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Quantifying density-independent mortality of temperate tree species

H.E. Lintz[a,*], A.N. Gray[b], A. Yost[c], R. Sniezko[d], C. Woodall[e], M. Reilly[f], K. Hutten[g], M. Elliott[h]

[a] Oregon Climate Change Research Institute, College of Earth, Ocean, and Atmospheric Science, Oregon State University, Corvallis, OR 97330, United States
[b] USDA Forest Service, PNW Research Station, Corvallis, OR, United States
[c] Oregon Department of Forestry, Salem, OR, United States
[d] USDA Forest Service, Dorena Genetic Resource Center, Cottage Grove, OR, United States
[e] USDA Forest Service, Northern Research Station, St. Paul, MN, United States
[f] Department of Forest, Ecosystems, and Society, Oregon State University, Corvallis, OR, United States
[g] Department of Forest Ecology, University of Washington, Seattle, WA, United States
[h] Puyallup Research and Extension Center, Washington State University, Puyallup, WA, United States

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ABSTRACT

Forest resilience to climate change is a topic of national concern as our standing assets and future forests are important to our livelihood. Many tree species are predicted to decline or disappear while others may be able to adapt or migrate. Efforts to quantify and disseminate the current condition of forests are urgently needed to guide management and policy. Here, we develop a new indicator to summarize raw density-independent mortality of forested stands by species from the last decade of the 20th century to the first decade of the 21st century using forest inventory data. We define density-independent mortality to be stand mortality by species due to processes unrelated to natural mortality from succession or stand maturation, which is marked by overall increase in tree girth at the expense of density of individuals. We assess trends for 22 species on national forests in two U.S. states, Washington and Oregon. Populations of some species including timber species have no or low overall levels of density-independent mortality (*Juniperus occidentalis*, *Abies procera*, *Thuja plicata*, *Tsuga heterophylla*, *Pinus ponderosa*, and *Pseudotsuga menziesii*). In contrast, other species demonstrate unsustainable levels of density-independent mortality (*Pinus monticola*, *Arbutus menziesii*, *Pinus albicaulis*, *Abies lasiocarpa*, *Taxus brevifolia*, *Pinus contorta*, *Abies grandis*, *Picea englemanii*, and *Larix occidentalis*). Additionally, the net potential for unsustainable levels of density-independent mortality in standing populations does not necessarily warrant concern when examined across species for our study area and time period; however, when examined by species, the number of species in decline exceeds the number of species where mortality can be generally attributed to endogenous self-thinning. We argue that this work can aid management and policy decisions and our understanding of complex vegetation dynamics in a changing climate. Application of the indicator at larger spatial scales and in conjunction with data on migration and establishment may be used to address questions such as, how can we make cost-effective management decisions to ensure long-term sustainability of tree species and forests? Tree species distributions across the landscape are complex systems, and raw characterization of current trends occurring in forest inventories is important especially given the uncertainty associated with the modeling and prediction of complex systems such as tree species.

1. Introduction

The effect of global climate change on Earth will depend to a great extent on the response of trees and forests (Ozanne et al., 2003; Purves and Pacala, 2008). However, forest dynamics are the result of complex interactions and are difficult to understand, model, and predict (Pautasso et al., 2010; Sexton et al., 2009; Purves and Pacala, 2008). Forests are responding to unprecedented climate change and other drivers (Breshears et al., 2005; Beckage et al., 2008; USCCRP, 2009; Woodall et al., 2009; Hatfield et al., 2008; Williams et al., 2010), and shifts in forest location and composition will likely increase (IPCC, 2007). The uncertainty associated

* Corresponding author. Tel.: +1 541 829 3507.
E-mail address: hlintz@coas.oregonstate.edu (H.E. Lintz).

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with prediction of forest trajectories warrants better understanding of community dynamics and better integration of forest inventory data (Purves and Pacala, 2008). Guiding our forest resources toward a sustainable future is perhaps one of the most significant challenges facing natural resource managers, policy makers, and scientists. State governments and natural resource management agencies need metrics for tracking the effects of climate change on the status and trends of physical and biological systems.

Paleo-ecological evidence reveals that species respond to climate change through unique, species-specific migration paths (Prentice, 1986; Davis and Shaw, 2001; Thomas et al., 2004; Parmesan, 2006); for this reason, climate change can lead to non-analog assemblages, and our understanding of the effects of climate change on forests requires species as the currency of investigation. However, efforts to detect, understand, and report actual changes in the distribution and composition of forest species are not well studied or adopted as integral to national reporting on forest resources. For example, large-scale monitoring efforts from remote sensing provide early warning for forest threats in the U.S. but they do not warn specifically for changes in species distributions (e.g. Hargrove et al., 2009). Frameworks for assessing the threats and benefits of climate change for species distributions have been proposed using paleoecological data, experiments, direct observations on species decline from repeated measurements, and projections from computer models (Williams et al., 2008; Dawson et al., 2011; Thomas et al., 2011). However, such frameworks have yet to be widely implemented. As part of these frameworks, direct observations are considered applicable in the assessment of all aspects of species vulnerability (Dawson et al., 2011).

