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E-mail: christopher.w.woodall@usda.gov**Keywords:** downed dead wood, standing dead trees, forest biomass, carbon, US forestsSupplementary material for this article is available [online](#)**Abstract**

Due to global change, temperate forests are expected to face growing threats to forest health (e.g. insects/disease) and increasing probabilities of severe disturbances (e.g. wildfires), which may result in amplified tree mortality against a backdrop of a changing climate and associated ecosystem/atmospheric feedbacks (i.e. increased rates of dead wood decay/combustion). Despite these expectations, we lack a fundamental understanding of current forest biomass trends among live and dead components across large spatial and temporal domains. The goal of this study was to examine changes in forest biomass components (downed dead wood (DDW), standing dead trees (SDs), and live trees) across coterminous US forests using a nation-wide, multi-decade (~2006–2010 to ~2015–2019) repeated forest inventory at the scale of regional ecosystems. It was found that the total biomass stocks of DDW, standing dead, and live trees all increased (18.3%, 14.7%, and 3.9%, respectively) with biomass accumulation in large live trees coupled with increases in the biomass of smaller sized down dead wood illustrating the influence of stand development across US forests at the scale of individual forest ecosystems (i.e. self-thinning). Coupled with this observation, tremendous positive skew of biomass change across all biomass components and size classes demonstrates the ability of severe but episodic disturbance events to produce substantial biomass inputs to SD and DDW pools with legacy effects exceeding the period of this study. Overall, against a backdrop of expected future global change and growing interest in the maintenance of the terrestrial forest carbon pool, the incorporation of dead wood-focused analytics such as decay-related functional traits, microbial/fungal community assessments, or dead/live biomass relationships into broader forest carbon/biomass monitoring efforts is essential.

1. Introduction

For decades the fundamental role of dead wood (DW) in forest ecosystems (e.g. Harmon *et al* 1986) has been widely accepted, with consistent expansion in monitoring and basic/applied research of this resource (e.g. Stokland *et al* 2012, Kapusta *et al* 2020). Although the DW research foci of wildfire (Schoennagel *et al* 2004), carbon stocks (Bradford *et al* 2008, Domke *et al* 2013), biodiversity (Stokland *et al* 2012, Martin *et al* 2021), and tree regeneration substrates (Bolton and D'Amato 2011) have been somewhat independent in the past, global change requires bringing these

disciplines into closer alignment. Processes such as changing climate, invasive pests, and land-use change are accelerating global change (Canadell *et al* 2007, Pugh *et al* 2019) across forest ecosystems, creating novel conditions (Johnstone *et al* 2016) with important feedbacks (Allen *et al* 2015) where DW plays a role. More frequent extreme weather events will increase the scale and severity of catastrophic forest disturbances (Vose *et al* 2018), some of which may result in type conversion from forest to non-forest (Parks *et al* 2019), necessitating the need to further quantify relationships between global change and DW stocks. Increased tree mortality (McDowell and

Allen 2015), the progenitor of DW, coupled with concerns over fire hazards and/or carbon emissions associated with DW consumption and decay elevates the importance of monitoring DW change (Harmon *et al* 2020).

Large-scale monitoring and assessment of DW has expanded in recent decades (e.g. Fridman and Walheim 2000, Siitonen *et al* 2000, Crecente-Campo *et al* 2016, Gora *et al* 2019, Kapusta *et al* 2020, Martin *et al* 2021b) owing to reporting mechanisms such as IPCC Good Practice Guidance (IPCC 2006) where DW is an individual carbon pool. Downed DW (DDW) exceeding a minimum size is often termed 'coarse woody debris' (Woodall *et al* 2019), while smaller DW is often referred to as 'fine woody debris' in alignment with fire behavior modeling (Deeming *et al* 1977). For clarity and brevity, in this study DW in the form of coarse woody debris is referred to as DDW. In contrast, DW in the form of standing dead trees (SDs) is referred to as SDs. In this study we focused on the live tree, DDW, and SD pools of biomass as they account for the vast majority of forest biomass in the study focus area (Woodall *et al* 2013).

The US began implementing a nation-wide inventory of DW circa 2002 as a component of the national forest inventory (NFI; Woodall *et al* 2019) with SD sampled on all forest inventory plots and DDW sampled on a subset of plots across most US states. As the US' DDW inventory has evolved over time to address quality assurance and quality control issues (Campbell *et al* 2019) and sampling efficiencies (Woodall *et al* 2019), periodic assessments of DW biomass and carbon dynamics (Domke *et al* 2013, Woodall *et al* 2013) have been conducted to inform the strategic directions of the inventory itself while informing national-scale monitoring efforts (e.g. Domke *et al* 2020a see IPCC 2006). Despite continual investment in a remeasured US DW plot network, the very nature of DW (e.g. decaying and fragmented) increases the uncertainty of associated carbon estimates (Campbell *et al* 2019, Martin *et al* 2021b) when compared to live trees. Despite these uncertainties, the US has continued its field-based DW inventory with early work laying the foundation for empirical observation of DW across all forest biomes (Woodall *et al* 2013), which serves to improve our understanding of DW dynamics among a host of forest attributes (e.g. live tree biomass) and in the context of carbon cycling. Despite the large amount of data collected as part of the US NFI, these data have not yet been applied to long-term and broad-scale analyses of DW biomass. As a result, we currently have a poor understanding of changes in DW biomass through time and how these changes may vary across the diverse forest ecosystems of the US.

The overarching goal of this study was to evaluate biomass dynamics of DDW, SD, and live trees using a repeated NFI in the US. Our specific objectives

were to: (a) estimate change from ~2006–2010 to ~2015–2019 among the three biomass components and across primary attributes (e.g. size and decay-class distributions) of delineated US ecosystems (ecological Bailey 1995, 2016), and (b) evaluate the relationship of changes in DDW and SD in relation to live tree biomass across time and in the context of potential drivers (e.g. harvest or natural disturbances).

