breaches of the NVC increasing steadily to more than 200 per year, with only seven prosecutions commenced out of more than 700 alleged breaches from 1998 to April 2002.

There are many implications of the changes to the eucalypt forests across Australia. The clearing of native habitat is the single most threatening process for biodiversity loss and species extinction in Australia. The loss of species in Australia over the past two centuries due to human impact is conservatively estimated at 97 plants, 17 species of mammal, and three birds. However, several hundred vertebrates, several thousand plants, and an untold number of invertebrates are threatened with extinction due to loss of habitat. The extent and rate of deforestation in Queensland are comparable to that in Western Australia and Victoria in the past, which has given rise to significant salinity problems in these states, both in terms of dryland salinity and salinization of drinking and irrigation water. The release of carbon into the atmosphere by clearing operations also contributes significantly (13% in 1996) to Australia's greenhouse-gas emission, and there is a net loss of carbon dioxide equivalent to a ratio of 3 : 1 compared with that captured by vegetation acting as a sink. Although many of these consequences of the loss of eucalypt forests have been known for decades, and have been recognized by governments and addressed in recent policy initiatives, clearing of eucalypt forests continues.

See also: **Ecology**: Plant-Animal Interactions in Forest Ecosystems; Reproductive Ecology of Forest Trees. **Entomology**: Bark Beetles; Defoliators; Foliage Feeders in Temperate and Boreal Forests; Sapsuckers. **Pathology**: Diseases of Forest Trees; Insect Associated Tree Diseases. **Tree Breeding, Practices**: Genetic Improvement of Eucalypts; Mycorrhizae.

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Ficus spp. (and other important Moraceae)

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Introduction

Moraceae is a family of mostly tropical trees containing 37 genera and about 1100 species. The most important genus, both in terms of numbers and benefit to humans, is *Ficus*. The family is characterized as having milky or sometimes watery latex. Leaves are mostly alternate, simple, entire, and pinnately veined. The flowers are unisexual but variable in form, as are the inflorescences. The fruits are commonly drupaceous, embedded in a fleshy receptacle forming a syncarp. The seeds are large without endosperm or small with endosperm. Although a few of the species produce timber, bark, and yield medicinal products, the greatest benefit to humans and animals is from the fruits that many produce. Except for a few of the fruit-producing species, three or four timber species, and a number of *Ficus* and other species planted for ornament and shade, members of the family are little planted or actively managed.

Taxonomy/Genetics

Note: The following treatment is based on taxonomy that predates the publication of the Angiosperm Phylogeny Group's higher-level classification of the angiosperms. Moraceae (used here in the narrow sense) is one of the ewosid families of Rosales.

Moraceae is part of the order Urticales, which is believed to have descended from a single ancestral line. Because of morphological and molecular similarity, it has been suggested that Moraceae, Celtidaceae, Cecropiaceae, and Urticaceae should be merged. The genera of Cecropiaceae appear under Moraceae in older references. Moraceae currently contains 37 genera and about 1100 species (**Table 1**).

Table 1 Details of genera and species within Moraceae

Genus	*No. sp.*	*Range*	*Life forms*
Antiaris	1	Africa, Australasia	t
Antiaropsis	1	New Guinea	t, s
Artocarpus	~50	Asia, Australia	t
Bagassa	1	America	t
Batocarpus	4	America	t
Bleekrodea	3	Melesia, Madagascar	t, s
Bosqueiopsis	1	Africa	t, s
Brosimum	13	America	t
Broussonetia	8	Asia, Madagascar	t, s, c
Castilla	3	America	t
Clarisia	3	America	t, s
Dorstenia	~105	Pan tropical	s, h
Fatoua	3	Pacific, Madagascar	s, h
Ficus	~750	Pan tropical	t, s, c
Helicostylis	7	America	t
Helianthostylis	2	America	t
Hullettia	2	Malaya	t, s
Maclura	11	North America, Pan tropical	t, s, c
Maquira	5	America	t
Mesogyne	1	Africa	t, s
Milicia	2	Africa	t
Morus	10–15	Almost worldwide	t
Naucleopsis	20–25	America	t
Parartocarpus	3	Malesia, Pacific	t
Perebea	9–10	America	t, s
Poulsenia	1–2	America	t
Prainea	4	Malaysia-New Guinea	t, c
Pseudolmedia	8–9	America	t
Scyphosyce	2	Africa	s
Sorocea	~20	America	t, s
Sparattosyce	1	New Caledonia	t
Streblus	~25	Old World	t, s
Treculia	3	Africa, Madagascar	t, s
Trilepisium	1	Africa, Indian Ocean	t
Trophis	9	America, Asia	t, s
Trymatococcus	3	America	t
Utsetela	1	Africa	s

