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New times in old forests: How the past matters in European forest science

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ABSTRACT

This article tracks changing conceptions of time in European forest science over recent decades, and accounts for how they can affect forest conservation and management. Through semiotic analysis of 62 peer-reviewed articles published in ecology and forestry, we (1) characterize the temporal features of old European forests as they evolve over our study period (1997–2017), and (2) trace how new and changing temporalities in forest science have reconfigured what constitutes a problem for conservationists and managers. We describe in particular how two articulations of forest time and forest management—Forest Continuity and Forest Maturity—have evolved, identifying the emergence of two new temporalities in old forest science. Over the study period, changing conceptions of forest pasts have increasingly led to consider forests as complex and evolving ecosystems from which humans cannot be excluded.

1. Introduction

In recent decades, the temporalities of Nature have taken an increasingly important place in the environmental humanities (Ingold, 1993; Pastor-Barrué et al., 2000; Dahan, 2007; Bensaude-Vincent, 2021). The Anthropocene, as a proposed geological epoch (Crutzen, 2006), has in particular captured the minds and the imaginations of social scientists and humanities scholars. This is because it elevates humans to the status of agents of geological time and troubles the classic humanist distinction between natural and cultural history (Chakrabarty, 2009). Philosophers of history (Croce, 1913; Childe, 1951; Collingwood, 1994) have long conceptualized nature as essentially stable, with processes occurring on a scale with no common measure with most human activities. By way of contrast, global changes occur today at a pace and scale perceivable to humans and humans are understood to have the capacity to act significantly on global changes (Chakrabarty, 2009). As humans become agents of earthly time, it is more difficult to maintain the opposition between cultural, social and economic history, and evolutionary and natural history (Bonneuil and Fressoz, 2013; Latour, 2017; Quenet,

2017).

It is in this context that authors working in the social sciences have analyzed the temporalities of the environment and the environmental sciences as they relate to the politics and economics of nature conservation and landscape management (Granjou, 2016; Granjou et al., 2017; Skrydstrup, 2017). Forests, in particular, are increasingly recognized as good objects for the analysis of interactions between human and natural temporalities, especially in the scientific field of historical ecology (Kirby and Watkins, 1998). This is tied, in part, to the complexity of integrating the “unrushed temporality” and the “long-termism” of forests with the immediacy of human, political time (Nordblad, 2017: 165). Cronon's (1996) classic text is a case in point. His analysis of literary and historical texts highlights a “flight from history” (p. 16) linked to a “pristine myth” of the Old-Growth Forests of the Americas (Denevan, 1992). This ahistorical “myth” is based on the idea that North American forests, prior to European colonization, were remnants of “virgin” or “pristine” nature, “untrammelled by man”, as the 1964 American Wilderness Act formulates the idea. In this conception, such forests were gradually degraded by the effects of human activity, from which they

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require protection in order to conserve the essential traits of wild nature. Cronon proposes a counter model of forests past. He seeks to demonstrate that this “myth” elides the “history” of pre-Columbian land use, the effects of land abandonment following genocide, and centuries of colonial land grabbing (Denevan, 1992; Willis et al., 2004). It replaces this history with a Romantic ideal of sublimated nature, essentially stable absent human intervention and the advancing frontier of civilization (Cronon, 1996). Cronon critiques the specific form of conservation that the “mythical” environmental temporality implies. Wilderness is nature without humans, or nature where humans only visit on weekends for recreation. This suggests that differing conceptions of the past of forests have undeniable effects on the present of forests. A mythical past in which forests were wild and pristine supports initiatives that aim to conserve forests by removing humans from them. Oppositely, with Cronon’s environmental history, humans as a species cannot but leave our mark on the planet. The question for conservation is what kind of mark we will leave.

Over the last decades, *the past* of the European forests has become a major research problem shared by several programs in forest sciences taking the long-established forests of Europe as their object of study (Spencer and Kirby, 1992; Peterken, 2001; Hanski and Ovaskainen, 2002; Paradis-Grenouillet et al., 2018; Sabatini et al., 2018; Barredo et al., 2021; O’Brien et al., 2021). As a continent shaped by a historically high density of human presence, Europe appears to be a particularly relevant place to question the entanglement between human and nature temporalities.

Grounded in Science and Technology Studies, this manuscript tracks changing conceptions of time in European forest science over recent decades, and accounts for how they have altered the remit of forest conservation and management.

Recent work on forest temporalities in the social sciences has focused on their futures (Hölzl, 2010; Mårald and Westholm, 2016; Nordblad, 2017). This literature shows how different ways of calculating and modeling the future inform the present of forest management and conservation. Doganova (2024) highlights the effects of a formula developed by 19th-century German economists for calculating forest value by discounting future yields. First, when forest futures are envisioned using the tools of finance, forests become something else. Not complex ecosystems to be conserved, nor a commons essential to the well-being of a community, but financial assets whose value can be maximized. Second, such tools influence forest management by designating what counts by designating what counts as a “rational decision”, i.e., a decision that efficiently attains the objective of maximizing return on investment using a discounting formula. The effects on management are direct; they determine the optimal moment for felling trees (see also Vatin, 2008). Dolez et al. (2019) describe how French forest scientists anticipate the future of forests, given global changes, as they model tree growth. They identify three “micro-regimes of anticipation”, each affecting forest practice in the present in different ways. First, foresters and forest engineers model the effects of climate change on forest processes to maintain or increase forest production. Second, forest ecologists model changes in tree biology in order to mitigate the effects of a changing climate. Third, forest ecologists use forests as sentinels to detect ongoing global changes. Each of these micro-regimes of anticipation articulates a vision of the future, a vision of forests, and a vision of what management should look like. Important in this body of literature is the plurality of forest futures and the effects that the work of anticipation can have on the present of forests through their ability to make authoritative claims about what is to come.

Using a scoping review of scientific European literature published since 1997, this manuscript rather focuses on old-forest pasts in Europe. “Old forest” temporalities involve advanced states of “maturity”, with the rhythms of natural regeneration playing a key role, as well as forms of “ancientness”, which entail the continuity of forest cover and of disturbance regimes. All existing definitions of old forests (Old-Growth, ancient, primeval, primary, pristine, late-successional, mature, virgin...)

are subject to local variations (Cateau et al., 2015). What these forests have in common is that they are defined by the passage of long periods of time in the past.

First, we characterize the temporalities of old European forests, as they exist in the environmental sciences. Through our socio-anthropological reading of the literature, we describe how the temporal features of forest processes are integrated into definitions of old forests, and we track the changing conceptions of forest temporalities in the environmental sciences over time.

Second, we show how these different pasts can affect forest management and conservation. Common to these social science discussions of forest time is the assumption that scientific discourse has the ability to rearrange the world it describes. In the sociology of science and technology, the capacity of scientific discourse to modify, or even create the reality it describes, is called *performativity* (Austin, 1975; Callon, 2020). Biodiversity databases inform decisions about which species to save (Bowker, 2000); the CORINE Biotopes habitat classification scheme prioritizes some habitats for conservation over others (Waterton, 2002); the scientific classification of invasive species shapes targeted population control measures (Boonman-Berson et al., 2014). As scientific discourse informs management practice, the natural world can be reshaped in its image. In work on forest futures, performativity is linked to science’s recognized ability to anticipate and predict what comes next and, thereby, to aid conservationists and managers in adapting their practice (Doganova, 2024; Dolez et al., 2019). In this study, we propose to focus on the performativity specific to the past, by showing how changing conceptions of forest temporalities affect what constitutes a problem for conservationists and managers in the present.

