Ecological Indicators 70 (2016) 451–459

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Using structural sustainability for forest health monitoring and triage: Case study of a mountain pine beetle (*Dendroctonus ponderosae*)-impacted landscape

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ARTICLE INFO

Article history:
Received 5 January 2016
Received in revised form 9 June 2016
Accepted 13 June 2016

Keywords:
Baseline mortality analysis
Forest structure
Forest disturbance
Climate change
Bark beetle

ABSTRACT

Heavy disturbance-induced mortality can negatively impact forest biota, functions, and services by drastically altering the forest structures that create stable environmental conditions. Disturbance impacts on forest structure can be assessed using structural sustainability—the degree of balance between living and dead portions of a tree population's size-class distribution—which is the basis of baseline mortality analysis. This analysis uses a conditionally calibrated reference level (i.e., baseline mortality) against which to detect significant mortality deviations without need for historical references. Recently, a structural sustainability index was developed by parameterizing results of this analysis to allow spatial and temporal comparisons within or among forested landscapes. The utility of this index as a tool for forest health monitoring programs and triage decisions has not been examined. Here, we investigated this utility by retrospectively analyzing the structural sustainability of a mountain pine beetle (*Dendroctonus ponderosae*)-impacted, lodgepole pine (*Pinus contorta*)-dominated landscape annually from 2000 to 2006 as well as among watersheds. We show that temporal patterns of structural sustainability at the landscape-level reflect accumulating beetle-induced mortality as well as beetle-lodgepole pine ecology. At the watershed-level, this sustainability spatially varied with 2006 beetle-induced mortality. Further, structural sustainability satisfies key criteria for effective indicators of ecosystem change. We conclude that structural sustainability is a viable tool upon which to base or supplement forest health monitoring and triage programs, and could potentially increase the efficacy of such programs under current and future climate change-associated disturbance patterns.

1. Introduction

Global forest health is influenced by natural and anthropogenic disturbances (Gauthier et al., 2015; Millar and Stephenson, 2015). The impact and prevalence of some biotic (e.g., insect and disease outbreaks) and abiotic (e.g., drought and wildfire) disturbances are predicted to increase in severity and frequency in coming decades in response to climate change factors (Allen et al., 2015, 2010; Gauthier et al., 2015; McDowell and Allen, 2015; Millar and Stephenson, 2015; Wotton et al., 2010). While some level of disturbance is necessary for maintaining forest communities, more frequent or severe disturbances may surpass the resistance—the capacity to endure disturbances without substantial change to the existing community—and resilience—the ability of a community to recover from disturbance-induced change—thresholds of affected forests, potentially resulting in substantial mortality. This mortality inevitably alters forest structure as trees of certain sizes are killed (Pommerening, 2006). However, forest structure is integral in defining the forest environment because dominant trees are foundation species (Ellison et al., 2005). This environment can change in response to altered forest structure, potentially causing cascading positive or negative effects on wildlife and plant populations as habitat suitability changes (Cale et al., 2013; Foster et al., 2002). Further, altered structure can affect forest ecosystem functions

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http://dx.doi.org/10.1016/j.ecolind.2016.06.020
1470-160X/

and services. For example, recent climatic shifts have facilitated unprecedented mountain pine beetle (*Dendroctonus ponderosae* Hopkins; Coleoptera, Curculionidae; MPB) outbreaks in western North America, resulting in substantial changes in forest structure and function including reduced carbon sequestration and storage, altered watershed hydrology, and hindered forest regeneration potential by reducing fungal-mutualist diversity (Bearup et al., 2014; Kurz et al., 2008; Treu et al., 2014). These qualities of a healthy forest are maintained by stable environments created by a lack of disturbance, or natural disturbance regimes (Ellison et al., 2005; Pommerening, 2006). Thus, significant changes to these qualities could be predicted to occur following major disruptions, such as from novel disturbance events or regimes, to forest structure.

Teale and Castello (2011) define a healthy forest as one that satisfies ecological and/or economic management objectives and is structurally sustainability while ultimately considering the ecology of the species evaluated. Structural sustainability is the degree of balance between living and dead portions of a tree population's size-class distribution, and conceptually predicts that biotic and abiotic components are stable in forests where mortality and regeneration/growth are balanced (i.e., structurally sustainable) because demographic development and turn-over occurs unhindered (Castello et al., 2011; Duchesne et al., 2005; Manion and Griffin, 2001; Manion and Rubin, 2001; Teale and Castello, 2011). This balance is important as forest mortality increases space and resource availability to growing trees, allowing them to optimize growth and density for a given site. Although historical disturbance regimes (high-impact, infrequent or low-impact, frequent) are essential to natural forest dynamics, long-term shifts in the mortality-growth/survival balance could be a consequence of novel disturbances or changes to natural disturbance regimes (Bergeron et al., 1999; Teale and Castello, 2011). Imbalance can be evaluated from landscape-level census data of individual tree species or mixed-species forests using baseline mortality analysis (BMA). Using tree size (diameter) classes and density in each class, BMA compares observed mortality levels to a conditional reference level derived from and calibrated to the distribution of living trees (i.e., baseline mortality) (Manion and Griffin, 2001; Teale and Castello, 2011). The statistical significance of differences between observed and baseline mortality is tested for each diameter class to identify portions of the size distribution potentially experiencing overcrowding (i.e., observed mortality less than baseline) or heavy killing-agent activity (i.e., observed mortality greater than baseline) (Castello et al., 2011).