Changes in the geographical distribution of forest species from future changes in climate have been predicted at large geographic scales using computer models (e.g. Iverson and Prasad, 2002; Rehfeldt et al., 2006; Coops and Waring, 2011). However, works on temperate tree species that examine empirical trends are few, generally smaller scale, and often focus on shifts in geographic footprints rather than population biology (e.g. Crimmins et al., 2011; Zhu et al., 2012). Species assessments also exist to prioritize species for conservation efforts, and these identify vulnerable, endangered, and critically endangered species based on criteria that rely largely on principles from population biology (e.g. Mace and Lande, 1991; IUCN, 2012). While direct observations are valued, such conservation assessments may not be always based on direct observations. Further, the generality of criteria developed for species vulnerability assessment and conservation overlooks the unique population biology of tree species in forests.

Tree mortality is often considered a key indicator of forest change (e.g., Van Mantgem et al., 2009), but the balance of mortality with recruitment and growth will determine whether a species declines over time or not. Mortality must be considered in the context of stand development (Luo and Chen, 2013). Trees undergo mortality that can exceed population growth at a stand level because self-thinning is linked to stand aging in early- and mid-successional stages (Oliver and Larson, 1990; Franklin et al., 2002). This type of mortality is density-dependent and sustainable because a decrease in density is offset by a stable or increasing basal area for remaining individuals. However, if basal area decline coincides with mortality that exceeds population growth, the most likely reason is unrelated to stand self-thinning and represents stand dieback or senescence of early-successional species in late-successional stands (Breshears et al., 2005). Possible reasons include but are not limited to density-independent factors associated at least in part with environmental variance such as climate change, pests and pathogens, tree harvest, and fire.

Efforts to quantify density-independent mortality to inform forest management given climate change face a formidable challenge of accuracy. The use of static functions and their parameters to model and estimate density-independent mortality of co-occurring tree species is problematic. Many tree species differ markedly in their tendency toward stand dominance. Birth and death rates vary both within a population according to age, size, and genotype, and among populations depending on growing conditions (Lande et al., 2003). Tree species have unique functional and successional roles in the landscape that vary with shade tolerance. Additionally, density-dependent mortality can compensate for density-independent mortality in complicated ways for self-thinning plant populations depending on spatial context and other factors (as both processes can operate at once) (Clark, 1992). Owing to these hurdles, we aim to develop an empirical metric of density-independent mortality that is stand-specific and does not rely on parametric assumptions.

While some works have studied the average of mortality and recruitment, or turnover (Phillips and Gentry, 1994; Lewis et al., 2004; Stephenson and van Mantgem, 2005), we develop a metric that juxtaposes and harmonizes two processes key to forest health regardless of species, stand age, or ecological context. One is the directional change in stem density per unit area or the balance of population death and ingrowth. The other is directional change in basal area irrespective of density. Synchrony of these processes within a single indicator can account for the unique population biology of tree species to estimate the ability for existing populations to persist in a location. The summary of the stand-level indicator across a region can help discern whether declines in population numbers are due to density-dependent or density-independent causes. Specifically, the method supports the following premise: at a meta-population level, if basal area is in decline and mortality exceeds population growth for stands where they exist on the landscape, then the ability for species in the existing stands to persist is likely compromised and might need further examination to identify stressors.

2. Methods

Continuous Vegetation Survey (CVS) data collected by the U.S. Forest Service's Pacific Northwest Region (Max et al., 1996) were used. CVS data provided a strategic inventory of vegetation conditions on all National Forest Service lands in the Pacific Northwest Region using a probability-based sample design (Olsen et al., 1999). The sample consisted of a systematic square grid at a 5.47 km spacing across all lands providing a sample density of one plot per 3000 ha. Plots were installed using the CVS design between 1993 and 1997 and then remeasured between 1997 and 2007 in spatially and temporally-balanced panels (Fig. 1). The CVS plot remeasurement period ranged from 1 to 14 years with a mean of 7.1 years.

The CVS plot design consisted of a cluster of five points within a 1 ha circle, with four points spaced 40.8 m in cardinal directions from the central point. At each point, crews measured live and standing dead trees of different sizes (2.5–7.6, 12.7–33.0, and >33 cm diameter at breast height (DBH, 1.37 m from the ground)) in nested plots of 0.004, 0.020, and 0.076 ha, respectively. Seedlings greater than 15 cm tall and less than 2.5 cm DBH were counted by species on the smallest plot size. In addition, trees greater than 76 cm DBH east of the Cascades or greater than 122 cm DBH west of the Cascades were measured on the full 1 ha circle.

This difference in DBH accounts for differences in productivity to ensure a sufficient sample of trees to estimate change well at the plot scale. All trees in the sample across the Cascades were treated the same in our statistical evaluation.

CVS plot locations were incorporated into the Forest Inventory and Analysis Program (FIA, Bechtold and Patterson, 2005) base grid. The FIA base grid is now part of a nationally standardized

