Chapter 4

Seasonally Dry Tropical Forest Soil Diversity and Functioning

DIANA H. WALL, GRIZELLE GONZÁLEZ,
AND BREANA L. SIMMONS

Knowledge of biodiversity is key to sustainable management. For tropical dry forests, information on soil animal diversity is sparse compared with tropical wet forests, and considerably less than for grasslands and deserts. Nevertheless, given the rapid transformation of dry tropical forests, primarily due to land use change (Janzen 1988a), it is important to examine the uniqueness of its faunal diversity and functioning as well as its vulnerability to increasing rates of global changes (Sala et al. 2000).

Why are there so few studies on soil faunal diversity and ecosystem functioning in dry tropical forests compared with other ecosystems? Reasons include (1) an emphasis on wet tropical forests due to the high biodiversity and rapid deforestation (Lawton et al. 1996; Lawton et al. 1998; Ineson et al. 2004; Bignell et al. 2005); (2) the small area of dry forests relative to wet tropical forests (Murphy and Lugo 1986a); and (3) poor recognition of ecosystem services that soil biota provide to humans (see table 4-1; van der Putten et al. 2004; Wall 2004; Wardle et al. 2004), which include pollination and wild food when the edaphic phase of the life cycle of aboveground organisms is considered (Daily et al. 1997; van der Putten et al. 2004; Kremen 2005; Barrios 2007). Further, the assumption that belowground faunal diversity will follow a latitudinal gradient seen aboveground (sensu Swift et al. 1979) of highest biodiversity

and abundance in the tropics may be unfounded (Boag and Yeates 1998; Bardgett et al. 2005; Maraun et al. 2007). There is evidence that local factors such as microclimate, resource quality, and habitat complexity have a greater importance to diversity than regional and latitudinal factors (Hansen and Coleman 1998; Wardle 2002; Bardgett et al. 2005). Additionally, evidence is accumulating that several groups of soil taxa (earthworms, collembolans, nematodes, oribatid mites) do not follow this gradient (Seastedt 1984; Judas 1988; Foissner 1997a; Boag and Yeates 1998; Maraun et al. 2007), and a standardized assessment across latitudes is needed (Culik and Zeppelini-Filho 2003; Maraun et al. 2003). Oribatid mites, for example, have highest species richness in warm temperate systems (Maraun et al. 2007), and abundance of microarthropods is higher in boreal forests (greater than 300,000 per square meter) than in tropical forests (less than 50,000 per square meter) (Seastedt 1984).

Taxonomic impediments should also be considered for determining soil animal biodiversity (Wall et al. 2005; chap. 5). Worldwide, most soils have a high (greater than 95 percent) proportion of unknown or improperly described species (Lawton et al. 1998; Wall and Virginia 2000). Assessing soil animal biodiversity at the species level requires taxonomic

TABLE 4-1. Ecosystem goods or services, processes involved, and estimated contribution of faunal diversity in dry tropical forests

Good or service provided for humans	Ecosystem process	Relative contribution of faunal biodiversity
Food production	Bioturbation, wood decomposition	Small
Water quality	N-retention in biomass, physical stabilization, interception of runoff	Large
Watershed flow	Moisture retention by organic matter, evapotranspiration	Medium to small
Fiber production	Decomposition, organic matter/nutrient cycling, nutrient availability, N-fixation	Large
C sequestration	Organic matter formation, inorganic C deposition	Large
Trace gas regulation	Maintenance of C and N balances	Large

expertise and several types of extraction methods for the many different taxonomic groups (Adis 1988; Coleman et al. 2004; Barberena-Arias 2008). Use of different methods and identification categories contributes to an inadequate database for soil biodiversity and ecosystem analysis. Although summaries are available for a few taxa such as collembolans and oribatid mites in Brazilian ecosystems (Culik and Zeppelini-Filho 2003; Oliveira et al. 2005) and earthworms of Neotropical systems (Fragoso et al. 1995), Adis (1988) noted that soil animal biomass and population densities in the Neotropics were based on partial inventories, collected by various methods. This is in contrast to standardized techniques used in wet tropical forests by global projects (e.g., Giller et al. 1997; Bignell et al. 2005; TSBF 2007). Despite these inconsistencies, there are several studies that provide examples of drivers of diversity and the roles of soil biota in biogeochemical cycling and ecosystem service. The examples highlighted throughout this chapter are a basis for more-comprehensive and standardized studies of soil biodiversity and functioning in dry tropical forests.

