Spatial variability in tree regeneration after wildfire delays and dampens future bark beetle outbreaks

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Climate change is altering the frequency and severity of forest disturbances such as wildfires and bark beetle outbreaks, thereby increasing the potential for sequential disturbances to interact. Interactions can amplify or dampen disturbances, yet the direction and magnitude of future disturbance interactions are difficult to anticipate because underlying mechanisms remain poorly understood. We tested how variability in postfire forest development affects future susceptibility to bark beetle outbreaks, focusing on mountain pine beetle (*Dendroctonus ponderosae*) and Douglas-fir beetle (*Dendroctonus pseudotsugae*) in forests regenerating from the large high-severity fires that affected Yellowstone National Park in Wyoming in 1988. We combined extensive field data on postfire tree regeneration with a well-tested simulation model to assess susceptibility to bark beetle outbreaks over 130 y of stand development. Despite originating from the same fire event, among-stand variation in forest structure was very high and remained considerable for over a century. Thus, simulated emergence of stands susceptible to bark beetles was not temporally synchronized but was protracted by several decades, compared with stand development from spatially homogeneous regeneration. Furthermore, because of fire-mediated variability in forest structure, the habitat connectivity required to support broad-scale outbreaks and amplifying cross-scale feedbacks did not develop until well into the second century after the initial burn. We conclude that variability in tree regeneration after disturbance can dampen and delay future disturbance by breaking spatiotemporal synchrony on the landscape. This highlights the importance of fostering landscape variability in the context of ecosystem management given changing disturbance regimes.

disturbance interactions | heterogeneity | forest dynamics | landscape ecology | lodgepole pine

The degree to which one natural disturbance (e.g., wildfire, windstorm, or insect outbreak) amplifies or dampens another can be key to ecosystem resilience (the capacity to tolerate disturbance without shifting to an alternative ecosystem state) as disturbance regimes change with climate warming (1, 2). Interactions between natural disturbances can elicit unpredictable feedbacks that affect successional trajectories (3, 4) and trigger or prevent state transitions in ecosystems (1, 2, 5–7). Linked interactions occur when one disturbance alters the probability, severity, or size of a subsequent disturbance (7). The second disturbance may be amplified by positive feedbacks, as when wind-caused blowdown increases the availability of surface fuels for a subsequent fire (4, 8) or dampened by negative feedbacks, as when one wildfire reduces fuel availability for subsequent fires (9, 10). The likelihood that successive disturbances will overlap and thus interact is growing as disturbance frequency and extent increase with climate warming (11–13). However, mechanisms underpinning disturbance feedbacks are poorly understood, making it difficult to anticipate the direction and magnitude of such interactions (13, 14).

Spatial heterogeneity may be a key mechanism that affects linked disturbance interactions, because natural disturbances both create and respond to spatial pattern (15–17). Spatially mediated feedbacks can link disturbances if one disturbance changes the amount and arrangement of habitat that is susceptible to another, thereby altering its probability, severity, or size (18, 19). Large disturbances can amplify the spread of future disturbances if they homogenize landscapes, or they can inhibit the spread of future disturbances if they increase landscape heterogeneity (20, 21). Such relationships are difficult to isolate, however, because theory suggests a nonlinear relationship between the amount of susceptible habitat available and disturbance spread (22). Furthermore, the nature and strength of feedbacks also can change over time as forest development proceeds, because susceptibility to disturbance often depends on structural characteristics that vary with age or developmental stage. For example, host trees must reach a minimum size and abundance to be susceptible to a bark beetle outbreak (23, 24), and burned forests must develop sufficient fuels before they can burn again (9, 10). Thus, large disturbances might not only spatially homogenize susceptible habitat but also temporally synchronize susceptibility to a future disturbance by resetting a landscape to the same successional stage; for example, large, stand-replacing fires that produce even-aged forests may set the stage for future widespread pest or pathogen outbreaks. Land-management practices that homogenize forest structure may act similarly, as when production forestry creates extensive forests of uniform tree density and size that become vulnerable to pests or pathogens at the same time (24–26). As such, variation in the rate or pattern of ecosystem recovery across a disturbed landscape might disrupt that synchrony and have a dampening effect. A critical challenge in

Significance

Wildfires have increased in western North America, creating extensive areas of regenerating forests. There is concern that recent large, stand-replacing fires will synchronize forest development and commit landscapes to a future of increased disturbance, such as bark beetle outbreaks that require extensive, well-connected forests of large host trees. We analyzed forest development after large high-severity 1988 fires in Yellowstone National Park to assess future susceptibility to bark beetle outbreak. Although stands originated from the same event, persistent variation in postfire tree density and size protracted the onset of susceptibility to bark beetle attack among stands. Furthermore, postfire variability delayed emergence of the habitat connectivity required for broad-scale outbreaks, suggesting spatial variability is an important dampening mechanism for disturbance interactions.

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ecology is to determine whether and how disturbance and recovery change the amount and connectivity of habitat susceptible to another disturbance, whether feedbacks between disturbances are positive or negative, and how such feedbacks vary over space and time.

We explored linked disturbances in a forested landscape, focusing on how stand-replacing fire affects vulnerability of forests to subsequent insect outbreak over time, and whether spatial heterogeneity in tree regeneration mediates this disturbance interaction. Specifically, we studied postfire stand development following the large, severe 1988 fires in Yellowstone National Park (YNP) in Wyoming and how heterogeneity in stand development affects the timing, extent, and spatiotemporal synchrony of future outbreaks of native bark beetles (*Dendroctonae*). Wildfires and insect outbreaks are the two most important native disturbance agents in mountain forests of western North America, and recent decades have seen a marked increase in their extent and severity (11, 13, 24). Numerous studies have evaluated whether bark beetle outbreaks influence subsequent fire occurrence or severity (7, 27–31). However, few studies have considered the degree to which recent high-severity wildfires may synchronize forest development and commit landscapes in western North America to a future of widespread outbreaks (but see, for instance, refs. 30, 32, and 33 for analyses of historical fire–beetle interactions).