2. Methods

2.1. Study area

The study area was the coterminous US with NFI assessments of live trees, SDs, and DDW at two points in time (~2006–2010 to ~2015–2019), available for all states except Wyoming, Nevada, and New Mexico (figure S1 (available online at stacks.iop.org/ERL/16/104034/mmedia)). Despite the lack of time-one inventories for these few western states, estimates of DDW change were computed by Bailey's (1995, 2004, and 2016) ecological sections, which enabled calculation of DDW attributes across the entire study region because the sections occur independent of state boundaries (i.e. imputation across political delineations). The study area spans a range of climates/ecosystems (Bailey 1995) with varying rates of climate change (i.e. climate change velocity; Dobrowski *et al* 2013) enabling robust examination of DW biomass dynamics.

2.2. US National Forest Inventory (NFI)

The US NFI consists of an annual inventory of all US forests (US Department of Agriculture, Forest Service, Research and Development Forest Inventory and Analysis program) (Bechtold and Patterson 2005). Forest is defined by the NFI as having at least 10% canopy cover or the potential to support such cover if recently harvested/disturbed (i.e. with no land use change that would prevent establishment of such cover) along with a spatial size requirement of ~0.4 ha and at least ~37 m in width. The NFI design is based on a spatially balanced sample of one plot every ca. 24 km² at a base sample intensity (which can be intensified by spatial delineations such as states where supplemental funds are available). Each inventory plot consists of four points, referred to as subplots, arranged in a cluster with one point at the center and three points oriented from the central point at 0°, 120°, and 240°. The distance from the center of the central subplot to the center of the surrounding subplots is 36.6 m. These four points form the center of fixed-area subplots (7.32 m for most of the US) used to tally live and SDs. Numerous tree (e.g. diameter, species, and height) and site attributes (e.g. elevation and slope) are measured by field crews at each plot. For further information on the NFI sample design and field protocols, refer to Bechtold and Patterson (2005) and USDA (2011, 2019).

2.3. National inventory of DDW

DDW is sampled in the US NFI using line-intersect sampling with subplot centers serving as the origin of transects used to measure DDW pieces. The sampling intensity of the DDW component of the NFI varies by political boundaries (National Forests and/or states) across space and time. For estimating DDW change in this study, the time one DDW inventory is based on inventories conducted using uniform plot protocols from 2002 to 2011 (Woodall *et al* 2019). Likewise, time two DDW inventories were conducted using uniform plot protocols from 2012 to 2019. As plot protocols and sample intensities vary between the two time periods, comparing population estimates (i.e. ecological sections) between these two time periods is valid and unbiased (Woodall *et al* 2019) while comparisons of re-measured individual plots would be considered inappropriate for this study's objectives.

Although the NFI's DDW plot protocols have evolved through time, the general approach to quantify DDW populations has consistently employed line-intersect sampling which consists of arraying one-dimensional sampling transects, with any piece of DDW intersecting a transect being considered part of the sample. Population estimators are constructed based on the length of transect, diameter of the DDW piece at point of intersection, and the attributes of interest measured from each sampled piece. Although the NFI monitors a few sub-populations of DW based on size and assemblage including coarse woody debris, fine woody debris, and piles, this study is limited to examining coarse woody debris (termed DDW in this study), which is defined as dead and downed pieces or portion of pieces of wood that meet size (e.g. minimum diameter of 7.6 cm), orientation, and condition criteria detailed in USDA (2011) and Woodall *et al* (2019).

Plot-level estimates of DDW biomass are based on line-intersect sampling estimators (Woodall *et al* 2019) whereby the transect diameter of DDW pieces, in combination with other sampling parameters such as transect length, are used to estimate a per-unit-area estimate of DDW volume. Estimates of DDW volume are used in conjunction with DDW decay reduction factors and species-specific wood density values to estimate biomass (Harmon *et al* 2008, Woodall *et al* 2019). Plot-level estimates of SD biomass (aboveground) are based on fixed-area estimators (Bechtold and Patterson 2005), individual tree volume/biomass models (Woodall *et al* 2011) and SD decay and structural loss reduction factors (Domke *et al* 2011). In a similar manner, live tree biomass (total aboveground) estimates were based on the same process as used with SD except with the exclusion of decay and structural loss reduction factors. Population-level biomass estimates for all components were calculated from combined plots using the standard NFI post-stratification estimators (Bechtold

and Patterson 2005, USDA 2018). In a similar manner, the forest area by ecological section was estimated using these estimators across time for primary disturbances (e.g. fire, insects/disease, other, and undisturbed) to enable evaluation of drivers of DW dynamics.

2.4. Analytical approach

Bailey's ecological sections (Bailey 2004) were used as observational units of change, given that the spatial scale is appropriate for the NFI sample intensity, and these units are unbiased for varying sample intensities and plot protocols across space and time (Woodall *et al* 2019). The ecological sections are spatial delineations of a collective integration of physical and biological components including climate, physiology, lithology, soils, and potential natural communities. Although the standing live/dead tree inventory occurs at a greater spatial intensity across the study region than the DDW inventory, the same plot selection for calculation of DDW population attributes was used to determine standing live/dead tree attributes because our goal was to examine DW relationships within the pool itself (DDW versus SD and among size/decay classes) and with live trees. Hence, although using all plots where live trees were measured might reduce the sampling error associated with related population attributes, it might in turn weaken correlations with DDW attributes. As forest attributes can be estimated at the condition level (unique site/stand classification such as forest type) within NFI plots, observations were unique combination of plots and conditions within the coterminous US. There were 47 251 observations at time one (2006–2010) and 179 104 observations at time two (varying inventory cycles within the 2010–2019 timeframe) used in this study (table S1). Finally, it should be noted that if in the future the DDW inventory is remeasured using the same plot protocols as employed since 2010 that the resolution of DW biomass change dynamics can be resolved at the plot/stand level.

