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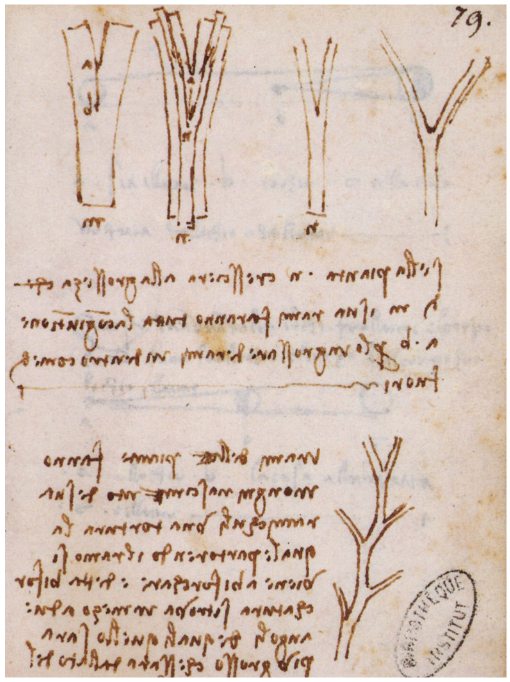


Da Vinci trees
Leonardo da Vinci became fascinated about rules that determine the branching patterns of trees. The far right sketch makes a critical prediction that the cross-sectional area of a tree trunk (the lowest line that crosses the trunk) is equal to the summed cross-sectional area at any distance from the base (that is, at the semicircles that represent successive distance from the trunk).

Variations

Leaf sizes also vary with environment: the mean and range of leaf sizes decrease from the tropics to the boreal zone, and from moist to dry forests. However, at any point on these environmental gradients there are usually tree species that vary along the architectural spectrum predicted by Corner's rules. Why does this variation occur? The answer to this is not clear. One theory suggests that because leaves represent a cheaper investment than stems, creating a crown of large leaves and/or a greater leaf area per annual increment of wood can allow such species to be faster in height growth and crown expansion, and thus ideal for the high light levels created by the death of canopy trees.

Leonardo's prediction

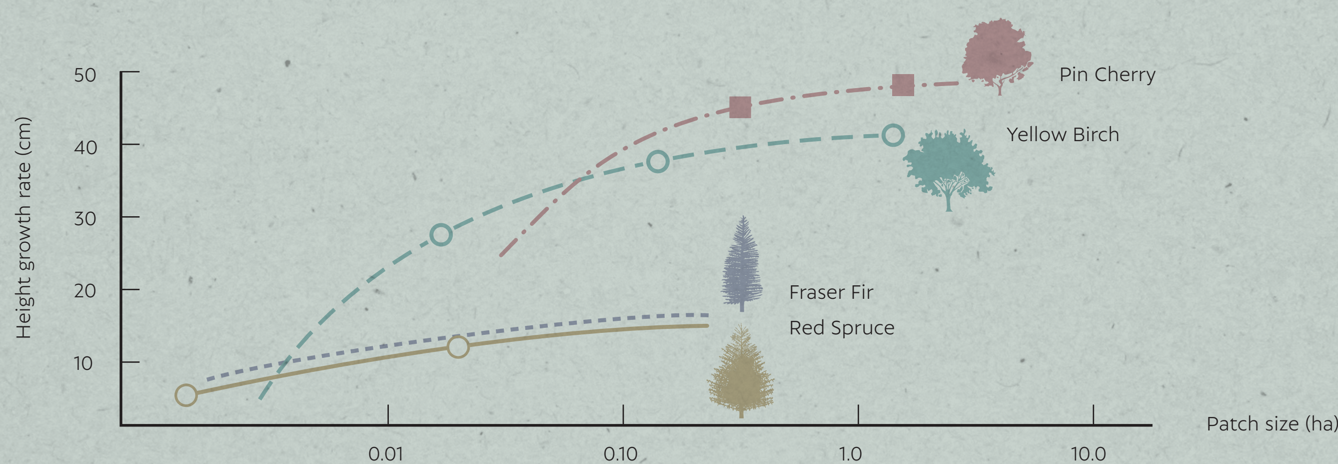
The Italian polymath Leonardo da Vinci (1452–1519) made a related prediction, saying that the cross-sectional area of a tree at its base is equal to its cross-sectional area at any distance from the base. In other words, if you gather all the twigs at the edge of a tree crown together as a bundle, the summed cross-sectional area of all the twigs will be the same as the cross-sectional area of the trunk at the base of the tree. To demonstrate this, imagine a set of 100 garden hoses, each 100 ft (30 m) long, gathered at one end as a round bundle. Moving along the bundle, at 30 ft (10 m) from the base, divide the 100 hoses into two sets of 50. Then at 50 ft (15 m) from the base, divide each of the two bundles into two sets (four in total) of 25. Continue this process until you are left, in each final "branch," with a single hose. Thus, we have Leonardo's prediction: the cross-sectional area of the hoses at the base is equal to the combined cross-sectional area of the individual hoses at the tips of the branching.

This simple model echoes one of Corner's rules: the more you divide the branches, the thinner those branches become. In reality, trees deviate somewhat from Leonardo's prediction, because they are not just made up of hollow tubes for water conduction, but also have structures for mechanical support that may vary from tree base to twig tip. It also seems that trees "overproduce" twigs, such that the summed cross-sectional area at the twig level is somewhat greater than the trunk diameter, although there are few direct observations from which to draw a conclusion.

Nonetheless, Leonardo's general idea is implicit in one of ecology's rules of thumb: the cross-sectional area of a tree trunk predicts the total leaf area of the crown. It being much easier to measure diameter than leaf area, field ecologists often take the diameter of the trunk as predictive of the tree's role (total leaf area being tied to total productivity). Because tree trunks often swell near the ground, this diameter is usually measured at "breast height," taken as 4½ ft (1.4 m) above the ground.

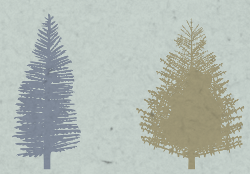
FAST AND SLOW CROWN GROWTH

Fast and slow crown growth are represented by height growth among four trees in the high-elevation spruce-fir forests in Great Smoky Mountains National Park (see Chapter 2, pages 70–71, for additional description of the disturbance dynamics of this ecosystem). The size of the disturbance patches (x-axis) is used as a surrogate for light availability.



Pin Cherry
A species with high leaf area per annual increment of stem growth and fast growth. This species requires high light (large disturbance patch size) and does not survive under shady conditions. It reaches 20 in (50 cm) extension growth per year in larger patches.

Yellow Birch
A species with intermediate leaf area per annual increment of stem growth. This species requires some disturbance for long survival. It reaches 12–16 in (30–40 cm) extension growth per year.



Fraser Fir and Red Spruce
These two species have low leaf area per annual increment of stem growth. Fir and spruce persist in the deepest shade in these forests, but grow in height only about 2 in (5 cm) per year. They grow faster (up to 6 in/15 cm per year) in disturbed patches but are outcompeted in the largest patches.

MONOLAYERS AND MULTILAYERS

Multilayers distribute leaves in a larger volume, monolayers tend to make fewer layers and, in extreme, just one.

Henry Horn's monolayers and multilayers

The second insight comes from the work of American ecologist Henry Horn, who in his 1971 book *The Adaptive Geometry of Trees* argued that the light environment predicts leaf arrangement. More specifically, he said that in low light tree branching should create less leaf overlap and, in the extreme, what he called monolayers of leaves, whereas in greater light trees can benefit from greater leaf overlap, creating what Horn called multilayers. For example, in the interior of a dense forest, with low light levels, seedlings and saplings are more like the monolayer extreme, and in patches created by windstorms, fields, and sunlit gardens, with higher light levels, trees should develop as multilayers. However, individual trees display plasticity and tree species also differ genetically. Early successional species (see pages 94–97) depend on high light levels and tend to be multilayers wherever they are found, whereas late successional species tend to be monolayers, except if they are large and old enough to dominate the sunlit forest canopy. Interestingly, a 2020 paper by Thomas Givnish pointed out that there may be other benefits to multilayered leaves, including a reduction in water loss in sunny environments, that may outweigh the importance of light interception per se.

The 23 models of Hallé, Oldeman, and Tomlinson

A third insight into tree forms comes from the work of Hallé, Oldeman, and Tomlinson. Their scheme overlaps with some features of Corner's rules in that it is particularly concerned with the pattern of branching. It is distinctive, though, in its emphasis on dynamics of development from seed to adult plant, its emphasis on the spatial position of growing points that produce branching, and its inclusion of where and how reproductive structures are produced. The authors described 23 models for the development of tree forms, naming each for a prominent botanist. Taking the palm form (single unbranched, thick stems and many large leaves) as an extreme in Corner's rules, they named it Corner's model.

Wood density

Our last insight is that, even within one set of environmental conditions, tree species vary greatly in wood density, creating, among other things, a great range of materials fit for different kinds of human use—the Balsa wood of gliding aircraft to wood so dense that it sinks in water. By definition, low-density wood is less costly in terms of the use of carbon products from photosynthesis. One possible consequence of this is that, for a given amount of carbon fixed, low-density woods can create faster volumetric growth rates—faster growth in height and in crown expansion. Indeed, in full sunlight the annual height growth of Balsa trees is ten or more times the height growth of ebony trees (genus *Diospyros*), which have high-density wood. But there's a trade-off: ebony trees, with their slow-growing, densely wooded strategy, are more durable and the lifespan difference between the two species is probably about the same, being ten or more times longer in ebony trees than in Balsa.

