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I. M. Turner
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Introduction

The tropical rain forest

Tropical rain forest is one of the major vegetation types of the globe (Richards 1996; Whitmore 1998). It is an essentially equatorial and strongly hygrophilous biome as its name suggests and is found on all the continents that the tropics touch. Tropical rain forest is defined physiognomically with typical features being a closed, evergreen canopy of 25 m or more in height dominated by mesophyll-sized leaves, with an abundance of thick-stemmed woody climbers and both herbaceous and woody epiphytes. Altitude has a marked effect on forest physiognomy above about 1500 m, and montane facies have to be distinguished. The so-called tropical diurnal climate has a temperature regime in which the major periodicity is the daily march from night-time lows to afternoon highs. The fluctuation through the year in mean monthly temperatures is usually of smaller magnitude than the typical daily temperature range. Temperatures usually average at around 27 °C at lowland weather stations in tropical rain-forest regions, and minima rarely, if ever, enter the chilling range below 10 °C. Rainfall is generally at least 2000 mm per annum, and a month with less than 100 mm is considered dry. Rain forests can withstand dry periods though prolonged, or particularly severe, droughts on a regular basis usually lead to drought-deciduous forest replacing the true rain forest. Many rain forests do persist despite annual dry seasons, though only if the trees have access to ground water in areas experiencing long periods without rain.

Edaphic factors including soil physico-chemical properties and drainage regime influence the floristic, physiognomic and structural characteristics of the tropical rain-forest community strongly. Forest formations can be recognised for major soil groups and inundation classes across the geographic range of tropical rain forest. For instance, heath forest that occurs on acidic, highly leached sands is readily distinguishable whether one is in Asia, Africa or America.

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Tropical trees

I include in the category of tree, any free-standing plant that attains a diameter at breast height (dbh) of at least 1 cm, as this has become the lower limit of inclusion for a global network of tropical forest plots (Condit 1995). As well as the arborescent dicotyledonous species the term tropical tree brings to mind, I also include gymnosperms, woody monocotyledons, tree-ferns and bananas and their kin (Table 1.1). The latter are herbaceous, but their large size means that they can be considered trees, at least in terms of the structure of the forest. All the other groups have many fewer species than the dicotyledons, particularly the non-angiosperm classes. However, palms are an important component of most tropical forests, and dominate some forest types. As with most ecological classifications, there are fuzzy edges to any definition of tree. Many large woody climbers have juvenile stages indistinguishable from tree saplings. Woody hemi-epiphytes, mostly figs (*Ficus* spp.), but also species of *Clusia*, some Araliaceae and a few others (Putz & Holbrook 1986), begin life as epiphytes, but grow roots down to the ground and become terrestrial. Their host tree may eventually die and the hemi-epiphyte is left mechanically independent: it has become a true tree.

Figure 1.1 gives a phylogeny of the seed plants to ordinal level with the pteridophytes indicated as a sister group. It is important to note that evolutionary relationships of some lines remain unresolved; for instance, it is not clear which of the gymnosperm clades gave rise to, or at least is closest to, the angiosperms. In addition, quite a number of angiosperm families are not yet placed within the orders, although these are mostly small. Many different evolutionary lines are represented among extant tropical trees (Fig. 1.1), but perhaps there is a concentration of species among the rosids and the more basal offshoots, orders Laurales and Magnoliales.

Species

The species is most often the unit of comparative ecology, although intraspecific comparisons of different populations can also be rewarding. If we are comparing species we have to consider what we mean by species. The definition has been a thorny problem in biology for many years, with considerable debate over the relative merits of biological and evolutionary definitions of species. From a practical point of view, it has to be realised that ecologists researching in tropical rain forests are nearly always working with a taxonomic species definition. They are forced to employ the species concepts of the taxonomist who wrote the flora or monograph that they are using. In most cases these are based on circumscription of morphological

