

1 **LOSS OF FOUNDATION SPECIES: CONSEQUENCES FOR THE STRUCTURE AND**
2 **DYNAMICS OF FORESTED ECOSYSTEMS**

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34 **Abstract**

35 In many forested ecosystems, the architecture and functional ecology of certain tree species
36 defines forest structure and their species-specific traits control ecosystem dynamics. Such
37 foundation tree species are declining throughout the world due to introductions and outbreaks of
38 pests and pathogens, selective removals of individual taxa, and over-harvesting. Through a series
39 of case-studies, we illustrate that the loss of foundation tree species changes the local
40 environment on which a variety of other species depend; disrupts fundamental ecosystem
41 processes, including rates of decomposition, nutrient fluxes, carbon sequestration, and energy
42 flow; and dramatically alters the dynamics of associated aquatic ecosystems. Forests in which
43 dynamics are controlled by one or a few foundation species appear to be dominated by a small
44 number of strong interactions, and may be highly susceptible to switching between alternative
45 stable states following even small perturbations. Ongoing declines of many foundation species
46 provide a set of important, albeit unfortunate, opportunities to develop the research tools,
47 models, and metrics needed to identify foundation species, anticipate the cascade of immediate,
48 short-term, and long-term changes in ecosystem structure and function that will follow from their
49 loss, and provide options for remedial conservation and management.

50 ***In a nutshell:***

- 51 1. In many ecosystems, a single foundation species controls population and community
52 dynamics and modulates ecosystem processes
- 53 2. The loss of foundation species acutely and chronically impacts fluxes of energy and
54 nutrients, hydrology, food webs, and biodiversity
- 55 3. Human activities including logging and the introduction of exotic pests and pathogens
56 often functionally remove foundation tree species from forests
- 57 4. Foundation species that are currently being lost from North American forests include
58 eastern hemlock, Port-Orford cedar, and oaks

59 We are living in an era of unprecedented and rapid ecological change (Reid *et al.* 2005).
60 Through habitat conversion, over-consumption of resources, and worldwide introductions of
61 pests and pathogens, humans are causing species extinctions at an unprecedented rate: the sixth
62 extinction crisis in the billion-year history of eukaryotic life on Earth (Eldridge 1998). The loss
63 of a common or abundant **foundation species** (*sensu* Dayton 1972; see Panel 1), which by virtue
64 of its structural or functional attributes creates and defines an entire ecological community or
65 ecosystem, can have dramatic effects on our perception of the landscape and broad consequences
66 for associated biota, ecosystem function, and stability. Foundation species differ from keystone
67 predators (Paine 1966) in that the former usually occupy low trophic levels whereas the latter are
68 usually top predators, and differ from core species (Hanski 1982) in that foundation species not
69 only are locally abundant and regionally common, but also both create locally stable conditions
70 required by many other species and stabilize fundamental ecosystem processes such as
71 productivity and water balance.

72 In forested ecosystems, trees are most likely to be foundation species. Their architecture
73 and functional and physiological characteristics define forest structure and alter microclimates,
74 while their biomass and chemical make-up contribute substantially to ecosystem processes.
75 Foundation tree species are declining throughout the world due to: introductions and outbreaks
76 of nonindigenous pests and pathogens; irruptions of native pests; over-harvesting and high-
77 intensity forestry; and deliberate removal of individual species from forests. We elaborate three
78 examples from North America to illustrate consequences for both terrestrial and aquatic habitats
79 of the loss of foundation tree species: the ongoing decline of eastern hemlock (*Tsuga canadensis*
80 (L.) Carr.) resulting from an introduced insect and preemptive salvage logging; the local
81 extirpation of whitebark pine (*Pinus albicaulis* Engelm.) caused by interactions among a non-

82 native pathogen, a native insect, and human alteration of fire regimes; and the functional removal
83 of American chestnut (*Castanea dentata* (Marshall) Borkh.) by an introduced pathogen. Our
84 examples focus on trees in systems we know best, but they are broadly representative of a wide
85 range of foundation species and illustrative of their role in forests throughout the world (Panel 2).

