Tropical Biomes: Equatorial Evergreen Forests, Tropical Deciduous Forests, and Savannas

ESP 30 Lectures 5 and 6
A quick tour of all the biomes
Even at the margins of glaciers, streams have some algae growing in them. Translucent rocks have algae growing in and under them. Lakes with thick ice but a little light filtering through have simple ecosystems. Life is very tough and “extremophiles” grow in hot springs, deep in the earth, in the bottom of ice shelves where liquid water exists among ice crystals, and other extreme environments as well as the margins of glaciers.
Tundra is the vegetation hugging the ground in the lower part of this shot. In the background, some very skinny conifers are established. Tundra vegetation hugs the ground because when the sun shines the “boundary layer” of air just a centimeter or two thick is rather warmer than the air above. Tundra climates are could as well as cold from high latitude. Boundary layer warmth is this important. The basic function of the pyramidal shape of so many conifers is to shed snow. When snow builds up on the branches, they bend down and dump the snow. Open branched trees are subject to heavy breakage if the experience heavy snow (or ice) loads. You will notice that we have an important open branched conifer, the California Grey Pine, in our foothills where snow is light and infrequent. In the Eastern US, storms with freezing rain sometimes load the bare limbs of deciduous trees so heavily that they are badly broken up.
This picture is from the Pawnee National Grassland east of Ft. Collins, Colorado. The light specks in the foreground are pronghorn antelope. Note a few scruffy conifers on the right horizon. This is short grass prairie, a signature sub-biome of the dry, higher elevation grasslands east of the Rocky Mountains from S Canada to Texas. Central Asia has huge areas of arid grasslands like this, a best barely suitable for crop production. Genghis Khan and Sitting Bull and their pastoral nomad follower are the classic human adaptation to the arid steppes. Further east in the US, the more humid tall grass prairie sub-biome is highly favorable for rainfed crop production.
Toothy leaves are a signature of the temperate deciduous forest. As far as I can discover, plant biologists don’t have a good explanation for why temperate deciduous leaves should so often be toothy.
These forests tend to be dominated by plants in the laurel family with un-toothy leaves shaped like lance points. The common culinary bay leaf and our more pungent California Bay are examples of laurel family plants that happen to grow in the Mediterranean Biome. But they are far from dominant with us. We grow lots of ornamental plants from Biome V from New Zealand, Australia, and South China. Most of the ornamental plants you see in California with smooth margined evergreen, soft-leathery leaves are adaptees from Biome V. With summer irrigation most of them do great in our climate. Citrus also do will with us. They are not from the laurel family, but they have the same lanceolate evergreen leaves.
The California coast near San Simeon. The mosaic nature of this scene is typical of Biome IV. Grasslands, shrub fields (chaparral—Spanish meaning you need chaps to ride a horse through it), and oak and pine forests form a patchwork. Conspicuously patchwork complexes of plant communities tend to form when the annual potential evapotranspiration (think of this as the amount of water plants would transpire if the had just what they needed in every month) to rainfall ratio is around 1. In places where rainfall from the rainy season collects, say in deep cracks in the rocks, shrubs or trees may be able to survive the dry season. On north facing slopes, the heat of the summer sun is less, and woody vegetation can survive the summer. In places where favorable summer conditions don’t exist, annual plants will dominate. The scene above is from April. What will it look like in June-October?
The signature plants of the subtropical desert are shrubs (creosote bush in background) and annuals that sprout when it rains (sunflower, foreground). Note that even in this fairly wet year, there is plenty of bare ground.
This sort of community is characteristic of a broad ecotone between proper tropical deciduous forest and proper savanna in Africa. The tall plants in the background are cactus-like succulents in the family Euphorbiaceae, very important group in arid Africa. These communities are extremely productive and are often quite rich in game animals.
Note people wearing rubber boots and giant leaves on understory plants. Both pretty good give-aways to Biome I
Note that my ESP30 web page has larger scale maps of the biomes for each continent.
Climates of the major biomes I

