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Is initial post-disturbance regeneration indicative of longer-term trajectories?

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Abstract. The ability to estimate and model future vegetation dynamics is a central focus of contemporary ecology and is essential for understanding future ecological trajectories. It is therefore critical to understand when the influence of initial post-disturbance regeneration versus stochastic processes dominates long-term post-disturbance ecological processes. Often, conclusions about post-disturbance dynamics are based upon initial regeneration in the years immediately after disturbances. However, the degree to which initial post-disturbance regeneration indicates longer-term trends is likely to be contingent on the types, intensities, and combinations of disturbances, as well as pre-disturbance ecosystem structure and composition. Our relatively limited understanding of why initial post-disturbance regeneration is sometimes a poor predictor of future ecosystem trajectories represents a critical gap in post-disturbance ecological forecasting. We studied the composition and density of regeneration of tree species following wind blowdown in 1997, wildfire in 2002, and compounded disturbances by blowdown and wildfire in subalpine forests of Colorado. We examined regeneration of *Picea engelmannii*, *Abies lasiocarpa*, *Pinus contorta*, and *Populus tremuloides* in 180 permanent plots across 12 sites (classified by pre-disturbance age and composition) in 2003, 2010, and 2015. At sites that were blown down but not burned, regeneration was dense and dominated by *Picea* and *Abies*. At these sites, regeneration observed from 2003 to 2005 (hereafter *initial regeneration*) was also highly predictive of regeneration 5–10 yr later. In contrast, at sites that were burned and sites that were blown down and burned, regeneration was less dense and dominated by a mix of species. At these sites, initial regeneration was a poor predictor of longer-term trends as species dominance and overall density fluctuated over the 13-yr period. These findings call into question our ability to confidently predict ecosystem trajectories based upon observations made in the years immediately after large, severe disturbances such as wildfires and compounded disturbances. As compounded disturbances become more common under climatically driven changes in disturbance regimes, post-disturbance ecosystem trajectories may become increasingly stochastic and unpredictable.

Key words: blowdown; compounded disturbance; ecosystem trajectories; legacy; linked disturbance; post-fire regeneration; resilience.

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Introduction

Although climate change can affect forest ecosystems gradually due to changes in atmospheric and climatic conditions, the most dramatic changes are likely to be abrupt and modulated by climatically driven disturbances (Frelich and Reich 2009, Turner 2010). Disturbances strongly influence the structure and composition of most ecosystems, and understanding the ways in which disturbances accelerate or introduce change is key to predicting future ecosystem trajectories (Sousa 1984, Pickett and White 1985). Disturbances cause mortality and often provide opportunity for new establishment or promote reorganization of surviving vegetation. The first few years of regeneration after a disturbance can be the best available indicator of future trajectories and therefore are relied upon for management decisions and individual-based ecological modeling (Egler 1954, Peet 1981, Veblen et al. 1991, Van Mantgem and Stephenson 2005, Zald et al. 2008, Donato et al. 2009*b*, Baker et al. 2013, Collins and Roller 2013, Grimm and Railsback 2013, Xiang et al. 2013). However, initial post-disturbance regeneration may not always be indicative of longer-term trends (Pickett et al. 2001), and it is critical to understand when initial post-disturbance regeneration versus stochastic processes dominate post-disturbance ecosystem dynamics. The lack of long-term monitoring of forest regeneration following large, severe disturbances has been stressed as one of the major deficiencies facing restoration efforts (Holl and Cairns 2002) and is seen as an urgent need in ecological science (Van Leeuwen et al. 2010), especially in the context of multiple interacting disturbances. Our relatively limited understanding of when and why initial post-disturbance regeneration is at times a poor predictor of future ecosystem trajectories represents a critical gap in post-disturbance ecological forecasting, with important implications for the resilience and vulnerability of ecosystem services (Turner et al. 2013).

For decades, succession theory was strongly influenced by Egler's (1954) Initial Floristic Composition Hypothesis (Finegan 1984), which predicts that successional pathways depend on the communities that are present from the start of succession (i.e., complete initial floristics; Wilson et al. 1992). However, understanding of succession and species composition evolved with the presentation of the intermediate disturbance hypothesis (Connell 1978), which states that maximum species richness is achieved not immediately following disturbance, but when sufficient time between disturbances allows for a balance of pioneer and late-successional species. Although this hypothesis spurred much research into the role of disturbances in determining biological diversity, this theory has been called into question because of lack of supporting theory and empirical evidence (Fox 2013). While contemporary ecology recognizes a more nuanced relationship between disturbance regime attributes and species richness, the fact remains that ecologists and managers often operate under the assumption that initial plant communities following disturbances are indicative of long-term successional pathways. This assumption should be adequately examined, especially as disturbances become larger, more frequent, and more severe, and ecosystems are increasingly affected by multiple disturbances over shorter periods of time.

