

Forest developmental trajectories in mountain pine beetle disturbed forests of Rocky Mountain National Park, Colorado

Matthew Diskin, Monique E. Rocca, Kellen N. Nelson, Carissa F. Aoki, and W.H. Romme

Abstract: A mountain pine beetle (*Dendroctonus ponderosae* Hopkins) epidemic has caused widespread mortality of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) trees across western North America. We characterized the initial effects of beetle-induced mortality on forest structure and composition in Rocky Mountain National Park, Colorado. In 2008, we surveyed stand structure and tree species composition across lodgepole pine dominated forests in the western portion of the Park. We defined five lodgepole pine forest types to describe variability in pre-epidemic forest conditions. This forested landscape appears to be resilient to the effects of the beetle. Surviving trees, including both canopy trees and saplings, were plentiful in most of the post-epidemic forests, even after accounting for anticipated future mortality. Subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and aspen (*Populus tremuloides* Michx.) had modestly higher relative abundances after the epidemic. Lodgepole pine remained the dominant species on approximately 85% of the landscape. The impact of the outbreak on forest structure and composition varied considerably among the five forest types, suggesting that post-epidemic forest developmental trajectories will vary according to pre-outbreak stand characteristics. Active management efforts to regenerate lodgepole pine forests, e.g., tree planting, will likely not be necessary on this landscape.

Résumé : Une épidémie de dendroctone du pin ponderosa (*Dendroctonus ponderosae* Hopkins) a causé beaucoup de mortalité chez le pin tordu latifolié (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) partout dans l'ouest de l'Amérique du nord. Nous avons caractérisé les premiers effets de la mortalité causée par le dendroctone sur la structure et la composition de la forêt dans le parc national des Montagnes Rocheuses, Colorado. En 2008, nous avons inventorié la structure et la composition en espèces d'arbres des peuplements parmi les forêts dominées par le pin tordu dans la partie ouest du parc. Nous avons défini cinq types de forêts de pin tordu pour décrire la variabilité de la forêt qui existait avant l'épidémie. Ce paysage forestier semble résilient aux effets du dendroctone. Les arbres qui ont survécu, incluant des arbres dominants et des gaules, étaient nombreux dans la plupart des forêts après l'épidémie, même en tenant compte de la mortalité anticipée. Le sapin subalpin (*Abies lasiocarpa* (Hook.) Nutt.), l'épinette d'Engelmann (*Picea engelmannii* Parry ex Engelm.) et le peuplier faux-tremble (*Populus tremuloides* Michx.) avaient une abondance relative légèrement plus élevée après l'épidémie. Le pin tordu demeurait l'espèce dominante dans environ 85 % du paysage. L'impact de l'épidémie sur la composition et la structure de la forêt variait considérablement parmi les cinq types forestiers, ce qui indique que la trajectoire du développement de la forêt après une épidémie variera en fonction des caractéristiques du peuplement avant une épidémie. Des efforts soutenus d'aménagement pour régénérer les forêts de pin tordu, tels que la plantation d'arbres, ne seront probablement pas nécessaires dans ce paysage.

[Traduit par la Rédaction]

Introduction

A severe mountain pine beetle (*Dendroctonus ponderosae* Hopkins) epidemic has severely impacted subalpine forests across much of western North America during the last decade. This recent beetle outbreak has caused widespread mortality of lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) and other pine species on tens of millions of hectares across western Canada and the United States

(Colorado State Forest Service 2009; Wulder et al. 2010). The severity of the outbreak within affected areas and the consequences of this epidemic for the future of impacted landscapes remain largely unknown. In this study, we describe the initial effects of mountain pine beetle induced mortality on lodgepole pine forest structure and composition in one heavily impacted landscape, Rocky Mountain National Park in northern Colorado. This study is a critical first step in characterizing possible future outcomes for beetle-

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disturbed forests in the Park, with implications for other affected landscapes in the Rocky Mountain region.

The mountain pine beetle is a native insect that infests many western conifer species. Mountain pine beetle populations typically persist at low, endemic levels, killing only weakened trees. Periodically, however, populations increase to epidemic levels and kill a majority of large-diameter trees over large areas. These beetle epidemics can last for a decade or more and typically subside due to either unseasonably cold temperatures or a depletion of large-diameter host trees (Safranyik and Carroll 2006). In this study, we focus on a recent, widespread outbreak in lodgepole pine, one of the beetle's preferred hosts. The extent and severity of the lodgepole pine mortality associated with the current epidemic is believed to be unprecedented in the recorded history of the Rocky Mountain region (Taylor et al. 2006; Kaufmann et al. 2008).

The overarching goal for this study is to describe future forest developmental trajectories in beetle-disturbed forests of Rocky Mountain National Park. To meet our goal, we sought answers to the following questions.

- How has forest structure on this landscape changed due to the lodgepole pine mortality? In other words, how abundant are surviving trees in each of the canopy, sapling, and seedling layers?
- How has the species composition of the forest changed following the outbreak? To what extent does lodgepole pine mortality increase the relative abundance of non-host tree species? Will lodgepole pine remain an important species on the landscape?

We approached these questions by emphasizing how variability in pre-epidemic forest structure and composition interacts with tree mortality patterns to influence post-epidemic forest conditions. Our results will help determine whether drought-induced insect disturbances, which may become more frequent under a changing climate, have the potential to cause large and unexpected changes to the structure and function of subalpine forests. This study will assess the resilience of the Rocky Mountain National Park landscape to the outbreak, providing land managers with much needed guidance on whether active restoration activities are necessary and (or) appropriate for maintaining a functional forest landscape.

