

# Contents

Introduction	8
<b>1</b> SEEING THE FOREST FOR THE TREES	14
<b>2</b> SCALE AND THE FOREST ECOSYSTEM	54
<b>3</b> THE FOREST AS A DYNAMIC MOSAIC	78
<b>4</b> MAPPING THE FORESTS OF THE WORLD	110
<b>5</b> THE DIVERSITY OF THE WORLD'S FORESTS	140
<b>6</b> TROPICAL RAIN FORESTS	174
<b>7</b> THE BOREAL FOREST OR TAIGA	208



► **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

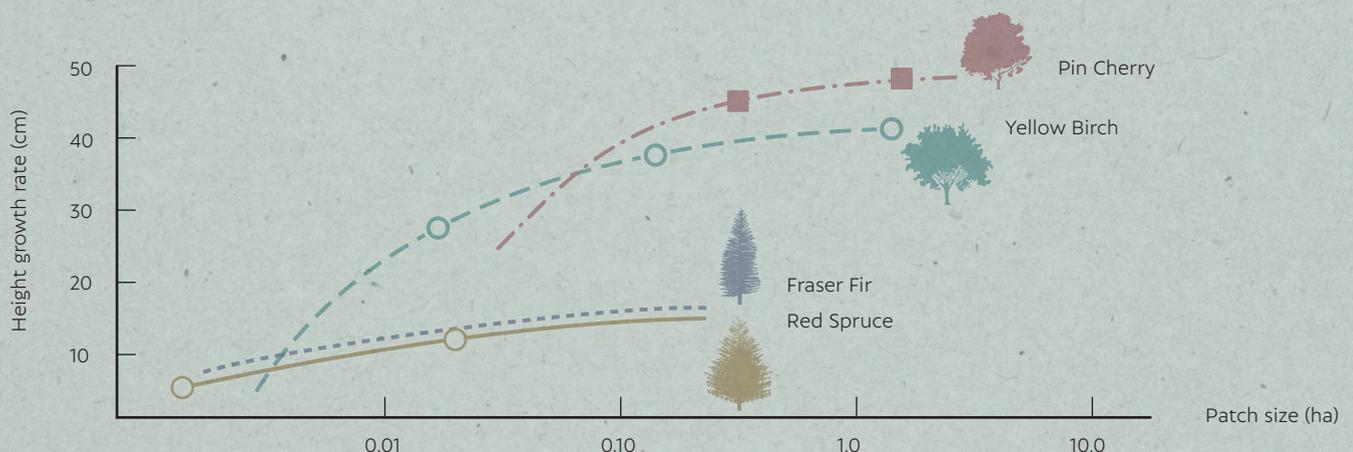
The Italian polymath Leonardo da Vinci (1452-1519) made a related prediction, saying that the cross-sectional area of a tree at its base is equal to its cross-sectional area at any distance from the base. In other words, if you gather all the twigs at the edge of a tree crown together as a bundle, the 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.



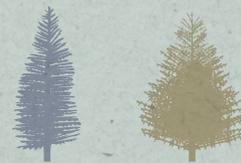
### Pin Cherry

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.

### Monolayer



### Multilayer



## 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).

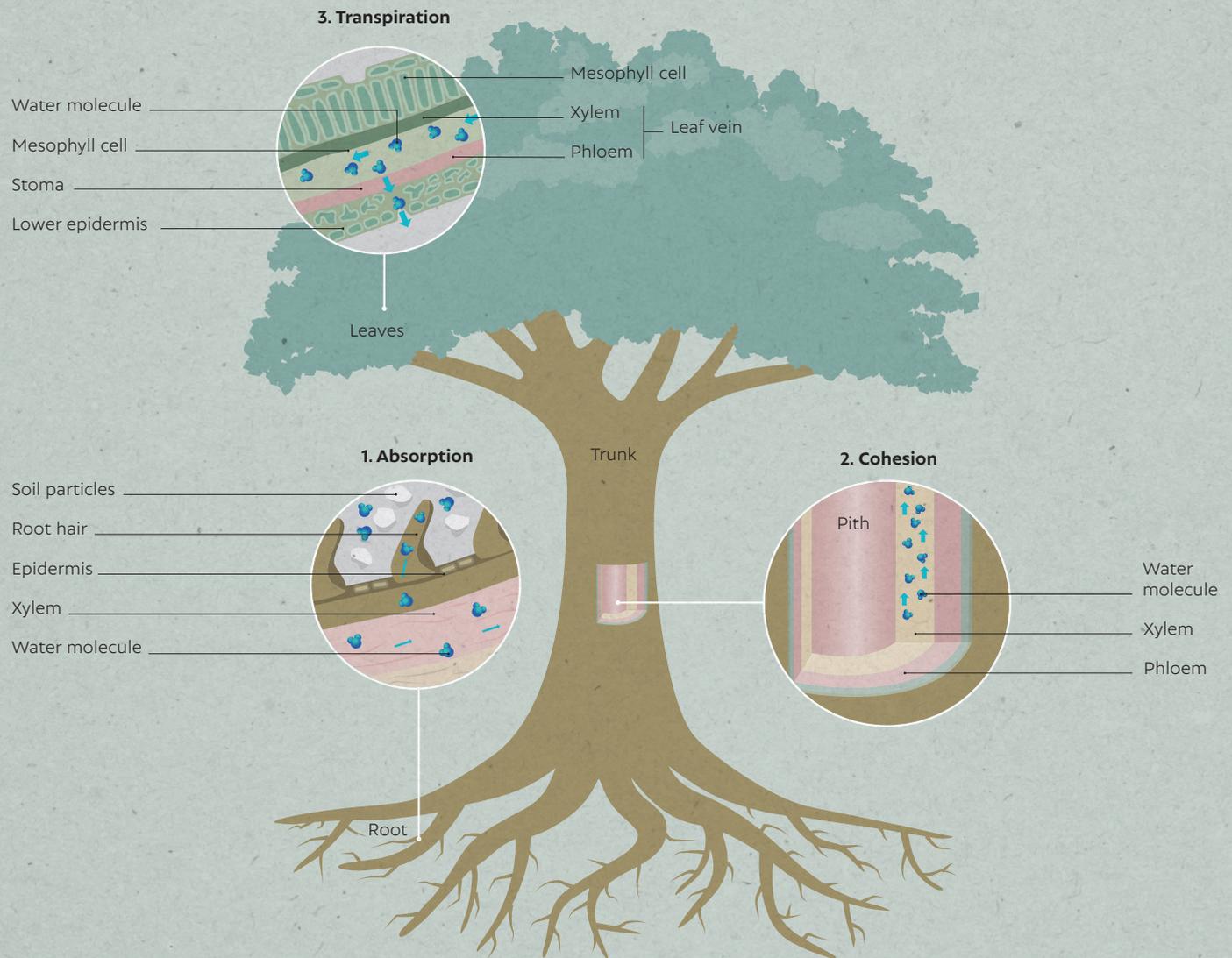
## Drought stress

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.