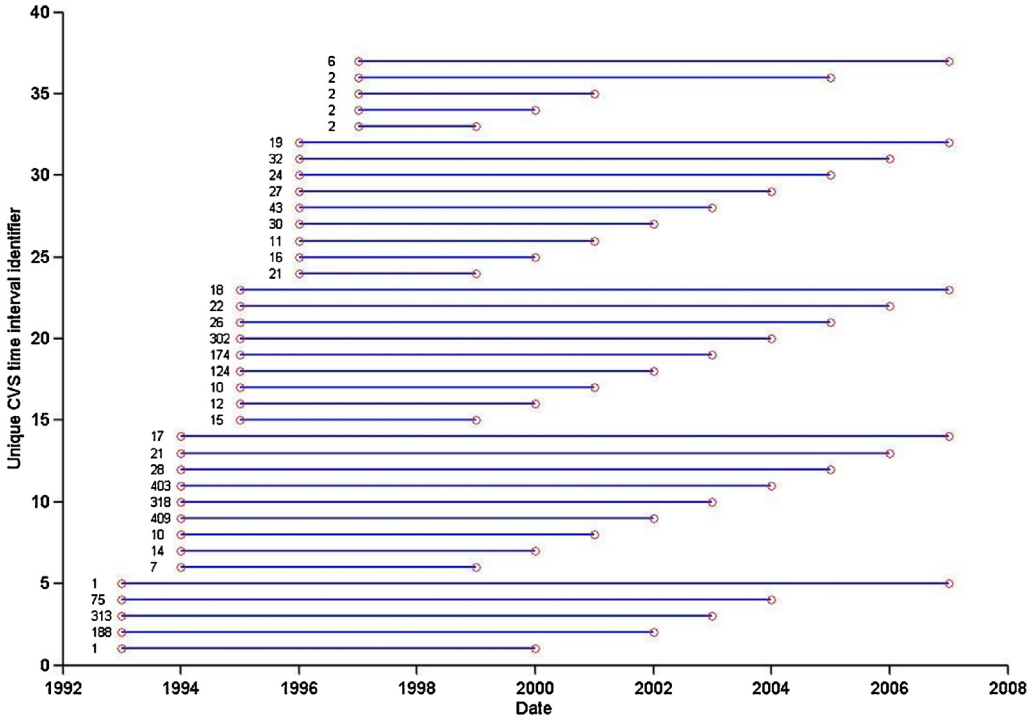

Fig. 1. Unique time intervals of tree re-measurement for CVS plots. Red circles indicate the endpoints of the intervals. Numbers shown beside intervals indicate number of plots that correspond to a remeasurement interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

inventory. We analyzed the intersection of CVS plots that were also measured using FIA protocols to couple re-measurement of trees with records of disturbance coded in the FIA measurement. The intersection represented a total of 2745 plots across Oregon and Washington (Fig. 2). Crews estimated disturbance types and dates that preceded the date of measurement for each plot included. Specifically, we used the disturbance data to identify plots where a fire or some type of cutting affected survival and density within the CVS re-measurement interval.

We determined that fire had not occurred in the re-measurement intervals of 2667 plots (Fig. 2). Mortality rates and population growth rates were calculated by plot and species for all trees greater than 2.54 cm DBH occurring within the CVS plot. First, the proportion of mortality was derived as the ratio of the number of trees that died between time 1 and 2 to the number of live trees at time 1. Only plots with more than 3 live trees of a species were included to reduce the number of extreme values that would skew the mean among plots. Each tree was assigned a weight to reflect differently sample areas on which different size classes of trees were measured. These "tree per hectare" values were then used for the calculation of mortality, ingrowth, and basal area change rates instead of individual tree counts. Since the time intervals for the tree re-measurement varied for the CVS plots, mortality rates were standardized using a negative compound interest formula to a 1-year basis (Lorimer, 1981; Sheil et al., 1995):

$$Q_1 = 1 - (1 - Q_n)^{1/n} \quad (1)$$

where Q_1 is the annual mortality rate, n is the interval of time or the number of years for which the mortality rate is measured, and Q_n is the mortality rate or proportion mortality for period n.

Population growth rate or plot ingrowth was similarly standardized to a 1-year basis using a compound interest formula (McCune and Cottam, 1985):

$$P_1 = (1 + P_n)^{1/n} - 1 \quad (2)$$

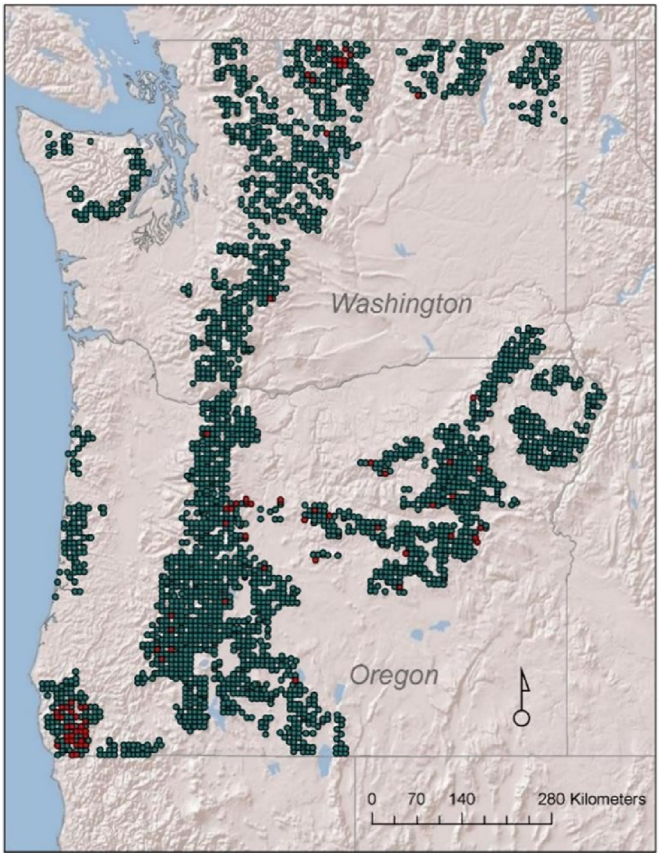

Fig. 2. All CVS plot locations that intersect with FIA mortality by species and per plot was plot locations in Oregon and Washington. The intersection represents the study sample. Red circles indicate plots where fire occurred during the re-measurement interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

where P_1 is the annual population growth rate, n is the interval of time for which the population growth rate is known, and P_n is the population growth rate or proportion growth for period n. Proportion growth was calculated as the ratio of the number of trees that grew into the 2.54 cm DBH size class on the plot by time 2 over the number of live trees at time 1.