86

87 **The rise and fall of eastern hemlock**

88 Majestic hemlock groves (Fig. 1) evoke reverence, affection, and poetry (Frost 1923).
89 Eastern hemlock, one of the most long-lived, shade-tolerant trees in North America, dominates
90 *ca.* 1×10^6 ha of forest from the southern Appalachians to southern Canada and west to the
91 central Lake states (McWilliams and Schmidt 2000). In the north, hemlock typically occurs in
92 nearly pure stands with species-poor understories. In the south, hemlocks grow in mixed stands
93 in narrow riparian strips and moist coves, often with dense understories of rhododendron
94 (*Rhododendron maximum* L.). In hemlock-dominated stands, the combination of deep shade and
95 acidic, slowly-decomposing litter results in a cool, damp microclimate, slow rates of nitrogen
96 cycling, and nutrient-poor soils (Jenkins *et al.* 1999). Canopies of evergreen hemlocks have
97 higher leaf area index and lower transpiration rates per unit leaf area than canopies of co-
98 occurring deciduous trees (Catovsky *et al.* 2002). Although hemlocks have much greater whole-
99 tree respiration rates in the spring and fall when deciduous trees are leafless, during the summer
100 hemlocks transpire ~50% of the water transpired by deciduous trees (J. Hadley, *unpublished*
101 *data*). These characteristics of hemlock, along with its high snow-interception rates, mediate soil
102 moisture levels, stabilize stream base-flows, and decrease diel variation in stream temperatures.
103 As a result, streams flowing through hemlock forests support unique assemblages of

104 salamanders, fish, and freshwater invertebrates intolerant of seasonal drying (Snyder *et al.* 2002).
105 Hemlock stands also shelter deer and other wildlife.

106 Populations of eastern hemlock have declined precipitously three times since the
107 Pleistocene glaciation: ~5500 years ago coincident with regional climate change and an
108 outbreak of an insect similar to the extant eastern hemlock looper (*Lambdina fiscellaria* Hulst.)
109 (Bhury and Filion 1996); ~200 years ago following forest conversion to agriculture, increases in
110 fire, and extensive logging for timber and tannin (McMartin 1992); and from the mid-1980s to
111 the present, due to an introduced insect, the hemlock woolly adelgid (*Adelges tsugae* Annand).
112 This rapidly spreading insect kills trees of all sizes and age-classes within 4-15 years of
113 infestation (Orwig *et al.* 2002). Hemlock has no apparent resistance to the adelgid; it rarely
114 recovers from attack (Orwig *et al.* 2002), and there currently are no effective biological or
115 chemical controls of the adelgid in forested ecosystems. The adelgid's impact is further
116 exacerbated by preemptive salvage logging, in which hemlock, which has modest economic
117 value, is cut in anticipation of future infestation (Orwig *et al.* 2002).

118 Hemlock could functionally disappear from eastern forests in the next several decades.
119 Hemlock generally does not re-establish following adelgid-induced mortality (Fig. 1), but is
120 replaced throughout its range by hardwood species including birch (*Betula* spp.), oaks (*Quercus*
121 spp.) and maples (*Acer* spp.) (Orwig *et al.* 2002). In the southeastern United States when
122 *Rhododendron* is absent, hemlock is replaced by yellow poplar (*Liriodendron tulipifera* L.) (J.
123 Vose *et al.*, unpublished). Decline of hemlock may lead to the local loss of its uniquely
124 associated ants (Ellison *et al.* 2005) and birds (Tingley *et al.* 2002), cause regional
125 homogenization of floral and faunal assemblages (Ellison *et al.* 2005), change soil ecosystem
126 processes (Fig. 2; Jenkins *et al.* 1999) and alter hydrological regimes (Fig. 2).

127 The effects of adelgid-induced hemlock mortality on stream ecosystems will be
128 extensive. For example, hemlock streams support significantly more taxa of aquatic invertebrates
129 than paired mixed-hardwood stands, and nearly 10% of the taxa are strongly associated with the
130 presence of hemlock (Snyder *et al.* 2002). Hemlock death may result in a rapid pulse of large
131 amounts of wood that decays more slowly than coarse woody debris from hardwoods. Large
132 hemlock logs in streams retain sediment and organic matter and create novel habitat types. In
133 general, large hemlock logs are abundant in streams draining forest where hemlock is an
134 important riparian species. Although logs from adelgid-killed hemlocks may persist in streams
135 for decades to centuries, eventually the loss of hemlock will reduce in-stream wood, leading to a
136 loss of in-stream sediment retention and productivity.

