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Regeneration strategies and forest resilience to changing fire regimes: Insights from a Goldilocks model

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Abstract

Disturbances are ubiquitous in ecological systems, and species have evolved a range of strategies to resist or rebound following disturbance. Understanding how the presence and complementarity of regeneration traits will affect community responses to disturbance is increasingly urgent as disturbance regimes shift beyond their historical ranges of variability. We define "disturbance niche" as a species' fitness across a range of disturbance sizes and frequencies that can reflect the fundamental or realized niche, that is, whether the species occurs alone or with other species. We developed a model of intermediate complexity (i.e., a Goldilocks model) to infer the disturbance niche. We parameterized the model for subalpine forests in Yellowstone National Park (USA) adapted to infrequent stand-replacing fires and included the three major tree-regeneration strategies: (1) obligate seeders that rely on ex situ seeding into burned areas (non-serotinous lodgepole pine, *Pinus contorta* var. *latifola*), (2) obligate seeders that depend on in situ seedbanks (serotinous lodgepole pine, *Pinus contorta* var. *latifola*), and (3) species that can resprout from surviving roots following fire (quaking aspen, *Populus tremuloides*). Our results showed which regeneration strategies increase or decrease in prevalence as fire rotation declines. Non-serotinous pines were extirpated when fire rotation was below 50 years in a monoculture and 100 years in a mixed forest; serotinous pines were extirpated when fire rotation was below 20 years; and aspen was extirpated when fire rotation fell below 6 years. The fundamental and realized disturbance niches pinpointed the key mechanisms limiting regeneration for each strategy, namely, increasing fire size for non-serotinous pine (ex situ seeders), decreasing fire frequency for serotinous pine (in situ seeders), and interspecific competition for aspen (resprouters). In a mixed forest, the three regeneration strategies were complementary and each dominated at different combinations of fire size and frequency. Consequently, diversity of regeneration strategies enhanced forest resilience to declining fire rotations. Despite its simplicity, our Goldilocks model produced realistic dynamics and could be readily adapted to other disturbance-prone ecosystems to explore the generality of these results. The disturbance niche is a key concept for anticipating community resilience to changing disturbance regimes.

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KEYWORDS
biodiversity, competition, diversity, extirpation threshold, fire ecology, individual-based model, portfolio effect, resilience, response diversity, stand-replacing fire, subalpine forest

INTRODUCTION

Disturbances are ubiquitous in ecological systems, and species have evolved a range of strategies to resist or rebound following disturbance (Grime, 2006; Johnstone et al., 2016; Pausas & Keeley, 2014). In forest trees, traits such as thick bark (e.g., *Pseudotsuga menziesii*), dense wood (e.g., *Prestoea acuminata*), and adventitious roots may allow species to survive fires, hurricanes, and floods, respectively (Parolin & Wittmann, 2010; Uriarte et al., 2019). Epicormic (e.g., some Eucalypts) or basal (e.g., *Populus tremuloides*) resprouting or a well-developed seedbank (e.g., *Pinus banksiana*) may lead to rapid regeneration following fire and wind disturbances (Clarke et al., 2013; Pausas & Keeley, 2017). Such adaptations are tuned to disturbance regimes rather than individual disturbance events (Keeley et al., 2011), yet disturbance regimes are changing (McDowell et al., 2020; Turner, 2010). The frequency and severity of hurricanes, floods, fires, and insect outbreaks are increasing in many regions throughout the world (Higuera & Abatzoglou, 2021; Seidl et al., 2011, 2017; Sommerfeld et al., 2018), and species adapted to historical disturbance regime are increasingly vulnerable to decline (Baltzer et al., 2021; McDowell et al., 2020). A central question is whether populations, communities, and ecosystems will be resilient (Holling, 1973; Scheffer, 2009) to future disturbance regimes, defined as the ability to avoid qualitative state changes, and more specifically, which combinations of regeneration strategies maximize resilience under a range of disturbance regimes.

Generalizing the responses of a community composed of species with different regeneration strategies to projected increases in the frequency and size of disturbances remains challenging. The presence and relative abundance of species with different regeneration strategies should influence how the community responds to disturbances that vary in size, frequency, and severity (Elmqvist et al., 2003; Grime, 2006). These responses can be represented by the "disturbance niche," that is, how fitness varies along key axes of a disturbance regime. For instance, for fires this would include the size, frequency, and severity of fires. The niche can be divided into fundamental and realized niches depending on the absence or presence of competitors, respectively (Hutchinson, 1957). Inferring the disturbance niche will allow to both identify the optimal disturbance regime for different regeneration strategies along with the disturbance regime that leads to regeneration failure (the extirpation threshold). Extirpation thresholds occur in the disturbance space where community composition is expected to change qualitatively and a viable population becomes locally extinct. Here, we define the fitness as species' density at equilibrium. Although this version of the niche does not capture transient dynamics, equilibrium maps the long-term trajectory of the system, and reveals which species and traits can or cannot be maintained over the long-term for any combination of disturbance size, frequency, and severity.

High-severity disturbances that kill most to all reproductive individuals are most likely to trigger long-term change by resetting the system and initiating recovery. Recovery pathways depend on the identity and abundance of the establishing individuals following a disturbance, post-disturbance conditions, and long-term interactions among species (Johnstone et al., 2016; Seidl & Turner, 2022). Understanding how tree species traits interact with high-severity fire is increasingly important as fire frequency, size and severity increase in many regions of the world (Bowman et al., 2013; Ward et al., 2020; Westerling, 2016).

