) reported:

Perhaps the most striking characteristic of the timber region of northern California... is the very large area occupied by brushfields. The brushfields, for the most part, are the results of fires which have destroyed the timber and allowed the brush to occupy the ground; in round numbers 1,500,000 acres [607,000 ha] are now in this condition. Of this million and a half acres probably 75% is restocking naturally, scattered individuals and groups of trees having survived the fires of the past, and can be depended on to take care of themselves....

Forests often, but not always, recovered after intense fires, particularly if surviving seed trees were nearby; if so, trees regenerated and tree density and basal area increased, and forests often became denser (Fig. 4c). Probabilistic studies found dense middle-aged forests and created or maintained grasslands and shrublands in all dry-forest landscapes (Table 2). However, many pathways of forest recovery likely occurred (Kashian et al. 2007). In dry forests, open forest patches and some dense forest patches may have simply persisted and grown older, and some dense forest patches may have been thinned by competition or disturbances (Oliver 1995, Zhang et al. 2013) until a mature forest re-established (Moir and Dieterich 1988).

Including the lag before tree regeneration, recovery of a mature forest after high-severity fire historically required >100 yr (Table 6). Old growth could be reached within 150–200 yr (Mehl 1992, Hamilton 1993), but 150–300 yr for

Table 4. Historical lags in tree regeneration and the length of successful episodes of natural tree regeneration after high-severity fires in dry forests, based on tree-ring reconstructions and early observations.

Topic/Author(s)	Location	Observation
Huckaby et al. (2001)	Front Range, Colorado	Tree regeneration delayed on average by 18 yr after high-severity fires, ranging from 0 to 33 yr for 16 fires from A.D. 1531–1880
Boerker (1915:15)	Western Sierra, California	“Unlike the chaparral regions of southern California, this brush is only a temporary type and is, in most cases, the result of fire having destroyed the forest cover. . . In most cases, in from 5 to 10 years after the fire has consumed the timber, the brush takes possession of the land. . . after the brush has established itself, if seed trees are nearby, seedlings will get started and fight their way through the brush. It takes from 15 to 30 years for a seedling to get large enough to overtop the brush. . .”
Wu (1999)	San Juan Mts., Colorado	Tree regeneration concentrated within 20 yr after higher-severity fires
Baker (2017b)	Uncompahgre, Colorado	Tree regeneration sparse or lacking in a stand 24 yr after high-severity fire
Ehle and Baker (2003)	Front Range, Colorado	Tree regeneration concentrated within 20–25 yr after high-severity fires
Nagel and Taylor (2005:448)	Lake Tahoe Basin, California	“Tree regeneration into the chaparral stands was highest during the first two or three decades after the fire [6 fires in 1861–1882], but tree establishment continued for at least five decades after the last fire in all of the stands”
Lauvaux et al. (2016:82)	Southern Cascades, California	“Tree populations were multi-aged. Initial establishment [after 6 fires in 1864–1918] was slow and typically peaked five or more decades after the fire”
Duthie (1914:14)	Front Range, Colorado	Tree regeneration sparse or lacking for first 50 yr: “A careful reconnaissance of the region made in 1911 showed that there are over 10,000 acres of land from which all forest cover was consumed by these fires half a century ago, and upon which there has been practically no natural restocking”
Sherriff (2004)	Front Range, Colorado	Tree regeneration concentrated within 19–60 yr after high-severity fires
Huckaby et al. (2001:25)	Front Range, Colorado	“... openings were created by a fire in 1851, and remained unreforested 149 years later. . . the northern part of the area may have burned again in 1880, slowing tree regeneration”
Kaufmann et al. (2003:239)	Front Range, Colorado	“... historical mixed severity fires and delays of regeneration into openings created by fire contributed to a very open, spatially complex and temporally dynamic landscape structure”
Pearson (1914:249)	Arizona and New Mexico	“A characteristic feature of the timbered mountains in Arizona and New Mexico at altitudes above 8000 feet is the occurrence of extensive burns. The original forests below 9500 feet were composed mainly of western yellow pine (<i>Pinus ponderosa</i>), Douglas fir. . . , limber pine. . . , Mexican white pine. . . , and white fir. . . The greater portions of the burns have grown up to quaking aspen. . . , but extensive areas are practically bare. Scattering trees of the original forest usually remain, and where this condition exists or where the burn is comparatively small conifers are generally restocking the land. . .”

conifers to regain dominance over aspen in mixed-conifer forests (Table 6). Historical high-severity fire rotations of 2–8 centuries (Baker 2015) would have often allowed full recovery to old growth before the next high-severity fire.

Fluctuating historical dry-forest landscapes of recovery had heterogeneous structure

Overall, historical dry-forest landscapes in the western United States fluctuated from infrequent

large natural disturbances that included substantial severe fires, beetle outbreaks, and droughts that killed many trees, leaving a diversity of legacies, followed by 100–300 yr of natural recovery. Where tree density and basal area were reduced, vulnerability to droughts and beetle outbreaks often declined; where old trees persisted, vulnerability to severe fires was reduced. Slow, variable post-disturbance tree regeneration and growth made natural recovery after LIDs a dominant

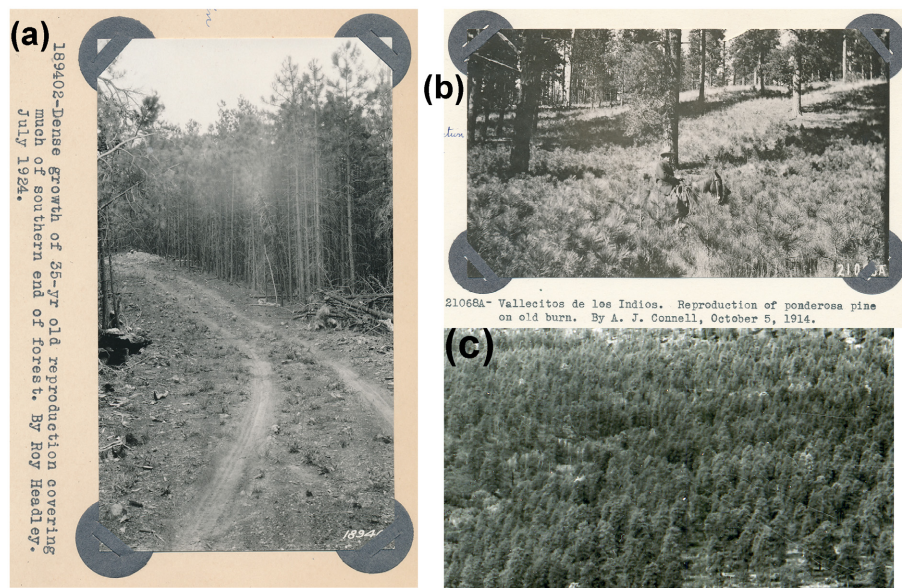


Fig. 4. Dense historical ponderosa pine regeneration after fire in the Southwest: (a) after likely large high-severity fire in the late 1800s in ponderosa pine forests, southern Coconino National Forest, Mogollon Plateau, Arizona, photograph taken in 1924 by Roy Headley, Historical Photo Collection, Region 3, U.S. Forest Service, Albuquerque, New Mexico; (b) after fire in the Jemez Mountains, New Mexico, photograph taken in 1914 by A. J. Connell, Historical Photo Collection, Region 3, U.S. Forest Service, Albuquerque, New Mexico; and (c) an example of a dense middle-aged historical forest, reproduced from a zoom of the right center of Fig. 2, an 1897 photograph by Whitman Cross.