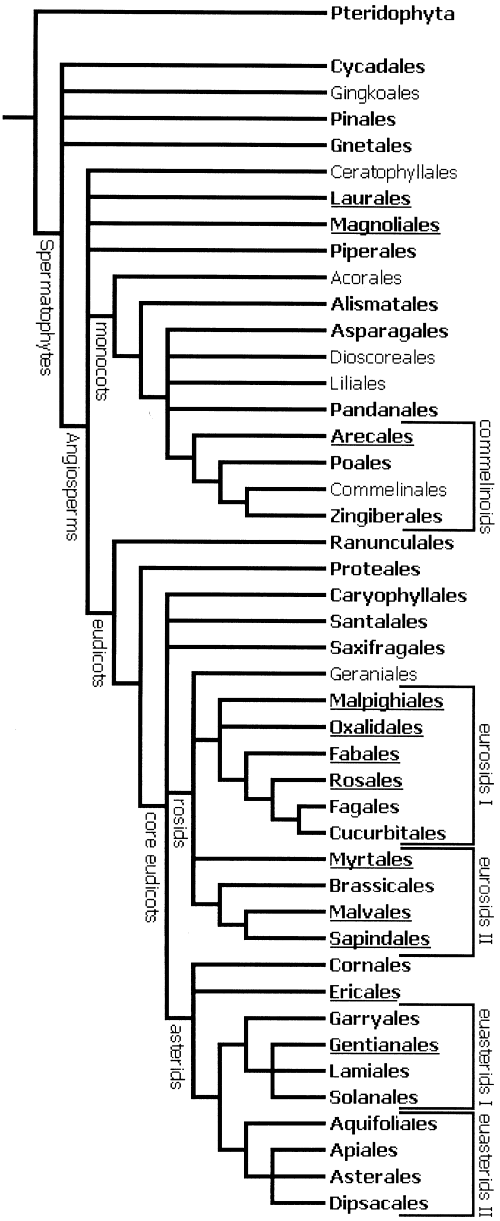

Figure 1.1 A phylogeny of the vascular plants to ordinal level (in part after Nyffeler (1999) based on Angiosperm Phylogeny Group (1998)). Names of orders given in bold indicate the presence of extant tropical tree species. Names underlined indicate that a majority of extant member species are tropical trees.

Table 1.1. *Taxonomic summary of extant tropical forest trees*

Inclusion of a genus implies at least one species considered to be a tree in tropical rain forest. Monocot families are presented in order of roughly decreasing degree of arborescence. Classification follows Brummitt (1992).

Pteridophytes	Gymnosperms		Monocots		Dicots (important families)	
FILICOPSIDA	PINOPSIDA	GNETOPSIDA	Woody:	Herbaceous:	Anacardiaceae	Malvaceae
					Annonaceae	Melastomataceae
Cyatheaceae	Araucariaceae	Gnetaceae	Palmae	Musaceae	Apocynaceae	Meliaceae
*Cyathea**	*Agathis*	*Gnetum*	(Arecaceae)	*Ensete*	Aquifoliaceae	Monimiaceae
	Araucaria	(*G. gnemon* and *G.*	many genera	*Musa*	Araliaceae	Moraceae
Dicksoniaceae		*costatum* seem to			Bignoniaceae	Myristicaceae
Cibotium	Cupressaceae	be the only species	Pandanaceae	Strelitziaceae	Bombacaceae	Myrsinaceae
Culcita	*Papuacedrus* (mtn)	that are trees, the	*Pandanus*	*Phenakospermum*	Boraginaceae	Myrtaceae
Dicksonia	*Widdringtonia*	rest are woody	*Sararanga*	*Ravenala*	Burseraceae	Ochnaceae
	(mtn)	climbers)			Capparidaceae	Olacaceae
Osmundaceae			Gramineae	Heliconiaceae	Celastraceae	Oleaceae
Leptopteris	Phyllocladaceae		(Poaceae)	*Heliconia*	Chrysobalanaceae	Piperaceae
	Phyllocladus (mtn)	CYCADOPSIDA	bamboos		Combretaceae	Pittosporaceae
also, but less convincingly				Zingiberaceae	Cunoniaceae	Rhamnaceae
dendroid:	Pinaceae	Cycadaceae	Dracaenaceae	*Alpinia*	Dichapetalaceae	Rhizophoraceae
	Pinus (dry)	*Cycas*	*Cordyline*		Dilleniaceae	Rosaceae
Blechnaceae			*Dracaena*	Araceae	Dipterocarpaceae	Rubiaceae
Blechnum	Podocarpaceae	Zamiaceae		*Alocasia*	Ebenaceae	Rutaceae
Brainea	*Acmopyle* (mtn)	*Ceratozamia*	Velloziaceae	*Montrichardia*	Elaeocarpaceae	Sapindaceae
	Afrocarpus	*Chigua*	*Vellozia*		Ericaceae	Sapotaceae
	Dacrycarpus	*Dioon*	*Xerophyta*	N.B. not all	Erythroxylaceae	Simaroubaceae
*in the broad sense, the	*Dacrydium*	*Lepidozamia*		members of these	Euphorbiaceae	Sterculiaceae
genus is split into two or	*Falcatifolium*	*Zamia*	Cyperaceae	genera attain tree	Fagaceae	Styracaceae
more by some pteridologists	*Nageia*		*Microdracoides*	size	Flacourtiaceae	Theaceae
	Podocarpus				Guttiferae	Thymelaeaceae
	Prumnopitys (mtn)		Xanthorrhoeaceae		(Clusiaceae)	Tiliaceae
	Sundacarpus		*Xanthorrhoea*		Icacinaceae	Ulmaceae

