



Tansley review

Forest ecosystems of temperate climatic regions: from ancient use to climate change

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Summary

Humans have long utilized resources from all forest biomes, but the most indelible anthropogenic signature has been the expanse of human populations in temperate forests. The purpose of this review is to bring into focus the diverse forests of the temperate region of the biosphere, including those of hardwood, conifer and mixed dominance, with a particular emphasis on crucial challenges for the future of these forested areas. Implicit in the term 'temperate' is that the predominant climate of these forest regions has distinct cyclic, seasonal changes involving periods of growth and dormancy. The specific temporal patterns of seasonal change, however, display an impressive variability among temperate forest regions. In addition to the more apparent current anthropogenic disturbances of temperate forests, such as forest management and conversion to agriculture, human alteration of temperate forests is actually an ancient phenomenon, going as far back as 7000 yr before present (BP). As deep-seated as these past legacies are for temperate forests, all current and future perturbations, including timber harvesting, excess nitrogen deposition, altered species' phenologies, and increasing frequency of drought and fire, must be viewed through the lens of climate change.

I. Introduction

Forest ecosystems have always been an integral part of human existence, whether as a source of food, fiber, and habitat, as an essential component in maintaining the atmospheric balance of O₂ and CO₂, or as a source of musical, artistic, or poetic inspiration.

Gilliam (2014)

I chose to begin my book on the ecology of herbaceous communities of forests of eastern North America with this

statement for both personal and professional reasons. I suspect that many, if not most, people who have had direct contact with forests eventually grow to establish an intimate connection with them, and at a variety of levels. It was such a personal intimacy that led to my scientific study of them. As this is a Tansley review, it is an appropriate aside to note that Sir Arthur Tansley himself conveyed a special sense of awe regarding forests, more specifically the Kingley Vale in his native England (Fig. 1), which offered a view that Tansley considered 'the finest in England,' a place that held both spiritual and professional significance for him, first as an



Fig. 1 Kingley Vale, West Sussex, England. Photo credit: David D. Williams.

11-yr-old boy and later as an international leader in the field of plant ecology (Ayres, 2012).

Although humans have long utilized resources associated with all forest biomes – tropical, subtropical, temperate and boreal – I suggest that it is the expanse of human populations in the temperate region that has left the most indelible anthropogenic signature among forested regions. Certainly, deforestation in the tropics has been, and continues to be, a serious environmental concern, for example, with projected loss of forest cover being up to 40% for the Amazon Basin by 2050 (Soares-Fihlo *et al.*, 2006), and a global annual loss rate of 0.4% (Hansen *et al.*, 2013; Malhi *et al.*, 2014). However, a far greater relative fraction of the original extent of temperate forests of the eastern United States has at one time been harvested, with estimates of <1% of these original forests remaining as primary (old-growth) forests (Davis, 1996). Older examples of anthropogenic alteration are wide-spread in Central Europe, where forest conversion dates back to the Neolithic Period (EEA, 2007). Dambrine *et al.* (2007) found evidence for 2000-yr-old ecological legacies created by temperate forest conversion and subsequent agricultural practices by the Romans in central France. Older still is the human imprint left on temperate forests of China, wherein extensive forest alteration dates back some 6000 yr before present (BP), to such an extent that the roles of climate and anthropogenic disturbance are essentially confounded in understanding long-term patterns of change in vegetation (Liu, 1988). Thus, if there is a common theme across the global distribution of temperate forests, it is that the human imprint on them is indelibly large and deep, and more so than with any other forest biome type.

Fig. 2 Anthrosequence in a stylized temperate woodland biome illustrating conceptual relationships among society types and social centrality, and their interactions with land suitability for agriculture and settlements in shaping the spatial patterning of human populations, land use and land cover, and their ecological consequences. Settlement patterns are drawn to allow interpretation as a chronosequence of societies from left to right; however, alternate transitions also are likely, for example, from hunter-gatherer to industrial. (a) Anthropogenic transformation of landscapes under different sociocultural systems (top) relative to spatial variations in social centrality (horizontal axis; same for all charts below) and land suitability (vertical axis). Landscape legend is at far left. (b) Anthrome level patterns across regional landscapes (black box frames landscape in a). (c) Variations in human population densities and relative land use and land cover areas (white represents no human use of any kind; ornamental land use includes parks, yards). (d) Relative variations in ecosystem processes, including net primary production, combustion of biomass *in situ* (natural fires, unintended anthropogenic fires and intended fires, e.g. land clearing), *ex situ* (hearth fires, cooking, heating), and fossil fuels, organic carbon accumulation in vegetation and soils, and reactive nitrogen and available soil phosphorus. (e) Relative variations in biogeographic and evolutionary processes, including woodland habitat patch size and relative isolation from other biotic communities, megafauna biomass (not including humans; native and domesticated), plant species richness of native, exotic and domesticated plants, and relative area of landscape without human populations or land use (wild), used directly by human populations ('used'; e.g. crops, grazing, settlements), and transformed by human influences, but not used directly (novel). Figure reprinted from Ellis (2015), with permission from author.

The term 'global change' is a collective term to describe anthropogenic modification of all aspects of the global environment that has the potential to alter the sustainability of the Earth for life. Often erroneously used interchangeably with anthropogenic climate change (hereafter, simply 'climate change'), global change comprises not only climate change, but also other essential facets of environmental change that interact with climate change, including land use, modification of local and regional hydrological cycles, changes in biogeochemical cycles, and biodiversity loss (Vitousek, 1994; Steffen *et al.*, 2011; Franklin *et al.*, 2016). Clearly, global change is not only quite evident in all temperate forests of the world, but also it has long been so.

Indeed, there is an ancient legacy of human alteration of landscapes of temperate forests on a global scale. In North America, notable evidence suggests that, far before the arrival of Europeans, use of fire by Native American peoples greatly impacted the composition of eastern hardwood forests, especially regarding tree species of masting or fruiting value, either directly for food or indirectly for game forage (Kay & Simmons, 2002). Even the English landscape that was so dear to Tansley (e.g. the Kingley Vale panorama; Fig. 1) was anything but pristine wilderness, given widespread deforestation of the English landscape by Romans 2000 yr BP (Williams, 2006). These observations challenge the very notion of what truly constitutes a primary or pristine state. Further, global change should never be considered a solely recent, modern phenomenon.

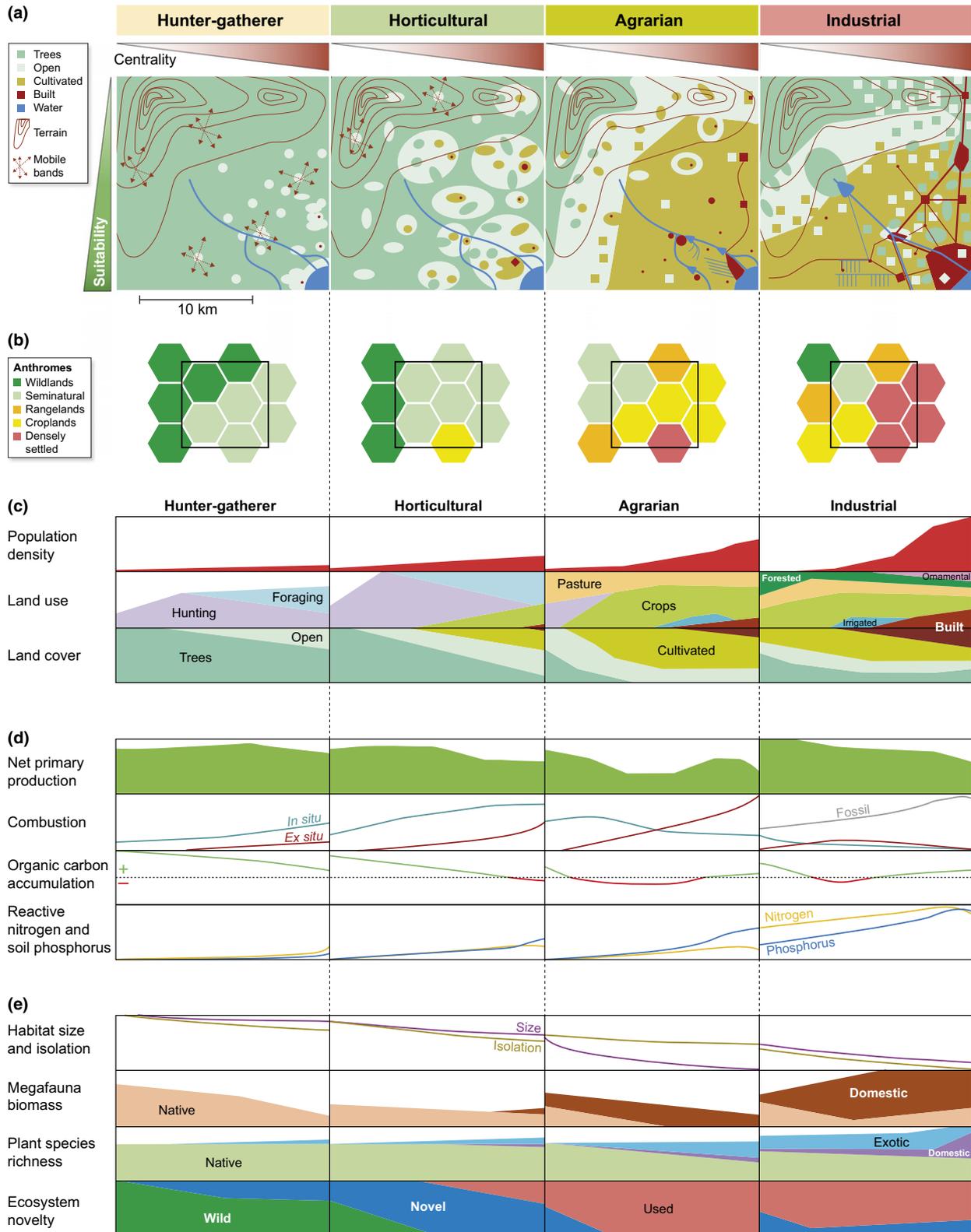
New terminology has recently been developed to address this awareness. Ellis *et al.* (2010) quantified anthropogenic change of global biomes (*anthromes*). Even our current epoch – the Holocene – is increasingly being referred to as the *Anthropocene* considering wide temporal and spatial scales of human alteration of all facets of the biosphere, from domestication of animal species and conversion of vast areas of land for cultivation, to long-term changes in atmospheric chemistry (Steffen *et al.*, 2011; Ellis, 2015; Lewis & Maslin, 2015).