While BMA is useful in identifying diameter classes with mortality-growth/survival imbalances, it does not objectively determine the structural sustainability of the distribution as a whole (i.e, all size classes together). Similarly, BMA results alone cannot be used to evaluate the relative structural sustainability among species nor over time or among regions for a single species. A structural sustainability index (SSI) was recently developed by Cale et al. (2014) to address these limitations by parameterizing several aspects of the BMA results, such as how clustered or numerous diameter classes with significant differences between observed and baseline mortality are in these results. This index does not predict a static estimate of structural sustainability but instead an estimate for a given point in time, which could be recalculated over time given new data. Further, SSI can discriminate between structurally sustainable and unsustainable forests. The conditionally-calibrated baseline mortality foundation (Teale and Castello, 2011) of SSI may make this index ideally suited for monitoring disturbance-associated changes in forest conditions (both biotic and abiotic) over time as climate change undermines the continued utility of historical references of healthy tree structures to monitoring programs. Similarly, SSI may be an equally valuable tool to prioritizing the allocation of forest management resources (i.e., ecosystem triage) by allowing managers to compare relative disturbance impacts among sites. However, the utility of SSI for these purposes has not been investigated.

Mountain pine beetle is a tree-killing insect native to western North America whose primary host is lodgepole pine (*Pinus contorta* Douglas ex P. Lawson & C. Lawson) (Amman and Cole, 1983; Amman, 1977; Safranyik and Carroll, 2006). Although MPB-associated mortality is minimal when beetle populations are at endemic levels, landscape-level mortality occurs when beetle populations reach outbreak densities and overcome defense mechanisms of healthy trees by attacking *en masse* (Raffa et al., 2008; Safranyik and Carroll, 2006). While considered invasive in parts of Canada (Cullingham et al., 2011; Erbilgin et al., 2014; Safranyik et al., 2010) where it has killed millions of hectares of pine forest, the beetle is a natural mortality agent in its native range where beetle outbreaks, as well as fire, are an essential part of the ecosystem that help regulate forest structure through stand-initiating mortality levels (Amman, 1977; Roe and Amman, 1970).

Here, we retrospectively analyzed the structural sustainability of a lodgepole pine-dominated landscape in Colorado during a MPB outbreak to investigate two questions: is SSI a viable tool for monitoring forest-change, and is SSI a useful platform upon which to base forest triage decisions? Further, we had two specific objectives: evaluate the utility of SSI for monitoring forest-change by assessing index score response to MPB-induced mortality over time, and for aiding triage decisions by comparing this mortality to SSI among several watersheds for a given year. The MPB-lodgepole pine system affords some advantages over other disturbance systems for this type of retrospective analysis: (1) the year in which each tree was killed by MPB can be estimated with high relative accuracy (Keen, 1955; Klutsch et al., 2009), (2) during an outbreak MPB is the dominant mortality agent allowing us to attribute forest structural changes solely to beetle activity, and (3) annual beetle-induced mortality follows a predictable exponential increase before declining after nearly all susceptible hosts have been killed (Raffa et al., 2008; Safranyik and Carroll, 2006). Further, the ability to accurately estimate mortality year allows us to recreate pre-outbreak structures by including MPB-killed trees among counts of living trees.

2. Materials and methods

2.1. Study site and data collection

We used data collected from lodgepole pine-dominated forests in the Sulphur Range District, Arapaho-Roosevelt National Forest in eastern Grand County (approximately 40°4′N, 106°0′W), Colorado. A MPB outbreak affected at least 90% of these lodgepole pine forests between 2000 and 2007 (USDA Forest Service, 2007). Lodgepole pine-dominated forest covers approximately 54% (158,000 ha) of the eastern Grand County study area, occurring at 2500–3500 m above sea level.

In 2006 and 2007, 221 plots (0.02 ha each) were established on US Forest Service land using a geographic information system (GIS) to select plot locations in areas with and without MPB infestation in lodgepole-dominated forests (Klutsch et al., 2009). Plots were a minimum of 400 m from each other and from roads. A total of 51 plots were classified non-infested, while the remaining 170 had varying amounts of infested lodgepole pine and infestation periods in 2000–2006. Although this dataset included other species, we extracted and analyzed records only for lodgepole pine trees with a diameter at breast height (DBH) $\geq$ 5.0 cm, which represented 69% of all species of all sizes and included DBH measurements, health status (live, dead from unknown cause, killed by MPB), and year of MPB infestation.