Tremendous spatial heterogeneity in postfire tree regeneration across the landscape was a striking consequence of the 1988 Yellowstone fires (16, 34). Postfire density of lodgepole pine (*Pinus contorta* var. *latifolia* Douglas) ranged from zero to >500,000 stems per ha (16, 35), and density of Douglas-fir [*Pseudotsuga menziesii* var. *glauca* (Mirb.) Franco] ranged from zero to ∼20,000 stems per ha (36). Lodgepole pine is well known for rapid, abundant, even-aged postfire regeneration and is the major host species of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins; MPB). Rocky Mountain Douglas-fir regenerates slowly in less dense, less uniformly aged stands and is the major host of the Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins; DFB). In these dominant forest types, we asked two key questions about how variability in postfire heterogeneity may influence future bark beetle outbreaks: (*i*) How does spatial variability in postfire tree regeneration affect the timing and amount of regenerating forest that is susceptible to bark beetle outbreak, and (*ii*) what is the importance of spatiotemporal variability in stand development for cross-scale amplifying feedbacks in future bark beetle outbreaks? Using extensive field data on stand conditions 24 y after fire and a well-tested simulation model, we projected forest dynamics for 130 y, coinciding with the window of time when stand structures vary within broad stand-age classes (37). We assessed susceptibility of the regenerating forest to bark beetle outbreak and compared susceptibility to hypothetical trajectories starting from homogeneous regeneration. We considered two alternative hypotheses. First, variability in initial postfire tree regeneration could persist over time to delay and disrupt the spatiotemporal synchrony in stand structure that is a prerequisite for widespread bark beetle outbreaks in forest landscapes. Alternatively, variability in initial postfire stand structure could diminish with time since disturbance to create spatiotemporal synchrony in stand structures, resulting in extensive, homogeneous, even-aged forests that promote broad-scale bark beetle outbreaks in the future. We then used a neutral landscape model (NLM) to address the second question and elucidate the role of among-stand variability in stand structure for spatiotemporal synchrony in susceptibility to bark beetle outbreak. Peters et al. (19), based on theoretical considerations, identified connectivity as a crucial prerequisite for cross-scale amplifying feedbacks in disturbance spread and distinguished four stages of connectivity related to nonlinear disturbance dynamics. Here we tested the hypothesis that postfire variability in stand development reduces the connectivity of susceptible forest and delays emergence of conditions conducive to widespread self-amplifying outbreaks [stage 4 *sensu* Peters et al. (19)]. Alternatively, critical connectivity of susceptible stands could be recovered within only a few decades after fire, regardless of the initial postfire heterogeneity in tree regeneration.

Results

Variability in Postfire Stand Development. The extremely high variability in stand structure (e.g., enormous among-stand differences in tree density, tree size, and stand basal area) measured in forests regenerating from the 1988 fires attenuated somewhat over time, but substantial differences in tree size and stand basal area persisted over simulated stand development (Table 1 and Figs. S1 and S2). Stem density declined over time but still spanned two orders of magnitude among stands in both forest types 50 y postfire (Table 1).

Table 1. Variability in stand structure after the 1988 Yellowstone fires

	Lodgepole pine (n = 70)		Douglas-fir (n = 38)	
Time since fire, y	Mean (median)	Minimum–maximum	Mean (median)	Minimum–maximum
		Stem density, stems per ha		
24	21,445 (4,050)	32–344,052	3,185 (1,832)	15–19,664
54	4,216 (3,583)	689–12,367	2,925 (2,027)	235–16,104
84	2,949 (2,701)	1,320–6,733	2,122 (2,088)	452–6,434
114	2,430 (2,270)	1,586–4,883	1,494 (1,543)	670–2,560
154	1,953 (1,852)	1,285–3,741	1,069 (1,018)	638–1,492
		QMD, cm		
24	5.1 (5.2)	0.4–10.3	1.6 (1.2)	0.4–5.7
54	9.9 (9.7)	5.2–14.1	5.5 (4.6)	2.3–12.1
84	13.1 (12.9)	9.6–18.1	10.3 (10.1)	5.6–16.5
114	15.6 (15.7)	12.0–20.8	15.5 (15.0)	11.2–20.3
154	18.5 (18.7)	14.2–23.6	21.8 (21.9)	17.0–29.7
		Basal area, $m^2 \cdot ha^{-1}$		
24	13.2 (10.6)	0.0–51.4	0.9 (0.2)	0.0–9.2
54	30.0 (35.5)	1.4–56.7	8.2 (4.8)	0.0–35.8
84	39.1 (44.0)	9.6–57.9	19.3 (19.1)	1.1–45.0
114	45.4 (48.3)	21.6–61.8	29.7 (36.8)	6.7–52.1
154	51.1 (52.0)	36.5–64.5	40.2 (44.0)	21.8–57.4

Year 24 marks observed data (35, 36), and all other years are from simulations using FVS. n = number of stands; basal area is the sum of the cross-sectional area of all trees in a stand at 1.3-m height.

Simulated stem densities decreased rapidly for lodgepole pine and more gradually for Douglas-fir (Table 1) but 154 y postfire still ranged from 1,285–3,741 (mean: 1,953) stems per ha in lodgepole pine and from 638 to 1,492 (mean: 1,069) stems per ha in Douglas-fir. Among-stand variation in the size of regenerating trees also decreased with forest development but remained substantial over the 130-y simulation. The quadratic mean tree diameter (QMD) increased with stand development and ranged from 4.5 to 13.6 (mean: 9.3) cm among stands 50 y postfire and from 14.2 to 23.6 (mean: 18.5) cm 154 y postfire for lodgepole pine. Trends were similar for Douglas-fir (Table 1). Among-stand variation in QMD was related to stem density; trees in lower-density stands had initially larger-diameter growth, and this advantage persisted through stand development despite converging stem densities. Stand basal area also increased over time (Table 1), and among-stand variability in basal area of simulated postfire stands remained large even 154 y after fire, when basal area ranged from 36.5 to 64.5 (mean: 51.1) $m^2 \cdot ha^{-1}$ in lodgepole pine and from 21.8 to 57.4 (mean: 40.2) $m^2 \cdot ha^{-1}$ in Douglas-fir. An evaluation of simulated stand development trajectories against independent data showed good agreement between observations and simulations for both lodgepole pine and Douglas-fir forests (Figs. S1 and S2).

