

Biogeography and Phylogenetic Community Structure of Soil Invertebrate Ecosystem Engineers: Global to Local Patterns, Implications for Ecosystem Functioning and Services and Global Environmental Change Impacts

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3.6.1 Introduction

Biodiversity is the variety of nature in terms of the abundance and distributions of, and interactions between genotypes, species, communities, and ecosystems (Ash *et al.* 2009). Ecosystem services are the benefits people derive from nature. If we want to establish the links between the two (if any, and causal or not), we have to recognize that biodiversity differs, both in absolute terms and in terms of what we know of it, between different global locations, continentally, regionally, or locally. The same holds true for the ecosystem services required by people from nature and the existing or desired governance structures to manage biodiversity and ecosystem services. Hence, the objective of this chapter is to assess global-to-local scale geographical patterns of soil biodiversity and to relate those to ecological processes as a prerequisite for understanding and managing the provision of ecosystem services and the responses to drivers of global environmental change.

This chapter deals specifically with the soil invertebrate ecosystem engineers *sensu* Hastings *et al.* (2007),

notably the termites, ants, earthworms, and enchytraeids, which leave physical traces on or in the soil that can outlive the engineers: excrements, mounds, burrows, moved particles, and soil aggregates.

The geography of the soil ecosystem engineers cannot be understood without considering the geography of soils. Following Jenny (1941), organisms, including the soil biota, are one of the soil-forming factors, in addition to (and interrelated with) parent material, climate, topography and time. Our entry point for the connection between the geography of soil and soil ecosystem engineers is that any location on earth has experienced considerable change over time due to the drift of the continents, changes in topography, climate changes, and evolutionary changes of the biota, all imprinting a legacy on the thin skin of the earth that currently constitutes the living soil. The current variation in solar energy interacts across the globe with that legacy and with the current complex patterns of global water distribution to form the major biomes that are the playgrounds of today's evolutionary and ecological processes (Fig. 3.6.1).

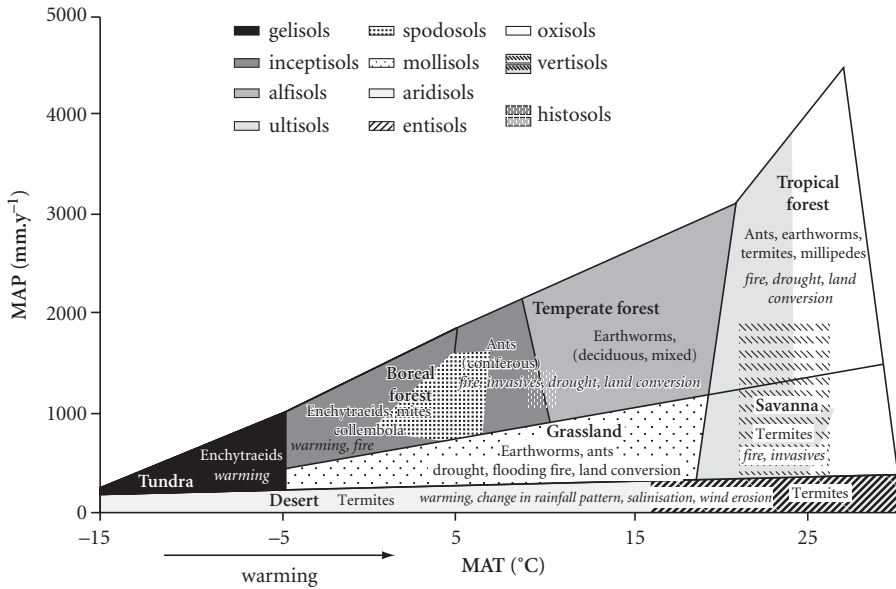


Figure 3.6.1 Dominant soil types, typical soil forming invertebrates and major global change threats across biomes with characteristic mean annual temperature (MAT) and precipitation (MAP). Warming causes increased nutrient cycling rates, extreme precipitation patterns, increasing catastrophic disturbances (floods, droughts, erosion, fires). Land conversion is an important non-climatic disturbance factor. Mean Annual Temperature was calculated from Climatic Research Unit (CRU) monthly temperature data (2000–2006), <http://www.cru.uea.ac.uk/cru/data/temperature/>. Mean Annual Precipitation was calculated from Global Precipitation Climatology Centre (GPCC) monthly precipitation data (2000–2006), <http://www.esrl.noaa.gov/psd/data/gridded/data.gpcc.html>. Global soil order map for 2006 was obtained from the United States Department of Agriculture (USDA). Biomes were derived from the International Geosphere-Biosphere Program (IGBP) Land Cover Characterization (LCC) database. (Recalculated after De Deyn *et al.* 2008 by Rogier de Jong.)

A comprehensive understanding of how these evolutionary and ecological factors have shaped present-day communities is aimed at in the analysis of phylogenetic community structure and in trait-based ecology. The conceptual foundation of trait-based ecology consists of observed trait distributions, initially derived from the pool of possible traits of individual organisms and selected by performance filters, i.e. environmental (biotic and abiotic) filters selecting against traits with inadequate local fitness. The filtering results in a certain community composition, associated with a certain level of ecosystem functioning (Fig. 3.6.2).¹

¹ The hypothesis of environmental filtering and subsequent density-dependent processes has to be tested against the null hypothesis of random species assembly (Hubbell 2001). Testing this hypothesis is not the subject of this chapter, but we note that in one area in which much research has been done, i.e. plant–herbivore ecology, random patterns of plant community phylogenetic structure are less frequently observed than non-randomness, resulting in clustering of trait distributions in species assemblages (Cavander-Bares *et al.* 2009).

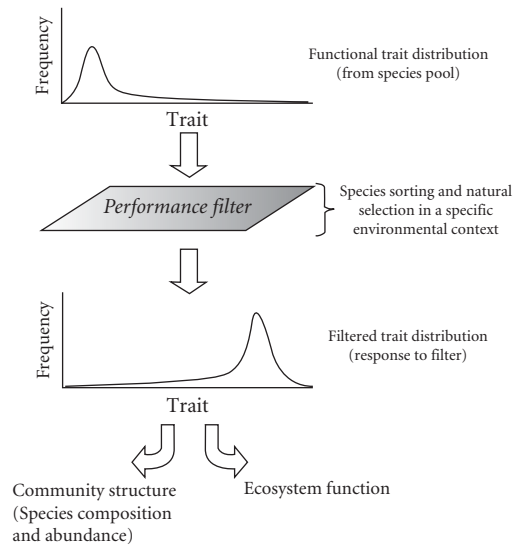


Figure 3.6.2 Relationship between trait distribution and performance filter. The functional trait distribution is filtered by the environment based on performance (the match between the trait and the environment) via natural selection and/or ecological sorting at a particular space/time location. (From Webb *et al.* 2010, with permission from John Wiley & Sons.)

In trait-based ecology, a trait is a well-defined property of organisms, usually measured at the individual level and used comparatively across species (McGill *et al.* 2006). In general, organisms are characterized in terms of their multiple biological attributes such as physiological, morphological, behavioral, or life-history traits. They can henceforth be encompassed in *functional trait groups*, depending on the ecosystem function under study, making the functional group concept less static. For further details see Brussaard (Chapter 1.3, this volume).

Phylogenetic community structure is the pattern of phylogenetic relatedness of species distributions within and among communities. The concept goes beyond a mere phylogenetic approach to biogeography at species level in that phylogenetic attraction of related species, driven by environmental filtering, and phylogenetic repulsion, possibly caused by competition, simultaneously occur and can be made explicit (Helmus *et al.* 2007). Hence, phylogenetic community structure and trait-based ecology help to reveal the historical and contemporary processes driving the assembly of biological communities and how they determine ecosystem functioning.

The processes that drive the organization of species in a focal area operate over varying temporal scales and depend fundamentally on the spatial scale of analysis (Fig. 3.6.3). At the broadest, (supra-) continental spatial scale, species distributions are determined largely by biogeographical processes that involve speciation, extinction, and dispersal. These processes occur over long temporal scales. At intermediate, regional/biome scales, as depicted in Fig. 3.6.3, dispersal varies with the dispersal ability of the organisms. Dispersal can alter patterns of species distributions as they become established through ecological sorting processes which occur when species are filtered out or added, as related to their physiological tolerances. The environment can include both abiotic factors (temperature, soil texture, soil moisture, light availability, pH) and biotic factors (symbionts, pollinators, hosts, prey). It follows that similar habitats in different regions may have different numbers of species, because differing histories of the areas have led to occupancy by different clades of the major taxa (in our case: of the soil invertebrate ecosystem engineers). In addition, different clades have different potentials for diversification, while dif-

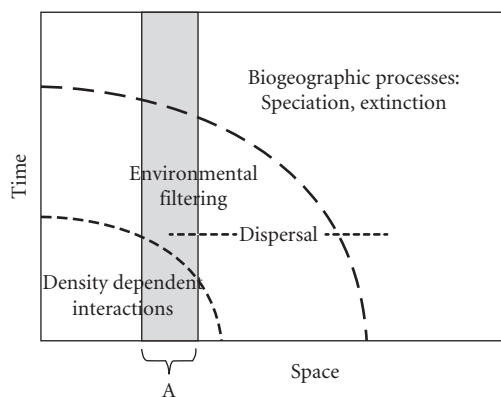


Figure 3.6.3 At a given spatial scale A, species distributions depend on multiple factors. (From Cavander-Bares *et al.* 2009, with permission from John Wiley & Sons.)

ferent lengths of time of occupancy also play a role in determining the numbers of extant species (Webb *et al.* 2002). At the smallest, local, i.e. neighborhood scales, density-dependent processes are likely to operate most intensively. These processes may include competition, disease, herbivory, interspecific gene flow, facilitation and mutualism, and may interact with the abiotic environment to reinforce or diminish environmental filtering (Cavander-Bares *et al.* 2009).

Following a section with an account of macroecological patterns in soil invertebrate community distributions, we give phylogeny-based accounts of biogeographic patterns of the major soil invertebrate engineer groups (termites, ants, earthworms, and enchytraeids). We also provide examples of phylogenetic community structure at continental-to-local levels and explore the possible effects of drivers of global environmental change on community composition and associated ecosystem functioning and services. Following these group-specific sections, we will discuss trait-based ecology of soil invertebrate ecosystem engineers more generally, with a view to the possible effects of global environmental change on ecosystem functioning and services.

3.6.2 Macroecological patterns in soil invertebrate communities

3.6.2.1 Area–diversity relationships

Area–species richness relationships have been documented for a number of aboveground organisms,

but have seldom been studied for soil organisms (Decaëns 2010). The theory of island biogeography predicts that species richness of a given group increases with island area and decreases with island distance from the mainland (Gaston 2000). In mainlands, it is also predicted that species richness increases with spatial observation scale. The few studies that describe such patterns for soil invertebrates include community assessment of ants of the Melanesian archipelago (Wilson 1974), of mites in islands and mainlands (Maraun *et al.* 2007), of springtails (Ulrich & Fiera 2009), and of European earthworms (Judas 1988). In most of these cases, species richness of ants and micro-arthropods also tends to be lower in islands than in mainlands for a given area (Wilson 1974; Stanton & Tepedino 1977; Maraun *et al.* 2007; Ulrich & Fiera 2009), which highlights a negative impact of habitat isolation on community species richness (Blondel 1995). On the other hand, Jonsson *et al.* (2009), while studying the community structure of six groups of soil invertebrates (i.e. ground-dwelling spiders, web-building spiders, beetles, collembolans, mites, and nematodes) in boreal lake islands of northern Sweden, found that taxonomic richness was either neutrally or negatively related to island size, and either neutrally or positively related to island isolation.