▲ **Ebony**
Ebony is a slow-growing, long-lived tree with very dense wood.

▼ **Balsa wood**
In contrast to ebony trees, Balsa is a fast-growing, short-lived tree with light wood with specialty uses such as building model airplanes.

Dragon Blood Tree

The Dragon Blood Tree (*Dracaena cinnabari*) is a striking tree with bright red sap found only on the Socotra Islands (Yemen) of the Indian Ocean—155 miles (250 km) east of the Somali coast and 235 miles (380 km) south of the Yemen on the Arabian Peninsula. Of the vascular plant species on the Socotras 37 percent are found only there (endemic), which is comparable to other oceanic islands such as Mauritius, the Galápagos, and the Canary Islands. The flora of the Socotras have been evolving independently for the past 35 million years when they separated from the Arabian Peninsula. The trees are potentially vulnerable to an extinction under a climatic warming.

The Dragon Blood Tree has a striking umbrella shape and complies to one of Hallé, Oldeman, and Tomlinson's tree architectural models discussed on page 43. It is a great example of what they called Leeuwenberg's model, in which the dominant bud at the end of a twig first flowers and then new twigs are produced that grow around the former flower bud. The stems are a joined assemblage of Y-shaped elements and the trees are made of Y-shaped twigs, which show up well in these photos as well as in the da Vinci tree diagrams on page 40.

Building tall trees

Human architectural wonders pale in comparison to the tallest *Eucalyptus* trees of Australia or *Sequoiadendron* trees of California. From an engineering standpoint, one can only marvel at the fact that a living organism can reach heights of more than 380 ft (115 m). We understand that trees grow tall in order to outcompete their neighbors and harvest as much light as possible, but why is the limit slightly over 380 ft (115 m)? Why is no tree 500 ft (150 m) tall? Why is the limit not 150 ft (45 m)?

One explanation for the cap on tree height is that it is constrained by the mechanics of building tall structures from wood. Tree trunks are tall, slender, vertical wooden columns anchored to the ground. As with any other slender, vertical object, like a tower of wooden blocks, any small displacement may cause it to collapse by buckling. In 1757, Swiss mathematician Leonhard Euler (1707–1783) found that the maximum height a vertical column can reach before buckling under its own weight is related to the column diameter raised to the power of $2/3$. So, if the base diameter of a column doubles, the column's maximum height is multiplied by only a factor of 1.587. However, trees are generally not columnar, instead mostly have a conical, tapered shape, and they are not all made of a homogeneous material. Trunk shape and structure both slightly modify the coefficient of Euler's buckling formula, but they do not change the way maximum height scales with trunk diameter.

Environmental factors

So long as the base of a tree is large enough, Euler's formula does not set a maximum limit on its height. Two other processes must be considered: the risks of being damaged by wind, and the physiological constraints of the tree's hydraulic system. In many parts of the world, strong wind gusts are a major threat to trees; so long as they are sheltered by other trees, the risks of breakage are limited. Yet, the towering giants of the forest are fully exposed to wind, which is therefore a potent selective force against tall trees.

▶ **General Sherman**
*A Giant Sequoia (*Sequoiadendron giganteum*) tree located in the Giant Forest of Sequoia National Park, California.*

Tree hydraulics

The other explanation for the cap on tree height involves water. For a long time, observers thought that trees acquired their water through the condensation of air vapor at the surface of their leaves. However, it was later found that trees lift water from the soil. The control in lifting water upward is the difference in water density in the air relative to that in the leaf. This difference creates a water potential, which the plant tries to balance by transpiring water. The process creates a surface tension in the slender conduits in the tree, and by capillarity the water column is pulled upward from the roots. This theory was first formulated in 1914 by plant biologist Henry Dixon (1869–1953).

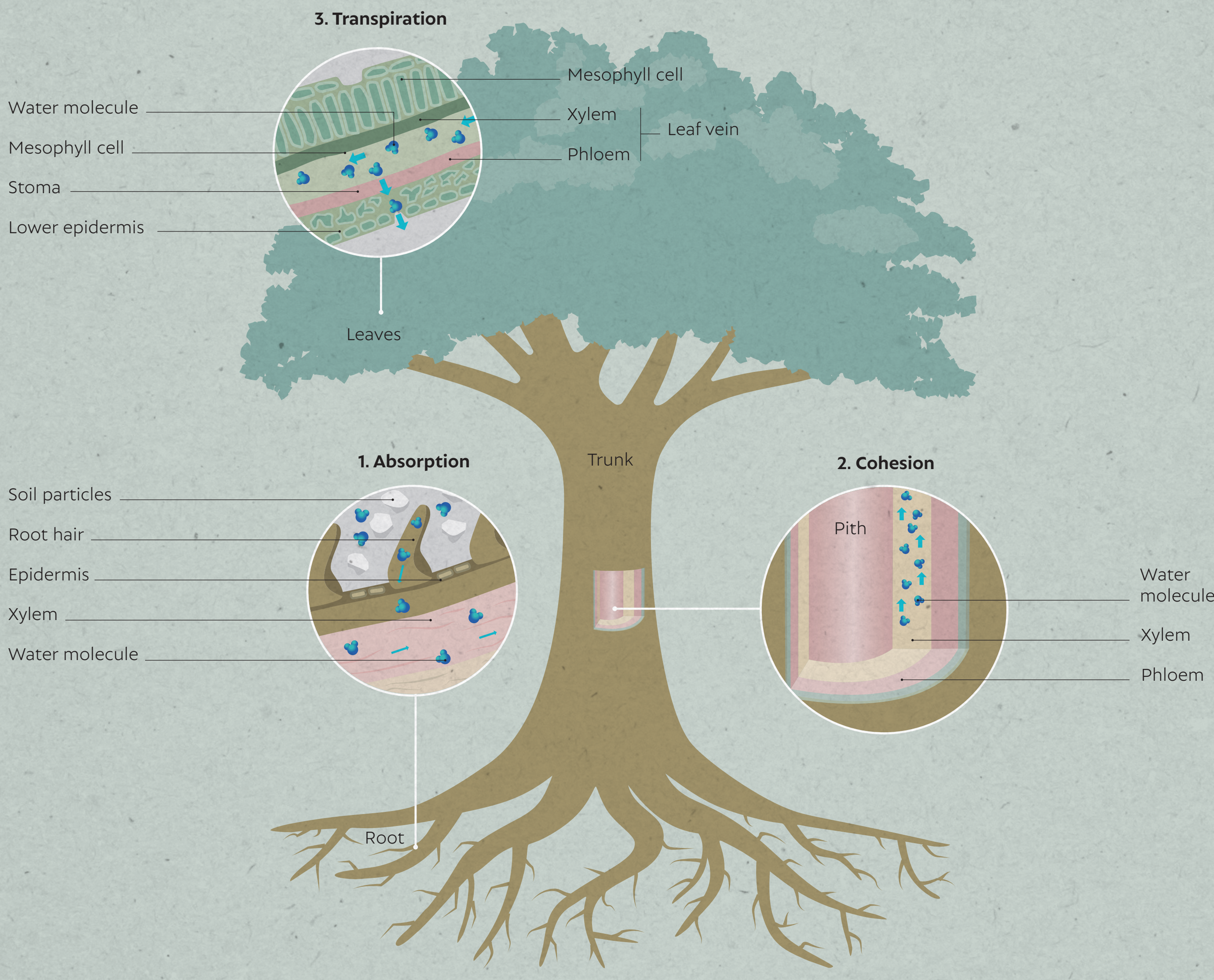
Drought stress

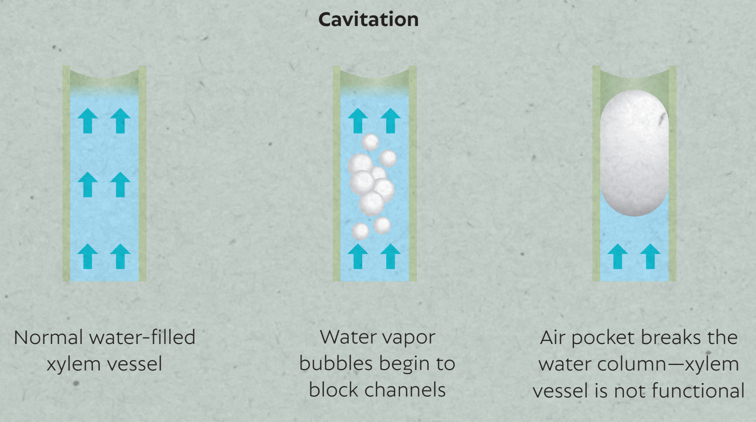
Taller trees must compensate for a greater gravitational force, and the pulling force for the ascent of sap should therefore be higher. However, if the tension of the water column is too high, this may create a phenomenon called cavitation, similar to the breakage of a rope under high tension. Water does not "break," but it does undergo a phase transition from a liquid to a gas, and this generates small water vapor bubbles in the otherwise liquid water column. Cavitation under tension produces a major alteration of the inner sap transportation conduits, leading to tissue death and even potentially the death of the entire tree. During extreme droughts, when the air surrounding leaves is very dry, plants lose large amounts of water through their leaf stomata (microscopic openings; see page 213) when they open these to let in carbon dioxide for photosynthesis. Under these conditions, the resultant tension on the water column is high enough to cause cavitation and eventually drought-induced death. Plants are adapted to their climate, and thin water conduits are much less likely to cavitate than wide water conduits, so it usually takes an exceptional drought to result in an actual increased mortality in trees.