Species Diversity and Distribution in Seasonally Dry Neotropical Forests

Light (1933) and Thorne et al. (1994) published termite species lists for western Mexico, which includes some dry tropical forest habitats. Within the tropics, termites are known to be numerically and ecologically important (Thorne et al. 1996). Fragoso et al. (1995) synthesized earthworm diversity and biogeography in northern Neotropical countries and proposed a framework for regional and global distribution of earthworm functional groups based on multiple interacting factors of phylogenetic constraints, moisture, temperature, and soil fertility, which helps explain the presence of earthworms in dry and seasonally dry forests. Biogeographical distribution of larger soil macrofauna appears to vary at local and regional scales of dry tropical forests, as has been noted in other ecosystems (Fragoso et al. 1995). Hanson (chap. 5) notes that while some groups of insects with soil-inhabiting larvae are common in dry tropical forests, others are rare or absent, which may be linked to inherent characteristics of this particular ecosystem, such as soil type. However, factors affecting the distribution of smaller biota (microbes and protozoa) are just being examined. Foissner (1995) found 80 ciliate species in a single soil sample from a seasonally dry tropical forest (SDTF) in Puerto Rico and from this described four new

genera and seven new species. Soils vary on the microhabitat scale, which suggests many more species of protozoa to be discovered.

Most studies of soil fauna have concentrated on microarthropods (Acari and collembolans). Neotropical collembolan diversity is about 1200 species (Mari Mutt et al. 1996—2001), which is considered an underestimate (Culik and Zeppelini-Filho 2003), compared with 7500 species globally and 812 species for North America. Culik and Zeppelini-Fihlo's (2003) synthesis of Brazil's collembolan diversity (199 species, of which 127 are endemic) across ecosystems indicates about 66 percent are from forests, and the remainder are found in other or undescribed habitats. The Brazilian dry tropical and seasonally dry forests have about 46 collembolan species, of which 13 are considered endemic to Brazil (Culik and Zeppelini-Filho 2003). Underestimates of species diversity occur not only with Collembola but also with other groups. A yearlong study of prostigmatid mites living in litter of two dry forest watersheds in the Chamela Biological Station in Mexico noted 31 of 43 species in the family Cunaxidae as new to science (Mejía-Recamier and Palacios-Vargas 2007; Palacios-Vargas et al. 2007). These are important findings as the Cunaxidae are predators of smaller microarthropods in the food chain (Walter and Kaplan 1991) found in soils, litter, and decomposing bark.

Many factors, such as seasonality, soil heterogeneity, and plants, can affect faunal species diversity and abundance (Swift et al. 1979; Coleman et al. 2004). Adis et al. (1989) examined wet and dry season soil arthropod densities (58,000 per square meter) in a moist campinarana forest near Manaus, Brazil, and found no differences and no evidence of animal migration to deeper depths during the dry season. Sixty-three percent of all arthropods measured at 0 to 14 centimeters depth were in the top 3.5 centimeters of soil. This was in contrast to studies during the dry season in seasonal tropical soils, showing lower arthropod abundance and vertical migration (Wallwork 1976; Lieberman and Dock 1982). In a dry forest of Mexico, Palacios-Vargas et al. (2007) examined arthropod abundance in soil and litter on a monthly basis for a year and noted different responses of microarthropod taxa to wet and dry seasons. Mite abundance was greater in the dry season, while collembolans were more abundant during the wet season. As with other arthropod studies (Adis 1988; Barberena-Arias 2008), Acari and collembolans dominated in soil and litter, comprising 90 percent of total arthropods, with total abundance greater in soil than litter (Palacios-Vargas et al. 2007). Seasonality of plant root growth and death as a source of carbon to soils (Kummerow et al. 1990) could be a factor regulating soil abundance in this dry forest but has yet to be quantified.

In many ecosystems, plant litter quality and quantity appear to govern diversity and density of soil and litter animals. For example, within a dry subtropical forest site, taxonomic composition of soil fauna varied in wood and litter of the same tree species (González and Seastedt 2000; Torres and González 2005). Whether diversity and composition of plants and litter quality across sites govern belowground (soil and plant litter) diversity and abundance is inconclusive for soil fauna in many ecosystems (see Maraun et al. 2007). Southwood et al. (1979) proposed that higher tree diversity could explain higher aboveground arthropod diversity. However, evidence varies as to whether plant diversity, identity, or composition drives soil diversity and abundance in ecosystems. Maraun et al. (2007) and others (Hansen 2000; St. John, Wall, and Behan-Pelletier 2006; St. John, Wall, and Hunt 2006) note that microarthropods have limited possibilities to adapt to a particular tropical or temperate site, since food resources (fungi, plant litter, physicochemical composition) are similar. Salamon et al. (2004) tested the relationship of collembolan diversity with plant species diversity and found little correlation and suggested that coevolutionary processes with plant species probably were not important.