Patterns supporting the predictions of island biogeography theory have been explained by a number of factors (Gaston 2000; Decaëns 2010). For instance, larger observation scales may encompass higher habitat diversity and greater environmental stability, thus leading to a higher ratio between immigration/speciation and extinction processes. Increasing observation scales also encompass a higher number of nested levels of organization (from habitat patches to successional stages and landscape units), which results in a larger size of species pools through higher potential spatial and ecological segregation. Additionally, species richness calculation at increasing spatial scales requires the compilation of increasingly larger data sets, which may result in an enhanced probability of detecting rare species. Patterns that depart from island biogeography predictions such as those described by Jonsson *et al.* (2009) have been attributed to the combined and confounding effects of several factors, but not necessarily those predicted as important by island bio-

geography theory, in determining invertebrate species richness in some island systems. For instance, they propose that an increase in species richness with island isolation may result from increased habitat heterogeneity due to greater disturbance from climatic events, and lower levels of predation from birds.

3.6.2.2 Latitudinal gradients

A remarkably low number of studies have explored latitudinal variations in soil animal communities (Bardgett *et al.* 2005; De Deyn & van der Putten 2005; Decaëns 2010). A few studies have described such variation for oribatid mites (Maraun *et al.* 2007), ants (Kusnezov 1957), springtails (Ulrich & Fiera 2009), and termites (Eggleton 1994; Lavelle & Spain 2001). Some authors suggested that this pattern may not apply for all soil organisms due to the cosmopolitan nature of many edaphic species or to a relatively low latitudinal variability of soil conditions (Wardle 2002; De Deyn & van der Putten 2005; Maraun *et al.* 2007). In many cases, however, the absence of a recognized latitudinal pattern for soil animals can easily be ascribed to a deficit of sampling in intertropical regions. For instance, Maraun *et al.* (2007) only found an increase in diversity going from boreal to temperate latitudes, after which diversity leveled off, but Decaëns (2010) suggested that this was mainly due to an unbalanced amount of data in favor of temperate countries. Lavelle (1983, 1986), using data on earthworm communities, suggested that enhanced efficiency of mutualism under tropical climates may be one of the causes of latitudinal gradients in soil animal communities. Other factors classically proposed, to explain the increase in species richness from high to low latitudes, include the increase in geographic areas towards the equator or the increase of the heterogeneity, productivity or environmental stability (both past and actual) of habitats (Huston 1994; Brown & Lomolino 1998; Gaston & Spicer 1998; Gaston 2000).

A frequent feature of latitudinal patterns is that the shape of the variation in biodiversity is often asymmetric (Gaston 2000). This was, for example, described by Dunn *et al.* (2009) for ants and by Eggleton (1994) for termites, who found that southern hemisphere sites were more diverse than northern

hemisphere sites. Dunn *et al.* (2009) emphasized that most of this asymmetry could be explained statistically by differences in contemporary climate, local species richness of ants being positively correlated with temperature, and negatively associated with temperature range, and precipitation. Another part of the asymmetry in the pattern was explained by the greater climate stability of the southern hemisphere during the Eocene epoch.

3.6.2.3 Altitudinal gradients

The few studies that explored altitudinal variation in soil biodiversity have focused on invertebrates. Some have described a continuous decrease in the total number of species by altitudinal stratum in a given geographical area, like earthworms in France (Bouché 1972; Dahmouche 2007), ants in the Smoky Mountains (Cole 1940), termites in Sarawak (Collins 1980), and dung beetles in Spain (Romero-Alcaraz & Ávila 2000). These patterns may be explained by different factors including the increasingly harsh abiotic conditions (in particular temperature), the reduced levels of primary productivity and ecosystem carrying capacity, and the smaller habitat areas at higher elevation.

On the other hand, as reported for many above-ground organisms, altitudinal variations in soil biodiversity may present strong local and/or taxonomic specificity (Brown & Lomolino 1998; Decaëns 2010). Many taxonomic groups show a humpback response to elevation gradients. For example, Collins (1980) reported a peak of taxonomic diversity at 500–1,200 m for beetle communities, and at 1,300–1,700 m for dipteran assemblages in Sarawak. Loranger *et al.* (2001) reported a humpback distribution of springtail species richness across an altitudinal transect from 950–2,150 m in the French Alps. These results may partly be explained by altitudinal variation in environmental factors (e.g. rainfall, temperature, pH or organic matter quality) and an increased influence of dispersal barriers (Gaston 2000).

3.6.2.4 Landscape modification gradients

A related pattern to the area–species diversity relationships is the response of communities to habitat

fragmentation gradients (Gaston & Spicer 1998). This has been directly addressed in a few studies focusing on micro-arthropods (Rantalainen *et al.* 2005), termites (Fonseca De Souza & Brown 1994), ants (Suarez *et al.* 1998; Carvalho & Vasconcelos 1999; Vasconcelos *et al.* 2006), and ground beetles (Barbosa & Marquet 2002; Driscoll & Weir 2005).

Some recent studies have underpinned the complexity and the specificity of the responses within or between broad taxonomic groups. For example, Davies (2002) illustrated opposite responses of two termite functional groups to the fragmentation of Amazonian rain forest (positive response for litter and wood feeders, negative for geophagous species). Sousa *et al.* (2006) studied Collembolan community patterns in comparable gradients from forested to agricultural dominated landscapes in eight European countries. Although species richness patterns were not fully concordant among the different countries, they found that high species richness was associated with high landscape heterogeneity (i.e. high number of land use units). They also report that the average local richness of forest patches decreased along the gradient, whereas the opposite pattern occurred for open habitat assemblages, showing that both ecological groups were sensitive to the fragmentation of their preferred habitat at the landscape scale. Assuming that different soil organisms have different dispersal and colonization capacities, Hedlund *et al.* (2004) predicted a relative resistance of bacterial-based communities, and a higher vulnerability of fungal-based organisms.

3.6.2.5 Concluding remarks

Understanding the driving factors of soil invertebrate communities across different spatial and temporal scales is of primary importance if we wish to predict soil responses to global changes and the impact these changes will have on the delivery of ecosystem services. We are, however, far from reaching a clear picture of these patterns, in part because of the still unsatisfactory knowledge of the taxonomy and phylogeny of most groups of soil animals (Decaëns *et al.* 2006, 2008a). It is thus of prime importance to address the strong taxonomic deficit

in most groups of soil organisms. This will likely be achieved through implementing new genomic taxonomical methods such as DNA barcoding (Rougerie *et al.* 2009; Richard *et al.* 2010). As suggested by Decaëns *et al.* (2008a), this approach has great potential for species identification, for stimulating accurate soil biodiversity surveys or any ecological or biogeographical research based on species lists, and for helping soil taxonomists to solve taxonomic and phylogenetic problems. In light of these exciting new tools, the efforts in the next sections to connect biogeography, taxonomy, and phylogeny within ants, termites, earthworms, and enchytraeids, have to be seen as preliminary rather than conclusive for gaining insight in the effects of global environmental change drivers on ecosystem functions and services, associated with the community structure and abundance of soil invertebrate ecosystem engineers.

3.6.3 Termite biogeography and phylogenetic community structure

3.6.3.1 Introduction

Termites are eusocial insects, phylogenetically nested within cockroaches (Inward *et al.* 2007). Colonies show complex division of labor, with reproductives, soldier and worker castes. Workers forage, and dead plant material is the main food source of almost all species. However, the plant material used is diverse, ranging from wood to organic material present in soil. Termites are renowned soil ecosystem engineers (Lavelle *et al.* 1997) as they have a highly significant impact on pedogenesis, soil properties, and soil functions. Hence, they play an important role as mediators of soil ecological processes (e.g. Lee & Wood 1971; Pearce 1997; Bignell & Eggleton 2000). They can translocate large quantities of soil, promote soil stability and water permeability, and change soil chemistry (Bignell 2006), and they can degrade and utilize even the most recalcitrant residues of dead plant material such as lignin, cellulose, and humus (Rouland-Lefèvre & Bignell 2002). Termites owe a large part of this efficiency to their gut symbionts, which include microorganisms of all major taxa: Archaea, Bacteria, and Eucarya (Bignell 2000). Any

extant termite is associated with representatives of at least two of these groups. The “higher termites” (family Termitidae) have retained their bacterial symbionts, but typically lack the protozoan gut symbionts that most other termite families have. A single subfamily in this terminal clade, the Macrotermitinae has evolved a unique “agricultural” ectosymbiosis with basidiomycete fungi of the genus *Termitomyces*. This niche differentiation has allowed termites to gain an immense impact on the global terrestrial carbon cycle, exceeding the cumulative decomposition roles of other arthropods and only being surpassed by the mammalian herbivores (Bignell *et al.* 1997). It is believed that termites mediate between 2–5% of the CO₂ flux from all terrestrial sources (Sanderson 1996; Bignell *et al.* 1997; Sugimoto *et al.* 2000). For example, in moist savannah systems, estimations of population respiration rates indicated that roughly 20% of carbon mineralization could be attributed to, mostly fungus-growing, termites (Wood & Sands 1978). In contrast, in the African rainforests, their relative contribution to decomposition is relatively low—about 1–2% of all C mineralization—in spite of their much higher taxonomic diversity in this habitat (Bignell & Eggleton 2000). In forests, tree metabolism dominates the carbon fluxes, making the relative contribution of the termites small, although the absolute abundance and biomass may be higher than in the savannahs (Bignell *et al.* 1997). Fungus-growing termites are only found in the Old World. In the New World, their ecological role may be covered to some degree by other fungus-growing social insects, the attine ants. However, attine ant food consists mainly of fresh rather than dry plant material (Mueller *et al.* 2005).