The balance between mortality and population growth rates at the plot level for a species, S_1, was the difference between the standardized annual mortality rate and the standardized population growth rate for the plot and species:

$$S_1 = P_1 - Q_1 \quad (3)$$

Positive values of S_1 mean that population growth exceeded mortality during the re-measurement interval, while negative values of S_1 means mortality rates exceeded population growth rates. A value of zero indicates an exact balance between mortality and population growth rates. This analysis excludes situations where individuals are new to a plot or only detected during the second plot visit.

In addition to calculating a tree density-based indicator representing the balance between mortality and population growth rates, S_1, we also derived the proportional change in basal area per species and per plot. We took the difference in live tree basal area per acre per species between time 2 and time 1, and divided the difference by the basal area at time 1. We called this proportional change BA_n. We standardized BA_n for each plot and each re-measurement period to a 1-year basis (or BA_1), by using the compound interest formula.

$$BA_1 = (1 + BA_n)^{1/n} - 1 \quad (4)$$

BA_n is unique from P_n or Q_n as it can be either positive or negative allowing the use of one formula.

We derived confidence intervals for species-level means of S_1 and BA_1 using the bootstrap percentile method. We used this method to accommodate the skewed distributions exhibited by different species. Inference from each confidence interval does not include plots where a species doesn't occur at the initial measurement. Data for each species were sampled with replacement, and this process was repeated 200 times to generate a frequency distribution from which the 95th percentile confidence intervals were derived. We restricted our study to species with a minimum of 50 occurrences; 19 conifer species and 3 hardwood species were included for study (Table 1). Confidence intervals were computed for species listed in Table 1. We also lumped two species, *Abies grandis* and *Abies concolor*, because CVS crews arbitrarily identified these species based on geography rather than taxonomy. Additionally, the two species hybridize in nature and can be difficult to discern taxonomically.

We reduced both dimensions, S_1 and BA_1, to a single dimension for geographic analysis by projecting each point in S_1 and BA_1 space perpendicularly to the 1:1 line (see Fig. 3). This facilitated a summary in both S_1 and BA_1 at the same time through geographic space. The projected distances for each species and population along the 1:1 line were averaged by Omernik's Level 3 Ecoregion (Omernik, 1995). The average values of density-independent mortality were mapped by Level 3 Ecoregion for each species. The standard deviation for each mean was mapped using a circle symbol within each respective ecoregion (Appendix A). The circle diameter represented the standard deviation of the estimate for an Ecoregion (Appendix A).

3. Results

Population measurements made individually for each plot location and each species display a diagonal hourglass pattern for the scatterplot of BA_1 versus S_1. The top right quadrant and the lower left quadrant show greater scatter compared to top left and lower right quadrants (Fig. 3). Thirty-four percent of the points falling fully within quadrants populate the top right quadrant. This is the region where the proportional change in basal area is positive and population growth exceeds mortality. The top left quadrant contains 23% of the points falling fully within the quadrants. This region of the graph shows an increase in basal area along with mortality that exceeds population growth. Thirty-seven percent of points falling fully within the quadrants reside in the lower left region denoting negative population growth and negative basal area change ($-BA_1$ and $-S_1$).

Most plots where fire occurred during the re-measurement interval occupy the lower left quadrant (Fig. 4A). Conversely, population measurements for plots where some form of cutting occurred during the re-measurement interval are more centralized in the

Table 1
Scientific names corresponding to species codes.

CODE	Common name	Scientific name
ABAM	Pacific silver fir	*Abies amabilis*
ABGR	grand fir	*Abies grandis*
ABLA	subalpine fir	*Abies lasiocarpa*
ABPR	noble fir	*Abies procera*
ABSH	Shasta red fir	*Abies x shastensis*
ACMA3	big leaf maple	*Acer macrophyllum*
ALRU2	red alder	*Alnus rubra*
ARME	madrone	*Arbutus menziesii*
CADE27	incense cedar	*Calocedrus decurrens*
CUNO	Alaska yellow cedar	*Cupressus nootkatensis*
JUOC	Western juniper	*Juniperus occidentalis*
LAOC	larch	*Larix occidentalis*
PIAL	whitebark pine	*Pinus albicaulis*
PICO	lodgepole pine	*Pinus contorta*
PIEN	Englemann spruce	*Picea engelmannii*
PIMO3	Western white pine	*Pinus monticola*
PIPO	ponderosa pine	*Pinus ponderosa*
PSME	Douglas fir	*Pseudotsuga menziesii*
TABR2	Pacific yew	*Taxus brevifolia*
THPL	Western red cedar	*Thuja plicata*
TSHE	Western hemlock	*Tsuga heterophylla*
TSME	mountain hemlock	*Tsuga mertensiana*