Timing and Amount of Postfire Forest Susceptible to Bark Beetle Outbreak. Persistent among-stand variability in the structure of postfire forests strongly influenced their susceptibility to future bark beetle attacks. Following fire, it took several decades for enough host trees to reach the size preferred by their respective bark beetle species (lodgepole pine diameters >15 cm for MPB and Douglas-fir diameters >23 cm for DFB). However, the emergence of trees of suitable size for bark beetles in postfire stands was not temporally synchronized in either forest type. For lodgepole pine, the first postfire stands became highly susceptible to MPB attack (susceptibility index of >50) at 79 y after fire in the simulations, and it took another 36 y until more than 50% of the stands were highly susceptible (Fig. 1). For Douglas-fir, the first postfire stands became highly susceptible to DFB attack at 99 y after fire, and it was another 31 y until more than 50% of the stands were highly susceptible. Most, but not all, simulated stands (89.0% of lodgepole pine and 93.3% of Douglas-fir) were highly susceptible at the end of the 130-y simulation period. Thus, although all analyzed stands originated after the same fire, the window of time between initial and complete susceptibility of regenerating forest stands to bark beetle attack was substantially protracted.

Role of Variability for Spatiotemporal Synchrony. Relating these results to hypothetical trajectories in which the differences in initial stand structure were homogenized in the simulation clearly identified among-stand variation in postfire regeneration as an important dampening factor for vulnerability to future bark beetle outbreaks (Fig. 2). Compared with simulations that assumed homogeneous initial stand structure, spatial variability delayed the earliest time since fire when 50% of the burned landscape could support even moderate-severity outbreaks (>25% of the basal area killed by beetles) by 34 y in lodgepole pine and by 44 y in Douglas-fir. The effect of spatial variability was even stronger for high-severity outbreaks (>50% of the basal area killed by beetles). Under homogeneous initial conditions, high-severity outbreak was supported over the entire burned landscape after 79 (MPB) and 104 (DFB) y, respectively. With the observed spatial variability in stand structure, however, high severity-outbreaks were supported in only 58.1% (lodgepole pine) and 34.6% (Douglas-fir) of the burned landscape after 154 y.

NLMs further demonstrated the role of variability in postfire regeneration in dampening spatial connectivity and the potential for nonlinear amplifying feedbacks. Lodgepole pine and Douglas-fir forests reached levels of spatial connectivity of susceptible habitat that allowed within-patch expansion of bark beetles [a stage 2 event *sensu* Peters et al. (19)] by postfire years 71 and 87, respectively (Fig. 3). Between 17 and 23 additional years were necessary to reach connectivity sufficient for between-patch spread [a stage 3 event (19)]. Due to among-stand variability in postfire stand development, the habitat connectivity associated with broad-scale outbreaks and amplifying feedbacks [a stage 4 event (19)] could be supported only after 139 y in lodgepole pine. In Douglas-fir, this level of connectivity was not reached during the first 154 y postfire. In contrast, stage 4 connectivity among susceptible stands was reached 69 (MPB) and 79 (DFB) years postfire, when spatially homogeneous initial conditions were assumed. Furthermore, under the trajectories started from spatially homogeneous conditions, both bark beetle–host systems transitioned from being able to support only very localized beetle attacks (stage 2) to a critically connected landscape (stage 4) within a 10-y simulation time step. This further indicates that the highly variable tree regeneration after the 1988 fires will delay the emergence of conditions that can support large, high-severity stage 4 bark beetle outbreaks relative to homogeneous regeneration.

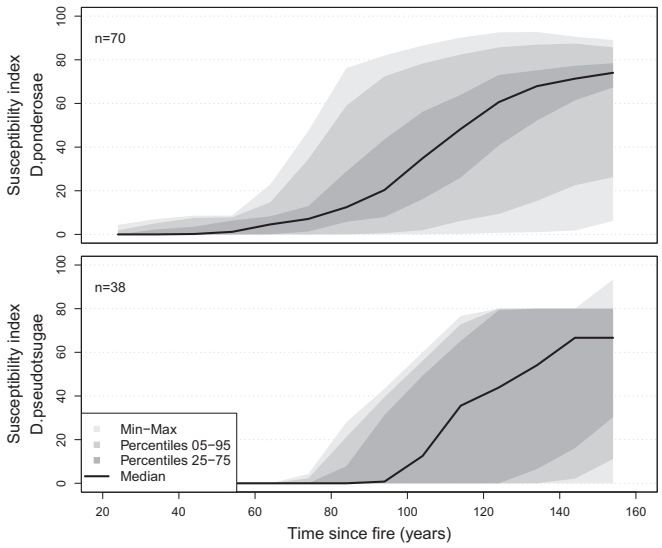

Fig. 1. Susceptibility to bark beetle attack as forests regenerate after stand-replacing fire in lodgepole pine forests (mountain pine beetle, *Top*) and Douglas-fir forests (Douglas-fir beetle, *Bottom*). Shown is the distribution of susceptibility indices in simulated stands (*n*) over time. Susceptibility indices are dimensionless and scaled to [0,100], where an index value >50 represents high susceptibility to attack.

Discussion

Our results highlight that variability in tree regeneration following past disturbances can dampen and delay future disturbances. Initial among-stand variability in postfire forest structure persists for many decades and modulates the availability and distribution of stands susceptible to bark beetle attack. Thus, the first hypothesis of dampened future bark beetle disturbance due to persistent postfire variability was supported by our analyses. The alternative proposition of a synchronous emergence of stand structures susceptible to bark beetle outbreaks was not supported by our simulations of 154 y of postfire forest development. Furthermore, and consistent with our second hypothesis, spatial variation after wildfire reduced the synchronous emergence of highly connected areas susceptible to bark beetle attack. Consequently, the time required for the susceptible forest area to exceed critical thresholds of connectivity was delayed by several decades because of postfire spatial variability. Thus, we have identified spatiotemporal variability as an important attenuating mechanism for interactions between fire and bark beetles.