3.6.3.2 Continental scale

Termites have been divided into seven families (Fig. 3.6.4), 281 genera, and about 2,600 species (Eggleton 2000). The highest diversity is found in the “higher termites,” comprising ca. 84% of the world termite species. Termites show rather extreme differences in their distributional range, so that at the same latitude, and under approximately similar environmental conditions, there are huge differences

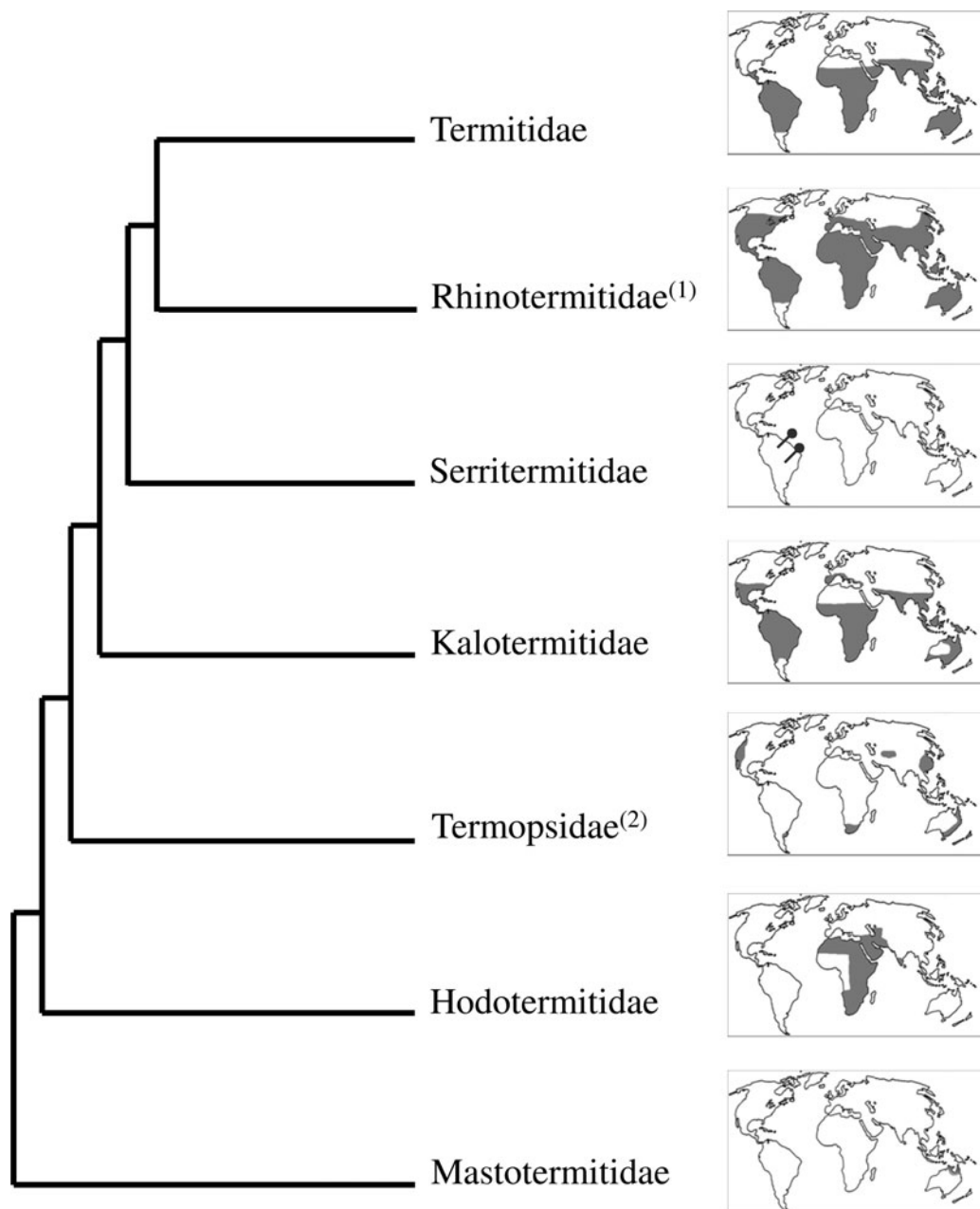


Figure 3.6.4 Schematic representation of termite family relationships (Inward *et al.* 2007) and their general patterns of distribution (based on Eggleton 2000). Rhinotermitidae is shown as a monophyletic group whereas it appears paraphyletic because the Brazilian Serritermitidae nest within this family. However, the status of the monotypic Serritermitidae as a separated family is debatable (see Kambhampati & Eggleton 2000). Termopsidae is likewise a paraphyletic group with the Hodotermitidae clade nesting within it and not being basal to it as represented here. On the distribution patterns: Mastotermitidae has only one extant member restricted to the non-rainforest parts of northern Australia; Hodotermitidae are restricted to the Old World and can be found in habitats ranging from dry savannah to arid grassland; Termopsidae are the most widely scattered of all the major termite groups and nest and feed on rotting logs; Kalotermitidae are widely distributed and live in water-stressed habitats; Serritermitidae consist of only two known species present at Santarém and Coxipó da Ponte in Brazil (Emerson & Krishna 1975) and likely inhabit savannah-like habitats (*cerrado*); Rhinotermitidae are widely distributed in habitats ranging from wet to dry; Termitidae comprise, amongst others, the fungus growers restricted to the Old World, and soil feeders present in the Neotropical and Oriental regions.

across regions and continents which can be explained by historical factors but also, to some degree, by habitat differences. Overall, in temperate and cold regions, they are virtually absent, whereas they are very abundant in tropical regions. Within their distributional range, termite species richness drops very fast from roughly 10° north and south of the equator (Eggleton 2000). This drop is much stronger north than south, which has been attributed to the relative protection of the south from the effects of glaciation (Eggleton 2000). The African fauna has a much higher genus richness than both neotropical and oriental faunas.

Some authors (e.g. Pearce 1997) suggest that termites might have been present since the end of the Permian period (Paleozoic era), but there are no fossil records to indicate that they have a pre-Cretaceous history (Thorne *et al.* 2000). Recently however, Engel *et al.* (2009) suggested that termites have diverged from cryptocerid roaches in the Late Jurassic, making termites the oldest group of eusocial animals, pre-dating the origin of ants by some 35 million years. A strong historical effect is apparent: phenetic patterns of the genus structure composition are closely explained by the paleogeographic history of the continents and it seems that the divergence from the basal groups happened already on the separating landmasses (Eggleton 2000). In this way, vicariance has played an important role for basal groups. The other (more diverged) groups, however, have recently dispersed over long distances (Emerson 1955).

It is unknown which factors have been causal in determining termite global distribution, but it has been suggested that differences in the histories and relative ages of the various forest blocks of the continents are important (Eggleton 2000). Additionally, an interesting correlation has been found between nesting habit and genus range size and species richness within each genus (Eggleton 2000): genera with at least one species nesting in wood have wider overall ranges than subterranean or mound-building genera. This has been interpreted as evidence for the hypothesis that nesting in wood facilitates dispersal by rafting, or, more recently, by humans via timber transport (Bess 1970).

A case in point is the fungus-growing termites (subfamily Macrotermitinae), which have evolved

an ectosymbiosis with basidiomycete fungi of the genus *Termitomyces* (Aanen *et al.* 2002). Their ancestral habitat has been identified through phylogenetic reconstruction (Aanen & Eggleton 2005) as African rainforests, where their taxonomic diversity is highest. The main radiation leading to the extant taxa probably took place in this habitat just before the expansion of the savannah, at least 30 million years ago (mya; Brandl *et al.* 2007; Nobre *et al.* 2011). Subsequently, four out-of-Africa migrations have occurred into Asia and a single one into Madagascar (Aanen & Eggleton 2005; Nobre *et al.* 2010), so that historical reasons have constrained this group to the Old World only, whereas it seems that their preferred habitat is not restricted to this geographic region.

Several functional classification schemes have been proposed, based on nesting type and primary food (Fig. 3.6.5; Abe 1987; Donovan *et al.* 2001; Eggleton & Tayasu 2001). Abe (1987) was the first to separate termite species according to the degree to which their nesting and feeding substrates overlap, temporally and spatially. In Abe's classification, single-piece nesters corresponds to termites that feed and nest in the same discrete substrate and intermediate nesters are the ones that, besides nesting in their feeding substrate, also forage outside their colony centre. In these two categories, we can only find wood feeders. The separate-piece nesters actively forage for their feeding substrate away from the nest and these termites have a wide range of feeding substrates. The soil feeders were given a separate status because this term is used for termites that nest and feed in soil, a substrate that is not discrete but continuous. Later, Donovan *et al.* (2001) presented a new quantitative functional classification of four feeding groups. Their classification was based on the consistent match between morphological character states of the workers and their gut contents across the humification gradient between living plant tissue and soil organic matter. Based on the consideration that the substrate's positional relation to the nest centre and the humification state of the substrate consumed were of more ecological importance than the substrate itself, Eggleton and Tayasu (2001) proposed a "lifeway" classification from a combination of the Abe and Donovan classifications.

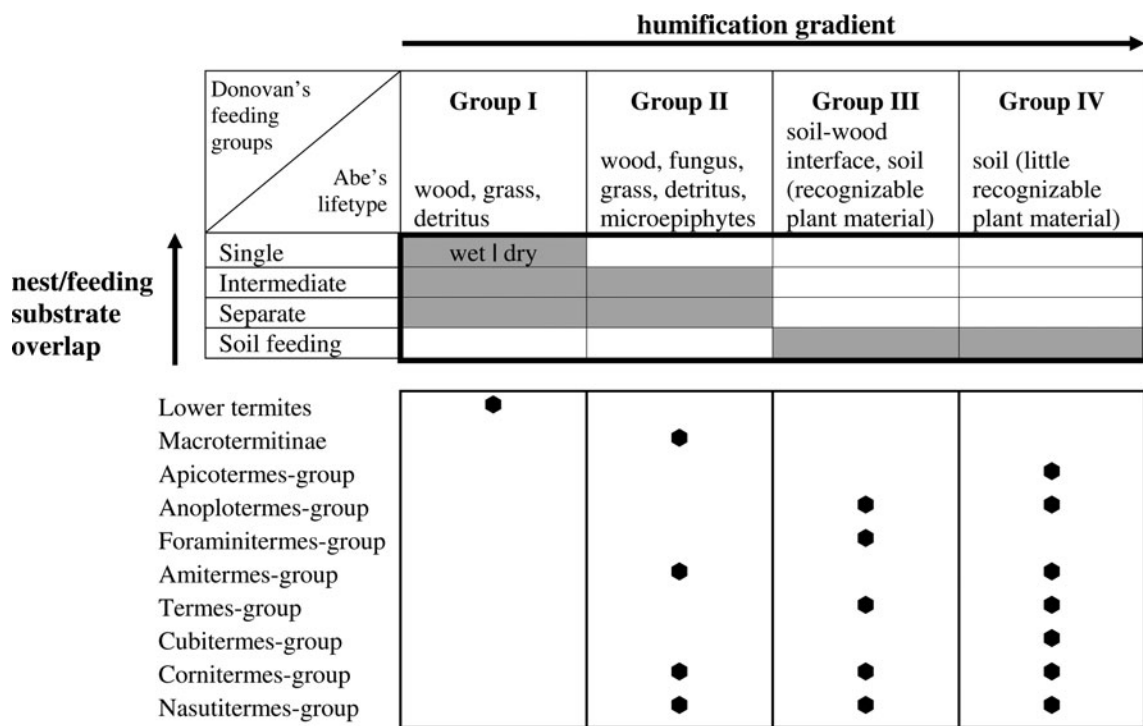


Figure 3.6.5 Diagram showing the eight lifeway categories (grey boxes). Distinction between Donovan’s feeding groups III and IV is based on worker morphology, and especially intestinal anatomy. The soil feeders are not classified by lifestyle because the distinction between single-piece and separate-piece breaks down for many species. (Adapted from Donovan *et al.* 2001 and Eggleton & Tayasu 2001.)

