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Original article

The values of soil animals for conservation biology

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Abstract

It has taken time for the international community to accept the idea of biodiversity values, a concept which had previously been restricted to the limited aesthetic and touristic aspects of wildlife. This situation changed following the International Convention on Biodiversity in Rio de Janeiro (1992), which focussed on "the forgotten environmental problem" of biodiversity erosion and made the first clear reference to the values of living species. Biodiversity values refer to direct or indirect, economic or non-economic interest, a given species or ecosystem may represent for human populations. These values are generally split into intrinsic and instrumental (use) values, the last category itself being divided into direct and indirect economic values. Obviously, each of these values carries different weights, and cannot be considered as being weighted equally in terms of justification for species or ecosystem conservation. Soil is probably one of the most species-rich habitats of terrestrial ecosystems, especially if the definition is extended to related habitats like vertebrate faeces, decaying wood, and humus of hollow trees (i.e. epiphytic soils). The diversity of soil communities (*sensu lato*) thus probably encompasses a large part of terrestrial animals. This highly speciose fauna has been the subject of recent research efforts, and current trends in soil fauna studies include aspects of biology, autecology, ecotoxicology, or functional ecology. During the past 20 years, recognition of the importance of soil fauna in the functioning of soils and by extension of terrestrial ecosystems has been continuously growing, ending in some important applications in agronomy. However, despite the general agreement about the ecological importance of soil fauna and its economic consequences, the absence of concern about this group from conservationists in their studies is conspicuous. This paper aims at presenting soil fauna within the scope of conservation biology concepts, trying to identify the different values of soil fauna and how they participe to the provisioning of key ecosystem services. Finally, the enormous gap between their recognised usefulness and their consideration in protection policies is discussed.

Keywords: Soil animals; Soil biodiversity; Biodiversity values; Ecosystem goods and services; Conservation biology; Concepts

1. Introduction

It has taken time for the international community to accept the idea of biodiversity values, a concept previously associated only with the limited aesthetic and touristic aspects of wildlife [29]. This situation has changed, mainly since the International Convention on Biodiversity in Rio de Janeiro (1992), which focussed on "the forgotten environmental problem" of biodiversity erosion and made the first clear reference to the values of living species [60]. Biodiversity was at this occasion defined as "the variability among living organisms from all sources including terrestrial, marine and other aquatic ecosystems and the ecological com-

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plexes of which they are a part; this includes diversity within and between species, and of ecosystems" [63]. Biodiversity values thus refer to the direct or indirect, economic or non-economic interest a given species or ecosystem may represent for human populations. Identifying species values comes down to answering the question: What is a species worth [13]? These values are generally split into intrinsic and instrumental (use) values, the last category being itself divided into direct and indirect economic values [29,52,66,106]. Obviously, each of these values carries different weights, and may not be considered equally powerful in terms of justification for species or ecosystem conservation.

Soil is probably one of the more species-rich habitats of terrestrial ecosystems [129]. If extending the definition of soils to related habitats like vertebrate faeces, decaying wood, humus of hollow trees, the diversity of soil communities (sensu lato) probably encompass the majority of terrestrial animal species. This highly speciose fauna has been the subject of recent investigation efforts, with current trends including biology, autecology, ecotoxicology and functional ecology. During the past 20 years, the recognition of the importance of soil fauna in the functioning of soils and by extension of terrestrial ecosystems has been continuously growing, ending in some important applications in agronomy (see e.g. [82]).

Despite the general agreement about the ecological importance of soil fauna and its economic consequences, the absence of concern about this group from conservationists in their studies is conspicuous [129]. This paper aims at presenting soil fauna within the scope of conservation biology concepts, trying to identify the different values of soil fauna and how they rely on key ecosystem services. The enormous gap between their recognised usefulness and their consideration in protection policies is finally discussed.

