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Review

Look Down to See What's Up: A Systematic Overview of Treefall Dynamics in Forests

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Abstract: The study of treefall and its after-effects is a common theme in studies of forest structure and local dynamics, yet its value as descriptor of broader-scale ecological dynamics is rarely explored. Here we synthesize the most highly cited literature on treefalls, from 1985 to 2016 (in three-year blocks), highlighting the importance of the causes, characteristics and consequences of such events. We then ask how this knowledge might contribute to the broader conceptual model of forest dynamics, and develop two conceptual models, which we use to illustrate both the classic and alternative views of how forests 'work'. Treefalls are one of the few 'integrating' attributes of forests, because of their ubiquity and longevity, and therefore can inform a variety of processes (e.g., tree mortality, turnover rates, structural impacts, recruitment, and fire frequency) due to their impacts occurring simultaneously over space (patterns), and time (legacy effects). The substantial knowledge that already exists on localized treefall dynamics should be combined with more integrative approaches to studying forest ecosystems, to investigate landscape-scale patterns of treefall and reconstruct past disturbance events.

Keywords: canopy gap; coarse woody debris; disturbance; forest dynamics; plant population and community dynamics; treefall

1. Introduction

As threats to global biodiversity from land-use change and other anthropogenic influences (e.g., climate change) mount, the future of the world's forests has become progressively more uncertain. As a consequence, studies focussing on the impact and sustainability of activities associated with human development on forest biomes (e.g., logging, cultivation), and their interaction with the agents of global change (e.g., climate change, fire regimes, non-native species), have become prolific over the last two decades [1–4]. However, to forecast future forest distribution and biodiversity, it is also essential to have a comprehensive understanding of the eco-evolutionary forces that shape the structural features and dynamic processes that occur within forests (such as mortality, turnover rates, rate of treefall, gap-phase regeneration, recruitment, nutrient cycling), as well as feedbacks between ecological and biophysical attributes. Forest community composition and turnover are influenced by many ecological processes [5–7]. While some factors are consistently important and ubiquitous (e.g., climate, plant-plant interactions, mortality rates), others are spatially heterogeneous in effect and can be highly context dependent (e.g., disturbance) [8,9]. However, forests are inherently complex systems [10], and strong interactions among processes can lead to reinforcing or diminishing feedbacks that are difficult to detect unless measurements over multiple spatial scales or temporal snap-shots are combined. These dynamic mechanisms cannot be studied effectively in isolation; moreover, the further back in-time we try to reach with our inferences, the more indiscernible the imprints of past processes become (e.g., legacy treefalls) [11].

Much of the focus of the forest-ecology literature has been on the position, size and species identity of growing and mature trees, and the consequences of their removal (gap dynamics). Additionally, it is well known that trees can die standing, and remain in this 'state' for years as stags or stumps. As a forest attribute, stags and stumps are important as they provide critical habitat for fauna (e.g., Leadbeater's possum, *Gymnobelideus leadbeateri*) and constitute an integral component of the forest structure [12]. However, unless the wood is harvested, the tree will eventually fall to the forest floor, either due to biotic (pathogens, competition) or abiotic factors (e.g., wind, fire).

This now-dead residue of the once-living forest is usually called 'coarse woody debris' (CWD), or treefall when the fallen log is still relatively intact. The age and volume of the dead wood contains signatures of past tree mortality, and so opens a temporal window through which we might perceive forest turnover rates, disturbance frequency, die-off events, past recruitment pulses and species-trait responses. For example, the presence of heliophilous species in an old-growth forest may be indicative of a past disturbance event that enhanced light availability by opening canopy gaps [13]. In systems where decay rates are slow (e.g., cool-temperate or boreal forests) or regions where disturbances such as fire are rare, the fallen wood can persist for decades to centuries [14], thus providing a long-term record of change in the forest.

Yet there remains ambiguity about the structural effects of treefalls on the spatial distribution of the living components of forests at different scales [15]. Is treefall a forest attribute worth studying for its intrinsic ecological value, or in the overall context of forest dynamics, is its importance defined by how it opens canopy gaps for the recruitment, growth and competition of new living trees? The current definition of a treefall typically relates to the size, frequency and purported causation of the fallen wood (e.g., windthrow or blowdown, forest or canopy gap, or average size and density of the CWD). However, ecologically, treefalls might equally refer to both structural characteristics and temporal features simultaneously, including the dead (but still standing) trees, the act and consequences of a tree falling, the fallen log on the forest floor, and the legacy effects (e.g., past physical displacement of large trees, root pits and mounds) that persist as an imprint after the dead wood has decayed.