As trees grow taller, they are more exposed to dry air and to gravitational forces. In 2004, ecosystem scientist George Koch and his colleagues climbed a tall Coast Redwood (*Sequoia sempervirens*) and measured leaf water tension at different heights during the driest hour of the day. They found that water tension increased linearly from the ground to the treetop, and the highest values were close to values where cavitation occurs. One could imagine that taller trees could avoid cavitation risks by having thin water conduits, but these would make it difficult for them to transport the large amounts of water they need. According to plant physiologist Ian Woodward, the plant hydraulic system should cavitate without other adaptations at an absolute limit at around 330 ft (100 m). Several physiological adaptations can push this limit to a maximum height of 400–425 ft (122–130 m).

WATER TRANSPORT AND CAVITATION

Trees must move water through the xylem in a continuous stream from the roots below to the leaves above. This movement is driven by the evaporation of water from the leaves, called transpiration, which produces tension in the water column. Under drought conditions, the tension becomes so negative, that bubbles of water vapor form, leading to a complete break in the water column—a phenomenon called cavitation.



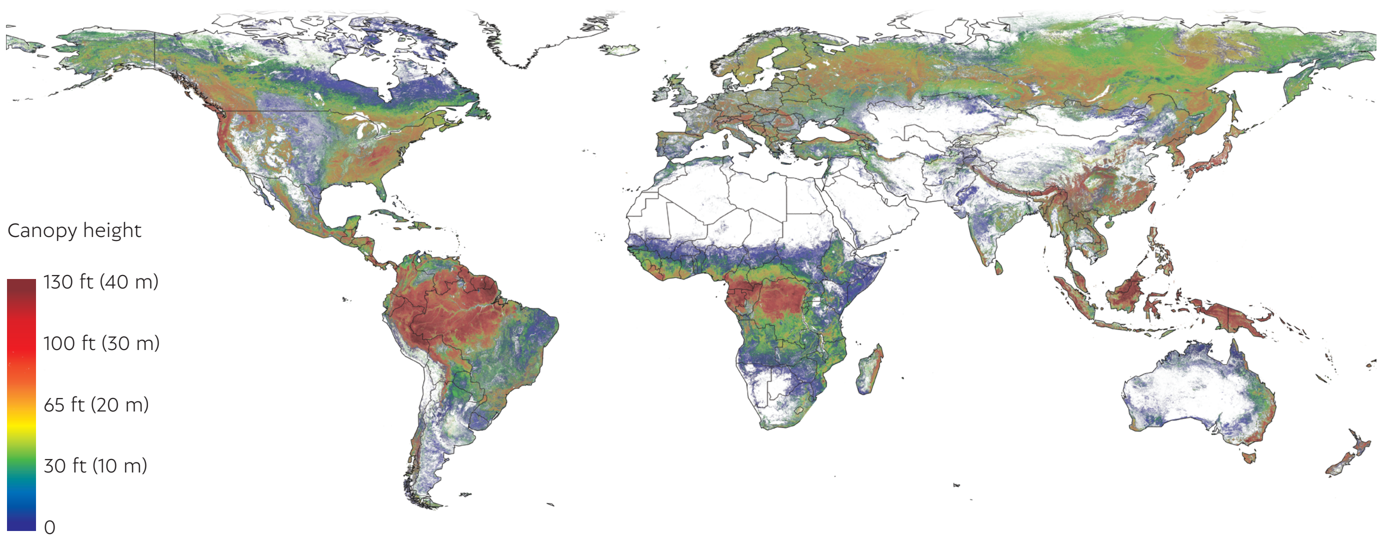


Reaching for the sky

The height of forests is an essential measurement, as forest vegetation is typified by verticality. The striving of trees to dominate the canopy, to gain the light they need to drive photosynthesis in their leaves and to gain control of local resources, drive the processes that ultimately produce forest patterns.

GLOBAL FOREST CANOPY HEIGHTS

In 2010, the ICESat satellite provided the first global lidar reconnaissance of the heights of the world's forests measured as height of the tallest 10 percent of the trees.



Often a tree's primary allocation to its growth of sugars derived from photosynthesis is to activate the top bud(s) and prioritize their elongation to add height. For ecologists, height reveals much about the status and future of each of the trees comprising a forest. For foresters, the height that a single-species forest of trees of equal age can reach at a given time is called the "site index" and it reveals the value of land for forest management. Site index tells a forester when to thin a forest, when to harvest it, and how densely the seedlings should be replanted in the regenerating forest after harvesting.

The use of lidar (light detection and ranging) instruments from ground, airplane, or satellite platforms has revolutionized local, and now global, capacity to measure forest height and its change. The map above shows the average heights of the tallest 10 percent of the trees in forests as seen from space using a 1,650 ft (500 m) spatial resolution. In this study, scientists used the Geoscience Laser Altimeter System on

board NASA's ICESat satellite to collect and calibrate 1,058,380 forest patches. ICESat was originally designed to measure the amount of ice in the Earth's polar ice sheets; that it has also proved able to measure forest heights is very fortuitous.

The temperate conifer forests were the tallest forests measured by ICESat, but globally they were also the most variable in height. The boreal forests were the shortest forests, and among these the shortest were the extensive deciduous larch (genus *Larix*) forests of northern Asia. The Indo-Malayan region has notably tall tropical and subtropical coniferous forests. Menara, the Yellow Meranti (*Shorea faguetiana*) tree, is a record height for a tropical tree and is from this region. The African tropics has taller temperate broad-leaved and mixed forests, but shorter tropical forests than other regions.

▲ **Lidar search**
*Mountain Ash (*Eucalyptus regnans*, left) and Yellow Meranti (*Shorea faguetiana*, right). Scientists continue to seek out the tallest trees. New discoveries are on the increase with the availability of remote sensing to survey the heights of forest canopies.*

WORLD'S TALLEST TREES

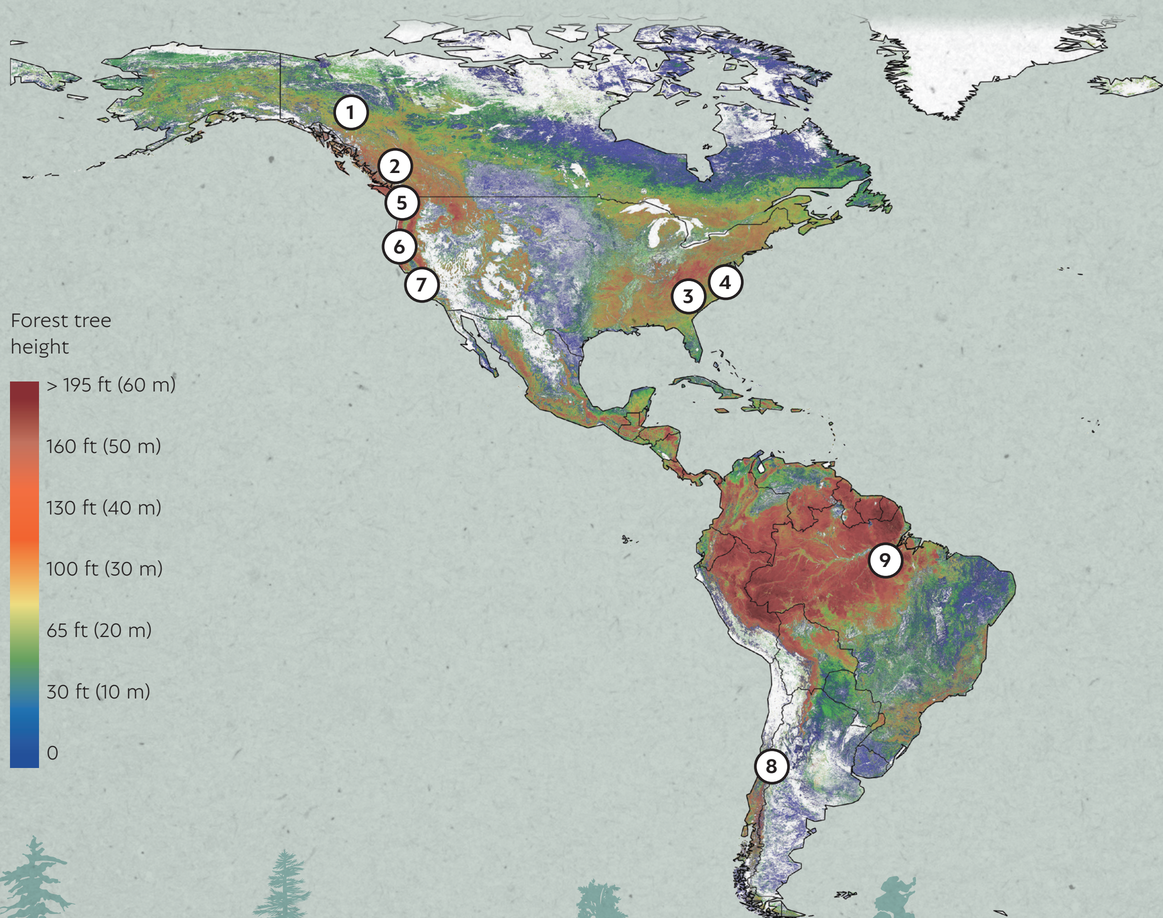
Species of extremely tall trees and the locations where they can be found on a map of observed maximum tree heights.