137 Logging of hemlock initiates more rapid and greater ecosystem changes than the adelgid
138 because of the abrupt vegetation and environmental changes, removal of wood of hemlock and
139 other species, soil scarification, and presence of extensive slash left by logging operations
140 (Kizlinski *et al.* 2002). Nitrogen availability and nitrification rates are significantly higher in cut
141 forests than in adelgid-damaged ones, increasing the threat of nutrient losses and changing food
142 availability in nearby aquatic systems (Kizlinski *et al.* 2002, C. Swan, *unpublished*).

143

144 **The shifting mosaic of whitebark pine**

145 Whitebark pine forms extensive contiguous stands in high elevation forests of the Rocky
146 Mountains of Wyoming, Montana, Idaho and Alberta, and smaller disjunct populations in eastern
147 and southwestern Oregon, California, and Nevada. This dominant late-successional species (Fig.
148 3) grows as dense krummholz at its upper elevational limit, whereas at lower elevations and less
149 extreme sites, it grows in association with other conifers and its dominance is maintained by

150 periodic fire (Arno 2001). Whitebark pine has occupied its current range for ~8000 years. In
151 western North America, extensive forests of whitebark pine, spruce (*Picea* spp.) and poplar
152 (*Populus* spp.) developed after glacial retreat. As warming continued 8000 – 4000 years ago,
153 whitebark pine became restricted to high elevation sites (MacDonald *et al.* 1989).

154 Whitebark-pine cover at upper elevations retards snowmelt and modulates runoff and
155 stream flows (Farnes 1990). At lower elevations, post-fire mid-successional whitebark pine
156 stands provide shade and cool soil, facilitating establishment of diverse plant communities and
157 associated cryptogams, invertebrates, and microbes. Its seeds serve as a major seasonal food
158 source for bears, small mammals, and birds (Mattson *et al.* 2001).

159 Throughout its range, whitebark pine is declining due to the combined effects of: an
160 introduced pathogen, *Cronartium ribicola* J.C. Fischer; a native bark beetle, *Dendroctonus*
161 *ponderosae* Hopkins; and fire-suppression policies (Kendall and Keane 2001). The pathogen *C.*
162 *ribicola*, which causes white pine blister rust, was introduced from Eurasia into western North
163 America in 1910 on imported white pine (*Pinus strobus* L.) seedlings planted near Vancouver,
164 British Columbia (MacDonald and Hoff 2001). After its introduction, *C. ribicola* spread in a
165 series of episodic pulses throughout western North America, and by the late 1930s it was
166 established throughout the west, where it devastated pine stands (MacDonald and Hoff 2001).
167 Fire exclusion further allowed replacement of whitebark pine by more shade tolerant species, and
168 at lower elevations promoted growth of dense stands of lodgepole pine (*Pinus contorta* Dougl.
169 ex. Loud.). In turn, lodgepole pine supports high populations of *D. ponderosae* beetles that
170 disperse into adjacent whitebark pine stands when beetle populations irrupt. In a positive
171 feedback loop, drought- and disease-stressed whitebark pines are further susceptible to beetle
172 attack.

173 Loss of whitebark pine alters watershed hydrology immediately as flashiness of streams
174 increases, and changes dynamics of wildlife populations and succession over longer time scales.
175 Cone crops of whitebark pine have declined due to interactions among white pine blister rust,
176 fire exclusion, and bark beetles, and carrying capacities of species dependent on whitebark pine
177 seeds have declined with the cone supply of this irreplaceable species (Mattson *et al.* 2001).

178

179 **The shrub that was a tree: the saga of American chestnut**

180 American chestnut was once a foundation species in eastern North American forests (Fig.
181 4). Chestnut and oak were co-dominants in the southern Appalachians for nearly 4000 years and
182 reached the northeast 2500-1500 years ago (Paillet 2002). Chestnut provided important resources
183 for wildlife and humans, and locally exerted a strong influence on ecosystem structure and
184 function (Paillet 2002). Chestnut blight, caused by the canker pathogen *Cryphonectria parasitica*
185 (Murr.) Barr, was introduced from Asia in the late 19th century. The blight was first noted in
186 New York in 1904, spread rapidly (~37 km/yr) across the range of chestnut, and within 50 years
187 had converted this stately tree to a rarely-flowering understory shrub across ~3.6 million ha
188 (Anagnostakis 1987).