Here we present a systematic overview of the last three decades of literature on treefalls and dead wood, and show that although treefalls have been repeatedly demonstrated as important facilitators of forest structure and process, their relationship to the living components is usually overlooked or implicitly downplayed. Here, we use the term 'treefall' to refer to not only act of the tree falling, but also the physical consequences of the fallen tree, and the gap-phase regeneration that it triggers. In this context, treefall is not only an event, but also a legacy record of past forest dynamics, and a driver of turnover processes. Specifically, we sought to: (i) examine the causes, characteristics and important consequences of treefalls, drawing attention to current gaps in our knowledge of treefall events; (ii) critically evaluate the importance of treefalls as key components of forest ecological processes; (iii) highlight areas for future study, including a re-evaluation of the conceptual model of forests when treefall is given explicit priority (and measured regularly and systematically, alongside attributes of the living forest). In pursuit of our final aim, we compare an example of a classic model of forest dynamics (traditionally focused on the life cycle of a tree) with an alternative approach, where tree death and treefall are seen as complementary windows into hidden underlying ecological processes.

2. Methodology

To sample the literature representatively, we undertook a series of searches using different combinations of key words relevant to treefall, disturbance, woody debris and forests (for example: TS = (treefall AND log AND forest); TS = ("fallen tree" AND log AND forest); TS = forest AND ("coarse woody debris" OR CWD); TS = (forest AND disturbance AND dead trees AND stumps, etc.)). The subsequent references and citations in the most highly cited of these papers were also scrutinised. We then combined the results and cross-referenced across the searches to remove duplicates, leaving a useable tally of ~2500 papers. To ensure a comprehensive yet tractable synthesis of this literature, we then created two summary tables, one that listed the most highly cited literature from 1985 to

2016 (separated as sequential three-year blocks; Table S1; 73 papers), and another (Table 1; 25 papers) that focused on four examples (not duplicated in Table S1), each representing a classic, well-cited, review/meta-analysis, and recent study (published within the last two years). Our choice of categories for grouping the selected papers was dictated by the most common themes that were covered in the literature. These were: (i) **causes** of treefall; (ii) **consequences** of a treefall and; (iii) **characteristics** of the fallen tree and the landscape, which is typically influenced by (i) and has an effect on (ii) (Figure 1). Within this ecological context, for Table S1 we broke the studies into six categories within each of the three-year blocks, being: (a) canopy gaps; (b) decay and nurse logs; (c) extreme-weather events and disturbance; (d) modelling and forest management; (e) non-living and structural effects; and (f) tree mortality and standing dead.

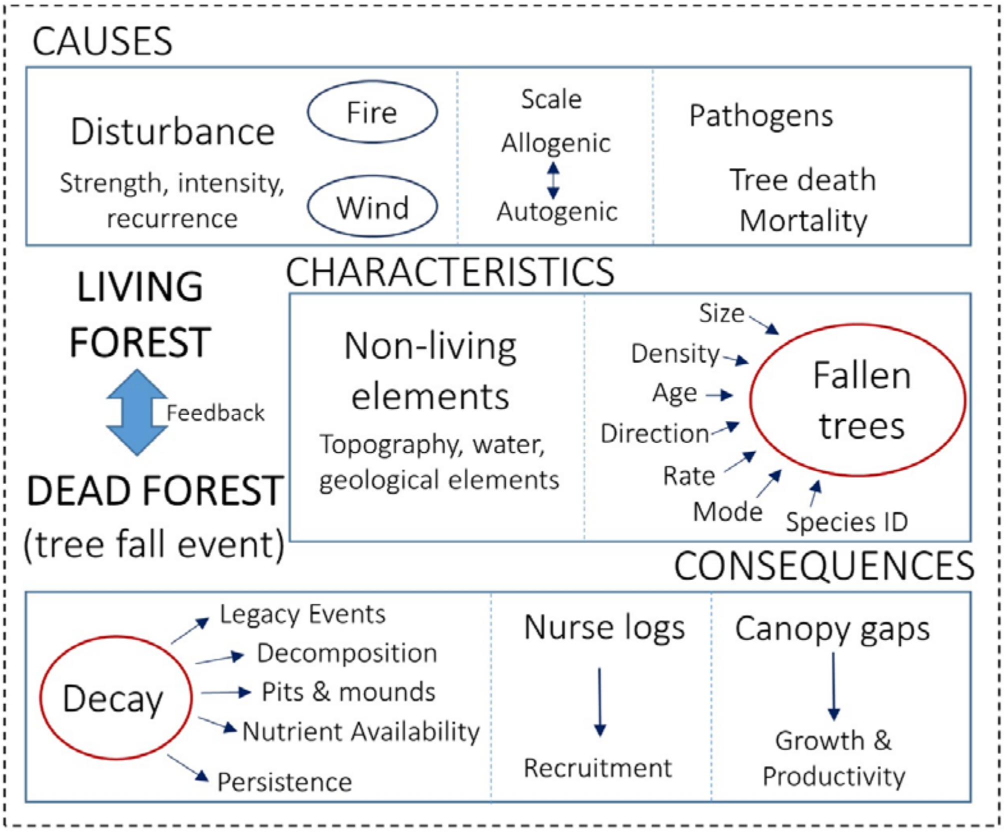

Figure 1. Summary of the most commonly studied research themes in the treefall literature (broken down by the categories shown in Table 1). Each theme relates to whether the study predominately explored the causes, consequences, or characteristics of the treefall.