Current understanding of regeneration following multiple disturbances suggests that an interacting effect may emerge in two ways—through the effect of a first disturbance on the occurrence, intensity, severity, or other attributes of a subsequent disturbance, or through a compounded effect that alters the nature of post-disturbance development (Donato et al. 2009*a*, Simard et al. 2011, Kulakowski and Veblen 2015). In extreme cases, compounded disturbances may push a community to an alternate stable state (Paine et al. 1998). For example, a short interval between two disturbances may lead to immaturity risk whereby seed may be less available at the time of the second disturbance, causing a shift to non-forest (Enright et al. 2015). Promoting ecosystem resilience through a deeper understanding of natural disturbance regimes is commonly a central management objective (DeRose and Long 2009, Nagel et al. 2014), but questions remain as to how resilience can best be achieved in the context of compounded disturbances or how to recognize cases in which compound effects are most likely. Such effects may not be immediately evident after disturbances, but emerge many years later in post-disturbance development through the presence (or absence) of biotic legacies (Pickett et al. 2005, Turner 2010, Royo et al. 2016) and may be sensitive to varying spatial scales of disturbance (Svoboda et al. 2014, Jogiste et al. 2017).

The subalpine forests of the Colorado Rocky Mountains are influenced by a variety of natural disturbances including wildfires, native beetle outbreaks, and wind blowdowns (Veblen et al. 1994, Kulakowski and Veblen 2003). These disturbance agents have played key roles in forest dynamics for thousands of years, but recent climatic warming has accelerated their frequency, enhanced their intensity, and increased their size (Westerling et al. 2006, Bentz et al. 2010, Evangelista et al. 2011). Colorado subalpine forests are composed primarily of Engelmann spruce (*Picea engelmannii*), subalpine fir (*Abies lasiocarpa*), lodgepole pine (*Pinus contorta*), and quaking aspen (*Populus tremuloides* Michx.), each of which utilizes a different regeneration strategy and fills a unique ecological niche.

Picea engelmannii and *A. lasiocarpa* are *avoiders* (Rowe 1983, Veblen 1986*a*, Buma and Wessman 2012), which are not particularly adapted to disturbances, but generally have a competitive advantage in the shadier conditions prevalent in the years after regeneration has established. *Picea engelmannii* and *A. lasiocarpa* both produce high seedling densities but differ in that *P. engelmannii* tend to have fewer seedlings but a higher rate of survivorship, while *A. lasiocarpa* regenerate in greater abundance initially but thin out as seedlings become saplings and saplings eventually become mature adult trees (Veblen 1986*a*, Maher et al. 2005). *Pinus contorta* exhibit an *evader* strategy (Rowe 1983) through the dispersal of seed by serotinous cones. Adult *P. contorta* are consumed in severe wildfires such as the Mount Zirkel Fire Complex of 2002, but many *P. contorta* are serotinous, and therefore, high fire temperatures allow cones to release plentiful seed, potentially leading to very dense regeneration. This is especially effective in dense stands of sexually mature and serotinous *P. contorta* (Tinker et al. 1994). *Populus tremuloides* can take an *endurer* approach (Rowe 1983) by regenerating asexually through vegetative resprouting. *Populus tremuloides* are also capable of regenerating from seed, although there is disagreement over the frequency of this occurrence in the subalpine forests of the Rockies (Kay 1993, Howard 1996, Romme et al. 1997, Quinn and Wu 2001). A majority of regenerating aspen in the study site in the years immediately after the 2002 wildfires resprouted vegetatively (Kulakowski et al. 2013), but increased aspen seedling regeneration in more recent years has been documented in stands that were previously dominated by spruce and fir (Buma and Wessman 2012). Both *P. tremuloides* and especially *P. contorta* have a competitive advantage over *P. engelmannii* and *A. lasiocarpa* in full sunlight, as is typical following a stand-replacing disturbance (Parker and Parker 1983). The general strategies of these four species are common among tree species worldwide, and are well-studied following single disturbances (Rowe 1983), but the efficacy of these strategies is highly complex following compounded disturbances and not well understood (Buma and Wessman 2012, Kulakowski et al. 2013). Here, we examine regeneration over a 13-yr period following individual and compounded disturbances in four major forest types to identify scenarios under which initial post-disturbance regeneration is indicative of longer-term trends and under which it is more stochastic.

