Limitations to Propagule Dispersal Will Constrain Postfire Recovery of Plants and Fungi in Western Coniferous Forests

NATHAN S. GILL, MONICA G. TURNER, CARISSA D. BROWN, SYDNEY I. GLASSMAN, SANDRA L. HAIRE, WINSLOW D. HANSEN, ELIZABETH R. PANSING, SAMUEL B. ST CLAIR, AND DIANA F. TOMBACK

Many forest species are adapted to long-interval, high-severity fires, but the intervals between severe fires are decreasing with changes in climate, land use, and biological invasions. Although the effects of changing fire regimes on some important recovery processes have previously been considered, the consequences for the dispersal of propagules (plant seeds and fungal spores) in forest communities have not. We characterize three mechanisms by which changing fire regimes disrupt propagule dispersal in mesic temperate, boreal, and high-elevation forests: reduced abundance and altered spatial distributions of propagule source populations, less effective dispersal of propagules by wind, and altered behavior of animal dispersers and propagule predators. We consider how disruptions to propagule dispersal may interact with other factors that are also influenced by fire regime change, potentially increasing risk of forest conversion. Finally, we highlight urgent research topics regarding how dispersal limitation may shape twenty-first century forest recovery after stand-replacing fire.

Keywords: fire refugia, fire regime change, legacy, seed dispersal, spore dispersal

Pathways to forest recovery following disturbance are becoming less certain (Johnstone et al. 2016, Halofsky et al. 2020) as the frequency, size, and severity of forest fires increase in many regions across the globe (Bowman et al. 2013, Westerling 2016, Ward et al. 2020). Forest taxa, including trees, understory plants, and fungi, have evolved an array of traits and recruitment strategies that align with selective forces of historical disturbance regimes, such as the ability to withstand fire, thrive in postfire habitat, resprout, or regenerate from spore banks or seedbanks in the soil (Crowther et al. 2014, Glassman et al. 2015) or canopy (e.g., serotiny; see box 1; Enright et al. 2014, Stevens et al. 2020). Historically, such strategies supported post-disturbance recovery, leading to predictable successional development and eventually mature stand composition (e.g., Lloret et al. 2012, Romme et al. 2016). However, recruitment strategies that sustained recovery for millennia may be maladapted to rapidly changing fire regimes (box 1; Enright et al. 2015, Johnstone et al. 2016, Barton and Poulos 2018, Coop et al. 2020). Propagule dispersal is a key process in the recovery of communities but will diminish in effectiveness, not only where altered disturbance regimes change or reduce biological legacies (box 1; Turner et al. 1998, Johnstone et al. 2016, Hughes et al. 2019) but also as changing climate influences regeneration niches (Hansen et al. 2018, Hoecker et al. 2020). In this article, we extrapolate from literature and our collective understanding the probable consequences of altered fire regimes and especially the rising pressure of propagule dispersal limitations on forest recovery. We illustrate how fire regime change has long-lasting effects on fundamental ecological processes that determine forest structure (i.e., dispersal) and discuss research needs that will clarify these effects and management practices that mitigate the consequences.

Mesic temperate, boreal, and high-elevation forests of western North America provide examples of how a wide variety of dispersal processes and recovery strategies are responding to changing fire regimes (Stevens-Rumann and Morgan 2019). The area burned and the lengths of the fire season in these forest types are increasing with warming climate (Kasischke and Turetsky 2006, Flannigan et al. 2009, Sanford et al. 2015, Westerling 2016, Bowman et al. 2017), and high-severity fires, which leave fewer patches with propagule production, are also increasing (Parks and

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Box 1. Key terms.

Biological legacies: Residual elements such as organisms, organic materials, and organically generated environmental patterns that persist through a disturbance and influence the recovering ecosystem (Franklin et al. 2000).

Fire refugia: Patches of organisms that endure many fires by consistently burning less severely or not at all relative to the surrounding matrix (e.g., persistent refugia, Meddens et al. 2018) as a result of rocky outcrops, cool, moist conditions maintained by topography, or other areas afforded protection by topographic position. Stochastic factors including fire weather are important drivers of surviving patches that are less likely to persist through multiple fire events (Krawchuk et al. 2016).

Fire regime: The generalized description of the historical or prevailing role of fire in an ecosystem over the long term, described by parameters such as frequency, severity, size, and seasonality, among others (Krebs et al. 2010).

Mycorrhizal fungi: Symbiotic fungi associated with the roots of 80%–90% of plant species, often providing nutrients and other benefits in exchange for photosynthetically derived carbon (Brundrett and Tedersoo 2018)

Propagule dispersal: The movement of propagules (i.e., seeds and spores) from their origin source to a site at which they may establish as new individuals (Nathan 2013).

Pyrophilous fungi: "Fire-loving" fungi—any fungi adapted to withstand fire, although a subclass of pyrophilous fungi are specifically stimulated by fire or may fruit only on burned substrates (Bruns et al. 2020).

Serotiny: A plant adaptation by which seeds are stored in closed capsules (e.g., cones) that open under the high temperatures of fire, releasing seeds into the postfire seed bed

Zoochory: Animal-mediated dispersal of seeds and spores through scatter hoarding (propagules are cached in large or small numbers), epizoochory (e.g., burrs latched to an animal's fur or skin) and endozoochory (propagules that are digested and remain viable when deposited in feces).

Abatzoglou 2020). In some regions, not only are natural ignitions more frequent than in the past (Veraverbeke et al. 2017, Bieniek et al. 2020), but anthropogenic ignitions are also on the rise, further lengthening the fire season (Balch et al. 2017). However, not all recent fire activity has meant a departure from historical fire regimes. In dry, mixed-conifer forests of western North America, which are adapted to frequent, low-severity regimes, fire suppression decoupled fire activity and climate, creating a fire deficit (Marlon et al. 2012). Recent increases in fire frequency in these forests mark a return to historical fire frequencies and are, in some cases, moving landscapes back toward historical conditions, whereas in other cases, fires burning after long periods of suppression have been at higher severity than historical fires and may therefore diverge from historical conditions. These processes in dry, mixed-conifer forests are not addressed in this review. Forests that fall within the scope of this review are mesic temperate, boreal, and high elevation forests that historically burned at long intervals (e.g., hundreds of years) and are now burning more often. We define fire severity as the quantifiable effects of fire on organisms, communities, and ecosystems (e.g., percent damage or mortality) and frequency as the number of fires burning at a specific location within a given period of time (e.g., fires per 100 years; Turner 2010).

The mechanisms of propagule dispersal vary and are therefore affected in different ways and to different degrees by altered fire regimes. First, we define propagule dispersal as the movement of propagules (i.e., seeds and spores) from their origin source to a site at which they may establish as new individuals (Nathan 2013). For many forest communities in which propagules are dispersed primarily by wind and gravity, distance from propagule sources strongly influences both patterns and rates of forest regeneration (Stevens-Rumann and Morgan 2019). Seed dispersal by wind typically follows a negative exponential pattern over distance, with most seeds falling close to the source (Greene and Johnson 1996, Nathan and Casagrandi 2004). This distribution pattern is also true of fungal spores (Galante et al. 2011). Plants and fungi that are readily killed by fire and lack resprouting mechanisms or seed or spore banks must rely on dispersal from surviving patches within the burned area or from the surrounding live forest. Most conifer and understory plant seeds exhibit a two-phase mode of seed dispersal, where primary seed dispersal by wind, gravity, or animals is followed by seed movement to new locations through granivorous or frugivorous birds, mammals, or insects (Nathan and Muller Landau 2000, Vander Wall 2003, Vander Wall and Longland 2004, Tomback 2016, Pessendorfer et al. 2016, Vander Wall et al. 2017). Fungal spores can also disperse in a one- or two-stage process by air movement, rain and water, invertebrates, or vertebrates (Malloch and Blackwell 1992, Vašutová et al. 2019). Given that fungi associations facilitate growth for many forest trees and understory plants (Read et al. 2004, Martin et al. 2016), stabilize soil (Rillig and Mummey 2006), and play critical roles in recycling nutrients (McGuire and Treseder 2010), postfire fungal spore dispersal is required for forest and soil recovery (Hart et al. 2005). As fire regimes change, dispersal processes may be disrupted by limitations in primary propagule dispersal, secondary disperser

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availability and behavior, or microsite availability, affecting the timeframe of forest tree, understory, and fungal recovery.