2. How many species in the soil?

Estimating the diversity of soil animal communities first requires a definition of a "soil animal". Wolters [129] distinguishes between the "full-time inhabitants" (many micro- and mesoarthropods, earthworms and macroinvertebrates) and the "part-time inhabitants" of soil (like many vertebrates, soil dwelling insect larvae or mound-building insects). But what about species that mainly live in/on the litter layer like for example Carabidae predators? Where does soil began and end? What about vertebrate dung, decaying wood, rocks, hollow trees and other "epiphytic" soils; all habitats termed "soil annexes" by Gobat et al. [54]. In this paper we adopt a sensu lato definition of soil animals and will take into consideration examples from these habitats highly connected to the soil sensu strito.

Soils probably represent a necessary substrate for a large part of global biodiversity. For example, the majority of animals in terrestrial habitats are soil inhabitants for at least one stage of their life cycle [7,129]. A rapid survey of invertebrate and vertebrate groups reveals that at least 1/4 of described living species are strictly soil or litter dwellers, the main part of which is insects and arachnids (Fig. 1). This prodigious belowground diversity led to the proposal of the "enigma of soil diversity" [2], demanding why biotic mechanisms that normally reduce diversity (e.g. the competitive exclusion process) have allowed such a large number

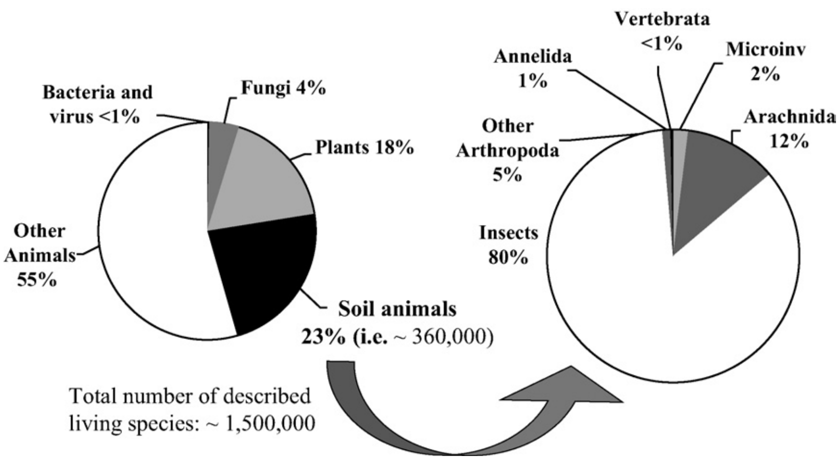

Fig. 1. Importance of soil animals for the global biodiversity (a) and relative importance of major taxa within soil communities worldwide (b) (data from [27,68,104,120,124]).

of coexisting soil dwelling species [127]. A set of concepts and ecological theories are proposed to explain this pattern [33,85,118], involving local processes shaping the interactions between individuals and populations, such as trophic niche partitioning, spatial and temporal segregation, relaxation of density dependant regulations by adverse soil conditions, and a high diversity of micro-habitats [53,129]. All these mechanisms are probably favoured by the nature of the physical environment, as the three-dimensional structure of the soil, the wide range of pores, surface types and microclimates, may reduce competitive exclusion and promote greater species coexistence through resource partitioning. Despite its supposedly critical contribution to global biodiversity, soil fauna has received comparatively little taxonomic attention when compared with other groups such as higher plants and vertebrates. To date, in many groups, there is a considerable imbalance of knowledge of tropical and temperate species, reasons why the soil community has been referred as the "Poor man's rainforest" by Giller [53], and as a new biotic frontier [6,60]. In fact, the more optimistic estimates suggest that soil and leaf litter arthropod richness is about five times larger than in the canopy [91,117].

Fig. 2 presents an overview of the number of described species vs. the estimated number of species that remain undiscovered for the major taxa of soil animals (modified from [124] with additional web sources). In general, the smaller the taxa are, the more they are disregarded in biodiversity surveys (but see [93]). This synthetic figure corroborates conclusions of André et al. [5] who estimate that the ratio of 'number of described species/number of existent species' converge on values inferior to 10 for most groups of microarthropods. Additionally, even for higher body-sized groups for which the taxonomic knowledge may be higher, basic species biology, ecology and distribution patterns remain unknown (see e.g. [50] for earthworms).