2. Methods

2.1. The scoping review

We conducted a scoping review of peer-reviewed, English language literature on old forests in Europe. This method serves to map a field of research, identify existing programs, catalog points of discussion, and identify important methodological developments (Arksey and O’Malley, 2005; Pham et al., 2014). It does this by maintaining both breadth and depth in the final corpus. There is a large body of literature dealing with definitions of old-growth forest, ancient forest, mature forest, etc. and their ambiguity (see for instance Wirth et al., 2009). The aim of this review was to track recent evolution of scientific approaches dealing with European forests overall characterized by the passage of long periods of time. To embrace the full diversity of studies dealing with such type of forest, we selected our corpus through a Web of Science search for the terms “old growth forest” or “primary forest” or “ancient forest” or “ancient woodland” or “virgin forest” in the title or abstract of research articles published on forests in European countries. This produced a corpus of 1076 articles published between 1978 and 2021.

Descriptive statistics of this larger corpus lead us to make two preliminary remarks about the field of research we seek to describe. First, there is a marked increase in the scientific output on old European forests over this period. Only four papers were published between 1978 and 1988, while 63 papers were published in 2018 alone. Second, there is a diversification of publications by regions of Europe. At the start of the period, publications from and on Western Europe predominated. Starting in 2000, there were more publications from Northern and Central Europe. Starting in 2005, there were regular publications from Southern and Eastern Europe. These dynamics reflect bias in article selection, which excluded important bodies of literature in national languages. They do demonstrate the development of an intellectual space at the European scale, where discussion between and across national forestry traditions is facilitated. It is in this light that it has become pertinent to provide analysis of the scientific production on old European forests, as this article proposes to do, since it is only in recent decades that such a body of literature has come to exist.

We then selected articles for qualitative analysis from this larger corpus. We first restricted our initial search to top ranked journals in the following subject areas: Forestry; Ecology, Evolution, Behavior and Systematics; General Earth and Planetary Sciences; Ecological Modeling; Ecology; Global and Planetary Change; Nature and Landscape Conservation. Using a journal ranking metric based on the average yearly citations to recently published articles was meant to focus analysis on texts with a greater potential to excite discussion and emulation and to capture articles more likely to be discussed in media with a readership that includes forest managers. This reduced our corpus to 267 documents. We then removed 35 articles published between 2018 and 2021. This was justified by the fact that it is more difficult to evaluate the reception of such recently published articles. Finally, through an iterative process that implied reading the abstracts and methods sections of all articles, and making our reasons for retaining or excluding any given document explicit, we reduced our corpus to 62 articles published between 1997 and 2017 (see full list in [Appendix 1](#)). Articles were retained according to two objectives. First, we sought to retain articles that generate discussion, taking the number of citations as a proxy indicator of this ability. Second, we retained as much diversity as possible in the corpus, in terms of methods and approaches, disciplines and objects, publication dates and regions.

A detailed presentation of this entire selection process is available in [Appendix 2](#). We acknowledge that the choices made are not innocuous and in particular regarding the terms used in the web of science query, the choice of this platform in itself, the subject areas selected, the prioritized journals. However, we assume that the selected articles are still representative of the scientific literature published throughout the study period on European old forests.

2.2. Qualitative analysis

We developed a mixed Qualitative Data Analysis scheme, based on the grounded theory of the sociologists Bernard [Glaser and Strauss \(2005, \(2017\)\)](#), and Greimasien semiotic analysis, as developed in the work of Bruno Latour and Paolo Fabbri for use on corpora of scientific texts ([Latour and Fabbri, 1977; Latour and Woolgar, 1996; Latour, 1993](#)).

Glaser and Strauss' grounded theory served to render the process of coding more rigorous, ensuring that the analytical categories put forward emerge inductively from the material and not from a predefined theoretical framework. This is what it means to say that the theory is "grounded". In concrete terms, as the codes or tags applied to terms or concepts in the corpus gradually accumulate, we articulated them with one another into higher order analytical categories. In addition, all new codes were accompanied with a short note that justified their creation and explained how they differ from other existing and similar codes ([Dodier, 1993: 63](#)). This process was facilitated by the use of ATLAS.ti QDA software (ATLAS.ti 9 for Windows).

Glaser and Strauss' approach accounts for the continued negotiation of social order (2005); we were interested in the processes of ordering specific to a corpus of scientific articles. Following [Latour and Woolgar \(1996: 87–89\)](#), scientific activity is primarily oriented towards the production of scientific literature. It is therefore possible to study scientific activity in terms of its discursive ordering.

Analysis paid particular attention to two things. First, we were interested in which entities were given the capacity to have significant effects on forests - referred to as *actants* in semiotics - in the methods, key results and management recommendations. It is through this process of coding for actants that the temporal features of forests emerged as key agents in scientific discourse. We see this in such phrases as "*Ancient woods are indeed richer in species than recent woods*" (Peterken and Game, 1984: 180); "*The low colonization capacity of ancient forest species severely restricts the possibilities of habitat re-creation*" (Hermy et al., 1999: 20) and "*The 33 lichen and fungi 'indicator species' reflected the presence of old-growth qualities*" (Ohlson et al., 1997: 226). The ancientness of forests

is attributed the capacity to determine species richness; the low colonization speed of ancient forest plant species determines possibilities for habitat recreation; the forest dynamics producing old-growth attributes determines species presence. This is what we mean when we say that we analyze how temporal features are enacted as determinants of important forest processes ([Moi, 2002](#)).

Second, we were interested into how the temporal features of old forests reformulate the problems and challenges faced by forest management and conservation. For example, "*[Our results] suggest that great changes in forestry are required to prevent a wave of extinction cascades*" ([Komonen et al., 2000: 125](#)); "*It must be questioned whether the nature of stand development described for the studied sites is desirable, or whether management should be redirected to mimic former disturbance regimes*" ([Linder et al., 1997: 30](#)). It is through such problematization that forest science has the potential to inform conservation practice and, thereby, to reshape the forested landscapes of Europe.

3. Results

While the literature analyzed was broad and deep, two primary articulations of forest time and forest conservation and management emerged through 53 articles ([Table 1](#)). First, Forest Continuity (23 articles), which refers to the uninterrupted time that a landscape has spent with forest cover. Second, Forest Maturity (30 articles), which refers to structural characteristics specific to the age of the trees. We present four versions of each (see appendix for the distribution of the different articles in each version). For Forest Continuity, we will see Patches of Stability, Species Lists, Plant migration, and Extinction Debt. For Forest Maturity, we will see Climax Microsuccession, Indicators of Old-growthness, Coarse Woody Debris, and Changing Disturbance

Table 1

How each version articulates forest time and forest conservation.