Forest recovery will continue to be sensitive to structure, composition, and spatial pattern of propagule sources (McDowell et al. 2020, Peeler and Smithwick 2020) and the balance of different dispersal modes, which are all influenced by fire regime change. The size and spatial pattern of high-severity burned patches can limit propagule dispersal for tree (Greene and Johnson 2000), understory (Whitman et al. 2019a), and fungal (Adams et al. 2013, Glassman et al. 2017) species. Therefore, small fires with complex mosaics and high edge-to-area ratios will facilitate propagule dispersal into burned patches for certain species. Increased frequency of high-severity fires can prevent maturation of species that seedbank (e.g., immaturity risk, Keeley et al. 1999; interval squeeze, Enright et al. 2015) or spore bank (Glassman et al. 2015) and influence surrounding forest structure and composition. More frequent fires can also reduce richness of fungal decomposers, slowing decomposition rates, influencing nutrient availability, and altering forest structure (Hopkins et al. 2020).

Forest recovery after disturbance is not necessarily a binary phenomenon of success or failure. Rather, it is a continuum (Tepley et al. 2013). Densities of forest plants and fungi can recover throughout succession to varying degrees, as can community diversity. Relative abundances of species may change even while community composition remains the same, or conversions to novel forest types or to shrub or grasslands may occur. These changes may aid system adaptation to new climates and fire regimes (Messier et al. 2015, Tepley et al. 2017) but may also create positive feedbacks leading to more frequent fire and loss of key species. For example, invasive species may introduce self-reinforcing compositional change, because they often exhibit traits that are advantageous under frequent fire (D'Antonio and Vitousek 1992, Fusco et al. 2019). Or postfire recovery may follow a trajectory toward the prefire compositional state but be substantially delayed (Anderson-Teixeira et al. 2013, Freund et al. 2014). In some cases, conversion to nonforest (Coop et al. 2020) or compositionally different forest (Johnstone et al. 2010, Millar and Stephenson 2015, Gill et al. 2017) may be how ecosystems adapt or adjust to new climate and fire regimes.

In settings in which patches of high-severity fire are homogeneous and large, plant (Tomback et al. 1990, Turner et al. 2003, Pansing et al. 2020) and fungal (Peay et al. 2012) species from the regional pool that are adapted to long-distance dispersal may gain advantage. Propagules may also disperse from sources within burned patches, according to a few general mechanisms. Within-patch propagule sources may include those with adaptations to withstand fire. Live forest patches can also persist through multiple fires where topography consistently maintains cool, moist conditions or where fuel breaks occur (i.e., fire refugia; see box 1; Camp et al. 1997, Kolden et al. 2017, Meddens et al. 2018, Coop et al. 2019; note that we distinguish fire refugia, which persist through multiple fires, from survivors of a single fire due to spatial heterogeneity in burn severities). Therefore, survivors are able to disperse propagules from within the burn, which can accelerate recovery of the prefire community. Individual surviving trees can serve not only as propagule sources but also as microsites for other species (Fuller and del Moral 2003). On an even finer scale, microtopography and variation in surface fuels create heterogeneity in soil heating, leading to patchiness in plant seedbank and fungal spore bank legacies. Some propagule sources have traits that allow them not necessarily to withstand fire, but to have new establishment stimulated by high-severity fire (e.g., heat-stimulated release of seeds from cones in *Pinus contorta* var. *latifolia* and heat stimulation of *Ceonothus velutinus* seeds and *Neurospora crassa* fungal spores).

Mesic temperate, boreal, and high elevation coniferous forests of western North America have historically had abundant propagule sources, interspersed in fine, heterogeneous patches after long intervals between stand-replacing fires but are now under pressure from dispersal limitation because of increased fire frequency (figure 1; Harvey et al. 2016a). We explore how changes in these fire regimes may confer relative advantages and disadvantages to certain trees, understory plants, and fungi on the basis of their dispersal modes and legacies that will influence propagule dispersal. Changing fire regimes alter the arrangement of seed and spore bank forest legacies within and surrounding burn perimeters (see the "Breaking the bank" section), alter wind-mediated dispersal via changes to the structure and composition of propagule source populations (see the "Blowing in the wind" section), and change the behavior of animal propagule dispersers and predators (see the "Fat tails" section; figure 2). We then consider the changing fates of propagules before and after dispersal and suggest key questions to address the rising influence of dispersal limitation resulting from fire regime change.

Breaking the bank: Reduced seed and spore bank legacies within and surrounding the burn

Seed and spore bank legacies result when refugia (box 1) and other patches of surviving organisms preserve sexually mature individuals, or when dispersal of propagules in burned patches occurs despite mortality (either through adaptive traits or before delayed mortality after fire). Ecological legacies also include postfire features that facilitate forest regeneration, such as nurse logs and snags (Swanson et al. 2011, Wolf et al. 2021), but seed and spore bank legacies are key to forest recovery and may be threatened by frequent, high-severity fire (Landesmann and Morales 2018). Distance to live seed source strongly influences the density of tree regeneration following high-severity fires (Donato et al. 2009, Kemp et al. 2016, Hansen et al. 2018). Patches of live forest within burn perimeters enhance edge complexity, reducing the distance between centers of burned patches and propagule sources. Such elements of spatial structure help improve the effective reach of dispersal (Johst et al. 2002), particularly for species with limited

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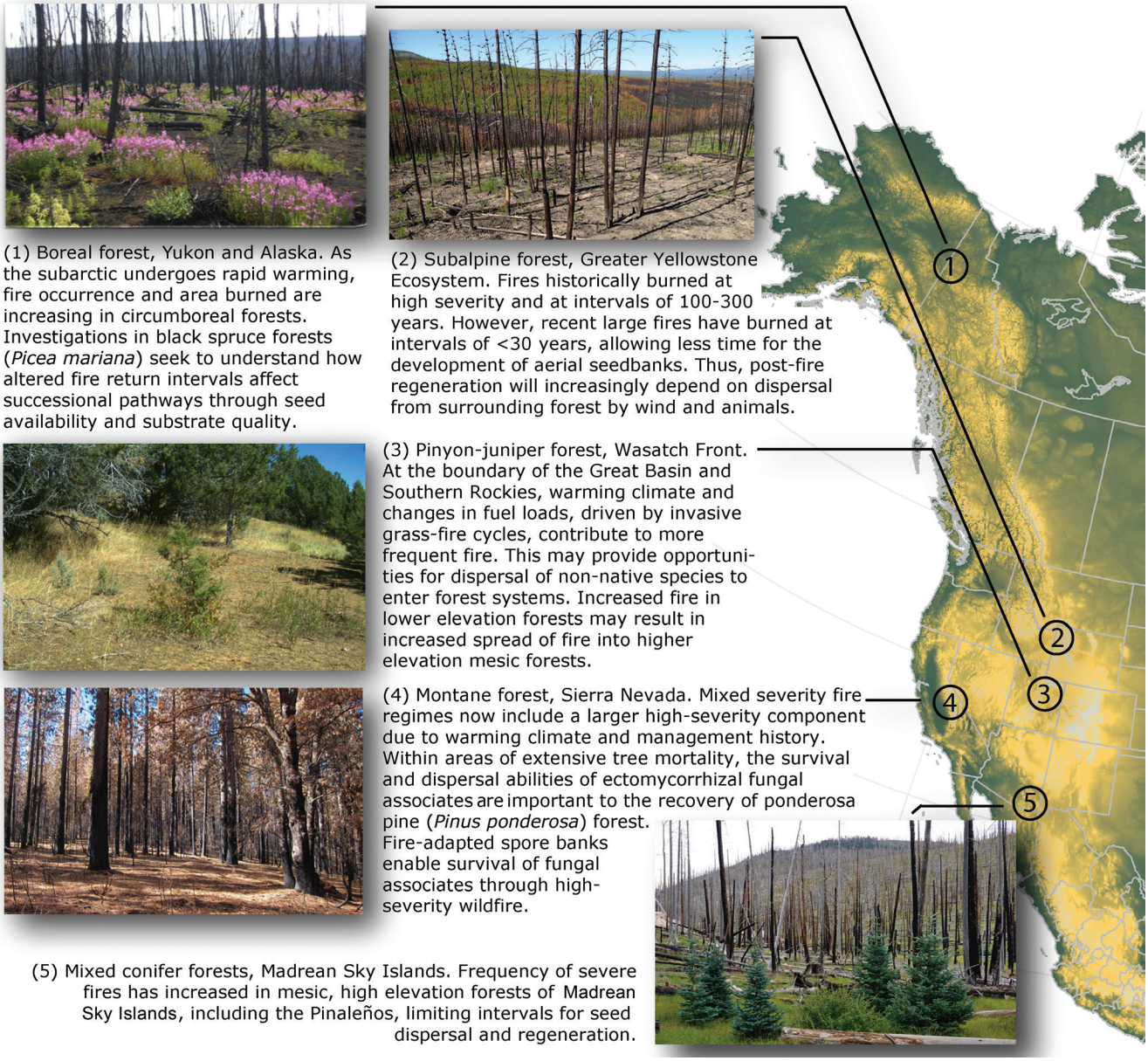