Differences in biomass density were evaluated among study populations (i.e. components and/or size/decay classes) across time using two-sided Z-tests, Kolmogorov–Smirnov tests of distributional differences, and Shapiro–Wilk tests for evaluation of biomass change distributions (i.e. tests of normality). As an additional evaluation biomass dynamics based on initial findings, the total biomass stock and stock change across the study period (T_g) was for the study area and time periods with significant differences evaluated using a two-tailed Z tests ($\alpha = 0.05$). Coarse mapping of changes in biomass density for DDW and SD among ecological sections was achieved by choropleth mapping ratio estimates (population total of DW divided by forest land area) to ecological sections with application of a non-forest mask. To further evaluate the relationship between the DW components of DDW and SD to live biomass, changes

in the ratios of these individual DW components to live biomass were evaluated across ecosystems in terms of density distributions (density mirror plot). As an initial exploration of drivers (forest area subjected to harvest or natural disturbances) of these ratios across time, a set of potential independent variables were evaluated using an ensemble learning approach via a random forests algorithm (Liaw and Wiener 2002) to assess changes in the ratios of DDW and SD to live biomass. Given the uncertainty associated with resource estimates of relatively small ecological sections due to small sample sizes, the first quartile of study observations in terms of forest land area at time one (less than $\sim 470\,000$ ha) were removed from the random forests analysis to achieve the highest r^2 while retaining all the largest ecological sections that support forest ecosystems. All analyses were conducted using R version 3.6.3 (R Core Team 2020) with the following packages central to analysis: randomForests (Liaw and Wiener 2002), ggridges (Wilke 2021), Basic Statistics and Data Analysis (BDSA) (Arnholt and Evans 2017), and moments (Komsta and Novomestky 2015).

3. Results

The estimated biomass population totals for DDW, SD, and live trees for the study region were 2101, 1448, and 23 425 Tg for time one and 2486, 1661, and 25 372 Tg (respectively) for time two (table S1) which constituted significant increases of 18.3%, 14.7%, and 3.9% (p -values < 0.0006 , < 0.0006 , and 0.0012 , respectively). When examining changes in mean biomass density, two-sided Z-tests detected significant increases in the mean biomass density of DDW (0.22 Mg ha^{-1}) and live tree (0.62 Mg ha^{-1}) biomass across coterminous US forest ecosystems during the two decades this study covers (table S2). The most frequently observed biomass densities of DW and live trees across coterminous ecosystems was of relatively minor DW biomass ($< 3\text{ Mg ha}^{-1}$) but moderate amounts of live tree biomass ($< 40\text{ Mg ha}^{-1}$) (figure S2). The distribution of biomass was positively skewed for DDW and SD due to zero-inflation, as a plurality of plot-level observations estimated zero DDW and SD biomass (figure S2, for population total skew see table S3). Live tree biomass density is roughly six times greater than that of DDW and SD, with a more normal distribution. Correlations between estimates of time one and time two DDW and SD biomass suggested variation across time, with r^2 s of 0.49 and 0.80 for DDW and SD, respectively (figure 1). When coarsely mapped by ecosystem provinces across the US, forests of the eastern US (especially the Gulf Coast) and west coast exhibited a general increase in DDW biomass over time, while forests of the upper Lake States and Rocky Mountain region exhibited a decrease in DDW biomass (figure 2(a)). In comparison, SD biomass appears to have increased in forests

of the Rocky Mountains with minor decreases in the upper Lake States (figure 2(b)).

To further investigate DW biomass dynamics, biomass changes by size class (for DDW, SD, and live trees) and by decay class (for DDW and SD) were explored. In terms of changes in the distribution of DDW biomass among size classes, there were no differences (table S2) across time, although qualitatively the distributions appear to trend towards an increase in smaller-sized DDW pieces compared to larger-sized pieces (figure 3). A similar result was found for live tree biomass where there were no differences among size classes (table S2), although a visual assessment of density plots (figure 3) suggested a potential decrease in the biomass of smaller sized trees with a concomitant increase in the biomass of larger sized trees. Hence, although two-sided Z-tests indicated differences in the population totals of DDW, SD, and live biomass over time (p -value < 0.05 , table S1), examination of biomass density changes (Z-tests) among components (SD or DDW) and size-classes suggested more subtle changes (table S2). Examination of the distributions using Kolmogorov–Smirnov tests of differences between the DDW size-class distributions at two points in time showed differences among most size classes (i.e. more biomass among the classes), while SD biomass only differed for the largest SD trees (table S3). Most biomass components among size classes exhibited greater kurtosis and positive skew at time two compared to time one (table S3).

In terms of changes in the distribution of DW biomass among decay classes, DDW biomass was positively skewed across all classes, while SD biomass increased among the least decayed classes, coupled with high positive skew (figure 4, table S3). The lack of normality in the DDW and SD decay distributions (Shapiro–Wilk's tests, table S2) due to episodic disturbances and/or high levels of sampling error for sparsely forested ecosystems precluded more rigorous testing of differences among decay class distributions except for moderately decayed SD, which showed increasing biomass (Z-test, table S2). Kolmogorov–Smirnov tests suggested differences in the distributions of biomass change for moderately decayed DDW (decay classes two through four) and SD (decay class two through three) (table S3).

Given the diversity of forest ecosystems across the US, examining DW change in the context of live tree biomass change may assist with detecting ecologically relevant changes such as forest health decline or the effects of insects/disease outbreaks. Our results indicate the distribution of SD to live tree biomass ratios have been static over the past two decades, apart from a few occurrences of ratios exceeding 0.25 (figure 5). In contrast, for DDW there may be a slight increase in the occurrence of DDW to live tree biomass ratios exceeding 0.1. Taken together, at the scale of the coterminous US there is stability between DW and live tree biomass ratios, while results at finer