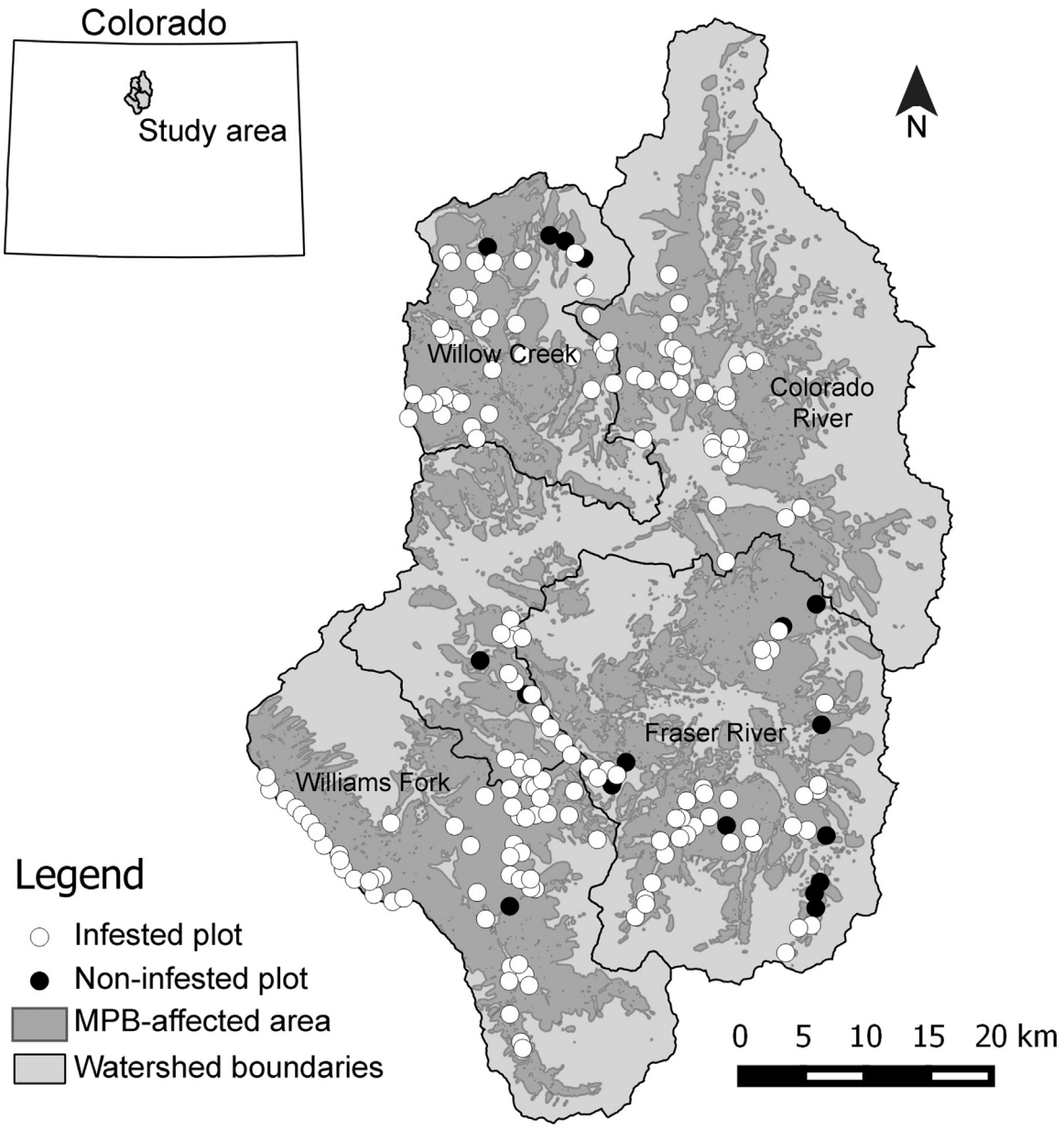

Fig. 1. Locations of mountain pine beetle (*Dendroctonus ponderosae*; MPB)-affected (infested) and non-infested plots in four watersheds (Colorado River (combined Headwaters Colorado River and Little Muddy Creek-Colorado River watersheds), Fraser River, Williams Fork, Willow Creek) in eastern Grand County, Colorado.

2.2. Defining outbreak area and watershed boundaries

To accurately represent the proportion of infested and non-infested area in eastern Grand County, we used a GIS to calculate the percent of lodgepole pine trees not affected by MPB. The extent of MPB outbreak in 2006 was estimated by merging the annual areas of lodgepole pine affected by MPB-induced mortality for 2000–2006 indicated in USDA Aerial Detection Surveys (ADS; USDA Forest Service 2007).

We used LANDFIRE Existing Vegetation Type for 2001 (Wildland Fire Science Earth Resources Observation and Science Center U.S. Geological Survey, 2010) to identify the area covered by lodgepole pine-dominated forest at the beginning of the beetle outbreak. In mixed-species areas containing lodgepole pine, we used the MPB-affected area, as identified by ADS, overlaid in a GIS with the Existing Vegetation Type identified as Rocky Mountain lodgepole pine as the total area covered with lodgepole pine forest type. Thus, the proportion of lodgepole pine area affected by MPB was calculated by dividing the MPB-affected area by the total area occupied by lodgepole pine. This estimate indicated that the MPB outbreak encompassed 90% all lodgepole pine-occupied area in Grand Country by 2006. To construct a dataset for analysis representative of this percentage and thus landscape conditions, we randomly selected 19 plots from among the 51 non-infested plots. This resulted in a subset dataset consisting of 189 plots (170 infested and 19 non-infested plots; 3.78 ha total area) containing 3425 lodgepole pine, 33% of which were large (≥20.0 cm DBH) trees. All further analyses were conducted using this dataset.