Figure 1. Illustrative examples of fire regime change and consequences for dispersal from mesic temperate, boreal, and high elevation forest systems across western North America. (1) Boreal forest, Yukon. Brown and Johnstone (2012). Photograph: Carissa Brown. (2) Subalpine forest, Greater Yellowstone Ecosystem. Gill and colleagues (2021). Photograph: Nathan Gill. (3) Lower-elevation pinyon juniper forest in the Southern Rockies. Kerns and colleagues (2020). Photograph: Sam St Clair. (4) Montane forest, Sierra Nevada. Glassman and colleagues (2016). Photograph: Sydney Glassman. (5) Mixed conifer forest, Madrean Sky Islands. Villarreal and colleagues (2020). Photograph: Jose M. Iniguez, USDA Forest Service, Flagstaff, Arizona.

dispersal ability (Padial et al. 2014). Fire-tolerant trees, such as Douglas fir (*Pseudotsuga menziesii)*, and pyrophilous fungi (box 1), such as *Pyronema* spp., have traits that increase the likelihood of individuals surviving a high-severity fire (e.g., thick lower bark for Douglas fir, Agee 1996; and heat-resistant propagules, sclerotia and spores, for fungi, Smith et al. 2015, Bruns et al. 2020). Mature western larch (*Larix occidentalis*) trees develop thick bark on their lower trunks that can resist fire while producing most seeds high in the tree canopy (Arno et al. 1992). *Eriophorum vaginatum* resists fire through its dense tussock morphology (Rowe 1983). Although it has been established for over a century that pyrophilous fungi that are infrequent or undetectable before fire can fruit intensively after fire (Seaver 1909, Petersen 1970), the specific mechanisms that enable them to survive fire are only beginning to be tested (Day et al. 2020, Raudabaugh et al. 2020). Some researchers have recently hypothesized that pyrophilous fungi exhibit

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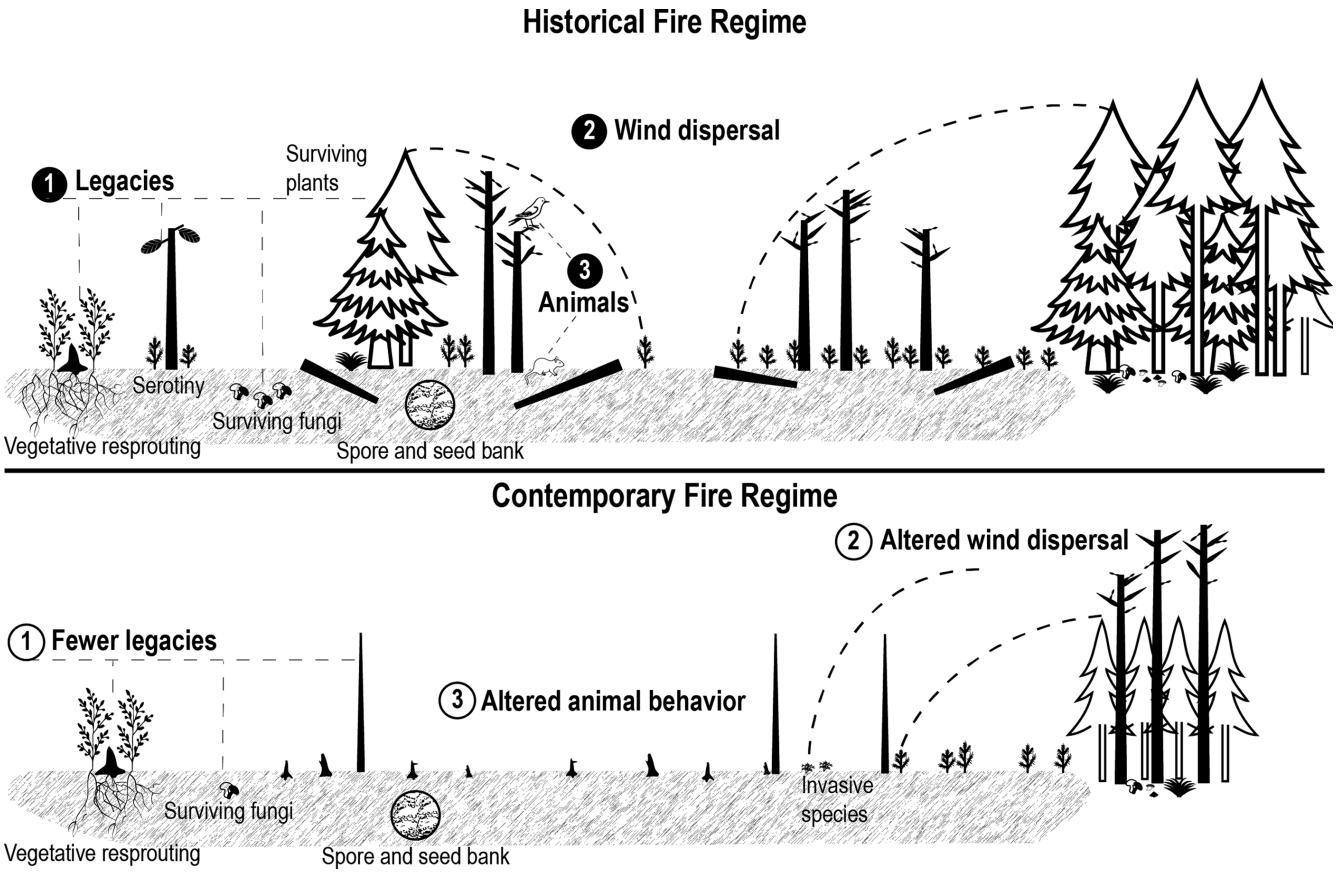

Figure 2. Fire regime change alters the dispersal process in three primary ways. If biological legacies (e.g., islands of surviving plants and fungi, fire-stimulated propagation) are few within burned patches after short-interval, high-severity fire, mesic temperate, boreal, and high elevation forest recovery will increasingly depend on dispersal from out-of-patch sources that remain living. The legacy that persists despite the rising pressure of dispersal limitation may benefit, because propagule dispersal is sensitive to fire regime change in the following ways: (a) the loss of legacies that serve as propagule sources within and surrounding burned patches, (b) increased fire frequency filters stand age and species composition of propagule sources at burn edges, altering effective wind dispersal range and success. (c) More frequent and higher severity fire alters postfire habitat mosaics and structure of resources, altering the behavior and local communities of animal dispersers and seed predators.

similar traits and strategies to plants (Whitman et al. 2019b). The roots and rhizomes of many native understory herbaceous plants (and some trees) can also survive high-severity fires, resprouting quickly then flowering and seeding within burn perimeters (e.g., Turner et al. 1997, Romme et al. 2016). For tree species that employ cone serotiny as an adaptation to historical fire regimes, dispersal of stored propagules is triggered by the heat of fire, when resin-sealed cones open and release seed from fire-killed trees within the burn. Lodgepole pine (*Pinus contorta* var. *latifolia*), jack pine (*Pinus banksiana*), and black spruce (*Picea mariana*) produce canopy seedbanks of serotinous cones (e.g., Buma et al. 2013). Similarly, some saprobic ascomycete fungi are not only heat-resistant, but their fruiting is even catalyzed by fire (Emerson 1948), and it is possible that spores of certain ectomycorrhizal fungi such as *Rhizopogon olivaceotinctus* may also be heat activated or at least heat tolerant (Glassman et al. 2016, Bruns et al. 2020).