The abundance of surviving trees — and how they are distributed among the canopy, sapling, and seedling layers — is an important indicator of future developmental trajectories. The reduction in competition that results from beetle-induced mortality increases resources for surviving trees. The resulting growth increase is thought to be more important for forest development than the establishment of new trees in many stands (Veblen et al. 1991; Hawkes et al. 2003; Astrup et al. 2008). Indeed, a recent study of mountain pine beetle disturbed lodgepole pine forests in British Columbia found that almost half of the stands remained fully stocked with surviving trees (Coates et al. 2006). A quarter of the stands were poorly stocked, however, indicating that the establishment of new seedlings will be important in some cases. Despite the high profile of the bark beetle epidemic and the associated impacts, little quantitative information is available to characterize surviving trees. In particular, for most affected land-

scapes, we do not know whether forests retain adequate densities of surviving trees to regenerate beetle-disturbed stands or what proportion of stands will require abundant new seedling establishment for regeneration.

The broad ecological amplitude of lodgepole pine further inhibits our ability to predict post-epidemic forest regeneration patterns. Because lodgepole pine trees grow with many other tree species (Peet 1981), we expected that beetle-induced mortality would cause a shift to forests dominated by the non-host species in our study area (subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), aspen (*Populus tremuloides* Michx.), Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), and limber pine (*Pinus flexilis* James)). Past research from the southern and central Rocky Mountains supports this hypothesis but also demonstrates that lodgepole pine remains dominant in areas that are unsuitable for other species or where seed sources for other species are not present (Moir 1969; Amman 1977; Sibold et al. 2007). The outbreaks studied in the past, however, were less extensive than the current epidemic, and it remains uncertain to what degree these patterns hold for the current large-scale, high severity epidemic.

Patterns of survivorship and forest renewal following a severe and widespread beetle outbreak may differ qualitatively from those observed during previous outbreaks of lesser extent and (or) severity. Although previous outbreaks have tended to accelerate development of late seral forests dominated by spruce and fir (Veblen et al. 1991; Sibold et al. 2007), a severe outbreak that kills the majority of large trees may release enough resources such that early seral species such as aspen and lodgepole pine are favored. Spatially patchy patterns of mortality resulting from past outbreaks generated landscape heterogeneity by triggering tree regeneration or favoring non-host species only in affected portions of the landscape. In contrast, it remains uncertain whether widespread mortality will tend to increase or decrease structural or compositional heterogeneity at the landscape scale (but see Nelson 2009). In an extensive outbreak, a greater variety of forest stand types within a landscape may be impacted, compared with a moderate outbreak in which only the most vulnerable or stressed forest stand types (such as those at low elevations) experience mortality. This variability in pre-outbreak conditions across a landscape, therefore, may require consideration of a greater diversity of forest developmental trajectories following a widespread mortality event. Finally, following an extensive outbreak, seed sources for post-outbreak recruitment of lodgepole pine may be limiting; as a consequence, tree, sapling, and seedling survivorship patterns may be the most important determinants of whether lodgepole pine remains an important component of the forested landscape.

Methods

Study area

Rocky Mountain National Park (Fig. 1) covers 108 000 ha along the spine of the Rocky Mountains in north-central Colorado's Front Range. The Park spans elevations from 2240 to 4350 m, and the Continental Divide runs approximately north-south, bisecting the Park. Weather records for the

neighboring town of Grand Lake approximate the climate in the study area. The average minimum January temperature is -16.5°C , and the average July maximum temperature is 24.6°C . Precipitation averages 480 mm/year, with no pronounced dry season. Measurable snow frequently falls in September, and snow typically remains on the ground until May (Western Regional Climate Center 2010).

We restricted the study to the Park's lodgepole pine dominated forests west of the Continental Divide. The study area comprises approximately 11 200 ha of lodgepole pine forest and represents the portion of the Park most severely affected by the epidemic as of 2008. At the time of field measurement in 2008, the epidemic was subsiding in much of the study area. Historically, stand-replacing fires occurred regularly in the western portion of the Park, and many of today's lodgepole pine forests regenerated following extensive fires in the mid- and late 1800s (Sibold et al. 2006). Lodgepole pine forests dominate the lower elevations of the western portion of the Park at elevations ranging from approximately 2500 to 3500 m (Rocky Mountain National Park 2007). The fire-free interval at higher elevations appears to be longer, and these areas are dominated by Engelmann spruce – subalpine fir forests (Sibold et al. 2006).

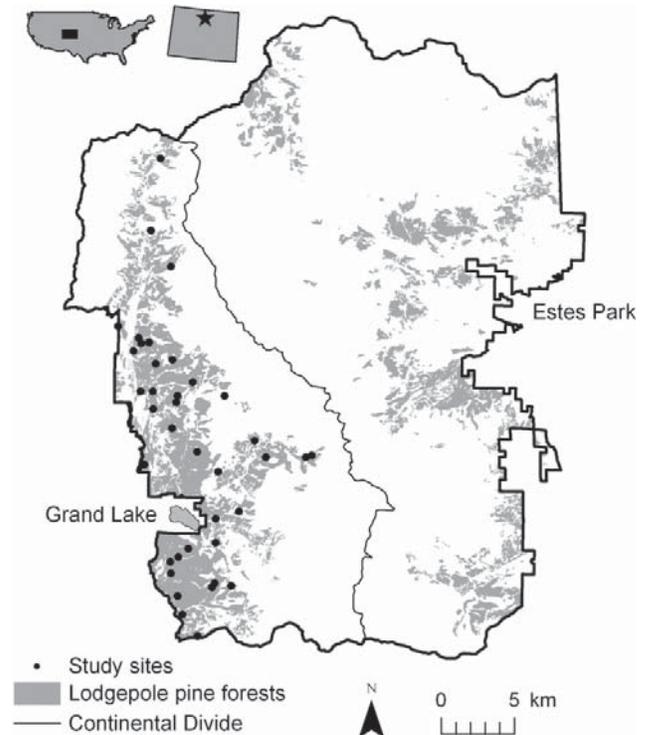
Data collection

Plots were randomly located across the study area, providing us with a representative sample of pre-outbreak stand conditions and outbreak severities. The study area was delineated by the extent of all lodgepole pine vegetation types according to the Park's vegetation map (Rocky Mountain National Park 2007). Prior to visiting the field, we implemented a spatially balanced random sampling scheme in a GIS; this ensured that samples were spatially well distributed across the study area while maintaining randomness (Theobald et al. 2007).