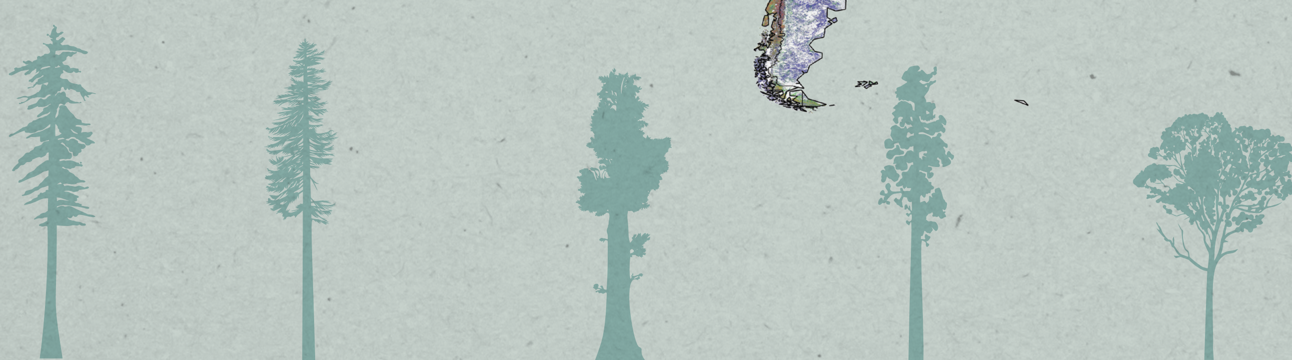
1 *Picea sitchensis*
(Sitka Spruce)
230–330 ft/70–100 m

2 *Abies procera*
(Noble Fir)
195–295 ft/60–90 m

3 *Liriodendron tulipifera*
(Yellow Poplar)
80–160 ft/25–50 m

4 *Pinus strobus*
(Eastern White Pine)
130–195 ft/40–60 m





5 *Sequoia sempervirens*
(Coast Redwood)
230–375 ft/70–115 m

6 *Pseudotsuga menziesii*
(Douglas Fir)
160–330 ft/50–100 m

7 *Sequoiadendron giganteum*
(Giant Sequoia)
195–330 ft/60–100 m

8 *Fitzroya cupressoides*
(Patagonian Cypress)
160–230 ft/50–70 m

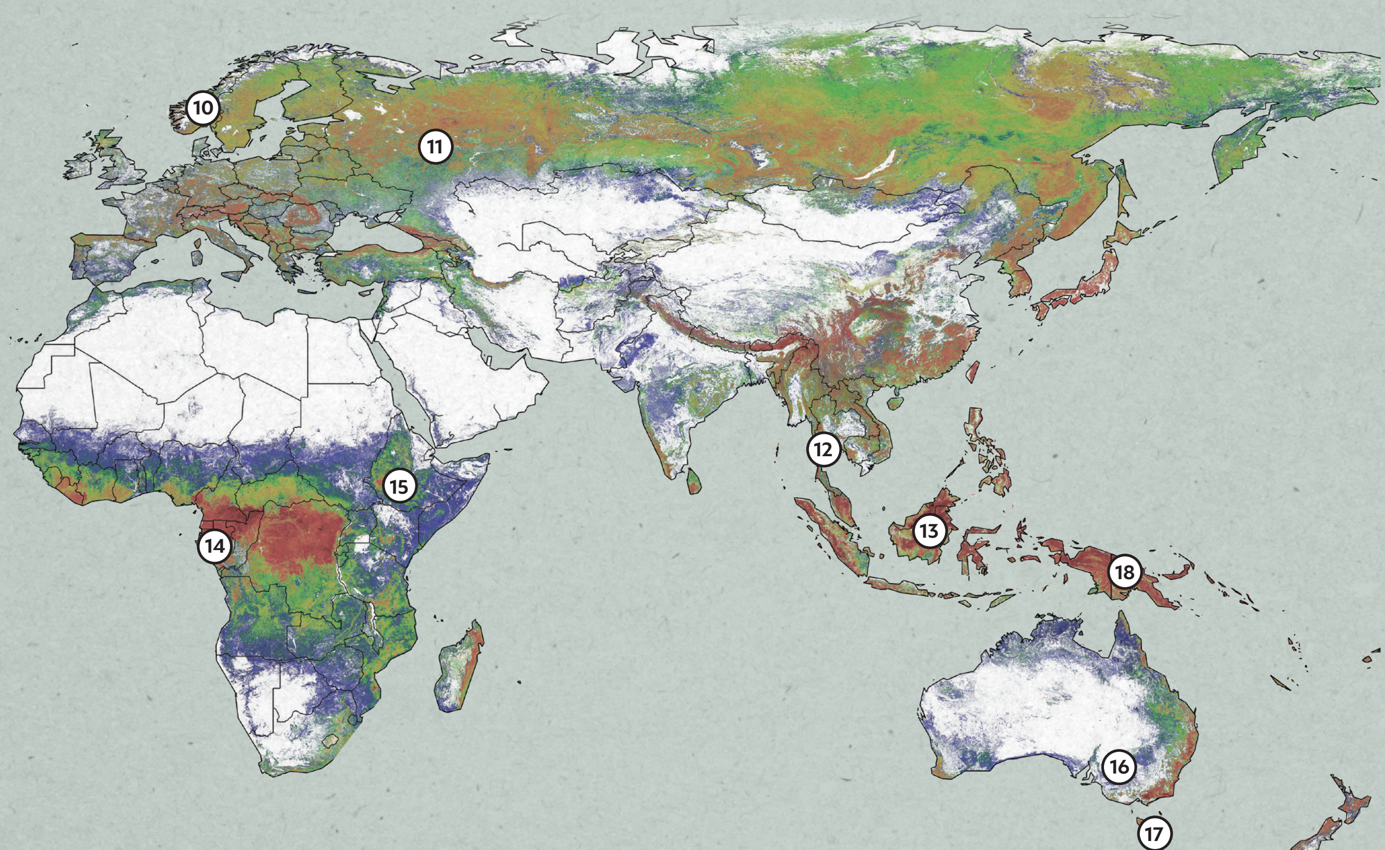
9 *Diniza excelsa*
(Angelim Vermelho)
160–280 ft/50–85 m

10 *Picea abies*
(Norway Spruce)
130–160 ft/40–50 m

11 *Abies normandiana*
(Nordman Fir)
160–195 ft/50–60 m

12 *Koompassia excelsa*
(Tualang Tree)
160–230 ft/50–70 m

13 *Shorea faguetiana*
(Yellow Meranti)
230–330 ft/70–100 m



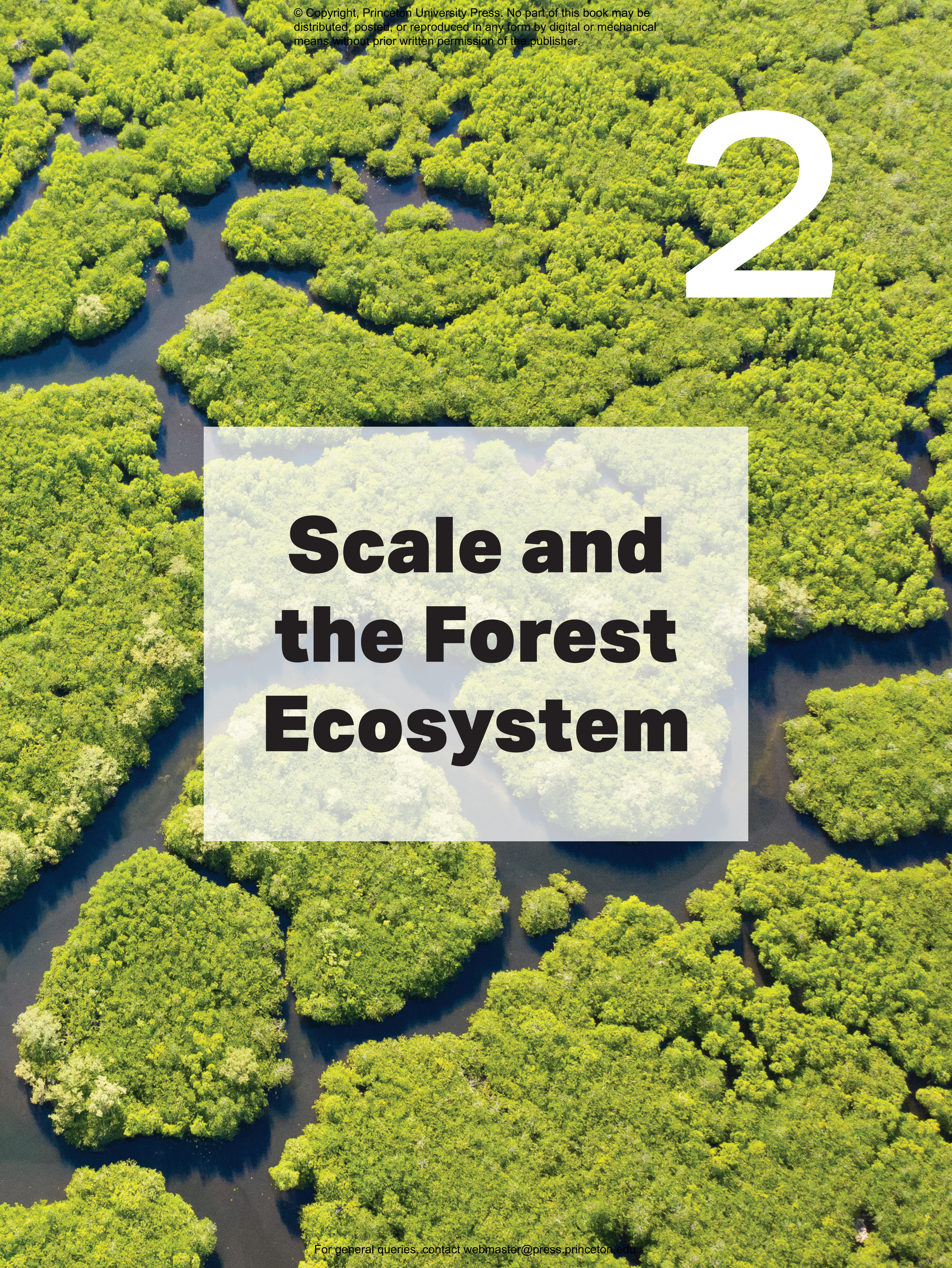
14 *Baillonella toxisperma*
(Moabi)
130–230 ft/40–70 m