### Cavitation



Normal water-filled xylem vessel



Water vapor bubbles begin to block channels



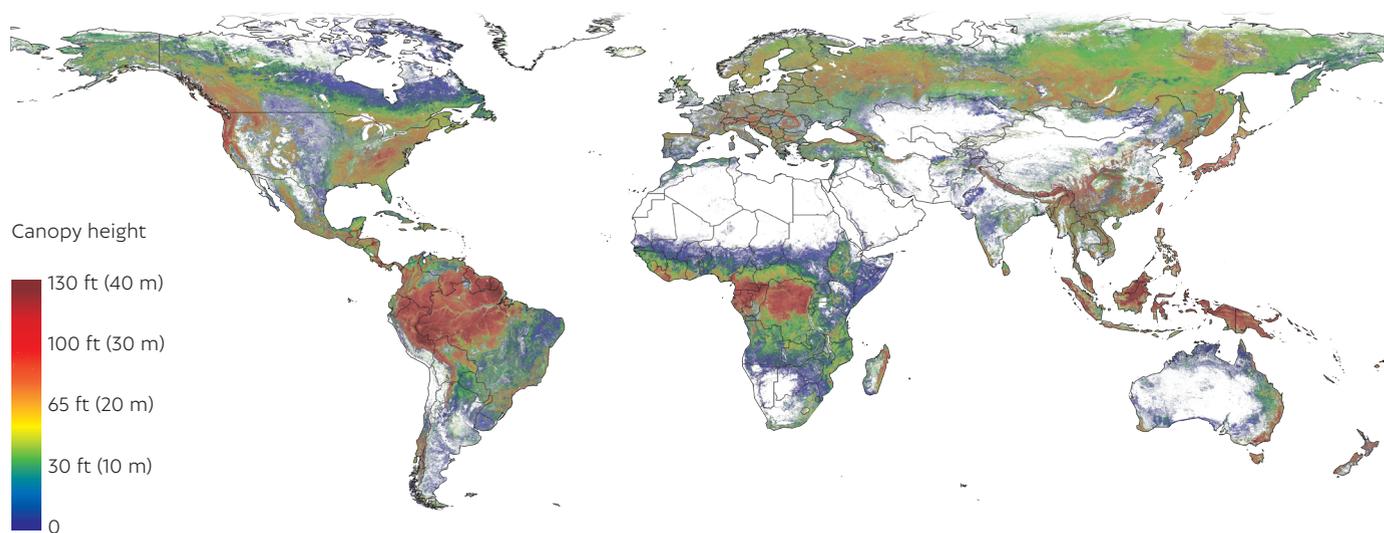
Air pocket breaks the water column—xylem vessel is not functional

## 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



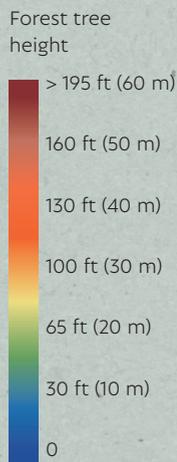
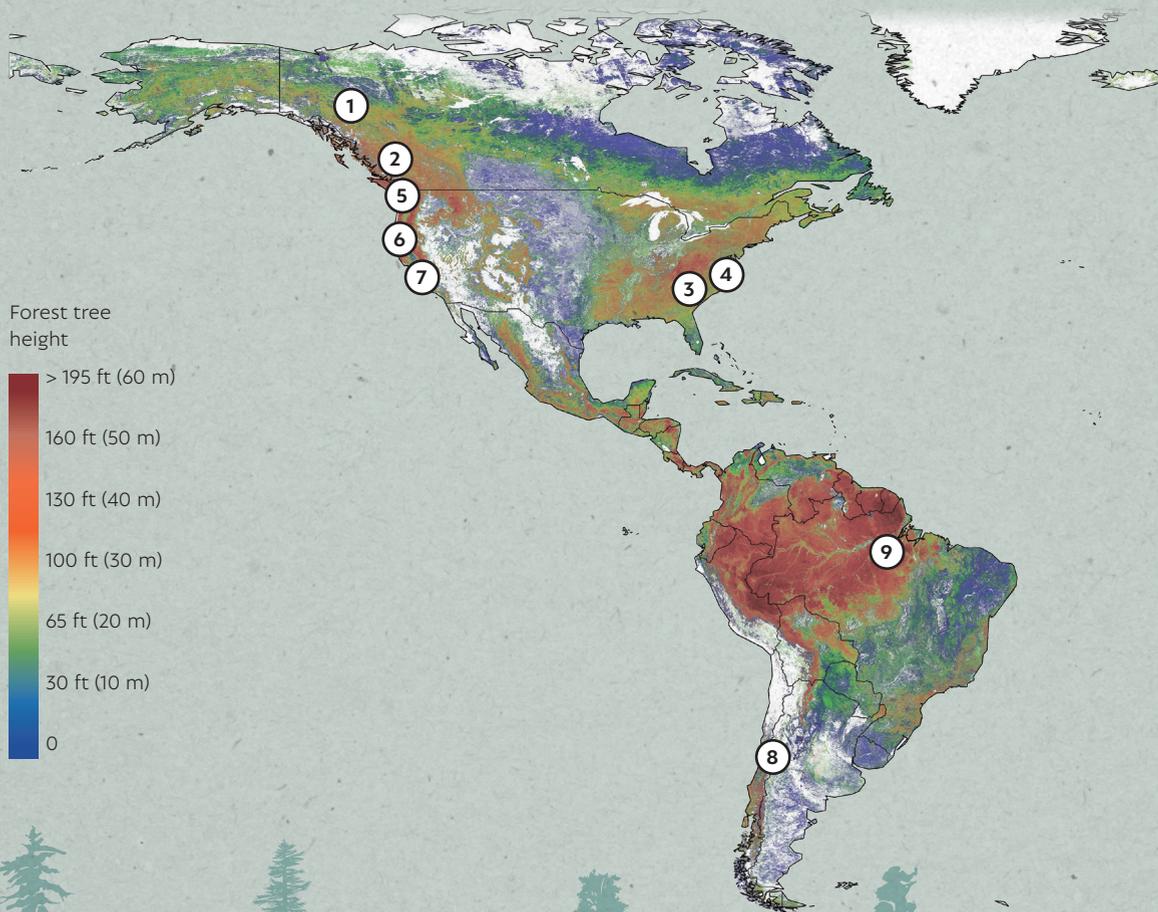
**2** *Abies procera*  
(Noble Fir)  
195–295 ft/60–90 m



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



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



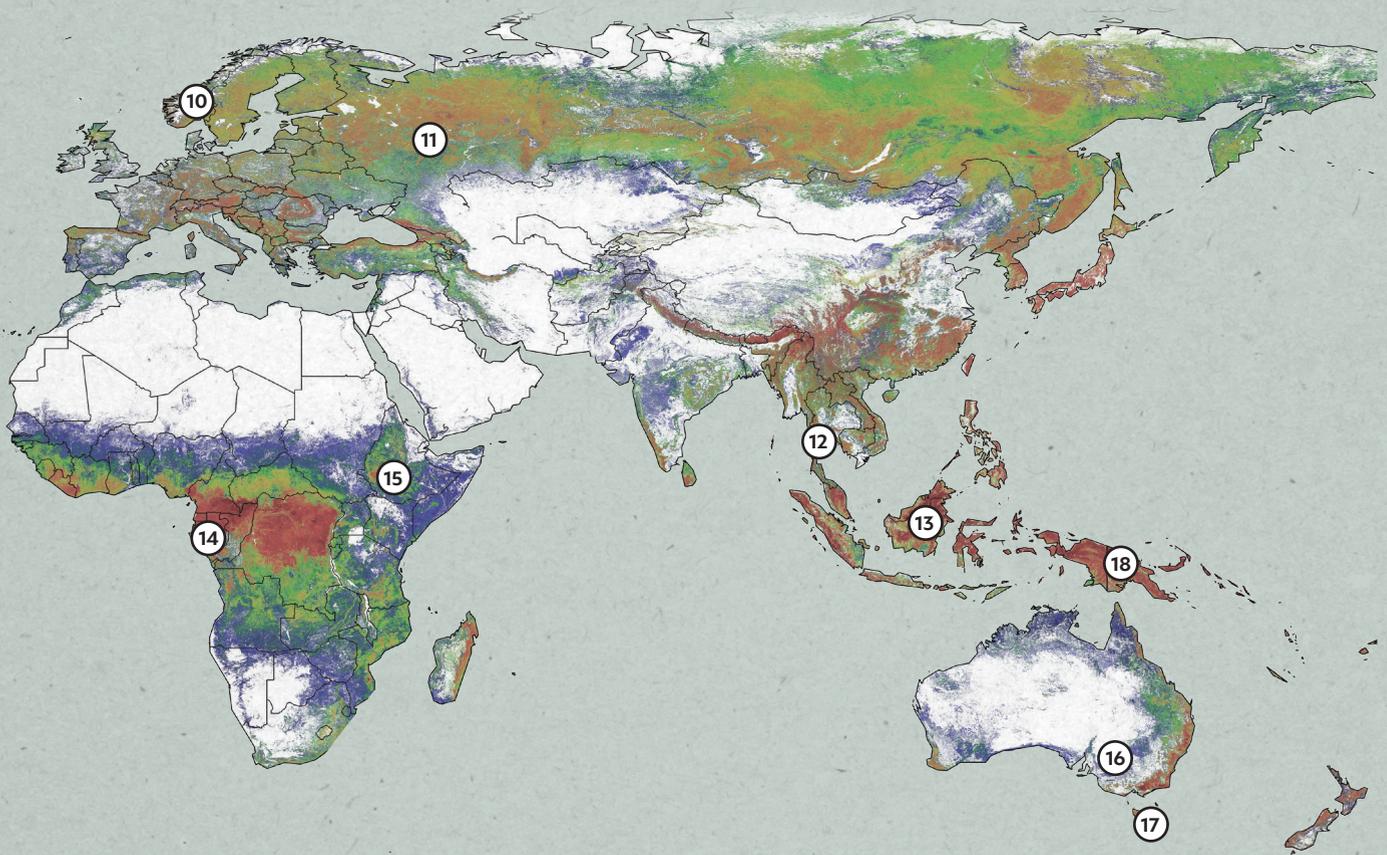
**11** *Abies nordmanniana*  
(Nordman Fir)  
160–195 ft/50–60 m