Tree re-establishment following stand-replacing fire arises from three general regeneration strategies: obligate ex situ seeders, obligate in situ seeders, and resprouters (Baker, 2009; Bellingham & Sparrow, 2000; Grime, 2006; Rowe, 1983; Rowe & Scotter, 1973). Ex situ obligate seeders rely on seed dispersal from live trees in undisturbed patches (Gill et al., 2022). Such species include lower montane conifers, such as Douglas-fir (*Pseudotsuga menzeisii*) and ponderosa pine (*Pinus ponderosa*); and high-elevation or north-latitude conifers, such as subalpine fir (*Abies lasiocarpa*) and Englemann spruce (*Picea engelmannii*) in the western United States, white spruce (*Picea glauca*) in boreal North America, and Norway spruce (*Picea abies*) in northern Europe. In situ obligate seeders develop a seedbank that provides an abundant post-disturbance supply of propagules. For example, serotiny has evolved independently several times, including lodgepole pine (*Pinus contorta* var. *latifolia*) in western North America, jack pine (*Pinus banksiana*) in eastern North America, black spruce (*Picea mariana*) in boreal forests, *Banksia* spp. in Australia and South Africa, and manuka (*Leptospermum scoparium*) in southeast Australia and New Zealand (Battersby et al., 2017). In contrast to obligate seeders, resprouters can produce new stems from surviving tissues after aboveground

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tissues are killed by disturbance (e.g., basal or epicormic resprouts). Examples include quaking aspen and birches (*Betula* spp.) in North America, and many woody plants in fire-prone savannas, including sumacs (*Rhus*), *Acacias*, and eucalyptus (Clarke et al., 2013; Ratajczak et al., 2017). Many species use at least one of these strategies and some species rely on multiple regeneration pathways (Enright et al., 2014).

Disturbance and vegetation dynamics have been simulated using many different types of models, and models are already used for assessing resilience across a wide range of conditions (Albrich et al., 2020; DeAngelis & Yurek, 2017; Keane et al., 2019; Seidl et al., 2012). At one end of the spectrum are models that are highly abstract and theoretical (e.g., Levin & Paine, 1974). Theoretical models focus on fundamental questions such as coexistence of species with different traits (Clark, 1991a, 1991b; Hastings, 1980; Miller & Chesson, 2009; Tilman, 1994) and provide general understanding and hypothesis generation, but the level of abstraction often limits site-specific applications. At the other end of a spectrum are models that attempt more realism and represent processes that require many detailed, site-specific parameters (e.g., forest landscape models such as LANDIS-II [Scheller et al., 2007], Fire-BGC [Keane et al., 2019], aDVGM [Scheiter & Higgins, 2009], and iLand [Seidl et al., 2012]). Detailed process-based models can better represent a real-world system well (e.g., iLand, [Seidl et al., 2012, Turner et al., 2022], but often at the expense of generality). Models of intermediate complexity that incorporate key processes yet retain the flexibility to be applied in a wide range of systems are valuable tools for exploring resilience under any hypothetical range of disturbance regimes, and for exploring the fundamental and realized disturbance niches.

Here, we develop and use a model of intermediate complexity—a "Goldilocks" model that strikes a balance between abstract (e.g., theoretical models) and detailed (process-based models) approaches—to explore characteristics of the disturbance niche in temperate forests adapted to infrequent, high-severity fires. The model is individually based and incorporates the three major tree regeneration strategies; basic demographic processes including dispersal, maturation, mortality, and competition; and spatial and temporal dynamics of stand-replacing fire. The model is based on a spatiotemporal point-process approach that has been used in ecology (Bolker & Pacala, 1997; Cornell et al., 2019; Ovaskainen et al., 2014), but such models have not, to our knowledge, been extended to disturbance-recovery dynamics. First, we asked for each regeneration strategy, how do the fundamental and realized disturbance niches vary with fire regime? We assessed disturbance niches by determining equilibrium density and extirpation thresholds as a function of fire rotation—a synthetic metric for fire size and frequency (see *Methods*). Second, we asked if and when the presence of all strategies enhances resilience and what is the expected forest composition (i.e., coexistence of regeneration strategies) under different disturbance regimes?

CASE STUDY REGION

We explored difference in tree densities across different combinations of fire size and frequency using the well-studied subalpine forests of Yellowstone National Park (Wyoming, USA) as a model system. Much of this forested landscape is dominated by lodgepole pine, with both non-serotinous and serotinous individuals present across the landscape but the prevalence of serotiny decreases with increasing elevation and the associated longer fire-return intervals (Schoennagel et al., 2003; Tinker et al., 1994). Aspen, which can resprout prolifically when aboveground stems are killed, is also present (Romme et al., 1995). The historical fire regime is characterized by large, infrequent, stand-replacing fires, which have occurred at intervals of approximately 100 to 300 years throughout the Holocene (Higuera et al., 2011). Paleoecological analyses (Iglesias et al., 2018; Stegner et al., 2019), chronosequence studies (Kashian et al., 2013; Kashian, Turner, & Romme, 2005; Kashian, Turner, Romme, & Lorimer, 2005), and assessments of postfire forest recovery (Turner et al., 1997, 1999, 2016) have demonstrated substantial forest resilience to the historical fire regime. However, climate change is increasing the frequency and size of wildfires (Moritz et al., 2012; Westerling, 2016)—a trend that is projected to continue through the 21st century (Westerling et al., 2011) and increasingly observed in other regions (Baltzer et al., 2021). How tree species with different regeneration strategies may respond to novel fire regimes, with more frequent and larger fires, is not known.

METHODS

The model simulates individuals from their initial recruitment through stage transitions (e.g., from juvenile to adult) until death (Figure 1). Life-history stages (Figure 1) and regeneration strategies differ among the species (see below and Figure 2). Biological events, such as recruitment, growth, or mortality, are stochastic and occur as a Poisson process. A reproductive individual produces new recruits at an average rate β according to a Gaussian dispersal kernel D with a scale (i.e., standard deviation) σ, the recruit transitions to the next life stage at an average rate γ, and dies of natural cause at an average rate μ. These rates are species- and stage-specific (e.g., the transition rate γ from seedling to sapling is different from sapling to tree) but we omitted the