Forest continuity	Forest maturity
<p>Version 1: Patches of stability Past forest cover loss has reduced Ancient Forest to relics; in the present, increased protection of Ancient Woodland sites is necessary in order to avoid the extinction of Ancient Forest species.</p>	<p>Version 1: Climax microsuccession Past succession dynamics have created a complex climax ecosystem; in the present, these dynamics must be protected in large forest reserves, protected from human disturbance, in order to maintain habitat complexity on which biodiversity depends.</p>
<p>Version 2: Species lists The loss of forest cover and traditional management practice has isolated and impoverished Ancient Woodland habitat; in the present, the extension of existing reserves and increased active management is necessary in order to avoid the extinction of Ancient Forest species.</p>	<p>Version 2: Indicators of old-growthness Habitat fragmentation and loss threaten biodiversity; in the present, we can reproduce the structural attributes of Old-Growth Forests in managed forests in order to restore habitats and maintain forest biodiversity.</p>
<p>Version 3: Plant migration Past loss of forest habitat connectivity has isolated patches of Ancient Woodland habitat; in the present, re-establishing connectivity with refugium in the agricultural matrix is essential in order to avoid the extinction of Ancient Forest species.</p>	<p>Version 3: Coarse woody debris Past disturbance events have produced Coarse Woody Debris; in the present, these dynamics must be protected and mimicked in order to maintain the structural and compositional complexity responsible for biodiversity.</p>
<p>Version 4: Extinction debt Past forest cover fragmentation has contracted an extinction debt; spatial connectivity of forests must be restored in the present or the debt will be paid in the future in the form of cascading biodiversity loss.</p>	<p>Version 4: Changing disturbance regimes Looking at the long-term, anthropogenic disturbance events are increasingly integrated into the natural disturbance regimes of old forests; in the present, key natural disturbance events of past regimes should be restored and/or allowed to run their course, and decisions are necessary regarding the conservation of heritage species composition.</p>

Regimes. In order to capture changing conceptions of time over the study period, we present these versions in the chronological order of their apparition in the literature. However, none of these versions has disappeared and they all continue to exist in parallel to one another, influencing each other and informing ongoing discussions.

Nine articles out of the 62 present in our corpus were not integrated in our analysis. They represent two other potential modes of recent forest temporalities related to climate and genetic, for which we did not have a sufficient number of articles in our final corpus to develop.

3.1. Forest continuity

Forest Continuity is based on a corpus of 23 articles. The methodological foundations are archive-based knowledge of woodland history. The first published and most cited article is Peterken and Game's (1984) "Historical Factors Affecting the Number and Distribution of Vascular Plant Species in the Woodlands of Central Lincolnshire". They make a distinction, which has since become common, between two primary "historical forest types". First, Ancient Forests are areas that are known to have been continuously forested from a given threshold date. This threshold date varies between countries (Matuszkiewicz et al., 2013; Palo et al., 2013), and corresponds to the oldest reliable records from before the "forest minimum" for Europe, i.e., the moment when the area of forest cover was at its lowest, in the mid-19th century for most European countries. Second, Recent Forests are areas which have been afforested in the time since this threshold date.

Using historical maps, this body of research constitutes historical inventories of disappearing Ancient Woodland sites taken as *Patches of Stability*. This is the first and earliest version of Forest Continuity in our corpus. This approach proposes histories of land cover change and sees in disappearing ancient woodland remnants of a rich and stable past. The premise of this version is that "the pattern of woodland [has been] reasonably stable" (Peterken and Game, 1984: 158) since the last period of glaciation. The claim is that if a patch of woodland was forested when forest cover in Europe was at its minimum, it is likely part of a landscape pattern that had endured for over ten thousand years (Peterken and Game, 1984; Bossuyt et al., 1999). We can therefore expect to find patches of primary forests in Ancient Woodland sites. Importantly, these authors also demonstrate how traditional landscape management participated in creating stable, species-rich forested landscapes, by increasing connectivity between patches and habitat diversity within patches. As "cultural woodland" (Rotherham, 2007; Bobiec, 2012), it is both the loss of ancient forest cover and the loss of traditional land management practices that have contributed to their impoverishment. In the *Patches of Stability* version of Forest Continuity, it is the continuity of this assemblage of traditionally managed agricultural landscapes, connecting patches of potentially primary woodland, that is understood to determine species presence in Ancient Forests.

Central to the conservation problem posed by this version of Forest Continuity is the *irreversibility* of forest cover loss (Peterken and Game, 1984; Kirby, 1988; Spencer and Kirby, 1992). Spencer and Kirby (1992) demonstrated that the loss of Ancient Forest cover has accelerated over the five decades preceding their inventory of Ancient Forests in the UK in the 1980s. Even as overall forest cover increased, Ancient Woods existed in small and isolated pockets, surrounded by intensively managed landscapes. These authors - and most authors working from the perspective of Forest Continuity - insist that it is impossible to recreate the habitat qualities associated with ancient woodland on human time scales: "Claims that secondary woods will one day become as rich as ancient, presumed primary woods seem unfounded (Peterken and Game, 1984: 180). Strict conservation through active management is needed immediately if habitat diversity and associated species richness is to be maintained.

"Floristic richness is more likely to be maintained by a policy of active treatment than a policy of non-intervention. It is widely believed that the

number of species is influenced mainly by habitat diversity which is partly an expression of vegetation structure. The structure created by non-intervention will at least temporarily be less diverse than that created by most treatments." (Peterken and Game, 1984: 181).

The second version of Forest Continuity is the elaboration of *Species Lists*, for several taxa, specific to Ancient Woodland. Here, authors demonstrate how the continuity of forest cover determines the presence of a unique set of species dependent on these habitats for their continued survival. The most frequently studied of these taxa are vascular plants. To establish such lists, authors define the "ecological profile" for "ancient forest plant species". These plant profiles build on Ellenberg indicator values for site conditions - water and light availability, soil chemistry... - and plant dispersal strategies (Ellenberg, 1978). The continuity of forest cover determines the presence of the Ancient Forest Plant Species guild for two reasons. First, long term forest cover produces its own site conditions. Second, "The low colonization capacity of ancient forest species severely restricts the possibilities of habitat re-creation" (Hermy et al., 1999: 20). This suggests that "even temporal land use changes may have dramatic effects on the survival of the ancient forest flora, and reduces the probability of successful restoration of degraded habitats" (Hermy et al., 1999: 20).

Again, decreasing forest cover is implicated in habitat loss. But authors in this version focus on the loss of traditional landscape management practices, which increases the habitat diversity inside Ancient Forests. Hermy et al. (1999) - an early article in this version, and by far the most cited - prone traditional deciduous forest management systems that favor these species, active interventions to reduce competitive plant species, with conservation focusing on extending existing reserves to allow for migration.

The third version focuses on *Plant Migration* between Ancient Forests and adjacent land. Here, the capacity of plants to disperse from patches of stable woodland and to colonize recent forests is measured in order to gauge the possibilities of habitat recreation (Bossuyt et al., 1999; De Frenne et al., 2011; Honnay et al., 1999; Honnay et al., 2002). Most often, these papers study the "colonization" capacity of ancient forest plant species in recent woodland or the agricultural matrix (Bossuyt et al., 1999; Honnay et al., 1999; De Frenne et al., 2011), but there are also studies on the "invasion" of ancient forests by weedy plants (Honnay et al., 2002).

These studies recognize the irreversible nature of habitat loss, but the focus on plant migration offers a response to the problem of species-poor recent woodland. De Frenne et al. (2011) show new, species rich forests can be created by connecting them to existing stretches of ancient hedgerows where Ancient Forest plant species find refuge.

The fourth version of Forest Continuity relates to *Extinction Debt* (Tilman et al., 1994). Several studies (Kruys and Jonsson, 1997; Komonen et al., 2000; Bailey et al., 2002; Brotons et al., 2003; Petit et al., 2004) have built on the early intuition that patches of Ancient Woodland in an agricultural matrix could be analyzed according to the principles of island biogeography (MacArthur and Wilson, 2001). They demonstrate that patches of Ancient Woodland are so isolated and fragmented that they can no longer support viable plant communities. Many extant taxa are doomed to certain, if delayed extinction (Hanski and Ovaskainen, 2002; Berglund and Jonsson, 2008). In other words, these species express a time-lagged response to the loss of their habitat or key resources. Naaf and Folk (2015) claim we cannot count on the "colonization credit" we might expect Ancient Forest species to extend to adjacent post-agricultural forests, precisely because of their limited dispersal capacities and habitat loss. The future of ancient woodland is one of cascading biodiversity loss.