Taxaceae	Lauraceae	Urticaceae
Taxus	Lecythidaceae	Verbenaceae
	Leguminosae (Fabaceae)	Vochysiaceae
	Loganiaceae	
	Magnoliaceae	

mtn = genera only represented in montane regions

dry = genera only represented in seasonally dry regions variation to the degree that the taxonomist considered typical of a species. Taxonomists can vary in their opinion of where to draw these lines (see, for example, Wong (1996) for discussion of *Fagraea* in Borneo), leaving ecologists in the difficult position of choosing whom to follow.

Additional problems are faced with the identification of plants in the field. The high diversity makes identification difficult. It may be annoying and confusing to find that you have been using the wrong name for a species. For example, many papers were published concerning *Virola surinamensis* on Barro Colorado Island, Panama, but this was a mis-identification, and is correctly *Virola nobilis*. What is worse is when your species contains individuals of other species. This happened for a study of buttressed trees in Malaysia (Crook *et al.* 1997) where one pinnate-leaved species turned out to be several.

Tropical rain-forest diversity

Tropical rain forests are the most diverse of terrestrial ecosystems. Many lowland forests contain more than 100 species among the trees of 10 cm dbh or over on 1 ha (Fig. 1.2), and in some more than 200 species may

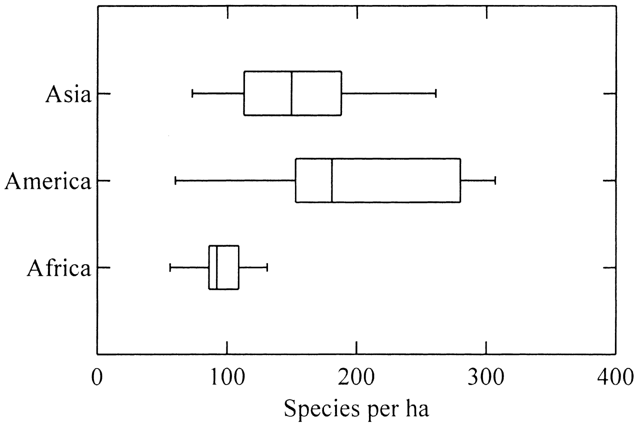

Figure 1.2 Box-and-whisker plot of species richness for trees greater than 10 cm dbh of rain-forest sites for the major tropical regions (Asia–Pacific, America and Africa). The line inside the box represents the mean value of the average number of species per hectare. The box extends for the range of 50% of the values above and below the mean. The whisker covers the complete range of the recorded values. Data from compilations by Phillips *et al.* (1994) and Turner (2001).

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be found. Species richness rises very rapidly with area or number of individuals sampled in a forest (Fig. 1.3) and plots of 5 ha or more may be required to sample local diversity adequately. Topographic and edaphic variations will often lead to landscapes of patches of different forest communities that further add to the high diversity of a lowland tropical region. The high diversity of species within a particular forest frequently involves the co-existence of species in the same genus. For instance, of the 814 species recorded in 50 ha of forest at Pasoh, Malaysia, by Manokaran *et al.* (1992), 82% of the species had a congeneric present in the plot, with 70% having a congeneric in the same broad height category.

A commonly asked question, for which we are still seeking the answer, is: why are the tropical rain forests so diverse? Various responses have been put forward. One solution is to turn the question around. Why are extra-tropical regions so poor in species? There is clearly a general inverse relation between environmental harshness and diversity. The tropics have many species because it is easier to survive there than in less favourable environments.