Ellis (2015) conceptualized how humans, more than any other multicellular organism, have transformed Earth's ecosystems, including temperate forests, leading to what he calls anthroecology theory. Figure 2 provides a visual representation of this theory for a temperate woodland. Beginning with earliest human inhabitation of the Earth, human populations have not only expanded in number, but have also changed socio-culturally, from hunter-gatherer, to horticultural, eventually to our current industrial status. The result has been chronic

anthropogenic change in land use and cover, patterns of energy consumption, ecosystem properties (e.g. carbon flux and nutrient cycling) and ecosystem state (from ‘wild’ to ‘novel’ to ‘used’) (Fig. 2). This provides a conceptual framework for

this review, as it links ancient use of temperate forests to current patterns of climate change.

The purpose of this review is to bring into focus the diverse forests of the temperate region of the biosphere, with particular



emphasis on crucial challenges for the future of temperate forests. Although these are generally found between 20° and 60° in each of the north and south latitudes, because land mass distribution of the biosphere is decidedly asymmetrical (more land occurring north of the equator) and due to a variety of climatic, oceanographic, and orographic factors, temperate forests of the Southern Hemisphere lack the widespread nature of their northern counterparts. Consequently, somewhat more emphasis will be placed on temperate forests of the Northern Hemisphere.

II. A brief biogeography and history of temperate forests

In North America, temperate forests span most of the eastern United States as hardwoods of widely varying species dominance, with conifer and mixed (conifer/hardwood) forests occurring in parts of the southeast, west and, especially, the Pacific Northwest, from the coastal United States into Canada. Temperate forests dominate essentially all of England and northern Europe, with a narrow band reaching far into Russia, much of eastern China and virtually all of Japan (Fig. 3). Distributions of temperate forests are more restricted in the Southern Hemisphere than in the Northern Hemisphere, including southern Chile, southeastern Australia and all of Tasmania, and parts of New Zealand, including all of the North Island, where it is referred to as oceanic temperate forest (McGlone *et al.*, 2016). Temperate conifers tend to dominate in more extreme conditions (e.g. cold climates and/or infertile soils) (Reich & Frelich, 2002; Waring, 2002), or in fire-dominated regions (e.g. the southeastern Coastal Plain and western regions of the USA), although conifer dominance in other regions (e.g. North American Pacific Northwest) has been ascribed to unusually long photosynthetic seasons arising from mild winters with abundant rainfall (Givnish, 2002) (Fig. 3).

The predominant climate of most of these forest regions is one of distinct cyclic, seasonal changes involving periods of growth and dormancy. Specific temporal patterns of seasonal change, however,

display impressive variability among temperate forest regions, a function of latitude (longer growing seasons toward at lower latitudes), topographic features (e.g. mountains) and proximity to oceans with marine currents of varying prevailing temperatures. The latter is evidenced by the development of temperate rainforests associated with coastal main lands or islands, including the Pacific coast of North America and small areas of Great Britain and Japan, and throughout most of southern Chile, southeastern Australia and southern New Zealand (Alaback, 1991).

Geological history and soil formation also vary greatly among temperate forests, thus precluding broad generalizations (Bally & Palmer, 1989; Ponge *et al.*, 2011). In North America the geological (continental) structure is generally symmetrical, beginning with the middle outward including shield, interior lowlands, mountains, coastal plains, continental shelves and ocean basins. By contrast, Eurasia lacks such symmetry, with Europe being geologically separated from Asia by the Ural Mountains (King, 2015). Thus, the broad spatial patterns of soil formation in North America contrast sharply with those for Asia (Bally & Palmer, 1989; Ponge *et al.*, 2011; King, 2015).

One aspect of geological history shared among temperate forests is the profound effects of glaciation (Clark *et al.*, 2009). Most relevant is the occurrence of the last glacial maximum (LGM), a period of widespread surface ice that ended *c.* 20 000 yr BP (Yokoyama *et al.*, 2000). Given the extent of LGM glaciers (Fig. 4a, b), any exposition of temperate forests necessitates at least a perfunctory understanding of their widespread nature. Glaciations of the LGM even have a diverse nomenclature, based on global location (Ehlers & Gibbard, 2007). Prominent in the Northern Hemisphere were the *Wisconsin* glaciation in North America and the *Devensian*, *Würm* and *Weichselian* glaciations in the British Isles, Alps and Northern/Central Europe, respectively. In the Southern Hemisphere, LGM glaciers include the *Llanquihue* and *Otira* glaciations in Chile and New Zealand, respectively.

Despite their widespread occurrence, temperate forests of many regions are similar in development toward their present state. Most

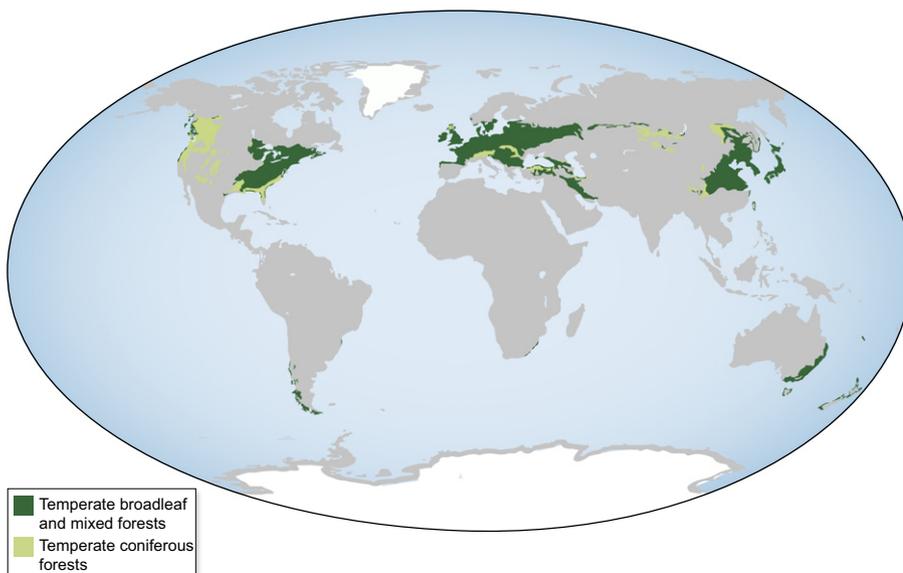


Fig. 3 Global distribution of temperate forests. Occurrence of temperate broadleaf and mixed forests is indicated in dark green, whereas occurrence of temperate coniferous forests is indicated in light green. Map data taken from Olson *et al.* (2001). Original map prepared by Annalisha Johnson (Marshall University, Huntington, WV, USA).