3. Treefall Literature: Current Knowledge

The most common terms used in the literature across all groups included 'gap(s)', 'coarse woody debris' and 'treefall' (Table 1). These terms were often used interchangeably and were chosen/defined at the researcher's discretion, depending on the question or the main finding e.g., [16,17]. Providing clear definitions is crucial to the understanding of treefall and its impact (e.g., at what point does a fallen tree cease to exist as its' components decay and are incorporated into the soil), but is beyond the scope of this study. Field measurements and observations were the most common type of study, and these were predominately done at an individual- to community-level (Table 1). For the papers that were included in this research synthesis, ecosystem and landscape-scale investigations included mainly reviews, meta-analyses or syntheses as these were the most likely to be heavily cited (Table 1).

Table 1. Contextualisation of the treefall, dead wood, and gap-phase regeneration literature, categorised into four major research themes: Causes of treefall, characteristics contributing to propensity of a tree to fall, consequences of a treefall event, and management or modelling applications. The papers that that were included in each category were chosen to represent the following four criteria: (i) a 'classic' study (for historical grounding); (ii) a highly cited example; (iii) the most recent published review; and (iv) a recently published study based on primary research.

Author(s)	Forest Type	Topic of Paper	Study Impact *	Key Development/Finding Type ^		Cites	Terminology
			CONSEQUENCES *Canopy gaps and gap dynamics*				
Brokaw, 1985 [18]	Tropical	An assessment of Watt's [19] description of mature forests as shifting mosaics and gap size dependence of regrowth using periodic observations at multiple sites.	FM	P	Accordance with Watt (1947): Gaps of different sizes and stages of regrowth are an important source of heterogeneity in composition and dynamics of tropical forests.	821	Treefall gaps
Uhl et al., 1988 [20]	Amazon forests	Effect of gap microhabitats on nutrient availability and regeneration, and the role of gap size in influencing regeneration within a gap within 4 years after gap establishment.	FE and FM	C	(i) Treefall gaps principally benefit pre-established seedlings and saplings; (ii) gap size has little effect on plant density, establishment and mortality; and (iii) gap microhabitats have negligible effects on vegetation dynamics and nutrient availability.	398	Treefall gaps
Muscolo et al., 2014 [21]	All forest types	A review of the roles of forest canopy gaps.	R	P	To further understand the impact of gaps on the forest as a whole, further investigation needs to be done on the below-ground communities (including: soil processes, organic matter trends, composition and activity of the microbial biomass, and soil characteristics).	3	Treefall gap
Zhu et al., 2014 [22]	All forest types	Meta-analysis on the effect of gaps on woody-plant regeneration.	M	E	Overall, forest gaps enhance woody plant regeneration, and the effects of gaps varies with forest type, gap characteristics, environmental factors and plant traits.	8	Forest gaps and treefall gaps

Table 1. *Cont.*

Author(s)	Forest Type	Topic of Paper	Study Impact *		Key Development/Finding Type ^	Cites	Terminology
CAUSES *Disturbance (Extreme weather events (fire and wind), uprooting)*							
Canham and Loucks, 1984 [23]	Hardwoo d forest	Assessment of the frequency and extent of catastrophic windthrow, and identification of the mechanisms.	FM	P	Return time for a catastrophic windthrow in these forests is 1210 years with catastrophic thunderstorms as the principle mechanism for large-scale blowdown.	379	Blowdown and windthrow
Attiwill, 1994 [24]	All forest types	A review of the literature on natural disturbances in forests.	R	P	An ecological framework of natural disturbances and its component processes and effects is synthesised and developed in this review. Provides the basis for sustainable forest management.	798	Tree fall
Ulanova, 2000 [13]	Boreal forest	A review of the literature on the ecological effects of windthrow and its effects on forest structure and composition at differing spatial scales.	R	L and C	The creation of gaps and microsites by windfall disturbances are two related major environmental components determining the regeneration niche of forest plant species. Windfall disturbances also increase biodiversity (for further information on how, see the paper).	310	Gap-phase dynamics, windthrow and fallen tree
Šamonil et al., 2010 [25]	All forest types	Investigation of the reported roles of tree uprooting in soil formation.	R	E	Knowledge of the effect of tree uprooting on soil formation is well understood across multiple scales, but there is limited quantitative data to date supporting much of the theory.	55	Tree uprooting
Bassett et al., 2015 [26]	Eucalypt forest	Development of a conceptual model of CWD dynamics pre- and post-fire to predict how topography, fire severity, and fire history interact to affect the availability of CWD in forests.	M	L	Both fire severity and fire frequency influenced CWD availability in gullies, where CWD on slopes was not. Gullies generally supported more logs than slopes, but longer inter-fire intervals in gullies may allow fuel loads to accumulate and lead to comparatively larger fire impacts.	2	CWD and logs and dead trees

