CORE
Metadata, citation and similar papers at core.ac.uk
Provided by Open Research Exeter

Tropical savannas and dry forests

R. Toby Pennington[1,2*]

Caroline E.R. Lehmann[3]

Lucy M. Rowland[1]

[1]Geography, University of Exeter, Rennes Drive, Exeter, EX4 4RJ, UK

[2]Royal Botanic Garden Edinburgh, 20a Inverleith Row, Edinburgh EH3 5LR, UK

[3]GeoSciences, Crew Building, The King's Buildings, Alexander Crum Brown Road, Edinburgh EH9 3FF, UK

Correspondence: t.pennington@exeter.ac.uk

In the tropics, research, conservation and public attention focus on rain forests, but this neglects that half the global tropics have a seasonally dry climate and are home to dry forests and savannas, which are the focus of this primer. The attention given to rain forests is understandable. Their high species diversity, sheer stature and luxuriance thrill biologists today as much as they did the first explorers in the Age of Discovery. Although dry forest and savanna may make less of a first impression, they support a fascinating diversity of plant strategies to cope with stress and disturbance including fire, drought and herbivory. Savannas played a fundamental role in human evolution and across Africa and India support iconic megafauna.

Tropical dry biomes are rapidly changing due to land transformation, the effects of rising atmospheric CO2 on tree growth, and climate change more generally. While dry forests are already highly fragmented and diminished, the savanna biome contains the majority of the world’s remaining arable land. With tropical environments rapidly changing, there is an urgent need to improve our understanding of savannas and dry forests and to ensure the conservation of their unique diversity that may represent vital resources underpinning sustainable futures in tropical countries.

Tropical biomes

Biomes are major vegetation formations with distinct physionogmies and ecological processes that can be characterised at a global scale. Historically, climate has been used to delimit biomes. However, in an age of earth observation, biogeographic analyses have demonstrated that in the seasonally dry tropics, multiple biomes, which vary widely in their physionogmy, species composition and ecology, occur under identical climates.

Tropical rain forests have high (>25 m), closed, evergreen canopies and generally occur where annual precipitation is greater than c. 2000 mm but with little to no dry season. Disturbance by fire seldom occurs, generally only following anomalous intense drought events. Where annual rainfall is less but distinctly seasonal, with almost no rainfall from four and up to nine months, large areas of savanna and smaller areas of dry forest dominate the global tropics. Of course there are formations that are transitional between tropical rain forests and tropical dry biomes, which are often semi-deciduous forests, and the location of biome transitions is not solely controlled by rainfall and its seasonality, but also by a diversity of environmental controls such as soil properties, temperature, drought, fire and mammalian herbivory. Some of these controls are geographic, such as soil properties across continents reflecting different tectonic geological histories, and it is this biogeographic and environmental complexity that makes predictions of the limits of savanna and dry forest difficult. However, to understand climate change impacts on the distribution and structure of tropical biomes it will be critical to resolve this complexity.

Savannas have open canopies, with tree cover from 0 – 80% and a generally contiguous ground layer of grasses (i.e., greater than 50%). Understanding of the co-dominance of the distinct life forms of trees and grasses has been subject of ecological research for a century, and it is now generally accepted that vegetation structure of savannas is maintained via interactions between climate, disturbance and plant life history traits. Open tree canopies permit growth of a grassy ground layer, which provides fuel for fire or forage for mammalian grazers such as rhino, zebra, buffalo and antelope. The processes of fire and herbivory retard the growth and recruitment of trees, keeping savannas open. The savanna biome is vast and covers around 20% of the global land surface spanning different ranges of rainfall across different continents from 300 – 1500 mm in Africa, 350 – 2000 mm in Australia and 800 – 2500 mm in South America.