To assess how SSI could vary among parcels at the sub-landscape-level we divided plots based on their location within boundaries of their respective watersheds (hydrologic unit digit level 10; Fig. 1) obtained from the USDA Geospatial Data Gateway version of the Watershed Boundary Dataset (US Geological Survey, 2015). This resulted in data from five watersheds whose structural sustainability was variously affected by MPB: Headwaters Colorado River, Little Muddy Creek-Colorado River, Fraser River,

Table 1
Total number of all trees, large (≥20 cm diameter at breast height, DBH) trees, and mountain pine beetle (*Dendroctonus ponderosae*) outbreak and non-infested plots by watershed.

Watershed	No. trees	No. of trees DBH ≥ 20 cm	No. plots	No. outbreak plots	No. non-attacked plots
Colorado River	886	270	48	46	2
Fraser River	898	308	49	38	11
Williams Fork	976	271	53	52	1
Willow Creek	665	238	39	34	5

Table 2
Baseline mortality and structural sustainability index analyses by study year for a mountain pine beetle (*Dendroctonus ponderosae*)-impacted lodgepole pine (*Pinus contorta*) landscape in eastern Grand Country, Colorado in 2000–2006.

Year	Diameter classes with mortality differences		Baseline mortality	Model statistics			Sustainability class
	Deficient	Excessive		*F*	r^2	p-value	
2000	92%	0%	45%	140.7	0.94	<0.001	Unsustainable
2001	75%	0%	45%	141.8	0.94	<0.001	Unsustainable
2002	67%	0%	45%	132.2	0.94	<0.001	Unsustainable
2003	70%	0%	48%	78.0	0.91	<0.001	Unsustainable
2004	44%	0%	45%	111.9	0.94	<0.001	Sustainable
2005	33%	0%	50%	137.1	0.95	<0.001	Sustainable
2006	25%	50%	57%	102.6	0.94	<0.001	Unsustainable

Williams Fork, and Willow Creek. However, Headwaters Colorado River and Little Muddy Creek-Colorado River were combined into a "Colorado River" watershed because Little Muddy Creek-Colorado River encompassed a smaller area and contained fewer plots than other watersheds. These four watersheds contained similar total numbers of trees, but differed in the number of infested and non-infested plots (Table 1), which further simulated a landscape whose watersheds are variously impacted by MPB.

2.3. Data analysis

After assigning lodgepole pines into 5 cm diameter class bins, the dataset was subset to evaluate annual counts of live and dead trees from 2000 to 2006 as well as total counts for each watershed. For the annual counts, all plot data were aggregated to create a landscape-level dataset. A watershed-level dataset was created by aggregating live and dead tree counts recorded in 2006 from plots within each of the four watersheds. Further, forest structure in 2000 was reconstructed by including counts of MPB-killed trees among the counts of live trees while all other dead trees remained among dead counts. We compared the simulated structure of watershed in 2000 to that in 2006 to assess how MPB-associated mortality affected lodgepole pine structure in each watershed over time.

The structural sustainability of lodgepole pine was quantified annually over the study period as well as among the watersheds using the SSI developed by Cale et al. (2014), which parameterizes results of a BMA (Castello et al., 2011; Zhang et al., 2011). Although other distributions such as negative power and Weibull functions may in some cases more accurately fit the data, BMA was designed for landscapes where the non-transformed distribution of live trees fits a negative exponential function, such as observed in uneven-aged forests and landscapes comprised of many variously-initiated even-aged stands (Rubin et al., 2006; Zhang et al., 2011). Baseline mortality analysis compares recorded levels of mortality against a predicted level (i.e., baseline mortality) derived from the slope of a log-linear model of the distribution of live trees. Two calculations comprise this analysis. First, living tree density (N) and diameter class bin values (D) are regressed by a log-linear model using ordinary least squares:

$$\ln(N) = \alpha_0 + \alpha_1 \times D \quad (1)$$

where ln(N) is the natural-log of living tree density, α_0 and α_1 are estimated regression coefficients. Second, the slope coefficient (α_1) from Eq. (1) is then used to calculate baseline mortality (BM):

$$BM = 1 - e^{-\alpha 1 \times \Delta D} \quad (2)$$

where ΔD is the diameter class bin size. Chi-square tests are used in series to identify diameter classes with significant differences between the number of dead trees in the diameter class (observed mortality) and a predicted number of dead trees under a baseline mortality level. Diameter classes with significant differences are classified as having either deficient or excessive mortality depending upon whether observed mortality occurs below or above baseline mortality (Eq. (2)), respectively. The SSI (Cale et al., 2014) was developed to parameterize these BMA results to allow quantitative comparisons among results. The index uses a series of five metrics to grade different aspects of the BMA results: distribution of mortality (i.e., which range of diameter classes have significant differences; DM), aggregation (i.e., how clustered diameter classes with significant differences appear; AGG), magnitude (i.e., the summation of absolute differences in observed and expected mortality; MAG), relative abundance (i.e., the total number of diameter classes with significant differences; RA), and change (i.e., the absolute difference in the number of diameter classes exhibiting significant differences at the first and last distribution in an iterative simulation; CHG) (Cale et al., 2014). The grading scales for these metrics are described in Cale et al. (2014). Metric grades are input into a discriminant function (Eq. (3); Cale et al., 2014) which calculates a structural sustainability index score.

$$\text{Score} = (0.699)\text{AGG} + (0.684)\text{RA} + (0.535)\text{MAG} + (0.420)\text{DM} - (0.554)\text{CHG} \quad (3)$$

Cale et al. (2014) further describe that index scores can be used to classify BMA results into one of two groups: structurally sustainable or structurally unsustainable. Classification is made by comparing the calculated SSI score against a threshold score of 70.58 (as calculated by Cale et al., 2014). Species or forests with SSI scores surpassing this threshold are classified as structurally unsustainable while those scores at or below the threshold are classified as structurally sustainable.