Table 1. *Cont.*

Author(s)	Forest Type	Topic of Paper	Study Impact *		Key Development/Finding Type ^	Cites	Terminology
			CAUSES *Tree mortality and Standing dead*				
Franklin et al., 1987 [12]	All forest types	Description of tree death as an ecological process.	R	I to P	Tree death demonstrates key principles of ecological process, and defining the spatial and temporal context of the study is important.	683	Tree death
Fridman and Walheim, 2000 [2]	All forest types	Evaluation of the dead-wood inventory in Sweden.	FM/M	C	Logs were more decayed than stags. Forest management affects the amount of dead wood present, less dead wood using clear-cut and thinning methods. Inventories are important and are usable as a tool for assessments of dead wood.	403	Dead wood, standing dead
Lugo and Scatena, 1996 [27]	Rainforest	Causes and consequences of tree mortality.	R	C	Tree mortality events vary extensively across time and space. These events often differ depending on stand conditions, and stem densities (higher mortality with higher densities). Ecological impacts of a sudden tree mortality event contrast with gradual background mortality.	28	Tree mortality, tree fall gaps
Soderberg et al., 2014 [16]	Boreal forest	Assessment of the choice of definition on the amount of dead wood that is reported in the literature.	FM	C	The different definitions of 'dead wood' used in studies, substantially affects the quantity of dead wood that is reported –in most cases leading to underestimates of dead wood volume.	1	Dead wood

Table 1. *Cont.*

Author(s)	Forest Type	Topic of Paper	Study Impact *		Key Development/Finding Type ^	Cites	Terminology
			CONSEQUENCES *Decay and nurse logs (recruitment)*				
Sollins, 1982 [28]	Douglas-fir forest	Decay rates and turnover in an oldgrowth forest, assessment of prior measurements that may have been misleading.	FM	C	Densities of fallen boles were lower than previously reported due to methodological and field measurement differences. Highlights the value of permanent plots (undisturbed) for accurate representation of decomposition and nutrient dynamics.	330	Tree mortality, fallen boles, fallen and standing dead woody material
Siitonen et al., 2000 [14]	Norway spruce forest	Differences in stand structure between managed and unmanaged stands (comparing mature and oldgrowth).	FM	C	Average volume of CWD was much higher in old-growth (managed) than mature (managed) and over mature stands. Logs contributed the most to CWD volume.	376	Coarse woody debris (CWD), living trees, logs, dead standing trees
Weedon et al., 2009 [29]	All forest types	A global meta-analysis testing the hypothesis that interspecific differences in wood traits affect decomposition of woody debris.	R	E	Found support for their hypothesis. Gymnosperm wood decomposes more slowly that angiosperm, and key nutrients such as nitrogen and phosphorus correlate with decomposition of angiosperm woody debris.	152	Woody debris
Cousins et al., 2015 [30]	Mixed conifer forest	Developing an understanding of decay rates of standing dead (SD) trees and the implications for carbon accounting in forests.	FM	C	Carbon density of the most decayed SD trees was 60% that of live trees. Species identity, surface area:volume ratio and relative position within the tree are all important characteristics that explained the SD patterns.	1	Standing dead (SD) trees, woody debris, deadwood

Table 1. *Cont.*

Author(s)	Forest Type	Topic of Paper	Study Impact *		Key Development/Finding Type ^	Cites	Terminology
CHARACTERISTICS *Non-living and Structural Elements*							
Maser and Trappe, 1984 [31]	All forest types	Synthesis of the available data on fallen trees in unmanaged forests with the aim of highlighting research needs and knowledge gained.	R	E	We know a lot about fallen trees their importance. Future research should focus on the effect of changes in and around the fallen tree on the overall functioning of forest ecosystems. Soil-log interface may be important.	327	Fallen trees, wood, woody debris
Harmon et al., 1986 [32]	Temperate forests	Describes CWD and its flow/movement into, from and within an ecosystem.	R	E	Rates of input/accumulation of CWD in forests ranges from 0.12 to 30 Mg/year. This input depends largely on the size of the tree (rate of decomposition), and frequency of disturbances (particularly big ones!). CWD mortality is expected to be aggregated (due to the processes governing tree death such as wind, pathogens affecting multiple individuals of the one area).	3166	Woody debris, coarse woody debris (CWD), dead trees, downed boles, logs
Woldendor p and Keenan, 2005 [33]	Australian forest	Assessment and literature review of CWD in Australian forests.	R	E	CWD can be high in exotic pine plantations if substantial amounts remain from the once native forest. There were differences in CWD quantity depending on stand age; young <20 years = lowest percentage of CWD, older >70 years = highest CWD and stag biomass. Tree size influences CWD amounts (i.e., tall open forests CWD much greater because of taller trees).	67	Coarse woody debris (CWD), standing and fallen dead wood, snags
Oberle et al., 2015 [34]	Temperate forest	Importance and movement of deadwood after treefall.	FM	C	While logs can fall in many different directions; snags, logs and branch average direction was consistent with downhill deadwood movement as trees fall. Relationships between log and landscape attributes (movement, shape and topography) suggest that downhill rotation during treefall drives most of the deadwood distribution over their study site.	1	Logs, deadwood, snags