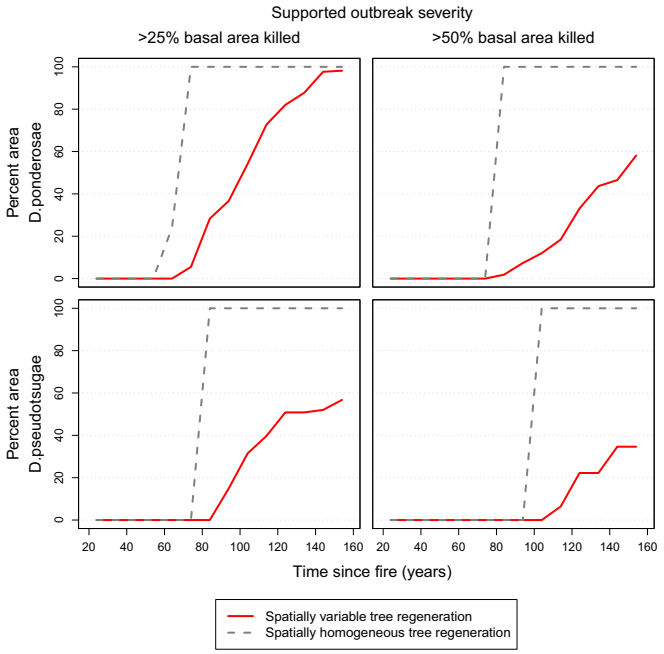

Fig. 2. The proportion of the area burnt in 1988 that is conducive to moderate (*Left*) and severe (*Right*) outbreaks of mountain pine beetle (*Top*) and Douglas-fir beetle (*Bottom*) as postfire stands develop through time. To isolate the effect of variability in postfire tree regeneration, results based on actual stands (solid red line) are compared with hypothetical trajectories initialized with spatially homogeneous conditions (dashed gray line).

Our estimate of the dampening effect of spatial variability on the fire–bark beetle interaction is in some ways conservative. Many factors contribute to variability within and among ecosystems, and we focused solely on variability in postfire forest regeneration in our simulations. Other agents of heterogeneity that could further reduce synchrony in outbreak susceptibility include variations in forest composition (e.g., mixing with nonhost tree species), fire severity, additional herbivores and pathogens, site productivity as influenced by topoedaphic setting, and a broader range of stand development pathways not captured by a deterministic model such as used here (e.g., stochastic variations in mortality, regeneration, and growth). For example, tests showed that simulated stand development trajectories matched observations well (see also ref. 38 and *SI Text*) but that variation in simulated stem densities was underestimated in later stages of forest development. This suggests that the variability in postfire forest development and its effect on future bark beetle outbreaks might not be fully captured by the applied simulation approach. Nevertheless, holding other sources of variability constant allowed us to isolate the apparently strong effects of variable regeneration density in mediating disturbance interactions.

Important caveats include that we did not explicitly consider bark beetle population dynamics in our assessment of disturbance interactions but have focused on the amount and connectivity of suitable bark beetle habitat. A series of thresholds from the within-tree to landscape scales need to be surpassed for an actual outbreak to develop (24, 39). Second, we use susceptibility here to refer only to the size, age, and density at which trees can potentially support beetle development and hold constant inter-tree variation in defense ability, which is highly heterogeneous in nature and increases with increased tree spacing. Furthermore, our analyses did not include the matrix of unburned forest, which is likewise characterized by considerable heterogeneity due to complex disturbance history (30, 33) and environmental variance and is a variable source of beetle immigration. Also, additional dampening and augmenting feedbacks exist between bark beetle outbreaks (e.g., beetle reproduction reduces the abundance of susceptible hosts available for future outbreaks) and high populations negate tree defenses that otherwise constrain low populations (24, 40).

The mitigating effect of disturbance-created variability on future disturbances documented here is likely applicable to a wide range of other systems characterized by spatially contagious disturbances. Our study documented qualitatively similar effects in two distinct forest types that differ substantially in their postfire regeneration mechanisms (immediate dense regeneration in lodgepole pine and slower sparse regeneration in Douglas-fir) and environmental settings. Attenuating feedbacks between fire and bark beetles have also been observed in other forest types (30, 33), and the importance of spatial connectivity for beetle outbreaks has been reported in other systems (41, 42). More broadly, such feedbacks may influence landscape-level vegetation dynamics (22) or the spread of diseases among human, animal, or plant hosts (43, 44).

Increased disturbance activity in the future (12, 13, 45) could reduce or increase the dampening effect of disturbance-mediated variability reported here. A reduction could be expected if eruptive disturbance agents spread simultaneously from multiple epicenters, as can happen when drought impairs tree defenses or elevated temperatures increase beetle survival, thus reducing the importance of landscape connectivity. An increasing frequency of disturbances of moderate severity and size could, however, amplify the negative disturbance feedback reported here through further increasing landscape heterogeneity. However, climate change is also expected to increase the frequency of extreme, historically rare fire years (45). Such extreme events could eventually lead to a homogenization of the landscape, for instance if frequent reburns change successional trajectories or if biological legacies are increasingly lost to reoccurring disturbances (1, 46, 47). Climate change could also alter relationships between stand structure and beetle susceptibility (24, 32), which is an aggregate of beetle attack behavior and tree defensive ability, both of which are influenced by climate. In our current effort to isolate and test a key mechanism of disturbance