The problem conservation faces in this version is that extinction debt must be reimbursed, either through the dramatic, cascading extinction of species of several kingdoms, or by increasing habitat connectivity (Komonen et al., 2000). According to the most cited article in this version (Hanski and Ovaskainen, 2002), the power of these approaches

lies in their ability to anticipate the impending extinction of the “living dead”:

“In the case of landscapes that have recently experienced substantial habitat loss and fragmentation, it would be a fatal mistake to assume that all extant species would have viable populations if any additional loss and fragmentation of the habitat were to be prevented. The only way to save such “living dead” species is to improve the quality of the landscape for these species” (Hanski and Ovaskainen, 2002: 672).

In the articles in this version, “improving the quality of the landscape” means increasing spatial connectivity between “patches of stability”. This can be achieved by establishing reserve networks (Brotans et al., 2003), and by conserving or replanting hedgerows in the agricultural matrix, which can serve as habitat corridors (Naaf and Kolk, 2015). In short, extinction debt takes us from the temporal continuity of ancient forests to the spatial connectivity of ancient woodland habitats at the landscape scale.

3.2. Forest Maturity

Forest Maturity is based on a corpus of 30 articles, which share a few oft-cited references in the German-language tradition. This is the “gap-phase dynamics paradigm”, and refers to analysis of *Climax Microsuccession* in the work of Hans Leibundgut (1959) and Štefan Korpel (1982), (1995). Authors place “small-scale forest disturbance events”, causing the death of single or small groups of trees, at the center of the cyclical and cumulative temporality of forest ontogenesis. Such tree deaths are caused, for example, by wind, disease, lightning, insect infestation, or old age. These small-scale, endogenous disturbance events drive the forest through a dynamic cycle of “development phases”, from the post-disturbance regeneration of trees to maturity and senescence. This cycle produces a “shifting mosaic” of forest patches in different development phases, with complex horizontal and vertical tree structures, tree species composition, and tree age distribution. Such complexity creates high habitat variability within such forests (Petritan et al., 2014; Garabarino, 2012). Over time, the “dynamic equilibrium” of “climax microsuccession” reaches a “steady state”, producing and reproducing local site conditions, soil chemistry, and light and water availability. We call this version Climax Microsuccession to highlight the relation to the stable state of climax ecosystems, while retaining the small-scale dynamics of forest microsuccession.

In our corpus, two articles propose Climax Microsuccession-based analysis. Boncina (2000) describes the horizontal structure of “virgin forest” patches, using a series of nine development phases, and then compares species presence in each successional phase to an adjacent close-to-nature managed site. The virgin forest is richer. Similarly, Emborg et al. (2000) account for the average time spent in a series of five, pre-defined sequential successional phases, noting that there is a nearly direct proportionality between time spent in a given successional phase, and the percentage of area in that phase. This is taken as a sign of climax stability.

An important mark of such approaches is the claim that the virgin forests of *Mitteleuropa*, in addition to being “untrammelled by man”, are also essentially untouched by large-scale disturbances. Large-scale disturbance, of the type that would flatten an entire stand, are taken to be “exogenous” and “anthropogenic”, the direct or indirect result of human degradation of the environment. Human activities have reduced forest resilience and increased the frequency and intensity of disturbance events. Such events, pushing forest ecosystems out of the cyclical microsuccession, are taken to be “unnatural”. As Emborg et al. note:

“In steady state, the condition of the system, for example expressed by the total biomass, is characterised by fluctuations and oscillations rather than directional processes at whole-system level. The shifting-mosaic steady state can be regarded as a preliminary dynamic end-point to succession” (2000: 174).

These approaches see human intervention as problematic. Boncina (2000) claims that “*The more the forest is influenced by man, e.g. by clearfell forestry, the more the composition, structure and productivity of forest community is changed, and the greater are the possibilities for unexpected and potentially undesired developments of its constituent communities*” (2000: 209). Where natural small-scale succession dynamics create “extreme variations in structure” (Emborg et al., 2000: 187), human interventions - even through near-to-nature management (Boncina, 2000: 209) - homogenize forests, leading to habitat and biodiversity loss. In contrast to all four versions of Forest Continuity, which prescribe active intervention to conserve Ancient Woodland and improve the spatial structure of the landscape, this approach to forest temporality prones non-intervention as the conservation strategy most likely to improve the quality of old forests.

The second version of Forest Maturity shifts focus towards the structural elements that result from the natural dynamics of microsuccession in order to develop *Indicators of Old-growthness* (Nilsson et al., 2003; Ugo et al., 2012; Lombardi et al., 2015; Di Filippo et al., 2017). These studies tend to intentionally avoid sites with recent large-scale disturbance events, integrating their unnaturalness into indicators:

“Densities and volumes of dead trees are very much dependent on the time since a catastrophic disturbance such as a hurricane or a crown fire. We intentionally avoided sites with such events in the recent past, since it is self-evident that extremely high values of dead wood will be recorded then. Instead, we wanted to show conditions that are more representative of the entire landscape” (Nilsson et al., 2003: 366).

Such indicators are used in two ways. First, to identify priority forests for conservation (Jonsell and Nordlander, 2002; Ugo et al., 2012; Lombardi et al., 2015; Di Filippo et al., 2017). Indicators help select forests to protect when more complex and more precise studies are inconvenient or expensive. Second, to develop silvicultural techniques which mimic natural structures in managed forests (Humphrey, 2005; Bauhus et al., 2009). The promise of “silviculture for old-growth attributes” is to maintain such biodiversity in the future by reproducing mature forest habitats in managed forests.

The third version focuses on the presence of dead wood in mature forests. Such dead wood is most often referred to as *Coarse Woody Debris* (CWD). These studies test the volume, continuity (Jonsell and Nordlander, 2002), and availability (Edman et al., 2007) of CWD, against disturbance histories, forest succession pathways, and wood decay rates. Methods are based on dendrochronology and soil charcoal analysis (Ohlson et al., 1997), and also build on historical sources and structural indicators (Siitonen et al., 2000). Comparing CWD in “virgin” and managed forests (Debeljak, 2006), or in forests with differing disturbance histories (Ohlson et al. (1997), these studies test CWD availability against species richness.

The CWD approach problematizes forest conservation in a similar manner to the Indicators of Old-growthness version. They claim, however, that the presence of dead wood is a particularly important “old-growth attribute”, since it is a key microhabitat for many forest species (note that, later on, several studies have also shown the key role of tree-related microhabitats for forest-dwelling species (Larrieu et al., 2018)). A distinguishing feature of this version is the rehabilitation of large-scale exogenous disturbance events as a natural feature of forests and a determinant of CWD availability. According to the most cited article in this version: “*In natural conditions, recurring disturbances, either small-scale gap perturbations or stand-replacing catastrophic events, continuously replenish and create CWD*” (Siitonen et al., 2000: 212). It is in this light that these authors condemn the practice of “salvage logging”, which removes dead wood following large scale disturbances to recover the economic value of the downed wood (Mikolas et al., 2017).