189 Chestnut has a rapid growth rate and sprouting ability, wood with an extremely high
190 tannin content, and leaves with a relatively low C:N ratio. Therefore, fundamental forest
191 ecosystem processes including decomposition, nutrient cycling and productivity likely changed
192 significantly following chestnut's replacement by other species. Decomposition of chestnut
193 wood is much slower than other co-occurring hardwoods and its high tannin concentrations
194 could restrict the mobilization of nutrients in soils. Additionally, chestnut's fast growth rate
195 (Jacobs and Severeid 2004) might have resulted in rapid sequestration of carbon and nutrients.

196 Chestnut dominated a wide range of environments and its decline is thought to have
197 altered both terrestrial and aquatic processes. There is evidence to suggest that the abundance of
198 chestnut along riparian corridors of the southern Appalachians was due to production of
199 allelochemicals that prevented establishment of what we now consider “typical” riparian shrub
200 and tree species, including eastern hemlock and rhododendron (Vandermaast *et al.* 2002).
201 Ironically, therefore, the loss of one foundation species – American chestnut – may have
202 facilitated the establishment of another – eastern hemlock – which itself is now threatened.

203 In most forested headwater streams, autumn leaf inputs serve as the predominant energy
204 base for aquatic ecosystems. Where chestnut was replaced by oak, relatively rapidly decaying
205 chestnut leaves with high nutritional quality for aquatic macroinvertebrates were replaced by
206 more slowly decaying oak leaves with lower nutritional quality (Smock and MacGregor 1988).
207 As a consequence, leaf-processing and consumption rates would have declined, decreasing
208 growth rates, and adult body mass in macroinvertebrate shredder communities. Many stream
209 macroinvertebrates have life cycles closely synchronized to the dynamics of detrital decay, and
210 this change in detrital quality undoubtedly affected the macroinvertebrate assemblage though
211 there are no data to support this supposition. Further, slowly decomposing chestnut wood persists
212 for decades in stream channels, altering channel structure and providing habitat for fish and
213 invertebrates. For example, in an Appalachian headwater stream sampled in the late 1990s,
214 Wallace *et al.* (2001) found that 24% of the large (>10 cm diameter) woody debris still consisted
215 of American chestnut that had died over 50 years earlier.

216

217 **Functional loss versus total loss**

218 As foundation species decline, their control of ecosystem structure and processes may
219 wane long before the species itself disappears completely. For example, as hemlock stands
220 decline, tree death opens the canopy, drastically altering the understory microclimate and causing
221 the loss of the unique habitat hemlock creates. Similarly, shrubby chestnut contributes little to
222 leaf area, wood production, or nuts, so that while it is still present in many forests, the American
223 chestnut tree is functionally extinct.

224 The potential effects on ecosystem function and community composition caused by the
225 loss of foundation species can be either exacerbated or ameliorated by patterns of decline in time
226 and space. For example, logging and diseases such as chestnut blight or white pine blister rust
227 have resulted in rapid loss of foundation species over broad areas. This contrasts with the slow
228 death of individuals over decades or partial loss of a species through removal or death of only
229 one age or size class, as in beech bark disease (Griffin *et al.* 2003). Similarly, whether the spatial
230 pattern of individual deaths occurs in mosaic fashion or as an advancing wave of death
231 influences the timing and magnitude of loss of a foundation species (Holdenreider *et al.* 2004),
232 and perhaps the ultimate outcome. Forest fragmentation often occurs in mosaic patterns across
233 the landscape (*e.g.*, Halpern *et al.* 2005), whereas epidemiological models of plant pathogens or
234 species invasions suggest that changes in forest structure occur in wave-like patterns (Johnson *et*
235 *al.* 2004). Such studies suggest that where complex spatial and temporal patterns of species loss
236 occur, the effects at any particular location are unlikely to be a linear function of area altered or
237 changes in species' dominance. Indeed, threshold responses, including transitions to new types
238 of ecosystems, should be expected where key dependent variables, such as mast production,

239 herbivore or detritivore abundance, or adult survival, result from a complex web of indirect
240 relationships (*e.g.*, Ebenman and Jonsson *in press*).