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



**13** *Shorea faguettiana*  
(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?

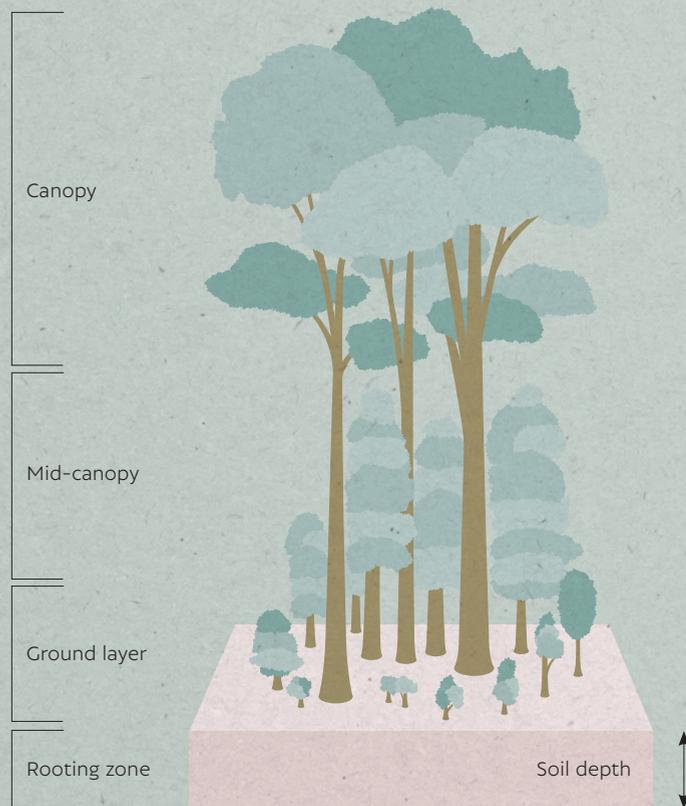
As we saw in Chapter 1, “tree” is a biologically complicated term. It follows that if a forest is composed of trees, then its definition could inherit some of that complexity as well. However, dictionary definitions that a forest is “an area dominated by trees” seem straightforward enough. For the sake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

### ▼ **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.*

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.





## 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”

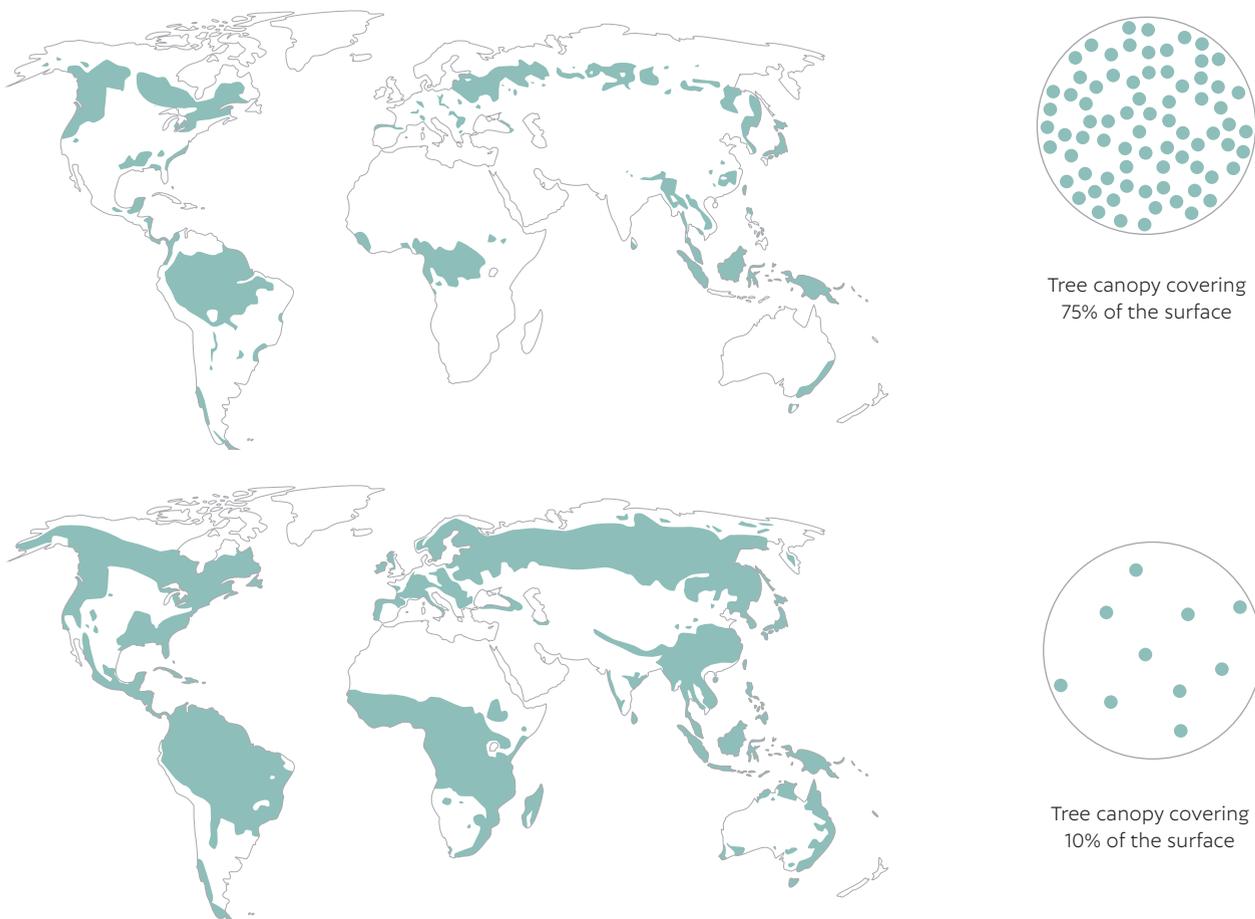
“Forest” as a word derives from ancient law and more precise definitions are important in modern law and environmental policy. Etymologically, it originates from the Latin *foris*, meaning “outside.” The Latin root *for(s)* carries this meaning in several European languages—for example, in the English 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.)