Tropical dry forests occur under similar seasonal climates to savannas. They have closed canopies and are generally deciduous in the dry season; in some savannas, especially in Latin America, trees are evergreen. In Latin America, dry forests occur on richer, less acid soils than savannas, and this fertility may be the factor promoting tree growth, enabling closed canopies that supress grasses and fire. How such edaphic controls operate globally is unclear and there is a surprising lack of comparative soil-vegetation studies across continents, and this should be a research priority. Tropical dry forests are home to some charismatic plants that show extraordinary adaptations to store water, such as the swollen trunks of the baobab trees of Africa and Madagascar, and their lesser-known relatives *Ceiba* and *Cavanillesia* in the same family (Malvaceae) in the New World. In drier climates, tropical dry forests are of lower stature and succulent plants form a more conspicuous element of the vegetation. In the New World, these succulents are cacti, and in Africa and Arabia their ecological analogues in other families, especially Euphorbiaceae (the spurges). As rainfall declines further, dry forests and savannas merge into deserts.

Defining the limits of rain forests globally has been relatively uncontroversial compared to doing so for dry forests and savannas. Confusingly, some tree-dominated vegetation in seasonally dry regions that have traditionally been termed “forests”, such as the dry dipterocarp “forests” of continental SE Asia and the African Miombo “woodlands”, are better regarded as savannas than dry forests. They have an open structure with a grassy ground layer and regularly burn. In our view, much of tropical continental Asia, including most of India, had an original vegetation of savanna, though this is now hard to discern because of extensive historical landscape modification.

The history of tropical biomes

The fossil record shows that tropical rain forests originated in their modern form – dominated by large trees with buttressed trunks, leaves with characteristic "drip tips" and composed of tree families such as palms and legumes – shortly after the demise of the dinosaurs at the end of the Cretaceous period. The following geological epochs were warm and wet, and it was not until global climates started to aridify in the mid-Eocene that the first fossil evidence appears for subtropical forests adapted to aridity, such as the Green River flora of Utah (45-48 million years ago [Ma]). An additional and independent source of information about the origin of biomes comes from evolutionary (phylogenetic) trees constructed from DNA sequences and calibrated with a dimension of time using molecular clock techniques. These suggest that some plant groups that now dominate modern dry forests, for example the genus *Bursera* (frankincense family) in Mexico, started to diversify in the Miocene. Such phylogenetic studies therefore corroborate late Miocene evidence for the presence of dry forest in Ecuador from beautifully preserved fossils of several tree genera that still dominate Andean tropical dry forests.

Unfortunately, the plant fossil record is poor, and in dry areas this problem is exacerbated because of a lower likelihood of structures becoming encased in sedimentary rock. However, the fossil record for savannas is good because it can be inferred from charcoal, phytoliths and the isotope content of herbivore teeth that have been preserved in great numbers because of the durability of dental enamel. These records documents a global rise of tropical savannas that is recent, starting c. 10 Ma, though estimates of the ages of thorny plant lineages found in drier African savannas based upon DNA sequence divergences suggest that these may have arisen 5-10 million years earlier . It seems that fire, the key ecological driver for tropical savannas, must have been too rare until the late Miocene to cause forest formations to open. The rapid expansion of savanna in the Pliocene, which occurred with remarkable co-ordination across continents, required a remarkable conjunction of climate, fire and C4 grass abundance, and how this occurred is poorly understood.

Examination of the similarity of composition of the woody floras of savannas, dry forests and rain forests across the global tropics shows groupings according to continent rather than by biome – for example rain forests, dry forests and savannas from the New World cluster in one group. This suggests independent origins of the savanna and dry forest floras in the Americas, Africa and Asia. For savannas at least, this is supported by evidence from evolutionary trees based upon DNA sequences, which show different evolutionary origins of lineages of woody plants found in the Americas and Africa.

The biodiversity of tropical dry biomes

The latitudinal gradient of species diversity is a pervasive theme in the literature of 'macroecology', the discipline which seeks to document and explain global patterns of species diversity. The premise of the latitudinal gradient is that species diversity is always highest near the equator and that it declines towards the poles. This pattern of high equatorial diversity is broadly true, but for the plants dominating some biomes it requires greater scrutiny. For example, tropical dry forests have their highest woody plant species diversity in Mexico, far from the Equator, so there is apparently no latitudinal gradient for dry forest plants. The pattern may reflect the large area of dry forest in Mexico over geological timescales, which has allowed accumulation of species. Interestingly, this is one of the explanations put forward for the latitudinal diversity gradient more broadly – for example that the area of tropical rain forests has been more extensive historically in equatorial regions.