To explain this major drawback in soil biodiversity knowledge, authors generally stress the lack of taxonomic expertise [4,11,23,53,124] and of standard sampling methods and protocols [5,23,93]. All this deserves much effort in methodological and taxonomic knowledge to allow meaningful estimation of species richness in soil communities, its main patterns and how it affects soil processes and ecosystem functioning [5,23].

3. The intrinsic values of species

Many conservation biologists believe that every species has intrinsic values, i.e. values not related to any economic or other aspect of usefulness [52,66]. This conception mainly ensues from ethical considerations, from which emerges the idea that a species has value without reference to anything else but its own existence. This value recognises its cultural, social, aesthetic, and ethical benefits. High social and religious values are attributed to individual species or communities of organisms by some groups in society.

Secular and religious standpoints often allow a spiritual value to each species, maintaining that people have a moral responsibility to protect earth's wildlife [47,52]. Early in the last century this thinking constituted the intellectual framework of the political conservation movement of John Muir (1838–1914). While Muir wrote about the equality of species in religious terms, the ecologist Aldo Leopold (1886–1948) was probably

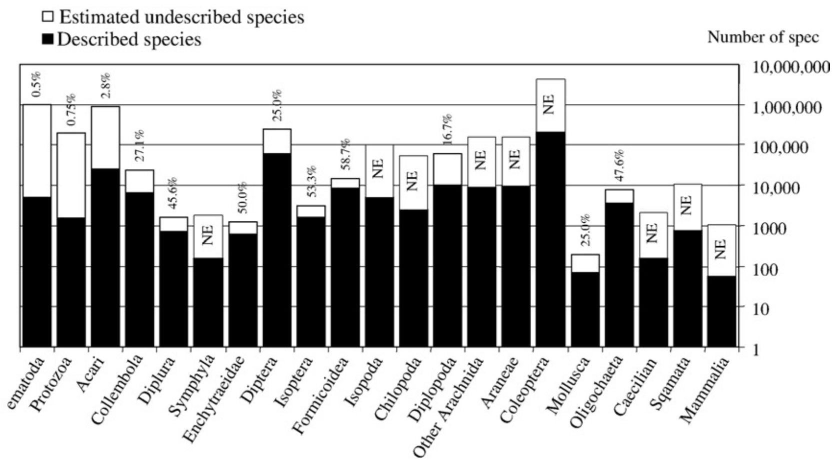

Fig. 2. Estimated numbers of described and un-described species for major soil animal taxa (data from [124], various web sites); NE = no estimation available.

one of the first scientists expressing equality in ecological terms and questioning the well-founded species utilitarian perspectives (see [66]). He argued that the study of the multiple functions played by any given species in an ecosystem is a so complex task that no man can say where utility begins or ends [88]. Leopold's works were the basis of an evolutionary-ecological ethic that considers the importance of preserving species as unique evolutionary links and functional elements of ecosystems.

Accepting the idea of species having an intrinsic value is still highly useful in conservation biology because of its simplicity and equity. As this value is by definition the same for all species, assigning a conservation status to a given plant or animal species may thus be done using extinction probability as the more relevant criteria.

4. The instrumental values of species

Instrumental values refer to the effective or potential use of species by human populations [66]. The ways of using wild species are diverse and allow conservation biologists to assign different kinds of instrumental values to biodiversity. On an economic basis, soil fauna has both direct (the organisms themselves and/or their metabolic products) and indirect (the long-term outcome of their activities) uses. Direct economic values are assigned to species that are directly harvested; e.g. for food, fuel, recreation. Indirect economic values refer to aspects of biological diversity such as ecosystem processes and environmental services that provide economic benefits without being directly harvested [106].

4.1. Direct economic values of soil animals

Direct economic values are probably the easiest to evaluate by observing representative groups of people and market activities from a local to international scale. Primack [106] distinguishes consumptive use values (i.e. goods that are consumed locally) and productive use values (i.e. products sold in markets).