ongoing process in most historical dry-forest landscapes. Episodes of LIDs across large areas meant that large land areas may have been synchronously recovering from natural disturbances. Infrequent disturbances and slow, variable natural recovery explain why historical dry-forest landscapes were spatially heterogeneous with a mix of old forests, middle-aged forests, recently disturbed forests, large and small openings with incipient or nearly completed regeneration, and more persistent openings, as documented by probabilistic landscape-scale studies (Table 2). This stand and landscape diversity conferred resistance, resilience, bet-hedging, and adaptation to diverse, unpredictable future disturbances, but substantial fluctuation still occurred.

EMERGING PATTERNS OF TRANSITION TO COMMITTED WARMING

Tree-mortality agents in dry forests over the last few decades

Increased tree mortality and regeneration decline or failure are expected during the

transition. Increasing tree mortality is evident around the world (Allen et al. 2010). In dry forests, mortality is occurring from fires, beetle outbreaks, and directly from drought and temperature stress (Anderegg et al. 2013). Background rates of tree mortality (non-catastrophic, including all agents) increased significantly (3.3% per year, a doubling time of 22 yr), likely from warming, in the 15 old-forest plots most likely in dry forests, since they had short mean fire intervals (Van Mantgem et al. 2009: Table 1). In all plots censused from 1955 to 2007 across the western United States, 19% of trees died over the roughly 50-yr period (Van Mantgem et al. 2009), which is a 263-yr rotation (50/0.19). That would not lead to lasting loss of old forests, as 263 yr is ample time to regrow old trees, but if mortality doubled further, then it could become very limiting, and drought and heat stress could become the main cause of tree mortality (Allen et al. 2010).

Even with more severe (non-background) mortality from beetle outbreaks, droughts, and fires, there are survivors that play key stand-level roles

Table 5. Longer-term studies and observations of post-fire creation or maintenance of grasslands and shrublands after historical high-severity fires in dry-forest landscapes of the western United States.

Author(s)	Location	Years after fire	Observation
Guiterman (2016)	Jemez Mts., New Mexico	>115	Most of the area of 5 large patches (totaling 1142 ha) of mixed montane shrubland, dominated by Gambel oak (<i>Quercus gambelii</i>) that originated primarily in 1894–1900 remained largely unforested. Originating fires were likely mixed- to high-severity
Baker (2014)	Sierra Nevada, California	109–118	About 22% of montane chaparral, likely burned in high-severity fires in the late 1800s, did not become forested, and instead remained as montane chaparral, over periods of 109–118 yr
Nagel and Taylor (2005)	Northern Sierra, California	~ 120–140	About 38% of montane chaparral patches that originated after high-severity fires in 1861–1882 had not become forested by the 2000s
Lauvaux et al. (2016)	Southern Cascade Mts., California	~ 100–150	About 35% of montane chaparral patches that originated after high-severity fires in 1864–1918 had not become forested by the 2010s
Huckaby et al. (2001), Baker (2009:249)	Front Range, Colorado	~ 120–150	By about A.D. 2000 [120–50 yr after fires], some forests burned in high-severity fires in 1851 or 1880 had recovered to dense, middle-aged forests, but some openings were still unforested grasslands that were slowly reforesting
Baker (2017b)	Uncompahgre Plateau, Colorado	~ 130–150	About 40% of a large ponderosa pine and mixed-conifer landscape with evidence of high-severity fire in the late 1800s was nonforested (e.g., shrubs, small trees, grasslands); about half the nonforested area that was a mixture of grasslands, shrublands, recent burns, and areas with small trees was not forested by 2010, likely indicating at least century-scale stability after high-severity fires

in forest resilience (Table 3). In beetle outbreaks, most smaller trees survive as do some percentage of larger trees. A 1965–1978 MPB outbreak in the Colorado Front Range killed 25% of ponderosa pines of all sizes, especially 20–36 cm dbh, and reduced basal area by 38% (McCambridge et al. 1982). In British Columbia, a more severe 2005–2008 MPB outbreak, also with western pine beetle (*Dendroctonus brevicomis*), killed ~80% of trees, including 23–42% <15 cm dbh, 81% 15–30 cm, and 94% >30 cm over >175,000 ha, with little variation across a wide range of tree densities (Klenner and Arsenault 2009). In the Black Hills of South Dakota and Wyoming, an MPB outbreak over ~157,000 ha in 2004–2014 mostly killed ponderosas 23–43 cm dbh (Graham et al. 2016). Stands with <21 m²/ha of basal area were little affected, but mortality increased up to 28–34 m²/ha, where 74% of trees were killed, but 60% for >34 m²/ha (Graham et al. 2016). Many trees survived, with means of 141 trees/ha of tree density and 11.7 m²/ha of basal area. After beetle outbreaks, there were surviving trees of all sizes,

especially small trees, as well as patches of surviving trees (Six et al. 2014). Dry forests were substantially renewed, and yet able to persist.

Mortality from droughts in dry forests has not been isolated, as beetles often ultimately kill many drought-affected trees. However, similar mortality patterns were evident with trees of all sizes killed and the highest percent mortality in larger trees (Ganey and Vojta 2011). Droughts put tall, old conifers especially at risk of replacement by shorter trees and shrubs (Bennett et al. 2015, McDowell and Allen 2015, McDowell et al. 2015), because taller trees are more physically vulnerable to failure to conduct water. A surprising 70% of a global sample of trees, in both dry and wet environments, operates with low physiological safety margins for escaping mortality from drought (Choat et al. 2012). Mortality consistent with these drought vulnerabilities is already occurring (Bennett et al. 2015). In contrast, larger trees generally better survive fires, because of thicker bark, elevated branches, and other adaptations (Baker 2009).

Table 6. Longer-term studies and observations of post-fire recovery to forest after historical high-severity fires in dry-forest landscapes of the western United States.