MATERIALS AND METHODS

Study area

The study area lies within Routt National Forest and the Mt. Zirkel Wilderness in northern Colorado and is defined as the sum of the areas affected by severe blowdown in 1997 and fire in 2002. The elevation of the study area ranges from 2400 to 3600 m above sea level. The climate is continental, and mean monthly temperatures since 1893 range from a minimum of −17.1°C in January to a maximum of 28.1°C in July. Mean annual precipitation is 60.2 cm of rain and 423 cm of snowfall (Western Regional Climate Center, http://www.wrcc.dri.edu/). Upland forests in this region are underlain by coarse-textured soils consisting of glacial deposits and Precambrian crystalline parent material, while low-lying valleys are derived from poorly drained alluvial deposits (Snyder et al. 1987). Forests are dominated by *Pinus contorta*, *Populus tremuloides, Picea engelmannii*, and *Abies lasiocarpa*. Portions of the study area were burned by stand-replacing fires in 1879 and 1880 (Kulakowski and Veblen 2002).

In October 1997, ~10,340 ha of the National Forest was blown down in a severe windstorm. Five years later, 12,354 ha of the forest burned in the Mount Zirkel Fire complex, and an additional 1724 ha burned in the Green Creek Fire that same year. Approximately 40% of the blown-down forest was burned in 2002.

Data and analysis

In 2003, we established 540 2 × 1 m microplots nested in 180 10 × 2 m macroplots across 24 sites within the study area. Sites were located according to a stratified random sampling scheme across classes of species composition (>90% *P. engelmannii*/*A. lasiocarpa*, >40% *P. contorta*, or >50% *P. tremuloides*) as determined by Kulakowski and Veblen (2002), stand structural stage (understory reinitiation stands that originated after fires in the 1880s or old-growth stands >200 yr old; Oliver 1981), and a combination of recent disturbances (severe 1997 blowdown, 2002 stand-replacing wildfire, or both). Other differences among sites such as elevation and precipitation were not included in the analysis because these factors were fairly consistent among sites by design.

We measured and recorded the regeneration density of all tree species in each plot in 2003, 2010, and 2014–2015. Sites that burned were also measured in 2004 and 2005. All saplings (individuals >140 cm in height but <4 cm dbh) were counted within each macroplot. We sampled the density of seedlings (conifer individuals <140 cm in height) and *P. tremuloides* ramets <140 cm in height in each microplot. Ramets were counted as separate stems if they were not adjoined above the soil. The average density from three nested microplots was then averaged with the single macroplot density of saplings and sapling-sized ramets to yield an estimate of regeneration density (juveniles per hectare) for each species within each macroplot (equal weight given to seedling density and sapling density to yield regeneration density).

Linear regression models were created in R (R Development Core Team 2008) using total initial regeneration density (2003 after blowdown or 2005 after wildfire) as the independent variable and subsequent regeneration densities (both 2010 and 2014/15 for all stands) as the dependent variable. One model was created for each category based upon pre-disturbance stand structural stage (Stage III understory reinitiation or Stage IV old-growth; Oliver 1981), pre-disturbance composition, (spruce/fir dominated or lodgepole dominated), and disturbance type(s) (blowdown, fire, or both). Adjusted R^2 and the F statistic were used to measure significance.

RESULTS

In stands that were affected by the 1997 blowdown but not the 2002 wildfire, initial regeneration density was generally a strong indicator of the dominant species (Table 1) and densities (Table 2) of regeneration both 7 and 11 yr later, with the exception of old-growth *Pinus contorta* stands (Table 2). In all cases, blowdown-only stands were typified by early *Abies lasiocarpa* dominance followed by gradual increases in the densities of *A. lasiocarpa, Picea engelmannii* (Fig. 1), and some *P. contorta* regeneration in the case of stands that were in Stage III of structural development at the time of blowdown (Fig. 1a, b). Rankings of regenerating species by density in later years were very similar to 2003 for all stand categories that were blown down and not burned (Table 1, Fig. 1).

In stands that burned but were not blown down, initial regeneration tended to be sparse in most cases (Fig. 2) and exhibited numerous changes in ranking of species by density (Table 3, Fig. 2). Spruce/fir stands of either stage and old-growth lodgepole pine stands exhibited no more

Table 1. Rankings of post-1997 blowdown regeneration of *Abies lasiocarpa* (AL), *Picea engelmannii* (PE), *Pinus contorta* (PC), and *Populus tremuloides* (PT) for stands of different pre-blowdown structural stage and composition.

Year	Stage III PE/AL	Stage III PC	Stage IV PE/AL	Stage IV PC
2003	AL, PE, PC, PT	AL, PC, PE, PT	AL, PE, PC-PT	AL, PE, PC-PT
2010	AL, PC, PE, PT	AL, PE, PC, PT	AL, PE, PC, PT	AL, PE, PC-PT
2014	AL, PC, PE, PT	AL, PC, PE, PT	AL, PE, PC, PT	AL, PE, PC-PT

Notes: Species are ranked from highest to lowest density. None of the sites presented in this table were burned in 2002.

Table 2. Dynamics of regeneration for stands that were blown down but not burned.