4.1.1. Consumptive use values

The use of soil animals as protein source in human nutrition is still widely represented in indigenous populations in most regions of the world [42,43] and was first reported by Wallace [125,126] more than 100 years ago. More than two thousand invertebrate species are utilised worldwide as a food resource by humans [109]. In Amazonia for example, at least 32 ethnic groups consume a significant amount of small terrestrial invertebrates, and the total number of edible invertebrate species used as food in this area is more than one hundred [100,102]. The variety of invertebrates that have been adopted as food is impressive and include numbers of soil inhabitants, including geophagous, detritivorous, saproxylophagous, leaf cutters, predators and generalists [100]. Among the more widely used soil animals figure leaf-cutting ants (Formicidae: *Atta* sp.), litter-consuming termites (e.g. *Synthermes* sp.) and earthworms (e.g. *Andiorrhinus* sp.) [102].

Examples of local populations consuming soil invertebrates are currently reported in the literature. Entomophagy (including root feeding Lepidoptera larvae and different ant species) is for example particularly important in the culinary culture of Australian Aborigines, and in many cases concerns soil insects [59]. In Colombia, native habitants of the Orinoco Llanos are very fond of swarming females of *Atta laevigata*, locally named "culonas", which they consume like peanuts after toasting the large abdomen in its own butter (TD and JJJ, personal observation/tasting). In sub-Saharan Africa, termite alytes are a highly prized foodstuff and are fried in their own oil with salt to produce a delicious and nutritious snack (GJM personal observation/tasting). In Venezuela, the Ye'Kuana ethnic group collect and consume at least two different edible earthworm species locally called "motto" and "kuru" and recently described under the name of *Andiorhinus motto* and *A. kuru* [101].

In many indigenous populations, the use of edible soil invertebrates corresponds to an important strategy that takes advantage of a highly abundant and renewable resource [59,102]. Invertebrate consumption can provide significant amounts of animal proteins, especially during difficult periods of the year (e.g. rainy seasons) during which fish and game is scarce (e.g. 60% of animal protein diet during rainy season for Guajivos Amerindians of Venezuela).

4.1.2. Productive use values

In a few cases, soil animals used as food may be found in local markets. This is the case for *A. laevigata* in Colombia, which is sold at 1–1.5 Euros 100 g^{-1} during the swarming season in the street of Santafé de Bogotá and other large towns of the country (Bonilla pers. com.). Smoked earthworms consumed by Venezuelan Ye'Kuana also has a high commercial value in local markets, three times higher than the price of smoked fish, game, pork or chicken [101]. In 1981 in Mexico, the demand for "escamoles" (immature stages of the ant, *Liometopum apiculatum* Mayr.) was so great that the price per kilogram went up to 1000 pesos (>1.5 Euros at the then- prevailing exchange rate) [43].

A high number of coleoptera species, which larvae live in the soil sensu lato (mainly rhizophagous, saproxylophagous and predators), are currently sold at insect fairs and specialised internet markets. A proportion of this business concerns scientific material, which is characterised by a high number of specimens generally sold to museums or private scientists at relatively low prices. Other specimens are prized for their ornamental interest to make decorative elements (e.g. Rutelinae, Cetoninae, Carabidae etc.). Finally, the larger and/or more charismatic species may be sold to collectors, even as dried adults of live stock, sometimes at extremely high prices for the more spectacular individuals of some giant Dynastinae or Cerambycidae species or some colourful Rutelinae or Cetoniinae species (arround 2000 Euros). This particular productive use value is directly proportional to the aesthetical value of the species.

4.2. Indirect economic values

Indirect values, although more difficult to evaluate from a monetary point of view, may in some cases be extremely important to support economies. If the services related to these values are not performed, substitute resources must be found, often at great expense.

4.2.1. Ecological values and ecosystem services

Ecological values of soil animals refer to the way this biota provides ecosystem services via ecological functions. Part of this functional significance may be of direct utilitarian value for humans in the production of goods and services that can be priced. Beyond this lie a range of ecosystem services that are of acknowledged benefit to humans but which generally lie outside the boundaries of recognised utilitarian benefit. It is probably one of the more documented aspects of soil animal values.