This classification provides a useful basis for understanding termite phylogenetic community structure and how it relates to their functioning in terms of carbon substrate use. For example, both wood feeders and soil feeders are biogeographically widely distributed. However, whereas wood feeders inhabit a very wide range of habitats, from wet to dry—with even one genus being able to survive in true desert (*Psammotermes*)—soil feeders are more restricted to savannahs and especially tropical forests (Eggleton & Tayasu 2001). Their contribution to carbon and nitrogen mineralization in relation to feeding habits is summarized in Eggleton and Tayasu (2001), where they show that $\delta^{13}\text{C}$ values are determined mostly by the vegetation in which the termites live, whereas $\delta^{15}\text{N}$ correlates more tightly with the feeding groups. Soil feeders—(III) and (IV)—thus face low carbon availability so that their nutrient strategy (C and N) delivers a high throughput as both C and N are limiting.

The ecological consequences of the much higher proportion of soil-feeding termites in Africa, compared to both Oriental and Neotropical faunas, have not been studied but may be important for the turnover rate of organic material in the soil (Eggleton 2000). The separate nest builders—Sep(I) and Sep(II)—form underground or aboveground nests, made externally of soil, and thus resulting in an even higher impact on soil turnover. This effect is even more pronounced in mound builders, as they bring soil from deep horizons to the surface, affecting soil characteristics, especially physicochemical properties, as well as infiltration, water status, and rainfall use efficiency, leading to nutrient-enriched microhabitats. Termite mounds, therefore, trap water and nutrients when compared to the surrounding soil, and in this way provide for increased primary production, which in turn fosters the build-up of food chains (herbivore and predator secondary production), making mounds hotspots

of ecosystem productivity (reviewed in Schmitz 2010).

3.6.3.3 Regional scale

The known habitats of termites range from dry deserts, steppes, prairies, and Mediterranean shrublands to the wettest tropical forests, with different assemblages occurring in different habitats (Bignell & Eggleton 2000). Not only phylogenetic community structure is strongly influenced by historical processes, but as a consequence, also the functional diversity. The majority of studies on the ecological importance of termites are focused on tropical forests and savannahs, where functional diversity patterns and the influence of environmental factors on assemblages have been analyzed (e.g. Bignell *et al.* 1997; Eggleton & Tayasu 2001; Eggleton *et al.* 2002; Davies *et al.* 2003, Jones *et al.* 2003), and where the impact of termites in the ecosystem (on the decomposition process, on soil physical and chemical properties, on carbon and nitrogen mineralization, on vegetation composition and thus in shaping higher trophic levels) is acknowledged as substantial (Wood & Sands 1978; Bignell 2006). In warm temperate and subtropical biomes, termite diversity is much lower, but their impact on forest systems is still apparent (Nobre *et al.* 2009).

3.6.3.4 Local scale

Local species richness strongly depends on environmental factors such as rainfall, vegetation type, temperature, and altitude (Williams 1966; Eggleton 2000). In general, wood and grass feeding termites are favored by decreasing rainfall, in contrast to soil feeding termites (Bignell 2006). Because most termites are soil-dwelling, creating extensive gallery systems in the soil and excavating mineral material to build mounds and runways, soil type is crucial for them. Some soils do not support termites at all, like excessively sandy soils, semi-permanently waterlogged soils, and severely cracking vertisols, (Holt *et al.* 1980; Wood 1988; Bignell & Eggleton 2000).

Over the entire group, the food sources of termites are (in different taxa) extremely diverse, and include both live and dead vegetation, wood, humus, dung, fungi, and even lichens. However, they all depend on cellulosic material to some extent. Different termite species are adapted to handle different stages in the decomposition process. This ranges from hardly humified plant material (wood, litter, and grass), via more degraded plant material to the most humified substrate present, on which the soil-feeding termites feed. Even within the wood feeders some groups feed preferentially on wood previously decomposed by microorganisms (e.g. Lenz *et al.* 1991; Rouland-Lefèvre 2000), probably owing to an enhanced nutrient content, decreased wood density, and a probable reduction of toxic allelochemicals (e.g. Waller *et al.* 1990). In parallel, also soil feeders can use a range of soils, from humus layers on organic rich soil with high levels of recognizable plant material to soil with high mineral content. Generally, wood feeders feed on a higher energy resource that is patchily distributed, and soil feeders make use of low energy but universally abundant substrate.

3.6.3.5 Global change drivers, termite community structure, and ecosystem functioning

Global change may impact termites in three ways. First, increasing temperatures are expected to extend distributional ranges. The distributional range of termites is concentrated in tropical and subtropical areas and quickly drops at higher latitudes. Within Europe, there is evidence that species of the genus *Reticulitermes* are moving north (Clément *et al.* 2001). However, some of this movement has been linked mainly to human interference as some species seem to be restricted to cities (Vieau 1993; Kutnik *et al.* 2004). However, though global warming is a factor, the cities' central heating systems seem to be more important, as illustrated by the now well-established *Reticulitermes* colonies near the harbor of Hamburg, inhabiting the pipe work of the district heating system. Colonies of this subterranean termite could be found in locations as far apart as Sauton, north Devon (UK), and Santiago and Valparaiso (Chile) and in numerous French and

Italian cities north of the natural distribution area of the genus.

Second, global change results in conversion and fragmentation of habitats. For example, human impact has led to increased fragmentation of tropical forests. The effects of forest fragmentation on the species composition of tropical termite assemblages have been addressed in several studies (Fonseca de Souza & Brown 1994; Eggleton *et al.* 1996, 1997; Davies 2001; Davies *et al.* 2003). These studies have generally shown that termite assemblages are very sensitive to habitat disturbance in the medium-to-long term, but rather insensitive in the short term (<5 years). The long-term effect of fragmentation is thus a change in species composition and decrease in species diversity.

Third, deforestation and conversion to agriculture can result in very considerable declines in species richness and changes in the composition of termite communities (Eggleton & Bignell 1995; Lavelle & Pashanasi 1989). The drop in species richness seems to be accompanied by the appearance of r-strategy species (Collins 1980; Johns 1992), i.e. species that are favored by disturbance and are good colonizers. Amongst the favored species one may find those with the potential to become pests. A further consequence of global change may therefore be the increased likelihood of the spread of invasive species (Leniaud *et al.* 2009).

3.6.4 Ant biogeography and phylogenetic community structure

3.6.4.1 Introduction

The common ancestor of all living ants probably lived in the early Cretaceous period, although there is not a consensus on this (range between 115–169 mya), (Brady *et al.* 2006; Moreau *et al.* 2006). Since this time ants have radiated to produce >20,000 species (Fig. 3.6.6; Bolton 2010), with 12,606 described (Agosti & Johnson 2010). They have come to abound around the world, only being absent from the very coldest areas. Although most species are predatory to a greater or lesser degree, the group performs a wide variety of ecosystem functions. Many species fill primary consumer roles either by feeding on honeydew (Blüthgen *et al.* 2003; Davidson *et al.*

2003) or by cultivating fungus on harvested leaves (Wilson 1974). The seeds of 35% of all herbaceous plants may be distributed by ants in some habitats (Beattie 1985) and ground nesting species can turn over large volumes of soil (Lyford 1963; Whitford 2000). It is not our intention to provide an exhaustive review of studies detailing the contributions of ants to ecosystem functioning. For this, see reviews by Folgarait (1998) and Crist (2009). Rather, this section uses examples from what is known about the broad patterns of this radiation and to discuss how ant biogeography and phylogeny might impact the contribution of this group to ecosystem functioning.

3.6.4.2 Continental scale

The main large-scale biogeographic division in ant communities is that between the Old and New World faunas. There are numerous genera, and even some subfamilies, that exist only on either one side of the Atlantic or the other. The impact that this division has on the ways that ants contribute to ecosystem functioning depends to a great extent on the time at which particular traits evolved. For example, army ants (the clade comprising the Aenictinae, Dorylinae, and Ecitoninae, nested within the “dorylomorphs,” Fig. 3.6.6) are abundant predators in most tropical forests and affect not only their prey but also the many other species that live within or around their colonies. Army ants evolved once in the mid-Cretaceous (94–116 mya) Period, and the current pan-tropical distribution of this group seems to be due to their Gondwanan origin (Brady 2003). On the other hand, the existence of traits that only evolved relatively recently may mean that certain contributions to ecosystem functioning are restricted to one side or the other of this inter-continental biogeographic divide. For example, leaf cutter ants (tribe Attini in the Myrmicinae), which harvest living plant material and use it to cultivate the fungus on which they feed, can be dominant herbivores in tropical forests (Rao *et al.* 2002). However, because the trait of leaf harvesting and fungal cultivation evolved only 8–12 mya in the Neotropics (Schultz & Brady 2008), the ants carrying out this function are presently only found in that region. The cultivation of fungus for food from live plant material might in turn directly

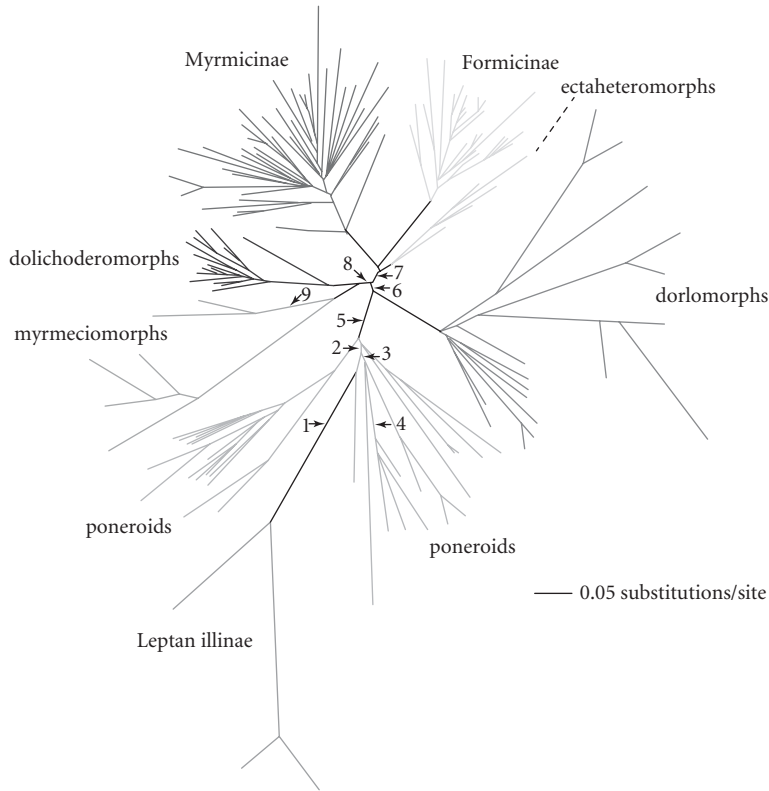


Figure 3.6.6 Unrooted molecular phylogeny of ants constructed using sequences from 162 species representing all 20 ant subfamilies. Numbers denote various possible rootings. Rooting 1 is most likely, although rootings 2–5 are also possible. Rootings 6–9 give significantly worse fits to the data. The “ectaheteromorphs” comprise the subfamilies Heteroponerinae and Ectatomminae; the “dolichoderomorphs” the Aneuretinae and the Dolichoderinae; the “dorylomorphs” the Leptanilloidinae, Cerapachyinae, Aenictogitoninae, Dorylinae, Aenictinae, and the Ectoninae; the “myrmeciomorphs” the Myrmeciinae and the Pseudomyrmecinae; the “poneroids” the Agroecomyrmecinae, Amblyoponinae, Paraponerinae, Ponerinae, and Proceratiinae. (After Brady *et al.* 2006, with permission from National Academy of Sciences, U.S.A.)

affect the distribution and longevity of the clade. Obligate mutualisms such as this one mean that both partners need to arrive simultaneously for colonization to be successful, and extinction of one partner inevitably leads to the extinction of both (coextinction; Koh *et al.* 2004), potentially making the clade both less dispersive and less long-lived.