The fourth version Forest Maturity accounts for the *Changing Disturbance Regimes* of old-growth European forests. In the late-1990s, research from this perspective began mixing methods, using historical archives, dendroecological and paleoecological data, and descriptions of

stand structure, to demonstrate how logging had replaced fire as the primary agent of disturbance events in Fennoscandia (Linder et al., 1997). The disturbance regime - the frequency, extent, and cause of disturbance - had changed. Axelsson and Ostlund (2001) demonstrated that as disturbance regimes changed, so did microsuccession dynamics of forests. This body of literature demonstrated that, under the effect of fire suppression, flood control, increased frequency of windthrow, the transition from traditional forest management to modern forestry..., evolving disturbance regimes have had and continue to have continent-wide impacts on tree species composition in old forests (Svoboda and Pouska, 2008; Kucbel et al., 2010; Nagel et al., 2013; Janik et al., 2016; Jaliouvar et al., 2017; Mikolas et al., 2017). These multidisciplinary approaches to long term changes in disturbance regimes also demonstrated that large-scale disturbances were within the “historical range of variability” in European forests (Kucbel et al., 2010; Bruna et al., 2013; Clear et al., 2013).

Focusing on the long-term disturbance histories of old European forests has important effects on how forests are defined. It integrates anthropogenic changes into the disturbance regimes of natural forests, and naturalizes large-scale disturbance events. This adds directional, historical time to the cyclical and cumulative temporalities of the dynamic equilibrium of forest ecosystems in Climax Microsuccession. This leads authors to recommend allowing natural disturbance regimes to run their course whatever their spatial scale and intensity. Fire should be reintroduced in the Boreal forests of Fennoscandia (Linder et al., 1997; Clear et al., 2013) and regular flood regimes should return to the alluvial forests of central Europe (Janik et al., 2016). This long-termism demonstrated that forests should not be characterized by continued production and reproduction of the same; it is *natural* for new things to happen in old forests and it is *natural* for their composition and structure to change. The question this version poses to conservationists is whether it is desirable to maintain, through active management, the species composition associated with disturbance regimes that no longer exist.

4. Discussion

In this article, we tracked and described changing conceptions of forest temporalities in old-forest science in Europe over recent decades and showed how they reformulated the problems and challenges faced by forest managers and conservationists. We particularly highlighted two ways of articulating old forest times with old forest conservation and management and identified the arrival of two new temporalities in this field of research.

At the start of our study period, historical ecologists working from the perspective of Forest Continuity identified the increasing isolation and fragmentation of patches of Ancient Woodland. With the rise of island biogeography in ecology, these landscape changes were analyzed in terms of a yet to be paid *extinction debt*. The importance of the economic metaphor of debt, contracted in the past and payable in the future, cannot be overstated. It introduced a new temporality - a new way of articulating the past, present, and future of forests - into old forest science. Past changes in the landscape pattern upset the stability of Ancient Woodland patches. The species guilds associated with each patch of forest are, likely “living dead”, zombie remnants on sites now so small and isolated that they are unable to support a viable population. This anticipated, catastrophic future, articulated with a stable past, is enacted as a determinant of ongoing forest processes. Throughout our study period, researchers working from the perspective of Forest Maturity have identified the cyclical and cumulative temporalities of forest succession as a key determinant of forest biodiversity. The structural and compositional complexity of these forested landscapes is the result both of the continual and faithful reproduction of the same, and the superimposition of natural succession as a new layer of the forest palimpsest. A focus on the long term of mature forests introduced two important changes, rehabilitating large disturbance events as an important and natural feature of forest histories, and identifying

continent-wide anthropogenic changes in disturbance regimes. The cyclical and cumulative temporality of forest ontogenesis was articulated with the directional, historical temporality of changing disturbance regimes. Therein lies the new time in old forest science that we identified in this body of literature. This long-termism upsets the debated notion of climax stability.

In both cases, changing conceptions of forest temporalities came to question notion of forest stability but as well reorganize the articulation between past, present and future. Within Forest Continuity, isolated patches of Ancient Woodland acquired a potentially catastrophic future, distinct from a rich and stable past while in Forest Maturity, long-term historical ecology takes us away from stable state systems towards an understanding of forests as having a future inherited but distinct from their past. As we can see, in both cases, the past of the forest comes to matter in very different ways. In forest continuity, historical fragmentation threatens future biodiversity and calls for immediate action. In forest maturity, past disturbances inevitably shaped what forest are and opens doors into accepting that future disturbances will continue to shape them.

Our account of new times in old forest science leads us to claim that the performativity specific to the *past* lies in its ability to make forests what they are but as well to influence how they should be managed or conserved. In short, the past is not a temporal context that “contains” an object with a stable and invariable definition - forests - that moves unaffected through time. Forest time is not an empty shell. The plural pasts of forests make them what they are and tell conservationists and managers what they should be. The past is given agency in the present because it is constitutive of the object “old forest”.

The effects of the described new times in old forest science on conservation and management are notable. One example is the French National Forest Office’s “FRENE Network”, in the Auvergne-Rhône-Alpes region, which aims to connect “islands of senescence” in order to increase spatial connectivity between isolated and fragmented pools of biodiversity. Another is the Black Forest in Germany, recently labeled as UNESCO’s Man and Biosphere Reserve, recognizing the shared long-term history between forest ecosystem and cultural identity.

By showing how they evolved over time, our study demonstrated that notions of forest continuity and maturity cannot be taken for granted. Forest pasts as scientific objects are constantly changing and so are forest policies’ recommendations. However, the different versions of both forest continuity and maturity did not exclude each other. They have been integrated into more and more complex conceptions of forest pasts. Such transformations of forest temporalities have increasingly led to understand forests as ecosystems from which human cannot be excluded. For authors working from the perspective of Forest Continuity, the stability of ancient forest patches may be lost due to historical changes in the landscape pattern. Conserving those forests means re-establishing spatial connectivity in fragmented landscapes of high human pressure. For the ones working on Forest Maturity, it became clear that forest ecosystems have always been shaped by a wide range of disturbances including direct and indirect human-induced land use changes. Thus, not only old growth forests cannot anymore be considered as stable virgin nature excluding humans, but there are also increasing calls in forestry science to reproduce old-growth forest attributes by fostering natural dynamic of post-disturbance succession in managed forest.

While some authors call for considering the capacity of non-humans in the making of environmental changes (Granjou, 2016), our results suggest that forest science over the last 40 years increasingly integrated humans as active participant in forest temporalities.

CRedit authorship contribution statement

Mélanie Roy: Writing – original draft, Writing – review & editing. **Liliana Doganova:** Writing – original draft. **Ruppert Vimal:** Conceptualization, Supervision, Writing – original draft, Writing – review &

editing. **Vanessa Py-Saragaglia:** Funding acquisition, Writing – original draft, Writing – review & editing. **Evan Fisher:** Conceptualization, Formal analysis, Methodology, Writing – original draft. **Laurent LARRIER:** Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Evan Fisher reports financial support was provided by French National Research Agency.

Data Availability

Data will be made available on request.

Appendix 1 - Articles in corpus organized according to the versions

Forest continuity

Version 1: patches of stability

Bobic A (2012) Białowieża Primeval Forest as a remnant of culturally modified ancient forest. *European Journal of Forest Research* 131(5). New York: Springer: 1269–1285. DOI: 10.1007/s10342-012-0597-6.

Kirby K (1988) Changes in the Ground Flora Under Plantations on Ancient Woodland Sites. *Forestry* 61(4). Oxford: Oxford Univ Press United Kingdom: 317–338. DOI: 10.1093/forestry/61.4.317.

Matuszkiewicz JM, Kowalska A, Kozłowska A, et al. (2013) Differences in plant-species composition, richness and community structure in ancient and post-agricultural pine forests in central Poland. *Forest Ecology and Management* 310. Amsterdam: Elsevier Science Bv: 567–576. DOI: 10.1016/j.foreco.2013.08.060.