Author(s)	Location	Years after fire	Observations of post-fire succession in dry forests
MacKenzie et al. (2004)	Western Montana	60–100	Tree density/basal area approached pre-fire level within about 60–100 yr, basal- area increase slowed ~ 100 yr after high-severity fire
Baker (2014)	Sierra Nevada, California	109–118	About 78% of chaparral, likely burned in high-severity fires in the late 1800s, became forested over periods of 109–118 yr
Smith and Smith (2005), Baker (2017b)	Uncompahgre Plateau, Colorado	100–137	Conifers can begin to overtop aspen within about 100 yr, with mixed conifer–aspen stands at about 137 yr after high-severity fires
Nagel and Taylor (2005)	Northern Sierra, California	~ 120–140	About 62% of montane chaparral patches that originated after high-severity fires in 1861–1882 had become forested by the 2000s
Lauvaux et al. (2016)	Southern Cascade Mts., California	~ 100–150	About 65% of montane chaparral patches that originated after high-severity fires in 1864–1918 had become forested by the 2010s
Huckaby et al. (2001), Baker (2009:249)	Front Range, Colorado	~ 120–150	By about A.D. 2000 [120–150 yr after fires], some forests burned in high-severity fires in 1851 or 1880 had recovered to dense, middle-aged forests, but some openings were still reforesting
Baker (2017b)	Uncompahgre Plateau, Colorado	~ 130–150	About 40% of a large ponderosa pine and mixed-conifer landscape was nonforested (e.g., shrubs, small trees, grasslands) in the late 1800s; about half that area had become forested by 2010, likely indicating natural recovery after high-severity fires
Leiberg (1902:74)	Western Sierra, California	150	“The yellow pine on these tracts is mostly old growth; that is, the greater percentage of suitable size for mill timber is over 150 years of age”
Wu (1999:134)	San Juan Mts., Colorado	~ 150–200	“Even-aged stands still maintain their structure, such as a prominent post-fire cohort of aspen or ponderosa pine, 150 years after their last lethal fires, which occurred in the period from 1850 to 1880. . .therefore, this study estimates that all-age structure requires at least two hundred years to develop”
Kercher and Axelrod (1984)	Western Sierra, California	~ 250	Simulation suggested that about 250 yr would be required for Sierran mixed-conifer forests to recover and stabilize after severe disturbance
Baker (1925:89)	Central Rocky Mountains	≥250	“On the assumption that conifers found in the aspen zone will bear seed at 80 years, most areas ought to be well seeded in with reproduction in three tree generations or about 250 years in the Douglas fir-white fir zone. . .certain areas in the lower zones may require more than 250 years. . .”
Duthie (1914:14)	Front Range, Colorado	200–300	“It is estimated that two or three centuries would elapse before these burns would again be fully reforested if natural regeneration were depended upon to produce a satisfactory forest cover” (describing recovery after high-severity fires that occurred a half century earlier)
Zier and Baker (2006:261)	San Juan Mts., Colorado	Long periods	Over about a century, 40% of mixed-conifer forests visible in 25 scenes in early photographs showed increased conifers, while in 60%, there was no change in proportions of aspen and conifers, suggesting that “...long periods of time may be needed for conversion from aspen to conifers, if it occurs at all”

Given these vulnerabilities and documented mortality effects, what were recent sources of mortality; were severe fires, beetle outbreaks, or droughts the largest cause of non-background

tree mortality over the last few decades? Details of analysis are in Appendix S1. Most important from this analysis is that insects-disease, on average, overall led to 2.1 times as much mortality

area as did moderate- to high-severity fires, 1.7 times in ponderosa, and 2.6 times in dry mixed conifer (Table 7). Estimated rotations were 565 yr for moderate- to high-severity fires and 221 yr for insects-disease in dry mixed-conifer forests (Table 7). Rotations were 408 yr for moderate- to high-severity fires and 247 yr for insects-disease in ponderosa pine. These are similar to 2003–2012 mortality rotations of 500 yr for fire and 286 yr for beetles across all forests of the western United States from the inverse of annual mortality of 0.20% for fire and 0.35% for beetles, and the ratio of insects-disease to moderate- to high-severity fire of 1.75 is also similar (Berner et al. 2017). Under a hypothetical California-type drought scenario moving across dry forests (Appendix S2), an affected area of 5.5 million ha every six years would have a mortality area of 1.3 million ha (24%); if half from direct drought mortality, this would be a drought mortality rotation of 191 yr (6 yr/(0.65 million ha/20.7 million ha)). If so, droughts and insects-disease would likely account for about 3–4 times as much mortality area as severe fires.

Recent sizes and rates of beetle outbreaks, droughts, and moderate- to high-severity fire in dry forests are probably not yet outside the historical range of variability (Table 8), although evidence about historical variability is limited and

some individual events have been exceptional locally (e.g., 2012–2016 California drought). Large beetle outbreaks have individually affected up to about 175,000 ha in dry forests, approaching the same scale as the 200,000- to 300,000-ha outbreak in the Black Hills in 1895–1909. The estimated recent beetle mortality rotation of 241 yr would not preclude full recovery of old-growth forests during or after the transition. The historical beetle-outbreak mortality rotation is too poorly known to be certain that this recent rate is or is not similar. Available evidence is insufficient to be able to assess historical vs. recent drought impacts on dry forests, but drought rates themselves are in general not outside historical variability in the western United States (Wuebbles et al. 2017; Appendix S3). However, if the frequency distribution of droughts does not change, $\sim 1^\circ\text{C}$ elevated temperature alone will cause an increase in drought events sufficient to kill ponderosa pine seedlings by about 1.8 events by A.D. 2100 under RCP 2.6 (Adams et al. 2017). Larger recent moderate- to high-severity fires have individually affected about 30,000–60,000 ha, except for the 128,000-ha Rodeo–Chediski fire in Arizona (Table 8). Historical fire-size evidence is limited, in general, but the area burned at moderate to high severity on the Uncompahgre Plateau, Colorado, likely in 1879, was at the scale of about

Table 7. Affected area and estimated mortality area in dry forests across the western United States from 1999 to 2012 ($n = 14$ yr) from moderate- to high-severity fire and insects-disease.

Area and measure	Ponderosa pine	Dry mixed conifer	Total
Affected area			
Fire area (ha)	518,580	415,971	934,551
Insects-disease area (ha)	2,319,651	2,874,101	5,193,752
Fire rotation (yr)	265	367	311
Insect rotation (yr)	59	53	56
Ratio: insects-disease/fire area	4.5	6.9	5.6
Mortality area from multiplying affected fire area by 0.65 and affected insects-disease area by 0.24			
Fire area (ha)	337,077	270,381	607,458
Insects-disease area (ha)	556,716	689,784	1,246,500
Fire rotation (yr)	408	565	478
Insect rotation (yr)	247	221	233
Ratio: insects-disease/fire area	1.7	2.6	2.1
Fire area in 40 yr (% of total), if no change	9.8	7.1	8.4
Insects-disease area in 40 yr (% of total), if no change	16.2	18.1	17.2
Fire area in 40 yr (% of total), if projected	15.4	10.5	12.8
Total analysis area (ha)	9,825,679	10,910,705	20,736,384

Notes: Data on affected areas and total analysis areas are from Baker and Williams (2015). See Appendix S1 for an explanation of estimation of mortality area.

Table 8. Comparative sizes, durations, and rotations of recent large infrequent disturbances in dry forests and the expected mortality area during the 40-yr transition.