How will changing fire regimes affect the patterns of propagules dispersing from legacies within and around burn perimeters? Evidence from recent fires (since the mid-1980s) shows that area burned at high severity has increased throughout western North America (Parks and Abatzoglou 2020) and in the US northern Rocky Mountains (Harvey et al. 2016a); however, no substantial change in spatial patterns (i.e., patch size and shape complexity within burn perimeters) has been detected. In one study, up to 90% of the burned area was within 150 meters (m) of forests that did not burn in stand-replacing fire and likely served as a seed source (Harvey et al. 2016a). However, increased fire severity may reduce legacy propagules by leaving fewer or no surviving individuals within burned patches and reducing the number or size of surviving islands (Falk 2013, Cansler and McKenzie 2014, Johnstone et al. 2016, Stevens et al. 2017), including patches that historically may have served as persistent fire refugia (Krawchuk et al. 2016, Meddens et al. 2018).

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Table 1. Taxa with dispersal related advantages and disadvantages due to fire regime change.

Section of article	Advantages	Disadvantages
Breaking the bank	Resprouters, or others that are catalyzed by fire *Betula neoalaskana* (resprouter) *Ceonothus velutinus* (catalyzed) *Neurospora crassa* (catalyzed)	Fire-adapted species sensitive to immaturity risk (not of concern in understory plants and fungi) *Pinus contorta* var. *latifolia*, *Picea mariana*
	Resisters that are protected or not readily killed by fire *Pseudotsuga menziesii* *Eriophorum vaginatum* *Pyronema* spp.	Avoiders, if refugia become vulnerable *Picea glauca* *Linnaea borealis* *Mitella nuda*
	Those with high propagule production or early sexual maturation *Picea mariana* (early maturity) *Antennaria parvifolia* (high production) *Aspergillus* spp. (high production)	Those with low or slow propagule production *Pinus albicaulis* *Juniperus monosperma*
Blowing in the wind	Those that rely primarily on animals or other mechanisms instead of wind *Pinus flexilis* *Vaccinium membranaceum* *Gauteria* spp.	Those that rely primarily on wind for dispersal (but with limited range) *Abies lasiocarpa* *Calluna vulgaris* *Inocybe lacera*
	Wind dispersed, but rapid vertical growth or long distance dispersal, including by smoke Nonserotinous *Pinus contorta* var. *latifolia* (rapid vertical growth) *Chamaenerion angustifolium* (long distance) *Dothideomycete* spp. (smoke)	Trees with slow vertical growth, or obligate seeders with short dispersal range *Pinus aristata* (slow vertical growth) *Abies lasiocarpa* (short range) *Ceonothus velutinus* (short range)
Fat tails	Those with a secondary dispersal mechanism that extends range *Pinus ponderosa* *Rubus parviflorus*	Those that rely primarily on a single dispersal mechanism *Pinus albicaulis* (nutcracker that depends on older forest)
	Those with "directed dispersal" into postfire habitat, and that are well suited to establish in burned substrate *Pinus albicaulis* *Senecio eremophilus* *Phytopthora* spp.	Those with "directed dispersal," if microsites become less common, like logs after "crown fire plus" *Pinus edulis*

Note: Some species may receive relative advantages in one regard but disadvantages in another. Because of these possibly counter attributes and many unknown aspects of dispersal ecology of some species (especially fungi), the overall net effects of fire regime change cannot be determined with confidence at this time. However, we emphasize that conceptualizing, researching, and managing within a framework that considers relative advantages and disadvantages wrought by novel patterns of fire will be increasingly important.

Presumably, lack of surviving patches would affect fungi similarly to plants, because ectomycorrhizal fungi appear to adhere to island biogeography principles (Glassman et al. 2017) and air-associated fungi also follow distance decay patterns (Adams et al. 2013).

Over the long term, the potential for sustained propagule dispersal from within burned patches will depend on whether within-patch legacies can persist under changing fire regimes (Krawchuk et al. 2020, Meddens et al. 2018). Spatial heterogeneity in severity is required to ensure these legacies are maintained. Changes to the fire regime that reduce propagule dispersal effectiveness or lead to reproduction failure will compromise postfire regeneration. Dispersal success may be further reduced if the extent of burned area frequently falls beyond effective propagule dispersal distances (e.g., increased areal extent of the high-severity or core area, reduced patch complexity; Cansler and Mackenzie 2014, Johnstone et al. 2016). Statistical models suggest that burned area will increase markedly into the future (Westerling et al. 2011, Abatzoglou and Williams 2016), and dispersal limitation may become more pronounced if patch sizes increase alongside fire sizes (Cansler and McKenzie 2014). Fungi and obligate seeder plants recovering far in the interior of burned patches are likely to do so more slowly than those established near burn perimeters as burn patch size increases (table 1). Even long-distance-dispersing ectomycorrhizal fungi are unlikely to disperse farther than ten kilometers (Peay et al. 2012).

For serotinous plant species able to regenerate within a burn perimeter despite fire-induced mortality, regeneration requires that the interval between successive fires is longer than the time required to reach reproductive maturity and produce sufficient viable seed (e.g., Buma et al. 2013, Viglas et al. 2013). As stand-replacing fires occur more frequently (Harvey et al. 2016a, Parks and Abatzoglou 2020), serotinous species are vulnerable to immaturity risk (Keeley et al. 1999, Halofsky et al. 2020). Although complex fire perimeters leave surprisingly high percentages (58%–75%) of burned areas relatively close (95–200 m) to live forest edges (Turner et al. 1994, Donato et al. 2009, Kemp et al. 2016), in the most extreme cases, large, contiguous patches of forest have reburned at very high severity, creating a lack of surrounding propagule supply combined with in-patch immaturity risk, yielding no tree regeneration (Brown and Johnstone

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2012). This leaves severely burned immature stands dependent on dispersal from outside burn perimeters rather than through legacy propagules (Gill et al. 2021). Such dependence will render postfire recovery far more sensitive to the spatial pattern, age, structure, and composition of live forest.

Blowing in the wind: Changing structure and composition of wind-dispersed propagule source populations

Wind is a primary mode of propagule dispersal for overstory plants (Burrows 1975, Howe and Smallwood 1982), fungi (Allen et al. 1989, Brown and Hovmøller 2002), and some fire-sensitive obligate seeder understory plants (e.g., *C. velutinus*), but most understory plants depend more heavily on resprouting or dispersal by animals than dispersal by wind (Hughes et al. 1994). Most wind-dispersed conifer seeds disperse within 200 m of source trees, with the majority of seeds falling at shorter distances (McCaughey and Schmidt 1987, Greene and Johnson 2000), and most basidiomycete fungal spores fall within 1 m of their source (Galante et al. 2011, see also Chaudhary et al. 2020 concerning arbuscular mycorrhizal fungi). Understory herbaceous species known to colonize burned areas primarily by wind dispersal can do so rapidly (e.g., *Chamaenerion angustifolium*). Along with seed morphology, the effectiveness of wind dispersal for any species is influenced by wind direction, wind speed, and seed release height (Bohrer et al. 2008), all of which can vary with forest structure, tree morphology, and topography (Cousens and Rawlinson 2001, Savage et al. 2011, Damschen et al. 2014, Peeler and Smithwick 2020).