3.6.4.3 Regional scale

Large-scale biogeographical considerations such as the ones described earlier apply mainly to functionally relevant traits that evolve infrequently. Many of the traits that determine the contributions of ants to

ecosystem functioning are highly labile, i.e. easy to evolve and lose. For example, the trait of excavating a nest in the ground, and consequently contributing to soil turnover, can be found in many ant genera. In these cases, it is the overall density of colonies and their rates of activity that are important, although it should be noted that there will be some variation between species in terms of their contribution to this ecosystem process. Other such labile functional traits include seed dispersal (Garrido *et al.* 2002), predation (Jeanne 1979), and foraging for protein and other baits (Fayle *et al.* 2011; Gove & Majer 2006). For these traits, broader, non-phylogenetic patterns of ant presence and activity relating to environmental filters on community assembly

become more important; for example, the declining gradient of ant diversity and abundance from the equator to the poles (Dunn *et al.* 2009). We would expect the rates of processes in these cases to track these gradients, which have been shown for predation (Jeanne 1979), although not, to our knowledge, for any other process.

3.6.4.4 Local scale

Phylogenetic structuring of ant communities at local scales is likely to reflect interactions between species rather than the biogeographical history of the group. One of the most extreme examples of this is the case of invasive ant species that often displace native ants and other invertebrates, and can have profound impacts on entire ecosystems (e.g. O'Dowd *et al.* 2003). Not only do these invaders reduce the diversity of native species, they can also alter the phylogenetic community structure of the remaining species. In fact, the structure of the resident community is likely to have an impact on the functioning of the ecosystem in terms of resilience against invasion by non-native species. Lessard *et al.* (2009) conducted a meta-analysis of 12 published studies and found that the arrival of invasive ants changed the phylogenetic structure of ant communities, with invaded sites supporting a more phylogenetically clumped community than uninvaded ones. That is, species loss was non-random with respect to phylogeny. Interestingly, the native species that were lost to produce this clumped distribution were not always closely related to the invader.

There remains much we do not know about the way ant phylogeny and biogeography at a range of scales affect the contribution of this group to ecosystem functioning in natural habitats. Besides the continuation of taxonomic work to further reveal the phylogeny of ants, particularly at the species level, a critical area of future research is to examine the traits that determine the degree to which each species contributes to particular ecosystem processes. The creation of global databases for such traits, building on those providing taxonomic and distributional information (Dunn *et al.* 2007; Agosti & Johnson 2010; Fisher 2010), is the first step towards a more comprehensive understanding of ant biodiversity and ecosystem functioning.

3.6.4.5 Global change drivers, ant community structure, and ecosystem functioning

Since ants contribute substantially to the functioning of soil ecosystems, it is of vital importance to understand how global environmental change affects ant communities, and how this in turn alters the way that ecosystems function. There are three aspects of global environmental change that are particularly relevant for ants: habitat conversion, the spread of invasive ant species and climate change. Habitat conversion and invasion by non-natives usually result in loss of species richness (Dunn 2004) and a change in species composition (e.g. Fayle *et al.* 2010). In some cases the nature of interaction networks within communities is also altered, with an increase in the strength of negative interspecific interactions during habitat degradation (Floren *et al.* 2001), but a decrease in interaction strengths when the community is invaded by a non-native species (Sanders *et al.* 2003). The impacts of climate change are less clear, although the strong response of ant communities to latitudinal (Dunn *et al.* 2009) and altitudinal gradients (Brühl *et al.* 1999) in climate strongly indicate that this group will be affected.

While we have some idea about the ways that global changes affect ant communities, we know much less about how these changes will affect the contribution of ants to ecosystem functioning. Habitat fragmentation does not seem to substantially alter the mutualistic relationships between ants and plants (Bruna *et al.* 2005), nor is there any difference in foraging rate for ants beneath trees in plantations and those in the plantation matrix (Gove & Majer 2006). Ant species richness is related to the rate at which nutrients are redistributed in rain forest, but only at very small spatial scales, at which there is no response of species richness to even quite drastic habitat conversion (Fayle *et al.* 2011). It is not known how species richness and the functional composition of ant communities are tied to nutrient redistribution at larger spatial scales. Even less is known about the ways that climate change will affect ant-mediated processes contributing to ecosystem functioning. The gradient of decreasing ant species richness and predatory function away from the equator found by Jeanne (1979) indicates that

increasing temperature may increase ant species richness locally and also increase predation rates. Interestingly, this pattern only holds true in forests and not in cleared areas, indicating that the responses of ant diversity and related ecosystem functions to changes in climate potentially differ between habitat types. It is clear that large-scale manipulative experiments are required in order to fully investigate potential changes in ant contribution to ecosystem functioning. These are currently ongoing for both habitat fragmentation and conversion (Ewers *et al.* 2011) and for climate change (Dunn *et al.* 2010).

3.6.5 Earthworms

3.6.5.1 Introduction

Phylogenetic community structure and trait-based ecology of earthworms are not well-explored topics. We approach the coupling of both topics in a slightly backwards fashion, by first explaining the basics of earthworm functional groups, and then considering the phylogeography of earthworms. This order is dictated by the need to use the functional group terminology in the discussion of phylogenetic community structure. Eventually we return to the consideration of traits, and finally the responses of earthworms and associated ecosystem services to global change drivers.

Earthworms, like termites (Eggleton & Tayasu 2001), have been assigned a categorization of species into functional groups, known by the names given to them by Bouché (1977): epigeic, endogeic, and anecic. They are based on morphological and behavioral traits (Lee 1959; Bouché 1977). Epigeic earthworms live in and feed on nearly pure organic matter substrates, such as thick forest floor leaf packs, fallen tree trunks, epiphyte mats, suspended arboreal soils, and leaf axils of palms, bromeliads, Pandanaceae, and some ferns. They are usually small-bodied, darkly pigmented, have the ability to move rapidly, have minimal development of intestinal surface area, and have high reproductive rates and short life spans. Anecics form a relatively permanent burrow system and emerge to feed on surface organic matter such as dead leaves. A typical anecic worm has a large body with a pigmented

anterior end, and a minimal degree of intestinal surface development. Endogeics live in mineral soil and consume soil organic matter. Lavelle (1983) divided the endogeic category into three, based on the degree of decomposition or humification of the organic matter consumed, from less humified to more: polyhumic, mesohumic and oligohumic. The first can resemble epigeics in some characteristics of coloration, but they are usually less deeply colored, larger, and form burrows. Oligohumic endogeics are unpigmented, large bodied, with high degree of intestinal surface area augmentation, and have no escape behavior. Mesohumics are also unpigmented and otherwise are intermediate. These functional groups were analyzed across multiple biomes by Lavelle (1983; Fig. 3.6.7). On a biomass basis, tropical soils contained the greatest diversity and evenness of functional groups, dominated by endogeics and having a uniquely tropical group, the oligohumic endogeics feeding on low quality soil organic matter. Temperate zones (mostly European data) had roughly 50% of community earthworm biomass in the anecic category, bearing in mind that anecics are typically large-bodied earthworms. Cold climates trended towards dominance by epigeics and polyhumic endogeics.

Boreal forests generally lack earthworms for historical reasons (past permafrost, glaciations), but a few epigeic acid-tolerant species like *Dendrobaena octaedra* can live along the southern margins of the boreal forest biome. Low quality of soil organic matter (SOM) and plant litter in this biome (De Deyn *et al.* 2008) are significant obstacles to most earthworms, yet the epigeic gut morphology is quite different from that of the oligohumic endogeics also existing on low quality SOM. The difference is that the epigeics have access to large volumes of SOM and litter, and ingest nearly 100% organic matter. Temperate forests support the full range of earthworm functional groups, exploiting a range of resource types corresponding to the mix of plant tissue traits generated by the forest vegetation (De Deyn *et al.* 2008). Tropical wet forests are similar, except that rapid decomposition drastically reduces the resource base for epigeics, who may be found more reliably in suspended organic soils created within or by epiphytes. In seasonal tropical forests, though the range of plant resources may be broad

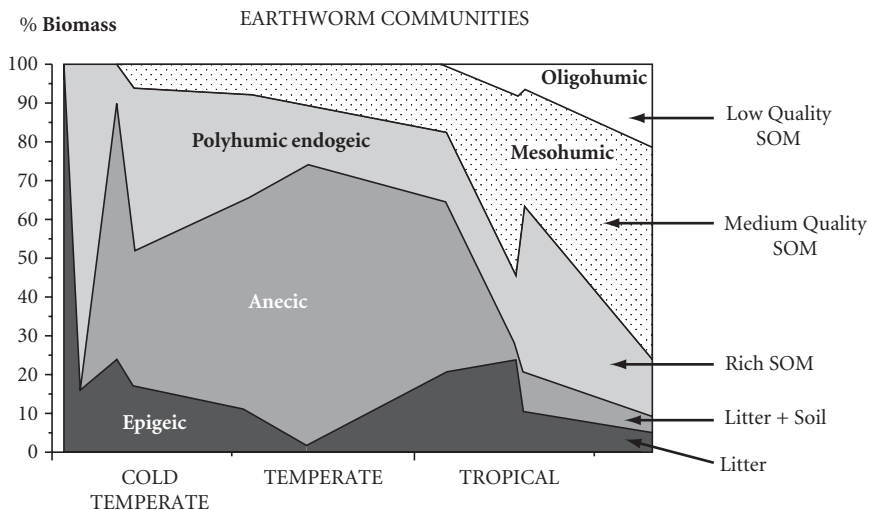


Figure 3.6.7 Percentages of biomass in different ecological categories of earthworm communities along a thermo-latitude gradient. Arrows to the right indicate the main food source used. (Modified from Lavelle & Spain 2001, with permission from Springer Science + Business Media B.V.)

and litter layers better-developed, the environmental stresses of the dry season eliminate most epigeic niches and promote endogeic or anecic earthworm activity. A similar result is found in all grassland/savannah biomes, with emphasis on endogeic functional groups and near absence of epigeics.