## 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.*

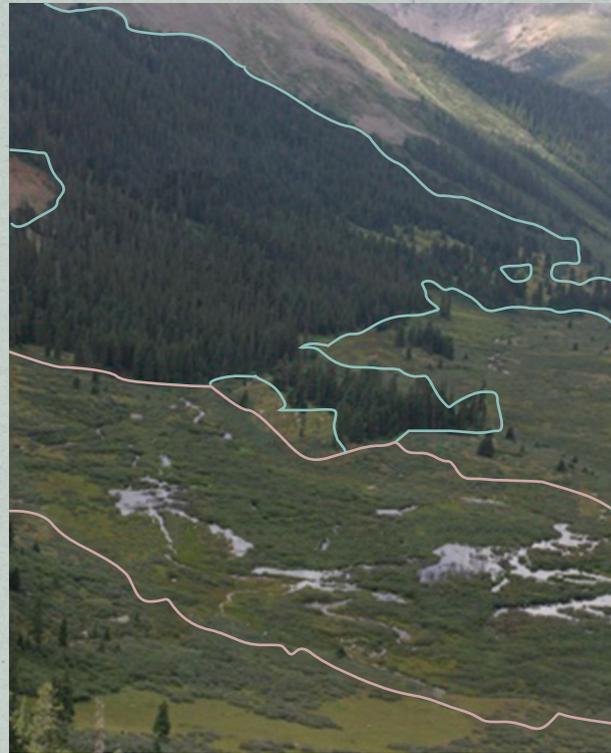
What Tansley referred to as an ecosystem would nowadays be called a system of definition, a clearly defined abstraction that includes the important parts of systems and their interactions but excludes irrelevant things. Forming abstractions is an essential procedure for progress in modern science in 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

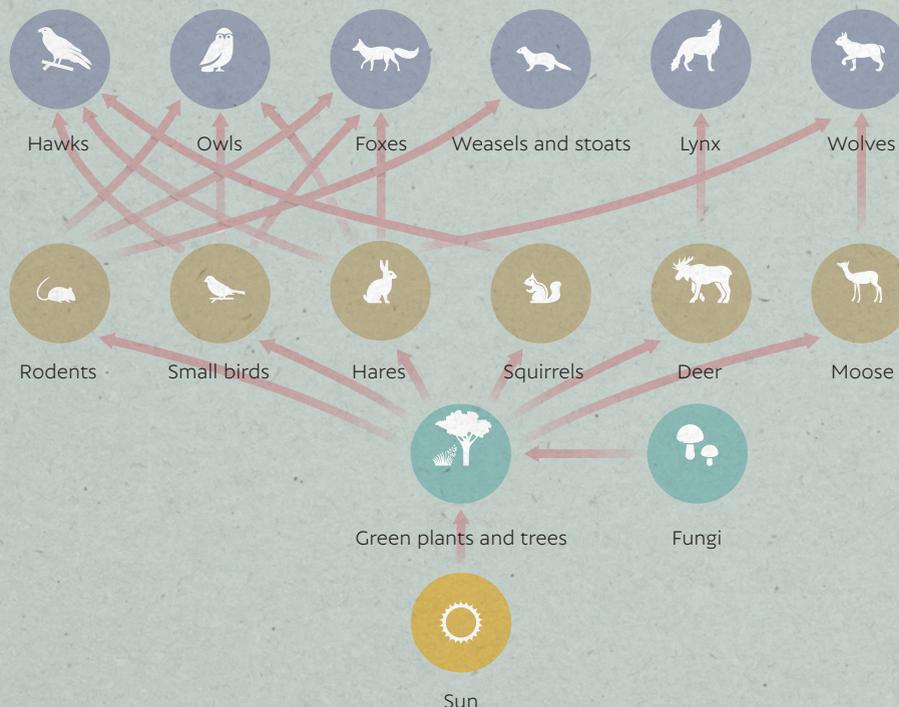
Another commonly used subset of ecosystems are food webs. These often emphasize plants and animals, and the transfer of food energy among them through predation. They are generally represented as “who eats whom” diagrams, with arrows indicating energy transfer and boxes indicating food energy stored 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.

### 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.

#### ▲ **Blending in**

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

## 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.



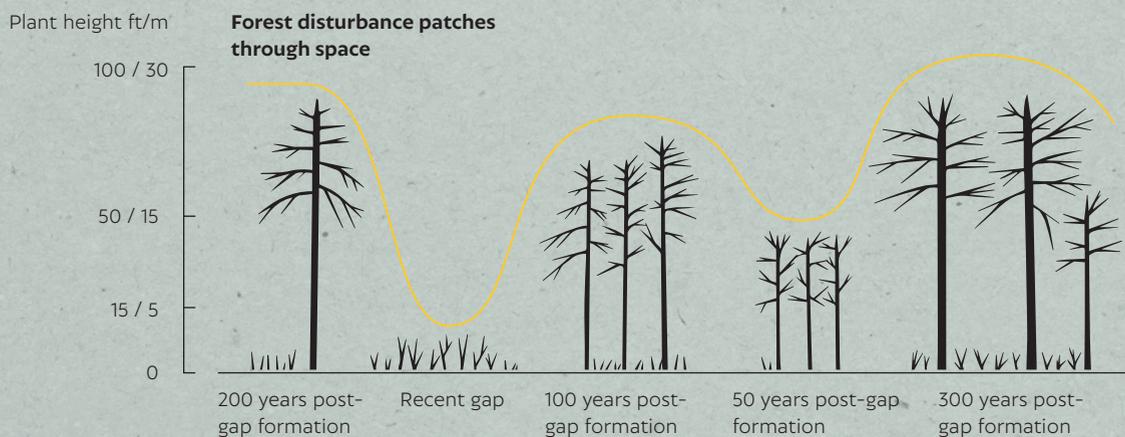
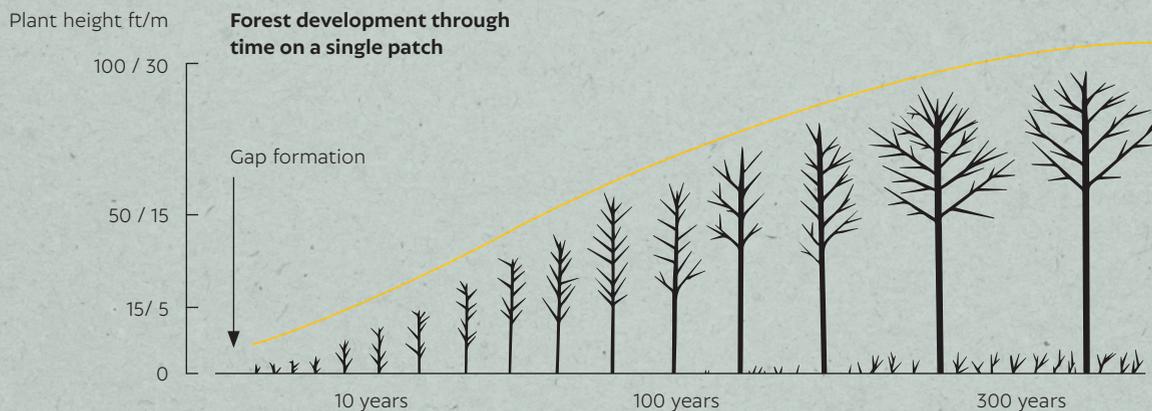
## Age and process

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.



(continued...)