Cumulative percent MPB-associated mortality was calculated annually for all or large trees (≥20 cm DBH) by dividing the number of MPB-killed trees in that and previous years by the total number of trees sampled or the number of large trees, respectively. Similarly, we calculated annual mortality by dividing the number of

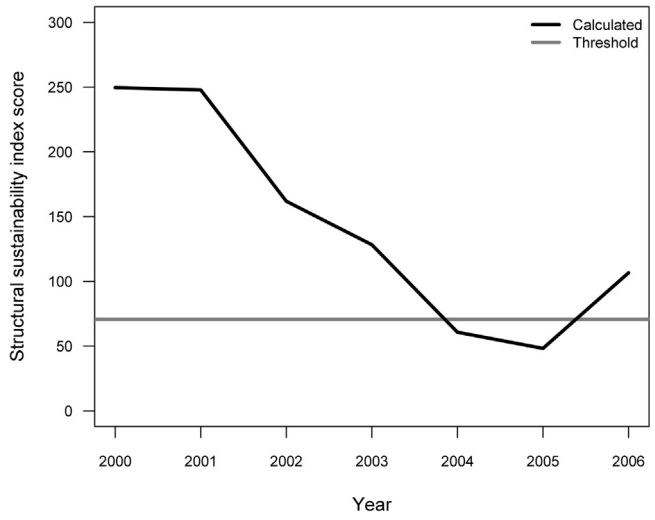

Fig. 2. Structural sustainability index scores for mountain pine beetle (*Dendroctonus ponderosae*)-impacted lodgepole pine (*Pinus contorta*) in eastern Grand County, Colorado calculated for 2000–2006 are indicated by the black line. The grey line indicates the structural sustainability index threshold calculated by Cale et al. (2014) which classifies structurally unsustainable (index scores greater than the threshold) from sustainable (scores lower than the threshold) index scores.

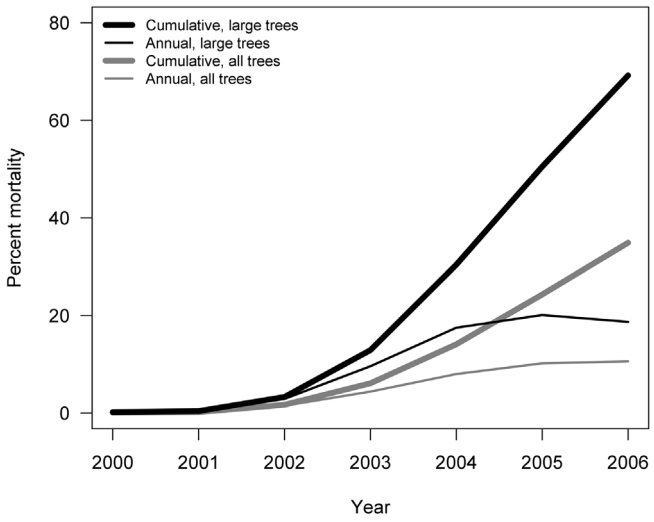

Fig. 3. Cumulative (thick lines) or annual (thin lines) percent mountain pine beetle (*Dendroctonus ponderosae*)-induced mortality in 2000–2006 for large (≥20 cm in diameter at breast height; black lines) and all (grey lines) lodgepole pine (*Pinus contorta*) trees surveyed in eastern Grand County, Colorado.

MPB-killed trees in a given year by the total number of sampled trees or the number of large trees, respectively. The fit of log-linear models were assessed using simple linear regression. Pearson's correlation was calculated to test co-linearity between SSI and study year. All statistical analyses were performed using the R software environment version 3.2.1 (R Core Team, 2015).

3. Results

Diameter distributions of live lodgepole pine trees each year from 2000 to 2006 had a negative exponential shape as indicated by parameters of their log-linear models, with all models being significant ($p < 0.05$) and having r^2 values of at least 0.91 (Table 2). Grades of each SSI metric for each year are provided in Supplementary Table 1. Baseline mortality analysis and SSI scores indicate that, at the landscape-level, the structural sustainability of lodgepole pine declined from 2000 to 2005 before increasing in 2006 (Fig. 2). SSI scores suggest lodgepole pine was structurally unsustainable from 2000 to 2003 as scores from these years were greater than the threshold of 70.58. Unsustainability was due to mortality levels significantly below baseline as no diameter classes exhibited mortality greater than baseline over this period (Table 2). However, the percentage of diameter classes with significant mortality deficiencies decreased over time with SSI, and lodgepole pine was structurally sustainable in 2004 and 2005 (SSI scores less than the threshold). In 2006, SSI increases above the threshold, and lodgepole pine again is unsustainable but this time due to 50% of its diameter classes exhibiting excessive mortality (Fig. 2 and Table 2).