Data were collected in the summer of 2008 at 38 sites (Fig. 1). In the field, sites were reassessed for suitability; suitable sites for sampling had at least five lodgepole pine trees of any size (live or recently dead), lacked evidence of anthropogenic manipulation (logging, roads, etc.), and were accessible on foot. Nearly all sites were deemed suitable — the rest were discarded. Evidence of past disturbance (recent fire, insects, windthrow, etc.), while rare, was considered to be part of the background variability in stand conditions and was not considered separately. At each site, crews established two $20\text{ m} \times 20\text{ m}$ square plots spaced 90 m apart along a random orientation. Minor alterations to this protocol occurred at a few sites to ensure that all plots met site selection criteria. In total, 75 plots were measured at the 38 sites.

In each plot, we measured the densities of canopy trees, saplings, and seedlings by species. Diameter at breast height (dbh) was recorded for each tree taller than 1.4 m. Canopy trees, saplings, and seedlings were distinguished by the following criteria: trees $\geq 10\text{ cm}$ dbh were defined as canopy trees; saplings were $< 10\text{ cm}$ dbh and taller than 1.4 m; and trees shorter than 1.4 m and at least one year old were considered seedlings. Canopy trees and saplings were measured in the $20\text{ m} \times 20\text{ m}$ plot and seedlings were counted in a $2\text{ m} \times 20\text{ m}$ transect that ran through the center of the plot. Living and beetle-killed lodgepole pines were tallied separately, allowing descriptions of pre-epidemic conditions.

Fig. 1. Map of Rocky Mountain National Park showing the locations of the 38 sample sites. The sampled area is the 11 200 ha of lodgepole pine (*Pinus contorta* var. *latifolia*) forests west of the Continental Divide. Lodgepole pine extent data are courtesy of Rocky Mountain National Park's Vegetation Map (Rocky Mountain National Park 2007).



Data analysis

We used a hierarchical agglomerative cluster analysis to define groups of plots with similar pre-epidemic species compositions and structures (McCune and Grace 2002). Subsequent analyses were conducted separately for each group of plots (hereafter "forest types"). Two species (Douglas-fir and limber pine) occurred in only two plots, and these species were not considered in the cluster analysis. Densities for each of the remaining four species (lodgepole pine, subalpine fir, Engelmann spruce, and aspen) were tallied separately for the canopy, sapling, and seedling layers, effectively treating each size class as a separate taxon and allowing us to distinguish between forest types with different structural attributes. Densities were relativized to give equal weight to canopy trees, saplings, and seedlings in the analysis. Compositional dissimilarity between groups was defined using Sørensen distance, and the cluster analysis proceeded using the flexible beta linkage method, with beta equal to -0.25 (McCune and Grace 2002). The PC-ORD software package was used for this and subsequent multivariate analyses (McCune and Meford 2006).

Multiresponse permutation procedures (MRPP; Mielke and Berry 2001) based on Sørensen distance tested for statistical differences between the groups identified by the cluster analysis. Nonmetric multidimensional scaling (NMS) using Sørensen distance was used to visualize patterns of tree species composition among plots and to confirm the distinctiveness of the groups found in the cluster analysis (Kruskal

1964; Mather 1976). Two gradients of species composition were extracted, and correlations were calculated between these axes and taxon abundance.

Although the epidemic appeared to be subsiding in most of the study area, we observed mortality in the year following field sampling and expect additional mortality. For this reason, we present results based both on documented mortality through 2008 and from a “hypothetical extreme scenario” in which we considered all lodgepole pine trees greater than 10 cm dbh to be dead. The 10 cm cutoff is based on the fact that, as of 2008, nearly all (99%) lodgepole pine trees less than 10 cm dbh were still living. Although the hypothetical extreme scenario probably overstates the ultimate severity of the epidemic, it provides an extreme bookend against which 2008 conditions can be compared.

We calculated standard forest descriptors to describe the abundance and species composition of surviving trees for each forest type defined in the cluster analysis. Absolute and relative stem densities and basal areas were calculated for the pre-epidemic forests, with observed 2008 mortality, and with hypothetical extreme scenario mortality. We also evaluated changes in species dominance by categorizing plots (before and after mortality) according to the species present with the highest basal area. Engelmann spruce and subalpine fir were grouped together as one taxon in this analysis of species dominance because they frequently occur together, distinguishing a unique forest type (Peet 1981).

The original intention of our nested sampling design (i.e., sampling two plots at each site) was to assess variability in beetle mortality at multiple spatial scales (Nelson 2009). However, preliminary analyses determined that plots within sites were not more likely to be in the same forest type than if forest types were assigned at random. Therefore, we assumed that spatial autocorrelation in forest type is not apparent at 90 m, and for the purposes of calculating confidence intervals on the proportions of the landscape represented by each forest type, we treated each plot as an independent sample for a total sample size of 75.

Results

Pre-epidemic patterns of lodgepole pine forest structure and composition

Five forest types defined from the cluster analysis effectively described pre-epidemic patterns of lodgepole pine forest structure and composition. The five types differed (*p* value < 0.0001; MRPP) with high homogeneity within types (chance-corrected within-group agreement $\Lambda = 0.291$). We used these forest types to describe variability in the abundance and species composition of surviving trees.

The five forest types varied with respect to their pre-epidemic species composition and structure (Table 1). Lodgepole pine dominated the canopy and sapling layers of all of the forest types, as would be expected because sampling was restricted to sites with a major lodgepole pine component in the overstory. Non-lodgepole pine species dominated the seedling layer in three of the five forest types. A description of the five forest types follows.

- Lodgepole – sparse understory: this type was nearly pure lodgepole pine and had extremely sparse sapling and seedling layers. It was found primarily on drier sites at lower

Table 1. Average pre-epidemic density (standard error in parentheses) by species for the five lodgepole pine forest types and the estimated percentage of the landscape occupied by each type.