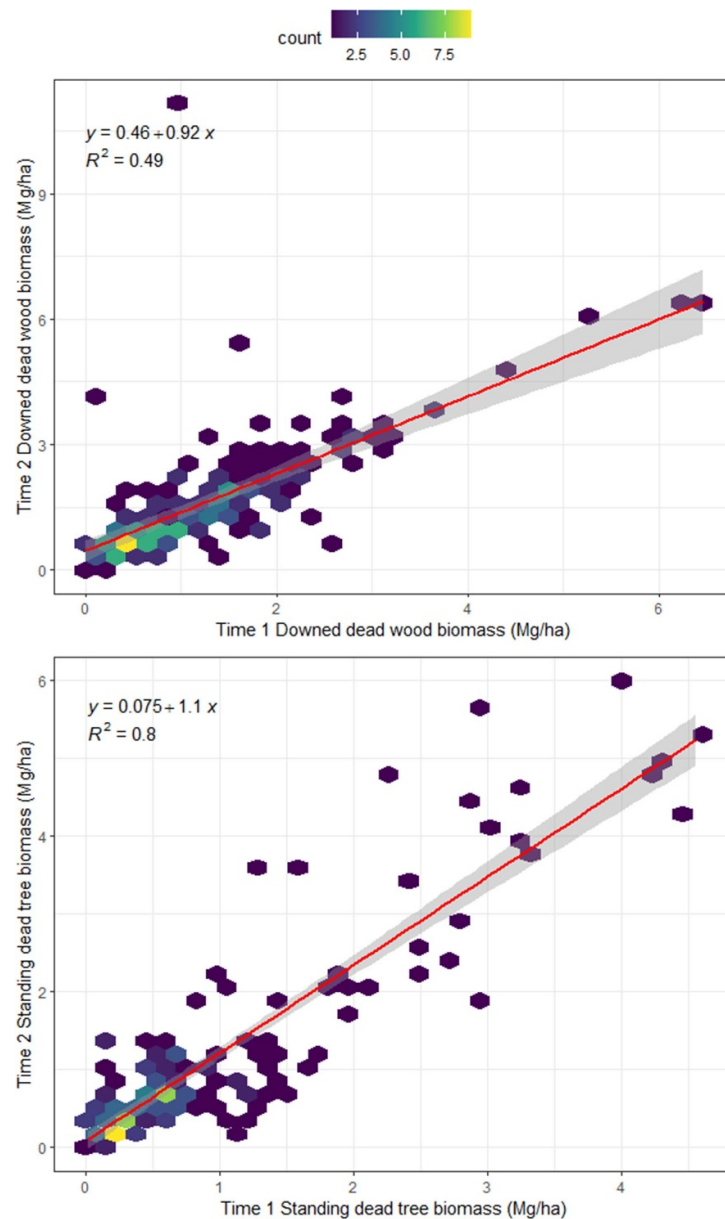


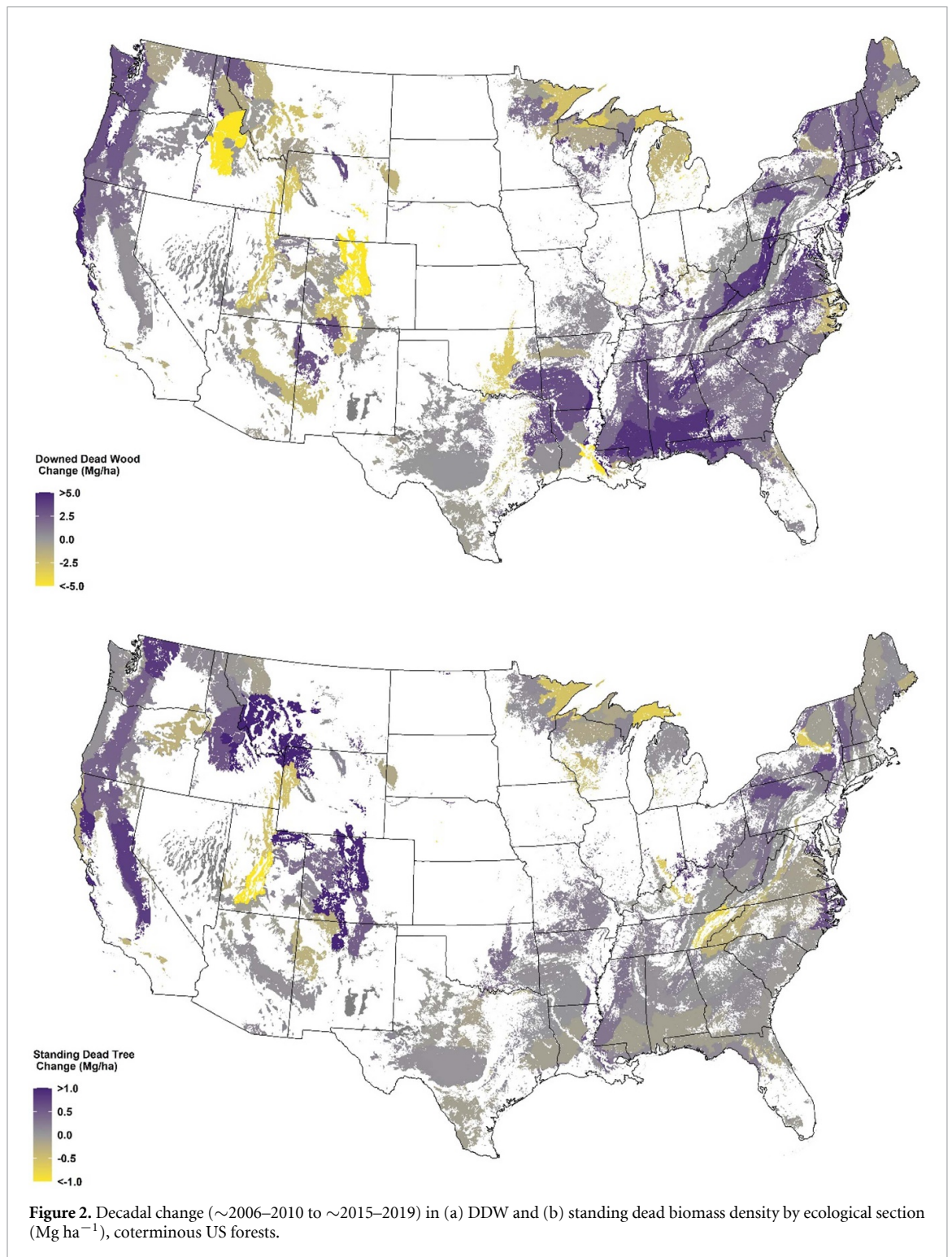
Figure 1. Two dimensional plots of population estimates (Mg ha^{-1}) of DDW and SDs at time 1 compared to time 2 (~2006–2010 to ~2015–2019) among ecological sections across coterminous US forests.

spatial scales would likely reveal less stability, especially in areas impacted by severe forest disturbances (figure 2(a)).

In the exploration of potential drivers of change in the ratios of DDW and SD biomass to live tree biomass, random forest classifications of a wide array of forest attributes revealed contrasting DDW and SD dynamics (figure 6). The DDW random forest classification attained a relatively weak r^2 of 0.15 with importance values across variables indicating that SD and large live tree attributes were most influential. Live tree gross growth, mortality, and harvests along with area estimates of disturbance (e.g. fire) were least influential. In contrast, for SD trees gross growth, mortality, and harvest of live trees followed by estimates of disturbed/undisturbed forest area were most influential (figure 6).