Pre-disturbance composition/ structural stage	Subsequent year	Adjusted R^2	*F*	*P*
Stage III PE/AL	2010	0.3937	58.8*	<0.001
Stage III PE/AL	2014	0.4582	76.3*	<0.001
Stage IV PE/AL	2010	0.1505	16.76*	<0.001
Stage IV PE/AL	2014	0.1512	16.85*	<0.001
Stage III PC	2010	0.5573	113.0*	<0.001
Stage III PC	2014	0.3832	56.3*	<0.001
Stage IV PC	2010	0.0000	0.9	0.336
Stage IV PC	2014	0.0497	5.7	0.020

Notes: Results of linear regression models using total initial (2003) regeneration density as the independent variable and total subsequent regeneration density as the dependent variable. Data are separated by pre-disturbance composition (PE/AL, *Picea engelmannii*/*Abies lasiocarpa* or PC, *Pinus contorta*) and stage of structural development. Asterisk denotes significance at the 1% level.

than 600 trees/ha of any one species of regeneration, with most species regenerating under 200 trees/ha. Even in cases where regeneration density was near 600 trees/ha, the most abundant species had been absent in previous years (Fig. 2a,c). These stands are characterized by low regeneration densities and numerous shifts in density rankings (Table 3, Fig. 2). Stage III *P. contorta* stands exhibited consistent dominance by very dense *P. contorta* regeneration (Fig. 2b), but older *P. contorta* stands and old and young *P. engelmannii*/*A. lasiocarpa* stands saw shifts in the most dominant species of regeneration (Table 3, Fig. 2). Early regeneration density in Stage III *P. contorta* stands was an effective predictor of later regeneration density through 2014, while early regeneration in Stage IV *P. contorta* stands was a good predictor for 2010 but not 2014 (Table 4).

Initial regeneration in stands affected by both disturbances exhibited high predictive power of later trajectories in some stands while others exhibited great fluctuations in regeneration density and species ranks. Regeneration of Stage III stands (of both *P. engelmanni*/*A. lasiocarpa* and *P. contorta*) was for the first two years dominated by *P. contorta*, but by 2005 *Populus tremuloides* regeneration became more dense and persisted as the dominant species of regeneration (Fig. 3a, b,

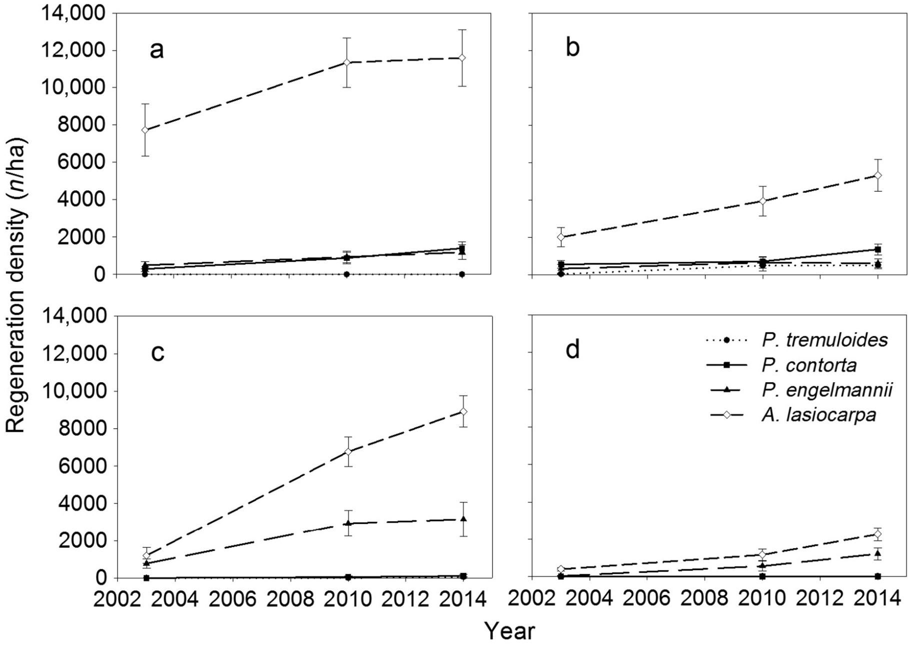

Fig. 1. Regeneration density (mean ± SE) of four species in stands affected only by 1997 blowdown, organized by pre-disturbance stand dominance and structural stage. Number of 20-m^2 plots = 30 per graph. (a) Understory reinitiation *Picea engelmannii*/*Abies lasiocarpa* stands. (b) Understory reinitiation *P. contorta* stands. (c) Old-growth *P. engelmannii*/*A. lasiocarpa* stands. (d) Old-growth *P. contorta* stands.