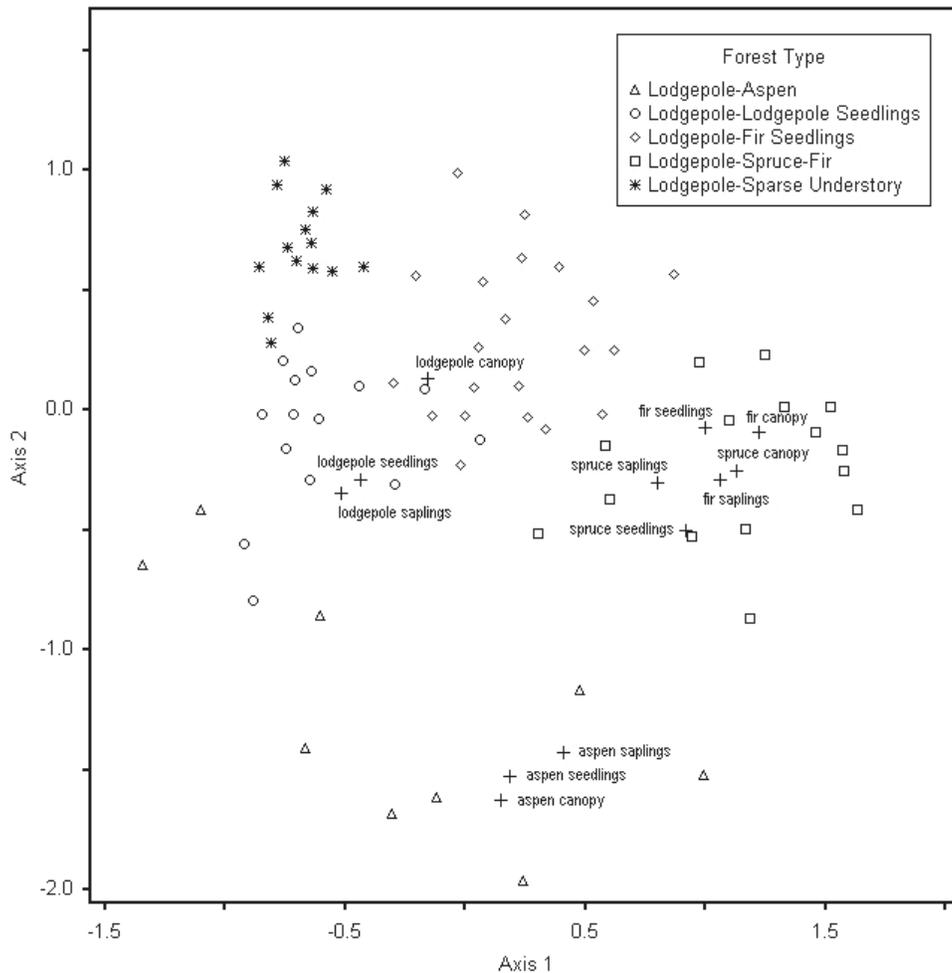
Forest type	% of landscape (±95% CI)	Canopy trees (stems/ha)				Saplings (stems/ha)				Seedlings (stems/ha)			
		Lodgepole pine	Fir	Spruce	Aspen	Lodgepole pine	Fir	Spruce	Aspen	Lodgepole pine	Fir	Spruce	Aspen
Lodgepole – sparse understory*	20 (±9)	1107 (132)	0 (0)	0 (0)	0 (0)	285 (72)	0 (0)	0 (0)	0 (0)	83 (31)	67 (52)	0 (0)	0 (0)
Lodgepole – lodge- pole seedlings	20 (±9)	997 (107)	0 (0)	3 (3)	0 (0)	717 (181)	7 (4)	22 (9)	0 (0)	2600 (625)	83 (40)	50 (27)	17 (17)
Lodgepole – fir seedlings	28 (±10)	983 (118)	15 (5)	25 (6)	0 (0)	323 (80)	42 (10)	46 (11)	0 (0)	393 (101)	1095 (212)	214 (65)	0 (0)
Lodgepole–spruce– fir†	20 (±9)	658 (137)	95 (22)	193 (40)	2 (2)	457 (225)	252 (51)	208 (40)	8 (5)	204 (79)	5402 (1623)	1483 (910)	117 (80)
Lodgepole–aspen	12 (±7)	488 (86)	0 (0)	22 (15)	53 (22)	456 (110)	91 (80)	59 (53)	216 (114)	375 (94)	156 (94)	125 (47)	2406 (776)
Average	100	892 (60)	24 (6)	49 (12)	6 (3)	436 (66)	74 (17)	66 (13)	25 (14)	737 (169)	1453 (404)	385 (192)	287 (118)

Note: CI, confidence interval.

*Douglas-fir is not shown here and was present in two plots.

†Lumber pine is not shown here and was present in two plots.

Fig. 2. Two-dimensional NMS ordination showing the segregation of the forest types and relationships with taxon abundance. Each symbol represents a plot and is coded according to its forest type, derived from a cluster analysis. Weighted average abundances for each taxon are indicated with crosses.



elevations (average 2860 m). Total vegetation cover on the forest floor was very low.

- Lodgepole – lodgepole seedlings: this type was also nearly pure lodgepole pine but had a high density of lodgepole pine seedlings. It too was found primarily at lower elevations (average 2780 m) but on flatter terrain than the lodgepole – sparse understory type.
- Lodgepole – fir seedlings: a moderate amount of fir seedlings characterized this type. Engelmann spruce and subalpine fir were present in low densities in the canopy and sapling layers. It was found on relatively dry sites at higher elevations (average 3000 m) and had low vegetation cover on the forest floor.
- Lodgepole–spruce–fir: Engelmann spruce and subalpine fir attained their highest relative abundance in this type. This type also had the highest absolute density of seedlings. It was found on relatively moist sites at higher elevations (average 3000 m) and had high vegetation cover on the forest floor.
- Lodgepole–aspen: this type was characterized by aspen suckers in the seedling layer. Aspen attained its highest relative abundance in this type as well. It was found on a variety of site types.