# Index

## A

*Abies* 214  
*Abies balsamea* 72  
*Abies fraseri* 70, 71  
*Abies mariesii* 72  
*Abies sibirica* 224-5  
*Abies veitchii* 72  
 Aboriginal people 252-3, 317  
 abscission layer 280  
*Acer* 277, 289  
*Acer saccharum* 75, 109, 283  
 acidity 103, 104  
 Acuña, Cristóbal de 187  
*Adansonia digitata* 246  
*Adansonia granddidieri* 246  
 adaptations 26, 178, 215, 314  
   cavitation 48  
   convergent evolution 146  
   disturbance recovery 86-7  
   fire 84-5, 148, 153, 295, 317, 324  
   freezing 217  
   leaf arrangement 42  
   mangroves 172  
   pollination 194  
   seasonality 286  
 adiabatic lapse rate 163, 164  
 aerial photography 364-5  
 African Baobab 246  
*Agarista salicifolia* 201  
*Agathis australis* 325  
 age  
   "pattern and process" 68, 69  
   regeneration 83  
   see also dendrochronology  
 agriculture 202-6, 303, 309, 320, 321, 331, 338, 368  
   Caribbean 340  
   climate control 358  
   Neolithic 318-19  
   New Zealand 326  
   temperate forests 296-7  
   see also grazing  
 air pollution 99, 104  
 Alexander the Great 19  
*Allium tricoccum* 285  
 alpine forests 213-14, 231  
 Amazon 182-3, 186-7, 207, 236, 372-3  
   fertilization 106  
   forest structure 377  
   IBIS model 349-50  
   MODIS 380  
   refuge theory 313  
 Amazonian Monkey Ladder  
   Liana 23  
*Amborella trichopoda* 36  
 American Basswood 109  
 American Chestnut 277  
 ancient forests see old-growth forests  
 Anderson Pond 355  
 Andes 116, 118, 128, 183, 314  
 angiosperms 28, 36, 118, 214  
*Angophora* 151  
*Angraecum sesquipedale* 176-7  
 Anthes, Richard 340  
 anthocyanins 282  
 ant mutualism 196  
 apical meristems 21, 24, 27  
*Aplectrum* 285  
*Arabidopsis thaliana* 27  
*Araucarioxylon arizonicum* 35

*Archaeopteris* 33  
 Arima, Eugenio 373  
 Aroids 192  
 Arrhenius, Svante 335-6  
 ashes 277  
*Aucoumea klaineana* 201  
 axial conformity 39  
**B**  
 backwards plants 285  
 Bald Cypress 279  
 Balsa 28, 43  
 Balsam Fir 72  
 Balsam Poplar 220  
 balsam woolly adelgid 277  
 banyans 19  
 baobabs 246  
*Baragwanathia longifolia* 32  
 bark 21, 32  
   *Cinchona* 116, 132  
   eucalypts 151, 153  
   fire adaptation 84-5, 295, 324  
 Bastard Gumwood Tree 191  
 Bates, Henry 176, 177  
*Bauhinia guianensis* 23  
 Becquerel, Antoine César 338  
 Beech 69, 277, 319  
 Berkeley, George 364  
 Betts, Richard 235  
*Betula* 214, 277  
*Betula alleghaniensis* 70, 71  
*Betula glandulosa* 220  
*Betula pubescens* 219  
 "Big leaf" models 348  
 biodiversity 25, 35, 314-15, 328  
   Amazon 313  
   Chablis concept 88-9  
   diversity anomaly 172-3, 289-91  
   global patterns 172-3  
   intermediate disturbance hypothesis 85  
   micro-habitats 91  
   rain forests 177-8, 182-3, 189, 190, 192  
   temperate forests 279, 288-91  
 bioengineering 360  
 biogeocenosis 62  
 biogeography 115, 117, 118, 131  
 biomass 82  
   dynamics 92-3  
   succession 98  
 biomes 131, 142  
 biophysics 27, 46-8, 349-50  
 birches 214, 218, 277  
 bird species 91, 299, 326  
 Black Dragon fire 223  
 Black, James Wallace 364  
 Black Oak 109  
 Black Pepper 17  
 Black Spruce 219, 220  
 bloodwoods 151  
 Boarwood 188  
 Bonan, Gordon 236, 338  
 Bond, William 250  
 Bonpland, Aimé 116  
 boreal forests 101, 143, 146, 208-37  
   bioengineering 360  
   browning 356  
*Brachyramphus marmoratus* 168  
 branches 27, 42-3  
   and leaf size 39

Leonardo's prediction 40  
 Braun-Blanquet, Josias 122  
 bristlecones 306, 308, 309  
 bromeliads 192, 193  
 Budyko, Mikhail 358  
 Bueno, Marcelo Leandro 255, 256  
 butterflies 177, 194  
**C**  
 Cahokia 321-2  
*Calamites* 32  
 calcium 100, 103, 104-5  
 Caldas, Francisco José de 116  
 cambium 21, 28, 84, 85  
 Canada Geographic Information System (CGIS) 125  
 Cannonball Tree 194  
 canopy  
   boreal forests 214-15  
   cover 58-9  
   gamblers and strugglers 76-7  
   height 50-1, 59  
   mosaic 64-7, 72  
   tropical forest 192-3  
*Carapa procera* 188  
 carbon  
   sinks 80, 92, 187, 205  
   source 80, 92, 347  
   storage 80, 220, 235, 347  
 carbon dioxide 138-9, 213, 335  
   Arrhenius' calculations 336  
   bioengineering 360  
   DGVMS 351  
   savanna 244, 245, 259  
 Carlowitz, Hans Carl von 302-3  
 carotenoids 280  
*Carpinus betulus* 319  
 Carvajal, Gaspar de 187  
 Cassini de Thury, César-François 115  
*Castanea* 277  
*Castanea dentata* 277  
 cavitation 48-9  
*Cecropia* 199  
*Cedrela odorata* 306  
*Ceiba pentandra* 188  
 Cenozoic era 314-15  
 Cerrado 254-6  
 Chablis concept 88-90  
 chainsaws 204, 323  
*Chamaecyparis obtusa* 306  
 chaparral 23, 148  
 Chestnut blight 277  
 Chestnut Oak 151  
 chestnuts 277  
 chlorine 170  
 chlorophyll 128, 219, 280, 378-9, 383-4  
 choropleth mapping 125  
 chronosequences 103, 106-9  
*Cinchona* 116, 132  
 Clements, Frederic 122-3  
 climate 106, 108, 143, 144  
   Amazon 313  
   biomass dynamics 92  
   boreal forests 213, 235  
   dendrochronology 306-7, 309-10, 321  
   ecological models 343  
   Köppen classification 134, 135  
   map 134-5, 345  
   modification 358, 360

New Zealand 324-5  
   savanna 256, 258  
   temperate forests 292  
   vegetation maps 131  
   see also drought; rainfall; temperature; wind  
 climate change 57, 82, 92, 205, 216, 222, 234, 236-7, 332-61  
   analysis 136-9  
   boreal forests 228-9, 232  
   cloud forests 165  
   mangroves 170  
   phenology 287  
   treelines 160  
   wildfires 153  
 climax vegetation 122-3  
 cloud forests 147, 154, 162-5  
 cloud-seeding 358  
*Coffea* 165  
 coffee production 165, 202  
 Colbert, Jean-Baptiste 301  
 Cole, Kenneth 346  
 colonialism 202  
 Columbus, Christopher 17, 182, 340  
*Commidendrum rotundifolium* 191  
 Common Hornbeam 319  
 compartment models 104  
 cone serotiny 84  
 conifers 28, 30, 33, 35, 143, 146, 167, 235, 236-7  
   boreal forests 214-15  
   dendrochronology 306  
   krummholz 158  
   New Zealand 326  
   temperate forests 271, 279, 292-5  
 Connell, Joseph 85  
 Cook, James 112  
 Cooloola Dune System 108  
*Cordaites* 34  
 Corner, Edred 39  
 Corner's rules 39, 40, 43  
*Corymbia* 151  
 Cotton Tree 188  
*Couroupita guianensis* 194  
 Cowles, Henry Chandler 60, 108-9  
*Crambe arborea* 26  
*Croton billbergianus* 195  
 crown  
   growth 41  
   shyness 65-6  
   structure 374  
 cryoturbation 216  
 Curtis, John 296-7, 298  
**D**  
 Daurian Larch 217, 219  
 Dangermond, Jack 126  
 Dargusch, Paul 160  
 Darwin, Charles 26, 36, 106, 116, 142, 176-7  
 Davis, Margaret 310  
 Dawn Redwood 290  
 day length 213  
 deciduous trees 51, 69, 115, 144-7, 156, 173  
   boreal forests 214, 218, 219, 231-2, 236-7  
   isothermal lines 118  
   physiognomy 128  
   temperate forests 270-1, 273, 276-99  
 decomposition 86, 101, 103, 164, 196, 215, 218, 220, 232, 263