241

242 **Responding to the loss of foundation species**

243 Because foundation tree species tend to be common, abundant, and large our responses to
244 their loss often come late and are conducted at inappropriate scales. For example, the on-going
245 attempt to recreate the American chestnut by back-crossing the few remaining fertile individuals
246 with resistant species from Europe and Asia holds out the promise of specimen trees in suburban
247 lawns but is unlikely to reforest *ca.* 4 million hectares with hybrid chestnuts. Similarly, chemical
248 control of the hemlock woolly adelgid requires injecting trees annually and can only target
249 isolated single trees or small groves. Biological control of the adelgid using non-native,
250 generalist, predaceous beetles is being explored with uneven regard for the long history of
251 unexpected impacts attendant to the importation of exotic insects (*e.g.*, Howarth 1991, Boettner
252 et al. 2000). Although several million beetles are released every year, there have been no
253 systematic attempts to determine whether self-sustaining populations have become established or
254 how effective they are at actually controlling the adelgid in the field. Overall, we would be much
255 more likely to conserve foundation species and the systems they create if we set aside very large
256 reserves of intact forests and adopted techniques that preserve ecosystem integrity in those forest
257 stands that we do manage (Foster et al. 2005).

258

259 **Conclusions**

260 There is no sign that the currently increasing rates of resource extraction, climate change,
261 or global movement of pests and pathogens will slow any time soon. Foundation species have

262 disappeared before and they will continue to disappear. Despite nearly half a century of research
263 on foundation species (Panel 1), our understanding of the consequences of their loss is based on
264 a small number of case studies, as we usually identify foundation species only after they have
265 declined dramatically. Our examples illustrate that foundation tree species can control both
266 terrestrial forest processes and the dynamics of aquatic systems within their watersheds. Detailed
267 information on the importance of foundation species to key ecosystem processes are scarce,
268 however. Likewise, the impact on water quality from the loss of foundation species could be
269 significant and merits further study.

270 Long-term monitoring can reveal how losses of foundation species alter successional
271 rates and trajectories, leading in some cases to novel forest types (such as black birch forests in
272 New England) with unexpected dynamics. But monitoring is not enough. Ecologists have long
273 appreciated the complex nature of interactions among species, and we encourage direct,
274 experimental approaches that use current foundational species' losses as an opportunity to
275 determine how the removal of a single species can have immediate and profound effects on other
276 species and ecosystem processes.

277 The dynamics of communities and ecosystems shaped by foundation species are
278 dominated by a small number of strong interactions (Fig. 2). Such systems are relatively fragile
279 and susceptible to switching between alternative stable states following even small perturbations
280 (Dudgeon and Petraitis 2005). At the same time that many forested systems are losing their
281 foundation species, they are simultaneously and synergistically threatened by climate change,
282 atmospheric deposition, drought, and invasion of exotic species, all of which may increase their
283 overall fragility. Temperate-zone forests, such as those we highlighted here, have few tree
284 species relative to the species-rich tropical forests that garner much attention from ecologists and

285 conservation biologists. When there are only one or two foundation species in a forest, there is
286 little functional redundancy in many important respects, and their loss is likely to lead to rapid,
287 possibly irreversible, shifts in biological diversity and system-wide changes in structure and
288 function (Ebenman and Jonsson *in press*). Regrettably, the lack of detailed knowledge of the
289 natural history of most species in most forests, and the abandonment of courses and curricula in
290 natural history (Dayton 2003) will leave us unaware of the collapse of the intricate webs of
291 interactions and processes that are lost when foundation species disappear.

292 Foundation species provide fundamental structure to a system, and thus they are by
293 definition irreplaceable. For example, without hemlock, hemlock forests cease to exist, and no
294 other native conifer possesses the same suite of structural and functional characteristics that
295 simultaneously define its position in the system and control system-wide dynamics and
296 processes. Many recognized foundation tree species (text and Panel 2) that have been identified
297 are conifers, but it remains an open question whether conifers are disproportionately represented
298 among foundation species. We need new research tools, models, and metrics that will allow us to
299 identify foundation species *a priori* and to anticipate the cascade of immediate, short-term, and
300 long-term changes in ecosystem structure and function that follow their loss. Community
301 viability analysis (Ebenman and Jonsson *in press*) may provide some of these tools, but its utility
302 awaits empirical evaluation. Ongoing declines of many foundation species (Panel 2) provide
303 timely, though unfortunate, opportunities to develop such tools and models.