Tropical evergreen forest

Deciduous tropical forest

Subtropical desert

Mediterranean

Temperate evergreen forest

Deciduous temperate forest
Remember that tropical climates are those influenced by the ITCZ and its seasonal movement. Biome I, Tropical Evergreen Forest, is under the influence of the ITCZ at least 10-11 months per year. Plants, in the average year, experience little or no drought. As you move away from the equator a few degrees, climates tend to become much more seasonal. The ITCZ moves north and south with the sun, leading to climates with highly seasonal rainfall. Where the summer rainy season is long and wet, Tropical Deciduous Forest, Biome II, exists. Still further from the equator, shorter dry seasons result in Tropical Savanna, Biome IIa.
Walter introduce the idea of “diurnal climates” to help characterize tropical climates. The concept is that climates near the equator have limited seasonal variation in temperature, so little that the average daily range of temperature exceeds the range of monthly means. In the above climate diagrams, the range of monthly means is only a degree or two while the average difference between night-time minima and daytime highs is ~ 10°C.
The Structure of Vegetation in the Tropical Biomes

Biome 1
- Evergreen seasonal forest

Biome 1-2 "ecotone"

Biome 2
- Semi-evergreen seasonal forest
- Deciduous seasonal forest

Biome 2a
- Thorn woodland
- Cactus scrub

Biome 3
Tropical soils are typically very heavily weathered and hold little nutrients in the soil. Plants are adapted to take up very dilute nutrients and store them in plant tissues. Exceptions exist. The “whitewater” rivers of the Western Amazon carry heavy loads of fresh sediment from the eroding Andes. The eastern flanks of the Andes also have areas of young soils on recent volcanic ash. Similarly, the islands of Indonesia and much of Central America are largely volcanic and have fertile, young soils even under hot, wet conditions. One of the reasons that volcanic eruptions in the tropics often result in such a heavy human death toll is that farmers in the tropics will tend to tuck themselves up close to active volcanoes because that is where the good soils are. People who live in climates where soils weather less rapidly can afford not to live so close to harm’s way.
Tropical forests in Ecuador

Pacific slope

Amazonian slope
Note that most leaves in tropical forests are “entire”, that is without toothy margins.
Tropical forests are actually complex mosaics if you get down to identifying species. The paradox is that the general form of the vegetation is very uniform but the species diversity is extra-ordinary. Forest stands with 100 or more species of trees per hectare (2+ acres) is not unusual.
Here the variation imposed by the presence or absence of seasonal flooding along the Amazon is depicted.