15 *Entandrophragma excelsum*
(Tiama)
160–260 ft/50–80 m

16 *Eucalyptus globulus*
(Blue Gum)
195–295 ft/60–90 m

17 *Eucalyptus regnans*
(Mountain Ash)
260–330 ft/80–100 m

18 *Araucaria hunsteinii*
(Klink Pine)
160–295 ft/50–90 m



2

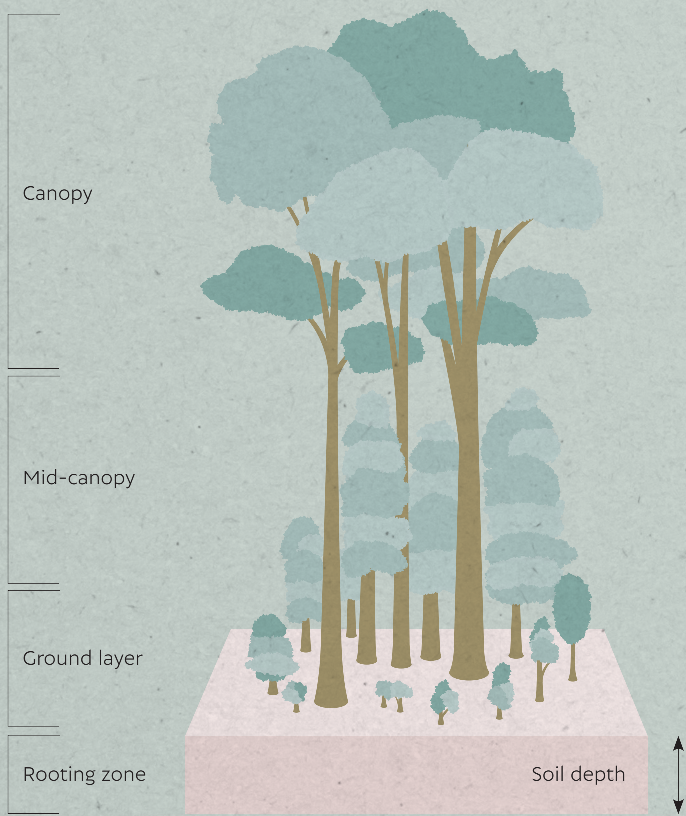
Scale and the Forest Ecosystem

What is a forest?

As we saw in Chapter 1, "tree" is a biologically complicated term. It follows that if a forest is composed of trees, then its definition could inherit some of that complexity as well. However, dictionary definitions that a forest is "an area dominated by trees" seem straightforward enough. For the sake of simplicity, this is the definition we will use in this book.

In this simple definition, the one tricky word is "dominated." In forests, trees usually dominate with respect to being the tallest, largest in mass, or most effectual in changing the local environment, but they are not necessarily dominant in terms of having the greatest number of individuals or the most species relative to other structural categories. Forests are structurally complex, and this complexity may be incorporated into one forest definition but not another. One reason a simpler definition for forest is preferred is that the term has hundreds of nuanced meanings, mainly because forests are important to people in so many ways and at so many scales.

▼ **Medieval forest**
In medieval Europe, forests were defined as any uncultivated land, which by law belonged to the Crown and were used as game preserves for royal hunts.



COMPONENTS OF A FOREST
In this case a survey plot in a forest is used for simplicity. The canopy is the top of the forest, the mid-canopy refers to trees below the canopy trees, and the ground layer is the vegetation near the ground. The leaf area of the forest is the total area of leaves per area of ground. The rooting zone is the depth into the soil that the roots can access. While tree roots can grow to great depths, in most forests 90 percent or more of the active roots are in the top meter of soil. Survey plots are arranged across an area. Sample systems of survey plots are averaged to obtain a measure of forests over a given area.

The word "forest"

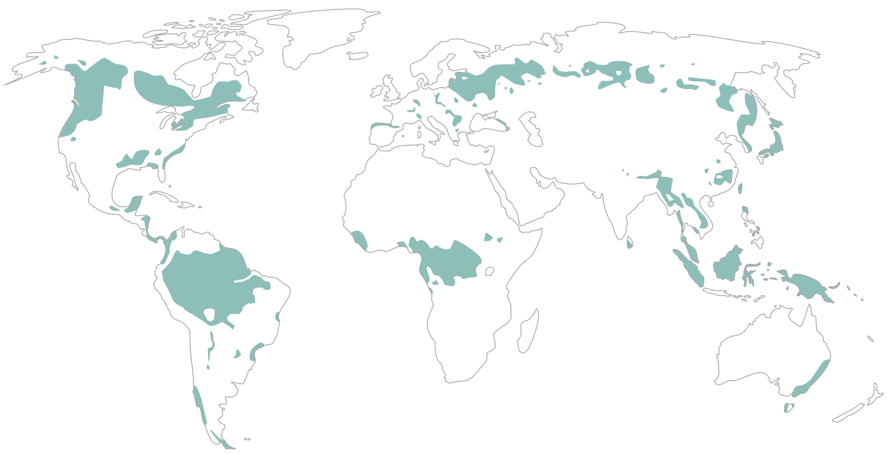
"Forest" as a word derives from ancient law and more precise definitions are important in modern law and environmental policy. Etymologically, it originates from the Latin *foris*, meaning "outside." The Latin root *for(s)* carries this meaning in several European languages—for example, in the English word foreigner, meaning "one from the outside." In medieval England, forests were land outside cultivation and by law belonged to the Crown, typically for use as royal hunting reserves. In Europe, the same concept appears for the first time in the laws of the Lombards, who ruled the Italian Peninsula in 568-774 CE, and in the capitularies of the Frankish emperor Charlemagne (724-814 CE), with forest (*foresta* in medieval Latin) again referring not to the nature of the land cover but to royal game reserves.

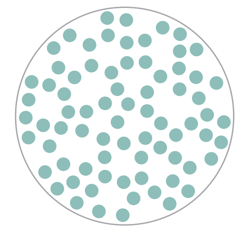
Forest legislation

Law and ecology still come together in defining a forest. Increasing the growth and expansion of forests can reduce greenhouse gas concentrations in the atmosphere and ameliorate global climate change, and this drives a significant focus on forests today. We are now deeply involved with policy and legislation of forests of trees at every scale, from patches of trees to forest parks, to state and national forest reserves, and to forests over the national and global levels. Forest consultant H. Gyde Lund has compiled a running list of 1,713 words that might be translated as "forest" in more than 500 languages, along with more than a thousand other definitions developed for use at international, national, state, provincial, or local levels. In these, a forest is defined as an area of land covered to some degree by trees, or at least potentially so.

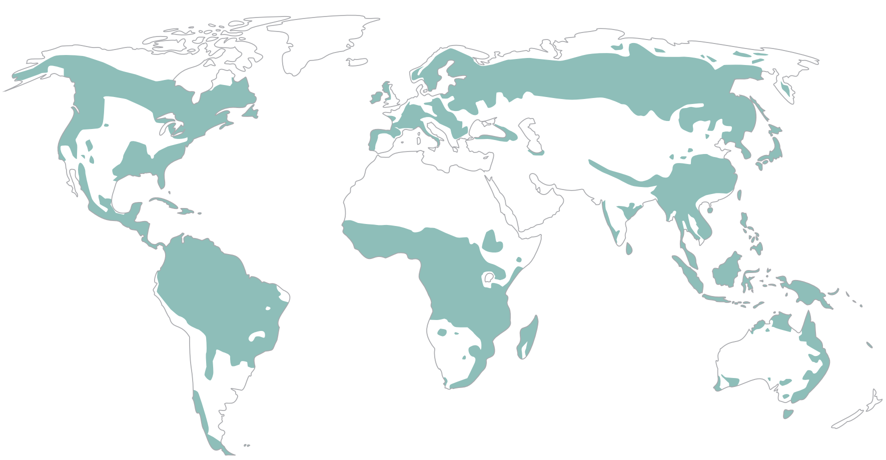
TREE CANOPY COVER

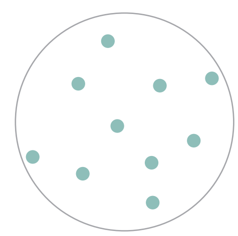
The amount of forest cover depends on how forests are defined. The maps shown here show the global extent of forest under the requirement that 75 percent of the surface is covered by tree canopies (top), and 10 percent of the surface (bottom). (Sources: Hansen et al. 2003; Kirkup 2001.)