The five forest types were found on roughly equal proportions of the landscape (12%–28%; Table 1), with the lodgepole – fir seedlings type slightly more common, and the lodgepole–aspen type slightly less common.

Distances between plots in the two-dimensional NMS ordination correspond well to the Sorensen's dissimilarities in composition between plots ($r^2 = 0.76$). The segregation of the five forest types in the ordination space suggests that the forest types follow a gradient along axis 1 from lodgepole – sparse understory, lodgepole – lodgepole seedlings, lodgepole–fir seedlings, to lodgepole–spruce–fir (Fig. 2). This pattern reflects increases along axis 1 in Engelmann spruce ($r = 0.71, 0.61, \text{ and } 0.28$ for canopy trees, saplings, and seedlings, respectively, where r is the Pearson's correlation between the density of the taxon and the ordination axis) and subalpine fir ($r = 0.70, 0.70, \text{ and } 0.55$). The lodgepole – sparse understory type is separated from the lodgepole – lodgepole seedlings type along axis 2. This separation is associated with a negative correlation between axis 2 and lodgepole pine saplings ($r = -0.23$) and seedlings ($r = -0.24$), which would be expected given the sparse sapling and seedling layers of the lodgepole – sparse understory type (Table 1). The lodgepole–aspen type has negative axis

2 values, which is associated with aspen ($r = -0.59, -0.46,$ and -0.67 for canopy trees, saplings, and seedlings, respectively).

Abundance of surviving canopy trees, saplings, and seedlings

Post-epidemic stands in 2008 had high densities of surviving trees and a moderate residual basal area on average (Table 2; Fig. 3). Although the average canopy tree density had been reduced to 495 trees/ha (from an average of 973 canopy trees/ha prior to the epidemic), the presence of hundreds of saplings per hectare and thousands of seedlings per hectare raised the average total stem density to nearly 4000 stems/ha. The average post-epidemic stand had a basal area of 12 m³/ha in 2008, down from over 33 m³/ha prior to the epidemic. Only 81 canopy trees/ha and a total basal area of 3.9 m³/ha would survive, on average, in the hypothetical extreme scenario. Even with hypothetical extreme scenario mortality, however, an average of over 3500 stems/ha would survive in the canopy, sapling, and seedling layers.

The forests types showed relatively minor differences in the abundance of surviving trees, with two notable exceptions. The lodgepole – sparse understory type had by far the smallest number of saplings and seedlings in 2008 and also had the smallest total residual density (Table 2). If mortality after 2008 removed all of the large surviving lodgepole pine trees, this type would average about 550 surviving stems/ha. Conversely, the lodgepole–spruce–fir type had by far the highest post-disturbance density and basal area, with averages of >8000 stems/ha and >10 m³/ha even under the hypothetical extreme mortality scenario (Table 2; Fig. 3).

Species composition of the post-epidemic forests

Lodgepole pine was still the dominant species in terms of both relative density and relative basal area in the average stand in the Park's western lodgepole pine forests in 2008 (Fig. 4). Even with hypothetical extreme scenario mortality, lodgepole pine would still have the highest average relative density (in the combined canopy, sapling, and seedling layers) and basal area (in the combined canopy and sapling layers) across the landscape. Engelmann spruce, subalpine fir, and aspen had a higher relative abundance in 2008 compared with the pre-epidemic forests, but the degree of change varied among the forest types. Decreases in the relative abundance of lodgepole pine were extremely small in the lodgepole – sparse understory and lodgepole – lodgepole seedlings forest types. Moderate decreases in the relative abundance of lodgepole pine had occurred in the lodgepole – fir seedlings, lodgepole–spruce–fir, and lodgepole–aspen types, with larger changes possible in the hypothetical extreme scenario. The low-moderate relative density and high relative basal area of lodgepole pine in these three forest types reflects high numbers of non-lodgepole species in the understory of stands dominated by lodgepole pine in the overstory. One plot in 2008 (eight plots in the hypothetical extreme scenario) had no surviving lodgepole pine trees.

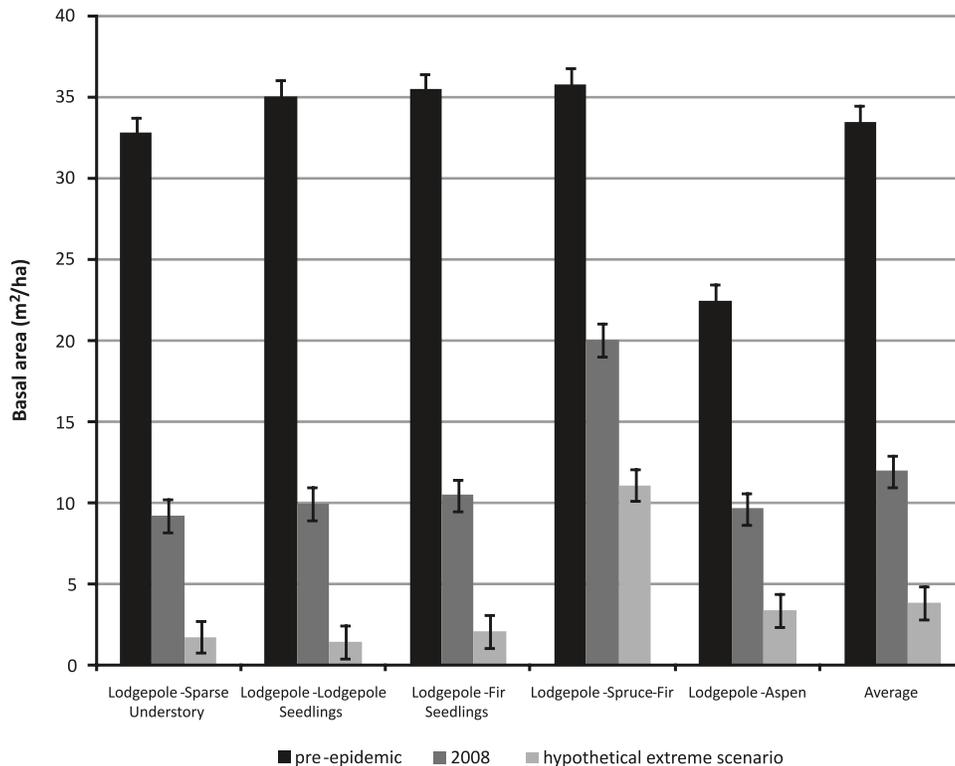
Stands in which lodgepole pine was the dominant species were still by far the most abundant type on the landscape in the beetle-disturbed forests in 2008 (Table 3). Non-lodgepole pine dominated stands were more abundant in 2008 than in the pre-epidemic forests, but even in the hypothetical extreme