Attribute	Insects-diseases	Droughts	Moderate- to high-severity fires
Example events among the largest (ha) events since 1984 in dry forests†	~ 157,000 ha SD/WY‡ >175,000 ha BC§	~ 5, 500,000 ha CA¶ ~ 700,000 ha U.S.#	30,146-ha 2012 Whitewater Baldy, NM 34,432-ha 2002 Hayman, CO 36,611-ha 2012 Ash Creek, MT 50,287-ha 2013 Rim, CA 56,174-ha 2011 Wallow, AZ 127,667-ha 2002 Rodeo-Chediski, AZ
Duration of these example events (yr)	4–14	5	1
Estimated recent mortality rotation (yr) across total dry-forest area††	233	191	478
Estimated historical mortality rotation (yr) across total dry-forest area for reference	>333‡‡	Unknown	362–491§§
Expected mortality area (% of total dry-forest area) in transition if no change in rotation¶¶	17.2	20.9	8.4
Projected mortality area (% of total area) in transition if climate change shortens rotation¶¶¶	Not available	Not available	12.8

Note: Province and state abbreviations: AZ, Arizona; BC, British Columbia; CA, California; CO, Colorado; NM, New Mexico; SD, South Dakota; WY, Wyoming.

† These are affected areas, in ha, not mortality areas.

‡ Graham et al. (2016).

§ Klenner and Arsenault (2009).

¶ From Tree Mortality Task Force (2017) and Potter (2017).

From Worrall et al. (2013) for roughly the area of aspen decline affecting dry mixed-conifer forests.

|| From MTBS data (www.mtbs.gov); the area is the sum of the moderate- and high-severity classes in the MTBS pdf map of each fire.

†† From the text, in the case of drought, and from Table 7, in the case of fire and insects-diseases; rotation is the time, in years, it is expected to take for these disturbances to affect land area equal to whole landscapes.

‡‡ The original rotation estimate of >80 yr for affected area is given in the text. The rotation for mortality area can be estimated by dividing by 0.24, which is the estimate from Hicke et al. (2016) used in Table 7.

§§ The original rotation estimate from Odion et al. (2014) was 235–319 yr for affected area, and the rotation for mortality area can be estimated by dividing by 0.65, as explained in the text and used in Table 7. After division, the original 235–319 yr range becomes 362–491 yr.

¶¶ From Table 7.

75,000–90,000 ha (Baker 2017b), thus similar to larger recent fires. The geometric mean higher-severity patch size was 47% lower in the recent than the historical period across 624,156 ha of dry forests in the Colorado Front Range (Williams and Baker 2012a). Moderate- to high-severity fire in dry forests was not operating from 1984 to 2012 at rates that exceeded historical rates, and the fraction of fires that burned at high severity had not increased (Baker 2015). The recent fire-mortality rotation for moderate- to high-severity fires of 478 yr is within, but toward the long end of the estimated historical rotation of 362–491 yr (Table 8).

Assuming no increase, in ponderosa pine, a resulting fire-mortality rotation of 408 yr would lead to expected mortality area of 9.8% over the 40-yr transition (Table 7). In dry mixed conifer, a

fire-mortality rotation of 565 yr would lead to mortality area of 7.1%. In ponderosa pine, an insects-disease mortality rotation of 247 yr would lead to mortality area of 16.2% over the 40-yr transition (Table 7). Similarly, in dry mixed conifer, an insects-disease mortality rotation of 221 yr would lead to mortality area of 18.1% (Table 7). Under a California-type drought scenario, a 191-yr mortality rotation would lead to a mortality area of 20.9%. Overall, if no change in rates over the 40-yr transition, actual mortality area from fire and insects-disease would total ~26% of dry-forest area, 1/3 from moderate- to high-severity fires and 2/3 from insects-disease, a mortality rotation of 154 yr, which could still leave substantial area of old forests by the end of the transition. However, if a California-drought scenario ensued, an added 21% in 40 yr could

lead to a total mortality area of $\sim 47\%$, a rotation of ~ 85 yr, which could leave much less old forest, since it is particularly vulnerable to droughts and beetles.

Projecting possible increases in these disturbances during the 40-yr transition period is only roughly possible, and only for fire (Table 7; Appendix S3). There are no specific projections for only 1.5–2.0°C of warming on drought, fire, and insects. The U.S. Global Change Research Program reported low-to-medium confidence in a current anthropogenic climate-change effect on fire in the western United States (Wuebbles et al. 2017). Nonetheless, to estimate an upper bound on possible increases in moderate- to high-severity fire in dry forests, I used the midpoint of the low range of projected increases in area burned by A.D. 2046–2065 across 23 analysis areas under moderate emissions (RCP 4.5), which is 1.57 in ponderosa pine and 1.48 in dry mixed conifer (Baker 2015). These were the most recent area-burned projections, which are needed to estimate future mortality area. Using these, the percentage of mortality area from fire would increase from 9.8% to 15.4% in ponderosa pine and from 7.1% to 10.5% in dry mixed-conifer forests (Table 7). If combined with the hypothetical California-drought scenario, the total could reach about 51%.

Recent and projected tree regeneration in dry forests

Is there evidence of tree-regeneration decline in dry forests that could make the forest loss from tree mortality more permanent? Current rates and patterns of tree regeneration in all dry forests are relevant, but the only systematic monitoring is by the Forest Inventory and Analysis Program (FIA). Since 1995, FIA data are remeasured at 5- to 10-yr intervals on plots each representing about 2429 ha (Bechtold and Patterson 2005). Forest Inventory and Analysis data were used to analyze recent recruitment of juvenile vs. adult trees relative to climate in the western United States (Bell et al. 2014, Dobrowski et al. 2015). Ponderosa pine and Douglas-fir seedlings were much less likely to be present than were adults (28,177 plots), particularly along the warmer western and southern range margins of ponderosa pine (Bell et al. 2014). Similarly, for most conifers (13 species in 33,665 plots) in dry forests, juveniles occupied moister sites than did adults

(Dobrowski et al. 2015). A caveat is that historical variability in tree regeneration was naturally high, as reviewed earlier, leaving in question whether these short periods of observation represent lasting trends.