- deforestation 189, 202-5, 296-9, 331, 360, 368-73  
 boreal forests 222, 226-7, 236  
 civilizations collapse 320  
 climate change 338, 340  
 Middle Ages 322-3  
 Neolithic Revolution 318  
 New Zealand 326-7
- de Gama, Vasco 17
- Delmarva study 126
- dendrochronology 306-10, 321, 325
- Diospyros* 43
- Diospyros tessellaria* 331
- Dipterocarps 194
- disjunct genera 288-9
- disturbances 368-73  
 boreal forests 222-8  
 natural 82-7  
 regime 83  
 savanna 258  
 succession 94, 99  
*see also* fire
- Dixon, Henry 48
- Dodson, Calaway 192
- dormancy 70-1, 86-7, 195, 198, 199
- Douglas Fir 66, 104-5
- Downy Birches 219
- Dracaena cinnabari* 44-5
- Dragon Blood Tree 44-5
- droughts  
 Cahokia 321  
 stress 48, 49  
 tree rings 309
- dry forests 206-7, 238-67
- dust movement 106
- Dwarf Ebony 191
- dynamic global vegetation models (DGVMs) 348-51
- dynamics 11, 43, 60, 68, 76, 78-109  
 boreal forests 220  
 forest structure 374-7  
 savanna 248-9  
 vegetation function 378-81
- E**
- early successional species 42
- ebony trees 43
- ecological models 136-9, 342-3
- ecological niche theory 131
- Ecological Society of America 60
- ecosystems 60-3, 106-8, 241  
 Kalahari Transect 256  
 metabolism 356  
 services models 62  
 succession 94-9
- edge effects 206
- electromagnetic spectrum (EMS) 367
- element cycles 63, 100-5
- elfin forest 164
- Ellenberg, Heinz 135
- elms 277
- El Niño 191
- Emanuel, William 134, 135, 137, 345
- embryophytes 30
- emerald ash borer 277
- energy-diversity theory 289, 291
- epicormic buds 153
- epiphylls 164
- epiphytes 19, 23, 164, 192
- equal-area projection 112
- ericoid tree 201
- Erwin, Terry 192
- Eucalyptus* 46, 151, 153  
*Eucalyptus regnans* 153
- Euler, Leonhard 46
- Euphorbia* 128
- European Beech 69, 319
- Evangeline-A Tale of Acadie* 8
- evapotranspiration 75, 132, 133, 163
- Evelyn, John 301, 302
- evergreenification 236
- evergreen trees 144-7, 215, 254, 270, 273, 278
- evolution 30-7  
 convergent 146, 172  
 disturbances 84-7  
 historical biogeography 290  
 rain forests 176-7  
 savanna 244-5  
*see also* adaptations
- Ewango, Corneille 189
- extinctions 30, 35, 63, 153, 173, 191, 245, 277, 290-1, 314, 326, 328, 340, 345
- F**
- Fagus* 277
- Fagus sylvatica* 69, 319
- Ferguson, Wesley 308
- fever tree 116
- Ficus* 19
- Ficus benghalensis* 19
- figs 19
- fire 82, 83, 106, 148  
 adaptations 84-5, 148, 153, 295, 317, 324  
 Black Dragon 223  
 boreal browning 356  
 boreal forests 220-1, 222, 223-4, 229-31  
 coniferous forests 295  
 fire hunting 253  
 Neolithic settlements 316-19  
 New Zealand 324, 326  
 savanna 244, 248-9, 250, 252-5, 259, 264-6  
 sclerophyll forest 152-3
- firebreaks 68
- firs 66, 70, 71, 72, 104-5, 214, 224-5, 236
- fir waves 72-3, 260
- Fisher, Howard 126
- floristic composition 128, 131
- flowering plants *see* angiosperms
- Foley, Jonathan 349
- Food and Agriculture Organization 58
- food webs 62-3
- FORCCHN model 356
- forest reserves 340
- forest stands 83, 374, 376
- fossil record 30, 32, 36, 136, 144, 178-9, 314  
 boreal forests 218  
 historical biogeography 290  
 humans 245
- Fourier, Jean-Baptiste Joseph 336
- fragmentation 206-7  
 Amazon 373  
 temperate forests 296-9  
*see also* mosaic
- Fraser Fir 70, 71
- Fraxinus* 277
- Friedlingstein, Pierre 351
- fungi  
 Chestnut blight 277  
 mycorrhizae 197
- fynbos 148
- G**
- gamblers 76-7
- gap colonization 68-9, 72-4, 76-7, 86-91, 92, 195, 199
- gap models 232, 352-7
- Garôé 20, 26
- Gaur 100
- Gaussen, Henri 135
- GBF-DIME 125
- general circulation models (GCMs) 136-7, 336
- genomes, migrations 312
- Gentry, Alwyn 192
- geoengineering 358-61
- geographic information system (GIS) 124-7, 372
- geological history 29-37
- Geoscience Laser Altimeter System 50-1
- germination 194-5, 198-9
- ghost gums 151
- Giant Baobab 246
- Giant Sequoia 295
- Gilbertiodendron dewevrei* 189
- Gilboa 32
- Ginkgo biloba* 34, 290
- girdling 85
- Givnish, Thomas 42
- Gleason, Henry 122
- Gondwana 168, 188, 190, 273, 274
- Google Earth 370
- Gray, Asa 288
- Gray's puzzle 288-9, 291
- grazing 322, 331, 368  
 cattle ranching 182, 205, 207, 246, 258, 368  
 savanna 244, 248-51, 258-9, 263, 266  
 temperate forests 270, 278, 295
- Great Bristlecone Pine 306, 308
- Great Frost 306
- Greeley, William 368-9
- greenup dates 380
- Grisebach, August 131
- Grove, Alfred 23
- Grove, Richard 331
- growth  
 crown 41  
 element cycles 101  
 primary 21  
 rings 29, 85, 306-10, 321  
 secondary 21, 25, 28-9  
 tall trees 46-53  
 wood density 43
- gymnosperms 28, 33
- H**
- habitat loss 298-9
- Haldane, "Jack" 192
- Hales, Stephen 340
- Hallé, Francis 27, 43, 44, 88
- Handroanthus ochraceus* 183
- Hansson, Amanda 160
- Harappan civilization 320
- hardwoods 28-9, 94
- Hardy, Thomas 10
- heartwood 28-9
- heliconid butterflies 177
- hemiepiphytes 23
- hill-and-hummock surfaces 90
- Himalayas 118, 154, 314
- Hinoki Cypress 306
- Hirtella physophora* 196
- historical biogeography 290-1
- Holdridge, Leslie 131, 345
- Holdridge vegetation map 132-5, 136
- Hornbeam 319
- Horn, Henry 42
- humans  
 as change agents 264-7  
 Maori 17, 35, 326  
 Neolithic settlements 316-19  
 savanna 244-5, 259  
*see also* climate change
- Hundred Rolls 323
- Hutchinson, George Evelyn 131
- hydraulic system *see* water, transport
- I**
- ice ages 290-1, 310, 312-13, 314, 317, 328, 336
- ice-out dates 287
- ICESat satellite 50-1
- ice sheets 51, 291, 310-11, 314, 336
- Indiana Dunes study 108-9
- Indian Banyan 19, 23
- Industrial Revolution 32, 259, 300, 368
- insects  
 butterflies 177, 194  
 diversity 192  
 moths 176-7, 194, 224-5  
 outbreaks 222, 224-5  
 pollination 194, 285  
 termite mounds 263
- Integrated Biosphere Simulator (IBIS) model 349-50
- intermediate disturbance hypothesis (IDH) 85
- International Union for Conservation of Nature (IUCN) 25
- "In a Wood" 10
- Ipê-do-cerrado 183
- iron 106
- islands 26, 27, 44  
 Caribbean 182, 191, 340  
 Madagascar 202  
 Saint Vincent 340  
 Sumatra 202  
 treelines 160  
 tropical forests 191
- isothermal lines 118
- isotherms 228
- isotope analysis 308, 309
- Isthmus of Panama 182
- Iverson, Louis 138
- J**
- James Dean strategy 199
- Jaramillo, Carlos 314
- Jefferson, Thomas 338
- Jenyns, Soame 340
- juniper 271
- K**
- Kalahari Transect (KT) 256-7
- Kauri 325
- Kava shrub 16-17
- Kawakawa 17
- Keeley, Jon 250
- keystone species 170
- Kharuk, Viacheslav 236
- Kingshill Enclosure Ordinance 340
- Koch, George 48
- Köppen climate classification 131, 134, 135
- Köppen, Wladimir 131