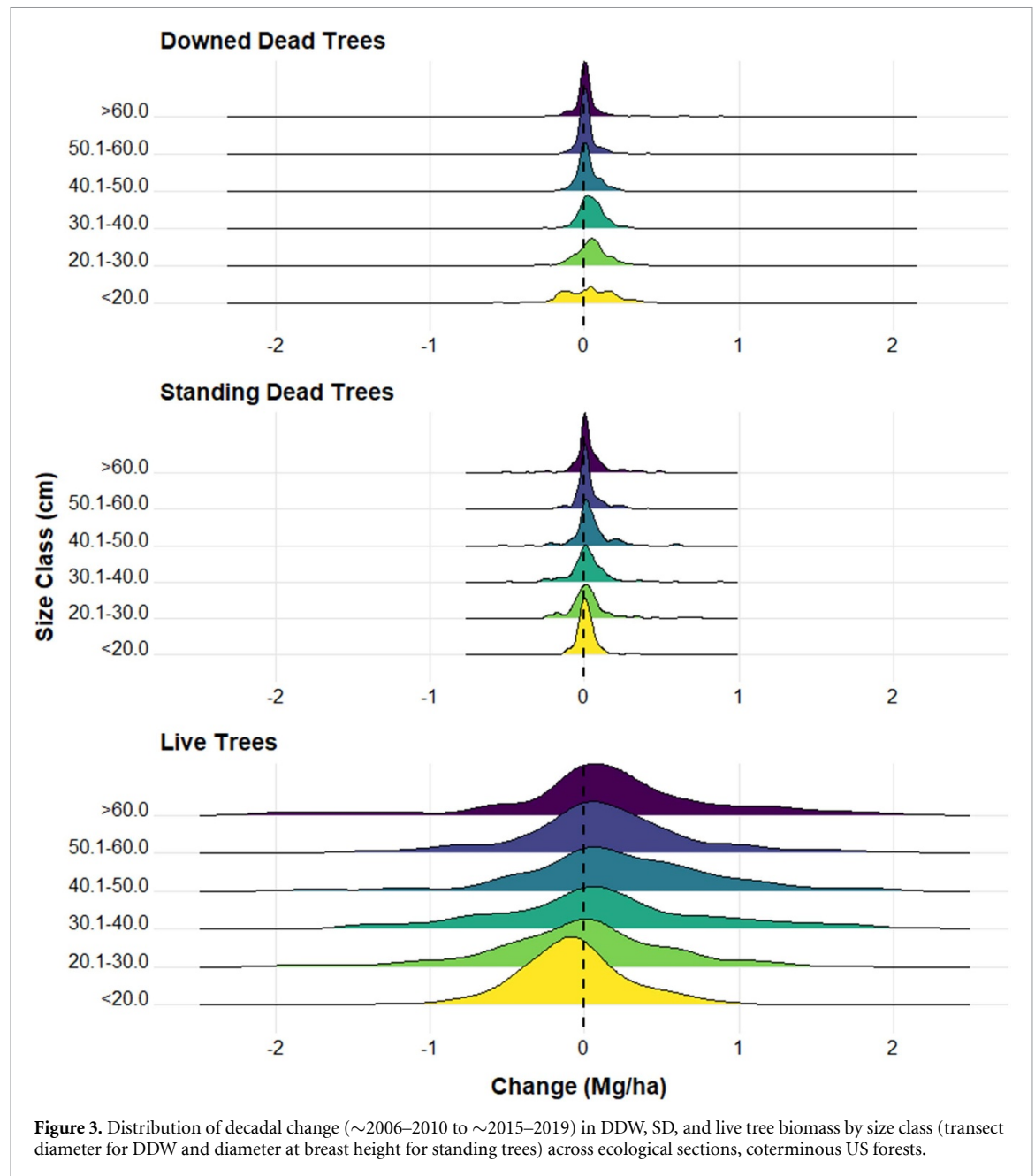
4. Discussion

Despite growing awareness of the role that DW plays in various forest ecosystem processes ranging from carbon cycling to tree regeneration, there has been a dearth of DW studies at spatial scales beyond local stand levels. Coupling the paucity of large-scale DW monitoring with the global change effects of increased disturbance activity (Vose *et al* 2018) and the emerging scientific paradigm of less recalcitrant soil organic matter (Lehmann and Kleber 2015) suggests that DW monitoring and associated sciences are vital to climate change adaptation/mitigation activities in forests. To the best of our knowledge, our study is the first to address temporal changes in DW biomass at a large (sub-continental) spatial scale, and it is one of few studies to address changes based



on repeated field inventories, even at smaller scales. Our results show definitive increases in the total biomass of live trees, SD, and DDW in coterminous US forest ecosystems over the past two decades with more subtle changes in associated biomass density among these components and related size classes. The few previous studies that have assessed overall biomass stocks and stock change inclusive of DW have produced mixed results. Kimberley *et al* (2019) assessed DW stock changes in natural forests of New Zealand,