There is also a general assumption that rain forest is the biome richest in species in the tropics. However, a recent evaluation of plant species diversity in dry forests across Latin America and the Caribbean suggests that they have more than 7500 woody species, almost certainly an underestimate because it is based on only 1600 inventories covering 125,000 square km across this vast region (for example, the dry forests of NE Brazil cover 750,000km^2 alone; see map). This suggests that in their entirety the dry forests of the New World may contain as many or possibly more species than the Amazon rain forest, where the most recent estimate of tree species numbers is c. 6200. Similarly, considering all plant growth forms, the savannas of Central Brazil contain 11.384species, 35 more than the Brazilian Amazon rain forest. Therefore, regarding agricultural expansion in dry forest and savanna areas in Latin America as unproblematic for biodiversity conservation because they are outside of the Amazon (e.g., Economist magazine: http://www.economist.com/node/16886442) is dangerously wide of the mark, especially given they have already suffered far greater deforestation than Amazonia.

The difference in the latitudinal gradient between rain forests and dry forests illustrates that the ecological differences defining biomes may underlie deeper distinctions in their evolutionary histories. For example, plant species may be on average younger in tropical rain forests than in tropical dry forests, despite the great geological age of rain forest as a biome. Phylogenies of dry forest plants show that regional communities are composed of related species, whereas local and regional communities of rain forest species are not related. Patterns in rain forests may reflect the vulnerability of individual plants to mortality caused by drought and landscape changes, opening space in the system for immigrant seeds to establish, which perhaps promotes speciation by geographic isolation of small, peripheral populations (peripatric speciation). In contrast, plant species in dry forests are adapted to survive even extreme drought events. This leads to a conception of major biomes as different “evolutionary theatres” and underlines the importance of key ecological drivers – such as drought and fire – in their definition.

Tropical dry biomes in times of change: research priorities

There is a general perception that the most urgent conservation issues in the tropics concern rain forests but their disproportionate scientific, policy and public profile has distracted attention from the vulnerability of tropical dry forests and savannas. The high population density in tropical drylands has led to widespread ecosystem impact and destruction. For example, in Latin America, because of their fertile soils, less than 10% of tropical dry forests remain intact. This stands in stark contrast with the Amazonian rain forest, which remains 80% intact. In many parts of the seasonally dry tropics, including Latin America, Africa and India, ecosystem modification for agricultural subsistence is historical, pre-dating European colonisation. However, where irrigation is possible, high levels of insolation and low pest pressure make tropical drylands perfect for rapidly expanding industrial agriculture. Intensive farming of cattle, sugar cane and soy has led to the destruction of 70% of the world's most species-rich tropical savanna in Brazil in just 40 years. The high rainfall savannas of sub-Saharan Africa are slated as the next frontier for agri-business expansion to meet increasing regional and global food and energy demands.

Conservation and restoration

Despite their widespread destruction, tropical dry forests and savannas are under-represented in protected areas. In order to conserve what remains, locating centres of species diversity and pinpointing areas which house the most unique (endemic) species is fundamental. Strong recent steps have been made in this area, for example a synthesis of plant species inventories in Latin American tropical dry forests, but better coverage there of savannas and especially the dry chaco woodlands is required because these are experiencing some of the most rapid deforestation rates on the continent. In addition, to understand how floristic composition varies globally and what controls it, new datasets are required that record the abundance of species in inventory plots where the characteristics of soils are analysed. Such data are essential for planning climate-smart regeneration strategies that take into account species preferences for climate and soil.

Understanding ecosystem function

Tropical dry biomes experience complex interacting environmental limitations on plant growth and survival caused by drought, soil nutrients and fire. The survival of individual plants is determined by functional traits such as drought deciduousness, water transport, tolerance of disturbance and photosynthesis. However, functional trait diversity is poorly studied in tropical dry biomes and consequently the value of these systems in carbon storage, carbon production, water cycling and biogeochemical cycling is not understood, nor is their resistance and resilience to climate change. With predicted substantial future shifts in rainfall patterns and elevated temperatures, and the prospect of more frequent and severe climate extremes, species adapted to survive in the seasonally dry tropics will be increasingly relevant in areas currently home to wetter vegetation but that are predicted to be subject to reduced or more erratic rainfall. However, in the seasonally dry tropics, climate predictions are geographically varied but uniformly suggest higher temperatures and increasing drought. There are suggestions that drylands may control the response of the global land carbon cycle to recent climate variability, and thus the efficiency of the land to mitigate climate change, so understanding how they will react to future climate change is critical.