Changes in fire frequency, size, and severity affect forest structure and composition, which, in turn, influence seed and spore dispersal by wind. When forests are immature, a propagule source may be absent, and even if adjacent stands are beginning to mature, seed dispersal from young forests of short stature into recent burns declines precipitously over very short distances (less than 5 m) from source trees (Gill et al. 2021). Taxa that overcome these limitations by surviving fire and retaining mature propagule banks will be at relative advantage as dispersal and regeneration unfold in the years after fire. Changes to forest structure may also influence wind turbulence (Damschen et al. 2014), but it has not been determined whether structural effects from increased stand-replacing fire might enhance or reduce propagule dispersal.

Although wind-dispersed tree species are affected by fire-determined structure in this way, understory plants are closer to the ground and exhibit less variability in vertical height. They reach maximum height more rapidly and do not have the same dispersal-enhancing effects that trees have from high release points of propagules. Therefore, we expect the propagule dispersal of wind-dispersed understory plants to be relatively unchanged by the fact that increased frequency of severe fires will promote younger forests. In addition to short-statured plants, those wind-dispersed tree species that exhibit rapid vertical growth and a tendency to colonize postfire environments (pioneers such as *Populus tremuloides*, *Pinus contorta* and *P. banksiana, and Chamaenerion angustifolium*) may gain relative advantages over slower growing wind-dispersed trees (table 1). The dispersal of fungi that tend to grow high off the ground on the stems and foliage of trees or on later successional tree species (e.g., Looby et al. 2020) may also be affected by increased fire frequency in the same way, as opposed to those that explicitly release spores from the forest floor.

In addition, certain plant and fungal taxa produce more propagules, disperse farther or colonize at a higher rate than others (Tomback et al. 1990, Vander Wall and Longland 2004, Peay et al. 2012). Therefore, increased fire frequency and increased size of patches of high severity may confer relative advantages to taxa with rapid reproductive maturity (e.g., *Picea mariana*) or long distance propagule dispersal (e.g., *Pteridium aquilinum, Suillus pungens*). It is likely that larger burned patches will disproportionately benefit plants and fungi with long distance dispersal capabilities. This long distance dispersal may occur through wind (e.g., *Chamaenerion angustifolium, Populus tremuloides, Thelephora terrestris*), through animals (e.g., *Pinus flexilis, Rhizopogon olivaceotinctus*, *Vaccinium* spp.), or in the case of some fungal spores, such as Ascomycetes in the *Hypocreales*, *Dothideomycetes*, and *Eurotiomycetes*, through wildfire smoke (Mims and Mims 2004, Kobziar et al. 2018). Species that rely on propagule dispersal by animals will be subject to other factors related to fire regime change, different from the factors affecting primarily wind-dispersed species.

Fat tails: Altered behavior of animal dispersers and granivores

Animal-mediated seed dispersal of conifers, understory plants, and fungi can facilitate postfire recovery, in part because it may substantially lengthen or fatten the tails of dispersal curves. Extended dispersal range and increased rates of propagule delivery come primarily from zoochorous (animal mediated; see box 1) dispersal mechanisms including scatter hoarding (seed caching), endozoochory (a consequence of frugivory where seeds pass through digestive tracts), and epizoochory (where propagules are carried outside of dispersal vectors, e.g., burrs attached to fur). Scatter-hoarding small mammals gather and cache already dispersed seeds, moving them up to an additional 70 m from their sources (Vander Wall 1993, 2003, Vander Wall and Longland 2004). Small mammals are key dispersers for many western forest fungal taxa, including ectomycorrhizal fungi that are critical partners with conifer trees (Flaherty et al. 2010, Vašutová et al. 2019, Stephens and Rowe 2020). Spore dispersal by small mammals occurs primarily through fruiting body (sporocarp) ingestion and subsequent defecation. Similarly, ungulates can be important propagule dispersers for understory plants (Albert et al. 2015) and arbuscular mycorrhizae (Vašutová et al. 2019). Invertebrates also may be important dispersers of both plant seeds (Warren and Giladi 2014) and fungal spores (Jacobsen et al.

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2017). Avian frugivores disperse understory plants throughout their territories through seed regurgitation and gut passage (e.g., Hagar 2007, Beck and Vander Wall 2011). Clark's nutcrackers (*Nucifraga columbiana*) will harvest seeds from coniferous forests across elevations and cache them within different forest communities and at distances as far as 32 kilometers (Vander Wall and Balda 1977, Tomback 1978, Lorenz et al. 2011).

In particular, seed-caching dispersers not only fatten and lengthen the tails of dispersal curves, they also often show directed seed dispersal, wherein they disperse seeds to specific microsite types (Nathan and Muller-Landau 2000), resulting in higher seed germination and seedling survival (Wenny 2001, Vander Wall and Longland 2004). The consequences with respect to potential seed germination and establishment of caching and cache microsite selection behavior vary with species of disperser. In western coniferous forests, important conifer seed dispersers include several granivorous birds of the family Corvidae (*Aphelocoma* spp., *Cyanocitta stelleri*, *Gymnorhinus cyanocephalus*, and *Nucifraga columbiana*), the deer mouse (*Peromyscus maniculatus*), and taxa in the squirrel family, primarily chipmunks (*Neotamias* spp.) and the golden-mantled ground squirrel (*Spermophilus lateralis*)—all widely distributed. These animals differ in their seed caching behavior not only in dispersal distances (Tomback 1978, Vander Wall and Balda 1981, Vander Wall 1993, Lorenz et al. 2011) but also in ways that affect the probability of seed germination and seedling establishment, including seed number, cache depth, substrate, and relation to microsite features such as shrubs and protective (nurse) objects (Tomback 1978, Tomback et al. 2001, Briggs et al. 2009). Animals may also exhibit preferences for caching seeds of certain plant species on the basis of seed size or nutritional quality (Lobo et al. 2013). Therefore, not all propagules are dispersed with the same probability to suitable microsites.

Changing fire regimes will broadly and indirectly influence zoochorous dispersal of propagules via modifications to habitat structure (including spatial pattern of mosaics, patch connectivity, and both horizontal and vertical structure) and resource availability. Fire severity and landscape heterogeneity are key covariates when considering fire-mediated changes to habitat structure for animal dispersers and the consequences for species occurrence and community composition (Kotliar et al. 2007, Fontaine and Kennedy 2012, Flesch et al. 2016, Tingley et al. 2016, White et al. 2016). Responses to these changes in landscape patterns are species specific and dynamic. For example, the abundance of certain granivore species may increase immediately after high-severity fire (e.g., Zwolak et al. 2010, Fontaine and Kennedy 2012), increase only after a temporal delay (Hutto and Patterson 2016), or increase only in patches that burned at low to moderate severity, while decreasing in patches that burned at high severity (Kotliar et al. 2007, Fontaine and Kennedy 2012). With extreme burn severity (e.g., crown fire plus; Turner et al. 2019), nearly complete loss of biomass would affect postfire habitat structure, including snag architecture for insects and birds, as well as downed logs (figure 2). Because animals often bury caches next to nurse objects (Tomback 1978, Vander Wall 1993), changes in the prevalence and pattern of these microsites with increased fire severity could change propagule caching and dispersal in ways yet to be explored. Refuges previously used by small mammals to avoid fire (e.g., shelter or underground) may become less effective, resulting in increased direct mortality of animals (Engstrom 2010) and, therefore, the loss of nucleated forest recovery (i.e., recovery from propagule caches within the fire perimeter) characteristic of some species (Banks et al. 2011). With higher fire severity, greater loss of vertical structure, snags, and downed coarse wood would leave fewer perches for avifauna, and less cover and fewer corridors for small mammals. Increasing fire severity, frequency, and size, and the resulting loss of propagule production through mortality or immaturity risk will reduce per capita seed availability. Seed availability for regeneration is negatively associated with seed consumption (McKinney and Fiedler 2010, Zwolak et al. 2010), suggesting that postfire environments may become more seed limited than the loss of legacies alone would suggest.