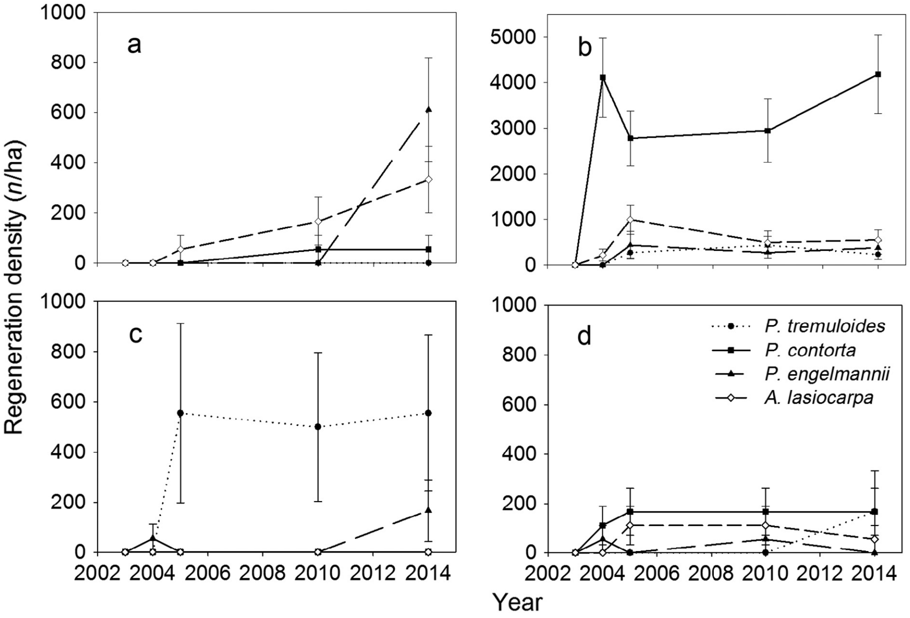

Fig. 2. Regeneration density (mean ± SE) of four species in stands affected only by 2002 fire, organized by pre-disturbance stand dominance and structural stage. Number of 20-m^2 plots = 30 per graph. (a) Understory reinitiation *Picea engelmannii*/*Abies* lasiocarpa stands. (b) Understory reinitiation *P. contorta* stands. (c) Old-growth *P. engelmannii*/*A. lasiocarpa* stands. (d) Old-growth *P. contorta* stands. Note the different scale for the *y*-axis of panel B.

Table 5). Similarly, in old-growth *P. engelmannii*/*A. lasiocarpa* stands that were blown down and burned, *P. contorta* is initially the only species regenerating, but from 2005 to 2010, *P. tremuloides* and *A. lasiocarpa* are ascending together and *P. contorta* becomes completely absent across these sites. Between 2010 and 2014, *P. tremuloides* also fails to persist, leaving *A. lasiocarpa* as the dominant regeneration species, while *P. contorta* establishes once again (Fig. 3c, Table 5). Old-growth *P. contorta* stands that experienced both disturbances are dominated by dense *P. tremuloides* regeneration from 2004 onward (Fig. 3d). Following compounded disturbances, Stage III and Stage IV *P. contorta* stands had early regeneration patterns which effectively predicted trends for 2010 and 2014, while patterns in Stage IV spruce/fir stands were effective predictors only through 2010, and patterns in Stage III spruce/fir stands predicted 2014 densities effectively but not 2010 densities (Table 6).

When regeneration plots were categorized by initial regeneration composition and density rather than by pre-disturbance stand structure,

Table 3. Rankings of post-2002 wildfire regeneration of *Abies lasiocarpa* (AL), *Picea engelmannii* (PE), *Pinus contorta* (PC), and *Populus tremuloides* (PT) for stands of different pre-fire structural stage and composition.

Year	Stage III PE/AL	Stage III PC	Stage IV PE/AL	Stage IV PC
2003	. . .	. . .	. . .	. . .
2004	. . .	PC, AL, PT, PE	PE, AL-PC-PT	PC, PE, AL-PT
2005	AL, PC, PE-PT	PC, AL, PE, PT	PT, AL-PC-PE	PC, AL, PE-PT
2010	AL, PC, PE-PT	PC, AL, PT, PE	PT, AL-PC-PE	PC, AL, PE, PT
2014	PE, AL, PC, PT	PC, AL, PE, PT	PT, PE, AL-PC	PT-PC, AL, PE

Notes: Species are ranked from highest to lowest density. None of the sites presented in this table were blown down in 1997. An ellipsis indicates complete absence of regeneration.

Table 4. Dynamics of regeneration for stands that were burned but not blown down.