The structural unsustainability in 2006 due to excessive mortality as well as the continuous decline in SSI score from 2000 to 2005 corresponded with changes in MPB-induced mortality over time. The cumulative percent MPB-induced mortality increased near exponentially over the study period when considering all study trees as well as only large trees (Fig. 3). Also for these sets of trees, annual percent MPB-induced mortality increased exponentially from 2000 to 2005 before nearly leveling or declining in 2006 when considering all trees or only large trees, respectively (Fig. 3). These changes in cumulative and annual mortality were due to increasing dead tree densities in 20–40 cm diameter classes (Fig. 4).

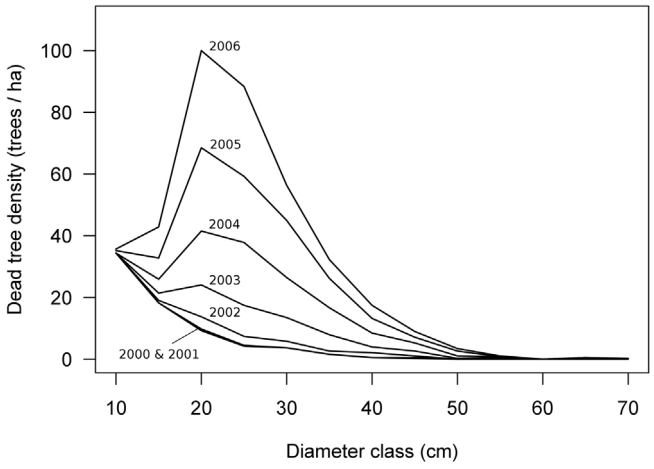

Fig. 4. Diameter distributions for the density (trees/ha) of mountain pine beetle (*Dendroctonus ponderosae*)-killed lodgepole pine (*Pinus contorta*) in eastern Grand County, Colorado during 2000–2006.

Structural sustainability varied among the four watersheds evaluated: Colorado River, Fraser River, Williams Fork, and Willow Creek (Table 3). Log-linear models indicated live trees in each watershed fit well to a negative exponential distribution, with all models being significant ($p < 0.05$) and r^2 values of at least 0.87 (Table 3). Structural sustainability index metric grades for each watershed are provided in Supplementary Table 2. When including MPB-induced mortality among dead tree counts (i.e., lodgepole pine structure in 2006), all watersheds exhibited mortality deficiencies in at least 29% of their diameter classes, while only Williams Fork and Colorado River had diameter classes with excessive mortality (Table 3). Williams Fork was the only unsustainable watershed (SSI of 77.9; Supplementary Table 2); likely due to mortality deficiencies in smaller diameter classes (trees ≤ 15 cm DBH) and excessive, MPB-induced mortality in larger diameter classes (trees ≥ 20 cm DBH) (Table 3). Further, this watershed had the highest percent MPB-induced mortality (42%) of all watersheds, which was concentrated in large trees as these showed 83% mortality (Table 3). All other watersheds showed SSI scores below the structural sustainability threshold (Table 3). However, 14% of diameter classes in the Colorado River watershed showed excessive mortal-

Table 3
Baseline mortality and structural sustainability index analyses by watershed for lodgepole pine (*Pinus contorta*).

Watershed	MPB-killed[a]	SSI	Diameter classes with mortality differences		Baseline mortality	Model statistics			Sustainability class	Cumulative Percent MPB-killed	
			Deficient	Excessive		*F*	r^2	p-value		All trees	Large trees
Colorado River	Included	57.9	29%	14%	55%	54.4	0.92	<0.001	Sustainable	41%	82%
	Excluded	116.7	67%	0%	39.3	47.3	0.87	<0.001	Unsustainable	–	–
Fraser River	Included	46.5	43%	0%	47.8	37.5	0.88	0.002	Sustainable	24%	51%
	Excluded	176.6	100%	0%	39.3	50.9	0.88	<0.001	Unsustainable	–	–
Williams Fork	Included	77.9	40%	40%	63.2	56.1	0.95	0.005	Unsustainable	42%	83%
	Excluded	132.8	70%	0%	42.3	138.3	0.95	<0.001	Unsustainable	–	–
Willow Creek	Included	36.3	29%	0%	47.8	47.1	0.90	0.001	Sustainable	30%	61%
	Excluded	100.0	67%	0%	36.2	63.4	0.90	<0.001	Unsustainable	–	–

[a] "Included" indicates that mountain pine beetle (*Dendroctonus ponderosae*)-killed trees were included among counts of dead trees, whereas "excluded" indicated beetle-killed trees were grouped with counts of live trees in order to simulate watershed structure prior to beetle-induced mortality.

ity that corresponded to 41% and 82% MPB-induced mortality out of all trees and large trees despite the watershed being structurally sustainable.

Including counts of MPB-killed trees from 2006 among the live counts of their associated diameter classes provided a structure likely similar to that occurring in 2000. These estimated structures suggest that each watershed was unsustainable when the MPB outbreak was beginning in 2000 (Table 3). The Fraser River watershed was the most unsustainable with an SSI score of 176.6 (Supplementary Table 2) and 100% of its diameter classes exhibiting mortality deficiencies (Table 3). Difference in watershed SSI between 2000 and 2006 (described above) indicated that MPB-induced mortality served to make the Colorado River, Fraser River, and Willow Creek watersheds more structurally sustainable (Table 3). Further, differences between the structural sustainability of 2000 and 2006 for each watershed were due to large increases in dead tree density for diameter classes 20–40 cm (Fig. 5).