Palo A, Ivask M and Liira J (2013) Biodiversity composition reflects the history of ancient semi-natural woodland and forest habitats-Compilation of an indicator complex for restoration practice. *Ecological Indicators* 34. Amsterdam: Elsevier: 336–344. DOI: 10.1016/j.ecolind.2013.05.020.

Peterken GF and Game M (1984) Historical Factors Affecting the Number and Distribution of Vascular Plant Species in the Woodlands of Central Lincolnshire. *Journal of Ecology* 72(1). [Wiley, British Ecological Society]: 155–182. DOI: 10.2307/2260011.

Rotherham ID (2007) The implications of perceptions and cultural knowledge loss for the management of wooded landscapes: A UK case-study. *Forest Ecology and Management* 249(1–2). Amsterdam: Elsevier Science Bv: 100–115. DOI: 10.1016/j.foreco.2007.05.030.

Spencer J and Kirby K (1992) An Inventory of Ancient Woodland for England and Wales. *Biological Conservation* 62(2). Oxford: Elsevier Sci Ltd: 77–93. DOI: 10.1016/0006-3207(92)90929-H.

Version 2: species lists

Hermý M, Honnay O, Firbank L, et al. (1999) An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biological Conservation* 91(1). Oxford: Elsevier Sci Ltd: 9–22. DOI: 10.1016/S0006-3207(99)00045-2.

Schmidt M, Moelder A, Schoenfelder E, et al. (2014) Determining ancient woodland indicator plants for practical use: A new approach developed in northwest Germany. *Forest Ecology and Management* 330. Amsterdam: Elsevier: 228–239. DOI: 10.1016/j.foreco.2014.06.043.

Watkinson AR, Riding AE and Cowie NR (2001) A community and population perspective of the possible role of grazing in determining the ground flora of ancient woodlands. *Forestry* 74(3). Oxford: Oxford Univ Press: 231–239. DOI: 10.1093/forestry/74.3.231.

Wilson BR, Moffatt AJ and Nortcliff S (1997) The nature of three ancient woodland soils in southern England. *Journal of Biogeography* 24(5). Oxford: Blackwell Science Ltd: 633–646. DOI: 10.1111/j.1365-2699.1997.tb00074.x.

Version 3: plant migration

Bossuyt B, Hermý M and Deckers J (1999) Migration of herbaceous plant species across ancient-recent forest ecotones in central Belgium. *Journal of Ecology* 87(4). Oxford: Blackwell Science Ltd: 628–638. DOI: 10.1046/j.1365-2745.1999.00379.x.

De Frenne P, Baeten L, Graae BJ, et al. (2011) Interregional variation in the floristic recovery of post-agricultural forests. *Journal of Ecology* 99(2). Hoboken: Wiley: 600–609. DOI: 10.1111/j.1365-2745.2010.01768.x.

Honnay O, Hermý M and Coppin P (1999) Impact of habitat quality on forest plant species colonization. *Forest Ecology and Management* 115(2–3). Amsterdam: Elsevier Science Bv: 157–170. DOI: 10.1016/S0378-1127(98)00396-X.

Honnay O, Verheyen K and Hermý M (2002) Permeability of ancient forest edges for weedy plant species invasion. *Forest Ecology and Management* 161(1–3). Amsterdam: Elsevier Science Bv: 109–122. DOI: 10.1016/S0378-1127(01)00490-X.

Version 4: extinction debt

Bailey SA, Haines-Young RH and Watkins C (2002) Species presence in fragmented landscapes: modelling of species requirements at the national level. *Biological Conservation* 108(3). Oxford: Elsevier Sci Ltd: 307–316. DOI: 10.1016/S0006-3207(02)00119-2.

Berglund H and Jonsson BG (2008) Assessing the extinction vulnerability of wood-inhabiting fungal species in fragmented northern Swedish boreal forests. *Biological Conservation* 141(12). Oxford: Elsevier Sci Ltd: 3029–3039. DOI: 10.1016/j.biocon.2008.09.007.

Brotans L, Monkkonen M, Huhta E, et al. (2003) Effects of landscape structure and forest reserve location on old-growth forest bird species in

Northern Finland. *Landscape Ecology* 18(4). Dordrecht: Springer: 377–393. DOI: 10.1023/A:1026148825138.

Hanski I and Ovaskainen O (2002) Extinction debt at extinction threshold. *Conservation Biology* 16(3). Malden: Blackwell Publishing Inc: 666–673. DOI: 10.1046/j.1523-1739.2002.00342.x.

Komonen A, Penttilä R, Lindgren M, et al. (2000) Forest fragmentation truncates a food chain based on an old-growth forest bracket fungus. *Oikos* 90(1). Hoboken: Wiley: 119–126. DOI: 10.1034/j.1600-0706.2000.900112.x.

Kruys N and Jonsson BG (1997) Insular patterns of calicioid lichens in a boreal old-growth forest-wetland mosaic. *Ecography* 20(6). Hoboken: Wiley: 605–613. DOI: 10.1111/j.1600-0587.1997.tb00429.x.

Naaf T and Kolk J (2015) Colonization credit of post-agricultural forest patches in NE Germany remains 130–230 years after reforestation. *Biological Conservation* 182. Oxford: Elsevier Sci Ltd: 155–163. DOI: 10.1016/j.biocon.2014.12.002.

Petit S, Griffiths L, Smart SS, et al. (2004) Effects of area and isolation of woodland patches on herbaceous plant species richness across Great Britain. *Landscape Ecology* 19(5). Dordrecht: Springer: 463–471. DOI: 10.1023/B:LAND.0000036141.30359.53.

Forest maturity

Version 1: climax microsuccession

Boncina A (2000) Comparison of structure and biodiversity in the Rajhenav virgin forest remnant and managed forest in the Dinaric region of Slovenia. *Global Ecology and Biogeography* 9(3). Oxford: Blackwell Science Ltd: 201–211. DOI: 10.1046/j.1365-2699.2000.00155.x.

Emborg J, Christensen M and Heilmann-Clausen J (2000) The structural dynamics of Suserup Skov, a near-natural temperate deciduous forest in Denmark. *Forest Ecology and Management* 126(2). Amsterdam: Elsevier Science Bv: 173–189. DOI: 10.1016/S0378-1127(99)00094-8.

Garbarino M, Mondino EB, Lingua E, et al. (2012) Gap disturbances and regeneration patterns in a Bosnian old-growth forest: a multispectral remote sensing and ground-based approach. *Annals of Forest Science* 69(5). Paris: Springer France: 617–625. DOI: 10.1007/s13595-011-0177-9.

Petritan IC, Marzano R, Petritan AM, et al. (2014) Overstory succession in a mixed *Quercus petraea*-*Fagus sylvatica* old growth forest revealed through the spatial pattern of competition and mortality. *Forest Ecology and Management* 326. Amsterdam: Elsevier: 9–17. DOI: 10.1016/j.foreco.2014.04.017.

Rozenbergar D, Mikac S, Anic I, et al. (2007) Gap regeneration patterns in relationship to light heterogeneity in two old-growth beech-fir forest reserves in South East Europe. *Forestry* 80(4). Oxford: Oxford Univ Press: 431–443. DOI: 10.1093/forestry/cpm037.

Version 2: indicators of old-growthness

Bauhus J, Puettmann K and Messier C (2009) Silviculture for old-growth attributes. *Forest Ecology and Management* 258(4). Amsterdam: Elsevier: 525–537. DOI: 10.1016/j.foreco.2009.01.053.