Pre-disturbance composition/ structural stage	Subsequent year	Adjusted R^2	*F*	*P*
Stage III PE/AL	2010	0.0000	0.1	0.831
Stage III PE/AL	2014	0.0242	3.2	0.077
Stage IV PE/AL	2010	0.0000	0.1	0.783
Stage IV PE/AL	2014	0.0000	0.4	0.528
Stage III PC	2010	0.2097	24.6*	<0.001
Stage III PC	2014	0.3302	44.9*	<0.001
Stage IV PC	2010	0.0949	10.33*	0.002
Stage IV PC	2014	0.0333	4.1	0.047

Notes: Results of linear regression models using total initial (2005) regeneration density as the independent variable and total subsequent regeneration density as the dependent variable. Data are separated by pre-disturbance composition (PE/AL, *Picea engelmannii*/*Abies lasiocarpa* or PC, *Pinus contorta*) and stage of structural development. An asterisk denotes significance at the 1% level.

composition, and disturbance agent(s), early observations in plots which exhibited regeneration densities of any species >1000 trees/ha were strong predictors of trajectories through 2010 and 2014. Plots with low early regeneration densities (<1000 but >0 trees/ha) had very little predictive power of future trends (Table 7). Plots with absolutely no regeneration through the first three years after disturbance often remained with little to no regeneration through 2014.

DISCUSSION

The current study shows that disturbance type and (secondarily) pre-disturbance stand structure and composition influence the ability to predict regeneration densities from the initial years of regeneration, even through the first 1–2 decades. The predictive power of models of regeneration for stands that were affected by a single disturbance agent varied strongly based on disturbance agent. In all cases, stands that were blown down but not burned were dominated by the same species in 2014 as they were in all prior years since the blowdown, across classes of structural stage and pre-disturbance species composition. Linear models of these regeneration trajectories effectively predict regeneration 13–17 yr following disturbance based on regeneration patterns

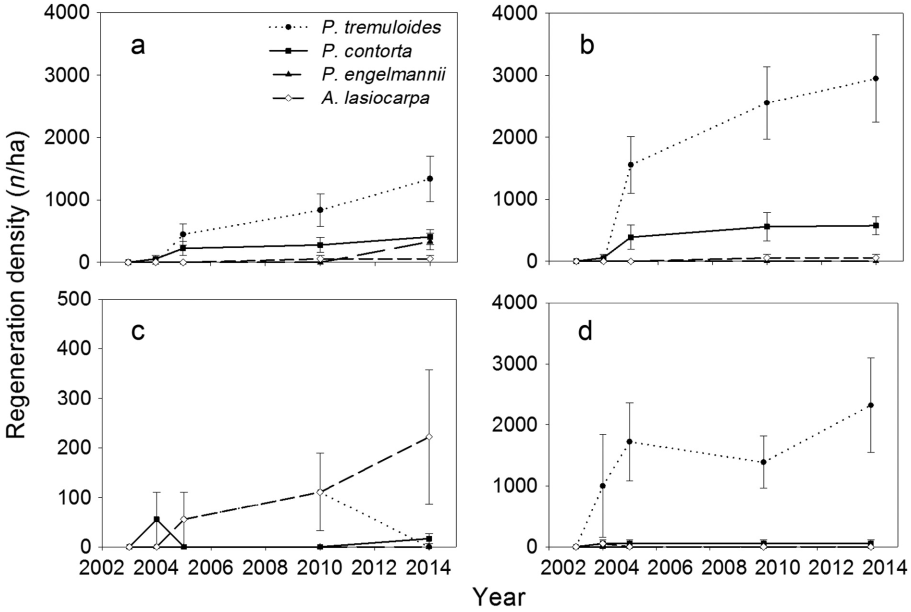

Fig. 3. Regeneration density (mean ± SE) of four species in stands affected by 1997 blowdown and 2002 fire, organized by pre-disturbance stand dominance and structural stage. Number of 20-m^2 plots = 30 per graph. (a) Understory reinitiation *Picea engelmannii*/*Abies lasiocarpa* stands. (b) Understory reinitiation *P. contorta* stands. (c) Old-growth *P. engelmannii*/*A. lasiocarpa* stands. (d) Old-growth *P. contorta* stands. Note the different scale for the *y*-axis of panel C.

Table 5. Rankings of regenerating *Abies lasiocarpa* (AL), *Picea engelmannii* (PE), *Pinus contorta* (PC), and *Populus tremuloides* (PT) following blowdown and wildfire for stands of different pre-blowdown structural stage and composition.