- krummholz 156, 158  
kwongan 148
- L**  
Lägern mountain 383  
Landsat satellites 370-3, 382  
larch 51, 214, 215, 217, 218, 219, 224-5, 236-7  
*Larix* 51, 214  
*Larix gmelinii* 217, 219  
Last Glacial Maximum (LGM) 310, 312, 313  
lateral meristems 21  
late successional species 42  
laurels 26, 154-5  
laurophyll forests 147, 154-5, 278  
Lawrence, George 365  
leaves  
    "Big leaf" models 348  
    bird correlation 91  
    color 280-3  
    display 39  
    evergreen and deciduous 144-6  
    foliage height diversity 91  
    leaf-fall 215, 217, 240, 280-5  
    margins 144, 154  
    monolayers and multilayers 42, 75  
    phenology 378  
    pigment 280-3  
    shape 178  
    size 39-40, 144  
    stomata 48, 213  
    structure 374  
    succession 98  
    total area 41  
    transpiration 49  
Leeuwenberg's model 44  
Leonardo da Vinci 40-1, 306  
*Lepidodendron* 32  
lianas 23, 176  
lidar 50-1, 367, 374-7  
life span 39  
life zone ecology 132-5, 345  
light-demanding species 74, 87, 92, 199, 201, 206  
lignin 30  
Linnaeus, Carl 288  
*Liquidambar* 283  
*Liriodendron* 283  
living fossils 290  
Loblolly Pine 138-9  
Lodgepole Pine 295  
London fossils 179  
Longfellow, Henry Wadsworth 8  
longleaf pine 279  
Lund, H. Gyde 57, 58  
Luther, Martin 328  
lycopsids 32
- M**  
*Macaranga* 199  
McGlone, Matt 326  
Mackie, William 30  
magnesium 100, 103, 104  
*Magnolia* 36  
Mahogany 201  
Maidenhair Tree 34  
Ma, Jianyong 356  
mallee 151, 153  
management 227, 319, 320, 322, 368  
    fire as 252-3  
    savannas 258-9, 265, 267  
    site index 50  
    sixteenth century 328  
    sustainability 302-3  
mangroves 147, 170-3  
Maori 17, 35, 326  
maples 75, 109, 277, 283  
maps 110-39  
    legends 128-31  
    projections 112, 115, 120  
    scale 112, 115, 120-2, 126  
    vegetation classification 122  
*maquis* 23, 148  
Marbled Murrelets 168  
Maries' Fir 72  
maritime temperate forests 166-9  
Martius, Karl Friedrich von 118  
matorral 148  
Mauritian Ebony 331  
Mencken, H. L. 317  
*Metasequoia glyptostroboides* 290  
*Miconia calvescens* 191  
micro-habitats 91  
migrations  
    Europe 312  
    Southeast Asia 313  
    southern hemisphere 313  
mimicry 177  
mineralization 101  
missing pollinator problem 176-7  
Moderate Resolution Imaging Spectroradiometer (MODIS) 380  
monolayers 42, 75  
Montezuma Cypress 18  
Morris, Jennifer 30  
mosaic 78-109, 232  
    gap models 352  
    savanna 252  
    see also fragmentation  
moths 176-7, 194, 224-5  
Mountain Ash 153  
mountains 132, 143, 147, 151, 213, 272, 291, 302, 347  
    Andes 116, 118, 128, 183, 314  
    cloud forests 162-5  
    packrats 346  
    The Rockies 292, 314  
    tepuis 184  
    see also treelines  
multilayers 42, 75  
*Musanga* 199  
mutations 30  
Mutis, José Celestino 116  
mutualisms 196-7  
Mycenaean civilization 320  
mycorrhizae 197
- N**  
*Nachhaltigkeit* 302-3  
Nadar 364  
near-infrared (NIR) light 365, 367, 372, 378-9  
Neolithic Revolution 318  
Neolithic settlements 316-19  
Neotropical Velvet Tree 191  
net primary productivity (NPP) 381  
Neubronner, Julius 365  
New World tropical rain forests 180-7  
niche conservatism 277  
nitrogen 104, 109, 232, 384  
Normalized Difference Vegetation Index (NDVI) 378-80, 381  
Northern Red Oak 109  
*Nothofagus* 168, 213, 273, 274-5, 324-5  
Novice Tree 196  
*Nyssa* 283
- O**  
oaks 94, 277, 300, 306, 310-12, 355  
*Ochroma pyramidale* 28  
*Ocotea foetans* 26  
Odyssey GIS 126  
Oldeman, Roelof 27, 43, 44, 76, 88  
old-growth forests 8, 69, 90, 99, 105, 168, 206, 376  
Old World tropical rain forests 188-91  
Olson, Jerry 109  
orchids 192, 196, 285  
Ordovician 30  
Oregon State University (OSU) 345  
Orellana, Francisco de 187  
organic matter cycling 101, 104  
overstory 83
- P**  
packrats 346  
Paleocene-Eocene Thermal Maximum 314  
paleoecological studies 136, 346-7  
paleogenomic studies 317  
Pallardy, Stephen 378  
paludification 218  
palynology 310, 313, 324-5  
Paraíso Cave 313  
parasites 196  
Pastor, John 232  
"pattern and process" 68-71, 72-4, 80, 352  
pattern-recognition techniques 382  
Payette, Serge 230  
Peach 27  
peat 220  
Peet, Robert 272  
pepper plants 16-17  
permafrost 216, 220-1  
pest species 83, 277  
phenology 135, 286-7, 370, 378-80, 382  
phosphorus 104, 106, 197  
photography, aerial 364-5  
photosynthesis 39, 43, 50, 65, 75, 89, 170  
    pigments 282  
    remote sensing 67, 380-1  
    savanna 243-4, 259  
physiognomy 17, 128, 131  
phytosociology 122  
*Picea* 214  
*Picea brachytyla* 306  
*Picea glauca* 220  
*Picea mariana* 219, 220  
*Picea rubens* 70, 71  
Pin Cherry 70-1  
pines 23, 75, 84, 94, 138-9, 214, 236, 279, 295, 306, 308  
*Pinus* 84, 214, 295  
*Pinus longaeava* 306  
*Pinus palustris* 279  
*Pinus ponderosa* 75  
*Pinus taeda* 138-9  
*Piper* 16-17  
*Piper excelsum* 17  
*Piper methysticum* 16-17  
*Piper nigrum* 17  
*Pitcairnia feliciana* 192  
pit vessels 29  
plant functional types (PFTs) 382-4  
pneumatophores 172  
podocarp conifer forests 326  
*Podocarpus hallii* 326  
*Podocarpus totara* 35, 326  
pollen 314-15, 317  
    gap models 355  
    Neolithic records 319  
    New Zealand 324-5  
    palynology 310, 313  
pollination 194-6, 218, 285  
pollution 99, 104, 177  
Ponderosa Pine 75, 295  
Ponomarev, Evgenii 224  
poplars 27, 214, 306  
*Populus* 27, 214  
*Populus balsamifera* 220  
*Populus tremuloides* 18, 280  
positive feedback 145, 232, 236-7, 244, 347, 351  
Post, W. M. "Mac" 232  
potassium 100, 103, 104  
Primack, Richard 287  
primary succession 96, 98, 109  
primeval forest 8  
Pruitt, Evelyn 367  
*Prunus pensylvanica* 70-1  
*Prunus persica* 27  
*Pseudotsuga menziesii* 66, 104-5  
Ptolemy 112, 115  
pyric heathlands 148
- Q**  
Quaking Aspen 18, 280  
*Quercus* 277, 306, 310-12, 355  
*Quercus alba* 151  
*Quercus montana* 151  
*Quercus rubra* 109  
*Quercus velutina* 109
- R**  
Rackham, Oliver 23, 323  
radar 367, 374, 376, 382  
radiocarbon dating 308, 324, 326  
Radkau, Joachim 322, 323  
rainfall  
    acid 104  
    deforestation 340  
    rainmakers 358  
    savanna 256, 258-62  
    temperate forests 270-2, 276  
rain forest see tropical rain forests  
Rampart Wood 201  
ramps 285  
Red Spruce 70, 71  
redwoods 35, 48, 163, 290, 292  
reforestation 205, 296  
refuge theory 313  
regeneration 50, 66, 82, 90-1, 194-5, 199  
    age 83  
    biomass dynamics 92-3  
    see also gap colonization  
remote sensing 67, 364, 366-7, 370-3, 374-8, 380-5  
Resin Birch 220  
retrogressive succession 109  
Rhynie chert 30, 32  
Richardson, Andrew 163  
The Rockies 292, 314  
Roman Empire 320  
Romantic environmentalism 331  
roots 24, 196  
    mycorrhizae 197  
    stilt 172  
Royal Navy 300-1  
Rübel, Eduard 131