3.6.5.2 Continental scale

At the largest time/space scale, earthworm community composition has been driven by evolution *in situ* on stable landmasses. Changing land area relationships have divided supracontinental faunas into the present continental faunas and, in a few cases, have delivered new taxonomic groups to a continent. Many paleogeographic interpretations of earthworm biogeography have been made (Bouché 1983; Omodeo 2000; James 2004; Blakemore 2006) in combination with phylogenetic hypotheses. We now have a more robust estimate of earthworm phylogeny at the family level (James & Davidson, unpublished), a simplified version of which is in Fig. 3.6.8. In this phylogeny there are many branching points which do not lend themselves to straightforward vicariance interpretations at the time scale of the separation of Gondwana from Laurasia, nor in relation to the breakup of those two superconti-

nents. For example, Glossoscolecidae (*s.s.*; South America) appears as the sister taxon to Eudrilidae (Africa), a simple transatlantic relationship which would in isolation be consistent with the opening of the South Atlantic. However, the Ocnerodrilidae are found on both sides of the divide, and share a more recent common ancestor with Eudrilidae than with the Glossoscolecidae. The same is true of the Benhamiinae, with genera on both sides of the South Atlantic, and an even more recent common ancestor than the Ocnerodrilidae–Eudrilidae node. If any of the above bifurcations was approximately contemporaneous with the opening of the South Atlantic, it was the division of the Benhamiinae. All others are of greater age. Pre-pangean continental earthworm faunas can only be speculated, but the existence of various apparent relicts far from their nearest relatives (e.g. Biwadrilidae, Kynotidae in Fig. 3.6.8; James & Davidson, unpublished data) suggests that there were such faunas, and that earthworms are an old element of terrestrial communities.

3.6.5.3 Regional scale

With most earthworm families distributed at continental or subcontinental scales, phylogenetic community structure is independent across the scale

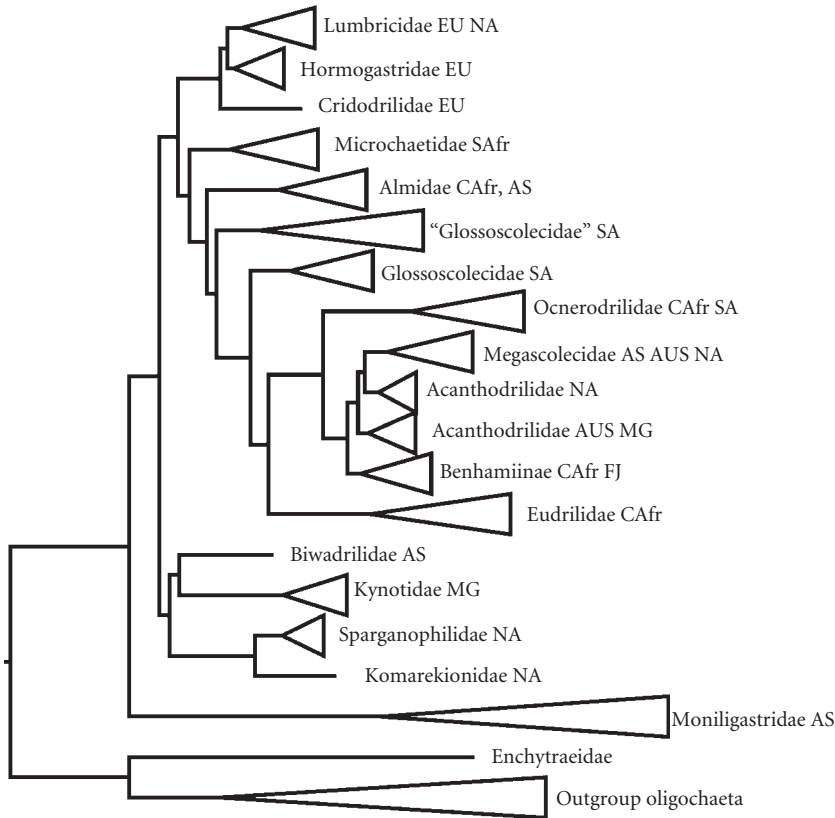


Figure 3.6.8 Phylogeny of earthworm families rooted with aquatic oligochaete outgroups (Bayesian analysis; 18s, 28s, and 16s genes), collapsed to family level. "Glossoscolecidae" indicates a section of that family which falls outside a more strictly defined Glossoscolecidae. Geographical locations of the sampled taxa: AS Asia, AUS Australia, CAfr Central Africa, EU Europe, FJ Fiji, MG Madagascar, NA North America, SA South America, SAfr South Africa.

units. Within continents, those families with diverse genera probably had a long history of evolution and occupation of the land mass. By comparison across higher taxonomic groups it is evident that the range of functional group characteristics has been repeated many times, though not in precisely the same way or to the same degree. Several of these, such as the number and locations of gizzards, pigmentation, pattern of musculature, the setal arrangement, and the degree of intestinal surface area enhancement, have clearly converged in many different earthworm lineages. In some faunas the anecic functional group appears to be missing, in spite of a long history. In one case the evolution of one functional group of species from another appears to have been rapid (Perel-Vsevolodova 1987).

Therefore, it is better to look within these units of scale at the diversity within families or other supra-specific taxa. In some earthworm faunas, earthworm functional group traits can be strongly linked to phylogeny. Forest epigeic worms in the eastern USA are exclusively *Bimastos*, while the endogeics are one or more of *Eisenoides*, *Diplocardia*, and *Komarekiona*. Southern Brazilian *Glossoscolex* contains separate wetland and mesic soil clades, and epigeics, if present at all, are typically *Urobenus* (James & Brown 2006). Southern France earthworm communities usually have *Scherotheca* anecic species, *Prosello-drilus* mesohumic endogeics, other endogeics such as *Gatesona*, *Aporrectodea*, and infrequently some *Dendrobaena* epigeic species (Bouché 1972). Details of distributions often show little range overlap

between congeners, exclusive of invasive species. For example, in most of Southern France one can only find a single species of *Scherotheca* on a given site, (Bouché 1972). This pattern is suggestive of phylogenetic repulsion driven by competition among similar taxa (Helmus *et al.* 2007). Considering that most earthworm species are narrow endemics, apparent phylogenetic repulsion could be quite common. Species pairs rarely or never coexisting in northern France included intrageneric pairs and intergeneric pairs, but all such infrequent pairings were between earthworms of the same ecological type (Decaëns *et al.* 2008b). This suggests that niche-based prediction of competitive exclusion is more likely to be correct than taxon-based prediction.

The other process mentioned by Helmus *et al.* (2007), the coexistence of related taxa under a phylogenetic attraction model driven by environmental filtering, is also possible. There is a clade of epigeic Lumbricidae including *Eisenia*, *Allolobophoridella*, *Dendrodrilus*, and *Bimastos* (North American) (James & Davidson, unpublished data). Forested habitats favorable to such worms should have a strong phylogenetic community structure and clustering of traits linked to the epigeic function. This is partially confirmed in Decaëns *et al.* (2008b), but there were also epigeics from other lumbricid clades. If phylogenetic attraction is to be invoked in this case, it implies that the most recent common ancestor of these epigeics was also epigeic, and other lifestyles evolved from that ancestral state. This hypothesis competes with the alternative that environmental filtering operated on independently-derived epigeic groups. It would be instructive to investigate the assembly rules of natural earthworm communities, rather than those generated by chance introductions influenced by human activity. Other functional groups are less strongly connected to Lumbricidae phylogeny, with anecics spread across at least five genera apparently by convergent evolution. However, the scale-dependence is important, because a given genus may provide the majority of anecic species functions within a given area.

One set of traits known for many decades, but only recently explored in detail, is the presence of nephridial symbiotic bacteria in many earthworm lineages (Knop 1926; Schramm *et al.* 2003; Davidson & Stahl 2006, 2008; Pinel *et al.* 2008; Lund *et al.* 2009;

Davidson & James, unpublished data). Best known in the Lumbricidae, where such bacteria are ubiquitous, the diverse lineages of symbiotic bacteria include obligate symbionts. One lineage, *Verminephrobacter* (Pinel *et al.* 2008) has many genomic rearrangements typical of symbiotic bacteria and has a large number of genes involved in nitrogenous compound transport and transformation. It is transmitted vertically by maternal means (the egg parent is the source of infection to the embryos in the egg capsules) and is only acquired during embryonic development (Davidson & Stahl 2006, 2008; Davidson *et al.* 2010). The phylogenetic distribution of symbiotic bacteria shows a potential ancestral symbiosis retained in the Lumbricidae, multiple independent acquisitions of other symbionts, one or more losses in the divergences leading to other earthworm families, and further independent acquisitions in some of those families (Davidson & James, unpublished data). Nephridial morphology and earthworm ecological type appear to have some relationship to the nephridial symbiont status of earthworms. Ecological significance, contribution to ecosystem processes, and impact on individual fitness remain to be investigated.

3.6.5.4 Local scale

Worms and many other soil biota are low-dispersal, and so are expected to have high inherent geographical structure. This is most relevant to the smallest spatial scales of phylogenetic community structure. In topographically complex regions, of which New Zealand and mountainous central Europe are the best known for earthworms, closely related species of very similar ecology occupy small ranges. Phylogenetic community structure and trait-based earthworm ecology should be meaningful and predictive. These could be combined with environmental data for niche-based range prediction, and further explored in global change models. Cryptic species diversity is a potential complication in this connection, and also in the examination of the ecology and distributions of common anthropochorous species (Novo *et al.* 2009, 2010; James *et al.* 2010). Earthworms have very deep mitochondrial COI divergence (10–20%; Pérez-Losada *et al.* 2005; King *et al.*

2008; Rougerie *et al.* 2009; Chang *et al.* 2009) in the DNA barcode region (Hebert *et al.* 2003a,b), even between some morphologically identical lineages. At this time there has been no investigation of the functional equivalence of cryptic species, but morphological evidence would indicate that any differentiation is probably small. Abiotic conditions and litter/SOM quality are important influences on earthworm community structure at local to regional scales (Fig. 3.6.7; De Deyn *et al.* 2008).

3.6.5.5 Global change drivers, earthworm community structure, and ecosystem functioning

Anthropogenic changes relevant to earthworm communities include habitat alteration, invasive species, and climate change. Assuming an indigenous set of earthworm species, intense disturbances such as deforestation typically result in the loss of a large percentage of those species. Disturbance intensity and frequency are important variables for both extinction of endemics and colonization by invasive species (Hendrix *et al.* 2008). Limited recolonization post-disturbance can occur depending on the extent and severity. Sanchez de Leon *et al.* (2003) observed that native Puerto Rican earthworms repopulated abandoned agricultural land, but that the soils were still dominated by an invasive species. The outcomes of habitat alteration and succession are variable across earthworm communities. The majority of earthworm ecology has been done on species tolerant of habitat alterations, most of which are now considered invasive earthworms.

Invasive earthworm success in population establishment varies with habitat disturbance factors and the presence or absence of a resident community of earthworms. Phylogenetic content replacement is the rule, and traits may be lost, gained, or redistributed as a result of invasions. In a typical tropical scenario, the invasive endogeic *Pontoscolex corethrurus* may be the only species present after disturbance and propagule arrival. Temperate zones globally typically acquire invasive European Lumbricidae or some of the East Asian *Amyntas*. In North America, where anecic species are unusual, *Lumbricus terrestris* introduces this trait set into forests and grasslands. However, the majority of the distribution of

the invasive Lumbricidae in Europe and North America is in regions previously earthworm-free in the wake of glaciation. In such locations earthworm invasions may be significant agents of ecosystem change (Hale *et al.* 2005; Hendrix *et al.* 2008).