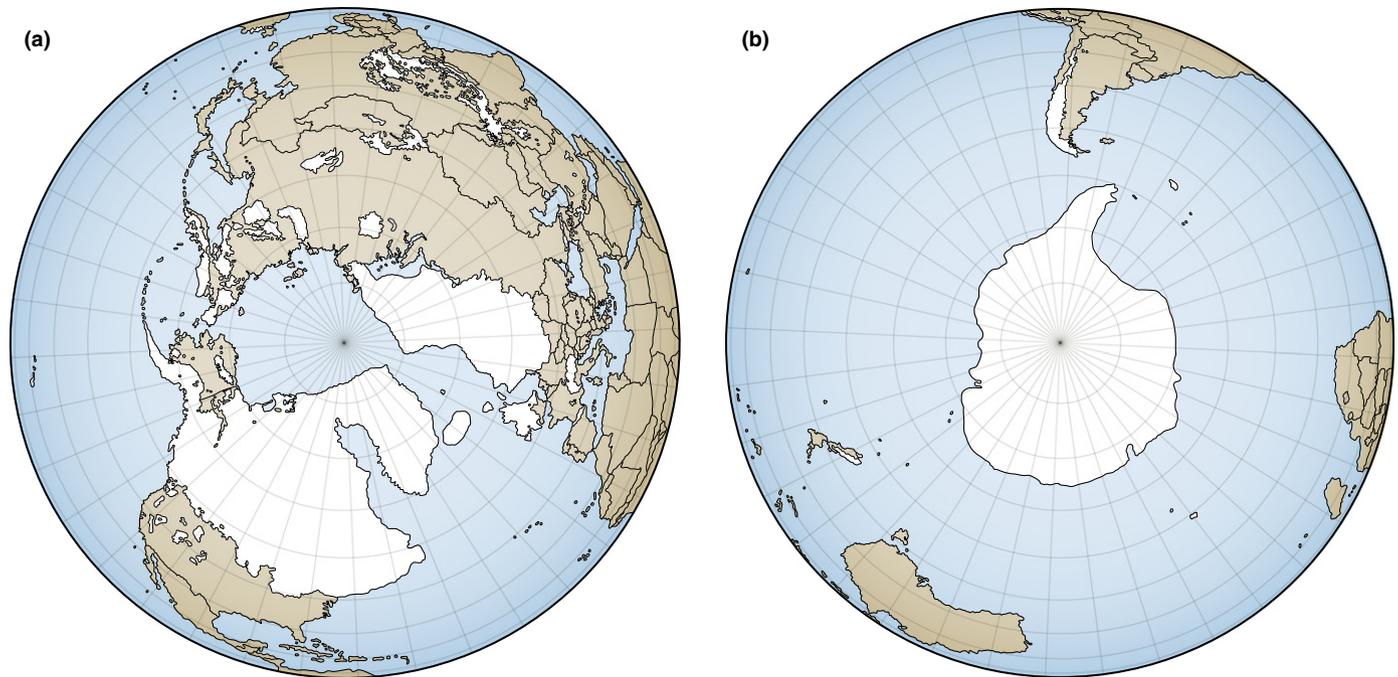


Fig. 4 Extent of the Last Glacial Maximum in (a) the Northern Hemisphere and (b) the Southern Hemisphere. Figure reprinted from Ehlers & Gibbard (2007), with permission from Elsevier.

of the Northern Hemisphere was once dominated by the Arcto-Tertiary geoflora (Cain, 1944; Axelrod, 1958; Whittaker, 1961). This was a time (*c.* 15 Myr BP) of a far warmer global climate than the present one, which was especially pronounced toward polar areas. Within this expansive forest were numerous gymnosperm genera, such as *Cedrus*, *Picea*, *Pinus* and *Tsuga*, and angiosperm genera – *Acer*, *Betula*, *Carya*, *Corylus*, *Castanea*, *Fagus*, *Magnolia*, *Quercus*, *Tilia*, *Ulmus* and *Liquidambar* (Xiang *et al.*, 2000; Graham, 2011). Increased warming during the Tertiary yielded to the cooler Quaternary, leading to the massive glaciers of the LGM over much of what is now boreal forest throughout the Northern Hemisphere (Fig. 4a). This pushed many species south toward the unglaciated refugia (e.g. Appalachian Mountains), which may have provided sources of remigration of species toward their current distributions (Davis, 1983; Graham, 1999; Stebich *et al.*, 2009).

Interestingly, the LGM is essentially irrelevant for temperate forests of China, largely unaffected by Quaternary glaciation (Liu, 1988). Pollen records reveal a diverse assemblage of tree genera at this time, varying from mixed conifer–hardwood to deciduous to widespread subtropical broadleaved evergreen forests; hardwoods comprised genera similar to other temperate forests of the Northern Hemisphere, with a diverse oak (*Quercus*) flora (Liu, 1988). Stratigraphy of mid-Holocene pollen demonstrates a period of maximum warmth (i.e. the Hypsithermal). Throughout northern regions at this time, forests increased in diversity with thermophilous hardwoods expanding, replacing both pine and, toward the south, birch (Liu, 1988).

Although glaciation also occurred in the Southern Hemisphere, other processes were equally significant in determining its temperate forest tree flora, including higher sea-to-land ratios creating

conditions leading to temperate rain forests on west-facing coasts (Alaback, 1991) and species of *Nothofagus* and conifers of the families Araucariaceae and Podocarpaceae (Beard, 1990; Kershaw & Wagstaff, 2001). During the Tertiary Period, drying occurred in continental regions, selecting more xeromorphic and even pyrophilic, fire-tolerant genera, such as *Eucalyptus* (Beard, 1990).

Fire – typically more prevalent among conifer-dominated stands than hardwood-dominated stands – has long been an integral factor in directing the development of temperate forest ecosystems. Marlon *et al.* (2009) used the paleorecord to examine the relationship between abrupt changes in global climate and enhanced frequency of fire. Using data from 35 charcoal/pollen records in North America to assess change in fire regimes during the past 15–10 kyr (the latest glacial–interglacial transition, and a time of profound climate change), they found clear links between fire frequency and degree of climate change. Implicit in their evidence is the intimate connection between occurrence of fire and the development of drought conditions in forested regions.

III. Climate, soils, composition and land use

1. North America

Temperate forests of North America occur in the eastern United States primarily as hardwood forests (except for extreme high elevations and southeastern Coastal Plain pinelands) and as conifer and mixed forests in parts of the western United States and Canada. Using the Köppen–Geiger climate classification (Kottek *et al.*, 2006), the predominant eastern climate would be classified as humid subtropical (Cfa) to the south, and humid continental (Dfa) to the north; prevailing climates for western

forests are predominantly warm temperate (Csb), with boreal zone-like conditions (Dfc) at high elevations of central western USA. Winter climate is dominated by fluctuations between cold, dry arctic air, along with cyclonic storms with marine-derived moisture to produce occasional heavy snows. Winter temperatures vary from means of -5°C in the north to 10°C toward the south. Spring brings thunderstorm activity through mixing of cold polar air with moist air from the Gulf of Mexico. Mean summer temperatures throughout the region range from 20° to 27°C . Frost-free periods are generally between 120 and 150 d in the north to >250 d in the south. Mean annual precipitation is 80–140 cm (Archibold, 1995). The prevailing climate of the Pacific Northwest forests is largely maritime, varying with latitude and elevation, with precipitation increasing with elevation (Franklin & Halpern, 2000).

Soils of eastern forests are generally Alfisols, Inceptisols and Ultisols, glaciated towards the north (Fig. 4a). Unglaciated soils are old, with soil pH decreasing with age. Soils of western forests are spatially variable. Montane conifer forest soils are usually young, derived from granites, gneisses and schists (Peet, 2000). Pacific Northwest conifer forest soils comprise Ultisols, Inceptisols and Spodosols, with many soils of volcanic origin (Franklin & Halpern, 2000).

With the exception of the virtual elimination of the American chestnut (*Castanea dentata*) by the chestnut blight (*Cryphonectria parasitica*) beginning in 1904, current eastern temperate forest types are largely similar to those originally described by Braun (1950). With the highest tree diversity occurring in the mixed mesophytic forest region of the Appalachians, dominant genera include oaks (*Quercus* spp.), maples (*Acer* spp.), hickories (*Carya* spp.) and birch (*Betula* spp.), along with American beech (*Fagus grandifolia*) and yellow poplar (*Liriodendron tulipifera*).

Conifer forests vary greatly within the broad temperate region of North America. At the higher elevations throughout the Appalachian mountain range (800–1200 m above sea level (asl) in New England to 1600 m asl in the Great Smoky Mountains), spruce (*Abies* spp.) and fir (*Picea* spp.) forests are common (Vankat, 1979). Southeastern Coastal Plain conifer forests are predominantly pines (*Pinus* spp.) of a primarily successional nature, the result of frequent natural (e.g. fire) and anthropogenic (e.g. harvesting) disturbances (Platt *et al.*, 2006); these typically change through secondary succession to *Quercus-Carya* forests (Peet *et al.*, 2014). Before European settlement *c.* 250 yr BP, this region was dominated by a single species – *Pinus palustris* – which is currently $<3\%$ of its original distribution (Gilliam & Platt, 2006).

Montane conifer forests of western North America contain more genera than those of the eastern United States. Important genera include fir (*Abies* spp.), juniper (*Juniperus* spp.), spruce (*Picea* spp.), pine (*Pinus* spp.), hemlock (*Tsuga* spp.) and Douglas-fir (*Pseudotsuga menziesii*). Some of these form mixed forests, especially those associated with elevation gradients and successional status following disturbances, such as fire; hardwoods include maple (*Acer* spp.), alder (*Alnus* spp.), poplar (*Populus* spp.) and mountain ash (*Sorbus* spp.) (Peet, 2000). The mild, moist climate of Pacific Northwest (coastal forests west of the Cascade crest) selects for a complex assortment of conifer species, including *Pseudotsuga menziesii*,

Tsuga spp., *Abies* spp., *Pinus* spp. and several genera of cedars (family Cupressaceae, e.g. *Calocedrus*, *Chamaecyparis*, *Thuja*), including the awe-inspiring redwood (*Sequoia sempervirens*), the tallest tree in the world (Franklin & Halpern, 2000).