Tree canopy covering
75% of the surface





Tree canopy covering
10% of the surface

Defining forest lands

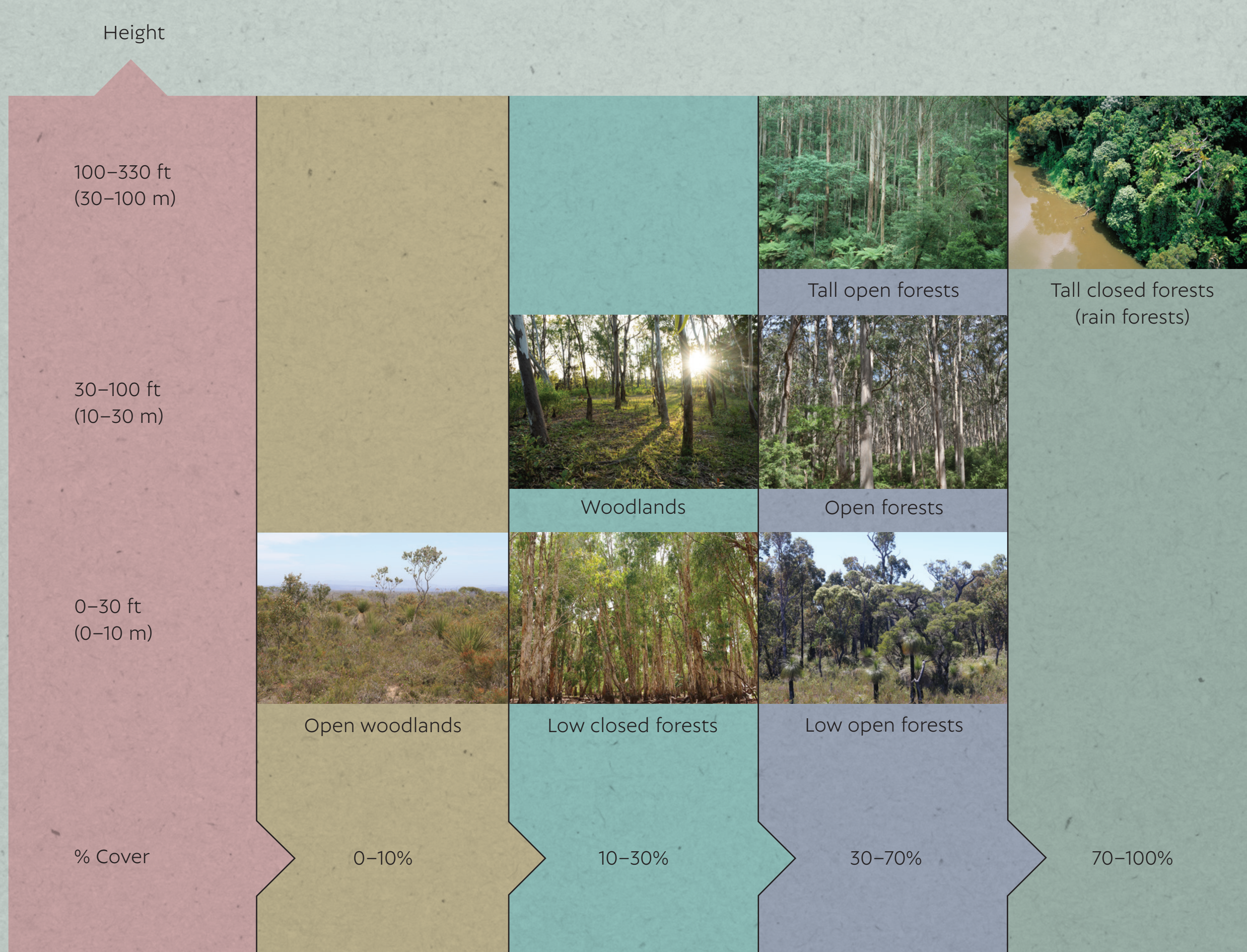
National laws and policies often attempt to bound forest definitions quantitatively by asking a set of questions. What is the minimum area a forest must occupy? What is the minimum tree cover in a forest? How tall must the trees in a forest be? In countries in which trees are planted in strips for erosion control, for shelter from the wind, for shade, or for aesthetics, how wide must these strips be to be called forests?

Minimum tree cover (the area of the sky blocked by leaves, stems, and branches) is sometimes not considered a necessary criterion in the definitions included among Lund's many terms. If it is considered at all, it ranges from as little as 10 percent up to 80 percent. It is important to note that the greater the lower limit of tree cover used to define a forest, the less "forest" there is in a particular area, region, or nation. The Food and Agriculture Organization of the United Nations defines a forest as an area of more than 1¼ acres (0.5 ha) with trees taller than 16 ft (5 m) and with the tree canopies covering at least 10 percent of the area. This definition is often used in international data compilations of forest cover and is the usual legal descriptor for a range of international forest issues, including storage of carbon or biomass (weight of organic matter per unit area), national inventories of forest cover, and rates of forest clearing or reforestation.

AUSTRALIAN CLASSIFICATION

The Australian government has a long tradition of systematically classifying its unique vegetation types using a combination of cover and height. Some examples of forests categories include the following:

- Tall closed forests (rain forests)—closed forests with tree heights above 100 ft (30 m) and reaching to 330 ft (100 m) in height; cover greater than 70 percent
- Tall open forests—tree heights above 100 ft (30 m) and reaching to 330 ft (100 m); cover 30–70 percent
- Open forests—tree heights above 30 ft (10 m) and reaching to 100 ft (30 m); cover 30–70 percent
- Low open forests—tree heights to 30 ft (10 m); cover 30–70 percent
- Woodlands—tree heights to 100 ft (30 m); cover 10–30 percent
- Open woodlands—tree heights to 100 ft (30 m); cover less than 10 percent
- Low closed forests—tree heights less than 30 ft (10 m); cover greater than 70 percent.



The ecosystem concept

The mid-1930s was a time of great challenge for ecologists. A horrific drought and poor farming methods in the North American Prairies combined to create the Dust Bowl, amplifying the effects of the Great Depression and leaving the nation and the world reeling from the consequences of past abuses of the land and natural systems.

Amid this worldwide turmoil, the Ecological Society of America produced a pivotal publication, the 1935 issue number 4 of the journal *Ecology*, dedicated to Henry Chandler Cowles (1869–1939), whose work on long-term change in ecosystems is discussed in Chapter 3. This publication was a kaleidoscopic interweaving of topics in an ecologically changed and still changing United States. At the start of the issue is a remarkable paper by the Cambridge professor Sir Arthur G. Tansley (1871–1955) entitled "The use and abuse of vegetational concepts and terms." This contained the first printed use of the word "ecosystem."

Tansley defined the term with the intent of transforming ecology beyond a mere description of nature and toward a scientific understanding of dynamic change in nature. Since the first usage of the word was in its definition, one might think this would make its meaning clear. However, the botanist's text is somewhat opaque to the modern reader:

▲ **Dust bowl**
Drought acerbated widespread land abuse across North America in the 1930s. In this setting, the ecosystem concept originated from attempts to predict dynamic systems of ecological/environmental change.

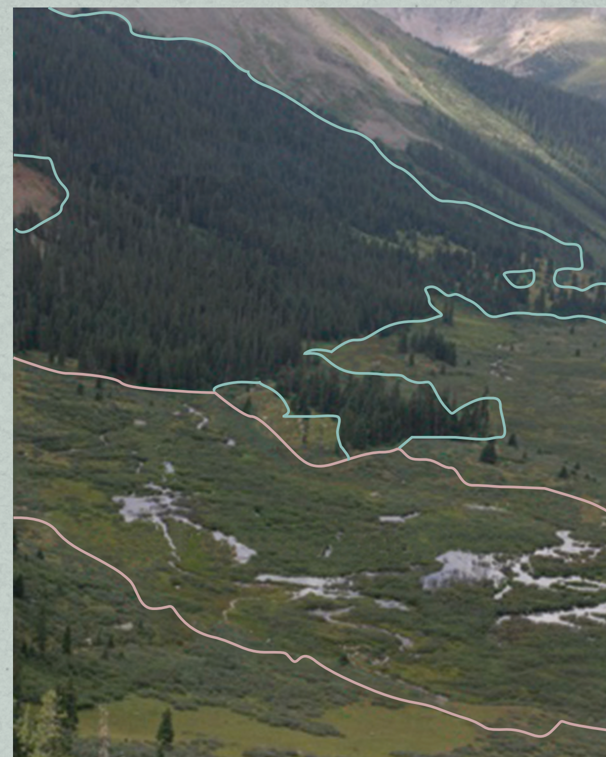
▶ **Ecosystem components**
An ecosystem is a specifically defined, interactive ecological/environment system. It is defined to understand and predict change.