Changes in habitat structure due to altered fire regimes that collectively reduce zoochorous propagule dispersal will influence trajectories of forest recovery. Increased fire frequency will shift habitats toward early successional stages; shortened-interval fires may increase avifaunal species richness and produce unique community assemblages of birds relative to single burns (Fontaine et al. 2009), but the effects of shifting intervals between high severity fires are uncertain (Thompson et al. 2007, Fontaine and Kennedy 2012). If wildfires burn larger but with continued fine-scale variation in severity, effects of altered fire regimes on habitat structure (and, in turn, propagule dispersal by animals) may be neutral or even beneficial for some species through increased landscape heterogeneity (Tingley et al. 2016, White et al. 2016). However, this may not be the case if burn patterns become more homogeneous, the proportion of high-severity fire increases, high-severity burn patches become more isolated from surviving legacies, and habitat connectivity decreases. Such changes may have negative consequences for propagules that are dispersed over relatively shorter distances (e.g., via small mammals or territorial birds, e.g., Steller's jays; table 1), and declining extent of mid- to late-successional forests may reduce populations of important avian seed dispersers such as Clark's nutcrackers. Competition-induced behavioral changes in dispersers associated with habitat use and cache site selection will further influence dispersal outcomes. For example, because availability of safe sites and seeds decline, many scatter-hoarding species modify caching behavior because of perceived pilferage risk, where risk is inversely related to seed availability (e.g., Dittel and Vander Wall 2018). Some individuals of some species are willing to risk predation to reduce the chance of cache pilferage by caching in more open habitats and traveling farther

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distances to cache (e.g., Munoz and Bonal 2011, Steele et al. 2014), suggesting that changing fire regimes may result in fatter or longer tails of dispersal curves. In contrast, Cao and colleagues (2018) found that higher pilferage risk led to increased larder hoarding (numerous seeds in a single deep cache) behavior, which is unlikely to result in seed germination (Steele and Smallwood 2002). These potential behavior changes underscore the context dependence and uncertainty concerning the effects of changing fire regimes on animal-mediated seed dispersal, and what they will mean for future forest trajectories.

Propagule fate: Dispersal is necessary but insufficient for forest regeneration

Successful forest regeneration after fire depends not only on dispersal of a sufficient number of propagules but ultimately on the establishment of individuals within the microenvironments to which they are adapted. Dispersal is one of many subprocesses of regeneration that determine patterns of establishment, in turn influencing ecosystem structure and composition over long time periods. We emphasize that an understanding of specific interactions with *each* of these subprocesses and fire regimes is necessary to project future forest dynamics (figure 3). Other factors, including species interactions and external factors such as climate and land management, can also affect these processes directly or can mediate the effects of fire regime change. We now focus on three important processes that are distinct from propagule dispersal but intricately connected and critical in determining propagule fates: the production, persistence, and establishment of propagules.

Propagule production. Successful dispersal requires an adequate supply of propagules. The major driver of changing fire regimes, climate warming, may also alter any step in the propagule production process (Giannini and Magnani 1994, Davis et al. 2018). Annual weather affects pollination, seed production, and masting in some tree species, but it is currently unclear how warmer temperatures and greater year-to-year variation will affect each of these processes and, therefore, seed production (e.g., Pearse et al. 2016). Spatial configuration matters in this situation as well; for example, pollination efficiency, seed production, and viability may decline if mature trees become increasingly isolated (Rapp et al. 2013, Brown et al. 2019). Earlier snowmelt, later snowpack, and summer drought increase mortality of mature trees, further reducing seed production (van Mantgem et al. 2009, Pederson et al. 2010).

Pests and pathogens also reduce propagule production potential. Warming has triggered widespread outbreaks of many native insects, especially *Dendroctonus* bark beetles (Raffa et al. 2008). For nonserotinous tree species such as Douglas fir, these outbreaks may kill a high proportion of mature trees (thereby ending seed production) such that they eliminate for decades the seed supply needed for regeneration if those forests burn (Harvey et al. 2013). Native and exotic pathogens that kill conifers (e.g., Oomycete *Phytopthora* root rots, fungal rusts *Cronartium ribicola*) or reduce growth rates (e.g., fungal *Dothistroma* needle blight) may increase in prevalence over time, influenced by regional or local climate (Sturrock et al. 2011) and compounded by wildfire (Metz et al. 2013).

Propagule persistence. The production of propagules in surrounding live forest does not guarantee their dispersal into burned landscapes; animals can influence propagule supply and fate through pre- or postdispersal predation (Connolly et al. 2014). Predispersal seed predation by red squirrels (*Tamiasciurus hudsonicus*) from serotinous cones and by various animals from nonserotinous cones can greatly reduce seed availability (Smith and Balda 1979, Benkman et al. 1984, McKinney and Tomback 2007), and postdispersal predation could be increasingly important where propagules are limited (Pansing et al. 2017, Frock and Turner 2018). Change in postfire environments can also alter the behavior of propagule predators (Sasal et al. 2017), just as it may alter the behavior of animal dispersers. Fires in desert, prairie, and forest ecosystems alter rodent community abundance and composition (e.g., Zwolak et al. 2010) and, therefore, rodent-driven seed fates.

Propagule establishment. Following propagule dispersal into postfire landscapes, regeneration will also be strongly influenced by microsite conditions (Stevens-Rumann et al. 2017). Conifer seed germination and seedling establishment are more sensitive to postfire environmental conditions than older age classes (Tomback et al. 2001, Dobrowski et al. 2015, Barton and Poulos 2018), and the postfire environment can be highly influenced by nonliving legacies such as snags (Wolf et al. 2021) and woody debris (Swanson et al. 2011). Exposure to unusually hot soil surface temperatures, low soil moisture, and freezing events can all trigger mass seedling mortality (Johnson et al. 2011). Indeed, declining soil moisture across postfire forests of the western United States has already begun to reduce tree seedling survival (Harvey et al. 2016b, Andrus et al. 2018, Kemp et al. 2019). Analyses of 33 fires across lower elevation forests of the Western United States identified clear climate thresholds for seedling establishment, and in the last 20 years, these thresholds have been crossed regularly (Davis et al. 2019). Further work is needed to explore whether similar thresholds have been crossed in boreal and subalpine forests. Projections of future climate for western forests suggest soil moisture will continue to decline with warming temperature and increasing evaporative demand (Mankin et al. 2017, Cook et al. 2020). Postfire climate plays a primary role in the regeneration niche of conifers (Jackson et al. 2009, Stewart et al. 2021), and experiments that simulate how future soil moisture affects seedling establishment and survival have found that tree regeneration failure could be widespread (Hansen and Turner 2019, Hoecker et al. 2020) with large consequences for landscape scale forest structure and composition (Hansen et al. 2020).

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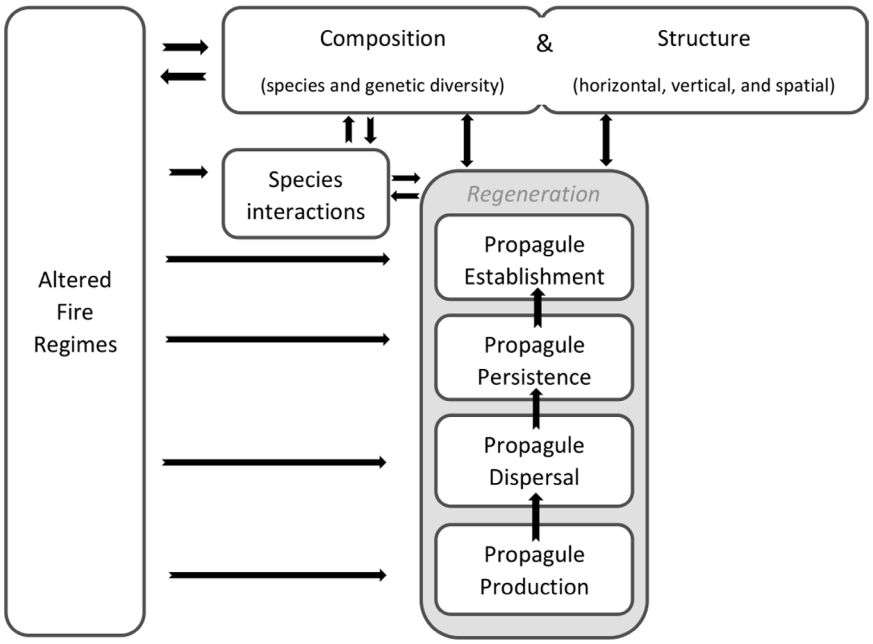

Figure 3. In mesic temperate, boreal, and high elevation conifer forests, patterns of forest composition and structure influence and are influenced by processes of change in fire regimes. Fire regime change also influences each step of the regeneration process directly, as well as indirectly through species interactions such as mutualistic symbiosis and predator–prey relationships. We define regeneration as being composed of at least four distinct subprocesses related to propagules: production, dispersal, persistence, and establishment. Although the focus of this review is on the relationship between fire regime change and propagule dispersal, each subprocess of forest regeneration is sensitive to changing patterns of fire occurrence and each must be considered.