2. Europe

The European Environment Agency divides Europe into 11 biogeographical regions, based on prevailing climate and proximity to bodies of water (EEA, 2007). Regions most germane to this discussion are the Atlantic, Black Sea, Continental and Pannonian, with Continental occupying by far the largest area (Finnie *et al.*, 2007). Temperate forests here are predominantly hardwood species, with conifer forests increasing in importance toward the north and with increasing elevation. These extend farther east into western Russia, wherein climate becomes increasingly continental and drier, contrasting with the maritime climate toward the west. The climate throughout this area ranges from temperate oceanic (Do) in the west to temperate continental (Dc) eastward (Kottek *et al.*, 2006). Winter temperatures vary from maritime means of 3° to 5°C to continental means of -4° to -15°C in central Russia. Mean summer temperatures generally range from 22° to 30°C . Mean annual precipitation is 50–75 cm, with snow uncommon in lowland parts of Europe (Archibold, 1995).

Many of the soils of Europe often are referred to collectively as brown earths, which are similar to North American Alfisols, except that many are developed from calcareous parent materials wherein they are more similar to Inceptisols. Other common soils are Spodosols, especially in northern latitudes (Jones *et al.*, 2005).

Human alteration of temperate forests over recent millennia is perhaps most pronounced here (Mitchell & Cole, 1998; Niklasson *et al.*, 2010), where only *c.* 25% of forests are considered primary (*sensu* FAO, 2010: 'forest of native species where there are no clearly visible indications of human activities and the ecological processes have not been significantly disturbed'), something that disconnects forest distribution with climate (Allen *et al.*, 2016). Evidence suggests that anthropogenic disturbance began there in the Neolithic, with widespread forest conversion beginning *c.* 7000 yr BP (EEA, 2007). Since these ancient times, forest condition has been closely linked with human populations and socio-economic development. Both historical and paleo-ecological records indicate periods not only of increased logging, but also of land abandonment and forest regrowth, including the plague years of the 1300s (EEA, 2007).

There are generally fewer tree species in Europe than in North America, a contrast further exacerbated by extensive planting of conifer species throughout hardwood ranges (Augusto *et al.*, 2002). Despite this, the two regions share many deciduous genera, including *Quercus*, *Acer*, *Betula*, *Ulmus* and *Fagus* (Pages & Michalet, 2003; Ellenberg, 2009). EEA (2007) recognizes a mesophytic deciduous forest type, quite analogous to that which dominates the eastern United States. Analogous to chestnut blight in eastern USA, European species of *Ulmus*, especially white elm (*U. laevis*), have been decimated by the Dutch elm disease (*Ophiostoma ulmi*), which has also decimated elm species of North America (Peterken, 1996).

The current extent of European temperate conifer forests is greatly modified by past and current policies to plant vast areas of productive conifer species. Again, widespread native deciduous forests have been replaced by conifer plantations, modifying the general composition of the western European temperate forest. Although some of these were transplanted from within Europe (e.g. Norway spruce, *Picea abies* and Scots pine, *Pinus sylvestris*), others were imported from North America (e.g. Sitka spruce, *Picea sitchensis* and Douglas fir, *Pseudotsuga menziesii*) (Augusto *et al.*, 2002). Not surprisingly, then, as with hardwood genera, predominant European conifer genera overlap greatly with those of North America, including *Abies*, *Picea* and *Pinus* (EEA, 2007).

3. Asia

Similar to their North American counterparts, temperate forests of Asia occur primarily as hardwood forests throughout the eastern part of the continent, extending to and including virtually the entire island of Japan, except for extremes of elevation and north latitude, where there are well-developed boreal conifer forests (Aiba, 2016), resulting from similar climates between the two regions, primarily humid subtropical and temperate continental, Cf and Dc, respectively (Kottek *et al.*, 2006). The most profound difference in climate between these regions is the existence of a monsoon season widespread in parts of Asia, arising from drastic pressure changes over the continent, that is, Monsoon Asia (Nakashizuka & Iida, 1995). Consequently, precipitation in Monsoon Asia has a pronounced summer maximum, with up to 90% falling between May and September. The wettest areas are on the Korean peninsula. Mean winter temperatures range from *c.* 3°C to –15°C in southern coastal and northern interior regions, respectively. Spring is dominated by moist tropical maritime air, with July temperatures averaging from 22°C to 28°C (Archibold, 1995).

Soils of Asian temperate forests are analogous to those of North American temperate forests. These vary from Alfisols in upland regions to Ultisols toward the south and east, with Entisols forming from alluvium along rivers. Spodosols develop in conifer-dominated regions associated with higher elevation and more northern latitudes (Archibold, 1995).

Although the temperate deciduous forests of Asia are the most species-rich temperate forests in the world, many of them have been altered irreparably by land use, particularly in the lowland plains, which are virtually entirely cultivated (An *et al.*, 2002). Many Asian tree taxa are quite common in North America (Ying, 1983; Nakashizuka & Iida, 1995; Fang *et al.*, 1998), including *Quercus*, *Ulmus*, *Tilia*, *Fraxinus*, *Acer* and *Lindera* (Henbo *et al.*, 2004; Takahashi, 2010), and close relatives such as Asian *Castanopsis* and *Distylium* (Miura *et al.*, 2001). Species vary greatly with elevation (Sang & Bai, 2009), with upland areas supporting species of *Betula*, *Populus*, *Acer* and *Tilia*; *Salix*, *Betula* and *Populus* are common in riparian areas (An *et al.*, 2002). Forest type varies greatly with latitude; from north to south, this grades from mixed conifer to deciduous to mixed deciduous, then to widely distributed subtropical broadleaved evergreen forests (Liu, 1988).

Asian conifers increase in importance with increasing elevation. Working in Chinese subalpine forests, Taylor *et al.*

(1996) reported extensive stands as mosaics of conifer (*Abies*, *Larix*, *Sabina* and *Tsuga*) and hardwood (*Betula*) patches. Other conifer genera include *Picea* and *Pinus* (Miyajima & Takahashi, 2007).

4. Southern Hemisphere

Because the distribution of land mass of the biosphere is decidedly asymmetrical, with far more land area being distributed north of the equator, temperate forests of the Southern Hemisphere lack the expansiveness so characteristic of the Northern Hemisphere. These forests are confined to relatively narrow bands along western South America, southeastern Australia (including all of Tasmania) and northern New Zealand, including the northwestern half of South Island. Climatic, oceanographic and orographic factors further limit forest development in many areas of the Southern Hemisphere. These regions display very high ocean:land mass ratios; consequently, they are generally of maritime temperate climates (Cf). The Andes range exerts a profound influence on the prevailing climate of temperate-forest South America, with the windward side receiving a relatively constant flow of maritime air from the Pacific Ocean (Perakis & Hedin, 2002), and many are temperate rain forests (Beard, 1990). Mean annual temperatures are generally 6–10°C, with a range typically < 10°C. In coastal areas, July-to-January temperatures vary only by 4° or 5°C, with a similar pattern found for coastal southwestern New Zealand. Indeed, summers average *c.* 20°C, with winters ranging from 10–15°C. Precipitation for most of these sites is very high, exceeding 300 cm, reaching as much as 850 cm (Sturman & Tapper, 2006).

Many of the soils throughout the temperate Southern Hemisphere are highly weathered Spodosols, the result of high amounts of rainfall and its associated fluctuating water table. These soils are generally highly acidic and infertile (Veblen *et al.*, 1996; Grubb *et al.*, 2013).

Forest genera, and even plant families, of the temperate forests of the Southern Hemisphere are quite dissimilar to those of the Northern Hemisphere. Prominent genera are *Nothofagus* (Nothofagaceae) and *Eucalyptus* (Myrtaceae), neither part of the native flora in the Northern Hemisphere. Conifer genera are in Araucariaceae (e.g. *Araucaria*) and Podocarpaceae (e.g. *Podocarpus*, *Dacrydium*) (Beard, 1990; Kershaw & Wagstaff, 2001). Forests of Chile and Argentina vary sensitively along the Andes-induced climatic gradient. *Nothofagus* species are dominant throughout these forests (Veblen *et al.*, 1996; Armesto *et al.*, 2009), but with *Araucaria araucana* replacing *Nothofagus* species under more stressful environmental conditions (Sanguinetti & Kitzberger, 2008). Mainland forests of Australia are dominated by *Eucalyptus* and *Acacia* species, especially in drier areas, whereas *Nothofagus* species, along with gymnosperms, are found in the cool, moist forests of Tasmania. *Nothofagus* is common in New Zealand, covering 84% and 40% of the South and North Islands, respectively (Beard, 1990). The current status of many forests of the Southern Hemisphere represents considerably altered states of the primary conditions, for example, the rainforests of Chile before the Conquest of Chile in the mid-16th Century by Spain (Smith-Ramírez, 2004).