These studies provide context, but tree regeneration after severe disturbances in dry forests is most relevant to the transition, since disturbances leave forests most dependent on regeneration. A focus has been on regeneration after high-severity fires; 24 studies, all I found, showed tree regeneration after these fires was almost universally heterogeneous (Table 9). Within the first 30 yr, substantial area lacked any conifer regeneration, while other area had adequate or dense regeneration (Table 9). Where studied, regeneration density was nearly always lowest in high-severity areas, relative to low- or moderate-severity areas. Ponderosa regeneration was commonly highest adjacent to the unburned margin of the fire and declined into the fire to low levels within 100–200 m, often attributed to seed-dispersal limitations, the hotter environment of open areas, or competition with shrubs or deciduous trees. Studies that analyzed topographic effects found regeneration especially deficient at low elevations and on south-facing slopes. Regeneration after high-severity fires in Colorado was concentrated in only three years with unusually high growing season precipitation over a 24-yr period, based on precisely dated seedlings (Rother and Veblen 2017). Less concentrated years of regeneration were evident in young adult trees, less precisely datable, after older New Mexico fires (Savage et al. 2013). Although regeneration was still sparse and favored near unburned margins at 28 and 45 yr post-fire, it was extrapolated to extend within ~ 50 yr across the 28-yr-old high-severity burn (Haire and McGarigal 2010). Substantial declines in post-fire tree regeneration occurred from warmer and drier conditions since 2000, suggesting possible declines with warming (Stevens-Rumann et al. 2018).

Tree regeneration after recent high-severity fires was often considered unnatural or deficient, but historical evidence now does not support this. Dense regeneration was earlier considered hyperdense and outside the natural range of variability (Savage and Mast 2005). Since then, we have found (1) dense regeneration occurred

Table 9. Studies of tree regeneration up to 64 yr after high-severity fires in dry forests of the western United States arranged by the number of years since fire.

Author(s)	Location	Years after fire	Post-fire seedling/sapling density (trees/ha)
Bonnet et al. (2005)	South Dakota Black Hills	2	>700 ha ⁻¹ in burn (19 transects in 1 fire) within 12 m of unburned edge, declining inward, still some at 120 m, 180 m; positive effect, scorched needles on burned mineral soil; negative, high understory cover
Keyser et al. (2008)	South Dakota Black Hills	2–5	By year 5 (36 sites in 1 fire), >1000 ha ⁻¹ in unburned, low and moderate severity; little in high severity
Meigs et al. (2009)	Oregon Eastern Cascades	4–5	Range 0–62,134 conifers/ha (64 plots in 4 fires); no difference among unburned, low, and moderate severity. In ponderosa forests, no ponderosa regeneration in high-severity fires and in mixed conifer limited conifer regeneration in high-severity fires
Ouzts et al. (2015)	Northern Arizona–New Mexico	7–10	Range 0–1433 conifers/ha (46 plots in 8 fires); 2 fires had 0 conifers/ha 7–10 yr after fire, 5 fires had <50 conifers/ha, 1 fire had 1500 conifers/ha; litter cover positively associated with seedlings
Crotteau et al. (2013)	California Southern Cascades	9–10	Mean 2235 conifers/ha in unburned (60 units in 1 fire), 2252 conifers/ha in low-severity, 7868 conifers/ha in moderate-severity, and 733 conifers/ha in high-severity fire; <i>Abies concolor</i> dominated regeneration over pines in more severe fire areas
Dodson and Root (2013)	Oregon Eastern Cascades	10	Mean 362 conifers/ha (18 plots in 1 fire); Range 0–1807 with 0 in 5 of the 7 plots <1000 m elevation
Collins and Roller (2013:1807)	Northern California Sierra	2–11	Omitting plots with post-fire management (leaving 21 patches in 5 fires), “there was no pine regeneration in over 90% of sampled patches”. No significant effect from distance to unburned forest. Negative effect from shrubs, low seed production or soil moisture
Welch et al. (2016: Fig. 5)	California Sierra, Klamath, Southern Cascades	5–11	Mean about 500 trees/ha in yellow pine (246 plots in 12 fires), about 2000 trees/ha in dry mixed conifer (489 plots in 10 fires), interpolated from a bar graph. Overall across all vegetation types, not just yellow pine and dry mixed conifer, 54% of plots had 0–1 conifers, in interiors of severe burns, in dry areas, where more shrubs
Hanson (2018)	California Sierra Nevada/San Bernardino Mts.	1–12	Mean 3803 conifers/ha at ≤50 m into fire (20 plots in 7 fires), 1850 ha ⁻¹ at 51–150 m into fire (15 plots in 7 fires), 798 ha ⁻¹ at 151–300 m into fire (22 plots in 7 fires), and 336 ha ⁻¹ at >300 m into fire (25 plots in 7 fires). More within 50 m, but no significant difference among other distances. Percent shrub cover not correlated with density of conifer regeneration
Kemp et al. (2016)	Idaho–Montana Northern Rocky Mountains	5–13	Mean 7047–8153 conifers/ha (182 sites in 21 fires); Range 0–127,500 conifers/ha, but 5% of 182 sites had 0 conifers within 500 m; seedling presence probable if within 95 m of live seed source, especially if high basal area; fire severity little effect as most burn area was within 95 m of live trees
Owen et al. (2017)	Northern Arizona	12–13	Mean 84.1 conifers/ha in edge plots (6 plots in 2 fires), 41.4 conifers/ha in interior plots having no surviving trees within 200 m (6 plots in 2 fires); Range 13.0–153.8 conifers/ha in edge plots, 12.0–124.0 conifers/ha in interior plots. Regeneration significantly lower in interiors. Some long-distance dispersal (>300 m) found
Rother and Veblen (2016)	Colorado Front Range	8–15	Mean 37–1424 conifers/ha (302 plots in 6 fires), nearly all lower than pre-fire density, and 59% of plots had 0 conifers in 100 m ² plot, with 83% of plots having <370 conifers/ha. Few seedlings in hot, dry lower elevations or on south-facing slopes, more seedlings within 50 m of live seed source, also in more southerly locations with summer rainfall
Ziegler et al. (2017)	South Dakota, Northern Colorado	11–15	Mean 43.0 trees/ha (18 plots in 3 fires)
Foxx (1996)	Northern New Mexico	0–16	Two sites in 1 fire had no seedlings in year 1, 0 and 210 trees/ha in year 8, and 218 and 318 trees/ha in year 16
Haffey (2014)	Arizona–New Mexico	6–16?	Only 24% of plots (179 plots in 9 fires) had ponderosa pine regeneration; within 150 m of a seed source, 38% of plots had tree regeneration; no regeneration beyond 250 m from a seed source. Nearly half of ponderosa pine seedlings were near a nurse structure, most often a log or large branch
Roccaforte et al. (2012)	Arizona	1–18	Range 0–11,234 conifers/ha (399 plots at 14 sites in 11 fires); 8 sites had 0 conifers/ha 1–12 yr after fire, 3 sites had 37–74 conifers/ha, 2 sites had 297–336 conifers/ha, and 1 site had 11,234 conifers/ha. Deciduous regeneration was dominant at all but 2 sites

(Table 9. *Continued*)