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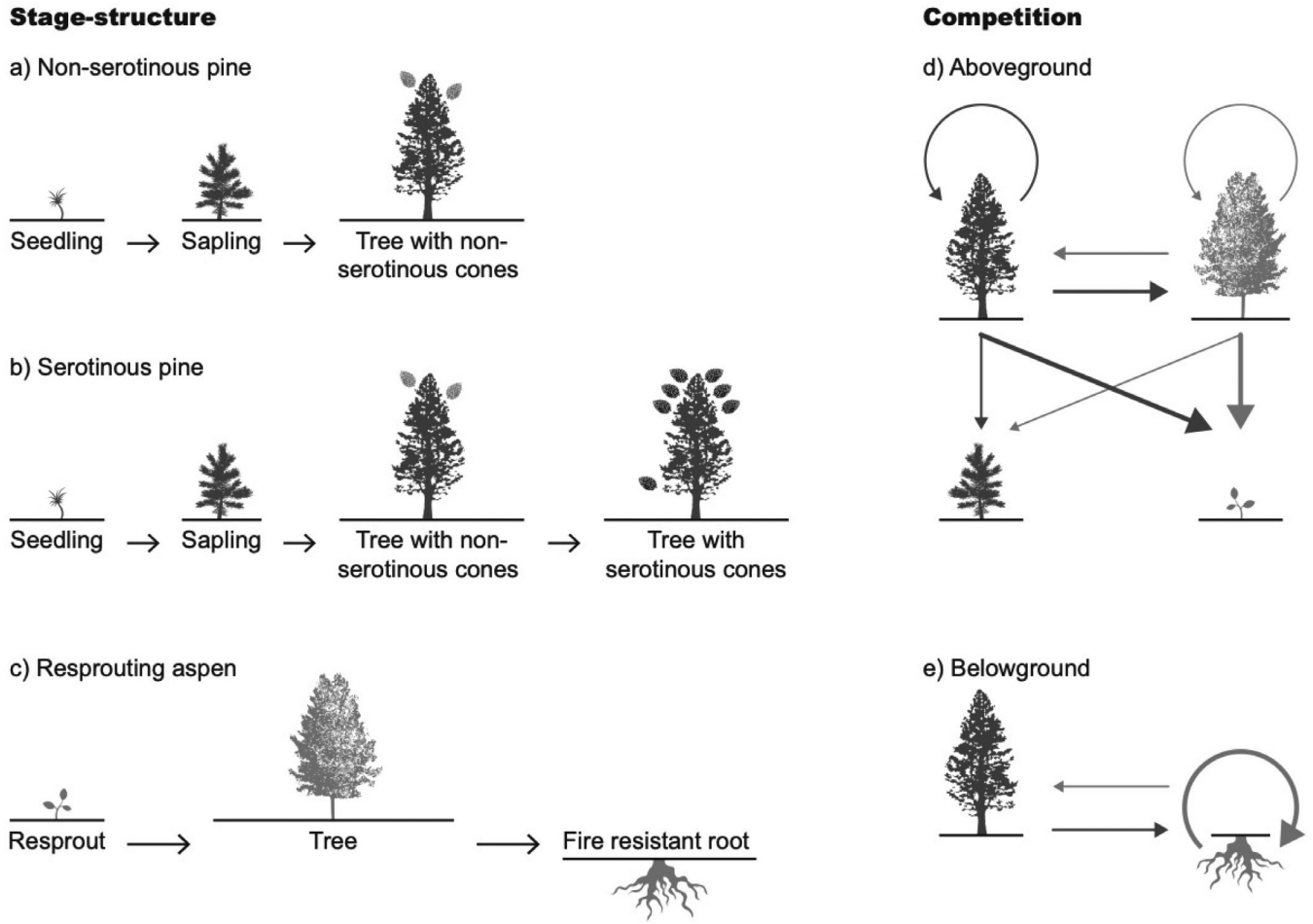

FIGURE 1 Model overview showing the stage transitions for (a) non-serotinous lodgepole pine, (b) serotinous lodgepole pine, and (c) resprouting quaking aspen, and the (d) aboveground and (e) belowground competitive interactions between individuals of each species. Black and gray arrows denote effect of the pines to the aspen and the aspen to the pines, respectively. The thickness of the arrow represents the relative strength of the interaction.

subscripts for brevity (see Appendix S1: Table S1). In our model, individuals also die due to competition and fire. Technically, the model is a spatiotemporal point process, commonly used in theoretical ecology (Bolker & Pacala, 1997) with spatially explicit Lotka-Volterra competition (stronger competition when individuals are in closer proximity) and stage-structure (e.g., passing from seedling, to sapling, to multiple adult tree stages).

Regeneration strategy and life-history stage

Non-serotinous pine has three life-stages: seedling, sapling, and tree (Figure 1a). Individuals are non-reproductive until they reach the "tree" stage (Figure 1a), after which they produce recruits until death. Individuals are subjected to stage-specific background mortality, competition-induced death, and fire mortality. Following a fire, recruitment only occurs from unburned trees.

Serotinous pine has four demographic stages: seedling, sapling, tree with non-serotinous cones, and tree with serotinous cones (Figure 1b). The first three life-stages are exactly the same as the non-serotinous pine; serotinous individuals initially produce primarily non-serotinous cones in line with empirical observations (Schoennagel et al., 2003; Turner et al., 2007, 2016), so the canopy seedbank takes time to develop. The serotinous tree with non-serotinous cones produces seedlings at the same rate as the non-serotinous tree until it transitions into a tree with serotinous cones. In that final stage, however, recruitment is halted and seeds are only released if the tree is burned.