Table 1. *Cont.*

Author(s)	Forest Type	Topic of Paper	Study Impact *		Key Development/Finding Type ^	Cites	Terminology
			APPLICATION *Modelling and For. Management*				
Lorimer, 1985 [35]	All forest types	How to infer past disturbance dynamics without using destructive techniques and using more than just age of trees.	R/M	P	Currently, it is difficult to identify past disturbance (severity) from the distribution of tree among age-classes. They advocate that to study disturbance history, random dispersal of plots of various sizes, across a large land area is recommended.	280	
Siitonen, 2001 [1]	Boreal forest	Exploring the relationships between CWD, forest management (intensively vs. unmanaged), and saproxylic species.	R	E	In managed forests, the average amount of CWD in the landscape has reduced by 90–98%. General species area relationships suggest that a reduction in available habitat (i.e., as logs), might lead to a reduction of >50% saproxylic species in the long term. It is important to assess how much CWD should be retained in managed forests.	904	Coarse woody debris (CWD), dead tree, decaying wood
Schliemann and Bockheim, 2011 [36]	All forest types	Review of the inconsistencies in gap terminology, and the methods and modelling used to investigate treefall gaps and the influence of gaps in a forest system.	R	E	Recommends a range of standard protocols when studying treefall gaps. For example the size of treefall gaps varied across studies; this study suggested a maximum gap size of 1000 m^2 (gap size can influence the results due to scale dependencies of processes). Gap shape varies and should be determined through extensive field survey.	70	Treefall gaps, canopy gap
Fischer et al., 2016 [37]	All forest types	Description of the development of the individual-based and process-based forest gap model FORMIND and its potential application to tropical forests.	M	E	Long-term modelling projects not only provide understanding of forest systems, but also provide benefits for ecological theory and empirical study design. They are powerful tools, and are becoming increasingly valuable in today's research.	0	Forest gap

^ Study type: field measurements (FM), field experiment (FE), review (R), modelling (M), glasshouse (GH), experiment in the field (EF), lab experiment (EL), management (MM). * Impact: population (P), community (C), ecosystem (E), landscape (L), individual (I).

3.1. Causes

Mortality of trees was a central focus of the literature across all categories (Table 1) and disturbance events were considered the main drivers of treefall [24,38]. While plant senescence leads trees to be more susceptible to biotic and abiotic factors, the death of the entire individual does not occur often without an external disturbing agent [12]. Fire, extreme wind events and knock-on effects to neighbouring living trees by a treefall event are common examples. It follows that the characteristics of treefall events are strongly correlated with type, magnitude and frequency of disturbance [39]. For instance, the severity of wind damage can vary from the death of a single tree to extensive windthrow [23], depending on storm intensity, timing, and its interaction with local conditions, tree size, and species involved [40,41]. Similarly, the interplay of fire regimes (frequency and intensity) and topography—which affects fire behaviour and fuel load—determines the extent of tree damage and recovery time [26]. Disturbance characteristics also influence the spatio-temporal distribution of standing and fallen dead wood [27,32] and consequently, treefall analysis can be a noninvasive technique for reconstruction of disturbance history and tree death.

3.2. Characteristics

Depending on tree size, treefall can occur through trunk snap or tree uprooting, the latter of which determines the formation of pit-and-mound microtopography [42]. At a fine scale, the common view is that pits and mounds inhibit soil development. For instance, Ulanova [13] found that microsites characterised by pit-and-mound topography differ pedogenically from undisturbed soil, and the time required for soil profile to recover was directly related to uprooting depth. Microsites can differ in light, soil moisture and temperature [43], and their extent is directly related to tree size [44]. However, at the scale of a forest ecosystem, the impact of tree uprooting on soil spatial variability is still poorly understood and more quantitative data are required to fully comprehend the ecological consequences of this phenomenon [25].

Dead trees themselves also provide, through accumulation of coarse woody debris, a sizeable fraction of a mature forest's stored carbon (biomass), and nutrient budget [12]. Consequently, CWD quantity, quality, and decomposition rates have a crucial influence on nutrient cycling, because large amounts of organic matter are transferred in the soil and/or in the atmosphere [32]. That said, the total amount of CWD in a given forest varies greatly with species composition, stand age, tree size, temperature, and humidity [29,33]. Moreover, landscape features such as slopes and valleys affect CWD spatial distribution and decomposition, with logs tending to move downhill where they are also susceptible to more rapid decay [34,45].