304

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434 **Panel 1 – The many definitions of foundation species.**

435

436 Following nomenclatural priority, we adopt Dayton’s (1972) terminology and general definition
437 of a foundation species: *a single species that defines much of the structure of a community by*
438 *creating locally stable conditions for other species, and by modulating and stabilizing*
439 *fundamental ecosystem processes.*

440 Subsequent authors, working in different habitats and apparently unaware of historical
441 antecedents, have suggested terms with some or all of the attributes of foundation species,
442 including:

443 *Core species* (Hanski 1982) are locally abundant and regionally common; associated *satellite*
444 *species* are sparse and rare. An associated metapopulation model (the *core-satellite hypothesis*)
445 explains relationships between a species’ local abundance and its regional distribution.

446 *Dominant species* (Grime 1984) competitively exclude subordinate species by garnering a
447 disproportionate share of resources and contributing most to productivity.

448 *Keystone predators* (Paine 1966) preferentially consume dominant competitors and enhance
449 local biodiversity by preventing exclusion of weaker competitors. Holling’s (1992) *extended*
450 *keystone hypothesis* posits that all terrestrial ecosystems are controlled and organized by a small
451 set of *keystone species*.

452 *Structural species* (Huston 1994) create physical structures of environments, produce variability
453 in physical conditions, provide resources, and create habitat for *interstitial species*.

454 *Ecosystem engineers* (Jones *et al.* 1994) cause physical state changes in biotic or abiotic
455 materials and modulate availability of resources to other species. Class 5 *autogenic ecosystem*
456 *engineers* are directly analogous to Dayton's foundation species.

457 **Panel 2. Additional examples of foundation species from forests around the world.**

458

459 **Bald cypress, *Taxodium distichum* (L.) Richard**, dominates deepwater swamps of southeastern
460 North America (Sharitz and Mitsch 1993). Its presence and density affect the water table and
461 flow of sediment and nutrients, and control structure and composition of associated plant and
462 animal communities (Sharitz and Mitsch 1993). Intensive logging and removal of bald cypress
463 dramatically alters hydrology and nutrient cycling, reduces primary productivity, and increases
464 sedimentation (Sun *et al.* 2001).

465 **Douglas fir, *Pseudotsuga menziesii* (Mirbel) Franco**, dominates young and old-growth forests
466 at low and mid-elevations west of the Cascade Range and at higher elevations in the interior of
467 the Pacific northwest of North America. Live trees, snags, and fallen logs provide unique habitat
468 for wildlife including endangered and rare species such as the spotted owl. The evergreen foliage
469 controls light levels, microclimate, and gas exchange from the forest floor to the canopy (Parker
470 *et al.* 2004). Logging alters C and N cycling, wildlife abundance, and plant successional
471 dynamics (Halpern *et al.* 2005). Unlike the other foundation species discussed in this paper,
472 Douglas fir is not currently threatened, as it is strongly favored by current forest management
473 practices in the Pacific Northwest. However, many old-growth stands in the Pacific Northwest
474 have been lost to logging over the past decades. High-intensity fires resulting from long-term
475 fire suppression practices, introduced pests or changes in the ecological dynamics of native pests,
476 or changes in forest management that pose mortality risks to old-growth Douglas fir stands could
477 have important ecological impacts in the future.

478 **Fraser fir, *Abies fraseri* (Pursh) Poiret**, is a locally abundant endemic species that occurs in six
479 discrete high-altitude areas in the southern Appalachians (Hollingsworth and Hain 1991). There,

480 Fraser fir defines high-elevation spruce-fir communities, with tightly associated animal and plant
481 species. Fraser fir has been declining since the balsam woolly adelgid *Adelges piceae*
482 (Ratzeburg) was introduced in the 1930s (Hollingsworth and Hain 1991). Its loss increases
483 susceptibility of its co-dominant, red spruce (*Picea rubens* Sarg.), to windthrow, and both
484 species are suffering additional effects of climate warming and air pollution (Hamburg and
485 Cogbill 1988).