IV. Climate change

Humans have, indeed, long utilized temperate forests for a variety of purposes (Fig. 2). Currently, temperate forests are managed worldwide for timber production, driven by an ever-increasing demand and resulting from relatively rapid growth among overstory dominant species, but also from the versatility of temperate tree species for numerous uses (e.g. paper, construction materials, furniture). Management practices potentially affect these forests across all spatial scales, from the landscape (Rhemtulla *et al.*, 2009), to the overstory (Beaudet *et al.*, 2004), and, often most sensitive, the herb layer (Moola & Vasseur, 2009; von Oheimb & Härdtle, 2009; Gilliam, 2014; Hedwall & Brunet, 2016). Furthermore, management practices historically often have been carried out using methods that are unsustainable in terms of maintaining forest ecosystem structure and function, including plantation forestry, especially conversion from slower-growing hardwood forests to faster-growing conifer plantations (Seidl *et al.*, 2011), and forest fragmentation (Smith-Ramírez, 2004). Naudts *et al.* (2016) suggested that broadscale conversion of temperate European hardwoods to conifer plantations contributes measurably to what is perhaps the most profound modern human influence on these forests – climate change (Lindner *et al.*, 2010; Parks & Bernier, 2010).

Thus, I suggest the following as the ‘bookends’ of anthropogenic impacts on temperate forests. The first is their historic – even ancient – and chronic use/conversion by ever-increasing human populations; the second is climate change. The spatial and temporal dimensions of these are superimposed (Fig. 5). The legacy effects of the recent and distant past are currently on a trajectory of future dynamics operating under the overriding influence of climate change (Dale *et al.*, 2001), and all that is associated with it, including altered phenology of organisms (Parmesan & Yohe, 2003) and extremes of weather-related phenomena (Min *et al.*, 2011) (Fig. 6). All responses of temperate forests to current land-use pressures must be viewed forever through the lens of climate change (Fig. 5).

In this final section, I emphasize challenges for future sustainability of global temperate forests. This is not meant to represent an exhaustive list of all critical issues. Rather, I emphasize those for which sufficient work has been done to provide an understanding of the nature of the problem. These include the effects of atmospheric deposition of excess N, global change-mediated alterations in phenology of temperate forest species and increases in drought/fire.

1. Excess nitrogen

More pronounced in the Northern than the Southern Hemisphere, a major human perturbation of temperate forests worldwide has arisen from emissions of reactive nitrogen (N_r) into the atmosphere leading to chronically elevated deposition of N_r and a cascade of environmental stresses for terrestrial and aquatic ecosystems and human health (Galloway *et al.*, 2013). The N comprising 78% of the atmosphere – N_2 – is considered nonreactive N because it enters into essentially no photochemical transformations in the atmosphere and no metabolic pathways in organisms, other than N

fixation by a small group of symbiotic and nonsymbiotic prokaryotes. However, numerous forms of N_r exist, including NH_3 , NH_4^+ , NO, NO_2 , NO_3^- , $2N_2O_5$, HNO_3 and several forms of peroxyacetyl nitrates (Horii *et al.*, 2005), all capable of undergoing photochemical transformations in the atmosphere and entering terrestrial and aquatic ecosystems.

Although more research on the effects of excess N has focused on herb-dominated than on forested ecosystems (Clark *et al.*, 2013; Simkin *et al.*, 2016), increasingly work is being devoted to understanding such effects on forest ecosystems, including those of the temperate regions (Sutton *et al.*, 2014). Whereas current increases in N deposition are occurring on a global scale (Bobbink *et al.*, 2010), N-mediated threats to biodiversity are particularly pronounced for temperate forests, especially given the spatial coincidence of high human population density – and associated N pollution – with temperate forests (Holland & Lamarque, 1997), the disproportionate contribution of the herbaceous layer to temperate forest diversity (Gilliam, 2007), and the sensitivity of the forest herb community to excess N (Gilliam, 2006). More vexing still is that chronically elevated N deposition is occurring contemporaneously and, indeed, interactively with climate change (Maes *et al.*, 2014).

Essentially all initial work on effects of excess N deposition on terrestrial ecosystems examined biogeochemical responses. These studies focused on changes in stream chemistry, generally showing increases in NO_3^- (from enhanced nitrification and leaching) and base cations (Ca^{++} , Mg^{++} and K^+) coupled with the movement of NO_3^- (Aber, 1992). Many areas of temperate forests of North America, especially those of the eastern United States, were shown to be sensitive to *N saturation*, a phenomenon which develops as atmospheric and microbial supply of available N exceeds biotic demand. Recent work has emphasized the effects of excess N on biodiversity of temperate forests (Thomas *et al.*, 2010; Clark *et al.*, 2013; Simkin *et al.*, 2016). Despite considerable inter-site variability, a broad consensus is that excess N decreases forest biodiversity in temperate forests of North America.

Gilliam (2006) provided a conceptual model to describe interactive processes that are sensitive to increased N loading in ways that can lead to loss of herb layer diversity, including altering interspecific competition, increasing herbivory and pathogenic fungal infection, inhibiting mycorrhizal associations and enhancing species invasions. Nitrogen-mediated declines in biodiversity are typically seen as loss of species in the herb layer from the increased cover of fewer nitrophilic species at the expense of numerous N-efficient species (Gilliam *et al.*, 2016). Fewer studies have focused on responses of tree species to N. Thomas *et al.* (2010) modelled the potential effects of N on temperate forest C sequestration and tree seedling survivorship. Chronically elevated N deposition enhanced C storage, but decreased survivorship in 8 of 11 common temperate tree species. Following N saturation, C sequestration is typically limited by another nutrient (Leuzinger & Hättenschwiler, 2013), often phosphorus (Gress *et al.*, 2007).

Research focusing on chronically elevated N deposition leading to N saturation began in Europe much earlier than in North America, primarily because N-related threats appeared earlier and were far more widespread there (Gilliam, 2006). Although a

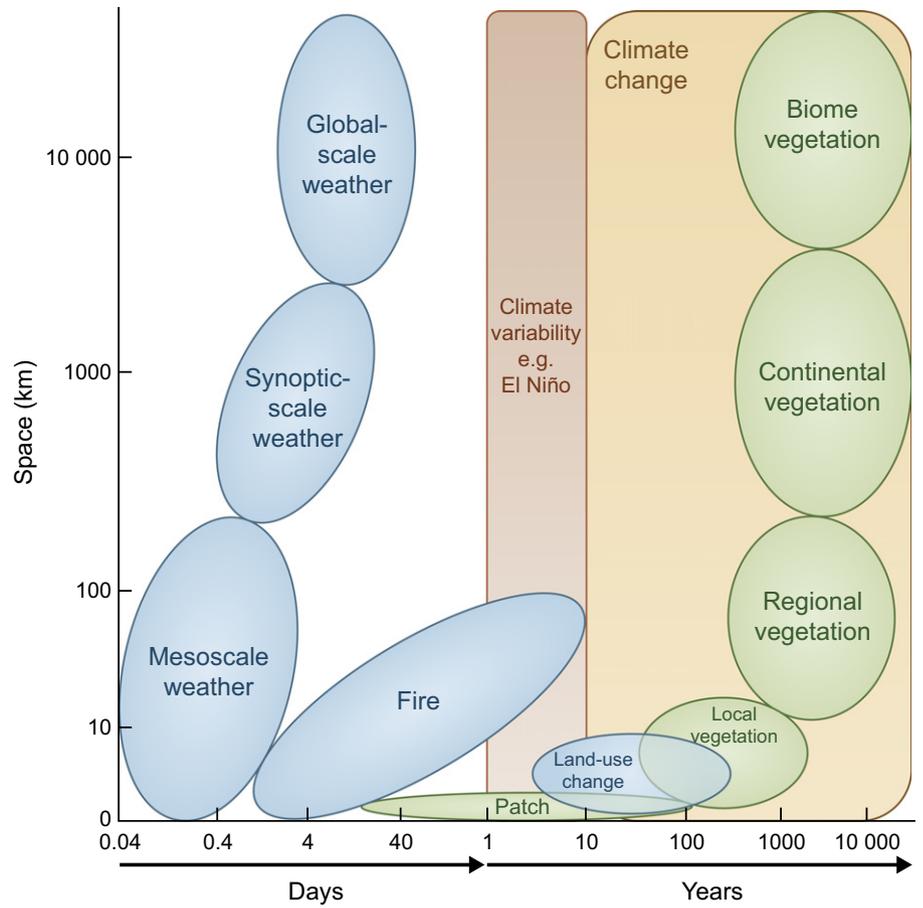


Fig. 5 Spatial and temporal scales of essential ecosystem drivers (weather, climate variability and climate change, fire and land-use change) and related distribution of vegetation. Figure reprinted from Mackey *et al.* (2012), with permission from Wiley Press.