However, this does not explain how all the tree species in the rain forest manage to co-exist. Classic ecological theory states that species can only co-exist if the levels of interspecific competition remain low enough to prevent competitive exclusion of some members of the community. One way in which this can be brought about is for all the species to occupy separate niches. Where do all the niches come from for the co-existence of hundreds of tree species on small areas of lowland tropical rain forest? Various mechanisms have been put forward by which tree species could be partitioning the environment and would thus exist in an equilibrium community. The light gradient from the shaded forest floor to the sunny canopy-top may allow specialisation in different heights at maturity (Kohyama 1993). The horizontal variation in light availability due to irregularity in canopy structure (presence of gaps, etc.) and in soil physical and chemical properties could also result in the subtle environmental variations needed for providing the many niches required.

However, the lowland tropical rain forest generally contains such a large number of species of very similar ecology that it is difficult to believe that strict niche partitioning is occurring. Another possibility is that factors other than niche partitioning may prevent competitive exclusion of species from the community. Compensatory mortality that places a ceiling on the local abundance of a species has been invoked as a means of species co-existence (Janzen 1970; Connell 1971). Species-specific causes of mortality, such as specialist seed and seedling predators and pathogenic diseases, may control the distribution of adult population density within the forest. Recent studies from Barro Colorado Island in Panama showed evidence for significant intraspecific density-dependent effects on recruitment for 67 out of 84 of the commonest tree species in the community (Wills *et al*. 1997). Givnish (1999) has argued that the fairly strong correlation between tropical rain-forest tree species diversity and total rainfall at a site is an indication of the increasing importance of compensatory mortality as dry spells become more infrequent in the local climate. The increasing rarity of periods of low rainfall allows invertebrates and plant-pathogenic organisms to maintain high population numbers and to provide the mechanism of compensatory mortality continuously.

Alternatively, the species in the forest may not have come to competitive equilibrium. Chance is seen as the major influence on community structure in this non-equilibrium view. There is growing evidence that recruitment limitation is common among species in the rain forest (Hubbell *et al*. 1999). That is, most species do not establish recruits successfully in all the sites in the forest that they are capable of occupying, either through failure in dispersal or through high mortality of juvenile stages. In a very species-rich community most species are so infrequent that no given pair of species will meet often enough for one to dislodge the other from the community through competi-

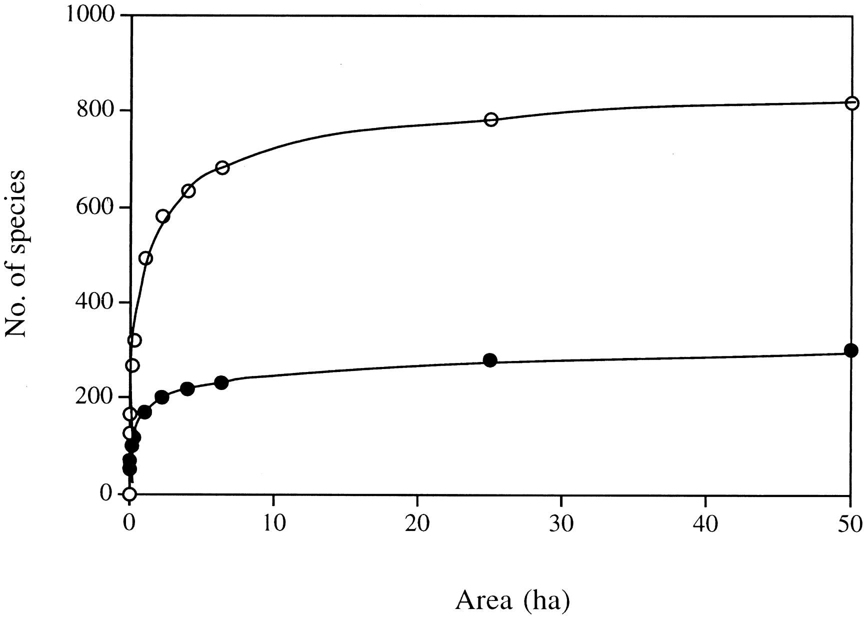

Figure 1.3 Species–area curves for 50 ha plots at Barro Colorado Island, Panama (closed circles), and Pasoh Forest Reserve, Malaysia (open circles). Trees ≥ 1 cm dbh. Data from Condit *et al*. (1996b).

tion. Recruitment limitation further increases the likelihood of an individual from a competitively inferior species reaching maturity by default.