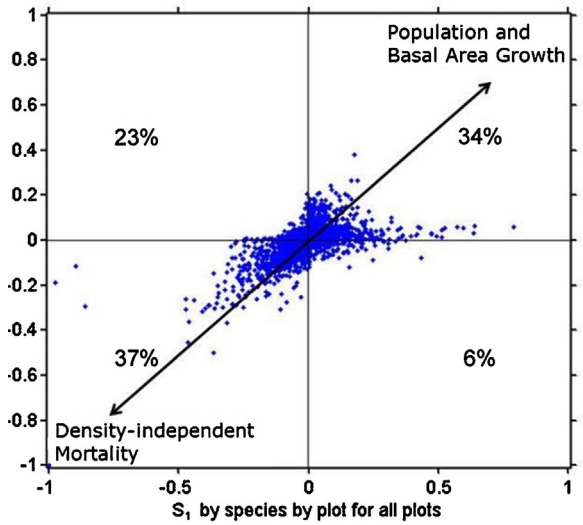

Fig. 3. Points represent plot-level measurements of BA_1 or directional change in basal area versus. S_1 or directional change in density per unit area for a species. The diagonal line represents a conceptual gradient of density-independent mortality. Percentages of points corresponding to points falling within each specific quadrant are shown. (Points falling directly on axes are excluded as they cannot be pinned to a specific quadrant.)

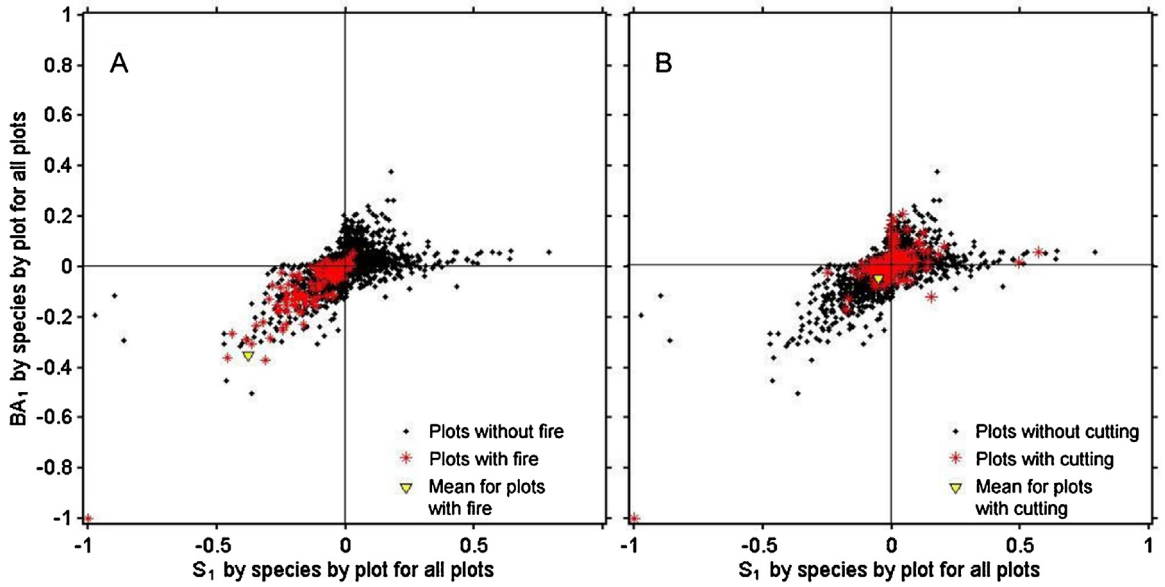

Fig. 4. Population measurements of BA_1 versus S_1 across plots and species for all plots. (A) Populations measured where fire occurred during the re-measurement interval are red. The mean for these populations is indicated with a yellow inverted triangle. (B) Populations measured where some type of cutting occurred during the re-measurement interval are red. The mean for these populations is indicated with a yellow inverted triangle. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

scatterplot but with proportionally more falling in the lower left quadrant (see mean, Fig. 4B). The dominant type of cutting that occurred was thinning across the re-measurement intervals, and thinning affected mainly the commercial tree species, *Pseudotsuga menziesii* and *Pinus ponderosa*.

Several species that are already known to be the most threatened regionally, *Arbutus menziesii*, *Pinus monticola*, and *Pinus albicaulis*, fell within the lower left-most position relative to other species examined for plots with or without fire (Fig. 5). The number of species in the lower left quadrant (indicating an unsustainable trajectory) with confidence intervals not overlapping zero for both BA_1 and S_1 is 9 or 41% of the species examined for locations where fire did not occur. The number of species in the lower left quadrant increases to 11 (or 50% of the species examined) when locations where fire occurred are included in the analysis (Fig. 5).