Summary

Up to a third of the global population lives in seasonally dry tropical areas and this includes the world's poorest people, who are reliant on the resources savanna an dry forest ecosystems provide, including food, water, medicines, building materials and fuel. Against a background of widespread ecosystem modification and a changing climate, better understanding of ecosystem function and improving restoration and conservation in tropical drylands is urgent to ensure a sustainable future for their rich biodiversity and especially their vulnerable human populations.

Further reading

Bond, W.J. (2008) What Limits Trees in C4 Grasslands and Savannas? Ann. Rev. Ecol. Evol. Syst. *39*, 641-659

Dexter, K.G., Smart, B., Baldauf, C., Baker, T.R., [50 additional co-authors], and Pennington, R.T. (2015). Vegetation in seasonally dry regions of the tropics: floristics and biogeography. Int. Forestry Rev. *17*, 10-32

DRYFLOR (2016) Plant diversity patterns and their conservation implications in neotropical dry forests. Science *353*, 1383-1387.

Edwards, E.J., Osborne, C.P., Strömberg, C.A.E., and Smith, S.A., C4 Grasses Consortium (2010) The origins of C4 grasslands: integrating evolutionary and ecosystem science. Science *328*, 587-591.

Lehmann, C.E.R., Anderson, T.M., Sankaran, M., Higgins, S.I., Archibald, S., Hoffmann, W.A., Hanan, N.P., Williams, R.J., Fensham, R.J., Felfili, J., Hutley L.B., Ratnam J., San Jose J., Montes R., Franklin D., Russell-Smith J., Ryan C.M., Durigan G., Hiernaux P., Haidar R., Bowman D.M.J.S., and Bond W.J. (2014) Savanna vegetation-fire-climate relationships differ among continents. Science *343*, 548-552

Lehmann, C.E.R., and Parr, C.L. (eds) (2016) Tropical grassy biomes: linking ecology, human use and conservation. Phil. Trans. R. Soc. B *373,* issue 1744

Parr, C.L., Lehmann, C.E., Bond, W.J., Hoffmann, W.A., and Andersen, A.N. (2014) Tropical grassy biomes: misunderstood, neglected, and under threat. Trends Ecol. Evol. *29*:205-13.

Pellegrini, A.F.A. (2016), Nutrient limitation in tropical savannas across multiple scales and mechanisms. Ecology *97,* 13-324

Pennington, R.T. , and Hughes, C.E. (2014). The remarkable congruence of New and Old Wold savannah origins. New Phytol. *204*: 4–6

Pennington, R.T., Lewis, G., and Ratter, J.A. (eds.) (2006). Neotropical savannas and dry forests: plant diversity, biogeography and conservation. CRC Press, Florida. 484 pp.

Figure Legends

Fig. 1. Schematic global map of tropical savannas and dry forests, based upon Olson et al. (2001; BioScience 51, 933–938), but with their tropical ecoregions reclassified into rain forest, savanna and dry forest biomes. The savanna classification follows Murphy et al. (2016; Phil. Trans. R. Soc. B 371, 20150319). Note that the scale precludes showing small geographic areas of dry forest and savanna biomes, for example dry forest enclaves scattered through central Brazil and isolated savanna areas within the Amazon rain forest.

Fig. 2. Savannas and dry forests. a) Wooded savanna, Brazil. b) Open savanna, Brazil. c) Savanna, Madagascar (Savanna); note in a,b,c the ground layer of grasses. d) Dry forest, Brazil; note the swollen trunks of the trees in the genus *Cavanillesia*. e) Dry forest, Brazil; in d and e, note the lack of grasses in the ground layer, contrasting with the savannas (a,b,c) nd the presence of succulent cacti. f) Savanna, India; in Asia, many savannas are termed “dry forest” but the presence of a grassy ground layer, as seen here, which provides fuel for dry season fires is more consistent with a classification as a savanna.