Ecological functions of soil animals have been widely addressed in the scientific literature, and functional classifications have been proposed by different authors. Some of these classifications, based on trophic relationships between species, are mainly issued from food web models [12,127]. Soil food web studies allow the aggregation of species into guilds according to their trophic level, although this approach inherits a multitude of difficulties mainly due to the dietary plasticity of many soil animals [113]. New molecular methodologies (e.g. fluorescence in situ hybridisation, natural variations in stable isotope contents in animal tissues) have recently given this discipline new and highly relevant perspectives (see review by [113]). An alternative and relatively recent approach is to focus on the impact of species on their physical environment through a 'functional domain' approach [3,77,78]. Functional domains are defined as the sphere of soil influenced by the activity of a single species, in which important soil processes are regulated and resources for other soil biota indirectly modulated [78]. This approach has proven its usefulness to address the functions of the so called 'ecosystem engineers' (*sensu* [71]) or 'bioturbators' (e.g. earthworms, ants, termites), which interact with the soil community through trophic, but also and above all atrophic (engineering) relationships. A just as a recent attempt to integrate these complementary concepts has proven its usefulness in drawing conceptual diagrams of interaction webs between above and bellow ground biota (Fig. 3; [22]).

Soil functioning is mainly controlled by a suit of factors ranging from abiotic with large scale domains (climate, mineral substrate) to biotic with smaller scale domains (vegetation and soil biota) (Fig. 4, [80,121]). At this last scale, soil animal communities are implicated in most key soil functions. Organic matter dynamics, nutrient cycling, C storage, energy flow, water infiltration and storage in soil are mediated by soil biota, wich therefore contributes to the maintenance of ecosystem integrity [22,23,60,77]. Many of the functions performed by soil animals rely on important ecosystem services at scales orders of magnitude above that of the organisms and their functional domains (Fig. 5; [3,7,79]). The only service of organic matter decomposition can be considered of maximum concern as 60–90% of terrestrial primary production is decomposed in the soil [53]. Available literature relating the functional importance of soil animals as mediators of ecosystem services provides growing evidence that without soil biota, all terrestrial ecosystems would collapse rapidly [60].

Finally, soil animals also constitute a food resource for many animals and hence feed a species-rich community of predators [56,60,86]. Earthworms constitute for example a keystone resource consumed by more than 175 species of mammals, birds, reptiles and amphibians in France [57]. In addition to these groups, predators preying upon earthworms may be found in a wide number of taxa, including fishes, insects (mainly

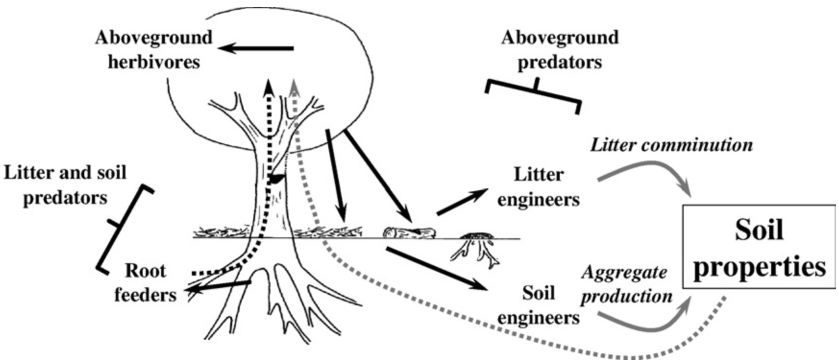

Fig. 3. Conceptual model of soil interaction web involving the main functional groups of soil animals and their relationships with aboveground biota. Dark arrows: trophic interactions; grey arrows: enfineering interactions; dotted arrows: feed backs (after [22]).