For locations that have not experienced a fire during the re-measurement interval, *Juniperus occidentalis* is the only species that clearly shows basal area increasing along with population size at a meta-population level across the study region (Fig. 5A). *Tsuga heterophylla* and *Abies x shastensis* show sustainable basal area increase with little or no net change to population size at the meta-population level for stands as they existed at first measurement (Fig. 5A). *Abies amabilis* and *Alnus rubra* show overall population decline and little or no net change in basal area. *Abies procera*, *Thuja plicata*, *Pinus ponderosa*, *Pseudotsuga meziesii*, *Tsuga mertensiana*, *Cupressus nootkatensis*, and *Calocedrus decurrens* do not exhibit notable change in basal area or population size over the study region and re-measurement period. The following species have potentially unsustainable levels of density-independent mortality where populations and basal area are in decline region-wide for existing stands: *Abies grandis*, *Larix occidentalis*, *Pinus contorta*, *Picea englemanii*, *Abies lasiocarpa*, *Taxus brevifolia*, *Pinus albicaulis*, *Pinus monticola*, and *Arbutus menziesii*. Every species showed variation in mean density-independent mortality across Ecoregions ranging from −1 to 0.15 (Fig. 6, Appendix A). The extremes of the means by species and region (−1, 0.15) were associated with regions that had either one or few occurrences (Appendix A).

4. Discussion

The net potential for unsustainable levels of density-independent mortality in standing populations does not necessarily warrant concern when examined across species for our study area and time period (e.g. Fig. 3). However, when examined by species, the number of species in decline exceeds the number of species where mortality can be clearly attributed to endogenous self-thinning or is generally low (Fig. 4). We independently and quantitatively confirm that forests in the western U.S. are undergoing density-independent mortality (for example, in the context of results presented by Van Mantgem et al., 2009). However, further investigations of species-specific mortality and new establishment across all forested ownerships in the region are warranted to elucidate cause. Additionally, more comprehensive efforts of seed collection and conservation of species in decline would help maintain genetic diversity and genotypes adapted to a range of environments. This capital could facilitate assisted mitigation of important timber as well as non-commercial species.

Metrics that can derive meaningful information on processes that contribute to forest and species sustainability from re-measurement data represent a valuable investment. Here, we argue that examining tree populations with respect to two metrics, directional change in basal area, BA_1, and directional change in density S_1, can reliably quantify the raw status of density-independent mortality. Specifically, the indicator we present gauges the effect of density-independent processes on meta-populations of tree species within a region, and it can complement other forms of species modeling and studies of causation and species sustainability. The indicator can help discern the relative effects of different types of disturbances on density-independent mortality including pests, pathogens, fire, and climate change.

While the measurement of each study species can change when plot locations with fire occurring are included in the analysis (Fig. 5B), fire is a natural part of forest succession that disturbs populations and often reduces basal area. Our results indicate that fire was a significant agent of change for several species during the re-measurement interval, but fire did not seem to substantially

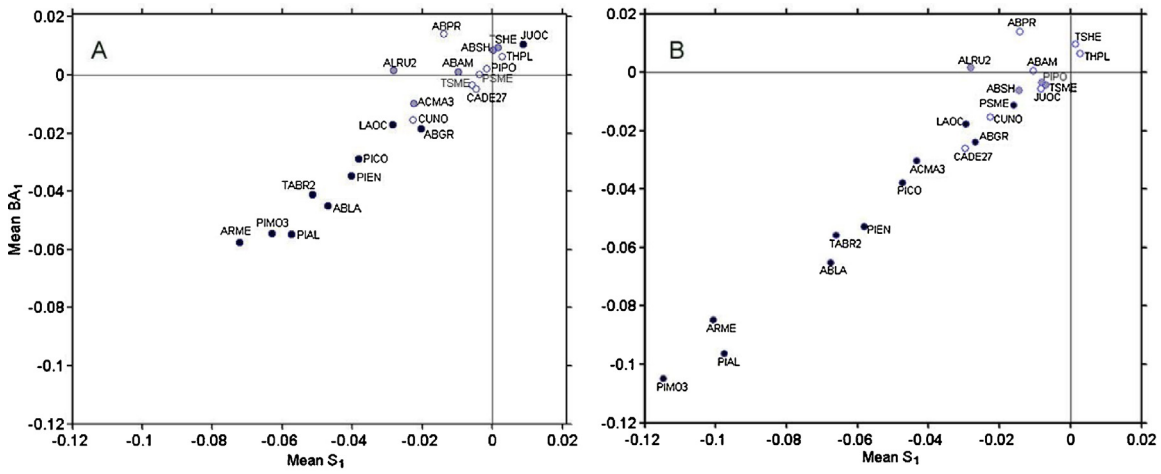

Fig. 5. Mean S_1 and BA_1 by species derived from fire-free plots (A) and all plots (B). Black circle indicates that the 95% confidence intervals for both metrics, S_1 and BA_1, do not contain zero. Grey circle indicates that the 95% confidence interval for one metric, S_1 or BA_1, does not contain zero. White circle indicates that the 95% confidence interval contains zero for both metrics.

change an outcome regionally for a species (i.e., from positive or neutral to negative). When coupled with disturbance data such as fire occurrence, the indicator we derive can start to distinguish some of the major causal drivers of change and their effects on species trajectories. Given decades of fire suppression in dry forests in the region (Hessburg and Agee, 2003; Stephens et al., 2013), the recent effects of fire on species and forest structure may not be undesirable or unsustainable particularly if stands are moving back to a pre-suppression structure through which future fires will move with less severity. In contrast to fire occurrence, tree harvest did not have a substantial effect on any species' trajectories during the study period. Tree cutting has been minimal on USDA Forest Service lands during this period, primarily consisting of thinning dense young stands (Campbell et al., 2010).