Resprouting aspen has three stages: sapling, tree, and root (Figure 1c). Trees produce roots, and roots produce saplings. We assume here that recruitment only occurs via resprouts from roots, not seeds. The functional form of the recruitment is the same as for the pines, but the parameters differ (Appendix S1: Table S1). Recruitment from root to sapling occurs continuously, but the

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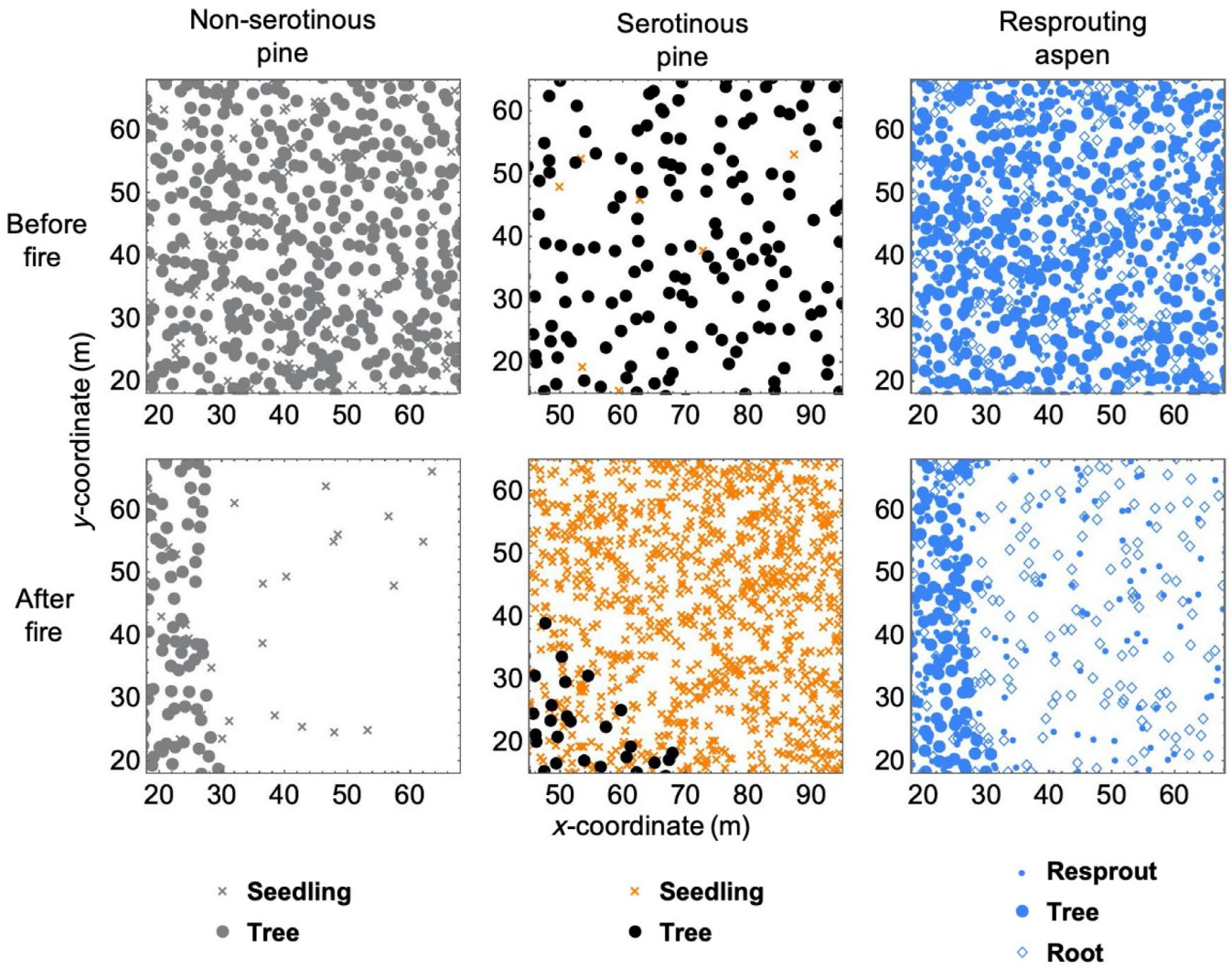

FIGURE 2 Snapshots of landscape configurations before (top row) and after a fire (bottom row) for monospecific forests. Gray, black, and blue represent non-serotinous pine, serotinous pine, and quaking aspen, respectively. Crosses represent seedlings, small dots represent aspen resprouts, large dots represent trees, and blue empty diamonds represent aspen roots. Fire radius is 100 m.

effective recruitment rate is higher after fires because sprouting is stimulated when mature aspen trees are killed by the fire.

We made two simplifying assumptions. (1) As the pines are not different species, we assume that their demographic parameters (stage transition rate, competitive effect, mortality) are the same. However, serotinous and non-serotinous pines are modeled separately to distinguish consequences of these two different regeneration strategies, which are conserved and passed down when propagules are produced (i.e., serotinous pines trees only produce serotinous pine seedlings). (2) We omit aspen establishment from seed to focus on resprouting and to contrast the three regeneration strategies. Although seedling aspen can establish in Yellowstone following high-severity fire, establishment is patchy (Turner et al., 2003), and the long-term fate of these seed-born trees is yet unclear (Hansen et al., 2016; Romme et al., 2005).

Intra- and interspecific competition

Trees in subalpine forests can be limited by competition for light, nutrients, and water (Figure 1d,e). Competition increases with abundance and proximity to other trees and induce density- and spatially dependent mortality. The total magnitude of competition experienced by an individual of type A (e.g., an adult aspen) at a location x is the sum of pairwise competition with all individuals in the domain,

$$K_A(x) = \sum_{y \in \Omega} \alpha_{AB} D(|y-x|, \sigma_B), \quad (1)$$

where Ω are the locations of all individuals that exert a competitive effect on A, B is the type of individual at location y (e.g., a pine tree or aspen tree), α_{AB} is the competitive effect of type B to type A, D is a Gaussian

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competition kernel normalized to one, and $|y - x|$ is the Euclidian distance between the individuals, and σ_B is the spatial scale of competition for type *B*.

For simplicity, we ignored the following competitive interactions: (1) seedlings were not affected by competition and had no competitive effect on any individual, (2) saplings exerted no competitive effects but were affected by trees, and (3) roots had no competitive effect on resprouts, saplings and seedlings. Thus, competitive effects were from trees to saplings and resprouts, between trees, between pine trees and aspen roots, and between roots (Figure 1d,e, Appendix S1: Table S2). Consistent with observations, we assumed that both pines are the superior competitor to aspen, and aspen exerts weaker intraspecific competition (Hansen et al., 2016).