## S

Sahara 106, 358  
Saint-Pierre, Bernardin de 331  
salinity 170-3  
salmon migration 167  
sand dunes 108-9  
Sankaran, Mahesh 258-9  
sapwood 28-9  
savannas 238-67  
    change studies 256-9  
    fire 244, 248-9, 250, 252-5,  
    259, 264-6  
    large herbivores 250-1  
    parkland 262  
sawing 323  
Schimper, Andreas 131  
Schulman, Edmund 308  
sclerophyll forests 146, 148-53  
sea ice 234, 236, 358  
sea level 147, 170, 313  
seasonality 280-7  
secondary insular woodiness 26  
secondary succession 96, 97-9,  
    220-1  
secondary woodiness 27  
seeds 70-1, 86-7  
    dispersal 189, 194  
    fire adaptation 295  
    germination 194-5, 198-9  
    seedbank 86-7  
    size 198-9  
seed trees 34  
*Sequoiadendron* 46  
serotiny 84  
shade-intolerance *see* light-  
    demanding species  
shade tolerance 74-5, 76, 86, 87,  
    201, 206  
    coffee 165  
    seeds 194-5, 199  
*Shorea faguettiana* 51  
shortwave infrared (SWIR) region  
    367  
Shulmeister, Jamie 160  
Shuman, Jacquelyn 352  
Siberian Fir 224-5  
Sirois, Luc 230  
site index 50  
Snow, John 124  
sodium 100, 170  
softwoods 28-9, 312  
soil  
    boreal forests 220  
    pH 103  
Sollins, Phillip 104-5  
Solomon, Allen 355  
southern beeches 168, 213, 273,  
    274-5, 324-5  
Spanish Cedar 306  
Spanish Moss 192  
speciation  
    pump 313  
    rates 291  
spectral classification 382-5  
spores 30  
spotted gums 151  
spring ephemerals 284-5  
spruces 214, 218, 236, 300, 310-11  
Steinitz, Carl 126  
stilt roots 172  
stinkwood 26  
stomata 48, 213  
stranglers 19  
Streeton, L. H. B. 153  
strugglers 76-7  
succession 42, 94-9, 109, 122-3, 220-1  
Sugar Maple 75, 109, 283

Sunda Shelf 313  
sustainable forestry 300-3  
Swap, Robert 106  
sweetgums 283  
*Swietenia macrophylla* 201  
SYMAP 126  
symbiosis 197  
*Symphonia globulifera* 188

## T

taiga *see* boreal forests  
Tank Bromeliad 193  
Tansley, Sir Arthur G. 60, 122  
Taubert, Franziska 206  
*Taxodium distichum* 279  
*Taxodium mucronatum* 18  
Teixeira, Pedro de 187  
temperate forests 101, 143, 146-7,  
    268-303  
    deforestation 202  
    maritime 166-9  
temperature  
    cloud forests 163  
    Dahurian Larch 217  
    isotherms 228  
    temperate forests 292  
    treelines 156, 160  
    *see also* climate change  
tepai forest 184-5  
termite mounds 263  
Thale Cress 27  
Theophrastus 23, 343  
thermal infrared (TIR) region 367  
thermokarst 216  
thinning laws 66-7  
Thoreau, Henry David 94, 287, 296  
*Thuja occidentalis* 271  
tiger bush 260-1  
*Tilia americana* 109  
*Tillandsia usneoides* 192  
*Tipularia* 285  
Tobago Main Ridge Forest Reserve  
    340  
Tomlinson, Philip 27, 43, 44  
Tomlinson, Roger 124-5  
topography 272  
Tournachon, Gaspard-Félix  
    "Nadar" 364  
tracheids 29, 30, 36  
tracheophytes 21, 30  
transitions, temperate forests 278  
transpiration 48, 49, 75  
tree architecture 27, 38-45, 88  
tree clumps 260-3  
tree competition 231-2  
treelines 118, 156-61, 218-19, 292  
*Triplaris americana* 196  
*Trochetiopsis melanoxydon* 191  
trophic cascades 299  
tropical rain forests 101, 143, 144,  
    172, 174-207, 314, 328  
    canopy top 192-3  
    as cradles 176-9  
    fragmentation 206-7  
    functional tree types  
    198-201  
    *see also* Amazon  
Tucker, Compton 378  
tuliptrees 283  
tundra 230  
tupelos 283

## U

*Ulmus* 277  
understory 83, 99, 165, 201, 284-5  
United Kingdom Meteorological  
    Office (UKMO) 345

## V

Veitch's Fir 72  
Venetian Arsenal 300  
vines 23  
*Virola* 194  
visible red (VIS) light 365, 367, 372,  
    378-9, 382  
*Vismia* 199  
vivipary 172  
volcanoes, New Zealand 324  
von Humboldt, Alexander 116, 118,  
    128, 228  
von Sternberg, Kaspar Maria 136  
*Voyria* 196

## W

Waldhufendörfer 322  
Wallace, Alfred Russel 176-7, 178,  
    190  
Wallace Line 190  
Warming, Eugen 176  
water  
    Cahokia 321  
    cloud forests 162-3, 164-5  
    cycle 100  
    evapotranspiration 75, 132,  
    133, 163  
    loss 213  
    runoff 260-1, 349-50  
    savanna 256, 258-62  
    transport 39, 46, 48-9  
    *see also* rainfall  
watersheds 104  
Watt, Alex S. 11, 68-9, 72, 232  
Webster, Noah 338  
White Cedar 271  
White Oak 151  
White Spruce 220  
Whittaker diagrams 272  
Whittaker, Robert 272  
Williams, Michael 368  
Wilmshurst, Janet 326  
Wilson, Edward O. 177  
wind 46, 83, 218  
wood craftsmanship 322  
wood density 43  
Woods, William I. 321  
Wood Thrush 299  
Woodward, Ian 48

## X

xanthophylls 280  
xylem 49

## Y

Yellow Birch 70, 71  
Yellow Meranti 51  
yellowwoods 35  
Yoda, Kyoji 66  
Yoda's law 66-7

## Z

Zeller, Otti 135