Table 2. Average density (standard error in parentheses) of all species combined for the five lodgepole pine forest types before the epidemic, in 2008, and with hypothetical extreme scenario mortality.

Forest type	Canopy trees (stems/ha)			Saplings* (stems/ha)	Seedlings (stems/ha)	Total canopy trees, saplings, and seedlings (stems/ha)		
	Pre-epidemic	2008	Hypothetical extreme scenario			Pre-epidemic	2008	Hypothetical extreme scenario
Lodgepole – sparse understory	1117 (129)	487 (113)	10 (10)	290 (72)	267 (105)	1674 (178)	1026 (178)	549 (145)
Lodgepole – lodgepole seedlings	1000 (108)	442 (78)	3 (3)	745 (178)	2750 (641)	4495 (698)	3932 (718)	3493 (733)
Lodgepole – fir seedlings	1024 (114)	504 (108)	40 (8)	411 (80)	1702 (256)	3137 (303)	2616 (313)	2152 (268)
Lodgepole–spruce–fir	950 (108)	635 (75)	292 (52)	928 (230)	7206 (2265)	9084 (2231)	8753 (2232)	8411 (2210)
Lodgepole–aspen	563 (92)	325 (81)	75 (24)	822 (272)	3063 (807)	4448 (971)	4210 (990)	3960 (962)
Average	973 (55)	495 (45)	81 (17)	603 (75)	2886 (551)	4462 (564)	3976 (572)	3562 (570)

*Pre-epidemic sapling densities are reported.

Fig. 3. Average basal area (all species) for the five lodgepole pine forest types before the epidemic, in 2008, and with hypothetical extreme scenario mortality. Error bars show standard errors.



scenario, stands dominated by lodgepole pine would cover 55% of the landscape. Engelmann spruce – subalpine fir dominated stands covered approximately 15% of the landscape in 2008, with further increases possible in the hypothetical extreme scenario. In the hypothetical extreme scenario, aspen would be dominant on 5% of the landscape.

Discussion

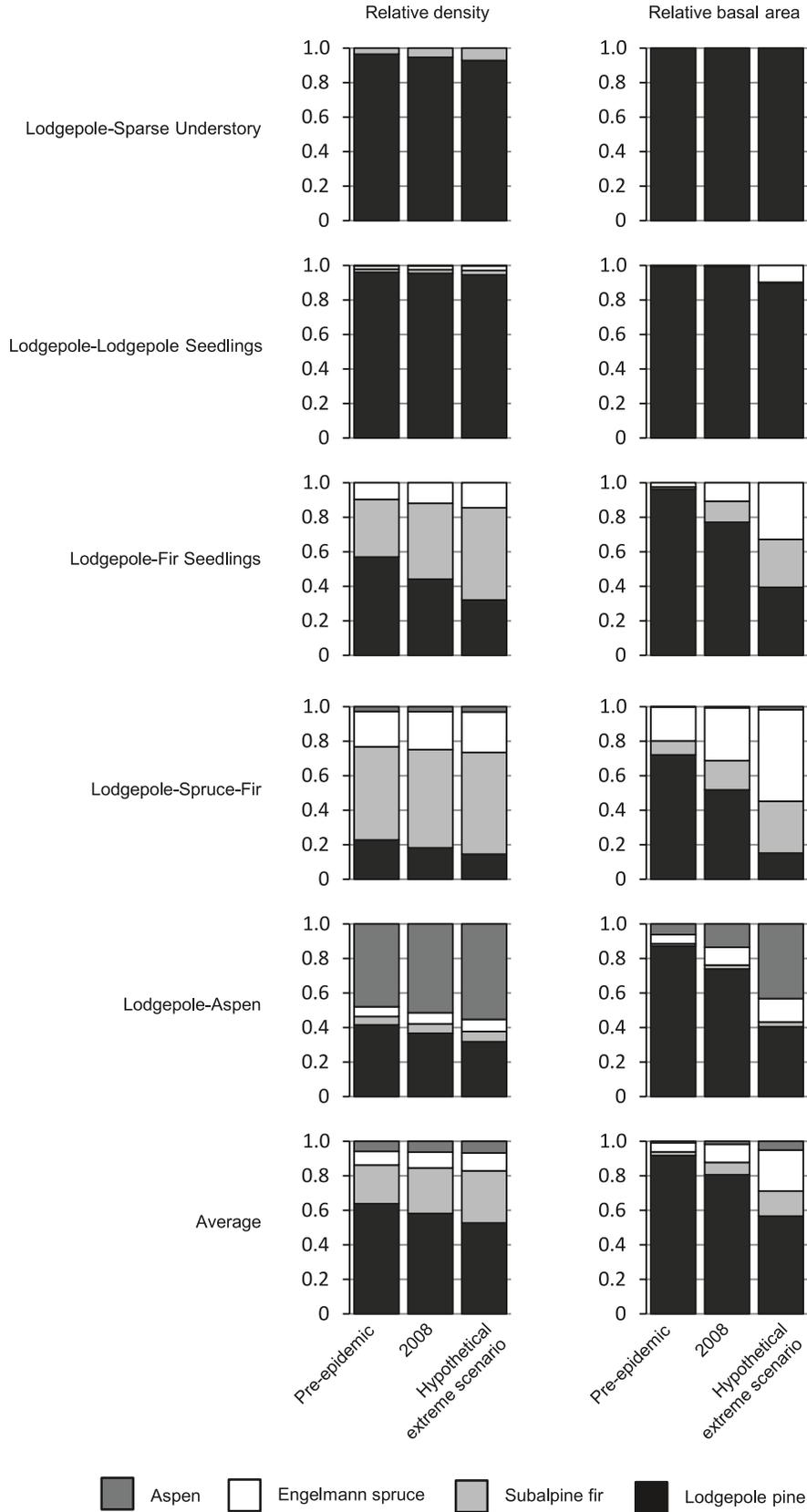
Forests on the western side of Rocky Mountain National Park remained fully stocked with surviving trees, despite widespread mountain pine beetle induced mortality in the canopy. The large decreases in basal area reflect substantial changes in forest structure associated with this epidemic. However, nearly all of the measured stands (96%) contained sufficient surviving trees to exceed the minimum post-harvest stocking requirement of 370 stems/ha used on adjacent National Forests (U.S. Forest Service 1997). This formal requirement does not apply in Rocky Mountain National Park, where the management emphasis is on maintaining natural ecological processes, but it is a useful general indicator of “successful” forest regeneration following disturbance.