t, trees; s, shrubs; c, climbers; h, herbs.
Information source: Kubitzki K, Rohwer JG, and Bittrich V (1993) *The Families and Genera of Vascular Plants*, vol. 2. Berlin: Springer-Verlag.

The family Moraceae consists of trees with lesser numbers of shrubs, climbers, and herbs, most of which are tropical. All (except for the genus *Fatoua*) secrete milky (sometimes watery) latex from laticifers in parenchymatous tissues in stems and sometimes leaves. Leaves are alternate or rarely subopposite, most frequently simple, entire, and pinnately veined. Stipules are present, although often fused and forming a cap over the bud. Inflorescences take various forms. Flowers are unisexual, often four-merous. Plants may be monoecious or dioecious. Although some species have dry fruits, most have drupaceous or achene fruits embedded in fleshy receptacles. The family is further divided into the tribes Moreae (*Morus*, *Broussonetia*, *Milicia*, *Maclura*, *Trophis*, *Streblus*, *Bleekrodea*, and *Fatoua*), which have 'urticaceous' stamens; tribe Artocarpeae (*Artocarpus*, *Paratocarpus*, *Triculia*, *Prainea*, *Hullettia*, *Antiaropsis*, *Sparattosyce*, *Batocarpus*, *Bagassa*, *Sorocea*, *Clarisia*, and *Poulsenia*), with generally unisexual inflorescences and seeds almost without endosperm; tribe Castilleae (*Perebea*, *Maquira*, *Castilla*, *Helicostylis*, *Pseudolmedia*, *Naucleopsis*, *Antiaris*, and *Mesogyne*), with spontaneous abscission of branches; tribe Dorstenieae (*Utsetela*, *Bosqueiopsis*, *Helianthostylis*, *Trymatococcus*, *Brosimum*, *Trilepisium*, *Scyposyce*, and *Dorstenia*) usually with uncinate hairs; and tribe Ficeae (*Ficus*), which have syconia enclosing the flowers.

The family follows various growth models. In Troll's model the architecture is built by the continual superposition of plagiotropic branches, each division alternating between main-line axis and determinate branch, and is followed by *Milicia excelsa*, in Rauh's model, a monopodial trunk grows rhythmically and develops tiers of branches and the branches are morphologically identical to the trunk, is exemplified by *Artocarpus heterophyllus*, *Ficus aurea*, and *Musanga cercropoides*. The architecture in Cook's model results when a monopodial trunk with spiral or decussate phyllotaxis adds branches phylomorphically. *Castilla* follows this model. Roux's model, followed by *Antiaris welwitschii*, *Milicia regia*, and *Perebea guianensis*, occurs when a monopodial orthotropic trunk meristem grows continuously and has plagiotropic branches that are inserted continuously. *Dorstenia* and *F. theophrastoides* grow by Corner's model in which vegetative growth of a single aerial meristem produces one unbranched axis with lateral inflorescences.

Sex determination in *F. carica*, and probably other members of the subgenus *Ficus,* is different from the XX/XY method used in most other life forms, from mosses through humans. It is believed to be determined by two pairs of alleles located on one pair of homologous chromosomes. Eleven possible combinations of dominant and recessive genes result in plants that produce caprifigs (with separate staminate male flowers and female pistillate flowers), and plants with edible figs (with only female flowers).