In dry semitropical systems, Barberena-Arias (2000) examined litter arthropods in three forest ecosystems of differing tree diversity (and management) across Mona Island, Puerto Rico, and found faunal diversity was positively related to a gradient of higher tree diversity. The managed mahogany plantation and a native plateau were dominated by a single tree species and exhibited lower litter microarthropod diversity, compared with the more diverse native coastal forest. Arthropod abundance was not related to litter quantity across sites and was highest at the native plateau forest where arthropod predators were considerably lower (Barberena-Arias 2000). In a study of two secondary dry forests (natural and planted) of Guadeloupe, Loranger-Merciris et al. (2007) reported that tree litter identity was related to greater abundance of macrofauna and microarthropods in a plantation of *Tabebuia heterophyla* than in other trees at the site. They attributed this to soil types and chemistry and lower levels of leaf tannins in the *T. heterophyla* plantation. Two anecic earthworm species occurred in soils only at the planted sites. Soil microarthropod (Collembola and Acari) composition varied in the soil profile at the two sites, with collembolans dominating the planted forest (Loranger-Merciris et al. 2007). These limited examples are insufficient to explain drivers of animal diversity in dry tropical forest soils but do illustrate that plant species and composition are a major factor for litter animal diversity, though soil fauna may be more influenced by physicochemical characteristics. Heterogeneity of soil habitats within

meters can govern faunal distribution, particularly for smaller biota such as protozoa and nematodes (Foissner 1995, 1997b; Anderson 2002). These few examples also indicate that seasonal responses to precipitation differ with animal group and may be characteristic of life history and physiological and behavioral response.

While the above examples describe the species richness of some groups of soil taxa, they were not designed to quantify or compare the effect of soil animal abundance and diversity on ecosystem processes among different forests; only a few studies compare soil fauna and ecosystem processes in wet and dry forests. Here we highlight some of these.

Soil Fauna and Ecosystem Processes

Wood debris is a major component of inputs to soils in dry tropical forests, and its decomposition rate varies with ecosystem (Eaton and Lawrence 2006). Wallwork (1976) postulated that soil fauna effects on wood decomposition were minimal in dry forests because of moisture constraints and in wet forests because soil fauna avoid the massive extent of fungal hyphal networks. Torres and González (2005) compared soil taxa in decomposing wood logs in wet and dry subtropical forests in Puerto Rico to test this hypothesis. They identified organisms, many to species level, in decomposing *Cyrilla racemiflora* logs after 13 years in the field at the Guánica dry tropical and the Luquillo wet tropical forest. They found higher species diversity and different taxonomic and functional groups (table 4-2) in the Guánica site (25 species) compared with the wet forest (12 species). For example, termites and ants occurred in greater abundance in wood in the dry forest (table 4-3), but termites were of different species in the wet site. Earthworms and fungi were more frequently associated with logs in the wet than dry forest. Reptiles occurred only in the dry tropical forest: the coastal blind snake, *Thyphlops hypomethes*, feeds on termites and ants and inhabits soils and logs, and the gecko, *Sphaerodactylus nicholsi*, lives in shaded but thick litter of dry forests (López-Ortiz and Lewis 2004). The presence of reptiles illustrates that soils are also habitats and food sources for vertebrates, a dependence that could be affected by land use change. The decomposition of logs also differed: the dry tropical forest logs had lower moisture content but higher decomposition rates (an average of 61 percent and 54 percent mass loss, respectively) than the Luquillo wet forest. Nutrient composition of the decaying bark of logs in the dry tropical forest appeared to be

higher in calcium, phosphorus, and nitrogen than in the Luquillo wet forest. González and Seastedt (2000, 2001) and González et al. (2001) hypothesized that the presence of certain functional groups, rather than taxonomic identity (order level), whose activities were not constrained by climatic conditions such as high temperatures and low moisture, were important determinants of litter decay in SDTF compared with other ecosystems they examined (e.g., alpine forest).

While the Torres and González (2005) study provides evidence that faunal biodiversity is higher in decaying wood in a dry compared with a wet forest, evidence varies on whether diversity is also higher in soil and litter of dry tropical forests. Barberena-Arias (2008) found no difference in taxonomic richness in soils and litter in wet and dry forests analyzed at a coarse level—class and order—but noted differences with extraction methods. Overall abundance, however, was considerably greater in the dry forest, with Acari and collembolans dominating the soil community (tables 4-2, 4-3). For certain taxonomic groups abundance was low or similar in dry and wet forests. These examples illustrate the need for comparative studies in dry and wet forests.

TABLE 4-2. Comparison of soil fauna diversity in wood, litter, and soil in wet and dry Neotropical forests

Location	Wet forest	Dry forest	Taxonomic level	Habitat type	Reference
Puerto Rico	12	29	Species	Wood	Torres and González 2005
	13 m^{-2}	13 m^{-2}	Order	Soil	Barberena-Arias 2008
	5 g^{-1}	8 g^{-1}		Litter	
	4 g^{-1}	1.5 g^{-1}	Order	Litter	González and Seastedt 2000
Mexico		32 m^{-2}	Order	Litter	Palacios-Vargas et al. 2007
		28 m^{-2}	Order	Soil	
Guadeloupe		71	Species	Soil (native forest)	Loranger-Merciris et al. 2007
		61		Soil (planted forest)	

A variety of collection methods were used. Diversity is represented per unit measure.