4. Discussion

A good indicator of ecosystem condition upon which forest health monitoring programs focus should be easily measured, sensitive to stressors (e.g., disturbances), predictable in their response to a given stressor, be indicative of impending ecosystem change, and predict changes avoidable by management (Dale and Beyeler, 2001; Niemi and McDonald, 2004). Our results suggest that structural sustainability, assessed through SSI and BMA, satisfy all these criteria. First, SSI and BMA are easy to calculate, allowing users with various technical and computational backgrounds access to these analyses. A Forest Structural Sustainability Calculator (http://www.esf.edu/efb/forsustcalc/) is available as free-to-download, non-commercial software to perform BMA and compute SSI for users. Further, these calculations are based on easily-collected forest census data commonly recorded during forest surveys and often available from a variety of private, municipal, and federal organizations.

Second, at least in cases where mortality can be attributed to a given mortality agent, SSI is sensitive to the effects of that agent. Here, we showed that SSI scores respond to slight, as well as large, changes in MPB-induced mortality levels. For example, the change in SSI from 2000 (SSI = 249.6; Supplementary Table 2) to 2001 (SSI = 247.8; Supplementary Table 2) corresponded to a 0.1% increase in mortality for all lodgepole pine trees (0.2% for large trees) during this period. Further, BMA can describe the nature of detected structural unsustainability. For example, we observed the percentage of diameter classes exhibiting deficient (lower than baseline) mortality to decline with SSI from 2000 to 2005. However, the rise in SSI in 2006 was not associated with a sudden increase of diameter classes with deficient mortality but instead with the occurrence of excessive (higher than baseline) mortality in half of all diameter classes.

Third, given prior knowledge of disturbance characteristics, we could predict changes to forest structural sustainability in response to that disturbance. Here we showed SSI changed little from 2000 to 2001 before steadily declining from 2001 to 2005, after which period it increased in 2005–2006. This pattern is expected given MPB-lodgepole pine ecology: beetle outbreaks cause near exponential increases in cumulative and annual host mortality before the latter declines from a lack of living, MPB-susceptible trees (Raffa et al., 2008; Safranyik and Carroll, 2006). This mortality decline corresponds to a heavily impacted structure, which reflects the SSI increase in 2006.

Fourth, SSI can indicate impending changes to current forest conditions. Mountain pine beetle is a natural regulator of lodgepole pine forest conditions as their outbreaks develop in and

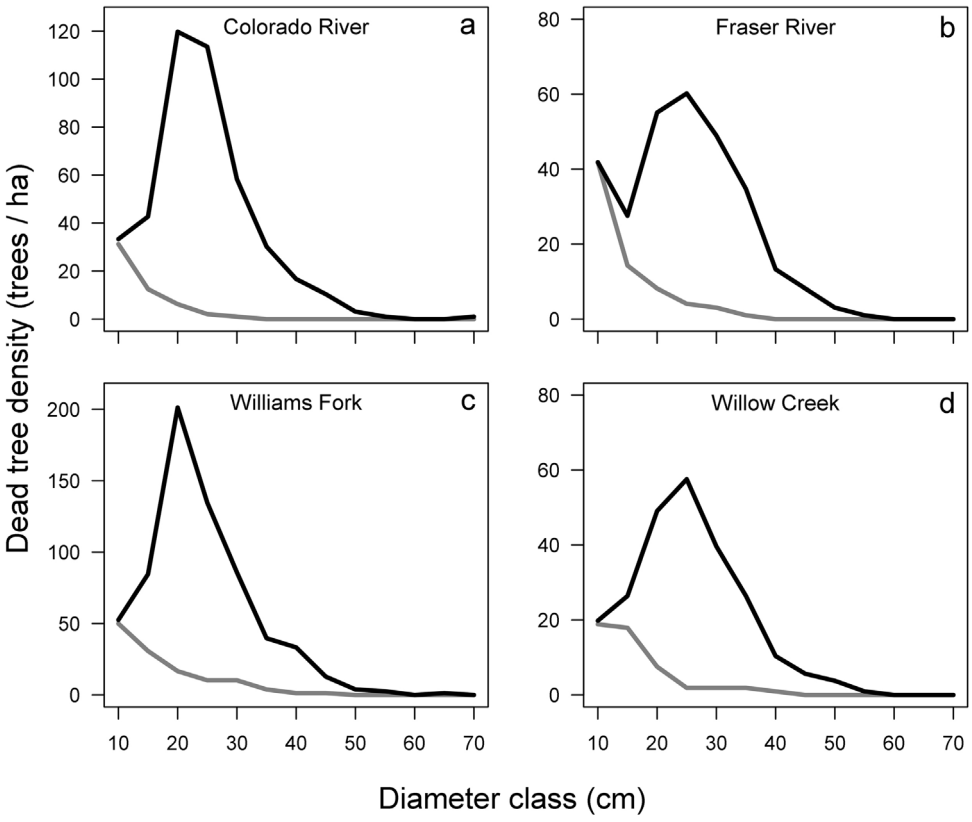

Fig. 5. Diameter distributions of mountain pine beetle (*Dendroctonus ponderosae*)-killed lodgepole pine (*Pinus contorta*) density (trees/ha) in the Colorado River ((a) combined Headwaters Colorado River and Little Muddy Creek-Colorado River watersheds), Fraser River (b), Williams Fork (c), and Willow Creek (d) watersheds of eastern Grand County, Colorado in 2000 (grey lines) and 2006 (black lines).