Climate change effects on earthworm communities have not been closely explored with experimental procedures. Distributional data in temperate zones indicate a strong influence of glaciation history on modern distributions, and a very slow rebound from refugia to deglaciated land, where invasive species now dominate (e.g. Frelich *et al.* 2006; Bouché 1972). The slowness indicates that range shifts of continental scale may take between 0.5 and 1 million years, with regional shifts an order of magnitude less. Here we assume a spread rate of 10 m year⁻¹, typical of invasive species in unpopulated soils (van Rhee 1969; Stockdill 1982) and no significant geographical barriers such as rivers, inhospitable soils, mountains, etc. Northern plant communities are out of equilibrium with modern climate (Davis 1989), and yet move faster than earthworms (~200 m year⁻¹). Rapid climate changes make it unlikely that earthworm communities and their ecosystem services will survive in current form, because the environmental filters may change faster than worms can respond. Ecological sorting depends on the mobility of the species pool as well as the rate of environmental driver change. Here we are considering a pool that is essentially immobile relative to the rates of environmental change anticipated. Under the conservative estimates of climate change, the future of earthworm ecosystem services may depend on invasive species in large, topographically simple regions. Topographic complexity provides steeper environmental gradients over short distances, which lend themselves better to climate driven range shifts by non-vagile soil organisms. Otherwise, medium-term evolutionary change may be the response mechanism available to earthworms.

3.6.6 Enchytraeids

3.6.6.1 Introduction

Enchytraeidae are small oligochaete worms (6–50 mm in length), adapted to semiterrestrial and terrestrial environments (Christensen & Glenner 2010),

including intertidal sands and ice sheets (Erséus & Rota 2003; Hartzell *et al.* 2005). They show a global distribution from the Arctic to the tropics (Nurminen 1965; Petersen & Luxton 1982; Standen 1988; Didden 1993). Up to 700 species have been described, of which 650 are considered valid (Erséus 2005). Traditionally, they are assumed to be mainly microbivores (Didden 1993). Recent research sustains that they are also saprovores, consuming organic matter that is on average 5–10 years old (Briones & Ineson 2002), but with great feeding flexibility, allowing them to access the more recalcitrant C sources when competitive pressures force them to switch to a different diet in response to warming (Briones *et al.* 2007a, 2010).

Most research on Enchytraeidae has focused on Europe and is based on a low number of samples from a few localities, taken over a short period of time (Briones *et al.* 2007b). However, from these studies it is possible to conclude that climate exerts profound effects in determining their geographical patterns. They are more abundant in temperate rainy climates with moderate or cold summers than in areas with dry, warm summers such as alpine meadows, tropical grasslands and tropical rainforests or in snowy areas and tundras (Briones *et al.* 2007b). In addition to climatic factors, soil pH, soil type, and vegetation cover also appear to play important roles in determining their presence and abundance. Accordingly, moorland soils, which are characterized as cold and extremely wet and having low-growing vegetation (shrubs, grasses, and mosses), high organic matter content and low pH (<4), sustain the highest numbers (Peachey 1959; Springett 1967; Briones *et al.* 2007b; see also review by Briones (2009)).

3.6.6.2 Continental scale

Detailed descriptions of biogeographical patterns are still scarce. Only recently the phylogenetic relationships of these small sized oligochaetes have started to be unveiled. The first studies using molecular data, which included not only enchytraeids but also other members of the Crassicitellata (such as earthworms) suggested that they are a monophyletic group (Siddall *et al.* 2001; Erséus & Källersjö

2004; Rousset *et al.* 2008). More recently, Christensen and Glenner (2010) produced the first phylogenetic analysis for 14 enchytraeid species representative of nine genera, which rendered two main clades: the early segregated paraphyletic group comprising *Lumbricillus* and *Enchytraeus*, exploiting sea shore habitats (r-strategists) and a later segregated larger monophyletic group including species living on decaying organic matter in more stable terrestrial ecosystems (K-strategists) (Christensen & Glenner 2010). According to this study, the sea shore could have then represented the first semi-terrestrial habitat which allowed early colonization until a well-established land vegetation provided an appropriate environment for later diversification. This is in agreement with the results from a previous phylogenetic analysis concluding that enchytraeids originated from an aquatic environment (Rousset *et al.* 2008), but contradicts early studies suggesting that the family has a terrestrial origin, either from South America or a contiguous southern land mass (Coates 1989) or from the Arctic (Dash 1990). This lack of agreement on a terrestrial or aquatic origin is a reflection of the inclusion of taxonomically problematic genera such as *Fridericia* and *Marionina* (e.g. Schmelz 2003; Schmelz & Collado 2008; Dózsa-Farkas 2009) in the phylogenetic trees, biased sampling towards a high proportion of non-terrestrial species (Rousset *et al.* 2008) and extensive radiation processes occurring in some genera (Erséus *et al.* 2010).

Interestingly, the most recent and more complete analysis of a multigene data set combining mitochondrial and nuclear genes (Erséus *et al.* 2010) and including 86 species (belonging to 14 genera) corroborated the existence of a basal dichotomy of the Enchytraeidae family but with a different evolutionary history. Accordingly, the Enchytraeidae root would be represented by those enchytraeid species with a tropical distribution, while the sister group would comprise the remaining enchytraeid taxa which can be further subdivided into two clades, each with both terrestrial and marine species (and including the previously considered ancestral genera, *Lumbricillus* and *Enchytraeus*) (Fig. 3.6.9). This different tree topology is the result of a much greater number of outgroups (17 in Erséus *et al.* 2010, and two in Christensen and Glenner 2010) and thus, a wider variety of Oligochaeta families

and provides stronger evidence that tropical soils were perhaps the first inland habitat successfully colonized by enchytraeids from where major genera diversification took place. It is also likely that the enchytraeid invasion of a greater range of habitats took place on several occasions (Coates 1989). The majority of the species included in the potentially most primitive clade (*Hemienchytraeus*, *Achaeta*,

Guaranidrilus, and *Tupidrilus*) are only found in the southern hemisphere, with many only known from South America (Fig. 3.6.9). Although detailed descriptions of biogeographical patterns are still scarce, it has been speculated that climatic factors (extreme temperatures, long periods of frost/snow cover) as well as soil factors (e.g. organic matter content and pH) exert control over their geographi-

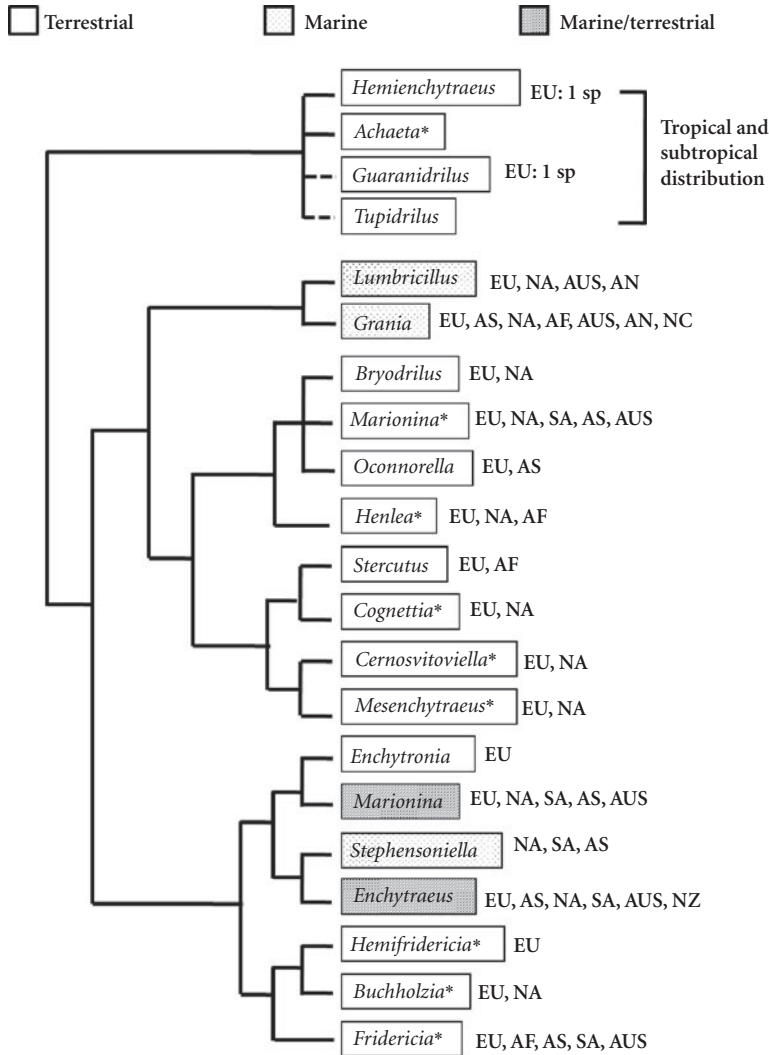


Figure 3.6.9 Schematic relationships among Enchytraeidae genera, redrawn from Erséus *et al.* (2010) together with their recorded geographical distributions. *Terrestrial genera with marine species (<http://www.inhs.uiuc.edu/~mjwetz/ENCH/MarEnchList.html>). Distributions from Rota (1995), Rota and Erséus (2003), Schmelz and Collado (2010) and the GBIF Data Portal, data.gbif.org (accessed on 12 December 2010). Geographical locations of the sampled taxa: AS Asia, AUS Australia, AF Africa, EU Europe, NA North America, SA South America, NZ New Zealand, AN Antarctica, NC New Caledonia.

cal distribution (Rota *et al.* 1998). Thus, species such as *Enchytronia parva* and *Enchytraeus lacteus* are mainly restricted to the southern boreal zone (Nurminen 1970; Kairesalo 1978) and *Buchholzia fallax* does not even reach this latitude (Nurminen 1967). Similarly, a mean annual temperature threshold of 16 °C has been found for *Cognettia sphagnetorum* (Briones *et al.* 2007b), above which it has never been recorded. Both ecological (habitat preferences, physiological tolerances, dispersal abilities, etc.) and historical data (geological history, vegetation patterns and geomorphology of the area sampled) are needed to elaborate a more complete picture of enchytraeid dispersal from the southern land mass.

3.6.6.3 Regional scale

Under a constant climate environmental factors such as soil pH, soil type, and organic matter quality and quantity also appear to have an important influence in controlling enchytraeid community structure. In non-wooded habitats, low organic matter content, together with higher pH values, usually result in a more diverse but less numerous enchytraeid community, whereas the acidic conditions of the organic-rich soils lead to high numbers of enchytraeids but dominated by two to three species (Standen 1984) and with *Cognettia. sphagnetorum* usually representing 95% of the total community. In forested ecosystems, the quality of litter materials and the concentration of microbial biomass therein appear to be most important for enchytraeid populations (Scheu *et al.* 2003). Indeed, changes in food quality as well as in abiotic conditions seem to explain the observed transient increases in enchytraeid abundance after clear-felling in the short term (Huhta 1976; Lundkvist 1983; Siira-Pietikäinen *et al.* 2001; Nieminen 2009). In contrast, the long term (>10 years) responses varied and numbers could either be lower than the control forests (Lundkvist 1983; Bengtsson *et al.* 1997) or leveled out (Siira-Pietikäinen & Haimi 2009). However, higher mortality rates of enchytraeids have been recorded a few years after tree-felling during the summer months and very few recovered in the following month, suggesting that microclimate conditions exert a much stronger influence and could

compromise their future existence (Uhia & Briones 2002).