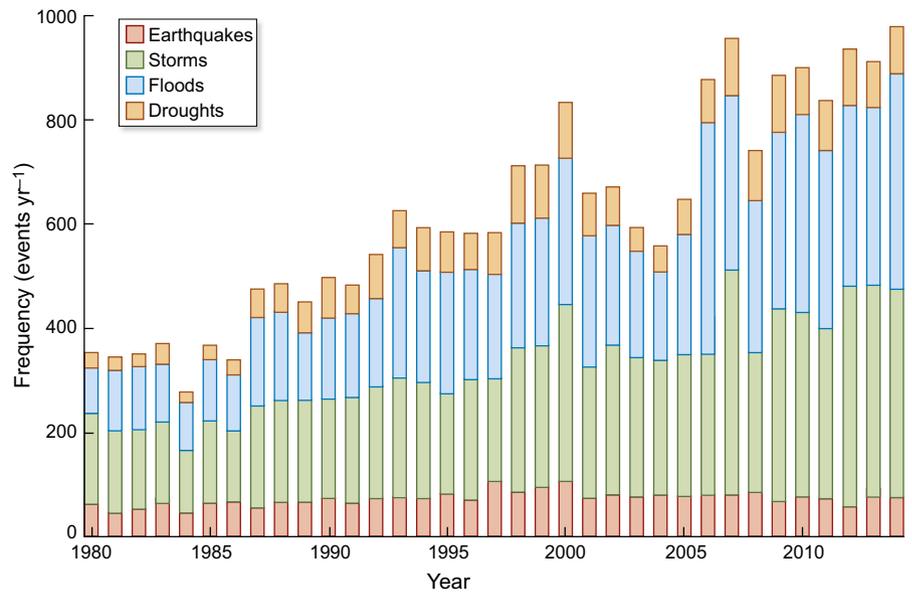


Fig. 6 Annual frequency of catastrophic natural disturbances globally from 1980 to 2014. Figure originally re-created by Annalisha Johnson (Marshall University, Huntington, WV, USA) from data taken from Münchener Rückversicherungs-Gesellschaft, Geo Risks Research, NatCatSERVICE.

notable amount of European work has been in the boreal region and in herb-dominated ecosystems, most recent work has been carried out in temperate forested regions, with much of that concerned with the response of the typically species-rich herbaceous layer to excess N, largely based on broad regional synthesis studies (De

Schrijver *et al.*, 2011; Verheyen *et al.*, 2012; Dirnböck *et al.*, 2014; Ferretti *et al.*, 2014).

Borrowing a phrase from my home state of West Virginia, where coal mining is common, many N-effects studies in Europe use the forest herb layer community as ‘the canary in a coal mine’ (wherein

caged canaries were once placed in a coal mine, whose death served as an early indication of impending peril for coal miners from coal gas). The wide spatial extent of sampling employed by these studies adds considerable validity and credibility to their findings. Verheyen *et al.* (2012) compiled data from 1205 permanent/semi-permanent sample plots among 23 carefully selected understory resurvey studies. Utilizing a wide gradient in N deposition across deciduous temperate forests in Europe, they assessed the importance of factors influencing forest herb communities, including rate of N deposition, change in density of large herbivores, and change in forest canopy cover and composition. Their results demonstrated the interactive nature of these factors, concluding that N-mediated increases in nitrophilous species can be obscured by changes in the forest overstory. Similarly, Dirnböck *et al.* (2014) synthesized long-term monitoring data from 1335 permanent samples among 28 forested sites from northern Fennoscandia to southern Italy, noting temporal trends in herb-layer species cover and diversity. They found a pattern of gradual replacement of N-efficient species by nitrophilous species in response to N deposition that was consistent on the European scale. Hedwall & Brunet (2016) attempted to separate effects of global change and altered land-use in both boreal and temperate forests of Sweden by documenting temporal variation in herb layer species over a 20-yr period in both boreal and temperate forests of Sweden, finding that most species changed in overall frequency. Comparing functional traits of both increasing and declining species, they found that current floristic dynamics were caused by combined effects of climate warming, nitrogen deposition and changing land-use (e.g. plantation forestry). Herb species' changes were more pronounced in temperate, rather than boreal, forests.

Less is known regarding the effects of excess N on temperate forests of Asia (Liu *et al.*, 2013) and the Southern Hemisphere. In China, this arises because of the chronically highly dissected extent of temperate forests (Liu, 1988) and the spatial distribution of highest amounts of N deposition occurring in tropical/sub-tropical regions (Lu *et al.*, 2015). In addition to elevated rates of N emissions to the atmosphere (Liu *et al.*, 2013), much of China's problems with excess N is associated with over-use of N fertilizers for summer maize agriculture (Zhang *et al.*, 2015). Kim *et al.* (2011) concluded that increases in N availability throughout Korea and Japan was most likely due to deposition of pollutant N from atmospheric sources from both industrial and agricultural regions. Perakis & Hedin (2002) found that, as a result of their location relative to oceans, with prevailing winds coming off those oceans, forests of the temperate regions of the Southern Hemisphere receive some of the lowest annual rates of N deposition anywhere in the world (Godoy *et al.*, 2001).

2. Altered phenology

Given that a prominent feature of all temperate forests is their distinct seasonality, phenology – seasonally recurring events of an organism's life cycle, for example, flowering, emergence of invertebrates, movement of migratory animals, and especially their timing and relationship with the physical environment – plays a key role in the structure and function of temperate forest ecosystems.

For plants, phenological changes can be triggered by environmental cues, for example, chilling, spring temperature, growing degree days and daylight (Elmendorf *et al.*, 2016). Because of their lack of thermoregulation, ectothermic animals (e.g. insects) can resemble plants with respect to environmental influences on and control of phenology, particularly temperature. Changes in phenology can affect several processes essential to survival, growth and reproduction of all organisms, especially critical when complex interspecific interactions are involved, such as plant–pollinator dynamics.

Many plant species are classified phenologically, based on seasonal patterns of flowering via photoperiod. Long-day plants flower in spring as day length increases, whereas short-day plants flower from late summer into the fall as day length decreases. Actually, it is the length of uninterrupted darkness that controls flowering, such that long-day plants are more accurately short-night plants and *vice versa*. Despite this importance of photoperiod, thermoperiod – daily and seasonal patterns of change in temperature – also affects virtually all phenologically controlled plant processes. Anecdotally, gardeners rue days of atypically warm temperatures in late winter that allow flower and leaf buds to break dormancy, only to be followed by seasonal temperatures < 0°C that kill new, susceptible tissues.

Evidence indicates that climate change has altered growing seasons in the temperate regions worldwide. Based on global meta-analyses of > 1700 wild species, including woody and herbaceous plants, birds, insects, amphibians and fish, Parmesan & Yohe (2003) found widespread changes in phenology and species distributions attributable to climate warming. Despite some species' temporal stability, most exhibited change as predicted by the United Nation's Intergovernmental Panel on Climate Change. They found advancing spring events of 2.3 d/decade, and shifting biogeographical ranges toward the poles of 6.1 km per decade (Parmesan & Yohe, 2003), calling such changes a 'coherent fingerprint' of the overall effect of climate change on natural systems.

Ibáñez *et al.* (2010) observed that climate warming has altered both spring and autumn phenologies of many species, but found considerable interspecific variation and, for a given species, spatial variation in response to climate change. Forecasting future change, they used a long-term (1953–2005) dataset including spring and autumn plant phenological events (flowering/leaf out and leaf coloring/leaf fall, respectively) of tree, shrub and herbaceous species of temperate forests of South Korea and Japan, finding that most species currently exhibit advanced spring phenology and delayed autumn phenology, consistent with expectations, but also that autumn-based changes are more rapid than those associated with spring. The latter observation contrasts with comparable studies in Europe which show that spring events are changing more rapidly than autumn events (Menzel *et al.*, 2006).

For temperate forests, three relevant factors affecting the phenology of dominant tree species are photoperiod, degree of winter chilling and temperature (Körner & Basler, 2010). There is, however, interspecific variability in which predominant factor(s) control phenology among temperate forest species, with photoperiod increasing in importance with forest succession; that is, it is more important for long-lived, late-successional species than for

short-lived, early-successional species. Although this may mitigate warming-induced change in temperate forest composition, Körner & Basler suggested that opportunistic (e.g. exotic invasive) species may benefit from a warming climate and claim a competitive advantage over photoperiod-sensitive species (Körner & Basler, 2010).

Altered phenology is a driver of change not only for plant species, but also for animal species, creating a complex scenario for plant–animal interactions, particularly pollination. Less a problem for climax canopy hardwood species, which are almost exclusively wind-pollinated, this is irrelevant for temperate conifers, but an especially serious threat for forest herbaceous species. Potts *et al.* (2010) reviewed patterns of global declines in numerous pollinator species, with an understandable focus on insects – especially bees – considering that they are the primary pollinators of both agricultural crops and wild species. Potential drivers of pollinator loss include habitat loss/fragmentation, agrochemicals, pathogens and introductions of novel species. Also included is climate change, and interactions among virtually all drivers. Effects of climate change on insect pollinators are seen on all hierarchical levels of organization, from the individual to population and community levels. Especially troublesome are the temporal and spatial mismatches between plant species and their insect pollinators, arising temporally from changes in phenology of plant and insect species, and spatially from altered distributions (Potts *et al.*, 2010).

Climate change-altered phenology has extended into changing life cycles among insects, an example of which is the mountain pine beetle (MPB; *Dendroctonus ponderosae*), native to western North America, and a generalist pest for the genus *Pinus*, often erupting epidemically, and killing wide swathes of trees throughout the region (Fig. 7a). Mitton & Ferrenberg (2012) studied a recent epidemic of MPB that was an order of magnitude larger than ever recorded and extending to higher elevations/latitudes than on record. They demonstrated that, following 20 yr of increasing air temperatures in the Front Range of the Colorado Rocky Mountains, the flight season of MPB began > 1 month earlier than historically known and extended twice that duration. More important was their novel finding that the life cycle of some broods of MPB increased from one to two generations per year (Fig. 7b). They explained that because this species lacks a diapause (suspension in development), its development is controlled solely by temperature. Accordingly, MPB populations currently respond to climate warming via faster development and expanse into previously inhospitable environments (Mitton & Ferrenberg, 2012). This work, however, was challenged by Bentz & Powell (2014), who agreed that MPB is influenced by climate change, but stated that such studies need to consider thermally dependent traits that have evolved to maintain seasonality.