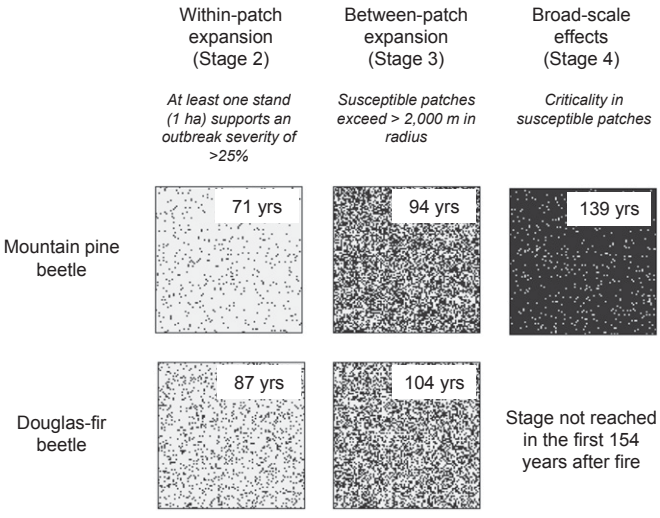

Fig. 3. Spatiotemporal synchronization of susceptibility to bark beetle outbreaks in simulated forests regenerating from stand-replacing wildfire. Stages refer to the conceptual model of cross-scale disturbance interactions proposed by Peters et al. (19). Years indicate when a stage was first reached in the simulation, and 10- × 10-km sections of a neutral landscape (1-ha grain and 302,500-ha extent) are shown for the respective time since fire. Dark shading indicates stands that can support an outbreak severity >25% in the NLMs. Analyses were conducted for the mountain pine beetle (*D. ponderosae*) and the Douglas-fir beetle (*D. pseudotsugae*) in lodgepole pine and Douglas-fir forests, respectively.

interaction we used historical climate and fire conditions and a fixed relationship between stand structure and susceptibility. Future studies could expand these analyses to incorporate how potential future climate change could alter disturbance interactions and feedbacks (14, 40).

Spatial variability provides a powerful means for land and resource managers to enhance ecosystem adaptation to changing disturbance regimes. Climatic drivers plus management-influenced patterns of forest structure have affected recent widespread disturbances, such as the extensive bark beetle outbreaks in western North America (24, 42). A focus on indicators of connectivity and spatial resilience (48) could improve the capacity to detect elevated vulnerabilities and counteract them through management. Our results suggest that ecosystem managers should embrace rather than reduce disturbance-created variability to strengthen negative feedbacks between successive disturbances. Such an approach is in stark contrast to current postdisturbance management interventions practiced in many places around the globe. Postdisturbance salvage logging, removal of legacy trees or undisturbed forest patches, and extensive tree planting (49–51) generally reduce disturbance-induced variability and thus likely weaken negative feedbacks between disturbance events. Because postdisturbance spatial variability can dampen and delay future disturbances, mitigate undesired ecological surprises (52), and enhance ecosystem service supply (53), we suggest that management foster a diverse range of structures on the landscape.

Materials and Methods

Study Area and Empirical Data. We studied forested areas of YNP that burned in stand-replacing fires in 1988. YNP encompasses 9,000 km^2 on a high-elevation (*ca*. 2,050–2,650 m) plateau in northwest Wyoming. Approximately 80% of Yellowstone's forests are dominated by lodgepole pine, but Douglas-fir is prevalent in the lower montane zone (54). Soils are derived from dry, infertile rhyolitic substrates as well as more mesic and slightly less infertile andesitic and former lake-bottom substrates. The climate is generally cool and dry, but the summer of 1988 was the driest on record since 1886 (55). Large, stand-replacing fires have occurred at 100- to 300-y intervals during warm, dry periods throughout the Holocene (56, 57). The 1988 fires burned under extreme drought and high winds, affected ~600,000 ha in Greater Yellowstone, and produced a complex landscape mosaic of burned patches that varied in size and shape (58). Ecological consequences of the 1988 Yellowstone fires have been well studied (16, 34). Postfire tree regeneration was rapid, abundant, and extremely variable across the burned landscape, with postfire lodgepole pine stem densities spanning five orders of magnitude (59–61). After 24 y, postfire lodgepole pine density remained high and variable [mean = 21,445 stems per ha, range = 32–344,052 stems per ha (35)]; Douglas-fir density was lower and also variable among stands [mean = 3,185 stems per ha, range = 15–19,664 stems per ha (36)].

Simulation Modeling and Bark Beetle Susceptibility Assessment. We used the Forest Vegetation Simulator (FVS) (62, 63) to simulate stand development and assess the persistence of variability in stand structure over time. FVS is an empirical, individual-based growth and yield model operating at the stand level. Diameter and height increment of a tree are estimated based on site information, the competitive status of a tree, and its current state variables. Tree mortality is calculated based on a species-specific maximum stand density index, which defines a size- and density-specific carrying capacity. The model variant used here was adapted to and parameterized with data from forest types of our study region (64) and has been successfully applied in previous studies at YNP (38). FVS was developed to be sensitive to stand density (as a main variable influenced by forest management) and thus allowed us to study the effect of a wide range of postfire regeneration densities on stand development. To evaluate FVS, we compared simulated stand development trajectories against independent observations from YNP (37, 38), particularly focusing on the variation in stand structure over time. FVS was well able to reproduce expected trajectories of forest structure for our study area (Figs. S1 and S2).

Analyses with FVS were conducted for stands in lodgepole pine (n = 70) and Douglas-fir (n = 38) forest types, respectively. Simulations were initialized with observed tree information 24 y after fire (35, 36) and run over 130 y using 10-y time steps. For low-density stands, infilling was assumed at empirically observed rates (35). From simulated stand structure we assessed the vulnerability of the burned area to mountain pine beetle and Douglas-fir beetle. Both are comparatively large bark beetle species that require trees of a certain minimum stem diameter for successful colonization and reproduction (i.e., a diameter at breast height of 15 and 23 cm for MPB and DFB, respectively). Stand density, stand age, and the proportion of host tree species within a stand also influence tree susceptibility and potential outbreak severity. We used previously established susceptibility indices to describe bark beetle susceptibility of simulated stands quantitatively over time (see *SI Text* for details). For MPB, we followed the approach of Hicke and Jenkins (23). For DFB, we used the susceptibility rating developed by Weatherby and Thier (65). Susceptibility indices were standardized to a [0,100] scale, with values >50 indicating high susceptibility. Maximum outbreak severities were estimated at 68.0% and 72.3% of basal area killed by MPB and DFB, respectively (7, 31), and severity was assumed to scale linearly with susceptibility (23, 66, 67).