Fire dynamics and effects

Fire is modeled as a process for which the size and average frequency of fires are external control parameters (i.e., we assume no fuel limitation, which is generally consistent with our case study system in which climate-driven fires dominate, e.g., Harvey et al., 2016; Westerling, 2016). For simplicity, we assume that fires are circular and defined by a radius *r*, that the location of each fire is random, and that all trees within the fire perimeter are killed. Fire appears as a Poisson process with rate β_F, which controls fire frequency. Note that the inverse of β_F is the expected (or average) time between two fire events within the spatial domain, that is, fire free interval (FFI). We use FFI (years) instead of frequency to quantify how often a fire occurs anywhere within the spatial domain. Thus, an increase in fire frequency is associated with shorter FFI. Different combinations of fire size and FFI can produce the same fire rotation (e.g., few large fires, or many smaller fires could burn an equivalent area over the same duration of time).

In the model, fire affects the reproductive stage of each species differently. Fire kills all individuals of ex situ obligate seeder, kills all of the in situ seeder but triggers seedling recruitment from serotinous cones, and kills the aboveground life-history stages of the resprouters, but does not affect belowground life-history stages that can resprout.

Model parameters and implementation

The simulation uses a recent implementation for spatio-temporal point process models (Cornell et al., 2019; Ovaskainen et al., 2014). The model is implemented in C and is based on the Gillespie algorithm. As the model is rather technical, we provided only general descriptions of the processes, implementations (above) and analyses (below). Further demonstrations of model behavior, including transient dynamics, alternative scenarios using different parameter values for postfire recruitment for serotinous pine, strength of competition between pines and aspen are reported in Appendix S1. Technical and additional details for implementation of initial conditions, serotinous pine (pre- and post-fire recruitment), a full description of how fire was parameterized, and guidance on how to run the simulations are reported in Appendices S2 and S3.

Model simulations and analyses

We ran the model in a 200 × 200 m domain but wrapped space as a torus; thus, the spatial domain is effectively infinite without boundaries. We ran each simulation for 1500 years, discarding the first 500 years then computing the equilibrium density during the remaining 1000 years. Each simulation began with specified initial conditions (presence, density, distribution, and relative abundance of each species) and a given fire regime (size and FFI of high-severity fire). For this study, we focused only on adult tree density.

Fire parameter space

Fire size was simulated by varying the proportion of area burned from 5% to 95% of the landscape with a 5% increment—a total of 18 different fire sizes. The FFI was varied in 5-year increments between 5 and 20 years and 10-year increments between 20 and 100 years—a total of 12 different FFIs. These parameter values generated a range of fire rotations roughly from 6 to 900 years. We ran 10 replicates, for a total of 15,000 years of simulation per combination of fire size and FFI.

Fundamental and realized niches

To obtain the fundamental niche, we simulated the model separately for each regeneration strategy, that is, representing a monospecific forest at the onset. To obtain the realized niche, we simulated the model for the mixed forest with all three regeneration strategies represented, then tracked the tree density of each species and as well as the total tree density of all three. For each combination of fire size and FFI, we computed the equilibrium

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density—our proxy for fitness—as the annual average tree density and then averaged among the 10 replicates. To determine the shape of the fundamental and realized niches, we plotted the equilibrium density for all combinations of fire size and FFI. The fire rotation demarcating regeneration failure or success represented the extirpation threshold. We assumed that a forest failed to regenerate if the tree density was less than 50 per hectare (Hansen et al., 2018).

Resilience and forest composition

To evaluate whether mixed forests are more resilient, we compared where along the axes of fire size and FFI the total density in the mixed forest exceeded that of monospecific forests. Finally, to assess change in forest composition in the mixed forest, we looked at the coexistence of the three strategies, that is, where their tree densities exceeded 50 trees per hectare.

RESULTS

Fire and the fundamental disturbance niche

For simulations of monospecific forests, equilibrium density of non-serotinous pines always declined as fire rotations became shorter (Figure 3a). Their density could reach up to 1600 stems per hectare in the longest fire rotations (~900 years). The equilibrium density declined from 1400 to 400 stems per hectare as fire rotation declined from 300 to 100 years. Non-serotinous pines were extirpated when fire rotation was below 50 years (Figure 3a). However, for the same fire rotation, the