Meanwhile, reduced snowpack and warming may lead to propagule establishment at upper tree lines at increasingly higher elevations where substrate allows (Harsch et al. 2009). In the following sections, we outline key uncertainties and next steps in research related to seed and spore dispersal under changing fire regimes (box 2).

Net effects of dispersal limitation on forest trajectories with more fire. Larger fires, bigger patches of high severity fire, and a surrounding matrix of early successional forests could affect dispersal processes synergistically, reducing the number of propagules that reach burned patches, slowing forest recovery. With continuing climate change, these processes in some cases may lead to a state shift in community type (e.g., Tepley et al. 2018, Andrade et al. 2021). (See box 2.)

More research is needed concerning these effects at a local landscape scale as well as a regional scale. An integrative approach including simulation modelling would enable us to test alternative scenarios, to test the magnitude of influence of different processes, and to anticipate and assess future constraints on propagule dispersal due to changes in seed and spore banks, live forest age structure and composition, and animal behavior. Furthermore, area burned and patch sizes affect dispersal processes in different ways, and the two must not be conflated. Increased size and frequency of fires, which, in boreal and high elevation forests, primarily result from climate change (Westerling 2016, Bowman et al. 2017, Alizadeh et al. 2021), will influence the matrix of surrounding forest over time, determining the source of propagules available to colonize burned patches from out-of-patch dispersal. Increased size of burned patches will alter the proportion of landscapes that are within range of propagule dispersal. Some species may benefit from these changes, whereas others may be disadvantaged, and others still may benefit in one regard and be disadvantaged in another (table 1). The potential for nonlinear interactions must be considered, including idiosyncratic effects of specific conditions, and the relative changes to elements of the dispersal process must be better understood if we are to anticipate future forest trajectories.

Biological invasions and novel species assemblages. Reduced dispersal of native propagules from within burned patches and live forest edges offers opportunities for other species to colonize or expand, including invaders. Some species could be regionally native but establish in new local settings as they track their climate niche. Whether this is truly a biological invasion is a point of debate. Either way, invasion success in postfire landscapes requires dispersal into the burned environment (Theoharides and Dukes 2007), which depends on propagule traits and characteristics of the postfire landscape (Bergelson et al. 1993). More, larger fires and higher burn severity are likely to facilitate nonnative propagule dispersal (Bergelson et al. 1993, Desprez-Loustau et al. 2007, Getz and Baker 2008). Even though some native species will also gain relative dispersal advantages in these settings, many wind-dispersed invasive species will be among those well suited to postfire environments. Compared with native species, nonnative plants may also be less reliant on mycorrhizal symbionts (Pringle et al. 2009, Busby et al. 2013) that are influenced by fire. For example, invasive species may introduce compositional change, because they often exhibit traits that are advantageous under frequent fire (D'Antonio and Vitousek 1992, Fusco et al. 2019). Invasive plants may also alter fungal trajectories because many are associated with arbuscular mycorrhizal fungi. These differences from the ectomycorrhizal fungi associations of native plants can have large impacts on carbon and nitrogen cycling (Averill and Waring 2018, Mushinski et al. 2021). (See box 2.)

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Box 2. Key questions to address the rising influence of postfire dispersal limitation.

1. What is the net effect of fire regime change on the dispersal of plants and fungi (via altered abundance of biotic legacies, spatial pattern, forest composition and structure, and behavior of animals that prey on or disperse propagules)?
2. How will the rising influence of propagule dispersal limitation interact with biological invasions and novel species assemblages?
3. What are the mechanisms that define pyrophilous fungi, and how will they be sensitive to fire regime change?
4. How can models that project trajectories of forest change incorporate the relationship between fire regime change and propagule dispersal limitation? What are the potential costs (errors) of not representing dispersal in projections of future forest trajectories?
5. What forest management strategies and treatments will best address the rising pressure of dispersal limitations due to altered fire regimes?

The introduction of invasive grasses (e.g., *Bromus tectorum*) that influence fire regimes may be driven in part by animal dispersers that thrive in postfire habitat, as has been observed at lower elevations (St Clair and Bishop 2019, Bishop et al. 2020). The introduction of invasive grasses into disturbed upland forest systems presents a legitimate threat to stabilizing feedbacks (Peeler and Smithwick 2018), and this threat has been underappreciated to date (Kerns et al. 2020). In addition, past fire suppression and land-use history contribute to increased high-severity fire in lower elevation, dry mixed-conifer forests (Allen et al. 2002, Miller et al. 2009), which can spread upslope to adjacent mesic forests (e.g., spruce fir) at higher elevations and result in more frequent severe fire than was observed historically in those systems (O'Connor et al. 2014, Alizadeh et al. 2021, Villarreal et al. 2020).

An increase in large patches of high-severity fire with reduced propagule supply (e.g., due to high mortality, repeated fire, and immaturity risk even in serotinous plants) will favor species with the ability withstand high-severity fire (e.g., pyrophilous fungi) or to resprout vegetatively (e.g., native trees such as *Populus tremuloides*, *Betula neoalaskana*, and native or invasive grasses if present at time of fire). How will novel assemblages that could arise from changing fire regimes shape future forest development? Further research is needed to understand the net effects on community composition and should include taxa ranging from microbes to herbaceous and woody vegetation. Because many invasive species exhibit traits that confer advantage under severe or frequent fire, the interaction between introduced species and native plants and fungi that are increasingly disadvantaged through fire regime change in mesic temperate and boreal forests should be closely monitored, of biological invasions into western North American forests has been underappreciated to date.

Effects of fire regime change on fungi

Our review indicated a lack of information about fire effects on fungal dispersal. Pyrophilous fungi exist, but most fire-related research on fungi is based on mushrooms or macroscopic fruiting bodies (McMullan-Fisher et al. 2011). The specific traits and mechanisms enabling their dispersal and survival after fire are largely unknown. Studies examining genomes (Steindorff et al. 2021) and biophysical assays to test the traits of pyrophilous fungi are in their infancy (Day et al. 2020) and ecological theory about their survival remains speculative (Whitman et al. 2019b). We are not aware of any studies specifically testing how directed dispersal may occur with fungi, although it is likely that such processes exist given the amount of fungi dispersed by animals (Vašutová et al. 2019). Furthermore, we know of no studies testing postfire fungal dispersal specifically, and we extrapolate from general studies of fungal dispersal (Adams et al. 2013, Peay et al. 2012, Glassman et al. 2017). Given these uncertainties, many of the mechanisms behind fungal dispersal, and specifically how they might be affected by fire regime change, remain unknown, and their organization into the framework presented in table 1 is somewhat tenuous. Although it is clear that there is differential temporal survival of fungal spores residing in spore banks, tests have not run longer than a decade (Bruns et al. 2009, Nguyen et al. 2012) as compared with plants where seedbank survival over many decades or longer has been studied and organized into synthesized frameworks (Csontos and Tamás 2003). (See box 2.)

Incorporating changes to propagule dispersal into models of future forest trajectories. The assumption that propagules are always available will become increasingly erroneous as climate warms and mesic temperate and boreal forests burn more than in the past. When exploring future forest dynamics in the context of environmental change, researchers should be cognizant of the key role propagule dispersal plays in developing forest cover, structure, and function. However, issues of scale limit insights from many current models. Seeds and spores are nearly always dispersed over shorter distances than the spatial grain of the Earth system models used to project vegetation responses to climate and disturbance at regional to global scales (Clark et al. 2018). Therefore, Earth system models rarely represent grid cell to grid cell dispersal (Fisher et al. 2018), often assume that seeds are always available, and largely ignore microbes completely. Furthermore, such models often group tree species into few plant functional types, limiting the diversity of dispersal modes that

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could be parameterized. Wildfires are also simplistically represented without considering the spatial heterogeneity in burn severity that is so important for creating within-perimeter legacies (Sanderson and Fisher 2020). (See box 2.)