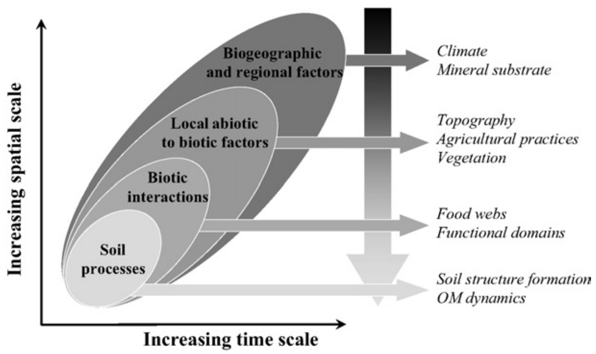

Fig. 4. Hierarchical model of the factors controlling soil functioning (after [40,80]).

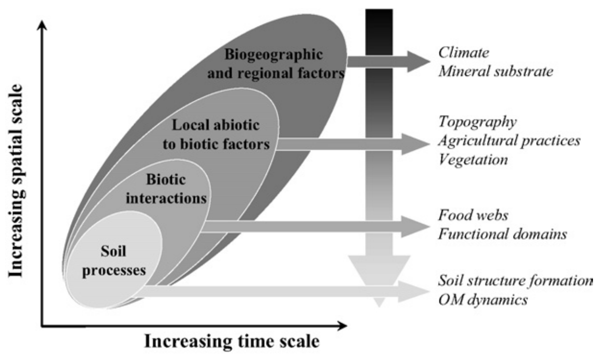

Fig. 5. Hierarchical model of the impact of microscale faunal-mediated processes on large scale ecosystem processes and emerging goods and services (after [40,80]).

Coleoptera), myriapods, gasteropods, annelids, shelled slugs, spiders, opiliones, dipteran larvae [86]. In a more applied domain, soil invertebrates have been considered to be of potential use for domestic animal nutrition [56, 57,59].

4.2.2. Patrimonial and recreational values

Many people throughout the world care about wildlife and are concerned with its protection, thus conferring to species or ecosystems a high "existence value". People value these feelings in a direct way by joining and funding conservation organisations that work to protect their favourite species or habitats [66,106]. This can represent enormous amounts of money when applied to representatives of the so-called "charismatic megafauna", but there is little or no evidence that the same occurs for soil animals, i.e. what is the attractiveness of a soil species to the general public?

Some tropical countries however are actually taking advantage of their high biodiversity to develop ecotourism. This local economy has its roots in an increasing interest for wild plants and animals (i.e. biophilia, [66]), which is generally related and proportional to the subjective notion of species "aesthetic" values. Thus, although obviously of lower importance when compared to more charismatic groups like tropical forest vegetation or large vertebrates, some tour operators often exploit the high diversity of soil invertebrates. In tropical America for example, an increasing number of countries provide "insect hunting tours" in which collectors are invited to collect their favourite families, including a number of soil dwelling taxa (mainly Coleoptera and Arachnida).

More indirectly, some vertebrates that prey upon soil fauna may represent a particular interest for human populations, either because of their potential use as game or, conversely, because of their presence on red lists of threatened species. The importance of soil macrofauna resource for declining bird and amphibian populations has been suggested by Haskell [61] for the forests of the Southern Appalachian Mountains. In France Granval [57] also underlined the importance of earthworm biomass as food resource for 63% of small game in France, and as an important factor for sustaining specialised predator populations like woodcock (*Scolopax rusticola*; Scolopacidae). He also provided a list of 114 vertebrate species of the French fauna that consume at least occasionally earthworms, 94% of which have some kind of legal protection (habitat of bird directive from the EC, Bonn or Washington conventions) and more than half are listed on IUCN red lists [49].

4.2.3. Scientific and educational values

A set of concepts and ecological theories are proposed to explain the extremely rich diversity in soils with the advent of soil ecology that is progressively making its way and becoming a truly interdisciplinary field of scientific innovation [33,85,118,127]. For example, one of the theories that relate the activities of soil macrofauna and the trigger of microorganisms depending on these activities has been explained by using the "sleeping beauty paradox" [76]. Besides, studies on the behavioural ecology of ants and termites have resulted in the development of theories that have served as models in social studies, by comparing how their societies are organised with those of humans.