Fig. 84. Schematic profile across a valley section of the lower Amazon river (white-water river) (after Sioli).
The seasonal fluctuation of the Amazon is more than 10 m here. This scene is at low water. The thick band of sediment exposed on this cutbank shows no sign of weathering to red soils. When the Amazon rises each year, it dumps fresh Andean alluvium in this region. This might be the Central Valley of Amazonia except that the whole area is flooded to a depth of 1 m or more during the high stand of the river. Except for a few people who live on the highest natural levees, no one has ever figured out how to exploit these lovely soils.
Tropical forests have adaptations that we don’t see in other biomes. Plank buttresses are very common. Tropical trees tend to have shallow roots with root hairs invading the decaying litter to compete for the mineral nutrients that are leaching out of them. Hence they are easily toppled by the wind. Buttresses are an adaptation to the lack of deep roots. Actually plank buttresses are more like guy wires than buttresses. They are weak in compression but strong in tension.
Pictures of forest are difficult because it is such a 360 degree environment. Here most of the forest has been dissected away by the cattleman's chain saws and we see an overstory tree with only a few friends left to provide shade for the cattle. Note the light colored bark on the trees here. This is due to lichens growing on the bark, not the color of the bark itself. The paradoxical principle is that drought adapted plants find all sorts of ecological niches in wet tropical forests. You can see that this tree has lianas (vines) growing up its trunk. You can also see that its branches carry a load of “epiphytes,” typically orchids, bromeliads (pineapple relatives) cacti, ferns and so forth. Epiphytes subsist on rainfall, but they have to be prepared to go without water for extended periods when rain fails to fall. Evergreen tropical forests have so much water that they can support an essentially rootless desert vegetation growing on the limbs! If the environment is near 100% relative humidity a lot of the time, it rains frequently, and is always warm, weird plants can thrive in weird niches that are too cold or dry to be livable elsewhere. The staggering diversity of wet tropical forests is partly built upon this principle.
Trees very diverse
We have some important vines in our Mediterranean vegetation, for example grapes and poison oak. But they are most conspicuous and diverse in Biome I.
Any ideas why? Humans are mostly right handed too. Is some general principle at work? If you can find it, you’ll be famous!
Tropical evergreen forest epiphytes are as spectacular or more spectacular than lianas.
The reserve where I took these pictures turned out to have ~ 60 species of orchids, most with spectacular flowers. Why do tropical flowers put so much energy into these gaudy displays? The theory is that each species is pretty rare. To attract a bird, bat, or insect to pollinate it, it has to be easy to find (bright big flowers, nice bouquet) and give a big nectar reward. The pollinator critter charges a steep fare to fly pollen so far between flowers and wants clear directions! The collection was pinned to a wire trellis, much like laundry hung out to dry. No dirt no nothing. The wet tropics are a trip!
Many tropical plants invest much energy in large flowers. We esteem them as objects of beauty. But why do they bother? Certainly not to please us!
A page from a field guide to Central American Birds. This is about 2/3rds of the hummingbirds in this region; more hummingbirds on the next page. The skinny slip of tropical land that connects North and South America has more breeding birds than the whole of NA north of Mexico. The flora of the small country of Ecuador is several multiples of the flora of the entire US. The tropics are crazy diverse! This diversity makes the wet tropical forests the mother cathedral for natural historians. Alexander von Humboldt, Darwin, Wallace, and every other naturalist finds the tropical forest a mystical experience I think. I know scientists are not supposed to be mystics. We could have a long philosophical discussion about this. Read the last paragraph of the Origin of Species for homework for this conversation. (Out-of-copyright classics like the Origin are easily found on the web.)