3.6.6.4 Local scale

Although vegetation cover and diversity do not seem to affect their abundance, some studies have associated enchytraeids to certain plant microhabitats. For example, in grasslands significantly higher densities of enchytraeids have been found under *Dactylis glomerata* and *Trifolium subterraneum* than under *Rumex obtusifolius* and *T. pratense* (Wardle *et al.* 2003). Similarly, *Juncus squarrosus* moors usually sustain relatively high population numbers (Peachey 1959; Springett 1967; Whittaker 1974; Briones *et al.* 1997, 2007b) and generally higher densities have been recorded in coniferous forest compared to deciduous woodlands (Kasprzak 1986 in Kapusta *et al.* 2003). This could be possibly related to changes in soil acidity, with numbers declining as pH increases (Standen 1984) and has led to the conclusion that enchytraeid communities are more sensitive to soil variations within the same plant communities than to successional vegetation changes (Nowak 2001). Furthermore, acidic conditions in soils usually prevent the colonization by other ecosystem engineers such as earthworms, with only a few exceptions of some acid-tolerant species; consequently, enchytraeids become the dominant faunal group in terms of live biomass in these ecosystems (Cragg 1961; Coulson & Whittaker 1978).

High population density does not often go with high species richness. For example, in peatland soils enchytraeid communities are not usually very diverse with typically only five to six species (Springett 1967, 1970; Standen & Latter 1977; Briones *et al.* 1997). This contrasts with the species-rich wet habitats such as river or lake banks (Rota *et al.* 1998), limestone areas (Springett 1967, 1970; Standen & Latter 1977; Rota *et al.* 1998) and taiga and tundra habitats (Piper *et al.* 1982; Christensen & Dózsafarkas 1999), where up to 18 species have been recorded but with lower overall enchytraeid densities. Again, changes in soil pH and organic matter content appear to be the main explaining factors and as a result, species richness has been reported to be

positively correlated to soil pH (Standen 1984; Nowak 2001) and negatively with organic matter content in the topsoil layers (Kapusta *et al.* 2003). However, life-history traits have also played an important role in shaping enchytraeid communities. For example, the more diverse enchytraeid communities in the Arctic tundras are characterized by a high degree of endemism which indicates an undisturbed long history (Christensen & Dózsa-Farkas 2006). This has led to the suggestion that enchytraeids are slow dispersers (Hartzell *et al.* 2005) and that the most likely sources of postglacial colonization were glacial refugia (Christensen & Dózsa-Farkas 2006).

In functional terms, enchytraeids have long been considered “litter transformers,” together with microarthropods (Lavelle 1996). Accordingly, their main role in ecosystems would be depositing casts (excrements) which are hotspots for microbial activity and, hence, mineralization. Their fecal pellets can constitute a large proportion of the soil horizons in upland grasslands and evergreen forest floors (Davidson *et al.* 2002; Bruneau *et al.* 2004; Tagger *et al.* 2008). Because their assimilation efficiency is very low, they have to ingest large quantities of organic matter (up to 0.75 Mg ha⁻¹ year⁻¹ of soil; Didden 1990), and considerable amounts of undigested material are deposited (Martin & Marinissen 1993).

Regarding their role as bioturbators, limited research has been done (Van Vliet *et al.* 1995, 1998; Tyler *et al.* 2001; Roithmeier & Pieper 2009), but from these studies it is obvious that enchytraeids reduce soil compaction and, consequently, increase hydraulic conductivity (Van Vliet *et al.* 1998) and, hence, nutrient leaching potential of water-extractable compounds such as dissolved organic carbon, nitrate, calcium and magnesium (Roithmeier & Pieper 2009). Furthermore, in moorlands and wetlands, bioturbation can increase oxygen concentration and modify the chemical gradients in soil profiles by increasing the fluxes of nutrients (Mermillod-Blondin & Lemoine 2010). In those soil systems where they coexist with earthworms, enchytraeids seem to have a more important role in soil structure dynamics because they comminute the feces of other animals and as a result they increase the pore volume of the soil (Topoliantz *et al.* 2000). In contrast, in soils without earthworms,

soil homogenization is much less complete, but by ingesting and excreting clay and organic matter, enchytraeids appear to be the dominant bioturbators within the subsurface horizons of such soils (Tyler *et al.* 2001). Therefore, enchytraeids could be considered to be the ecosystem engineers of the organic layers, whereas earthworms play an essential role in structuring the organo-mineral layers (Tagger *et al.* 2008).

3.6.6.5 Global change drivers, enchytraeid community structure, and ecosystem functioning

Among global change drivers, climatic factors, namely temperature and rainfall regimes, seem to shape global enchytraeid distribution (Briones *et al.* 2007b). And so, accordingly, cold and wet environments with mild summers are consistently linked to greater densities of enchytraeids, whereas summer droughts drastically reduce total numbers (Briones *et al.* 1997; Beylich & Achazi 1999). Because their response to abiotic factors is species-dependent (Briones *et al.* 1997), behavioral adaptations exhibited by certain species (namely *C. sphagnetorum*) could allow them to survive in the deeper layers, which would result in accelerated turnover of the less labile C substrates occurring there, and with implications for water quality, greenhouse gas emissions, and the fate of carbon stocks in general (Briones *et al.* 2007b, 2010). Therefore, any alterations in enchytraeid communities may have important implications for ecosystem services in those biomes where they are dominant.

3.6.7 Trait-based ecology of soil invertebrate ecosystem engineers with a view to the possible effects on global environmental change and ecosystem functioning and services

The community assembly of soil invertebrate ecosystem engineers cannot be understood without considering their food resources. With the exception of predatory ants and ants tending sap-sucking insects, their food is dead organic matter or fungi cultivated on it. The physical environment, resource quality and organisms control organic matter

transfers in terrestrial ecosystems (Swift *et al.* 1979) in a hierarchical fashion whereby the physical environment is of overall, and resource quality is of specific importance in structuring soil organism communities (Lavelle *et al.* 1993). This assumption also underlies Fig. 3.6.1 in that different major groups of soil invertebrate ecosystem engineers are globally associated dominantly with biomes that are characterized by combinations of climate and soil type. Yet, at regional to local scales a clear hierarchy of environment and resources is not straightforward in soil invertebrate ecosystem engineers, because, by definition, they modify their habitats to suit their niche requirements. Consequently, resource quality will be an important habitat-selecting factor, influencing ecosystem functioning and services (Tian *et al.* 1997; Wolters 2000; Fox *et al.* 2006).

The filtered trait distribution of Fig. 3.6.2 can be used to predict changes in either species composition and abundance or ecological processes (Fig. 3.6.10), such as decomposition, nutrient cycling and carbon sequestration, and responses to drivers of global environmental change.

We suggest that the distinct patterns across biomes in belowground community biomass and composition (Fierer *et al.* 2009) and in soil mesofauna-mediated litter decomposition rates, which is quantitatively important for the C balance, especially in temperate and wet tropical biomes (Wall *et al.* 2008), can be explained by trait associations of soil invertebrates and plants. Through plant tissue/litter quality, plants will elicit response traits in soil-

dwelling litter transformers, including soil invertebrate ecosystem engineers that are detritivorous or humivorous, and which result in effect traits on ecosystem functions and associated services. Trait associations are also to be expected between plants and leaf-cutter ants, but seem less probable between plants and the majority of predatory ants.

Plant associations with soil organisms are crucial for supporting soil carbon input from primary production as well as for carbon output and carbon stabilization in soil (Brussaard & Juma 1996; Wolters 2000; De Deyn *et al.* 2008). The carbon assimilation efficiency of decomposers (usually < 20%, but >50% in termites), the efficiency with which plants use mineralized nutrients, and the level of interactions between organic and mineral soil fractions throughout the soil profile (via rooting and soil invertebrate ecosystem engineers), determine the balance between soil carbon input and output (De Deyn *et al.* 2008).

These considerations are important, because, as traits arise as innovations along the tree of life, often reflecting their biogeographical origins, and tending to be shared by species that have common ancestry (phylogenetic history), it can be argued that phylogenetic diversity is better correlated with ecological processes than species richness (Cavander-Bares *et al.* 2009; Donoghue *et al.* 2009). Hence, the analysis of phylogenetic community structure should be helpful when using a trait-based, i.e. *functional trait-group* approach to understanding (environmental impacts on) ecosystem functioning and associated ecosystem services (Webb *et al.* 2010).

Kozak *et al.* (2008) suggest that the use of GIS data on environmental variation can be relevant in studying processes of speciation, genetic divergence among populations and evolution of traits. One application is in ecological niche modeling, which allows one to predict the range of a species from its known distribution, but evolutionary processes and species interactions also have to be taken into account (Fig. 3.6.11). By extension to the multiple species at a single site, it will eventually become possible to predict community composition, and therefore: 1) estimate the importance of phylogenetic community structure across landscape or regional-scale patches of habi-

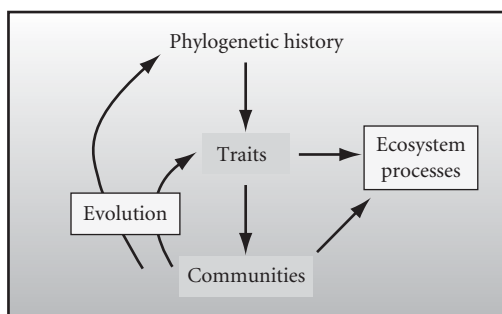


Figure 3.6.10 The central role of traits in understanding evolutionary and ecological processes. (From Cavander-Bares *et al.* 2009, with permission from John Wiley & Sons.)

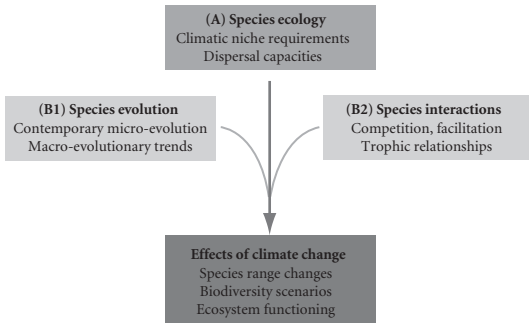


Figure 3.6.11 Mechanisms that should be considered in order to adequately project the effect of climate change on species ranges and species assemblages (*bottom box*). The top box (A) and main arrow represent the most widely used approaches of species distribution models. Boxes (B1 and B2) and side arrows represent the mechanisms that have been little envisaged to forecast climate changes effects, so far, namely that species evolve and interact. (From Lavergne *et al.* 2010, with permission from Annual Reviews.)

tat; 2) determine the degree to which species or phylogenetically-structured sets of species co-occur and are therefore non-random samples of a species pool; and 3) provide an analogous approach to the distribution of organismal traits, ecosystem processes and ecosystem services across spatial scales.

This approach will be a major challenge, not only because it will require the set-up of an appropriate trait database, but also because only a simultaneous approach of trait-based ecology of all major soil invertebrate ecosystem engineer groups will yield insight in their evolutionary and ecological relationships with ecosystem functioning and services and the impacts of global environmental change drivers. To take this approach is also urgent, because most soil invertebrate ecosystem engineers are K-strategists. Whereas their legacies in soil will outlive their presence for mostly unknown periods of time, they will be difficult to recover, once they are gone.

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