> *It is these systems so formed which, from the point of view of the ecologist, are the basic units of nature on the face of the earth. Our natural human prejudices force us to consider the organisms (in the sense of the biologist) as the most important parts of these systems, but certainly the inorganic "factors" are also parts—there could be no systems without them, and there is constant interchange of the most various kinds within each system, not only between the organisms but between the organic and the inorganic. These ecosystems, as we may call them, are of the most various kinds and sizes. They form one category of the multitudinous physical systems from the universe as a whole down to the atom.*

What Tansley referred to as an ecosystem would nowadays be called a system of definition, a clearly defined abstraction that includes the important parts of systems and their interactions but excludes irrelevant things. Forming abstractions is an essential procedure for progress in modern science in general, and is no less so in forest ecology. One isolates system components and interactions to gain understanding. The ecosystem is formulated in this same manner—identifying the components needed for understanding a given question at a given time and at a given scale.

Plant communities

A biogeocenosis is seen as a physical unit bounded in space by the limits of specific plant communities—for example here a Ponderosa Pine forest and a Beaver pond/marshland. The landscape shown here could be thought of as a single ecosystem for some objectives or alternatively, one of the small beaver ponds could be defined as a different ecosystem for other purposes.



Ponderosa Pine forest

Beaver meadow

Forest ecosystems

Since the term ecosystem is a concept, ecologists study an ecosystem not *the* ecosystem. Research objectives determine an ecosystem's case-specific definition. However, there are many ecological studies that have similar objectives and hence use similar ecosystem definitions. For example, an older but similar concept to ecosystem is biogeocenosis. This is defined as a community of plants and animals, along with their associated abiotic environment. A community in this case is an area with a similar assemblage of plants and animals across its extent or compared to other areas, and abiotic refers to inanimate components such as geology, the non-living parts of soils, and weather variables. Biogeocenosis is often applied by ecologists in central Europe somewhat analogously to the use of ecosystem. However, it differs from ecosystem as a definition by its reference to a specific area defined by the plant or animal community. It is a special case of an ecosystem—one in which its size or location size is defined by a community.

Ecosystem services models

Ecosystem services models are often based on the flows of commodities that people receive from properly functioning forests, including clean water, flood and erosion control, and wildlife populations. They are often constructed to determine the value forests have for people and/or indicate the risks if the forests producing these services were taken away. In this context, forest ecosystems are defined as environmental services delivery systems. As with food webs, transfers of valuable services of commodities coming from a forest are shown in diagram format, with the various services sometimes quantified as dollar values. Models based on these ecosystems are often developed to incentivize the offset of environmentally detrimental aspects of human activities.

Food webs

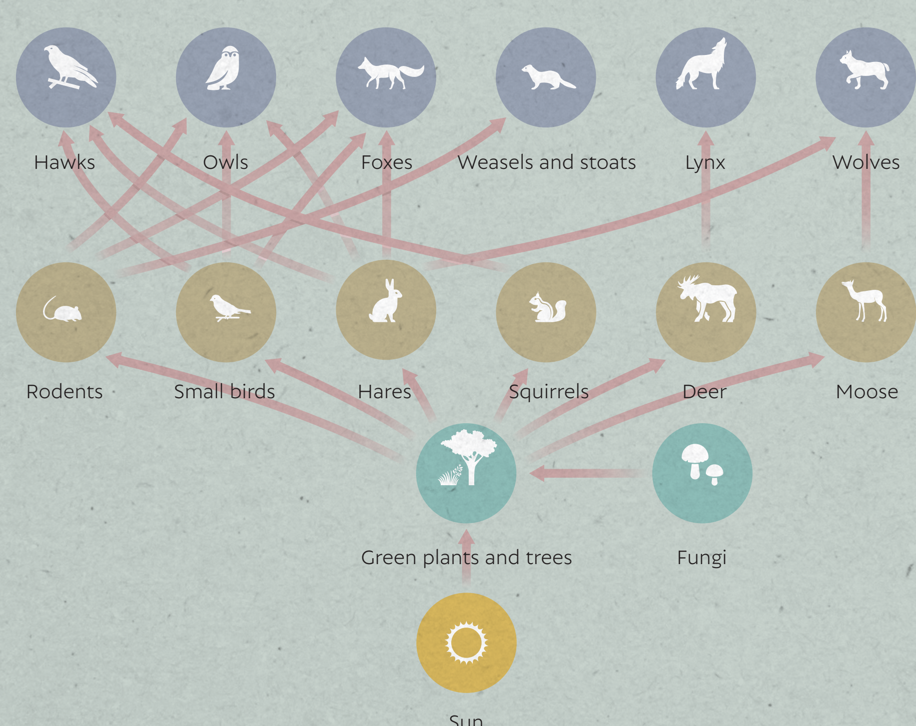
Another commonly used subset of ecosystems are food webs. These often emphasize plants and animals, and the transfer of food energy among them through predation. They are generally represented as "who eats whom" diagrams, with arrows indicating energy transfer and boxes indicating food energy stored in a particular population. This energy transfer is sometimes abstracted as a positive or negative effect of one species on another, and the complexity of the pathways varies under different conditions, which has implications for the maintenance of species diversity at a given location. One important issue concerns whether there are species in a location whose removal might cause a collapse in the total number of species there. Similar questions arise in assessing the effects on food web patterns of the introduction of exotic species. The current rate of extinction of species across the planet is high, and food web models are valuable tools for exploring the potential knock-on effects of one species' extinction on others.

Ecosystems that emphasize element cycling resemble food webs, but they trace the movement of elements through an ecosystem (see pages 100–105). Food energy is dissipated as it moves through food webs, but chemical elements are conserved in transfers within forests. Forest ecosystems often include large recycling loops, particularly with respect to essential elements for plant nutrition (see pages 92–93).

Boreal forest food web

This food web has the productivity of green plants from photosynthesis, supplemented by nutrients from fungi, supplying food energy to herbivores, which in turn supports an array of predators of different sizes.

All of the animals in this food web share a common problem of acquiring food energy while aiming to expend the minimum amount of food energy in obtaining this food.



The tiles of a mosaic

When one flies over a mature forest or views it from a high lookout point, a graininess of the canopy arises from the average size of a large tree. Depending on the forest and its age, this is in the order of 30–100 ft (10–30 m) in diameter. The grains or tiles, which are the crowns of large individual trees, tessellate to form the mosaic that is the forest canopy.

Crown shyness

Crown shyness is the tendency of tree canopy crowns to have open space between them.

Because buds often grow at or near the ends of tree limbs, the branches of adjacent trees knock them off when they are whipped about by the wind. This creates a phenomenon called crown shyness, in which the crowns of trees do not touch and there is space between them. Lie on your back on the floor of a forest and look straight up through the canopy, or look at the same view taken with the fish-eye lens of a camera. The pattern of light streaming through the canopy has a beauty that resembles the rose window of a Gothic cathedral, and much of that light comes from center (directly overhead), through openings created by crown shyness. Much less light comes through oblique side-view angles.

▲ **Blending in**

Juvenile mammals, such as fawns, often have white spots to help them blend with forest floor sunspots.

Crown shyness and the forest floor

The regularity of forest canopies, combined with crown shyness, implies that the forest floor is mostly shaded by the dominant canopy trees—a photograph taken at midday in a forest displays speckles of light. It is not surprising that many small forest animals, particularly young mammals, have light or white spots as camouflage in their light-speckled habitats. Spots of the brightest forest-floor illumination derive from shafts of light shining through direct, open paths from the sky to the ground, which are created by crown shyness. When the canopies of the trees are deep, crown shyness generates openings from the top of the canopy to the forest floor. If the angle of incoming sunlight matches the orientation of these openings, then shafts of sunlight shine through the canopy to the ground. Because the sun's angle changes with the time of day and time of year, these sun flecks blink on or off at locations through the canopy and on the forest floor. On the forest floor, green plants rely on the light provided by sun flecks and light shafts for their photosynthesis.

Yoda's law

When viewed from above, crown shyness sharpens the boundaries among the individual tree crowns and increases the apparency of the mosaic nature of forests. This is especially easy to see in conifer forests, such as Douglas Fir (*Pseudotsuga menziesii*) forests. Crown shyness among encroaching, adjacent trees causes the trees to carve away the edges of their neighbors, a phenomenon called crown-pruning by foresters. Tree-to-tree competition in closed forests generally favors the larger, "dominant" trees, with subordinate trees growing more slowly and suffering, leading to increased death. This drives a reduction in the overall number of subordinate trees (thinning) in a growing forest, a phenomenon called Yoda's law for the Japanese ecologist, Kyoji Yoda (1931–1996), who first described it. Thinning laws originated when Japanese forest ecologists were looking to predict the numbers and sizes of trees growing in regenerating stands from a theoretical basis because they did not have the extremely long records of forest yield that form the empirical basis for European forestry. Some important statistical issues vex the derivation of the relation between

the average size of trees and the total number of trees. Nevertheless, Yoda's law indicates a semi-crystalline regularity in the organization of forest canopies. In nature, this regularity may be one of the sources of the beauty of forests as an object of contemplation.

Granularity and self-organization

With modern remote-sensing technologies, one can detect the graininess of forest canopies, as well as quantify the rates of photosynthesis according to tree-scale granularity across entire landscapes. This is in no small part due to the many ways in which trees alter their local environments. A theoretical basis has developed for understanding the manner in which the forest mosaic self-organizes through predictable interactions into regular patterns and spacing. Further, the death of an individual canopy-level tree is a locally significant event in a closed forest, initiating a more-or-less predictable chain of responses over time that repair the holes in the ventilated canopy. The sections that follow discuss these essential forest processes in more detail.