Di Filippo A, Biondi F, Piovesan G, et al. (2017) Tree ring-based metrics for assessing old-growth forest naturalness. *Journal of Applied Ecology* 54(3). Hoboken: Wiley: 737–749. DOI: 10.1111/1365-2664.12793.

Hegland SJ, Lilleeng MS and Moe SR (2013) Old-growth forest floor richness increases with red deer herbivory intensity. *Forest Ecology and Management* 310. Amsterdam: Elsevier: 267–274. DOI: 10.1016/j.foreco.2013.08.031.

Humphrey JW (2005) Benefits to biodiversity from developing old-growth conditions in British upland spruce plantations: a review and recommendations. *Forestry* 78(1). Oxford: Oxford Univ Press: 33–53. DOI: 10.1093/forestry/cpi004.

Lombardi F, Marchetti M, Corona P, et al. (2015) Quantifying the effect of sampling plot size on the estimation of structural indicators in old-growth forest stands. *Forest Ecology and Management* 346. Amsterdam: Elsevier: 89–97. DOI: 10.1016/j.foreco.2015.02.011.

Nilsson SG, Niklasson M, Hedin J, et al. (2003) Densities of large living and dead trees in old-growth temperate and boreal forests (vol 161, pg 189, 2002). *Forest Ecology and Management* 178(3). Amsterdam: Elsevier Science Bv: 353–+. DOI: 10.1016/S0378-1127(03)00083-5.

Suorsa P, Huhta E, Jantti A, et al. (2005) Thresholds in selection of breeding habitat by the Eurasian treecreeper (*Certhia familiaris*). *Biological Conservation* 121(3). Oxford: Elsevier Sci Ltd: 443–452. DOI: 10.1016/j.biocon.2004.05.014.

Ugo C, Lorenzo S, Vittorio G, et al. (2012) Classification of the oldgrowthness of forest inventory plots with dissimilarity metrics in Italian National Parks. *European Journal of Forest Research* 131(5). New York: Springer: 1473–1483. DOI: 10.1007/s10342-012-0616-7.

Version 3: coarse woody debris

Andersson R and Östlund L (2004) Spatial patterns, density changes and implications on biodiversity for old trees in the boreal landscape of northern Sweden. *Biological Conservation* 118(4). Oxford: Elsevier Sci Ltd: 443–453. DOI: 10.1016/j.biocon.2003.09.020.

Debeljak M (2006) Coarse woody debris in virgin and managed forest. *Ecological Indicators* 6(4). Amsterdam: Elsevier: 733–742. DOI: 10.1016/j.ecolind.2005.08.031.

Edman M, Jonsson M and Jonsson BG (2007) Fungi and wind strongly influence the temporal availability of logs in an old-growth spruce forest. *Ecological Applications* 17(2). Washington: Ecological Soc Amer: 482–490. DOI: 10.1890/06-0852.

Hilszczanski J, Gibb H, Hjalten J, et al. (2005) Parasitoids (Hymenoptera, Ichneunionioidea) of Saproxylic beetles are affected by forest successional stage and dead wood characteristics in boreal spruce forest. *Biological Conservation* 126(4). Oxford: Elsevier Sci Ltd: 456–464. DOI: 10.1016/j.biocon.2005.06.026.

Jonsell M and Nordlander G (2002) Insects in polypore fungi as indicator species: a comparison between forest sites differing in amounts and continuity of dead wood. *Forest Ecology and Management* 157(1–3). Amsterdam: Elsevier: 101–118. DOI: 10.1016/S0378-1127(00)00662-9.

Mikolas M, Svitok M, Bollmann K, et al. (2017) Mixed-severity natural disturbances promote the occurrence of an endangered umbrella species in primary forests. *Forest Ecology and Management* 405. Amsterdam: Elsevier Science Bv: 210–218. DOI: 10.1016/j.foreco.2017.09.006.

Ohlson M, Söderström L, Hörnberg G, et al. (1997) Habitat qualities versus long-term continuity as determinants of biodiversity in boreal old-growth swamp forests. *Biological Conservation* 81(3): 221–231. DOI: 10.1016/S0006-3207(97)00001-3.

Sii-tonen J, Martikainen P, Punttila P, et al. (2000) Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. *Forest Ecology and Management* 128(3). Amsterdam: Elsevier Science Bv: 211–225. DOI: 10.1016/S0378-1127(99)00148-6.

Version 4: changing disturbance regimes

Axelsson AL and Ostlund L (2001) Retrospective gap analysis in a Swedish boreal forest landscape using historical data. *Forest Ecology and Management* 147(2–3). Amsterdam: Elsevier Science Bv: 109–122. DOI: 10.1016/S0378-1127(00)00470–9.

Bruna J, Wild J, Svoboda M, et al. (2013) Impacts and underlying factors of landscape-scale, historical disturbance of mountain forest identified using archival documents. *Forest Ecology and Management* 305. Amsterdam: Elsevier Science Bv: 294–306. DOI: 10.1016/j.foreco.2013.06.017.

Clear JL, Seppa H, Kuosmanen N, et al. (2013) Holocene fire frequency variability in Vesijako, Strict Nature Reserve, Finland, and its application to conservation and management. *Biological Conservation* 166. Oxford: Elsevier Sci Ltd: 90–97. DOI: 10.1016/j.biocon.2013.06.008.

Jaloviari P, Saniga M, Kuchel S, et al. (2017) Seven decades of change in a European old-growth forest following a stand-replacing wind disturbance: A long-term case study. *Forest Ecology and Management* 399. Amsterdam: Elsevier Science Bv: 197–205. DOI: 10.1016/j.foreco.2017.05.036.

Janik D, Adam D, Hort L, et al. (2016) Patterns of *Fraxinus angustifolia* in an alluvial old-growth forest after declines in flooding events. *European Journal of Forest Research* 135(2). New York: Springer: 215–228. DOI: 10.1007/s10342-015-0925-8.

Kuchel S, Jaloviari P, Saniga M, et al. (2010) Canopy gaps in an old-growth fir-beech forest remnant of Western Carpathians. *European Journal of Forest Research* 129(3). New York: Springer: 249–259. DOI: 10.1007/s10342-009-0322-2.

Linder P, Elfving B and Zackrisson O (1997) Stand structure and successional trends in virgin boreal forest reserves in Sweden. *Forest Ecology and Management* 98(1). Amsterdam: Elsevier Science Bv: 17–33. DOI: 10.1016/S0378-1127(97)00076–5.

Nagel TA, Svoboda M and Kobal M (2014) Disturbance, life history traits, and dynamics in an old-growth forest landscape of southeastern Europe. *Ecological Applications* 24(4). Hoboken: Wiley: 663–679. DOI: 10.1890/13-0632.1.

Svoboda M and Pouska V (2008) Structure of a Central-European mountain spruce old-growth forest with respect to historical development. *Forest Ecology and Management* 255(7). Amsterdam: Elsevier: 2177–2188. DOI: 10.1016/j.foreco.2007.12.031.

We identified the existence of two other potential modes of articulated forest temporalities with problems for conservation, for which we did not have a sufficient number of articles in our final corpus to develop.

Climate

Castagneri D, Nola P, Motta R, et al. (2014) Summer climate variability over the last 250 years differently affected tree species radial growth in a mesic *Fagus-Abies-Picea* old-growth forest. *Forest Ecology and Management* 320. Amsterdam: Elsevier: 21–29. DOI: 10.1016/j.foreco.2014.02.023.

Hattenschwiler S and Schafellner C (2004) Gypsy moth feeding in the canopy of a CO₂-enriched mature forest. *Global Change Biology* 10(11). Hoboken: Wiley: 1899–1908. DOI: 10.1111/j.1365-2486.2004.00856.x.