The large reduction in basal area that had occurred in most areas indicates that competition among surviving trees for limiting resources will be low in the years following this disturbance. Surviving trees are therefore likely to experience accelerated growth, similar to what has been found in other areas following beetle epidemics (Roe and Amman 1970; Heath and Alfaro 1990; Romme et al. 1986). Due to both their abundance and size advantage over newly established seedlings, it is likely that these surviving trees, legacies of

the pre-epidemic forest, will form the core of most future forests in the Park. Though post-epidemic tree seedling establishment will likely occur in most areas (Sibold et al. 2007) and be important in a few areas where surviving trees were scarce, it appears that the most important mechanism for forest renewal in the Park following this epidemic will be the release of surviving trees. These processes — canopy mortality, accelerated growth of surviving trees, and seedling establishment — will promote uneven-aged, multilayered forest structure in the Park (Roe and Amman 1970; Romme et al. 1986; Sibold et al. 2007).

Lodgepole pine still dominated the beetle-disturbed forests in the western portion of Rocky Mountain National Park as the epidemic was subsiding in 2008 and would remain dominant even if future mortality resembles the hypothetical extreme scenario. It appears highly unlikely that lodgepole pine will be eliminated from more than a very small percentage of stands in the foreseeable future. Moderate increases in the relative abundance of spruce, fir, and aspen had occurred in many areas, and on a small portion of the landscape, these species became dominant due to lodgepole pine mortality. However, about 40% of the area remained nearly pure lodgepole pine in 2008; this pattern holds true even in the hypothetical extreme scenario. Our results support previous studies showing that either shade-tolerant species or lodgepole pine can dominate following mountain pine beetle induced mortality (Amman 1977; Sibold et al. 2007). However, our results also indicate that increases in the relative abundance of shade-tolerant species are not always necessarily large and that aspen could potentially be favored as well.

Fig. 4. Relative species composition of the five forest types before the epidemic, in 2008, and with hypothetical extreme scenario mortality. The graphs on the left show the relative density by species of the combined canopy, sapling, and seedling layers, and the graphs on the right show the relative basal area by species of the combined canopy and sapling layers. Not included are Douglas-fir (present in two plots in the lodgepole – sparse understory forest type) and limber pine (present in two plots in the lodgepole–spruce–fir forest type).



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Table 3. Percentage of the landscape (95% confidence interval in parentheses) dominated by each species before the epidemic, in 2008, and with hypothetical extreme scenario mortality.

Dominant species	Pre-epidemic	2008	Hypothetical extreme scenario
Lodgepole pine	93 (± 6)	84 (± 8)	55 (± 11)
Engelmann spruce – subalpine fir*	5 (± 5)	15 (± 8)	39 (± 11)
Aspen	0	0	5 (± 5)
Douglas-fir	1 (± 2)	1 (± 2)	1 (± 2)

Note: Dominance is defined as the species with the highest total basal area in the plot. Columns might not add up to 100% due to rounding.

*Engelmann spruce and subalpine fir were treated as one taxon in this analysis.

Although often regarded as a “simple” forest type, lodgepole pine forests in fact exhibited highly variable structure and composition both prior to and after the beetle epidemic, as described by the five different forest types identified in this study (Table 1). These forest types resemble the community types described by Peet (1981) in his study of forest vegetation on the Colorado Front Range. The variability in lodgepole pine forest structure and composition is important because it means that the impacts of lodgepole pine mortality and subsequent developmental trajectories will not be uniform. Two of the five forest types are nearly pure lodgepole pine; these two types are distinguished by the density of lodgepole pine in the sapling and seedling layers. Although it appears likely that forest renewal in the lodgepole – lodgepole seedlings type will largely be characterized by the release of surviving lodgepole pine in the canopy and understory, the nature of post-epidemic seedling establishment will likely be an important determinant of forest development trajectories in the lodgepole – sparse understory type, where the lowest densities of surviving trees were found. Moderate to large increases in the relative abundance of Engelmann spruce and subalpine fir will likely occur in the lodgepole–spruce–fir and lodgepole – fir seedlings forest types, although lodgepole pine was still the dominant species in many of these areas in 2008. The fact that the lodgepole–spruce–fir type retained the highest surviving tree density and basal area indicates that forest renewal in these stands should occur relatively quickly. The degree to which the epidemic will promote the dominance of Engelmann spruce and subalpine fir in these forests is variable and will depend on the density of large-sized Engelmann spruce and subalpine fir and the ability of seedlings to grow into the canopy.