Climate change interactions have been reported for other forest pest insects. DeRose *et al.* (2013) combined empirical data, based on US Forest Service Forest Inventory Analysis data, with three global change models to evaluate and predict the effect of increasing temperature on the distribution of spruce beetle (*Dendroctonus rufipennis*), which attacks spruce forests of North America. They predicted that extent of attack should increase with temperature,

but that there should be time lag in response, given the long-lived nature of host spruce trees.

This phenomenon is not confined to North America. Netherer & Schopf (2010) reported similar findings from throughout Europe for defoliating insects, bark beetles and especially the pine processionary moth (*Thaumetopoea pityocampa*), a defoliating insect for numerous conifer species. Its altitudinal and latitudinal distributions are controlled primarily by temperature and are already modified by climate change. Because of the prevailing oceanic climate in the Southern Hemisphere (i.e. generally lower temperatures during the growing season), climate change is predicted to promote contrasting effects on insect cycles there, as well (Deutsch *et al.*, 2008).

Related to climate change-mitigated alterations in phenology are similarly altered changes in biogeographical ranges of species. Again, Parmesan & Yohe (2003) concluded that climate change has caused mean pole-ward range shifts of 6.1 km per decade. Using seven global circulation models (GCMs), Hansen *et al.* (2001) projected future distributions of prominent temperate forest types of North America, including the eastern deciduous forest and western mountain/coastal forests of the United States, focusing on major tree species. These models differ in their type – equilibrium vs transient – and in assumptions of change in temperature and precipitation. Equilibrium models are older and simulate instantaneous increases in CO₂, being run until equilibrium climate conditions are reached; the more recent transient models assume increases in glasshouse gases at 1% yr⁻¹ until 2100, allowing climatic adjustment. Although specific predicted outcomes for eastern forest species varied among models (Fig. 8), all concurred in predicting profound shifts in dominant species, especially the virtual elimination the maple–beech–birch forest type (one of the more species-rich forest types of the region) and loblolly–shortleaf pine, and expansion of oak–hickory and oak–pine types (Fig. 8). Potential ranges for several subalpine coniferous species are predicted to contract in the western United States (data not shown). Among their conclusions is that changes in climate and land use in the future will be of a magnitude to cause even greater changes in biodiversity. Although distributions of some species, communities and biomes are likely to expand, others will contract, creating novel communities (Hansen *et al.*, 2001).

3. Drought/fire

In their now-classic paper, Hansen *et al.* (1988) provided forecasts of several outcomes of global climate change using the three-dimensional model of the Goddard Institute for Space Studies. These included increased atmospheric warming globally, with degree of warming dependent on growth of trace gas emissions. Another prediction, one relevant for the present and future of global temperate forests, was a notable increase in the frequency of extremes of weather events and conditions. Indeed, this prediction is well-supported by current data collected by the *Münchener Rückversicherungs-Gesellschaft*, *Geo Risks Research*, *NatCatSERVICE*, wherein they examined global annual frequency of catastrophic disturbances 1980–2014 (Fig. 6). All types of catastrophic disturbance, save earthquakes, have

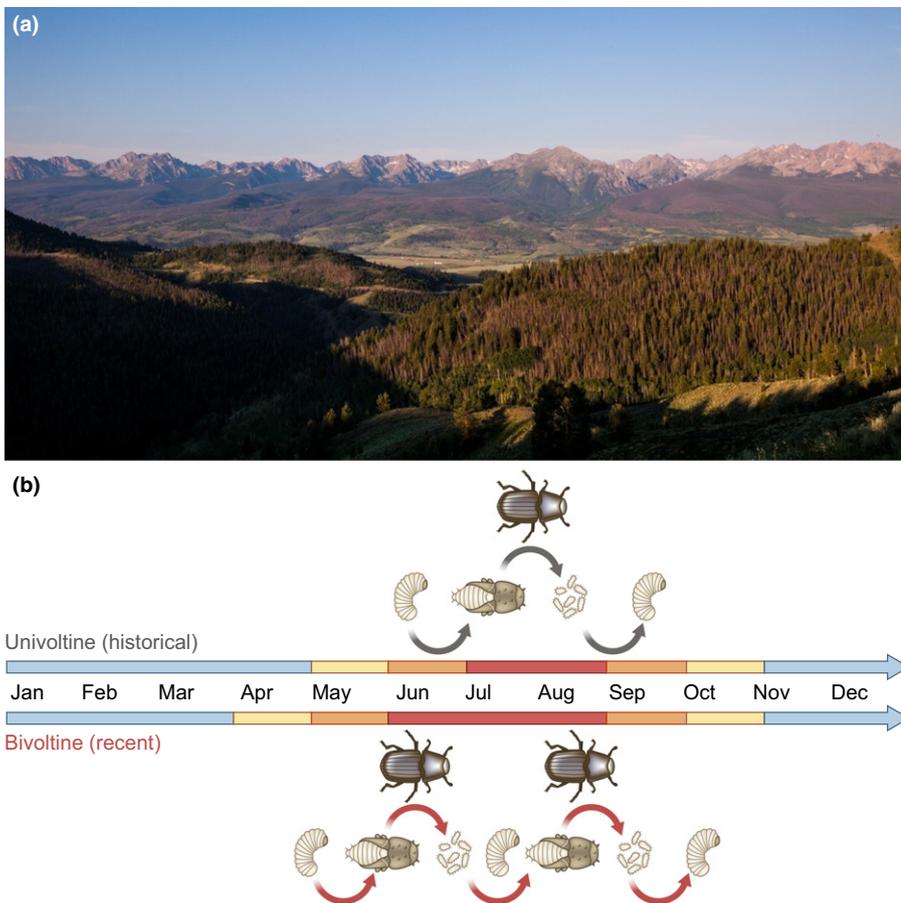


Fig. 7 The mountain pine beetle (MPB) of western North America. (a) Wide swathes of beetle-killed trees in the Williams Fork Mountains (foreground) and the Gore Range of northern Colorado. Photo credit: Jeffrey B. Mitton, used with permission; (b) Historical univoltine life cycle of MPB (above calendar arrows and linked by grey arrows) and observed bivoltine life cycle (below calendar arrows and linked by red arrows). Colors of calendar arrows indicate monthly temperature regimes: blue: $< 0^{\circ}\text{C}$, yellow: $0\text{--}4.99^{\circ}\text{C}$, orange: $5\text{--}9.99^{\circ}\text{C}$, and red: $\geq 10^{\circ}\text{C}$. Figure from Mitton & Ferrenberg (2012), with permission from authors.

increased during this period. These are true extremes, indeed, considering that frequencies of both flooding and drought exhibit large increases over the *c.* 35 yr time period. Relevant to the current discussion is the increased frequency of drought, a disturbance not directly associated with any particular biome, but representing an especially serious threat to temperate forests (Fig. 6).

Forests typically develop in the temperate zone wherever there is sufficient precipitation to maintain soil moisture amounts capable of supporting tree growth and survival. Thus, the occurrence of extensive drought will have directly damaging effects on tree species. In addition to the direct limitations of drought-induced moisture stress, however, is the drought-induced increase in the frequency of fire. Wildfire activity has not only been predicted to increase in the future under a climate warming scenario, but also such increases are hypothesized to bring about biogeographical shifts that reduce the resilience of fire-prone forests worldwide (Harvey *et al.*, 2016). Although the relative contribution of fire to forest decline is greatest in the boreal forest, fire still represents a threat to temperate forests, especially conifer forests already weakened by drought (Hansen *et al.*, 2013). Harvey *et al.* (2016) tested two hypotheses associated with this observation in fire-prone subalpine (largely conifer) forests in the Rocky Mountains of the United States: (1) availability of viable seeds will decrease in large patches following stand-replacing fire, and (2) seedling establishment and survival will decline measurably following post-fire drought. They found

that total tree seedling establishment declined sharply post-fire with greater drought severity and with greater distance to seed source. Many responses exhibited interspecific variation, suggesting fire/drought-induced changes in forest composition. They concluded that, given the predicted increase in frequency of drought and wildfire in the future, post-fire tree seedling establishment of these forests could be reduced substantially. Although some of these reductions might be offset by compensatory increases from lower montane and upper timberline species, important near- to mid-term shifts in the composition and structure of high-elevation forests will occur under continued climate warming and increased wildfire activity.

Not part of their study, yet no less important, is the interaction of drought and fire with increases in extent and severity of forests pests, as discussed in Mitton & Ferrenberg (2012) in North America and Netherer & Schopf (2010) in Europe. That is, the scene depicted in Fig. 7(a) of wide swathes of insect-killed stems is of trees more susceptible to insect death because of drought stress, and simultaneously represents substantial fuel for intense fires. Furthermore, McDowell *et al.* (2008) established a close connection between climate change-enhanced drought and increases in pests for temperate forests of North America.