Analyses. To assess persistence of postfire variability in stand structure over time we used FVS simulations, analyzing variation in stem density, diameter, and basal area among stands. We then evaluated structural variability in the context of bark beetle susceptibility, estimating the onset and progression of susceptibility over time. Specifically, we determined how many years after fire the first stand would become highly susceptible to bark beetles and when >50% of the analyzed stands would be at high risk. Furthermore, we estimated the length of the time window between the first stand reaching high susceptibility and all stands being highly susceptible (i.e., we quantified temporal synchrony in the emergence of stands susceptible to bark beetle attack on the burned landscape). To isolate the effect of spatial variability in postfire regeneration from other factors affecting stand development we also ran analyses in which we effectively eliminated heterogeneity in regeneration density and structure. Specifically, we initiated the simulations with identical conditions for all stands while keeping total postfire tree density the same (see *SI Text* for details).

To address our second question (effect of spatiotemporal synchrony on conduciveness of the landscape to widespread bark beetle outbreaks) we used NLMs. The extent of the neutral landscape was set to 302,500 ha, the grain was 1 ha, and analyses were conducted for an outbreak severity of >25%. For every 10-y time step of the simulation the supported stand-level severity was determined from FVS and susceptibility indices, and stands were distributed in the neutral landscape with replacement, accounting for the observed distribution of the respective stem density classes (60). Neutral landscapes were subsequently analyzed using the framework proposed by Peters et al. (19), which focuses on connectivity as a crucial factor for cross-scale amplification in spatially contagious disturbances (see *SI Text* for details). In the context of bark beetle outbreaks, this framework describes the process by which heterogeneity at the landscape scale provides beetles with a series of small resource pulses that are scattered in space and time, and hence less likely to favor large population increments, rather than a simultaneous large pulse from a more uniform and well-connected forest that ultimately favors a transition past eruptive thresholds.

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Supporting Information

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SI Text

Bark Beetle Susceptibility. We used susceptibility indices to quantify bark beetle risk based on the simulated stand development trajectories after fire. We applied stand structure susceptibility indices (*SSSI*) (i.e., indices solely addressing the variation of susceptibility with stand characteristics and disregarding the effect of site factors such as climate). For MPB, we used the index developed by Hicke and Jenkins (23), which is a modified version of earlier work by Shore and Safranyik (68) and Shore et al. (69). Susceptibility to MPB was calculated from stand age (A_{MPB}), stand density (D_{MPB}), and host availability within a stand (P_{MPB}) (Eq. **S1**):

$$SSSI_{MPB} = A_{MPB} \cdot D_{MPB} \cdot P_{MPB}. \quad \textbf{[S1]}$$

MPB susceptibility has a unimodal relationship with age, peaking in stands between 80 and 120 y (Eq. **S2**):

$$A_{MPB} = \begin{cases} 0.1 & age < 40 \\ 0.1 + 0.1 \cdot \left(\frac{age - 40}{10}\right)^{1.585} & 40 \le age \le 80 \\ 1.0 & 80 < age \le 120 \\ 1.0 - 0.05 \cdot \frac{age - 120}{20} & 120 < age \le 510 \\ 0.1 & age > 510 \end{cases}. \quad \textbf{[S2]}$$

Furthermore, susceptibility is highest in dense stands but decreases again at very high stem densities above 1,500 trees per hectare (tph) (Eq. **S3**):

$$D_{MPB} = \begin{cases} 0.0824 \cdot \left(\frac{tph}{250}\right)^{2.0} & tph < 650 \\ 1.0 - 0.7 \cdot \left(\frac{3 - tph}{250}\right)^{0.5} & 650 \le tph \le 750 \\ 1.0 & 750 < tph \le 1{,}500 \\ \frac{1.0}{0.9 + \left(0.1 \cdot e^{0.4796 \cdot \left(\frac{tph}{250} - 6\right)}\right)} & tph > 1{,}500 \end{cases}. \quad \textbf{[S3]}$$

The final component of MPB *SSSI* accounts for the share of potential host trees [i.e., pine trees with a diameter at breast height (dbh) of ≥15cm] within a stand, with susceptibility increasing with potential host tree share (Eq. **S4**):

$$P_{MPB} = \frac{basal\ area\ of\ pine \ge 15cm\ dbh}{basal\ area\ of\ all\ species \ge 7.5cm\ dbh} \cdot 100. \quad \textbf{[S4]}$$

The thus calculated $SSSI_{MPB}$ ranges from 0 to 100, with higher values indicating higher susceptibility to MPB.

For DFB we used the susceptibility rating system developed by Weatherby and Thier (65), which is also the DFB risk rating approach used by the US Department of Agriculture Forest Service (70, 71). Stand susceptibility to DFB ($SSSI_{DFB}$) increases with basal area (BA_{DFB}), the proportion of basal area in Douglas-fir (P_{DFB}), the average dbh of Douglas-fir (DBH_{DFB}), as well as stand age (A_{DFB}). We modified the original approach of Weatherby and Thier (65) by restricting compensation to occur only between parameters representing stand structure and composition, and by scaling the index to a [0,100] interval for better comparison with $SSSI_{MPB}$ (Eq. **S5**):

$$SSSI_{DFB} = min(BA_{DFB} + P_{DFB} + DBH_{DFB}\ ; A_{DFB}). \quad \textbf{[S5]}$$

Stands with a basal area above 57.4 $m^2 \cdot ha^{-1}$ are particularly susceptible to DFB attack (Eq. **S6**):

$$BA_{DFB} = \begin{cases} 6.7 & basal\ area < 27.5\ m^2 \\ 13.3 & 27.5\ m^2 \le basal\ area \le 57.4\ m^2 \\ 20.0 & basal\ area > 57.4\ m^2 \end{cases}. \quad \textbf{[S6]}$$