Juniperus occidentalis fell within the upper right quadrant of the S_1–BA_1 space created with the fire-free plots (Fig. 5A), indicating low levels of density-independent mortality.

Indeed, the area of land classed as juniper forest has increased over the last 60 years from 420,000 acres in 1936 (Cowlin et al., 1942) to 3.3 million acres in 1999 (Azuma et al., 2005). This increase is enormous and can have a profound effect on the landscape, lowering grazing carrying capacities, intercepting precipitation, and changing the quality and availability of wildlife habitat. As forest canopy cover becomes increasingly dense, the carrying capacity, resilience, and sustainability of sagebrush desert biomes will continue to decrease because of the significant competition from *Juniperus occidentalis* for moisture and nutrients. All indications are that the area of juniper forest will continue to increase (Azuma et al., 2005). If only half of the savanna lands continue to increase there might be as much as 5 million acres of juniper forest in the future, making juniper the forest type with the greatest area in eastern Oregon (Gedney et al., 1999). Fire reduced the positive trend for *Juniperus occidentalis* when fire-affected plots were included in the S_1–BA_1 space (Fig. 5B).

The two most important commercial species, *Pseudotsuga menziesii* and *Pinus ponderosa*, are at minimum on stable trajectories where populations currently exist in the study region. *Pseudotsuga menziesii* contributes the highest volume of softwood timber nationally and the highest carbon density of any terrestrial system (Smithwick et al., 2002; Smith et al., 2009).

Both conifer species are dominant, widespread, and keystone in forests of the Pacific Northwest. The Klamath Mountain Ecoregion and the North Cascades Ecoregion have lower mean density-independent mortality compared to other Ecoregions for both *Pseudotsuga menziesii* and *Pinus ponderosa* (Appendix A). The Blue Mountain Ecoregion also shows lower mean density independent mortality per population for *Psuedotsuga menziesii* compared to other Ecoregions (Appendix A).

Four species already recognized to be in substantial decline fell within the farthest corner of the lower left quadrant in Fig. 5, consistent with expectations, and demonstrating proof of concept for this method. *Pinus monticola* and *Pinus albicaulis* have been identified to be in decline due to a non-native fungal pathogen, *Cronartium ribicola*, and other causes such as change in climate (Neuenschwander et al., 1999; Tomback and Achuff, 2010; Bechtold et al., 2012; IUCN, 2013). In particular, *Pinus albicaulis* has been proposed for listing under the Endangered Species Act in the United States; Canada's Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has listed *Pinus albicaulis* as endangered. Also, *Pinus albicaulis* has been designated endangered globally by the IUCN (IUCN, 2013). Breeding programs for pathogen resistance and gene conservation and restoration have been established for five-needle pines including *Pinus albicaulis* (Mahalovich and Dickerson, 2004; Sniezko et al., 2007; Aubry et al., 2008; King et al., 2010).

Abies lasiocarpa and *Arbutus menziesii* also show high levels of density-independent mortality and fall in the lower left quadrant of Fig. 5 consistent with what has been independently recognized in the field and from aerial surveys. Regionally, *Abies lasiocarpa* has been experiencing mortality from the balsam wooly adelgid (*Adelges piceae*) for decades (Overhulser et al., 2004; Bechtold et al., 2012; Mitchell and Buffam, 2001), but relatively little work is devoted to managing or breeding the species for conservation. At a global level, the IUCN recognizes *Abies lasiocarpa* in the category of Least Concern because of the large extent of occurrence and large population size. However, our work supports that *Abies lasiocarpa* in the Pacific Northwest warrants more attention regionally. Additionally, *Abies lasiocarpa* is one of few tree species in the Pacific Coastal United States showing no sign of migration (Monleon and Lintz, 2015). Current populations are in greatest decline in the Blue Mountain Ecoregion (Appendix A).

Arbutus menziesii is a hardwood species endemic to the west coast of North America. It has been in decline for several decades mainly due to climate change, fungal pathogens, and management activities (Elliott et al., 2012a). Our work corroborates the status

of *Arbutus menziesii* throughout our study locations in the Pacific Northwest. Like *Abies lasiocarpa*, *Arbutus menziesii* also shows no evidence of migration or establishment in new locations where it previously did not exist (Monleon and Lintz, 2015). *Arbutus menziesii* is a species that clearly warrants conservation concern for three reasons: population decline where it currently exists, a relatively small range size, and lack of evidence for migration. Populations found in the Klamath Mountain Ecoregion show the least sustainable trajectories for our study region (Appendix A). Common garden field trials have been recently established for *Arbutus menziesii* to provide the first look at adaptive genetic variation and to examine the potential for pathogen resistance and adaptation to climate change (Elliott et al., 2012a).