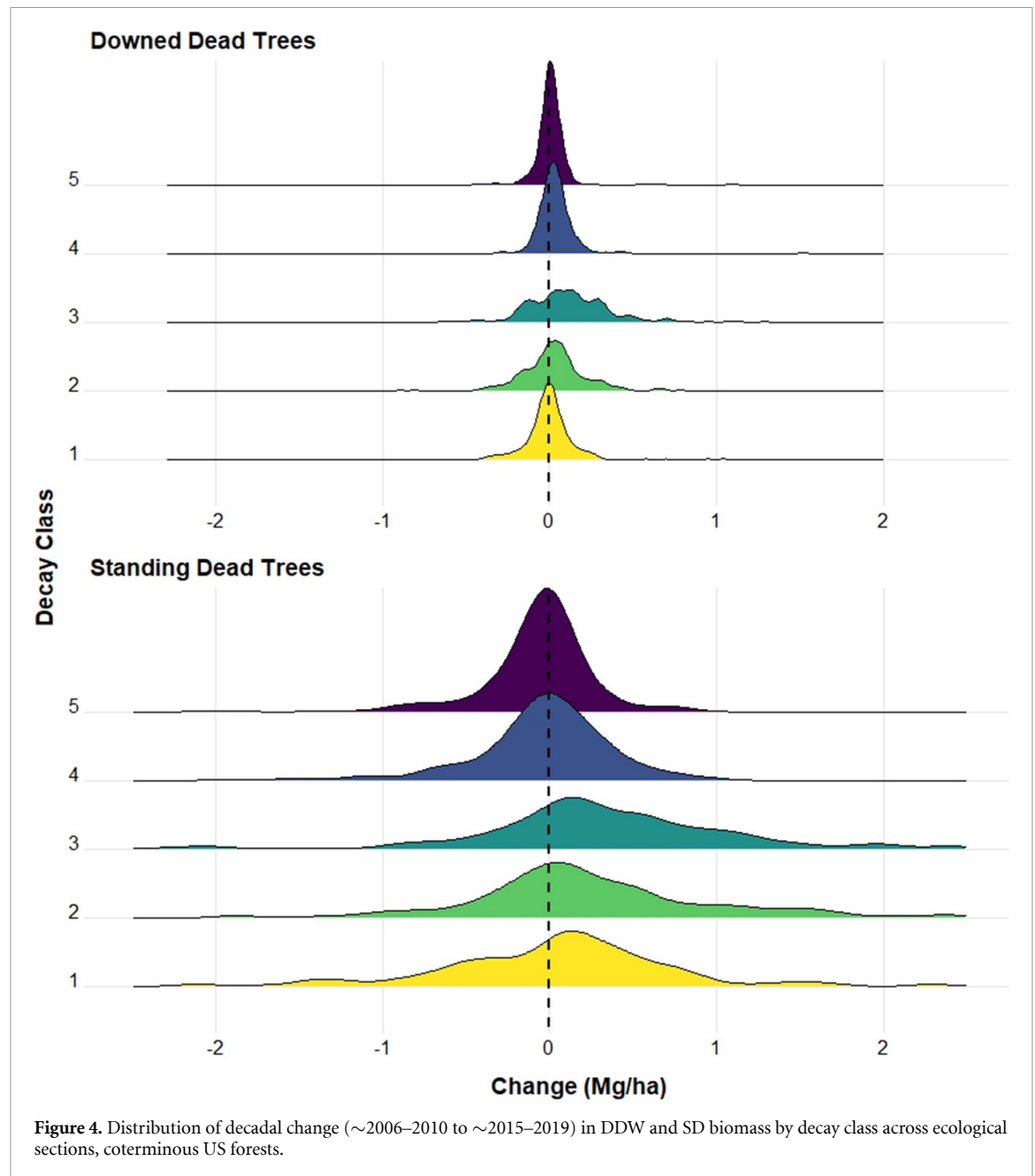
finding no change over a 7 years period. Woodall *et al* (2015) reported a slight increase in both large downed DW and SD (0.02 and 0.11 Mg ha^{-1} , respectively) using the same US NFI plot network but over a shorter, roughly 5 years period in the Eastern US. Working at the stand-level in New Hampshire, US, D'Amato *et al* (2017) found a slight decrease in large downed DW and a slight increase in SD over a 20 years period following a catastrophic hurricane ~ 75 years earlier, based on repeated field inventories. Although



the fundamental changes in overall DDW, SD, and live tree biomass stocks are critical for monitoring, we propose that evaluating changes in biomass density among DW components (e.g. piece size and state of decay) in the context of live tree dynamics and factors such as harvesting and natural disturbances is vital for robust monitoring and useful application to management.

Although our study found evidence of increases in the stock and density of live trees and DDW biomass across coterminous US forests, changes among individual piece size and/or decay classes suggested more nuanced dynamics further complicated by a limit to the statistical power of the current US sample intensity (Westfall *et al* 2011). As this study's Z-tests indicated no difference in the sub-populations of DDW, SD, and live tree by size class across time, we can

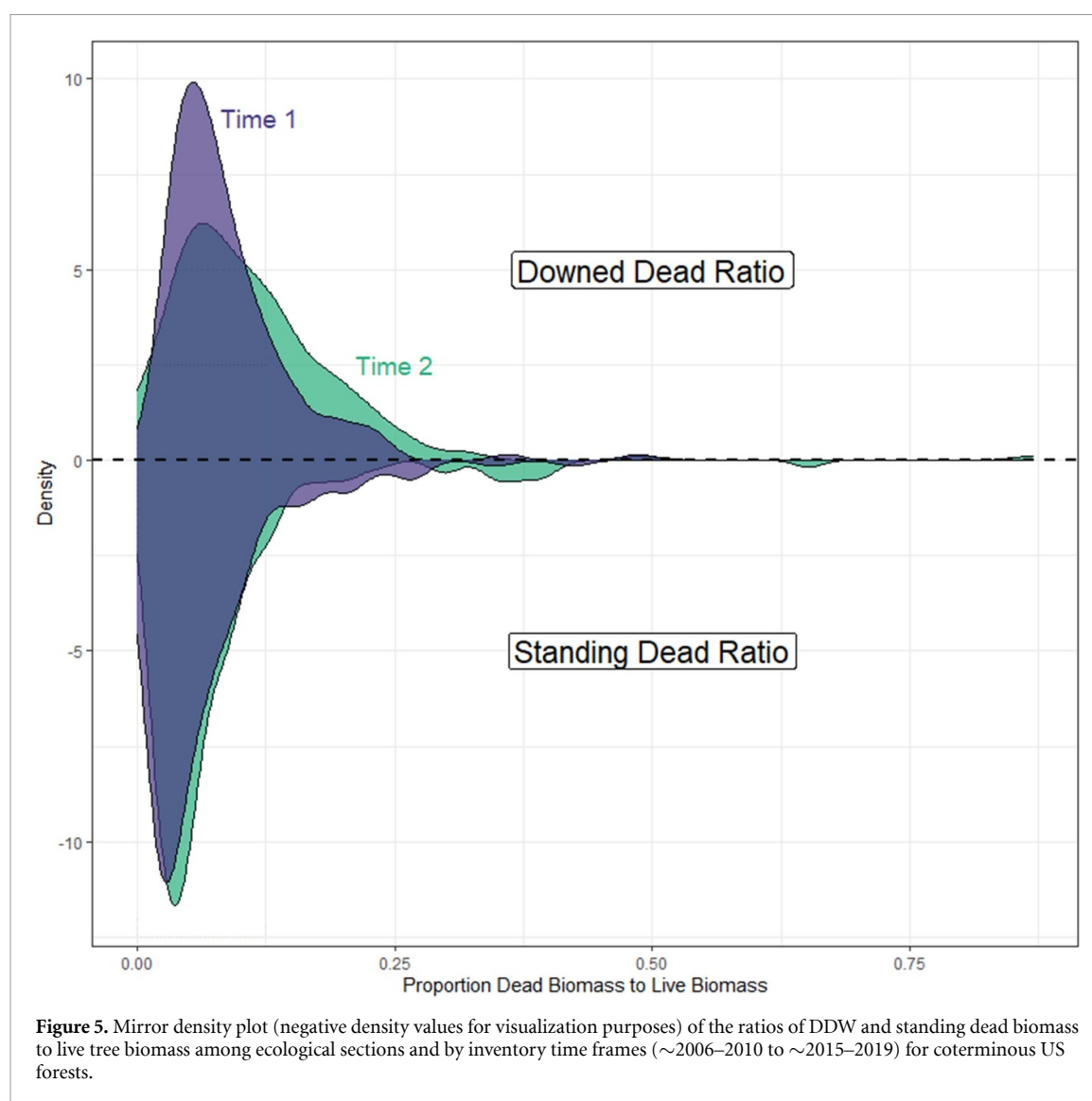
infer no fundamental changes in these populations. However, visual appraisal of density plots of change coupled with Kolmogorov–Smirnov tests of size/decay class distributions, as well as assessment of kurtosis and skew, suggest live biomass may be increasing for larger-sized trees with concomitant decreases for smaller-sized trees. In relation to these potential changes, we may be seeing increases in the biomass density of smaller-sized DDW and total biomass stock of SD following the self-thinning that accompanies natural stand development. We hypothesize that US forest biomass retains ecological memory (Johnstone *et al* 2016) via disturbance events that perpetuate DW biomass across the landscape coupled with accumulating live tree biomass via forest recovery, all at the temporal scale of decades/centuries. The future of this biomass pool may depend on how