With reference to education, it is well worth mentioning the importance of informal education, such as "Farmer Field Schools" or schools without walls. It is a learning-by-doing process for both farmers and scientists working with them. The impact of this process was revealed in the rice fields of South East Asia where by using this approach a reduction of 60% in the use of pesticides led to increases in rice production and sustained ecosystem diversity [90]. Or in the case of education for children, for example, soil biology web sites or journals (where a "soil wizard" guides children to discover the secrets of soil (see [96,119]).

4.3. Strategic values in conservation biology

From a conservation point of view, it is interesting to compare the abundance of species and the range of their impacts on ecosystem functioning. Hence, it is possible to rank, by increasing levels of conservation priority: common, dominant, rare, regulating and keystone species [106]. Another view is to focus on the strategic potential of species rather than on their ecological functions. "Flagship" or "umbrella species" are charismatic species with large geographic and/or habitat range, whose protection benefits a large number of non-targeted species. One of the rare examples in soils is provided with the scarabid beetle *Osmoderma eremita* (Scarabaeidae): a medium sized Eurasian beetle that is used as a flagship species by conservation biologists and may help with conservation of old European hedgerows that hold particularly speciose plant and animal communities (see below).

Many groups have been used as indicators of the level of disturbance caused by human activities. Different groups of soil invertebrates have also proven to be useful in this domain, like e.g. Nematoda [19], Collembola [105]. Soil macroinveretbrates comprises of a large range of taxa with diverse biological and ecological traits and patterns of response to different kind of anthropogenic perturbations [99]. Macroinvertebrate communities thus provide an accurate and relevant view of ecological risks that integrate a number of parameters like e.g. soil physico-chemical conditions, bioavailability of pollutants across time, etc [15,20,44,51, 85,89,95,112,122].

5. Ecological economics

The emerging discipline of ecological economics [35,103] considers the full range of services that society derives from nature, because ecosystems provide services that are non-extractive and some methods have been developed for valuing such services, even when these are not included in conventional markets. The inclusion of these non-extractive services changes drastically the outcomes of the economic analyses [62,65, 123].

One step is to identify and describe the values of soil organisms, but an important aspect is to evaluate these functions from a monetary point of view. Hence, if biodiversity could be assigned an economic value, it would provide very strong arguments to conservation biologists to justify biodiversity protection towards politicians or policy makers [13]. The total economic value of a given ecosystem may be considered as the sum of the different values listed in this paper (Fig. 6; after [106]).

Obviously this task is one of the more problematic as many values listed so far are indirect and difficult to express in economic terms. Intrinsic species values, for example, are by definition devoid of any economic values, and thus will lack persuasive power to be really useful. Conversely, some ecological values will be of high indirect monetary importance, especially in agricultural soils where animals will participate to cultivated plant productivity through their impacts on soil fertility [81].

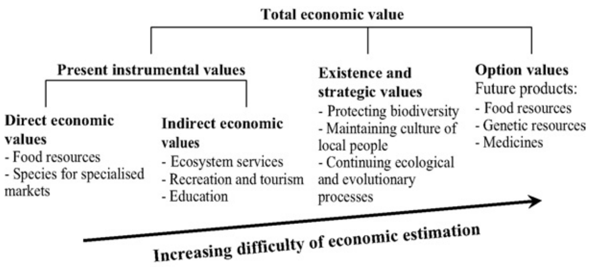

Fig. 6. Conceptual scheme of the global economic value of soil biodiversity in a given ecosystem (after [106]).

6. Threats on soil fauna biodiversity

Species vulnerability to extinction mechanisms is a function of several factors including species adaptive strategy, individual abundance, geographic range and specialisation for a given habitat [66,106,107]. An important point is that most of these species attributes are likely to be interdependent, as demonstrated by the general positive relationship between abundance and geographical distribution [21,52], which seems to also apply to soil invertebrates [129]. Species with narrow geographical ranges tend to have small local populations, making them more vulnerable to extinction by increasing the likelihood of stochastic and simultaneous extinction [106]. In a recent contribution on Amazonian fauna, Lavelle and Lapied [83] (Fig. 7) stressed the fact that earthworm and, to a lesser extent ants, present a very low local to regional richness ratio when compared to many other invertebrate groups. This means both taxa may comprise of a high proportion of geographically restricted species, suggesting that there is a high proportion of still undescribed species with a high risk of extinction under anthropogenic factors.