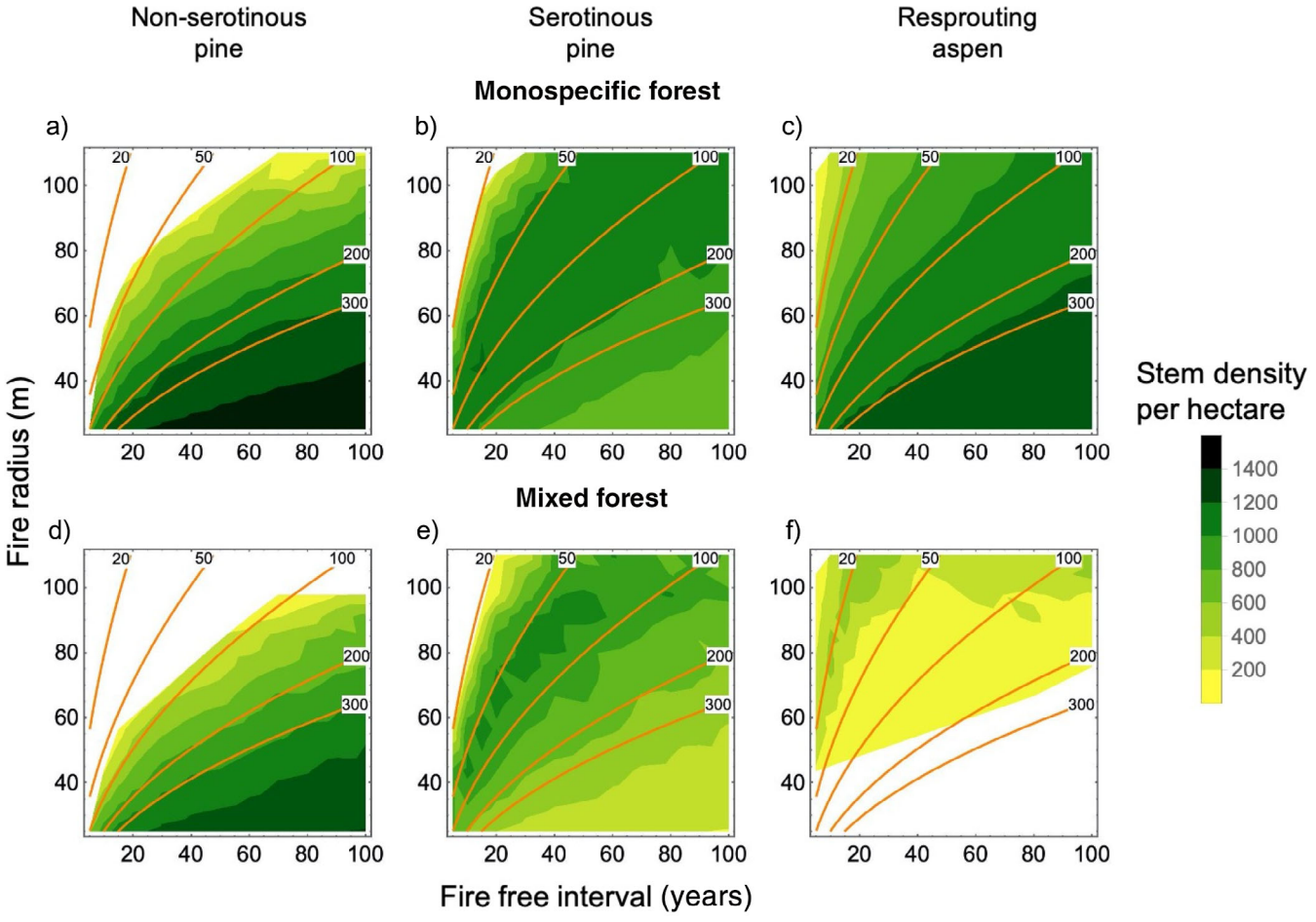

FIGURE 3 Total tree density at equilibrium as a function of fire size and fire-free interval for each species in the monospecific and mixed forest scenarios. Top panels (a–c) show the density of non-serotinous pine, serotinous pine, and resprouting aspen, respectively, in monospecific scenarios. Bottom panels (d–f) show the density of non-serotinous pine, serotinous pine, and resprouting aspen, respectively, in the mixed forest scenarios. Orange lines represent isoclines of fire rotations (years required to burn an area equivalent to the landscape area).

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equilibrium density declined with increasing fire size, indicating that regeneration was more sensitive to fire size than fire frequency (Figure 3a).

Equilibrium density in monospecific forests of serotinous pines had a hump-shaped response to declining fire rotations. Density was high (1200 to 1400 stems per hectare) at intermediate fire rotations of 50 to 200 years and low when fire rotations were longer or shorter (Figure 3b). Interestingly, serotinous pines plummeted from 1200 stems per hectare to extirpation as fire rotation declined from 50 to 20 years (Figure 3b). The equilibrium density did not vary much along the isocline of fire rotation, meaning that unlike non-serotinous pines, serotinous pines were not sensitive to increases in fire size (assuming unchanging fire rotation).

Equilibrium density in monospecific forests of aspen could be as high as 1400 stems per hectare in monospecific forests but declined monotonically as fire rotation declined (Figure 3c). Of the three species, aspen exhibited the shallowest decline from 1400 to 1200 stems per hectare as fire rotation declined from 300 and 100 years, and from 1000 to 600 stems per hectare from 50 to 20 years. Aspen was extirpated when fire rotations reached 6 years. Similar to the serotinous pines, the density of aspen did not vary along the isocline of fire rotation.

Fire and the realized disturbance niche

For both pines, the realized niche was qualitatively similar to the fundamental niche. However, in a mixed forest, non-serotinous pines attained lower maximal equilibrium density in mixed forest versus monospecific forest (1200 vs. 1600 stems per hectare, respectively) and declined more rapidly as fire rotations became shorter (Figure 3d). Non-serotinous pines were extirpated when fire rotation was ~100 years. Serotinous pines attained a density up to 1200 stems per hectare (compared to 1400 stems per hectare in the monospecific forests) and peaked at a lower and narrower range of fire rotation (50–100 years) compared to the monospecific forests (50–200 years in) (Figure 3e vs. b). The extirpation threshold of 20 years for serotinous pines was the same as in the fundamental niche.

The realized disturbance niche of aspen differed drastically from its fundamental niche. In a mixed forest, aspen maintained a low density (≤200 stems per hectare) for fire rotation ranging from 200 to 50 years. Aspen peaked at 600 stems per hectare when fire rotation was about 20 years to eventually decline (Figure 3f). However, aspen was extirpated when fire rotations were long, that is, >200 years. The response along the isocline was the inverse of the non-serotinous pine, with aspen benefiting from larger fire sizes.

Effect of forest composition on resilience

Total tree density was always higher in the mixed forest compared to the monospecific forests (Figure 4a vs. Figure 3a–c) although forest composition changed as fire rotation declined. For long fire rotations (above 300 years), aspen was competitively excluded by both pines. As fire rotation declined, aspen coexisted with both pines, but shortening fire rotations led to extirpation of non-serotinous pines and then serotinous pines (Figure 4b). In terms of coexistence of regeneration strategies, only the combination of non-serotinous pines and aspen was not possible. Finally, the range of fire sizes and fire free intervals in which all three strategies could coexist over the long-term was narrow: when fire rotation was roughly between 100 and 300 years (Figure 4b), that is, within the historical range of variability.