Forest landscape models that simulate individual trees often represent disturbance and dispersal explicitly and can be parameterized to capture various modes of dispersal (e.g., wind, animal), making them a promising approach for quantifying how changing dispersal may influence future forests (Seidl et al. 2012, Albrich et al. 2021). However, they are computationally expensive and cannot be run at continental scales. Therefore, to make species-level predictions of how dispersal modes may contribute to shifts in forest cover, species composition, and stand structure across western North America, new modeling techniques are needed that can scale from the processes that operate over meters to the outcomes that manifest more broadly (Rammer and Seidl 2019). Such scaling techniques would offer opportunities to address essential questions identified in this article. For instance, how will dispersal and colonization by invasive grasses influence postfire tree regeneration and feedback to alter fire in the West? How will expected changes in populations of important seed dispersers and predators influence forest trajectories? How do these changes in fine-scale forest processes such as propagule dispersal scale up to influence broader forest cover, composition, and structure, and what are the resulting feedbacks to fire regimes and subsequent regional to global climate change? How might limitations in propagule dispersal result in alternate postfire community trajectories (i.e., alternate states) or novel communities?

The identification of areas in which dispersal limitations are likely to contribute to the potential for delayed recovery or even transition to nonforest could help resource managers efficiently target areas for active management, including forest planting. Furthermore, identification of dispersal modes that are most and least sensitive to changes in fire regimes will allow managers to make more informed decisions as to which species and functional groups to monitor, preserve, and plant (Anderegg et al. 2020).

Implications for management of mesic temperate, boreal, and high elevation forests. The consequences of a changing fire regime may be acceptable in some forests, because fires can create opportunities for communities to reorganize and adapt to environmental change (Buma and Schultz 2020, Schuurman et al. 2020). However, forest managers should strive to maintain a heterogeneous burn-severity mosaic, even if change is deemed appropriate, because patches of live forest serve as propagule sources within fire perimeters (Downing et al. 2019). We suggest that managers keep a running map of fire history and severity. Where large patches have burned at high severity, forest managers could map surrounding areas as critical seed sources and eventually apply prescribed burning or fuel thinning treatments to protect these areas from future wildfire. However, burnout or backburn operations in which unburned or low-severity forest patches are deliberately and severely burned to reduce fuels increase the homogeneity of burned areas and contribute to the loss of propagule sources (Backer et al. 2004). Managed wildland fire use might include judicious application of thinning and prescribed fire to protect fire refugia or other patches of mature forest that sustain propagule supplies (e.g., Hansen et al. 2020) and maintain connectivity among protected patches. Fuel reduction and prescribed fire can be used to reduce wildfire severity and slow rate of spread (depending on weather conditions), perhaps achieving or maintaining a mosaic. (See box 2.)

Where sustaining forests in the face of increasing fire frequency is a goal, active management to alleviate dispersal limitations and direct recovery may be warranted. Dispersal limitations may need mitigation where atypical short-interval reburns have eliminated local seed supplies, where burned areas may be surrounded by immature forest, and where future climate conditions are expected to support forested ecosystems (e.g., Turner et al. 2019, Gill et al. 2021). Where forest recovery is a goal that is constrained by propagule dispersal, tree planting could be strategically implemented (Stevens-Rumann and Morgan 2019), targeting homogenous patches of high-severity fire that had been dominated by fire-sensitive tree species. Depending on goals, the species planted could reflect the prefire community or other native species better matched to projected future climate. In such cases, the critical choice is whether to manage for ecosystem persistence or change or, possibly, to hedge bets.

Fungi play an especially critical role in forests, influencing carbon and nitrogen cycling and plant nutrition, and their propagule dispersal should therefore be considered in management plans in addition to that of trees and other plants where possible (Van der Heijden et al. 2008, Crowther et al. 2019). For example, in many cases, the addition of fungal inoculum or soil amendments may be necessary to improve forest regeneration (Schmidt et al. 2020, Dickie et al. 2010) but particular attention must be paid to sources of inoculum (Maltz and Treseder 2015). Further research is needed to better understand which fungi are capable of surviving high severity fire and why. With this understanding will come an improved capacity to manage for success in postfire fungal communities, making possible efforts similar to those we have suggested for trees and other plants.

Conclusions

As fires across mesic temperate and boreal forests of western North America and around the world continue to increase in size, frequency, and severity, dispersal limitations of plant and fungal propagules are likely to constrain postfire forest recovery. These constraints may arise through altered patterns of legacies, immaturity risk, novel forest composition and size structure, or altered animal behavior influencing propagule dispersal and predation. We emphasize the importance of identifying and protecting fire refugia (i.e.,

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those patches that are truly persistent through multiple fires), as well as maintaining mosaics of mixed-severity burned and surviving forest after single fires that provide sources of within-patch propagules. Reforestation efforts may be highly effective where sites are suitable for forest regeneration but beyond the current range of seed and spore dispersal. Populations of important seed and spore dispersers and predators should be monitored, because their dynamics may drive timelines of postfire recovery for trees, understory plants, and fungi. The specific sites and success of propagule dispersal will increasingly shape the future trajectories of forests (McDowell et al. 2020), and past assumptions about the dispersal process may no longer apply.

Acknowledgments

The authors wish to acknowledge Amber McCord for providing the illustrations in figure 2 and Kevin Robertson for input to early outlines of the ideas presented in this review. Many thanks to three anonymous reviewers who suggested very helpful revisions to an earlier draft of this manuscript. The authors also acknowledge the organizers of the 104th Annual Meeting of the Ecological Society of America in Louisville, Kentucky, in 2019, which hosted an organized oral symposium that provided the impetus for writing this article. MGT acknowledges funding from the Joint Fire Science Program (grant no. 16-3-01-4) and the University of Wisconsin Vilas Trust.

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Nathan S. Gill and Monica G. Turner contributed equally as co-lead authors to this work. Nathan S. Gill (nathan.gill@ttu.edu) is an assistant professor in the Department of Natural Resources Management at Texas Tech University, in Lubbock, Texas, in the United States. Monica G. Turner (turnermg@wisc.edu) is the Eugene P. Odum professor of ecology and a Vilas Research Professor in the Department of Integrative Biology at the University of Wisconsin–Madison, in Madison, Wisconsin, in the United States. Carissa D. Brown (carissa.brown@mun.ca) is an associate professor in the Department of Geography at Memorial University, in St. John's, Newfoundland and Labrador, Canada. Sydney I. Glassman (sydneyg@ucr.edu) is an assistant professor in the Department of Microbiology and Plant Pathology at the University of California, in Riverside, California, in the United States. Sandra L. Haire (shaire@umass.edu) is a research landscape ecologist at the Haire Laboratory for Landscape Ecology, in Tucson, Arizona, in the United States. Winslow D. Hansen (hansenw@caryinstitute.org) was an Earth Institute postdoctoral fellow at the Lamont Doherty Earth Observatory, at Columbia University, in Palisades, New York, and is an assistant scientist at the Cary Institute of Ecosystem Studies, in Millbrook, New York, the United States. Elizabeth R. Pansing (epansing@americanforests.org) was a postdoctoral researcher in the Department of Geographical and Sustainability Sciences at the University of Iowa, in Iowa City, Iowa, and is a senior manager and forest and restoration scientist for American Forests, in Washington, DC, the United States. Samuel B. St Clair (stclair@byu.edu) is a professor in the Department of Plant and Wildlife Sciences at Brigham Young University, in Provo, Utah, the United States. Diana F. Tomback (diana.tomback@ucdenver.edu) is a professor in the Department of Integrative Biology at the University of Colorado Denver, in Denver, Colorado, the United States.

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