Also, a higher share of the host tree species Douglas-fir on the total basal area increases the susceptibility to DFB (Eq. **S7**):

$$P_{DFB} = \begin{cases} 13.3 & Douglas\text{-}fir < 25\% \\ 26.7 & 25\% \le Douglas\text{-}fir \le 50\% \\ 40.0 & Douglas\text{-}fir > 50\% \end{cases}. \quad \textbf{[S7]}$$

Furthermore, the size of the Douglas-fir trees within a stand is positively associated with susceptibility (Eq. **S8**). Here, only trees >22.9 cm in dbh were assessed (65); if no tree within a stand was above this threshold susceptibility was set to zero:

$$DBH_{DFB} = \begin{cases} 13.3 & dbh < 25.4\ cm \\ 26.7 & 25.4\ cm \le dbh \le 35.6\ cm \\ 40.0 & dbh > 35.6\ cm \end{cases}. \quad \textbf{[S8]}$$

With regard to age, the ordinal susceptibility rating of the original index (65) was converted to continuous scale, increasing linearly between 60 and 120 y (Eq. **S9**):

$$A_{DFB} = \begin{cases} 0.0 & age < 60 \\ 1.667 \cdot age - 100 & 60 \le age \le 120 \\ 100 & age > 120 \end{cases}. \quad \textbf{[S9]}$$

Potential Outbreak Severity. For both susceptibility indices, outbreak severity was found to be closely and nearly linearly related to susceptibility in previous analyses (23, 66, 67). We took advantage of these findings to also assess the proportion of the forest area affected by wildfire in 1988 that would support moderate (>25% of basal area affected) and severe (>50% of basal area affected) bark beetle outbreaks at any given point in time. To calculate potential outbreak severity we associated maximum *SSSI* levels with peak outbreak severities (OS_{max}) observed for the two bark beetle species [68.0% and 72.3% for MPB and DFB, respectively (7, 23, 31, 66)]. Subsequently, we assumed a linear relationship between *SSSI* and severity (23, 67) and calculated potential outbreak severity (*POS*) following Eq. **S10**:

$$POS = SSSI \cdot \frac{OS_{max}}{100}. \quad \textbf{[S10]}$$

Reference Trajectories Under Homogeneous Regeneration Density and Structure. To isolate the effect of postfire variability in regeneration on future beetle susceptibility we also ran analyses effectively eliminating heterogeneity in regeneration density and structure. In these runs we controlled for among-stand variability in postfire regeneration by initializing the simulations with identical

conditions for all stands. Densities were set to 1,200 and 700 trees for lodgepole pine and Douglas-fir forests, corresponding to levels that are considered fully stocked stands in forest management. Stands in the observed dataset matching those densities most closely were imputed over the entire study area. The trajectories resulting from spatially homogeneous regeneration were compared with the runs initialized with the observed variability in tree regeneration, with the latter weighted according to their represented area within the perimeter of the 1988 fires (60). In the subsequent analysis we focused on two levels of severity (>25% and >50% of basal area killed) and determined what proportion of the burnt landscape would be able to support the respective outbreak severity at any given point in time.

Stages of Connectivity and Nonlinear Disturbance Dynamics. Peters et al. (19), based on theoretical considerations, suggested that spatial connectivity is a crucial factor for cross-scale, amplifying feedbacks in disturbance. Spatial connectivity of susceptible beetle habitat was here assessed based on NLMs. NLMs are models that analyze spatial patterns in the absence of spatial processes and have been used widely in landscape ecology (72, 73). A variable of interest (here the stand-level risk for bark beetle attack, derived from susceptibility indices based on FVS-simulated stand development) is distributed randomly across a landscape, and the emerging patches are analyzed based on rules of spatial connectivity. The grain of our NLM was 1 ha, and stands were distributed on the landscape with replacement based on the proportion of the real postfire landscape occupied by stands of varying tree density (60). The extent of the neutral landscape was 302,500 ha, arranged in a square of 55 × 55 km. As the susceptibility of the individual stands increases with time since fire, the area susceptible (defined as stands with a POS of >25% for this analysis) also increases, and smaller patches coalesce to form fewer but larger patches. Indicators of spatial connectivity, such as percolation and criticality (i.e., the condition when all susceptible patches on the landscape are connected), can be calculated at each time step to quantify dynamics of the emerging patterns. Compared with actual landscapes, NLMs generally show similar qualitative trends in patch numbers, sizes, and connectivity, although actual landscapes have a wider range of spatial patterns than simple random NLMs (72). Thus, our NLM-based assessment of the landscape progression through the stages defined by Peters et al. (19) is likely conservative.

Peters et al. (19) identified four stages related to the spatial spread of disturbances and associated with nonlinear dynamics: initiation, within-patch expansion, between-patch expansion, and fine- to broad-scale feedbacks (19). Initiation (stage 1) is reached once at least one tree on the landscape exceeds the minimum diameter threshold for bark beetle attack. The landscape was already in this stage at the beginning of our study period 24 y after fire; stage 1 was thus not further analyzed here. Stage 2 describes a landscape in which within-patch expansion of the disturbance is possible, here defined as at least one 100- × 100-m stand being susceptible for attacks of >25% severity. In stage 3 the disturbance can expand between patches. Following a previous analysis (74) we here defined patches to be areas of <2,000 m in radius. Consequently, stage 3 was reached once the connected patches of susceptible forest exceeded this size in the simulation. Finally, stage 4 describes broad-scale effects within a disturbance and the presence of amplifying feedbacks (19). Here, we used criticality (i.e., full connectivity between susceptible cells) across the entire landscape to define conditions that are conducive to such effects in the context of a bark beetle outbreak. For all spatial analyses an eight-neighbor rule was used to define connectivity. Neutral landscape analysis was done at 10-y time steps and the temporal transitions between stages interpolated to annual values.