DISCUSSION

Understanding how resilience varies among different regeneration strategies is increasingly important as disturbance regimes shift beyond their historical range of variability. We formalized the concept of disturbance niche and developed a "Goldilocks model" to provide new insights into how communities with single (fundamental disturbance niche) and mixed (realized disturbance niche) strategies fare across a range of high-severity disturbance size and frequency. The obligate ex situ seeder (non-serotinous pines) was most sensitive to increasing fire size, the in situ reseeder (serotinous pines) declined sharply at short fire rotations, and the resprouter (aspen) could persist at short fire rotations but was extirpated at long fire rotation due to interspecific competition. Compared to monospecific forests, mixed communities that included all three regeneration strategies sustained higher equilibrium tree densities across all disturbance regimes, including when fire rotation declined. While forest composition changed with fire rotation, complementarity among the regeneration strategies allowed different species to dominate at different combinations of fire frequency and size. Collectively, these results are consistent with the hypothesis that resilience to changing disturbance regimes is enhanced by response diversity—which describes variation in the strategies by which organisms resist and recover from

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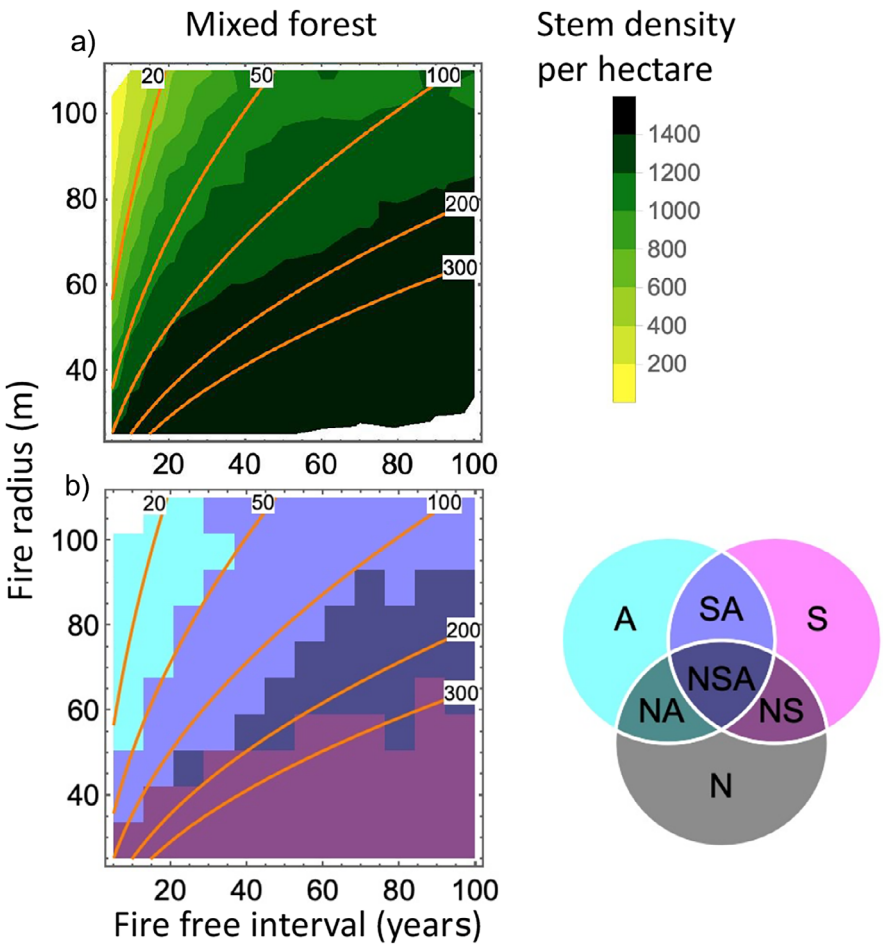

FIGURE 4 Total tree density at equilibrium in the mixed forest scenario and coexistence of the strategies as a function of fire size and fire-free interval. Panel (a) shows the total tree density at equilibrium for the mixed forest scenario (all species). Panels (b) shows the set of coexisting species where N, S, and A represent non-serotinous pines, serotinous pines, and aspens, respectively. White square means all species were extirpated. Orange lines represent isoclines of fire rotations.

disturbance (Carpenter et al., 2012; Elmqvist et al., 2003; Tilman et al., 2014; Walker & Salt, 2012). Furthermore, the model can be easily modified to simulate other types of disturbances (e.g., low severity fire, landslides, or hurricanes) and extended to incorporate other mechanisms such as fire-vegetation feedback processes (Cornell et al., 2019). Our results suggest that inferring the disturbance niche will improve our understanding of the effects of changing disturbance regimes on disturbance-prone ecosystems.

Our results provide insight into the regeneration strategies—and thus species—that may persist or be extirpated, increase or decrease in prevalence on the landscape as the frequency and size of stand-replacing fire increase. Comparing the fundamental and realized disturbance niche illuminates the key processes that limit the regeneration potential of each strategy. For ex situ seeders (represented here by non-serotinous pines), increasing fire size is detrimental. Empirical studies corroborate the effect of fire size in constraining regeneration, as postfire regeneration of ex situ seeders declines sharply with distance to unburned forest. For instance, in drier portions of Yellowstone, fewer than 10 Douglas-fir seedlings per hectare were observed at distances >100 m from live trees 25 years after large fires in 1988 (Donato et al., 2016), and distance to unburned forest predicts postfire density of other conifers that are ex situ seeders (Harvey et al., 2016). We found that the presence of competitors changed the extirpation threshold from 50 years to around 100 years. Although an extirpation fire rotation threshold of 100 years seems high, the non-serotinous lodgepoles in Yellowstone are associated with higher elevation areas where historical fire intervals were ~290 years (Schoennagel et al., 2003; Tinker et al., 1994). Dispersal is indispensable for ex situ seeders to regenerate, yet the mismatch between the scale of the dispersal and the scale of the fire as we explored here is only one aspect of the potential mechanisms

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of post-disturbance failure to disperse (Gill et al., 2022). Thus, our results are conservative.