Members of the family have $n = 12$, 13, 14, or more (sometimes much more) base numbers of chromosomes. Some notable genera are as follows: *Dorstenia* $2n = 24$–48; *Brosimum* $2n = 26$; *Broussonetia* $2n = 26$, 39; *Ficus* $2n = 26$; *Castilla* $2n = 28$, *Artocarpus* $2n = 28$–81; *Morus* $2n =$ mostly 28 with oddities up to 308.

Ecology

Species within the family Moraceae are tropical and subtropical, with a few exceptions such as *Maclura pomifera*, *Morus alba*, *M. rubra*, and *M. serrata*, which are warm temperate. Although a wide variety of soil, topographic, and precipitation conditions make a suitable habitat, most members of the family grow in humid, fertile conditions at low to middle elevations. They vary from highly intolerant of shade to shade tolerant. Most require full or at least partial sunlight to establish themselves, grow well, flower, and bear fruit. Many Moraceae species occur in primary remnant forests while others grow in secondary forests; a few are pioneer species. One group colonizing an unusual habitat are *Ficus* species that grow in the crowns of other trees, and on rocks, cliff faces, and masonry structures.

Form, structure, and life history are usually inexorably linked with the niche each species occupies in the forest ecosystem. *Dorstenia* are perennial herbs, subshrubs, or shrubs with rhizomes or tuberous subterranean parts. They usually grow in mesic habitat in the understory of primary and secondary forests. All, or nearly all, of the Moraceae rely on animals for seed dispersal. The form and presentation of the fruits and seeds help facilitate the particular disperser. *Morus* and the small-fruited figs, such as *F. citrifolia*, present their fruits near the ends of slender branches, ideal for small birds and fruit bats. Other species, such as *Artocarpus heterophyllus*, *F. racemosa*, and *F. heteropoda*, flower and fruit on their stems and major branches (cauliflory), where the fruits are more accessible to climbing mammals and large birds. Several figs bear fruits on pendulous branches near the ground (*F. capensis*, *F. ribes*, and *F. minahassae*), at least one at the base of the trunk (*F. auriculata*), and at least *F. geocarpa* and *F. cunia* produce fruits on underground branches (geocarpic fruiting) at a distance from the parent tree, where they are uprooted by deer, pigs, and other animals. Most species of the family have small seeds that easily pass through the gut of the dispersing animal. On the other hand, the *Artocarpus* spp. have large seeds that are mostly discarded by the dispersing animal as they consume the fruit pulp.

Most Moraceae species follow the common plant life history of seeds, being deposited by dispersers on soil or superficial organic horizons, germinating, and growing into adult plants. A significant part of the genus *Ficus* develops in a different way. The seeds, which are tiny, are deposited by birds or mammals through defecation in crotches or bark crevices of trees, or in irregularities in large rocks, cliff faces, or masonry structures. They germinate during rainy periods and grow slowly, developing short roots to attach themselves and absorb moisture and nutrients. After they have grown a few leaves they begin growing a vinelike root toward the earth. The process may take a few months to several years. After the long aerial root has reached the soil, it thickens and stiffens to become the plant's stem. Cutting the vine-size roots will not kill the epiphytic plant. Additional roots to the earth may be added and lateral roots begin to surround the host tree or interlace the stone surface. Some species remain vinelike but most become trees, often very large, smothering or sometimes strangling their hosts. Some species actually have modified roots that encircle their host's trunk for the purpose of strangling them. The aerial roots that become stems eventually coalesce to form a massive trunk.

The seedless variety of *Artocarpus altilis* (breadfruit) is totally dependent on humans for long-distance transport. Once established, it suckers from the roots, sometimes as much as 30 m away from the parent tree. The variety thus reproduces and competes successfully in secondary forests that develop after farm abandonment.