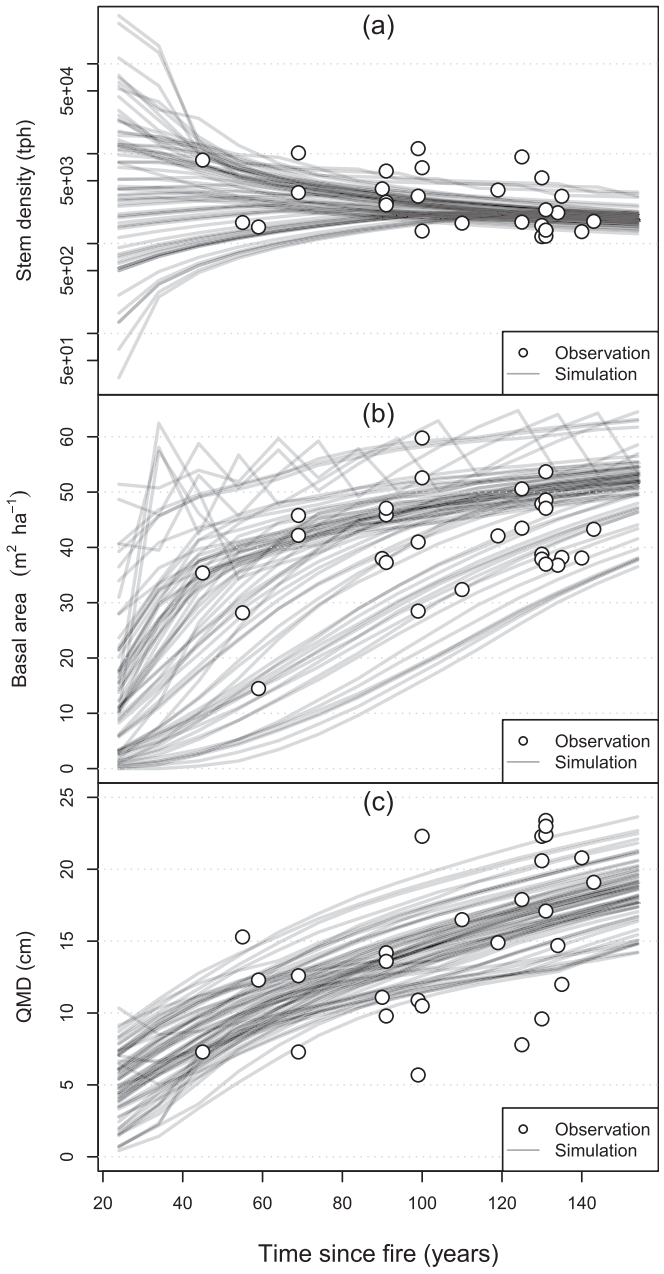

Fig. S1. Simulated trajectories of lodgepole pine stands after wildfires in 1988 compared with independent observations from a chronosequence of stand development at YNP (37). Lines indicate the development of 70 individual stands (see also Table 1) for (*A*) stem density (on a log scale), (*B*) stand basal area, and (*C*) the QMD of the stand.

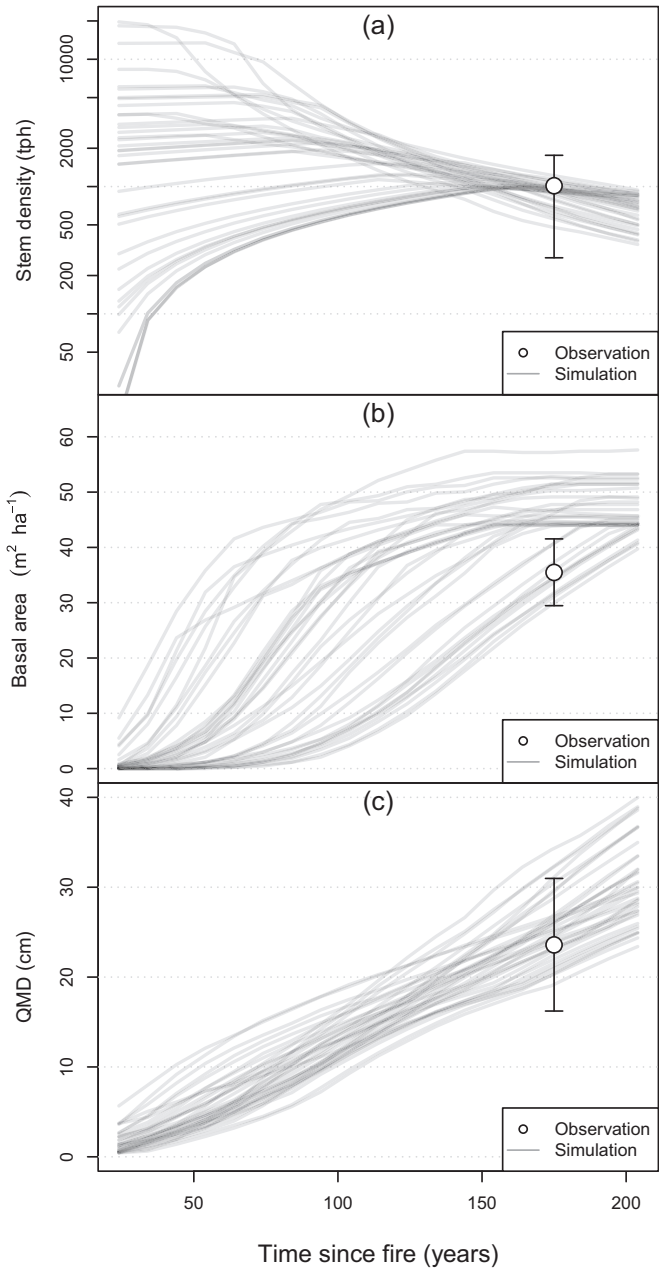

Fig. S2. Simulated trajectories of Douglas-fir stands after wildfires in 1988 compared with independent observations of mature stands (mean and SD) at YNP (38). Lines indicate the development of 38 individual stands (see also Table 1) for (*A*) stem density (on a log scale), (*B*) stand basal area, and (*C*) the QMD of the stand.