In situ obligate seeders (represented by serotinous pines here) were most affected by shortening of fire rotation, but their equilibrium density peaked at intermediate fire rotations. Other studies have also found that an intermediate fire rotation benefits serotinous trees, as propagule release following fires more than compensates for fire induced mortality (Schoennagel et al., 2006). However, we found an abrupt decline in density as fire rotation declined. With or without competitors, in situ obligate seeders declined abruptly in a narrow band of fire rotations (between 20 and 50 years). In a model of Mediterranean-type ecosystem, the transition from in situ seeders to resprouters was also observed between 20- and 50-year fire rotation (Batllori et al., 2019). The abrupt decline is driven by immaturity risk where fire occurs before the trees have developed their canopy seed bank (Brown & Johnstone, 2012; Buma et al., 2013; Enright et al., 2015; Keeley et al., 1999). Such declines have been observed in short-interval stand replacing fire in lodgepole pine (Turner et al., 2019) and black spruce (Baltzer et al., 2021; Brown & Johnstone, 2012) and likely foreshadows a qualitative change in community composition. Our results caution that even a fire-adapted trait like serotiny cannot ensure dominance or even persistence in novel fire regimes (Buma et al., 2013).

The qualitative difference between the fundamental and realized disturbance niche of the aspen revealed competition as a major limiting factor for these deciduous resprouters. The historical low abundance of aspen in Yellowstone could be explained by competitive exclusion due to the asymmetric competition from pines (Brown et al., 2006). With frequent fire, harsher environments, such as soil quality or aridity, might have favored the evolution of obligate seeders from resprouters (Pausas & Keeley, 2014) and the wide distribution of aspen in North America suggests that environmental conditions most likely shape competitive hierarchy (Béland et al., 2003; Cavard et al., 2011; Johnstone, 2005). However, resprouters could persist if fire intensities do not kill the roots. In our model, aspen only increased when serotinous pines started to decline. Consistent with our modeling results, recent studies showed that aspen and other deciduous trees could become more abundant with increased fire activity (Kreider & Yocom, 2021; Mack et al., 2021). However, of the three strategies, resprouters were most resilient, as their density declined the least as fire rotation declined and eventually was extirpated when fire rotation reached 6 years. A spatial model for *Banksia* in western Australia also found a higher extirpation threshold for seeders (*B. hookeriana* and *B. prionotes*) compared to resprouters (*B. attenuata*) (Groeneveld et al., 2002). These results suggest that the relative value of persistence (as evidenced by reprouters) may increase as the ability of obligate seeders to re-establish after fire is threatened as the frequency and size of stand-replacing disturbances increase.

Complementarity of the two in situ regeneration strategies promoted resilience of forest structure (total density), albeit at the expense of compositional resilience (species turnover). Equilibrium tree density decreased with shorter fire rotations, but equilibrium tree densities were greater for a given fire rotation when all three regeneration strategies were present relative to the three monocultures. Although there is some overlap in the disturbance niches (e.g., each strategy can regenerate when fire rotation is >100 years), negative consequences of interspecific competition were negligible compared to the benefits of having diverse regeneration strategies. The highest response diversity was attained at intermediate fire rotation. This result agrees with the idea that high response diversity increases ecosystem resilience (persistence of forest across different fire rotations) (Carpenter et al., 2012; Elmqvist et al., 2003; Tilman et al., 2014; Walker & Salt, 2012).

Caveats

While all models are abstractions, we recognize caveats for the interpretations of the model developed here. First, the persistence of aspen roots and resprouting parameters have less empirical studies to draw on (Romme et al., 1995; Turner et al., 2019), may be over- or underestimated, which could lead to an over- or underestimation of the fire-rotation extirpation threshold. We also assumed that demographic traits are constant in time and space. Changing climate conditions associated with increased fire activity can also alter reduce survival or tree fecundity, which can limit tree regeneration (Hansen et al., 2018; Stevens-Rumann et al., 2018). From a structural perspective, the stage-transitions lack memory and thus individuals sometimes transition to the next life stage in a short amount of time. We limited this effect by adding multiple life-stages that prevent individuals from becoming reproductive in an unrealistically short period of time (Caswell, 2001). Finally, serotiny was modeled as a binary state but often the abundance of serotinous cones increases gradually with tree age before reaching a plateau (Enright et al., 1998; Lamont et al., 1991). Despite these shortcomings, the model provided valuable insight on forest responses to stand-replacing fire regimes. Future work is needed to understand the effect of adding more details to the model. To our knowledge, no disturbance model presents such degree of flexibility.

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CONCLUSION

We developed a Goldilocks model to infer the disturbance niche and to understand the responses (or resilience) of three major regenerations strategies to high-severity disturbance regimes. Each regeneration strategy dominated at different ranges of fire rotation, such that benefits from complementarity outweigh interspecific competition, consistent with the hypothesis that response diversity will increase resilience to changing disturbance regimes (Carpenter et al., 2012, Elmqvist et al., 2003, Tilman et al., 2014, Walker & Salt, 2012). Diversity in regeneration strategies supported forest persistence across a wide range of fire rotations, consistent with expectations that some forests will persist as fire regimes change, though composition and structure will vary (Mack et al., 2021). General predictions from our models are testable; while field studies will never reach equilibrium conditions, shifts from pre- to post-disturbance can be evaluated for directional change in the relative abundance of regeneration strategies (Hoecker & Turner, 2022). As disturbance regimes exceed their historical ranges of variation, Goldilocks models of intermediate complexity might facilitate consideration of a wide range of future conditions and compared to parameter-rich models, be less biased to extrapolate responses from those unknown conditions (Clark et al., 2020). The flexibility of the approach and recent development in analyzing and simulating spatio-temporal point processes (Cornell et al., 2019) constitutes a promising avenue for studying disturbance-prone communities and to inferring disturbance niches.

AUTHOR CONTRIBUTIONS

Tanjona Ramiadantsoa, Zak Ratajczak, and Monica G. Turner conceived the ideas and developed the model; Tanjona Ramiadantsoa implemented the model, ran the simulations, and analyzed the outputs; Tanjona Ramiadantsoa, Zak Ratajczak, and Monica G. Turner wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Empirical data were not used for this research. Novel code (Ramiadantsoa, 2023) is provided in Zenodo at https://doi.org/10.5281/zenodo.7752448, with additional details provided in Appendix S3 of this paper.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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