Author(s)	Location	Years after fire	Post-fire seedling/sapling density (trees/ha)
Chambers et al. (2016)	Colorado Front Range	11–18	Mean 225 trees/ha (305 plots in 5 fires) across unburned, low, and moderate severity. Mean tree density lowest in high severity (118 trees/ha) and in only 25% of plots, whereas 60% of low- to moderate-severity plots had regeneration. Regeneration greatest at high elevations and adjacent to unburned, declining to 10 conifers/ha at 200 m
Shatford et al. (2007)	Southern Oregon–Northern California	9–19	Mean 1694 trees/ha (24 plots in 8 fires); Range 83–8188 trees/ha. Plots showed a wide range from immediate and rapid regeneration to slow and constant to chronically limited. No significant effect of distance from seed source on seedling density; up to 84–1100 trees/ha >300 m from a seed source. Positive effect of shrub and hardwood cover
Guiterman et al. (2015)	Northern New Mexico	20	Mean 11 conifers/ha (10 plots in 1 fire); conifers present in 4 of 10 plots; maximum distance from a ponderosa seedling to unburned edge was 77 m
Rother and Veblen (2017)	Colorado Front Range	8–23	Ponderosa pine and Douglas-fir regeneration was concentrated in years with especially high growing season precipitation (413 dated seedlings at 10 sites in 5 fires); for all sites combined, three years (1995, 1998, and 2009) in twenty-four (1988–2011) accounted for most of the post-fire regeneration. Regeneration lags after the 5 fires were 0–4 yr
Passovoy and Fulé (2006)	Northern Arizona	3–27	Range 0–1052 conifers/ha (210 plots in 7 fires). Four of seven fires in years 4–8 had <50 conifers/ha and one had 26 conifers/ha at year 27, the other two fires had 170 conifers/ha and 1052 conifers/ha in years 4 and 9, respectively
Haire and McGarigal (2010)	Northern Arizona–New Mexico	28, 45	Little within years 1–8 (68 plots in 1 fire) or 1–15 (79 plots in 1 fire); ~8000, 2000 trees/ha near low-severity edge; most within 200 m of low-severity edge, but some to 304 m, 410 m; could reach all of fire area within ~50 yr
Savage and Mast (2005)	Northern Arizona–New Mexico	25–54	Regeneration began within 1–2 yr at 7 sites, within 6–10 yr at 3 sites (300 plots in 10 fires); 5 sites <200 trees/ha, 5 sites >400 trees/ha
Savage et al. (2013)	New Mexico	47–64	Regeneration did not begin for 3–20 yr (5 fires); Range (from 150 plots in 5 fires) per fire: 96–443 adult conifers/ha (≥ 1.4 m height and >6 cm dbh), 94–1629 seedlings and sapling conifers/ha for a total of 201–2112 trees/ha

Note: ? indicates that the Years after fire entry is uncertain.

historically over 20–30% of dry-forest areas in Oregon, California, and part of northern Arizona (Baker and Williams 2015); (2) dense younger established forests were historically common in nearly all dry-forest landscapes, suggesting past regeneration had been successful and dense (Williams and Baker 2012b); and (3) very dense post-fire trees are shown here to have covered large area on the southern Mogollon Plateau in northern Arizona (Fig. 4a) and occurred in the understory of burned forest in the Jemez Mountains, New Mexico (Fig. 4b). Dense and even very dense regeneration, in general and after high-severity fires, was within the historical range of variability in dry forests.

Some also considered poor regeneration after high-severity fires to indicate potentially unnatural type conversion of forests to shrublands or grasslands (Savage and Mast 2005, Haffey 2014), possible indicators of emerging tipping points (Reyer et al. 2015). However, of 24 studies, 21

(88%) covered only up to 27 yr after high-severity fires (Table 9). In general, 27 yr is insufficient, as historical tree regeneration after high-severity fires in dry forests could extend over periods of up to 60 yr (Table 4). Some large areas could even lack regeneration for ≥ 50 yr (Table 4) in part because of few climatically favorable periods for tree regeneration (Savage et al. 1996, Rother and Veblen 2017). A way to offset insufficient post-fire records is to extrapolate spatially (Haire and McGarigal 2010), but this has not generally been done (Table 9). Evidence is insufficient to conclude that post-fire tree regeneration is outside historical variation.

Historical tree regeneration after high-severity fires in dry forests failed or was slow at times, creating forest openings (Tables 4, 5), but recent studies often did not show modern failure was outside historical variability (Lauvaux et al. 2016). Opening creation by high-severity fire is likely operating at or below historical levels, since

high-severity fires are at or below historical rates in dry forests (Baker 2015). Some openings have declined (Coop and Givnish 2007); thus, creation of new openings by high-severity fires is likely restorative (Baker 2017b, Boisramé et al. 2017). Openings also enhance resistance to fire spread (Boisramé et al. 2017, Owen et al. 2017) and increase the heterogeneity of landscape structure (Kaufmann et al. 2003), enhancing resistance and resilience (Table 3); thus, added openings in the transition are generally beneficial.

In contrast, tree regeneration after beetle outbreaks and droughts is not currently thought to be declining, because advance regeneration continues. In the multi-decadal period that background tree mortality increased in dry forests as temperatures rose, tree recruitment was unchanged (Van Mantgem et al. 2009). In beetle outbreaks, (1) 75% of trees <20 cm dbh survived (McCambridge et al. 1982), (2) 77% of trees <7.5 cm dbh and 58% of trees 7.5–15 cm dbh survived a severe outbreak (Klenner and Arsenault 2009), and (3) >95% of trees survived in stands with <18 m²/ha of basal area, about 170 trees/ha in trees up to 37 cm dbh (Graham et al. 2016).

Future regeneration of dry-forest trees in general, not just after disturbances, was projected. Dobrowski et al. (2015) modeled the recruitment niche of 10 dry-forest trees relative to minimum temperature, evapotranspiration, and climatic water deficit. They then projected recruitment prevalence across the West through A.D. 2100 under RCP 8.5 (high emissions) and found recruitment declines of only about 10% or less (estimated from graphs) by A.D. 2060, at the end of the transition. Petrie et al. (2017) modeled climatic effects on stages in ponderosa regeneration (Fedema et al. 2013, Savage et al. 2013) and then projected future conditions with a water-balance model under RCP 4.5 and 8.5. Regeneration potential would be increased by +50% ± 106%, at 47 sites across the West by A.D. 2020–2059, from more flowering, seed production, and germination, especially in Arizona, Colorado, and New Mexico. After A.D. 2060, at the end of the transition, tree regeneration would decline, due to lower seedling production and survival, especially in the Pacific Northwest (–67%), but less so in the Intermountain region (–29%).

In summary, background rates of tree mortality are increasing in dry forests, and major recent

droughts and beetle outbreaks have killed many trees. Recent droughts and beetle outbreaks together account for perhaps 3–4 times as much tree mortality as do moderate- to high-severity fires. Together, natural disturbances could cause tree mortality over 26–51% of dry forests in the transition. Tree regeneration is not apparently outside historical variability and is projected to only slightly decline or even increase. Some opening creation from tree mortality followed by tree-regeneration failure could actually restore grasslands and other openings. Current dry-forest area is not all at risk, as 1/2 to 3/4 could escape substantial mortality under committed warming, and the remainder could have more resistant and resilient forests that persist more than expected.