Year	Stage III PE/AL	Stage III PC	Stage IV PE/AL	Stage IV PC
2003	. . .	. . .	. . .	. . .
2004	PC, AL-PE-PT	PC, AL-PE-PT	PC, AL-PE-PT	PT, AL-PC, PE
2005	PT, PC, AL-PE	PT, PC, AL-PE	AL-PT, PE-PC	PT, PC, AL-PE
2010	PT, PC, AL, PE	PT, PC, AL, PE	AL-PT, PE-PC	PT, PC, AL-PE
2014	PT, PC, PE, AL	PT, PC, AL, PE	AL, PC, PE-PT	PT, PC, AL-PE

Notes: Species are ranked from highest to lowest density. An ellipsis indicates complete absence of regeneration.

observed 5 yr after the blowdown. In stands that were severely burned in 2002 and not previously blown down, most of the temporal trends in the composition and density of regeneration were volatile as the abundance and composition of regeneration fluctuated substantially. The exception is the highly serotinous younger *Pinus contorta* category, for which the model exhibited strong predictive power through 2014. Models of less-serotinous (though still partly serotinous) old-growth *P. contorta* stands demonstrated high predictive power for regeneration density through 2010, but not 2014. In this way, the strength of post-fire regeneration models appears to be associated with stand serotiny, although future research should analyze this relationship with greater specificity (i.e., measure percentages of serotinous cones and trees; Tinker et al. 1994).

Table 6. Regeneration dynamics for stands that were blown down in 1997 and burned in 2002.

Pre-disturbance composition/ structural stage	Subsequent year	Adjusted R^2	F	P
Stage III PE/AL	2010	0.1595	17.9	<0.001
Stage III PE/AL	2014	0.1711	19.37*	<0.001
Stage IV PE/AL	2010	0.1010	11.0*	0.001
Stage IV PE/AL	2014	0.0613	6.8	0.011
Stage III PC	2010	0.4626	75.8*	<0.001
Stage III PC	2014	0.2710	34.1*	<0.001
Stage IV PC	2010	0.5021	90.8*	<0.001
Stage IV PC	2014	0.8055	369.7*	<0.001

Notes: Results of linear regression models using total initial (2005) regeneration density as the independent variable and total subsequent regeneration density as the dependent variable. Data are separated by pre-disturbance composition (PE/AL, *Picea engelmannii*/*Abies lasiocarpa* or PC, *Pinus contorta*) and stage of structural development. An asterisk denotes significance at the 1% level.

In the current study, regeneration composition and density during the first 5 yr following compounded blowdown and fire were strongly indicative of future trajectories in some cases, especially when early post-fire regeneration was abundant, but not indicative in other cases (despite the relatively short study period). Kulakowski et al. (2013) found that *Populus tremuloides* regeneration was no less dense following compounded blowdown and fire disturbances than following fire only, unlike conifer regeneration, which was largely inhibited by compounded disturbances. Likewise, models of regeneration density in the current study

Table 7. Regeneration dynamics for stands of varying patterns of initial regeneration of *Abies lasiocarpa* (AL), *Picea engelmannii* (PE), *Pinus contorta* (PC), and *Populus tremuloides* (PT), with results of four linear regression models using total initial regeneration density as the independent variable and total subsequent regeneration density as the dependent variable.

Composition of early regeneration (2003–2005)	Subsequent year	Adjusted R^2	F	P
PE/AL ≥1000/ha	2010	0.3527	72.4*	<0.001
PE/AL ≥1000/ha	2014	0.3138	60.9*	<0.001
PC ≥1000/ha	2010	0.266	18.48*	<0.001
PC ≥1000/ha	2014	0.1723	11.8*	0.001
PT ≥1000/ha	2010	0.1854	10.33*	0.003
PT ≥1000/ha	2014	0.3957	27.84*	<0.001
Total regeneration <1000/ha	2010	0.000	0.3	0.568
Total regeneration <1000/ha	2014	0.000	0.0	0.892

Note: Model data are categorized by plot initial regeneration species, regardless of pre-disturbance stand dominance and disturbance agent(s). An asterisk denotes significance at the 1% level.

exhibited high predictive power when initial regeneration density was high, frequently due to *P. tremuloides* after compounded disturbance. In contrast, models were weak when initial regeneration was sparse, a condition associated with compounded disturbance in this landscape (Kulakowski et al. 2013).

The findings of the current study partly reflect differences between stand-replacing and less severe disturbance agents. While even a high-severity blowdown typically will leave surviving individuals, a stand-replacing wildfire by definition consumes all vegetation. The role of legacies is critical to the trajectory of ecosystem processes and should receive special attention as management strategies are developed (Grumbine 1994, Buma and Wessman 2011, Sturtevant et al. 2014). Considering that all stands in this study were >120 yr old in the late 20th century, the presence of understory juveniles would be expected. Wind blowdown events tend to cause mortality among the tallest trees, while understory vegetation is typically protected (Veblen et al. 2001, Kulakowski and Veblen 2003). With the elimination of competing taller trees, the understory individuals are able to access more resources and are effectively released from competition, resulting in sustained increases in annual growth (Marks 1974, Kulakowski and Veblen 2003). These individuals would have established over the years preceding disturbance and have a competitive advantage over post-disturbance regeneration. The presence of legacies brings a steadiness to the trajectory of post-disturbance ecosystem development.