In reality it seems likely that, to some extent, both equilibrium and non-equilibrium forces operate in the community simultaneously. The bulk of the diversity comes in the form of rare species that are probably not occupying separate niches. However, there seems to be more predictability in forest community structure than might be expected from a strongly stochastically driven system. Long-term studies of primary forest community composition show only minor variations, not random fluctuations, in species make-up and relative abundance over time (see, for example, Manokaran & Swaine 1994). Succession appears to follow relatively predictable trajectories in similar sites (Terborgh *et al.* 1996). We remain uncertain of what controls or constrains these processes. Hubbell (1997) has proposed that the main influences of chance are on the composition of the regional species pool and the relative abundance of species in the pool. These factors, together with environmental tolerances, are then responsible for community composition at any place in the region. Hubbell has produced some remarkably accurate simulations of community composition (dominance–diversity curves) from his model. However, the mechanics of the interface between regional and local community composition have yet to be explained in detail.

Adaptation

The fit between organisms and their environment is one of the main fields of study of ecology. The working hypothesis is that natural selection favours the inheritance of features that suit an individual to its typical environment and way of life. These features are called adaptations. Comparative ecologists use multi-species studies to identify strong trends for the possession of a certain character, or suite of characters, among species in a particular environment. This provides circumstantial evidence that an adaptation may be involved. Proving that a feature is an adaptation is very difficult. It requires a demonstration that individuals with the feature are fitter than individuals that differ solely in not having the putative adaptation. Comparative ecologists tend to rely on the weight of circumstantial evidence for convergent evolution rather than attempt the full burden of proof. This has led to criticism of the so-called adaptationist programme: what Gould & Lewontin (1979) termed the Panglossian paradigm. They argued that the assumption of adaptation is too readily taken up, when in fact adaptation is only one of several possible reasons for the presence of a character. Extant species are not perfect; many features may be selectively neutral or arise through complex interactions among different genes and the environment.

For much of the content of the remaining chapters in this book, it is difficult to refute the charge of promoting the Panglossian paradigm because insufficient studies have been conducted to confirm adaptationist speculation. It would be very repetitive to include warnings concerning the assumption of adaptation at each mention of a supposedly advantageous feature, so the reader is reminded to maintain a degree of scepticism throughout. I strongly believe that the correlations evident from comparative studies are invaluable as a base from which to formulate hypotheses and tests of the evolutionary biology and ecology of tropical trees.

The importance of phylogeny

There can be no doubt that a species is strongly influenced in many of its characters by its antecedents. We must therefore question whether the patterns ecologists see when they compare species, such as trees in the tropical rain forest, are not mostly reflections of phylogenetic relationships rather than recent ecological adaptations.

Can we estimate the degree of ‘phylogenetic constraint’ on the ecology of species? Or can we control for the influence of phylogeny when we design ecological experiments or observations? The answer to the first question is a qualified ‘yes’. Techniques exist that attempt to partition interspecific variation into ‘ecological’ and ‘phylogenetic’ components, or at least filter out the phylogenetic effects as error in the statistical model. Two main approaches are available (Gittleman & Luh 1992). Autoregression techniques can be used that partition variance to different phylogenetic distances within the data set, generally by using either nested analysis of variance (ANOVA) or spatial statistics (Moran’s *I*). The alternative is phylogenetically independent contrasts (PIC), which overcome the statistical dependence of species by restricting comparisons to adjacent branch pairs on the phylogenetic tree. The major problem with applying these techniques is that they require a phylogeny from which to work, although statistical ways round this have been suggested (Martins 1996). Only recently have detailed phylogenetic analyses of the higher plants become available, and these generally stop at the family level, although more are becoming available within orders and families. These phylogenies are mostly based on DNA sequences and rarely include more than one gene, often with no more than the barest minimum of sampling per taxon. Phylogenies drawn from data of this sort suffer from many interpretive problems (outlined by Donoghue & Ackerly 1996) and at present cannot be taken as definitive. It is not surprising therefore that some ecologists have argued that phylogenetic knowledge is still too fragmentary to consider any meaningful attempt at partitioning ‘ecological’ and ‘phylogenetic’ factors in