TRANSITIONING DRY-FOREST LANDSCAPES

Large, infrequent disturbances that will enact tree mortality during the transition are capable of rapidly affecting millions of hectares and are generally beyond control. The spatial extent (25.5 million ha) of dry-forest landscapes and associated human communities and infrastructure provides large inertia for preparations. Our ability to control LIDs by manipulating forest structure is limited, and structurally ideal or restored landscapes may help, but a broader tie-in strategy, with a refocus on bet-hedging to enhance resilience to natural-process management may be more feasible and effective.

Limited ability to directly prevent LIDs or reduce their impacts on dry forests in the transition

Our ability to directly prevent LIDs or reduce their impacts is limited. Graham et al. (2016) reviewed the long history of failed attempts at controlling bark beetles through direct suppression or indirect manipulation of forest structure. At best, evidence suggests thinning, the most common manipulation, might modify the extent and pattern of tree mortality over limited area. Fettig et al. (2014) found thinning treatments to reduce tree mortality from MPB were costly and did not work during outbreaks without added direct control; thinning worked in some cases in ponderosa pine forests but had no significant effect in others. Six et al. (2014) also found thinning could possibly work at times, but failures

occurred during outbreaks, and unthinned stands may actually have more survivors. Droughts are not directly controllable. Some drought treatments aim to protect particular trees by reducing competition (McDowell and Allen 2015), but this will likely ultimately fail under hotter droughts (Bennett et al. 2015). Fuel treatments to reduce fire spread and severity have also not been very effective: “Mechanical fuels treatments on U.S. federal lands over the last 15 yr (2001–2015) totaled almost 7 million ha...but the annual area burned has continued to set records” (Schoennagel et al. 2017:4586). Schoennagel et al. (2017) explained that treatments can reduce fire severity and increase low-severity fire in some dry forests, but the probability of having an effect is low, as only about 1% of treatments actually experience wild-fire each year. Thinning treatments have been ineffective for LIDs in dry forests, in general, and are best as short-term, small-area holding actions (Six et al. 2014).

Can ideal or restored landscapes discourage LIDs from crossing tipping points?

Evidence that ideal or restored landscapes can discourage tipping points is also limited. To maintain MPBs in an endemic condition, discouraging an outbreak, Graham et al. (2016:157) suggested, based on high tree survival in an outbreak: “...heterogeneous landscapes composed of stands with heterogeneous structures and containing densities in the neighborhood of 80 feet² [18.3 m²/ha] of basal area are resistant to MPB infestations...” However, they said forests in the late 1800s were dominantly in that condition when the largest known MPB outbreak in ponderosa pine forests occurred, the 200,000- to 300,000-ha 1895–1909 outbreak in the Black Hills. Thus, ideal landscapes might only be resistant to some beetle outbreaks. Lundquist and Reich (2014:472) said: “Existing models show that diverse composition and configuration is the best and possibly only long-term, large-scale approach to bark beetle management...” For droughts, ideal stands and landscapes have not emerged, and there is little historical evidence. For wild-fires, low-density stands with large, old ponderosa pines and few understory trees and shrubs are most resistant and resilient to subsequent wildfires (Allen et al. 2002). However,

probabilistic studies (Table 2) have shown this structure was a significant, but not dominant component of most historical dry-forest landscapes, which had more heterogeneous stands across heterogeneous landscapes (Table 2). Thus, historical and ideal landscapes appear congruent, and achievable through restoration, for droughts and beetle outbreaks, and at least partly for fires.

Idealized and historical stand and landscape structures are unlikely to prevent LIDs from causing substantial tree mortality, some tree-regeneration failures, and some opening creation, as these were natural components of historical processes of disturbance and recovery in dry forests. Large, infrequent disturbances occurred in historical dry-forest landscapes and led to substantial landscape change and large fluctuations. Dry-forest landscapes appear to have been capable of general recovery after LIDs (Table 6), but some nonforest, created by disturbance, persisted for 100–150 yr or more (Table 5). Whether tipping points were crossed or this simply represents slow natural recovery is uncertain, but in either case dry-forest landscapes were dynamic and subject to large fluctuations that created and renewed resistance and resilience features that fostered bet-hedging (Table 3).

Natural fluctuation means that restoration and management in dry forests are less a matter of restoring and managing forest structures (Table 3) and more a matter of restoring and managing natural disturbance and recovery processes. Most structures are inherently ephemeral, persisting for only years or decades, and are quickly recreated by disturbances, and thus do not warrant intentional restoration. Widespread micro-management of fuel loads and forest structures after LIDs, based on fears of hypothetical mass fires (Stephens et al. 2018), is likely a waste of resources, because extensive structure management to reduce severe fires has been ineffective (Schoennagel et al. 2017). However, old trees and their associated stand- and landscape structures could persist for centuries, are not recreated by disturbances, and have been lost to excessive logging. Structure restoration and management make sense for these long-persisting structures not created quickly by disturbances, but process management, and associated facilitative structures (e.g., bet-hedging) now make sense for most landscape restoration and management.

A tie-in strategy using bet-hedging and process management of disturbances in the transition

Given substantial uncertainty and limited ability to control LIDs, a broad tie-in strategy, using actions beneficial for people and nature no matter what occurs, could likely facilitate more forest persistence in the transition. Suggested actions include (1) refocusing intentional ecological restoration on bet-hedging using historically congruent structures that provide resistance and resilience to diverse future disturbances (Baker and Williams 2015), (2) expanding development of fire-safe landscapes for people and infrastructure (Schoennagel et al. 2017), (3) expanding managed fire, and (4) accepting that LIDs will beneficially revise resistance, resilience, and genetic adaptation (Six et al. 2014). Restoring forest structure is costly, and resistance structures may fail, favoring structures that facilitate more process-based restoration (Millar et al. 2007).

Droughts and beetle outbreaks are likely to be 3–4 times as important as fires during the transition, which means that abundant small trees and high tree species diversity are now the more important resistance and resilience structures for transitioning dry forests (Table 3). Most large restoration programs (Reynolds et al. 2013, Addington et al. 2018) are likely to be ineffective, as they are focused on structures resistant to fire, when it is more likely that drought and beetles will determine the structures that persist in the transition. These programs to thin forests to resist damage by moderate- to high-severity fires have unfortunately reduced the small trees and diverse tree species that most provide resilience to droughts and beetle outbreaks. These programs could be quickly modified to instead retain small and diverse trees. In forests already deficient in small and diverse trees, if only one prescribed fire occurs before managed wildfire for resource benefit ensues, that last fire will likely stimulate some tree regeneration to repopulate small trees. If low-severity fires are generally managed to mimic historical spatial and temporal variability, opportunities will likely occur for diverse trees to repopulate (Baker 2017a).