effectively thin over-crowded forests (Amman, 1977). Widespread outbreak-associated mortality acts as a stand replacing disturbance that changes the even-aged structure of lodgepole pine populations to uneven-aged stands not necessarily dominated by lodgepole pine by triggering post-disturbance seedling development and growth of advanced regeneration of both lodgepole pine and shade-tolerant species (Astrup et al., 2008; Axelson et al., 2009; Collins et al., 2011; Kayes and Tinker, 2012; Nigh et al., 2008; Vyse et al., 2009). Given this ecology, the SSI scores indicating structural unsustainability at landscape- and watershed-scales in 2000 suggested lodgepole pine was over-crowded and thus poised for a stand-replacing disturbance, such as MPB.

Lastly, SSI could similarly predict changes in forests avoidable by management. Mountain pine beetle outbreaks can leave forests prone to increased water runoff due to reduced forest interception and transpiration (Potts, 1984; Uunila et al., 2006), as well as the potential for increased wildfire intensity (Jenkins et al., 2014, 2012; Klutsch et al., 2011; Page and Jenkins, 2007). Given a previously determined threshold, programs could monitor SSI to predict when or where these cascading effects are likely to occur. Appropriate management strategies (Fettig et al., 2014) could be implemented prior to exceeding this threshold to circumvent the problem.

Many management priorities and triage decisions are, at landscape-scales, based on the amount of affected forest, or, at smaller scales, the density of killed trees as well as mortality levels (Fierke et al., 2011). This information is often provided by aerial surveys and annual risk assessments calculated from remeasurement data collected in permanent sampling plots (Potter and Conkling, 2014). Here, we showed that SSI reflects the MPB-induced mortality levels observed for each watershed in 2006, and therefore could aid forest managers and conservation planners in making triage decisions. In absence of municipal factors weighting management prioritization, SSI could aid managers in justifying resource allocation toward one impacted forest over another. Conversely, given municipal factors, SSI could be used alongside established tools and protocols to further support management decisions. The SSI (and BMA) encompasses both the degree to which a site is experiencing overcrowding and disturbance-associated mortality without the need for geographically appropriate stocking guides or non-disturbed mortality levels. When integrated into monitoring programs, such as those using remeasurement data, SSI could further enrich information-based management prioritization by allowing managers to compare and quantify the relative impact of a given disturbance among sites over time without the need for a common reference against which to evaluate differences.

While here we evaluated the utility of SSI for monitoring and triage of a single-species-dominated landscape comprised of even-aged-structured forests of various ages, our findings extend to landscapes more heterogeneous in species composition and/or structure. Indeed, BMA was originally designed to assess the structural sustainability of all species combined or individually in a northern hardwood (*Acer-Fagus-Betula*) landscape comprised of mixed-species, uneven-aged forests (Manion and Griffin 2001). For such types of landscapes, BMA and SSI using combined-species data can provide an aggregate picture of overall structural sustainability (Manion and Griffin, 2001). However, if this indicates unsustainability, SSI could be separately quantified for each component species in order to identify which is driving the overall unsustainability (Cale et al., 2014; Manion and Griffin, 2001).

In conclusion, SSI and BMA are valuable tools to forest monitoring and triage efforts. Here, we show that structural sustainability meets the criteria for effective indicators of ecosystem change used in monitoring programs while also providing critical quantitative data upon which to base forest triage decisions. In systems where

forest mortality can be confidently attributed to a particular disturbance agent (either abiotic or biotic), SSI could provide an estimate of the balance between mortality and growth/survival prior to this disturbance, as we showed for MPB-impacted lodgepole pine. Using this to compare pre-disturbance structural conditions among landscapes or watersheds could help elucidate potential pre-disposing factors to severe disturbance events. Following the definition of forest health proposed by Teale and Castello (2011), the lodgepole pine landscape investigated here would be considered healthy despite temporal and spatial patterns of structural unsustainability from MPB activity because the beetle is a natural regulator of lodgepole pine populations. As indicated by others (Cale et al., 2014; Teale and Castello, 2011), SSI and BMA could also allow monitoring programs to detect the occurrence of novel tree-killing disturbances through their impact on forest structure. Because it is based on a conditionally-calibrated reference level (i.e., baseline mortality), SSI seems ideally suited to monitoring future forest change scenarios as climate change undermines the continued utility of historically-defined healthy reference conditions. Further, SSI could serve as an important tool in developing monitoring and triage systems tasked with conserving forest communities or tree species threatened by climate change and/or other disturbances, thereby addressing the need for new techniques with which to manage forests under novel climate and growing conditions (Sturrock et al., 2011).

Acknowledgments

This work was partially supported by Natural Sciences and Engineering Research Council of Canada (Discovery grant to NE) and the Izaak Walton Killam Memorial Scholarship (to JGK). We thank Cortney D'Angelo as well as two anonymous reviewers for their comments on the manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2016.06.020.

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