Abies grandis, *Larix occidentalis*, *Pinus contorta, Picea englemananii*, and *Taxus brevifolia* are five more species that also fall in the lower left quadrant of Fig. 5A and show evidence for density-independent decline across Ecoregions. *Pinus contorta* is known to be susceptible to bark beetle infestation, and recent range-wide outbreaks have been severe (e.g. Johnson et al., 2014; Pfeifer et al., 2011). A full accounting for the decline of *Taxus brevifolia* is more challenging. Busing and Spies (1995) reported that natural populations of *Taxus brevifolia* had been harvested over large areas of the Pacific Northwest during clear-cut logging operations in the 1970s and 1980s and for taxol production with no provision for regeneration or consideration of the effects on populations as a whole. Fire is a factor limiting *Taxus* distribution (McCune and Allen, 1985); while scattered individuals may survive and resprout in unburned microsites, recolonization of burned sites depends on regeneration by seed (Busing and Spies, 1995). Clear-cut harvest without burning results in loss and slow recovery of *Taxus brevifolia*. Population growth rates of *Taxus brevifolia* are relatively slow; undisturbed populations show little change in size and structure over periods of several decades and disturbed populations require centuries to recover characteristics of old-forest stands (Franklin and DeBell, 1988; Halpern, 1989; Busing and Spies, 1995). *Taxus brevifolia* often occurs at low densities, and consequently, our minimum limit of three individuals in a plot for measurement likely underestimated the number of populations on the landscape. Accounting for the declining trend of *Abies grandis*, *Picea englemanii*, and *Larix occidentalis* will require further investigation.

While it may appear in Fig. 5 that BA_1 or basal area change can serve as a proxy for S_1 or density change at the population level, the spread of points at the plot level precludes this (where each point represents a single plot location and species) (Figs. 3, 4). The variation in these estimates across populations measured at the plot-level can yield important information depending on how the indicator is used or aggregated. Here we provide two levels of aggregation as an example, we examine BA_1 and S_1 at the species level across the study region (Fig. 5) and by Ecoregion where we retain information from both BA_1 and S_1 to create a single measure that can be easily mapped. The Ecoregion is one of many ways to classify a geographic area. One caveat of the approach is the possibility of incomplete overlap between a species range and the boundaries of an Ecoregion, which in some cases is misleading as far as inference in the maps provided. For example, in Ecoregions with few occurrences of a species, the reliability of the information for that region is compromised compared to other regions. However, we use Ecoregions here as a starting point to demonstrate that these metrics can apply to scales relevant to forest management. We also include measurements of sample size and variability by Ecoregion to communicate uncertainty.

The nature of this indicator makes it difficult to directly incorporate the process of recruitment of a species in a stand across the re-measurement interval in a manner that is comparable to density-independent mortality. More specifically, the event of zero individuals during the first plot visit followed by positive ingrowth upon the second visit poses an algorithmic challenge owing to the problem of having zero in the denominator of a proportion. Consequently, this indicator is intended for change detection specific to mortality processes rather than an indicator of meta-population sustainability where the net behavior of populations winking on and off across the landscape is estimated. Explorations of other indicators that estimate recruitment together with mortality to quantify sustainability are warranted. Notwithstanding, given that tree populations are long-lived and pre-existing forest stands can represent timber revenue on the order of tens of billions of dollars at state levels in the Pacific Northwest, this focus on mortality alone yields important conclusions. For example, our results could help timber owners assess whether it is prudent to harvest now or later.

Managing forests and forest species for sustainability requires working with naturally occurring processes to maximize their beneficial use and reduce undesirable losses (NRC, 2010). Movement toward sustainability requires knowledge of the current status and trajectory of tree species and populations. More specifically, our work can corroborate other research and inform tree planting decisions and when and where to thin stands to alleviate mortality risk and species population decline regionally. A forest manager can look at the overall density-independent mortality occurring for different species from the appended maps to inform new options for successive species in their region by considering species that have low density-independent mortality (or a neutral or high indicator score).

Further, a public land manager may take note of species with both high and low density-independent mortality in their region to determine the type and extent of thinning designed to alleviate drought stress, or if that is even necessary. The indicator can inform policy decisions that prescribe management actions or expenditures based on knowledge grounded in data, which can promote and ensure healthy forests nationally.

We aim to apply this and other indicators to the new re-measurement data from the Forest Inventory and Analysis (FIA) program, which, since 2001, offers a single standardized design nationally across all lands (not just the USDA Forest Service lands measured here). The FIA program started re-measurement of all these plots in 2011 where one-tenth of the plots across the inventory are re-measured annually in the western United States. The data used here have drawbacks that can be ameliorated by utilizing FIA data at a broader scale and across all lands to probabilistically represent all populations within a larger area (rather than just on Forest Service lands).

The dissemination of indicators like this one is perhaps the most important and challenging step toward innovative management of forest ecosystem resilience in changing climate (NRC, 2010). Resilience is the capacity of a system to absorb shocks and maintain function (Holling, 1973; Gunderson et al., 2009; NRC, 2010). Management for resilience recognizes that the future is unpredictable and requires an approach that connects knowledge, innovation, and social and institutional networks to facilitate learning (Folke, 2006; Walker and Salt, 2006; Gunderson et al., 2009; NRC, 2010). The ecological concepts of resilience and sustainability are mutually reinforcing. Indicators like ours can be used to help communicate observed changes to density-independent mortality, migration, recruitment, and fitness in our forests, all of which are central to our sustainability and livelihood. The type of information we distil can also allow for proactive measures to be taken at an early stage of decline of a species, which will provide more options for successful recovery of the species or ecosystems (Schoettle and Sniezko, 2007). Monitoring of species distributions from large-scale biological inventories can constrain modeled predictions and aid our understanding and modeling of complex natural phenomena in a rapidly changing climate (Stephenson and van Mantgem, 2005; Purves and Pacala, 2008; Thomas et al., 2011).

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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.2015.11.011.

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