The flowers of *Ficus* are pollinated by tiny wasps. The female wasps normally pass from their birth syconia, carrying pollen from male flowers that are located near the apical pore of the syconia to syconia on other trees where they oviposit in short-styled pistillate flowers. Long-styled flowers are pollinated without being parasitized. The male wasps emerge first to inseminate the females before they emerge to repeat the process. The relationship is obligately mutualistic for both the wasps and the figs. Most species of fig have their own endemic wasps. For this reason, exotic *Ficus,* which leave their endemic pollinators behind, rarely produce seed and do not become invasive. An exception to the rule, *F. microcarpa*, has naturalized in several counties in southern Florida. Members of the Moreae tribe with 'urticaceous' stamens that propel pollen into the air are wind-pollinated. Research is needed to determine how pollination is accomplished in other genera.

Silviculture

The cultivation of *Ficus*, *Morus*, and *Artocarpus* species for fruit, *Ficus* species for potted ornamentals, and *Morus alba* for silkworm fodder is well documented and beyond the scope of this silviculture treatment. Methods used for the production and establishment of seedlings for yards, streets, parks, greenbelts, and shelterbelts are similar to those used in restoration and plantation forestry. The large-seeded species and some of the small-seeded species are started from seed in nursery beds or germination trays, usually without pregermination treatments. The seedlings are then grown as bare-root or containerized seedlings by conventional methods. At least the small-seeded *Ficus*, while easy to germinate on wet peat or blotter paper, are difficult and slow to develop into plantable seedlings. They are routinely propagated vegetatively by stem or root cuttings or by air or ground layering. Field planting is done by conventional procedures. While none of the Moraceae are planted in large monocultures for timber, a few, for example *Bagassa guianensis* and *Brosimum alicastrum*, have been tested or are being cultivated in small plantations and may possibly find a place in major plantation silviculture in the future.

An alternative to monoculture plantations is enrichment planting and treatments to promote natural reproduction. *Milicia excelsa* has been produced in nurseries and outplanted. Because it is fire-sensitive, it can only be employed in enrichment planting where complete fire protection is maintained. In harvested areas in Mozambique where large *M. excelsa* were left as seed trees, reproduction occurred in the openings.

Management of *Ficus* species in natural stands is an extremely important issue but little studied and reported. One of the reasons that it is so important is that the wild figs are an important source of food (fruit) for mammals and birds in native forests, and they are dependent on those animals as dispersers of their seeds. If the principal disperser of the seeds of a species is eliminated from an area by hunting or critical habitat destruction, the *Ficus* species must eventually decline. The impact is greater because in most tropical forests, wild figs occur in low densities. The *Ficus* species, which are of low timber value, are also likely to be eliminated during timber stand improvement treatments. While killing large *Ficus* trees is difficult by cutting and girdling, and moderately difficult with herbicides, they can be eliminated with a determined effort.

Enrichment planting of *Ficus* species will probably not be much different from the establishment of ornamental figs or enrichment planting of other forest species: providing an opening with enough light for vigor of newly planted seedlings and protection from weeds and encroaching overhead shade until the planted trees show promise of reaching a codominant position in the canopy. Except for the one previously cited for *M. excelsa*, reports of successful treatments to encourage natural regeneration are not known to the author. A logical treatment for ground-seeding species would be to create openings with scattered patches of exposed soil near fruit-bearing *Ficus* trees. Treatments to encourage epiphytic species may not be possible other than the protection of potential seed trees and their animal dispersers.

Utilization

Probably the most important species in an economic sense is *F. cerica* (common fig), a low, bushy tree or large shrub. It apparently originated in western Asia, was domesticated in ancient times, and spread to the Mediterranean and to most subtropical areas of the world. Today, annual fruit production is an estimated 1 million tonnes. The fruits are eaten raw, dried, preserved, candied, made into jam, used in baking, brewed into wine, and toasted for a coffee substitute. The wood is used to some extent for boxes, small articles, and fuel. There are at least 87 other *Ficus* species whose fruits and vegetative parts are eaten by people in various parts of the world. A number are used in herbal medicine. The tissue used depends on the ailment treated. Maladies most commonly treated are skin lesions, ulcers, and other skin problems, and diarrhea and dysentery. Although used locally for lumber, crafts, and fuel, *Ficus* species do not figure in international commerce for wood. This could change with wider use of medium-density wafer board and similar products. However, great benefit is derived from many *Ficus* species as ornamentals and shade trees. A few should be noted. *F. benjamina* (benjamin fig) is one of the most common large indoor potted plants for homes and institutions. It is also grown outdoors as a street, yard, and park tree in frost-free climates. If allowed to grow freely, it may reach 30 m in height and assumes a banyan-like habit.