Regeneration following high-severity fires is free of competition from above-ground legacies but is more sensitive to environmental conditions. This fact may in part explain the observed fluctuations in regeneration density, shifts in species dominance, and the failure of some cohorts to persist (see St Clair et al. 2013). Cyclic wetting and drying and fluctuating temperatures are known inhibitors of early growth in aspen (McDonough 1985). Fluctuating temperatures may also influence seed production and availability—for example, current warming temperatures have been found to favor increased seed production of *Abies lasiocarpa* (Buechling et al. 2016). Post-disturbance climate appears to affect new seedlings more than established individuals (Turner 2010, Dodson and Root 2015), and vegetative versus sexual regeneration may be differentially sensitive to these factors. Because of monotonic shifts in temperature and moisture conditions, plant community reshuffling is expected to occur more frequently under future climate change (Dodson and Root 2015). The results of the current study may demonstrate exactly such a case and emphasize the important role of legacies in influencing the predictability of ecosystem trajectories.

The persistence of initial regeneration varies across species based upon competing regeneration strategies that are found not only in North America, but in forests around the globe. *Abies lasiocarpa* in this study appear to be least sensitive to environmental fluctuations, consistently persisting after establishment, while *Picea engelmannii*, *P. contorta*, and most notably *P. tremuloides* each exhibited sudden establishment, decline, and failure to persist in some cases. In stands affected only by blowdown, this may be primarily a result of the fact that *A. lasiocarpa* are typically more abundant among the advance regeneration, creating a competitive advantage for this species following a disturbance that was not stand-replacing (Schmid and Hinds 1974). *Abies lasiocarpa* regeneration was consistent from year to year, even in burned stands, and even while other regeneration fluctuated at the same sites. *Abies lasiocarpa* is a shade-tolerant species, and establishes at much lower densities immediately after stand-replacing disturbances, if at all (Veblen 1986*b*, Bigler and Veblen 2009), while *P. contorta* and *P. tremuloides* thrive in open sunlight and are sensitive to changes in light availability (Calder 2009). Otherwise, *A. lasiocarpa* tend to recruit high numbers of individuals in early years of regeneration, but few of these reach maturity due to high juvenile mortality rates (Veblen 1986*a*, Antos et al. 2000).

Interacting disturbances may have compound effects, even causing a shift to an alternate stable state (Paine et al. 1998), but drivers of forest trajectories following multiple disturbances may include nuanced differences in stand attributes, species-specific regeneration strategies, and a fluctuating microenvironment. Initially, prolific regeneration of *P. tremuloides* in Routt National Forest suggested that favorability for *P. tremuloides* may provide a negative feedback to the frequency of fire and beetle disturbances (Kulakowski et al. 2013). However, in some stand types, initial indications of trajectories have already shifted in a brief 13-yr period of post-fire stand development, highlighting the complexity of estimating trajectories in an environment with highly interactive disturbance regimes. The need to understand compound effects of multiple disturbances is of utmost importance (Turner 2010). The effects of multiple disturbances on regeneration are not necessarily synergistic, but depend on species regeneration strategies and the interactions of multiple species (Buma and Wessman 2012). To this, we add that the response varies not only by species, but also with pre-disturbance structural stage (White et al. 2015) and potentially with fluctuating environmental conditions.

CONCLUSIONS

Often, the regeneration density in the years immediately after a disturbance is indicative of the future trajectory of an ecosystem, but in some cases, particularly following stand-replacing or compounded disturbances, initial regeneration density and composition can be poor indicators of future trends. Competitive advantages in an environment void of advance regeneration, such as that following stand-replacing disturbance, may shift with subtle changes in resource availability caused by weather patterns, climate, or other factors. In contrast, regeneration in stands that have legacies that survive a disturbance tends to be consistent from the years immediately after the event into the next decades. Future research should measure the degree to which changing climate conditions may affect trends in post-disturbance regeneration, as these trends have important implications for forest management and ecosystem modeling. Patterns of regeneration after fire can directly influence patterns of future fire severity. Additionally, drier climatic conditions expected with climate change may alter fire regimes such that intervals between fires become shorter, decreasing the window of opportunity for the recruitment of fire-intolerant woody plants (Westerling et al. 2011). Often, management plans and models of future carbon stocks and other resources are based solely upon as little as one year of post-disturbance stand development, and rarely more than five years. As high-severity and compounded disturbances become more common under climatically driven changes in disturbance regimes, post-disturbance ecosystem trajectories may become increasingly stochastic and unpredictable, particularly when densities are low during initial years of regeneration.

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