3.3. Consequences

The creation of a canopy gap is arguably the most obvious consequence of treefall in a closed forest. Accordingly, the most common and highly cited research category in the literature on treefall was canopy-gaps and gap-dynamics (Table 1 and Table S1), with 50% of papers focussing on this topic alone e.g., [18,46–48]. Depending on their characteristics—particularly size, shape, distribution, and age—canopy gaps introduce environmental heterogeneity locally, determining changes in light levels, soil nutrient availability, litter depth, belowground competition and spatial patterns in regeneration at a landscape level [21,49]. These effects have been recorded in both temperate and tropical forest environments [46], although with exceptions, which were predominantly focused on single-treefall gaps in any forest e.g., [20]. The microhabitats generated by canopy gaps enhance plant regeneration, with the magnitude of this effect depending on forest type, gap characteristics, local conditions and plant functional traits [22]. Gaps can result in: (i) increases biodiversity by facilitating the establishment of pioneer, shade-intolerant species; (ii) rejuvenation of the gene pool, since gaps are mostly colonised by seeds and spores; and (iii) enhanced structural complexity, as species are represented by individuals at different life stages [13,18,21,24]. Gaps can be more or less important depending on the regeneration regime and forest type. For example, in continuously regenerating tropical forests, light is extremely limiting, and gaps here provide regeneration 'pulses' that would not otherwise occur without the gap [18]. Conversely, Australian tall eucalypt forests predominately regenerate via a stand-replacing disturbance event and rely less on the continuous availability of gaps [50], although gap size have been correlated with regeneration success in *Eucalyptus regnans* stands [51]. Despite the influence of canopy gaps on local conditions, both terminology and field work protocols are still inconsistent between studies and therefore results can be difficult to interpret and compare [36].

Other than creating a gap in the canopy, the physical presence of fallen logs also facilitates plant establishment for some tree species, particularly at advanced stages of decay when stored nutrients are more readily accessible [32]. Nutrients and water are released slowly from CWD and hence, when CWD is not removed, they are retained in the ecosystems until plant productivity recovers [52]. However, these dynamics are still poorly understood and results from different studies can be contradictory, or relate to very different process such as seedling establishment versus nutrient dynamics. For example, mounds and decaying wood are important substrates for the germination of the coniferous species *Picea abies* [13,53], but a study on meso-eutrophic forests found that only one of nine species investigated displayed higher seedling density on logs, suggesting that differences amongst species (in trait characteristics, presence or absence of mycorrhizal associations, for instance) might also play an important role [54]. Furthermore, Laiho and Prescott [55] inferred only a limited role for CWD in the nutrient cycle of north coniferous forests. The positive effect of fallen logs on seedling establishment could then be due to the lower competition with herbs and mosses occurring on CWD compared with soil, and only partially to enhanced nutrient availability [56]. The presence of decaying wood is also crucial for organisms other than plants, such as bryophytes and saproxylic fungi and invertebrates, which rely on spatio-temporal continuity of suitable host trees for their persistence in the forest community [1].

4. Living-Forest Dynamics

In models the dynamics of a forest classically begins with recruitment and seedling establishment, through growth, maturity and reproduction of the canopy tree, and ends with its death and eventual fall [12]. Over time, the fallen log decays, with this process in turn facilitating many important ecosystem services across space and time, including recruitment (as a nurse log, or via gap-dynamics), decomposition (nutrient turnover, microbial community growth and diversity), habitat for animals or bryophytes, and structural influences on the pattern and growth of living trees; so the cycle begins again (Figure 2).

Additionally, treefalls are obvious indicators of disturbance events e.g., [57]. In this context, it is apparent that an important driver of change and structure in this classical tree-focused conceptual model of a forest is the 'dead' component—and the dynamical processes that it facilitates. We recognise two defining and inseparable features of forests; the 'living' (seedlings, saplings, mature trees) and the 'dead' (stags, fallen logs, etc.). The transition between these states needs a stimulus, making a disturbance event (e.g., wind, fire, pathogens) and time, the key to maintaining this dynamic flux (Figure 3).

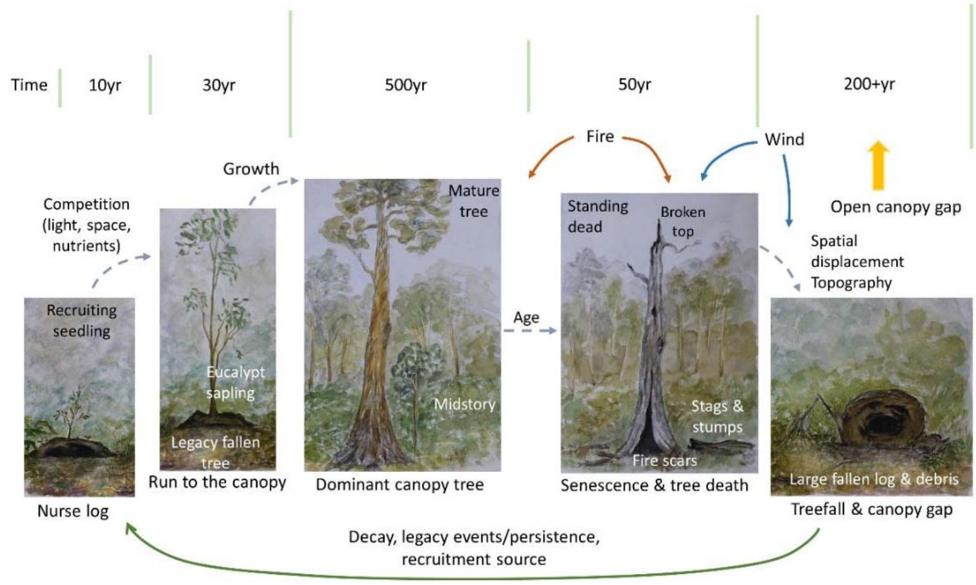

Figure 2. Example of a classical model of forest dynamics, in the context of canopy trees. It begins with recruitment and growth, and ends with treefall and log decay. The direction of the arrows show movement between states, and where key forest processes may be occurring. The green bars indicate duration of stages—in the case of a stand replacing event, the forest may transition from a living tree, or a stag, directly to regeneration following fire. In these circumstances however, it is unlikely that the fire will result in 100% removal of coarse woody debris (CWD).