The unpredictability of future disturbances suggests hedging bets (Millar et al. 2007, Baker and Williams 2015) in stand-level restoration by maintaining large and small trees and available tree species diversity. After restoration, most stands, even

open low-density stands, can have numerical dominance by small trees of all available species, but also sufficient replacement larger trees of all available species. Early land surveys across 1.7 million ha of dry forests showed small trees (typically <40 cm dbh) were, on average, 62% of total trees (Baker and Williams 2015). Given loss of large trees to logging, retaining all large trees, and mid-sized trees that are their future replacements, is sensible. After disturbances, successful tree regeneration is favored by large surviving trees that provide seed within about 100–200 m (Table 9). Larger trees may later be lost to hotter droughts and beetle outbreaks. However, if there were 20–50 larger (>40 cm dbh) trees per ha, and >5% survived, that could provide needed surviving large trees. Bet-hedging in restoration leaves abundant trees of all species and sizes with small trees dominant.

At the landscape scale, diverse historical forest structures could reduce the spread and effects of natural disturbances (Table 3) and bet-hedging at this key scale of LIDs is very important now. For fires, areas of large fire-resistant trees, openings, and naturally moist areas or shaded fuels provide resistance and favor survivors that aid post-fire resilience. For beetle outbreaks and droughts, diverse tree species and smaller trees provide the most important resistance and resilience. Recovering younger to middle-aged forests were common historically, based on studies in Table 2, and naturally conferred resistance and resilience to beetles and droughts. Kautz et al. (2017:534) found that "...more than 60% of global forests are in various stages of recovery from a past disturbance at any given time." Protecting young, naturally recovering forests is thus feasible, congruent with historical forests, and a key landscape part of a process-restoration approach (Baker 2017b). Young forests can survive beetle outbreaks and possibly droughts at much higher rates than older forests (Graham et al. 2016). To maximize bet-hedging, mixtures of diverse resistance and resilience structures across landscapes, with much more focus on beetle outbreaks and droughts, in addition to fire, are now more congruent with expected LIDs.

It would benefit both people and nature to rapidly increase protection of infrastructure, homes, and communities from increased wildfires, and this would also enable more managed use of natural disturbances. With ~7 million ha of fuel-reduction treatments, but fires still

burning homes (Schoennagel et al. 2017), we need to prevent the expansion of developments into fire-prone settings and finish full fire protection around all homes, infrastructure, and communities. Effective ways to reduce vulnerability and live with wildfire have been articulated (Cohen 2000, Baker 2009, Calkin et al. 2014, Moritz et al. 2014, Smith et al. 2016, Schoennagel et al. 2017). Tools include fire-safe construction, zoning, building codes, incentives, easements, growth boundaries, insurance policies, and other means (Kennedy 2006, Baker 2009, Schoennagel et al. 2017). Homeowners can use fire-safe construction focused on the home-ignition zone (Cohen 2000). Possibly most effective is for communities and developments to designate growth boundaries that enclose a wide margin of open, fire-resistant land uses that can serve as an effective fire break (e.g., ball fields, wetlands, irrigated agricultural fields), whether they are already in place or require construction. This alone would definitively stop expansion into fire-prone vegetation, protect key concentrations of people and infrastructure from fire, and make it more feasible to manage wildfires for resource benefit on adjoining public lands (Baker 2009).

Among LIDs, using more managed fire for resource benefit would be effective wherever it is safe and feasible, especially in the early part of the transition. Moderate- to high-severity wildfire has the longest recent rotation (Table 8) and is the only LID that can be directed. Prescribed fires are typically not sufficiently intense for effective restoration (Van Wagtendonk and Lutz 2007, Baker 2014), but prescribed burning once across landscapes and near homes and infrastructure is best before initiating managed fire (Baker 2017a). Managed wildfires can accomplish more renewal and enhancement of resistance and resilience, and also help prepare communities for future LIDs (Schoennagel et al. 2017). Expanding managed fire is scientifically supported (North et al. 2015, Schoennagel et al. 2017), and solutions to institutional barriers are identified (Stephens et al. 2016). Managed fires early in the transition are especially important to reduce tree density and basal area, which can lower vulnerability to droughts and beetle outbreaks more likely with higher temperatures later in the transition. Early managed fires could also stimulate tree regeneration, when it is

avored (Petrie et al. 2017). Recovering small trees and entire stands recovering after fires provide resilience to droughts and beetles and foster asynchrony in tree populations that can slow disturbance spread (Millar et al. 2007, Seidl et al. 2016). If openings or low-density patches are created by early disturbances, those could also reduce later vulnerability. Openings are less likely to ignite (Baker 2009), may slow fire, and could hinder beetle spread.

Acceptance of the benefits of LIDs and protection of the post-LID environment are sensible, since we cannot prevent LIDs in the transition. For example, bark-beetle outbreaks may naturally thin and diversify forest structures (Oliver 1995, Graham et al. 2016), updating resistance and resilience, while increasing biodiversity and furthering genetic adaptation to emerging climates and LIDs (Six et al. 2014, Beudert et al. 2015). Large, infrequent disturbances also provide selection against individual trees not resistant to the LID or post-LID environment (Six et al. 2014). Survivors and post-disturbance regeneration can revise tree adaptations to both emerging climate and patterns of LIDs. Rapid evolutionary response to extreme climatic events is possible, even in long-lived trees (Grant et al. 2017). For example, MPB outbreaks favor survival of slower-growing ponderosa pines, even though faster-growing trees may outcompete them at other times (De la Mata et al. 2017). Also, since post-LID tree regeneration is favored within 100–200 m of surviving trees (Table 9), and LIDs can leave isolated patches of surviving trees that, by chance, have different gene frequencies, the opportunity for locally adapted genetic change is high. As Howe (1976:263) said: “Prevention of major conflagrations... would eliminate the ingredients for drift, i.e., the replacement of large, continuous populations by tiny islands of isolated interbreeders from which most ensuing regeneration would emanate...” To preserve genetic adaptation of trees to emerging climate and LIDs, it is important to not prevent LIDs, not plant trees, and not log post-disturbance survivors (Lindenmayer et al. 2008). Genetic adaptation to committed warming could enhance possibilities for more dry-forest persistence in the transition and during the extended period of adjustment after the initial transition to committed warming.

CONCLUSIONS

Limiting warming, as with the Paris Agreement, should enable more persistence of current dry forests in the transition to committed warming than projected by models. Here, I reviewed evidence that (1) LIDs historically produced diverse forest stands and landscapes that naturally provided resistance and resilience to subsequent disturbances; (2) LIDs cannot be generally prevented through direct control or indirect manipulation of forest structure; (3) fires, droughts, and beetle outbreaks are not yet having effects in dry-forest landscapes that appear outside historical variability; (4) in the last few decades, droughts and beetle outbreaks have caused roughly 3–4 times as much tree mortality as fires; (5) primary opportunities to enhance forest persistence are from expanded bet-hedging at stand and landscape scales focused on resistance and resilience to droughts and beetle outbreaks, and facilitating adaptation as disturbances occur; and (6) 1/2 to 3/4 of dry-forest area could possibly escape most mortality during the transition.

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