V. Epilogue

Regrettably, climate change has been insinuated into the current political arena – especially in the United States, but also elsewhere

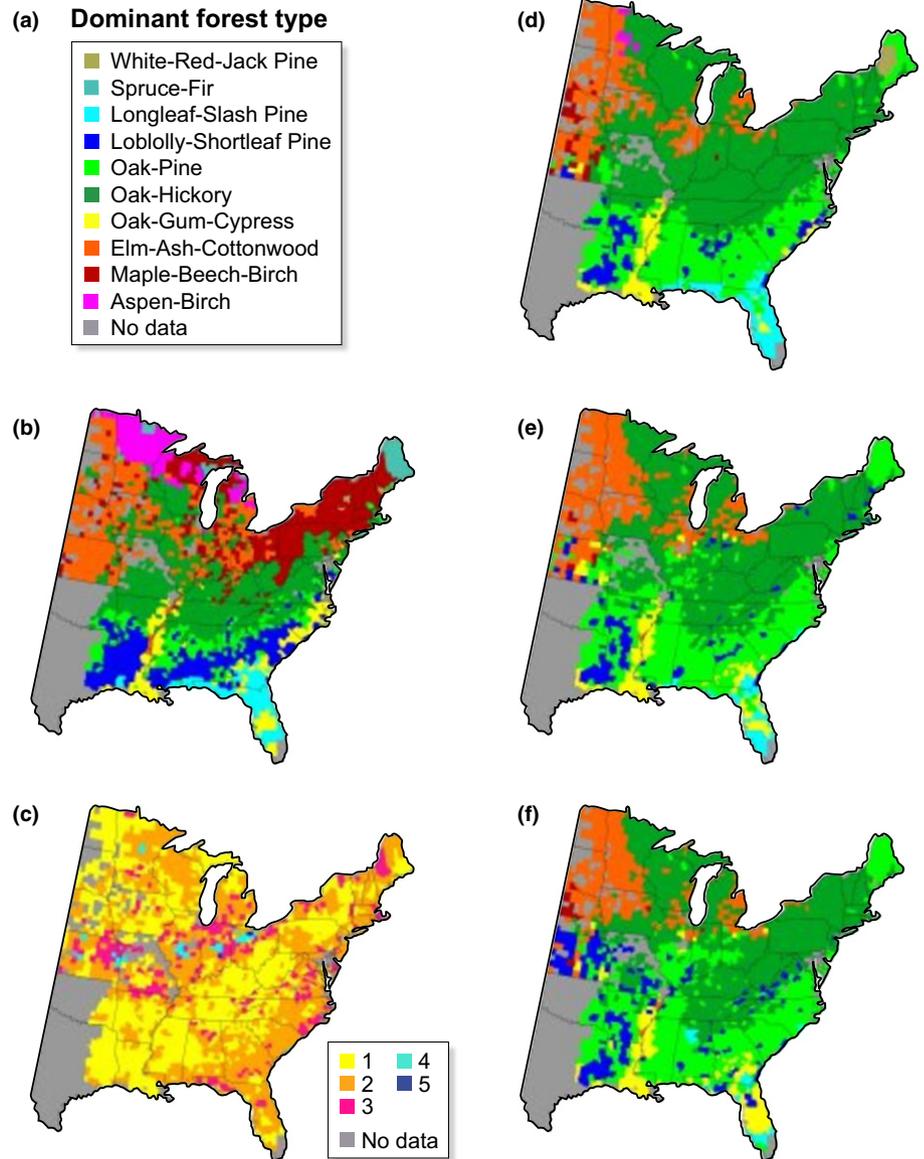


Fig. 8 Potential distributions of forest community types in the eastern United States as simulated with the DISTRIB model (an empirical model that uses a regression tree analysis approach) under five different global circulation model (GCM) scenarios and representing an approximate doubling of concentrations of CO₂ – see Iversen & Prasad (2001) for description of model and GCM scenarios. (a) Color key for forest types; (b) current forest-type distribution based on 100,000 forest inventory plots; (c) uncertainty map, with the number of unique forest community types simulated across all five future GCM scenarios plotted; (d) potential forest community type distribution under the HADCM2SUL scenario, among the coolest of future warming scenarios; (e) a modal map of future biome distributions (shown are the biomes most often simulated for the future across all five GCMs; refer to panel (c) for the ‘uncertainty’ associated with the modal map); and (f) forest community type distribution under the CGCM1 scenario, among the warmest of future scenarios. Figure from Hansen *et al.* (2001), with permission of Oxford University Press.

around the world – wherein agenda-driven politics seek to deny its scientific reality (I remind my students that mixing politics and science is like mixing manure and ice cream – it never helps the manure, but always ruins the ice cream). In spite of this, and to a real degree because of it, climate change will continue to threaten global ecosystems in general, and temperate forests in particular, for many years in the future. It is quite compelling that, in spite of misrepresentations to the contrary, numerous long-term predictions from the past regarding climate change have largely survived scientific scrutiny. Certainly, predictions of Hansen *et al.* (1988) nearly 30 yr ago have all been essentially supported, especially regarding climate change-mediated extremes of weather (Fig. 6).

Climate change, however, is only a part, albeit the lion’s share, of global change, comprising myriad other drivers, most of which have been explicated herein. Franklin *et al.* (2016) developed a conceptual model of the effects of these drivers – climate change, altered disturbance regimes, invasive species/novel species assemblages, land-use change – on terrestrial ecosystems using multiple

lines of evidence. These include observations for attribution, experiments for identifying mechanisms, and use of models at multiple scales of ecological organization for verification (Fig. 9). Although this model was developed as a set of general guidelines for all ecosystems of the biosphere, it seems particularly applicable to temperate forests, considering (1) the chronic alteration of these forests by human populations, and (2) their temperate nature, wherein growing/dormant seasons are an integral part of their structure and function. Such a model provides a strong base not only for ongoing scientific inquiry and understanding, but also in informing mitigation policy. Although the science to date has provided sufficient evidence providing the impetus for policy changes, there is still a clear need for further basic scientific research. Climate change is unquestionably a complex phenomenon that can be best understood only by a complex of scientific approaches, involving empirical field monitoring, manipulative field experiments and laboratory simulations, all coupled with modeling (e.g. DeRose *et al.*, 2013).

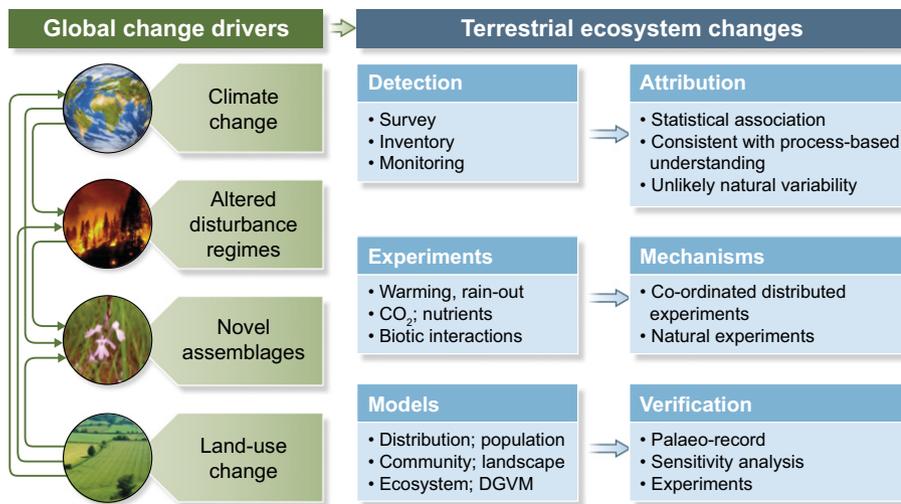


Fig. 9 Conceptual model of drivers of global change—climate change, altered disturbance regimes, invasive species/novel species assemblages, land-use change – on terrestrial ecosystems using multiple lines of evidence, including observations for attribution, experiments for elucidating mechanisms, and models deployed at multiple ecological scales for verification. Figure reproduced from Franklin *et al.* (2016), with permission from the author.

Finally, I suspect that I am not alone among plant ecologists in considering Sir Arthur Tansley as a professional ‘hero,’ a truly inspirational visionary in our field, and one who clearly articulated many ecological concepts we embrace today. Although it is an honor to write a review bearing his name, I cannot imagine that he, in his day, would have conceived the truly global scale of our ‘modern’ alteration of climate. Still, he deeply appreciated the profoundly negative influence human activity can have on the very ecosystems that he not only ‘coined,’ but on which our sustainability depends. Appropriately, I allow Sir Arthur to conclude:

It would be difficult, not to say impossible, to draw a natural line between the activities of the human tribes which presumably fitted into and formed parts of ‘biotic communities’ and the destructive human activities of the modern world. . . Regarded as an exceptionally powerful biotic factor which increasingly upsets the equilibrium of preexisting ecosystems and eventually destroys them, at the same time forming new ones of very different nature, human activity finds its proper place in ecology.

Tansley (1935)

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improved by their input. In my case, this goes far beyond cliché, as I am overwhelmed with the amount of time three peers put into reviewing the original version of this paper. Their keen collective insight leading to vast improvements in concepts and content is deeply appreciated.

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