Ficus elastica (Indian rubber tree) is used in much the same way indoors and becomes even larger in outdoor settings. Its tapped latex was once an important source of natural rubber, but has been almost completely replaced by latex tapped from *Hevea brasiliensis*. The banyan fig (*F. benghalensis*), although an interesting curiosity, eventually covers so much area by its expanding crowns and aerial roots that become trunks that it cannot be extensively used. *Ficus microcarpa*, *F. lyrata*, and *F. religiosa* are all beautiful and manageable figs planted in parks, estates, and along streets, and loved throughout the tropics. A large number of other *Ficus* species are occasionally planted as ornamental and shade trees. *Ficus pumila*, a climber that clings to surfaces by means of adventitious roots, is used like ivy (*Hedera helix*) to cover masonry walls.

Most of the *Ficus* species are relatively common but rarely abundant in tropical forests. However, many are important sources of food (mainly the fruits) for wildlife. Over 1200 species of vertebrates have been identified that eat the fruits of *Ficus* species. Some of the *Ficus* species in India and nearby countries are used as hosts in the cultivation of *Laccifer lacca* insects, the source of shellac and certain natural dyes. A number of the *Ficus* and several species of other related genera cause contact dermatitis, especially when persons come in contact with the latex.

Other important members of the Moraceae include *Artocarpus altilis*, an important food crop in the humid tropics; it occurs in two forms. Breadfruit produces abundant 1–2-kg starchy fruits eaten like potatoes. This large (to 30 m) tree produces no seeds but reproduces aggressively by root suckers. Breadnut (the seeded form) is grown for its large edible seeds. Although once used by Pacific Islanders for canoes and surf boards, the wood is little used today. A related species is the jackfruit, *A. heterophyllus*. It produces large (up to 20 kg) cauliflorous syncarps with sweet pulp eaten raw or cooked and large seeds that are roasted or boiled. The wood finds minor local uses for furniture and the extraction of a yellow dye. Another important genus is the mulberry (*Morus*) with important representatives white mulberry (*M. alba*), black mulberry (*M. nigra*), and American mulberry (*M. rubra*). All produce delicious fruits of minor importance and are used to some extent as ornamentals. White mulberry is the principal fodder grown for silkworms (*Bombyx mori*). American mulberry wood is used for fence posts, furniture, and caskets. *Morus serrata*, native of the Himalayan area, produces valuable wood used for furniture and carvings. Osage-orange (*Maclura pomifera*), a temperate representative of the family, has been used extensively for fence posts, cattle shade, windbreaks, and conservation plantings in North America. Its neotropical relative, *M. tinctoria*, is a timber tree producing wood used for flooring, and other uses requiring toughness, and is the source of a yellow-brown dye. Two African species, *Milicia excelsa* and *M. regia*, produce valuable timber often substituted for teak.

Some members of the genus *Brosimum* produce valuable wood used locally and traded internationally. The leaves and fruits are important food for domestic and wild animals during times of drought. The seeds are edible when cooked and the sap of some of the species is drunk as a tonic. The bark of *Broussonetia papyrifera*, native or planted through Southeast Asia and the Pacific, is used to make a high-quality bark cloth for clothes, mats, wall hangings, and funerary rites. *Antiaris toxicaria* of Africa through Australia is used in the same way to make cloth, and the sap is used as an arrow poison and to treat several medical conditions. *Castilla elastica* produces a copious latex that was once tapped to make natural rubber but is of low quality and has fallen into disuse. *Bagassa guianensis* and several species of the genera *Clarisia*, *Pseudolmedia*, and *Trophis* are harvested for timber. Finally, many lesser known members of the family are used in herbal medicine.