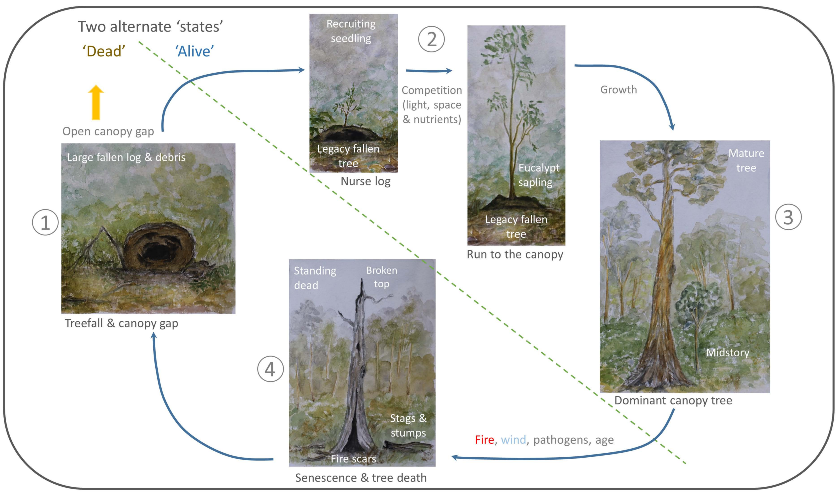

Figure 3. Example of an alternative conceptual model of forest turnover (cf. Figure 2), with large fallen logs (the 'dead' components of forests) as the central focus. The two alternative states of forest turnover are separated by the dotted line, and includes the 'living' (with the mature tree as the 'end' point of the 'living' state) and the 'dead' states. The direction of the arrows show movement from one state to the next (with the key processes involved in the movement between states written above the arrows where required). This image is conceptually similar to Figure 2, but depicts both stages being equally as important to the structure and dynamics of an example forest. Disturbances such as fire, wind, pathogens and age are key to the transition into the 'dead' state, where canopy gaps, for example in tropical forests, are the key to unlocking continual regeneration of the living state. Note that gap processes can often commence around stags, before the treefall has occurred, due to de-foliation, and stem breakage.

5. A Treefall's Eye-View of a FOREST—What Is Next?

When looked at from the perspective of treefall, the prevailing state of a forest centres on dead components; standing-dead trees, coarse-woody debris and fallen logs, which typically persist for much longer than it takes for a seed to establish, compete, and race to the canopy. From the perspective of the dead tree (fallen log), the living forest is arguably more unstable and in a constant flux, depending on inputs, environmental conditions (determining decay rates) and disturbance (fire, wind). Observations and measurements of the dead states (e.g., the size, spatial position, decay state and fire scars on a fallen log), can provide a powerful tool for inferring deeper-time ecoevolutionary processes—reaching much further back than the relatively evanescent information provided by observations of only the living components would allow [58,59]. As such, the analysis of treefall allows us to look back into the past using snap-shot patterns and log dating, and so measuring the attributes of the dead forest offers a crucial augmentation to measurements of the sizes, identities and positions of the living trees. Yet the measurement and use of the spatial locations of treefalls remains underexploited in plot-based studies, based on our survey of the literature (Table 1 and Supplementary Materials Table S1). A more explicit focus on the causes and consequences of treefall as more than just 'an opener of canopy gaps' might also be useful for improving pattern-oriented models (POM) of forests [60]. This is because analysis of the patterns of the fallen wood should permit an explicit filtering and verification of the adequacy of structural forest models that seek to characterise the interplay between living and dead forest components, and broader community dynamics.

6. Future Directions

The relative stability of the dead component of a forest is largely context-dependent. For example, the persistence of dead wood can, on average, last much longer in cool compared warm rainforests. Indeed, in the tropics, logs tend to decay at faster rates, and the trees often lack distinct growth rings due to a continuous growing season. In cool rainforests, by contrast, the dead wood of some species can persist on the forest floor for decades, and trees show marked growth rings due to seasonal growth periods. However, the general unresponsiveness of the 'dead forest' to short-term fluctuations in environmental conditions, allows information on past events and dynamics to be preserved through time.