486 **Jarrah**, is a unique Australian forest type comprised mainly of *Eucalyptus marginata* **Donn ex**
487 **Sm.** It experiences mass collapse and sudden death following waterlogging, which increases
488 infection of jarrah roots by zoospores of *Phytophthora cinnamomi* (Davison and Tay 1987), a
489 soil-born pathogenic fungus introduced into Western Australia in 1921 that affects ~2000 of the
490 9000 extant plant species there (Wills 1992). Following invasion by *P. cinnamomi*, richness of
491 woody perennial species in the jarrah understory declines significantly, whereas richness of
492 monocots, herbaceous perennials, annuals and geophytes are largely unaffected (Wills and
493 Keighery 1994).

494 **Port-Orford cedar**, *Chamaecyparis lawsoniana* (A. Murray) **Parl**, endemic to southwestern
495 Oregon and northern California, grows on ultramafic and non-ultramafic soils, in riparian and
496 upland sites, and occurs in the most diverse plant associations in the region. On ultramafic soils,
497 Port-Orford cedar often is the only riparian tree species. It is a foundation species for both
498 terrestrial and aquatic habitats: it recycles calcium to surface soils, provides shade, and stabilizes
499 soil and stream banks (Hansen *et al.* 2000), and its highly rot-resistant wood provides habitat
500 heterogeneity and alters hydrology. The non-native, water-dispersed, and generally lethal root
501 pathogen *Phytophthora lateralis* Tucker & Milbrath has spread into virtually all natural forest
502 stands from nursery plants infected in the early 1920s (Hansen *et al.* 2000).

503 **Mangroves, *Rhizophora spp.***, form dense, often monospecific stands in estuarine and coastal
504 forests throughout the tropics; these forests have some of the highest reported net primary
505 productivity of any ecosystem on the planet (Ellison and Farnsworth 2001). Removal of
506 mangroves leads to rapid build up of acid sulfides in the soil, increased shoreline erosion and
507 sedimentation onto offshore coral reefs, and collapse of intertidal food webs and inshore fisheries
508 (Ellison and Farnsworth 2001). More than 2% of mangrove forests are lost annually, as forests
509 are cut for fuel, coastal development, and wood fiber used to produce rayon.

510 **Figure Legends**

511 **Figure 1.** An old-growth eastern hemlock (*Tsuga canadensis*) stand (left), a stand declining
512 following 10 years of infestation by hemlock woolly adelgid (*Adelges tsugae*) (center and
513 inset), and dense regeneration of black birch (*Betula lenta*) saplings on a site formerly
514 dominated by eastern hemlock in southern Connecticut (right). Nearly all hemlock trees
515 in this 150-hectare in southern Connecticut forest were killed in the mid-1990s by the
516 hemlock woolly adelgid. Photographs courtesy of MD Abrams (Pennsylvania State
517 University, DA Orwig (Harvard Forest) and D Lee (Florida International University).

518 **Figure 2.** Conceptual model of shifts in terrestrial and aquatic ecosystem processes following
519 loss of eastern hemlock from northern (left) and southern (center) forests and conversion
520 to hardwood-dominated stands (right).