Herbst M, Mund M, Tamrakar R, et al. (2015) Differences in carbon uptake and water use between a managed and an unmanaged beech forest in central Germany. *Forest Ecology and Management* 355. Amsterdam: Elsevier Science Bv: 101–108. DOI: 10.1016/j.foreco.2015.05.034.

Pietsch SA and Hasenauer H (2006) Evaluating the self-initialization procedure for large-scale ecosystem models. *Global Change Biology* 12(9). Oxford: Blackwell Publishing: 1658–1669. DOI: 10.1111/j.1365-2486.2006.01211.x.

Piovesan G, Biondi F, Di Filippo A, et al. (2008) Drought-driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. *Global Change Biology* 14(6). Hoboken: Wiley: 1265–1281. DOI: 10.1111/j.1365-2486.2008.01570.x.

Seedre M, Kopacek J, Janda P, et al. (2015) Carbon pools in a montane old-growth Norway spruce ecosystem in Bohemian Forest: Effects of stand age and elevation. *Forest Ecology and Management* 346. Amsterdam: Elsevier: 106–113. DOI: 10.1016/j.foreco.2015.02.034.

Genetics and heredity

Cottrell JE, Munro RC, Tabbener HE, et al. (2002) Distribution of chloroplast DNA variation in British oaks (*Quercus robur* and *Q. petraea*): the influence of postglacial colonisation and human management. *Forest Ecology and Management* 156(1–3). Amsterdam: Elsevier Science Bv: 181–195. DOI: 10.1016/S0378-1127(01)00642–9.

Franzen I, Vasaitis R, Penttila R, et al. (2007) Population genetics of the wood-decay fungus *Phlebia centrifuga* P. Karst. in fragmented and continuous habitats. *Molecular Ecology* 16(16). Oxford: Blackwell Publishing: 3326–3333. DOI: 10.1111/j.1365-294X.2007.03394.x.

Paffetti D, Travaglini D, Buonamici A, et al. (2012) The influence of forest management on beech (*Fagus sylvatica* L.) stand structure and genetic diversity. *Forest Ecology and Management* 284. Amsterdam: Elsevier Science Bv: 34–44. DOI: 10.1016/j.foreco.2012.07.026.

Appendix 2 - selection protocol

We began by a search in the Web of Science database, for English language articles published on forests in European countries with “old growth forest” or “primary forest” or “ancient forest” or “ancient woodland” or “virgin forest” in the Title or Abstract fields, in the following categories: Forestry, Ecology, Biochemistry & Molecular Biology, Biology, Evolutionary biology, Plant Sciences, or Biodiversity Conservation.

This yielded 1076 results.

1. Selection of journals

To bring this down, we restricted our search to the 100 top ranked journals, according to the Scopus CiteScore, in the following subject areas: Forestry; Ecology, Evolution, Behavior and Systematics; General Earth and Planetary Sciences; Ecological Modeling; Ecology; Global and Planetary Change; Nature and Landscape Conservation. After perusing the resulting source list, we removed 8 journals considered too distant from our research interests (*GCB Bioenergy, Reviews in Aquaculture, Global Food Security, Food and Energy Security, GPS Solutions, Computers and Electronics in Agriculture, Elementa, Evolution, Medicine and Public Health*). For every journal excluded, we added an additional journal at the end of the ranking in order to obtain 100 source journals.

Only 6 of these 100 journals were in the domain of forestry. This is because forestry journals rank lower, on average, than generalist life science journals. To better capture the specificity of our research object, we wanted to be able to search at least 20 forestry journals. We therefore added the 14 top ranked forestry journals to our source list.

2. Web of Science search

We then used the same query string as above, applied to our new source list. This yielded 267 results, of which 123 were from generalist ecology journals, and 144 were from the forestry journals.

4. Removing articles where old forests are context and not topic

We then removed articles in which old forests are the context or site of the investigation, but are not the object of research. For example, we removed a study on the maintenance of forest roads, where the term “primary forest” appears in the abstract in the phrase “primary forest roads”. The selection process was based on the reading of abstracts, titles and keywords. At this stage, we applied an inclusive selection strategy: any doubts or hesitation led to the retention of articles rather than their exclusion.

This left us with a total of 169 articles, of which 79 were from generalist ecology journals and 90 from the specialist forestry journals.

5. Final Selection

We began by removing the 35 articles published between 2018 and 2021. This is justified by the fact that it is more difficult to evaluate the reception of such recently published articles. This also meant that more recent trends in forest science - specifically climate and eDNA - are under-represented in our corpus.

We then removed few articles focusing on study regions outside of continental Europe. Subsequent selection was meant to maintain both breadth and depth, while ensuring that the final corpus was of a size appropriate for qualitative analysis in the time allotted. To ensure this, we sought to make explicit the reasons to retain each article. We developed a set of codes to apply to the articles which would allow us to filter them according to country and approach. A total of 33 different approaches were identified (eg., fragmentation, herbivory, succession, climate, DNA, dendrometrics...). Several approach tags could be applied to each article.

We sought to reduce corpus size by approximately one third. To this end, we cross referenced, for each article, the approach, the number of citations, and the country of the study site. We relied heavily on the number of citation rankings and, in general, we retained the top $\frac{2}{3}$ of articles according to the number of citations. However, we also sought to retain geographical and methodological diversity. To illustrate, let us take the tag Approach_gapdynamics as an example (cf. the table below). Articles 3 and 4 in the table are by the same authors and from the same study site (Kucbel et al., 2010, 2012). To maintain diversity in our corpus, we retained only the most cited of the two (Kucbel, 2010), and took the next most cited article from the Approach_gapdynamics tag. We then removed the least cited of the 6 articles to meet our goal of reducing the size of the corpus by $\frac{1}{3}$.

	Authors	Date	Title	Journal	Cits	
1	Axelsson, A. L.; Ostlund, L.	2001	Retrospective gap analysis in a Swedish boreal forest landscape using historical data	Forest Ecology and Management	101	Sweden
2	Rozenbergar, Dusan; Mikac, Stjepan; Anic, Igor; Diaci, Jurij	2007	Gap regeneration patterns in relationship to light heterogeneity in two old-growth beech-fir forest reserves in South East Europe	Forestry	75	Slovenia, Croatia
3	Kucbel, Stanislav; Jaloviari, Peter; Saniga, Milan; Vencurik, Jaroslav; Klimas, Vladimir	2010	Canopy gaps in an old-growth fir-beech forest remnant of Western Carpathians	European Journal of Forest Research	71	Slovakia
4	Kucbel, Stanislav; Saniga, Milan; Jaloviari, Peter; Vencurik, Jaroslav	2012	Stand structure and temporal variability in old-growth beech-dominated forests of the northwestern Carpathians: A 40-years perspective	Forest Ecology and Management	51	Slovakia
5	Garbarino, Matteo; Mondino, Enrico Borgogno; Lingua, Emanuele; Nagel, Thomas A.; Dukic, Vojislav; Govedar, Zoran; Motta, Renzo	2012	Gap disturbances and regeneration patterns in a Bosnian Old-Growth Forest: a multispectral remote sensing and ground-based approach	Annals of Forest Science	42	Bosnia
6	Diaci, Jurij; Adamic, Tomaz; Rozman, Andrej	2012	Gap recruitment and partitioning in an old-growth beech forest of the Dinaric Mountains: Influences of light regime, herb competition and browsing	Forest Ecology and Management	28	Slovenia

We continued through this process for all identified approaches until we arrived at our final corpus of 62 articles.

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