▼ **Crown shyness from above**
Aerial view of a coniferous forest canopy in the Carpathian Mountains, Ivano-Frankivsk Oblast, Ukraine.

Pattern and process in forests

Alex S. Watt (1892–1985), a professor at Cambridge University, England, published a highly influential paper in 1947 entitled "Pattern and process in the plant community." The key insight of this paper is that all vegetation, whether grassland, heathland, or forest, consists of patches that differ in age—that is, time since the last disturbance (sudden destruction of living biomass) or mortality event (see pages 80–81).

▼ **Natural firebreak**
Firebreaks, whether man-made or natural, are areas with reduced burnable fuels and/or areas in which the potential fuels have a high moisture content. River channels have both low fuel and high moisture.

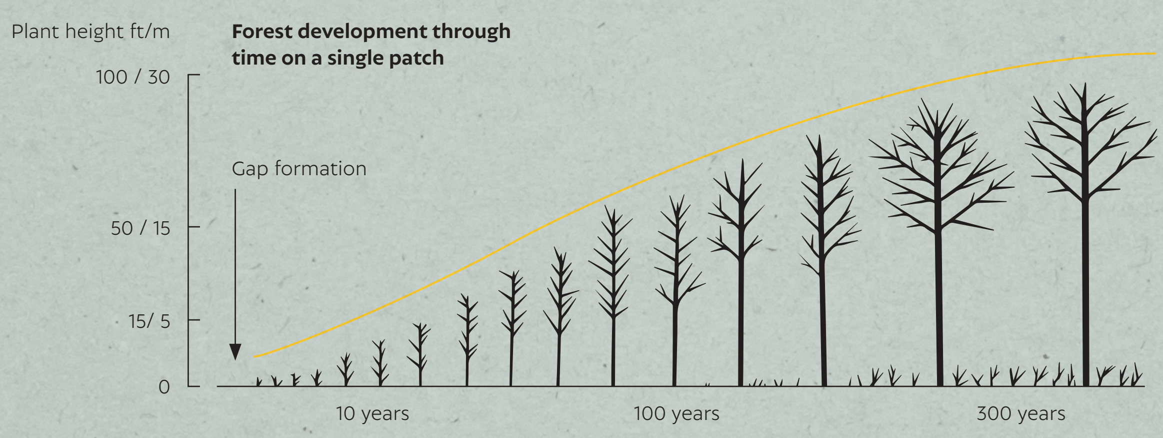
Watt stated that some patches are young due to recent disturbance or species decline, while others are old because they have been free of recent disturbances or deaths. He argued that a vegetation pattern is a snapshot of an ongoing dynamic process. Prior to this, vegetation ecologists had often focused only on the patterns themselves and, within these, usually only on the oldest patches. Watt's revolutionary "pattern and process" perspective links all patch types with the dynamic process—in other words, vegetation has to be understood as both pattern and process. While process creates pattern, the converse is also true. For instance, a flammable patch of forest may be surrounded by natural "firebreaks" like wetlands, such that a fire is unable to spread to that patch, thereby lowering fire frequency there.

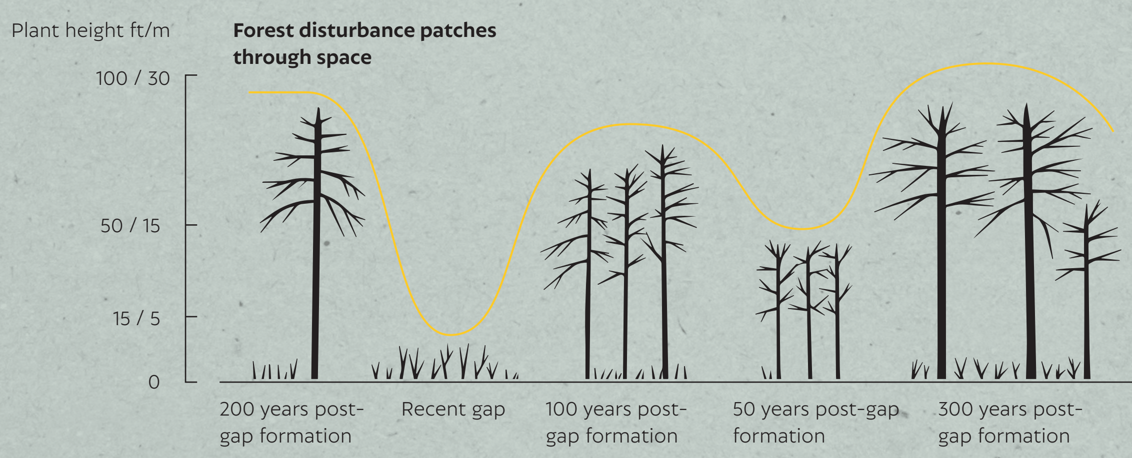
Age and process

We can take this a step further: the processes themselves can be correlated with patch age. One of the vegetation types Watt described in his paper is English deciduous woodland. With time, the dominant trees here become larger, but they also become more vulnerable to wind and insects. Thus, the probability of disturbance increases with patch age. In other words, regardless of whether wind and insects increase or fall over time for other reasons, there is a natural rhythm of forest disturbance that is a function of time since last disturbance. As time goes by, short-lived species that colonize disturbance patches are replaced by longer-lived species that are more tolerant of low-resource conditions. And so the cycle repeats—as long as all other conditions, such as external factors, remain constant.

PATTERN AND PROCESS

The concept of pattern and process was initially developed by Alex S. Watt in his doctoral work in 1924 on ancient beech forests on the Sussex Downs in southern England. Watt had the insight that the patchwork patterns of small areas occupied by trees of different sizes in a mature European Beech (*Fagus sylvatica*) forest that he studied arose from an ecological process filling the openings left in the forest canopy by the death of a large canopy tree. The patches of the forests could be resolved by reassembling them into a coherent sequence of regular underlying change.





Dominant species after disturbance

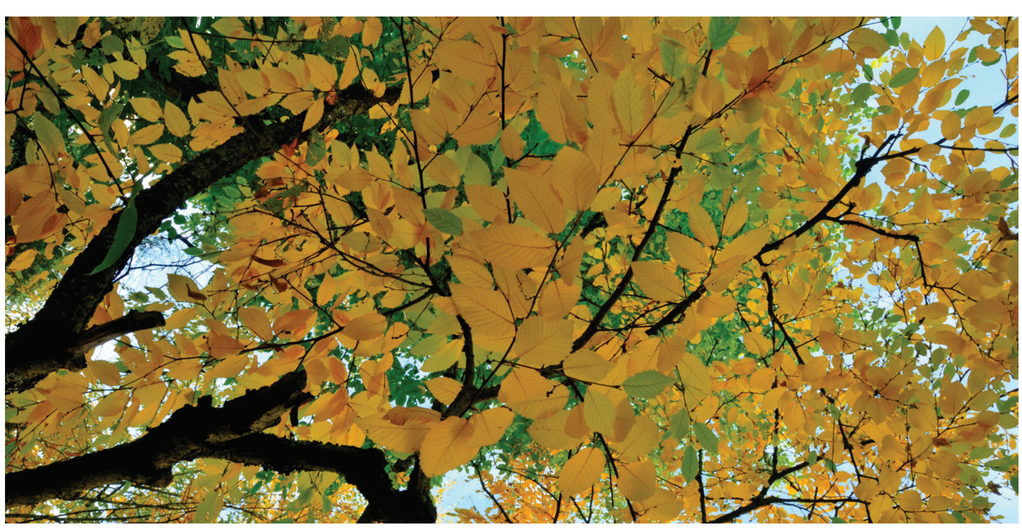
To further illustrate the importance of pattern and process, consider the high-elevation spruce- and fir-dominated forests of the southern Appalachians in Great Smoky Mountains National Park, North Carolina and Tennessee. There are four potential dominants of the forest, depending on disturbance characteristics: Pin Cherry (*Prunus pensylvanica*), Yellow Birch (*Betula alleghaniensis*), Red Spruce (*Picea rubens*), and Fraser Fir (*Abies fraseri*).

Trees that dominate large patches

Disturbances that cause the loss of tens to hundreds of canopy trees result in colonization by Pin Cherry, a species with a persistent pool of dormant seeds in the soil. These high-magnitude disturbances, causing the upheaval of many trees and exposing mineral soil, are rare. Pin Cherry seeds are capable of long dormancy (100 years or more) and the species is the fastest grower of the four species considered here. It soon dominates large disturbance patches but lives only 40-60 years. It reproduces at 5-10 years of age and goes on producing seeds, replenishing the dormant soil seed pool. Without disturbance, Pin Cherry declines and ultimately is represented by only the dormant seeds below ground.

Pin Cherry
*Pin Cherry (*Prunus pensylvanica*) is a rapidly growing but short-lived tree that colonizes large disturbance patches, usually from a buried pool of dormant seeds that accumulate in high elevation soils through bird dispersal.*

Yellow Birch
*The seedlings of Yellow Birch (*Betula alleghaniensis*) have a low survival rate in the shade but can colonize gaps resulting from the fall of three to five or more canopy trees.*



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