Leaves with pointy “drip tips” are common. If you cut these tips off, water tends to dam up at the lower end of the leaf. Why would tropical plants want to keep their leaves as dry as possible?

“Entire” leaves are the rule. They have smooth margins. (contrast the toothy edged leaves of maples and many other leaf shapes). Giant leaves like this are common. Think about the possible adaptive significance of such a shape and size variation. This plant is in the Calla Lily family.
Here is one theory about why rain forest plants try to keep their leaves as dry as possible. Here, lichen epiphytes have encrusted an old leaf and reduce its photosynthetic capacity. Bacterial and fungal diseases can also attack damp leaves. Humans find it a big struggle to keep clothes and other things dry enough not to rot promptly away in humid tropical climates.

Another odd fact about the leaves of rain forest plants is that they are generally rather thick and leathery. They can resist water loss rather well. The theory is that in these hot climates, shallow rooted plants can get quite drought stressed in short dry periods. Strangely, wet tropical plants must have some resistance to drought. This is most extreme in epiphytes that have no roots in the ground at all. It is probably no accident that the cactus family of plants’ most primitive members are rain forest shrubs.
The forest floor vegetation is not that dense because very low light levels limit photosynthesis. You don't need to whack about with a machete to get around. Despite the blazing tropical sun at the top of the canopy, down here photos like this require a tripod! This was a ½ second exposure. Many house plants are from this vegetation, and from the epiphytes clinging to branches over our head here. Think about why plants from the forest understory and the tropical epiphytic environment are “pre-adapted” to be house plants.
One of my old friends is a monkey-watcher (primatologist). Her first idea for her PhD thesis was to study New World monkeys in Costa Rica. She had undergrad experience observing chimpanzees in Africa. The new world monkeys were very frustrating! The monkeys were small, active creatures living in the thick forest canopy 40-50 m above the ground. You get brief glimpses of individuals amidst a lot of shaking leaves. Chimps live mostly on the ground and you can observe most things that they do fairly easily. She gave up on field studies of New World monkeys! So it is with much that goes on in Evergreen Tropical Forests. Much of the action is in the canopy that is impossible to observe from the ground.
Figs are another wildly diverse group in the tropical biomes. In Evergreen Forests, strangler figs are common. They start out as epiphytes but send branches down the tree-trunk to root. Then they are a sort of liana, but one that thickens up and gradually chokes its host, finally becoming an independent tree. N Queensland, Australia.
Forests are generally lousy places for herbivores. The most efficient style of herbivore digestion trades on large size to operate a gut brewery that converts plant cellulose to sugar. Cows and elephants are good at this, but they can’t climb big trees. (Elephants specialize in pushing over small trees to browse on the canopy.) Small herbivores are not so good. Leaf-eating monkeys can harvest only the tenderest and least chemically defended leaves. Cold blooded animals like snakes have a very efficient metabolism. They are disproportionately important in biomes like wet tropical forests and deserts where the ability of herbivores to harvest the vegetation is low.
This is a classic adaptive tradeoff; high energy fast active life versus an ultra conservative critter that only needs a meal a few times a year.
Many tropical forest browsing (leaf eating) mammals, like tapirs and duikers, are “primitive” meaning that they resemble species that are at the root of later mammalian radiations. This makes sense because moist tropical and warm temperate ecosystems are ancient ecosystems. Over the last 20 million years or so the earth has gotten cooler and drier. Deserts, savannas, and steppes are modern biomes. Tapir and duiker like ancestors gave rise to the horse and antelope radiations onto the emerging grasslands in the Miocene. In Australia, there was until humans arrive a 2-ton galloping terrestrial crocodile. The caiman of South America are mainly fish eaters, but like crocodiles they will take terrestrial animals that come to riversides to drink.
People live in wet tropical forests