expected (e.g. episodic precipitation or blowdowns) (Parks *et al* 2019) and unexpected future perturbations (Pugh *et al* 2019) influence this lineage of ecological memory to alter the course of US forest biomass. The added dynamic of DW decay, breakage, and/or fire consumption further complicates the influence of past disturbances on biomass trajectories. Examining changes in DW in relation to live tree biomass dynamics may be one path to assessing DW dynamics in a more robust manner.

Despite nearly two decades of change across coterminous US forests, we found that the biomass of DDW and SD was relatively stable in relation to changes in live trees (i.e. ratios of DW to live trees). However, analysis of potentially influential factors suggests that live tree dynamics (harvests or gross growth) and disturbances (fire, insects,

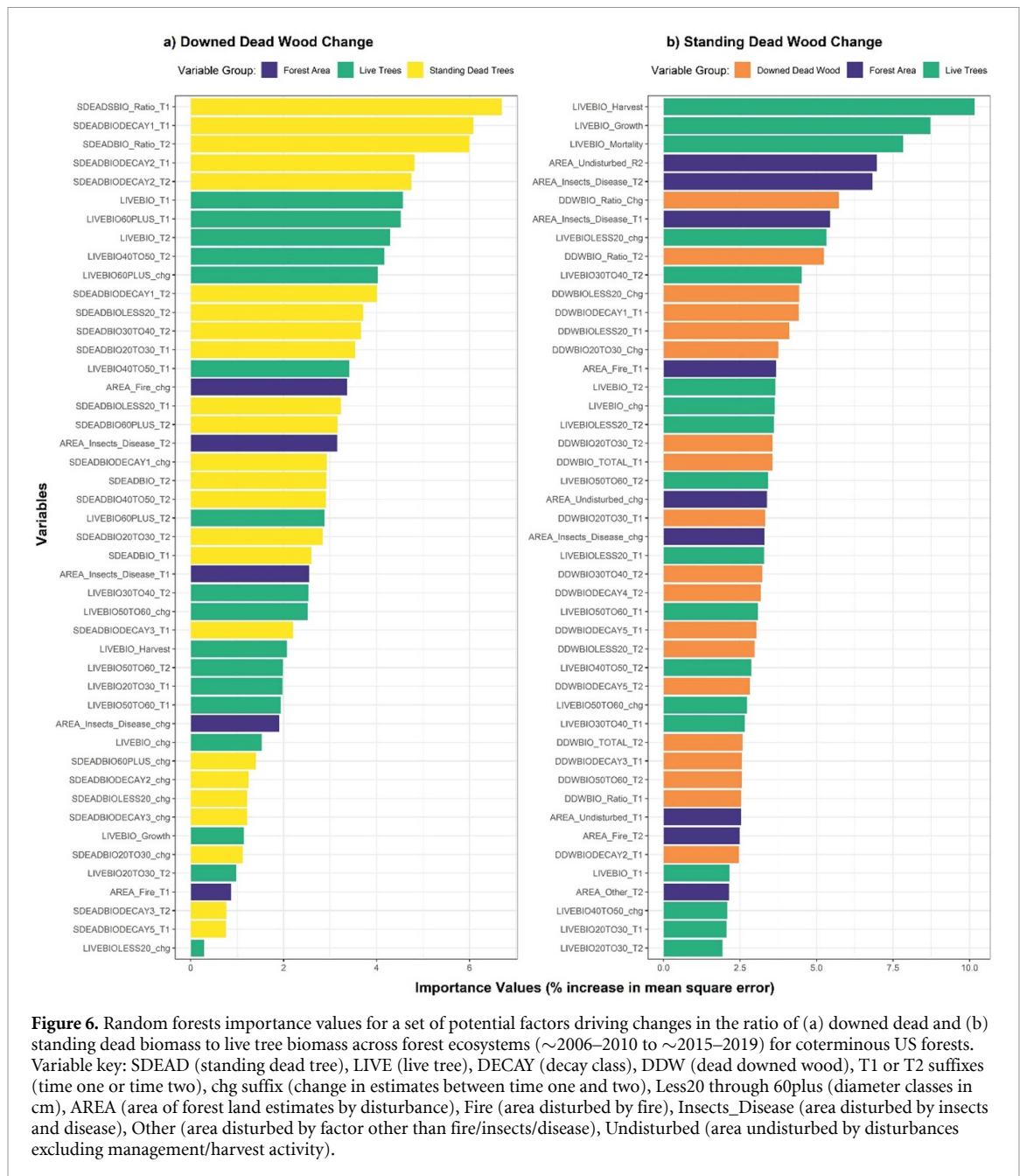
or disease) may be driving SD dynamics, while SD and large live tree attributes may be driving DDW dynamics, which aligns with expected outcomes of stand development. By viewing changes in the major components of forest biomass across decades and among ecological sections, our study presents a new paradigm of forest biomass dynamics: the behavior of the coterminous US forest biomass is not unlike that of individual stands except operating at a different temporal scale. For forest stands, in any given year individual tree mortality/growth coupled with DW decay causes minor fluctuations to the otherwise stable pool of biomass, excluding infrequent but severe small-scale disturbances (e.g. harvests or wind-throw). At the scale of the coterminous US these same dynamics are observed among ecological sections. That is, stable forest biomass with less frequent but