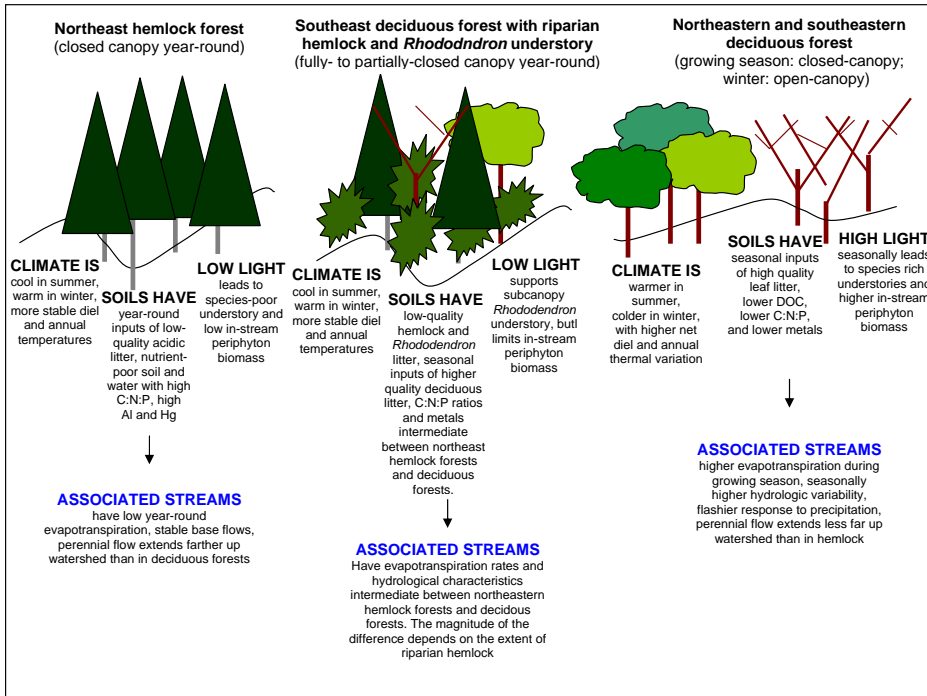
521 **Figure 3.** High-elevation stands of whitebark pine (*Pinus albicaulis*). This species is transformed
522 from healthy stands (left) to dead stands (right) through the interaction of fire
523 suppression, the introduced pathogen *Cronartium ribicola* that causes white pine blister
524 rust (inset), and the native bark beetle *Dendroctonus ponderosae*. Photographs courtesy
525 of S van de Gevel and E Larson (University of Tennessee).

526 **Figure 4.** American chestnut (left: Chestnut timber, Great Smoky Mountains of Western North
527 Carolina, photographed by Sidney V. Streator *ca.* 1910), a foundation species that was
528 transformed in the mid-20th century to an understory shrub (right: small shrub in center)
529 by the introduced pathogen *Cryphonectria parasitica* that causes chestnut blight (center:
530 chestnut in the Blue Ridge Plateau killed by the blight, photographed by Bluford W. Muir
531 1946). Archival photographs courtesy of the Forest History Society, Durham, NC;
532 chestnut understory photograph courtesy of DA Orwig (Harvard Forest).



533

534 Figure 1



535

536 Figure 2

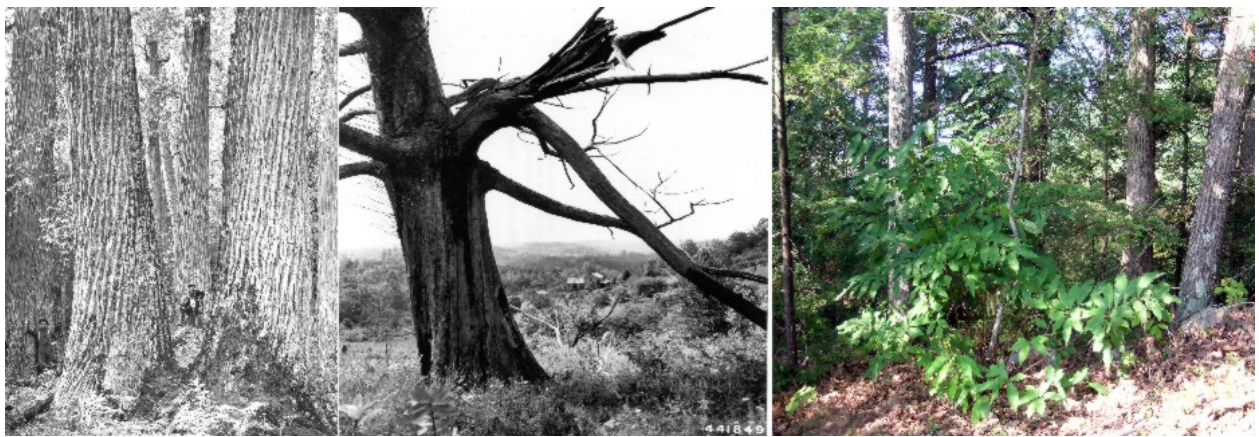
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538

539 Figure 3

540



541

542 Figure 4