TABLE 4-3. Soil fauna abundances in litter and soil from wet and dry
Neotropical forests

Location	Wet forest	Dry forest	Taxonomic level	Habitat type	Reference
Puerto Rico	10,189 m^{-2}	23,210 m^{-2}	Order	Soil	Barberena-Arias 2008
	3.5 g^{-1}	4.5 g^{-1}	Order	Litter	
	80 g^{-1}	2 g^{-1}	Order	Litter	González and Seastedt 2000
Mexico		26,497 m^{-2}	Order	Soil	Palacios-Vargas et al. 2007
		15,756 m^{-2}	Order	Litter	
Guadeloupe		100 m^{-2}	Species	Soil (native forest)	Loranger-Meciris et al. 2007
		183 m^{-2}	Species	Soil (planted forest)	
		51,000 m^{-2}	Order	Soil (native forest)	
		61,000 m^{-2}	Order	Soil (planted forest)	

A variety of collection methods were used. Abundance expressed as number per unit.

Global Change and Belowground Biota in Seasonally Dry Tropical Forests

Few studies examine how global changes will affect the linkages of soil bi-
ota in SDTFs to aboveground biota, and little evidence exists for assessing
the vulnerability of soil biota to climate change in either wet or dry tropical
forests (but see Wall et al. 1999). However, in both wet and dry tropical
forests many studies show that soil biodiversity and abundance change with
disturbance (Fragoso et al. 1997; Giller et al. 1997; Johnson and Wedin
1997; Allen et al. 1998; Lawton et al. 1998; Chauvel et al. 1999; Bignell
et al. 2005). In dry tropical forests, community composition can be altered
(Barberena-Arias 2000) and single species may dominate abundance with
varying effects on ecosystem processes (Barberena-Arias 2000; Decaëns et

al. 2004; Palacios-Vargas et al. 2007). For example, Yamada et al. (2006) studied nitrogen as an input to decomposition in two tropical forests, a dry deciduous forest and a dry evergreen forest in Thailand, and found that of a diverse group of termites, only wood- and litter-feeding termites fixed nitrogen. Two species, *Microcerotermes crassus* and *Globitermes sulphreus*, had nitrogen fixation rates of 0.21 and 0.28 kilogram per hectare per year, respectively (see also Genet et al. 2001; Decaëns et al. 2004). Disruptions of soil habitats and inhabitants may alter nutrient cycling such as nitrogen fluxes (Yamada et al. 2006) and carbon sequestration (Singh et al. 1991) as well as porosity, aeration, water capacity, and other physical and chemical properties of the soil habitat (Höfer et al. 2001; Decaëns et al. 2004; Barrios 2007). In fact, it has been hypothesized that the loss of termites, and the general decline in the abundance of macroinvertebrate decomposers along broad latitudinal gradients, reduces the ability of the fauna to uniformly affect decomposition rates in colder regions as well (González 2002). Alterations of rates of decomposition have rippling effects on other biota beyond soils (Wall and Moore 1999; Ineson et al. 2004).

Land use change is a major driver affecting soils. For example, human population pressures and fertile soil conditions are resulting in the conversion of dry tropical forest to agriculture (Murphy and Lugo 1986a). Agricultural lands increased in Mexico by 64 percent between 1977 and 1992; while forested areas decreased by 26 percent (Cairns et al. 2000). As more land is converted from dry tropical forest to agriculture, the benefits of managing for complex and complete soil food webs that provide many ecosystem services will become more important to growers, especially in areas where access to pesticides is limited by availability, economics, or environmental concerns.

Conclusions

Dry tropical soil biodiversity and abundance may be greater than in wet forests. The ecosystem services provided to humans by soil animals and microbes are a key reason for considering animals in the context of soil sustainability. While clearing of forests for agriculture may be an immediate need, examples presented here illustrate that changes occurring in the wealth of undescribed biodiversity belowground can be much longer lasting. We suggest the following are urgently needed: (1) a network of taxonomists and ecosystem scientists studying a critical ecological process in several dry tropical forest sites, (2) establishment of comprehensive and

long-term studies of management effects on the vulnerability of macro-fauna and selected groups (e.g., nitrogen fixers) as linked to soil carbon and nutrient fluxes and management, (3) research efforts comparing nearby tropical wet and dry forests, (4) assessment of conservation priorities at local and regional scales that include consideration of belowground biodiversity, and (5) assessment of ecosystem services for animals in soil habitats of dry tropical forests.