impactful larger-scale disturbances (e.g. regional hurricanes and/or county-scale wildfires) extends across landscapes and through time. If viewed as one pool of biomass, there are indications of biomass increasing with a shift towards larger-sized living individuals (i.e. standing trees) and smaller-sized DDW which may reflect the general process of self-thinning across the US. Coupled with this background of stand development, severe but episodic disturbances (Lugo and Scatena 1996) introduce substantial positive skew to distributions of biomass change especially for DDW and SD.

As DW accumulation in temperate forests is inherently derived from individual tree mortality, we suggest that focusing on the major drivers of stand development (i.e. live tree biomass) and episodic disturbances is a means to understanding DW biomass dynamics. Infrequent but severe disturbance events present a challenge to forest monitoring. First, there is temporal latency associated with the monitoring of large-scale disturbances, such that field

inventory measurements of DW following a disturbance may not occur for many years after the disturbance. While disturbances may be categorized in most national forest inventories, this temporal mismatch inhibits relying on field inventory data alone to understand biomass dynamics. Remote sensing techniques may identify broad trends in forest disturbances across states (e.g. Williams *et al* 2016, Vogeler *et al* 2020), but platforms that enable rapid post-disturbance measurement such as LiDAR (Bae *et al* 2019) and unmanned aerial vehicles (Gao *et al* 2020) are not yet capable of identifying the species and decay class of DW, which adds uncertainty associated with DW biomass and carbon estimates (Martin *et al* 2021b). Second, in ecosystems where forests may be sparse such as grassland or chaparral (e.g. Palouse Prairie Section), there is much higher sampling error associated with these estimates across time. Estimates of DDW biomass change in such ecosystems may be bounded by sampling error rather than attribution to any specific disturbance. In terms of



stand development processes, individual tree mortality and small-scale disturbances are another driver of DDW biomass dynamics that can be difficult to detect using strategic-scale forest inventories. Furthermore, these types of ecological processes can be gradually extended across a landscape through time. Species-specific mortality driven by agents such as emerald ash borer (*Agrilus planipennis*) or mountain pine beetle (*Dendroctonus ponderosae*) can perpetuate through a species' population across years/decades with important implications for DW biomass (Hansen 2014). We propose that episodic but severe disturbance events combine with more gradual stand development and/or gradual mortality drivers to create pulses of DW via live tree mortality (Fraver *et al* 2017). Perhaps in a manner similar to disturbance

ecology in tropical forests (Lugo and Scatena 1996), DW dynamics can be summarized across space and time using background and catastrophic tree mortality as a framing concept. However, an important addition to this framework would be the incorporation of decay/consumption processes driving ecosystem responses that stands in contrast to live tree growth response paradigms.

If society is collectively interested in maintaining or enhancing the forest biomass/C sink across large scales (e.g. Domke *et al* 2020b), then refining the monitoring and associated understanding of live/dead forest biomass is key under a changing climate. Understanding how DW decay rates will change under future global change scenarios allows us to better understand the contribution of DW in C

assessments (Russell *et al* 2014, Harmon *et al* 2020). As explored in this study, monitoring the ratios of DW to live biomass might be one approach akin to assessing the stability of the DW biomass resource. Based on the results of this study and increasing interest in the terrestrial forest C cycle, we propose that DW monitoring approaches might explore the concept of ‘delayed C emissions’ where drivers of decay and/or combustion associated with DW are part of monitoring efforts. In terms of decay this could relate to climate, piece orientation (i.e. ground contact status), tree species functional traits, and/or fungal/microbial community examinations. In terms of combustion, this could relate to fine fuel loads (not examined in this study), fuel moisture, fire weather, and/or longer-term drought monitoring. Overall, as DW biomass accumulation is derived from tree mortality, the incorporation of factors underlying DW biomass depletion into forest biomass analytics may greatly assist future efforts to lengthen the time span that DW C remains with avoided emission to the atmosphere.

5. Conclusions

The total biomass of live trees in coterminous US forests has increased over the past decades with significant transfer to SD and DDW biomass pools via gradual tree mortality and episodic but severe disturbance events. Such dynamics can be witnessed through significant increases in coterminous US live-tree and DDW biomass densities, where stand development (i.e. self-thinning) results in biomass accumulation in larger-sized live trees and smaller-sized DDW, while there is tremendous positive skew across all size classes for DDW and SD biomass components indicative of stochastic disturbance events. Forest stand development and/or gradual forest health issues may result in pulses of biomass inputs to the DW pool that can be subtle and perpetuate through time and space. In contrast, episodic and severe disturbance across large scales can be considerable factors in driving DW biomass dynamics with legacy effects lasting decades if not longer. Considered jointly, and against a backdrop of expected future global change and increased interest in maintenance of the terrestrial forest C pool (i.e. delayed C emissions from DW), the incorporation of DW-focused analytics such as climate, decay-related functional traits, microbial/fungal community assessments, or wild-fire metrics into forest biomass monitoring efforts is essential.

Data availability statement

All data that support the findings of this study are included within the article (and any supplementary files).

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