Of particular interest to land managers and the public is the lodgepole–aspen forest type. Aspen is the only major upland deciduous tree species in the southern and central Rocky Mountains, and aspen forests support a rich and distinctive biota. Aspen forests are declining in many areas due to recent climatic conditions, paucity of fires, and other causes (e.g., Worrall et al. 2008), but it is hypothesized that aspen will become more abundant in mixed stands where the lodgepole pine component has been largely removed by mountain pine beetles. In this study, surviving lodgepole pine trees were abundant in the lodgepole–aspen type, and minor increases in the relative abundance of aspen in these forests had occurred by 2008. The fate of aspen suckers in the seedling layer of these stands is uncertain. Recent research indicates that an extremely high proportion of aspen suckers in the study area is being heavily browsed by elk, although in-

creased growth, establishment, and density of aspen suckers was observed in areas with higher levels of beetle-induced lodgepole pine mortality (Nelson 2009).

The post-epidemic forest conditions described here serve as starting points that will influence future forest development. These initial conditions allow for informed projections of future forest structure and composition (Diskin 2010). Several unpredictable factors, however, will shape forests in the future. First, future disturbances, notably stand-replacing fires (Peet 2000), will alter forest developmental trajectories. Much attention has been devoted to the concern that bark beetle outbreaks increase fire risk in the short term and (or) set the stage for uncharacteristically severe wildfire in the decades following an outbreak. Assessing the validity of these concerns is beyond the scope of our study (but for a recent review, see Black et al. 2010). Regardless of whether future wildfires are exacerbated by beetle activity or not, subalpine forests will burn periodically during exceptionally dry seasons (Schoennagel et al. 2004), killing established trees and providing establishment opportunities for early seral species such as lodgepole pine and aspen.

Even without fire, blowdown of surviving trees could affect forest development, and evidence from lodgepole pine harvesting operations indicates that lodgepole pine is especially susceptible to blowdown following partial canopy removal (Lotan and Critchfield 1990). On the other hand, retrospective studies of historic beetle epidemics fail to report evidence of post-epidemic blowdown (Sibold et al. 2007; Dordel et al. 2008). Blowdown of both living and dead trees could also damage or kill trees in the understory (Griesbauer and Green 2006).

Second, the ability to respond to increased resources (light, water, nutrients, etc.) will likely not be uniform among the surviving trees and could depend on the species, height, age, and health of the tree, although relationships are not clear (Griesbauer and Green 2006). What is clear, though, from previous epidemics and studies of advance regeneration following timber harvests, is that surviving trees generally experience increased growth rates (Romme et al. 1986; McCaughey and Ferguson 1988; Veblen et al. 1991; Lewis Murphy et al. 1999). The spatial distribution of surviving subcanopy trees will affect their ability to replace beetle-killed trees in the canopy (Griesbauer and Green 2006). If surviving trees are clumped in small areas, post-epidemic tree establishment could be a more important mechanism for forest renewal than indicated by summaries of stand density.

The final unknown for the future development of the Park’s beetle-disturbed forests is the rate and composition of

future tree establishment. Sibold et al. (2007) found abundant lodgepole pine and subalpine fir establishment in the 20 years following a previous beetle disturbance in the Park, but studies elsewhere indicate variable rates of establishment (Astrup et al. 2008; Axelson et al. 2009). Our focus has been on surviving stems, most of which pre-dated the outbreak, so any new establishment of seedlings will add to the densities of stems reported here. Nineteen percent of seedlings included in our tallies were young enough to have germinated since the onset of the outbreak, but we found no relationship between canopy mortality and density of young seedlings (unpublished data). We suspect, therefore, that by 2008, we had not yet observed a pulse of new seedling recruitment brought on by the epidemic, in part because most dead trees still retained many needles and understory light levels had not appreciably changed. Measuring rates of future seedling recruitment will be an important next step towards refining our estimates of future forest trajectories.

Many of the changes associated with this epidemic are undesirable to society and command swift management action, including hazard tree removal around buildings and infrastructure. In wildland settings of Rocky Mountain National Park, however, we found that surviving trees — including larger trees in the canopy and sapling layers — were generally abundant and that lodgepole pine remained a dominant species even as the epidemic was subsiding in 2008. In the absence of future disturbance or rapid changes to climate, it is likely that this lodgepole pine dominated landscape will remain forested. Trees will be smaller for some time, but species composition will be similar to what existed before the epidemic. This implies that proactive efforts to “restore” mountain pine beetle disturbed forests such as planting seedlings or clearcutting to promote lodgepole regeneration are unnecessary in much of the Park. A second implication of the findings of this study is that uniform portrayals of the epidemic and one-size-fits-all management strategies are likely to be misguided, given the variability in beetle-disturbed forests both before and after the epidemic.

The most important insight from this study is that the bark beetle epidemic greatly reduced stand basal area and stem density, but it left almost all forests fully stocked with smaller trees that should grow well following the reduction in overstory dominance. In other words, this landscape appears resilient to the recent outbreak and, subject to the caveats listed above, is likely to remain forested, with a modest change in species composition. The key to forest resilience in Rocky Mountain National Park, i.e., the prevalence of high densities of saplings and seedlings, may or may not be matched in other subalpine forest regions experiencing high tree mortality rates. Despite the value of forest demography assessments like the one presented here for gauging forest resilience and the need for management intervention, we are aware of few studies that have explored post-outbreak stand conditions in other areas (but see Coates et al. 2006). More studies across the range of the current mountain pine beetle epidemic are needed to determine whether resilience to severe and extensive bark beetle outbreaks is a universal characteristic of subalpine forest ecology. Future efforts not only should describe the average post-outbreak trajectory of forest stands on a landscape, but also should capture the variability in stand

conditions and mortality patterns, which will interact to determine the effect of the outbreak on the future forest.

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