Simple swidden cultivation

Commercial citrus Belize

Maya: high civilization in Tropical Evergreen/Deciduous Forest. But the system collapsed.

Small scale logging, Brasil
Biome 2 Tropical Deciduous Forest

![Map of Biomes](image)

Fig. 13. Vegetational zones (much simplified, without edaphically or anthropogenically influenced vegetational regions). I. Tropical and subtropical zones: 1 Evergreen, rainforests of the lowlands and mountainsides (cloud forests). 2 semi-evergreen and deciduous forests. 2a dry woodlands, natural savannas or grassland. 3 hot semi-deserts and deserts, polewards up to latitude of 35° (see also 7a). II. Temperate and Arctic zones: 4 sclerophyllous woodlands, with winter rain. 5 moist warm temperature woodlands. 6 deciduous (hemiboreal) forest. 7 steppes of the temperate zone. 7a semi-deserts and deserts with cold winters. 8 boreal coniferous zone. 9 tundra, 10 mountains.
Climographs from stations in India with seasonal tropical climates. In the wettest example, Marmagoa, forests are still evergreen and many evergreens remain at Belgaum. Bidar and especially Jaipur are really in the Tropical Deciduous forest zone. Walter calls the wetter two stations the "zonocotone" between biomes 1 and 2.

Fig. 32. Climate diagrams of Indian stations in the evergreen, semievergreen, moist- and dry-monsoon forest. (From Walter and Lieth, 1967.)
Remember that even in equatorial evergreen forests with plenty of rain on average, plants suffer drought stress on their leaves exposed to the hot sun at the top of the canopy. Even understory plants are drought stressed when a few weeks without rain occur. Just as we experience in California, the weather fluctuates a lot around the averages in the tropics. If it were not so, weather forecasting would be trivial. Stressful droughts strike even the most humid climates. In the last few years, Indonesia and Florida have been struck by big forest fires caused by drought striking in humid forest biomes. Thus, evergreen forests persist under climates with short dry seasons, though they become shorter and more open.
1-2 Zonoecotone. Deciduous tree in bloom at Tikal, Guatemala. Many deciduous tropical trees bloom just before the start of the rains. Tikal has lots of evergreens too, as you can see in the lower right.
1-2 Zonoecoline in N Zambia. October, end of the dry season. The forest is short and open, but largely evergreen. Human disturbance (swidden horticulture) may account for short open stature.
Classic deciduous tropical forest in wet season. Much less diverse than evergreen tropical forest. We can speak of Mopane being dominant tree here. Inset, Mopane leaf w/caterpillar.
Near Batopilas, Mexico. Most but not all trees and shrubs are leafless. Tree in center with white spots on it is a kapok tree. Kapok was once used to stuff life preservers.
2a Savanna climographs are fairly variable. What unites them is having just a few months of ample rain, but not many. Examples marked 2a here Tropical Savanna.
When rainfall is rather low, intensively rooted grasses get almost all of the water and extensively rooted grasses out-compete woody species (a & b). Grasses are also exceedingly tolerant of heavy grazing. Every kid who has had to mow the family lawn knows why, even if they have not thought about it. Why does a heavily mowed lawn stay free of weeds and woody vegetation? In subtropical Australia and South Africa, burning is used as a “mowing” strategy to favor grasses at the expense of woody vegetation. But as some water leaks to deeper depths extensively rooted shrubs can find enough deep water to sustain themselves during the dry season (c). They can also cast a little shade and out-compete the grass that crowd too close for light. Some also exude poisons that inhibit competitors for water. As rainfall increases, more water drains into the subsoil and the shrubs and eventually trees became more aggressive (d). They use products of photosynthesis to build tall woody stems that shade low competitors and increase the water available to them. A tropical evergreen forest is the logical conclusion of this pattern. The struggle for light is won by the trees when water is no longer limiting at all. Soil texture complicates this story. Deserts tend to be dominated by shrubs, not grasses. Grasses are often absent. A meditation upon soil weathering will tell you why shrubs come back as climates get even drier than a.
Another classic East African Rift scene
Australia’s dominant genus, Eucalyptus, has evergreen sclerophyll leaves in several biomes. Even the Acacias, abundant in Australia, replace leaves with thick blade shaped “phylloides” that resemble Eucalyptus leaves. For geological reasons, Australian soils are exceedingly nutrient poor. The main part of the continent has seen very little mountain building or volcanic activity for a very long time. Soils are very heavily weathered. Could this explain why Australian plants are so weird? The unique attributes of Australia could be due to its very poor nutrient status or to its biogeographic long isolation from the rest of the world. The adaptive and historical explanations for Australia’s oddities remain topics of active research.
Legumes and their relatives are common in Biome 2, 2a and 3. These plants are important to ecosystem function because their bacterial symbionts “fix” atmospheric nitrogen. That is, bacteria they harbor in root nodules convert nitrogen gas to ammonium that plants can use to make protein. Soils in arid and semi-arid regions tend to be rich in P and K but short on N, this favoring species that can extract the abundant N in the air. N-fixation is energetically quite costly because the N-N bond of N₂ gas is very strong, so N-fixers generally don’t completely outcompete non-fixers. On the contrary, N-fixers sometimes lead to their own demise at the hands of competitors if they fix too much N.
“Secondary productivity” of ecosystems leaps upward in Thorn Forests and Savannas. Primary production is ecospeak for plant growth rate per unit area of land. Secondary production is the rate of plant eating animal growth per unit area. The most efficient herbivores use gut microorganisms to digest cellulose in complex stomachs (ruminants, cow, antelopes, deer and others, or in long blind sacs attached to their intestines (rhinos, horses, elephants). The most efficient users of cellulose in this way are large. Large animals have lower metabolism per unit kg. Small herbivores need more energy and have to eat higher quality plant parts than mature leaves. In fact, plants seem to have evolved to keep their leaf tissues both dilute in nutrients and often rich in toxic plant compounds. Grasses, for example, try to defeat grazers by having lots of silica (glass shards essentially) in their leaves. These make them unpleasant to eat and wear away the teeth of the grazers. The grazers of grass have responded by evolving specialized “high crown” teeth to mill abrasive grass leaves. Large animals can’t climb trees, and in the wetter, taller tropical forests trees can keep their leaves out of harm’s way. The understory is very unproductive and the numbers of tapirs and duikers and the like is low. As water becomes limiting and primary productivity falls, and plants can’t produce enough wood to keep their leaves safe. Browsers and grazers are now abundant and diverse. Plants do invest in thorns and poisons to defend themselves, but animals counter these strategies.