See also: **Ecology**: Biological Impacts of Deforestation and Fragmentation. **Environment**: Environmental Impacts. **Silviculture**: Natural Stand Regeneration. **Tree Physiology**: Forests, Tree Physiology and Climate. **Tropical Forests**: Monsoon Forests (Southern and Southeast Asia); Tropical Dry Forests; Tropical Montane Forests.

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Mangroves

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Introduction

The term mangrove is used to define both a group of plants and also a community or habitat type in the coastal zone. Mangrove plants are trees or shrubs that normally live in the intertidal zone. Mangrove communities are those in which these plants predominate. Other terms for these communities include coastal woodland, intertidal forest, tidal forest, mangrove forest, mangrove swamp, and mangal. The word mangrove can be traced to the Portuguese word 'mangue' and the Spanish word 'mangle,' both of which are actually used in the description of the habitats, rather than the plants themselves, but still have been joined to the English word 'grove' to give the word mangrove. It has been suggested that the original Portuguese word has been adapted from a similar word used locally by the people of Senegal.

Mangrove Species

Mangrove plants are not a simple taxonomic group, but are largely defined by the ecological niche where they live. The simplest definition describes: 'a shrub or tree which normally grows in the intertidal zone and which has developed special adaptations in order to survive in this environment.' Using such a definition a broad range of species can be identified, coming from a number of different families. Although there is no consensus as to which species are, or are not, true mangroves, a core group of some 30–40 species is agreed by most authors. These 'core' species are the most important, both numerically and structurally, in almost all mangrove communities. **Table 1** provides a more complete list of mangrove species (of tree, shrub, fern, and palm), highlighting the core species.

All of these plants have adapted to a harsh environment, with regular inundation of the soil and highly varied salinities, often approaching hypersaline conditions. Soils may be shallow, but even where they are deep they are usually anaerobic within a few millimeters of the soil surface. Many mangrove species show one or more of a range of physiological, morphological, or life history adaptations in order to cope with these conditions.

Coping with Salt

All mangroves are able to exclude most of the salt in sea water from their xylem. It would appear that most species operate an ultrafiltration process at the endodermis of the roots. *Bruguiera, Lumnitzera, Rhizophora*, and *Sonneratia* species are highly efficient in this initial salt exclusion. Others, including *Aegialitis, Aegiceras*, and *Avicennia*, are less efficient and hence also actively secrete salt from their leaves. This is done metabolically, using special salt glands. Evaporation leaves salt crystals on the leaf surface which are often clearly visible (**Figure 1a**).

Anaerobic Soils

The morphological feature for which mangroves are best known is the development of aerial roots. These have developed in most mangrove species in order to cope with the need for atmospheric oxygen at the absorbing surfaces and the impossibility of obtaining such oxygen in an anaerobic and regularly inundated environment. Various types of roots are illustrated in **Figure 1**.

The stilt root, exemplified by *Rhizophora* (**Figure 1b**) consists of long branching structures that arch out away from the tree and may loop down to the soil and up again. Such stilt roots also occur in *Bruguiera* and *Ceriops* although in older specimens they fuse to the trunk as buttresses. They also occur sporadically in other species, including *Avicennia*.

A number of unrelated groups have developed structures known as pneumatophores which are simple upward extensions from the horizontal root into the air above. These are best developed in *Avicennia* and *Sonneratia* (**Figure 1c**), the former typically with narrow, pencil-like pneumatophores, the latter with secondary thickening so that they can become quite tall and conical.

Root knees are more rounded knobs which, like pneumatophores, extend upwards from the roots. In *Xylocarpus mekongensis* these are the result of localized secondary cambial growth, but in *Bruguiera* (**Figure 1d**) and *Ceriops* they are the result of a primary looping growth. In these species branching may also occur on these root knees.