To properly identify and contextualise the importance of treefall as a key forest process, integrative modelling (e.g., POM) is a necessary approach [61] because it allows for an explicit mechanistic view of functions and feedbacks, as well as permitting sensitivity analysis of key parameters and scenario testing. For instance, a forest represented in silico (e.g., the BEFORE model; [62]) can be used to manipulate treefall frequency, density and occurrence patterns, and assess the role of treefalls in determining equilibrium dynamics, disturbance and the spatial positions and/or growth of living trees, via a simulation that encompasses anything from a cohort of canopy trees through to a model of the entire forest community or ecosystem. Further, 'bottom-up' model verification, based on pattern-oriented approaches, can be used to test the influence of multiple predictors on observations (e.g., treefall, in combination with other biotic and abiotic processes such as competition, facilitation, fire, humans). Using POM filters in this way could allow for testing the sensitivity of processes and centrality of treefall in shaping the character and definition of a forest, such as the probability of a phase transition into an alternative state (e.g., degradation into open vegetation, or continued thickening into a heavily closed, continuously regenerating, and gap-dependent system). This type of modelling approach might also help underpin decisions on the resolution and ecological basis of the structural thresholds currently used to define and characterise what a forest is, i.e., what is the biological basis of current thresholds of >10% canopy cover at 5 m in height and covering an area of at least half a hectare [63]?

Two of the key advantages to characterising the metrics of treefall in forest-plot protocols are: (i) the literature already contains ample information on the importance and function of treefalls in forest communities (Table S1, Supplementary Materials); and (ii) because a treefall is relatively easy to observe (it can be readily seen and measured) and persists (in the absence of fire) in the landscape, researchers can take advantage of mensurative experiments (e.g., patchy landscape fires) to infer temporal dynamics of a system based on 'snap-shot' patterns. For example, studies comparing different forest types with matched pairs that are either undisturbed or selectively logged (i.e., living trees remain intact but fallen logs are removed), or treefall-frequent (continuously disturbed) versus treefall-infrequent forests, can reveal the importance of fallen and legacy wood in shaping the structure and dynamics of a forest [31]. Additionally, uncovering which forest species benefit most from treefalls, and how treefalls fit in systems that are heavily reliant on mass disturbance and regeneration, could also be a key direction.

Of course, measuring and modelling the dynamic components of forests (e.g., treefalls) will, in some cases, be infeasible. For instance, mapping the size and position of potentially hundreds of fallen logs per hectare is a significant logistical undertaking. Furthermore, the reliability of LiDAR and remote sensing in the spatial analysis of treefall is, although promising, yet to be fully developed, particularly for what concerns logs [64]. The information that can be gained from treefall in any given forest will depend on a variety of factors, like climate, fire frequency, decay rates, and so on. Such factors will influence the rate of transition between the states. For instance, in warmer, drier forests, the frequency of fire and activity of termites will typically be high, removing any lasting legacy of the fallen trees (reaching an extreme in the tropical savannas). This contrasts strongly with cool, wet rain forests, where ancient logs on the forest floor are among the most persistent feature of the ecosystem, shaping its dynamics across time scales that last much longer than a typical plant lifespan [65,66].

The relative importance of treefall to a given forest's dynamics might also wax and wane over time, and in situations where the forests of a given region switch repeatedly between different states. For instance, in an old-growth forest, ecologically influential treefall events would be rare, because the mature, canopy-forming individuals are long-lived and the mid-storey trees are typically too small to cause consistent disturbance effects [67]. However, when a treefall does occur in such an ecosystem (i.e., after tree death or major disturbance), the magnitude and cascading after-effects of the event can be profound. Another case is forests in which stand-replacing events occur, such as after a rare but intense wildfire or catastrophic storm. This can lead to a persistent unimodal size distribution of trees, with common ages [68]. In such a situation, large individual treefalls might not constitute an important component of the system for decades or centuries; perhaps never, if the return interval of the disturbance is sufficiently frequent. Yet even in these cases, the process of succession might lead to multiple peaks in the frequency distribution of treefalls, derived first from the shortestlived, fastest growing colonist species, and eventually as a result of the stochastic deaths within the climax community of canopy trees.

7. Conclusions

Systematically incorporating dynamic components of a forest like treefall (dead wood) as legacy components into forest-plot measurements and studies of forest processes should encourage researchers to consider and apply more active and standardised approaches to exploring the ways in which patterns link to underlying processes. For instance, snap-shot observations of living trees in forest plots are collected largely because they are thought to capture a suite of deeper-time ecological and evolutionary processes [69]; here we emphasize that patterns in the dead forest are just as important in realising this goal. Forests should thus be envisaged as not just a static landscape type, but as a complex system that can be theorised, observed, experimented and modelled in a consistent way. This sentiment was echoed centuries ago by the French explorer, Bruni D'Entrecasteaux, who upon seeing the majestic tall forests of Tasmania wrote: *"nature in all her vigour, and yet in a state of decay seems to offer to the imagination something more picturesque and more imposing than the sight of this same nature bedecked by the hand of civilised man."* [70]. The science of forest ecology ought to capture the vigour of these systems that so impressed D'Entrecasteaux, and this begins by progressing and enhancing our understanding of forests, both vital (living) and decaying (dead), into more of an integrative framework.

Supplementary Materials: The following is available online at www.mdpi.com/1999-4907/8/4/123/s1. Table S1: Synthesis of the global literature on dead-wood forest components.

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