North American and Eurasian steppe environments once had the same diversity of herbivores and herbivore predators at Africa does today. Probably human hunters in the late Pleistocene and early Holocene were responsible for the demise of these spectacular faunas. As far as African farmers are concerned big game is a problem. An African farming friend of mine in Zambia can’t imagine farming with elephants around. Why didn’t African hunters and farmers do the same devastating number on their big game? Hint: think of human diseases.
Some of the competitive effects that lead to diversity are well known. Horses and their relatives are not as efficient digesters of cellulose as ruminants. But they can move further faster. They seek out rarer but higher quality plants than ungulates like cape buffalo. The white rhino, seen above, is also called the square-lipped rhino. It is an indiscriminant mowing machine. The related black rhino has pointed lips and is a discriminating forest browser that picks out high quality leaves quite selectively. The long muzzles of grazing animals have a rich array of odor sensory cells. Humans have very little olfactory epithelium and many of our ancestral genes for olfaction have been shut down. They are not expressed during development. We have a hard time understanding what it most be like to have a huge cascade of scents flowing into our brains.

Even quite efficient herbivores leave lots good stuff behind in their dung. Dung beetle candy! They roll the balls away and bury them with can beetle egg upon them. The biggest dung beetles I’ve seen are about half the size of golf balls.
Africa today has an amazing diversity of grazers and browsers like these ungulate antelopes. The interesting thing is that for most of the last several million years, so have all the more open biomes on all the continents. Lions lived in Europe. North America's big game fauna rivaled Africa's. Australia had giant Kangaroos and a terrestrial crocodile that ran on legs underneath its body not sprawled out sideways like the aquatic crocodile. Many of us think that the eruption of sophisticated human hunters out of Africa 50,000 years ago was responsible for the destruction of big game on the other continents. The African animals coevolved with modern humans and did not have us sprung on them unawares. Hence many more big game species survive in Africa.
Dale Guthrie, a mammalian paleontologist at the University of Alaska has proposed that much of Ice Age Eurasia was a biome completely different from any we know today. Although very cold in winter, it was fairly warm and productive in summer. Cold adapted grazers like giant bison (Guthrie holds part of a skull) and wooly mammoths he thinks lived at something like African densities and diversity in this biome. In the second picture, Guthrie holds a mammoth molar. We do know from pollen recovered from lakes that evolution by competitive exclusion rearranged Ice Age plants into biomes without any parallel in the modern world. We can recognize most of the same species that live today, but they were arrayed on the landscape in an entirely different way. 20,000 years ago, the blink of an eye on the geological scale, the world was a very different place! The Rancho La Brea tar pit fossils show that California was a completely different place only a short time ago as well.
Getting a good burn is easier and drier climate weathers soils more slowly. Uganda (pictured here) also has volcanic soils and somewhat cooler high elevation climates. Rwanda is almost entirely in such a favorable zone and is very densely populated.
A small town in northern Zambia. This could be one of a great many towns in rural Africa, Asia, and Latin America.
This area is in the “matrilineal belt” of Africa (kinship is reckoned via women not men; kids take mom’s family name not dad’s). In tropical forest horticulture, women do the lion’s share of the work. Here, men work about 500 hrs/yr; women 2,000 hrs. Formerly men “worked” as warriors, which may say something about the political chaos in Zaire and other African countries.
The problem in the Kpiri Mposhi area is that population has tripled in the last 40 years. The old style long fallow swidden cultivation is today impractical. People are rapidly cutting into forest to plant fields, but this is unsustainable.
Abandoned fields are readily invaded by forest, but the population is too high to let long fallow swidden work. If it takes 20 years of forest regrowth to accumulate nutrients for a year or two of crops, most of the landscape has to be in forest at any given moment. This worked historically but not with today’s population.
Put men (back) to work to bring water and nutrients to poor soils. On left, Richard Armstrong, ecologist, muddy boots philanthropist. This well is intended to be a source of water for small areas of high value crops in the dry season.
Soil here weathers onto quartzite, very low in clay-forming minerals and having virtually no iron. Hence, unusually for a heavily weathered tropical soil it is almost white. The soil is virtually beach sand. What can be done?
Use wells to irrigate dry season crops. Plan nitrogen fixing species to build up nitrogen in soils more rapidly. Find some way to get more phosphorus into soils. 1,500 hrs/man of unused labor!