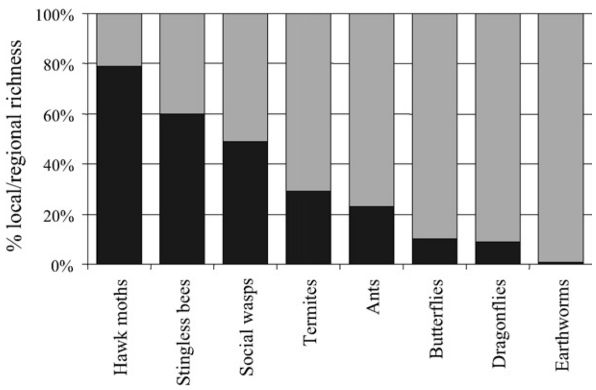

Fig. 7. Endemism in different Amazonian invertebrate groups, calculated as the ratio between regional and local species richness (after [83]).

Environmental factors are known to shape living community structure through all spatial domains, from patches to landscape and biosphere. Following this idea, the "species pool hypothesis" considers local species diversity as a subset of a regional species pool (i.e. the number of species potentially present in a given region) [1,17]. Biodiversity driving factors act as environmental filters, removing species from the original pool at different spatio-temporal scales according to their biological traits [1,73]. The impact of anthropic activities on community diversity may thus be considered as a result of modifications of these natural filters, or of the creation of new filters. This may occur even at the local scale (i.e. changes in biotic interactions through e.g. modification of the vegetation or introduction of exotics), the ecosystem scale (i.e. ecosystem alteration or conversion to agro-ecosystems), or larger scales (i.e. landscape fragmentation, global change) (Fig. 8).

6.1. Local scale filters: exotic plantations and invasive species

Introduction of exotic species into ecosystems is of major concern for conservation biologists [66,106,107, 124]. It may have severe impacts on soil biodiversity by altering the biotic and/or abiotic environment, or by modifying competitive interactions within communities (i.e. the finer-scale filters on Fig. 8). Here we discuss separately the impact on soil fauna communities of the deliberate introduction of plants for agricultural purposes and of the often accidental introduction of invasive soil animals.

Contradictory examples of the impacts of cultivated plant introduction may be found in the literature. In the tropics *Eucalyptus* spp. produce a poor-quality litter [14] that has detrimental impacts on soil macrofauna especially in young forest stands (e.g. termites; [92]). In temperate North America, the introduction of *Berberis thunbergii* and *Microstegium vimineum* modifies soil pH and organic matter levels, thus increasing earthworm density and, subsequently, soil porosity [75]. Conversion of the Amazonian forest into pastures sowed with introduced grasses and legumes is also known to eliminate native fauna which is thus replaced by exotic invasive species [30]. On the other hand, similar pastures in Colombian savanna areas have been found to conserve native soil communities [41, 70].

Exotic species dynamics in soil fauna communities have been little investigated, although examples are often quoted in the literature. Lee [87] reports more than 100 species of exotic earthworms worldwide, and Fragoso et al. [50] listed more than 50 species in tropical regions. Introduction of exotic macroinvertebrates is generally followed by significant impacts on communities or soil functioning [85,124]. For example, the expansion of the invasive earthworm species Amynthas hawayanus (Megascolecidae) in New York forests has been reported to generate deep modifications in soil organic matter composition, water infiltration patterns and soil chemistry [24]. In soils of the United Kingdom, northern Europe and United States the invasion of exotic planarian flatworms has led to an increased predation pressure on native earthworm species [18,98] In Amazonian pastures, forest endemic-earthworms largely disappear and are rapidly replaced by monospecific populations of *Pontoscolex corethrurus* (Glossoscolecidae), a peregrine earthworm which causes severe compaction in surface soil [30]. On the other hand Lee [87] also pointed out the potential functional interest of peregrine species in agricultural lands where native species have disappeared.

6.2. Land use changes and agriculture intensification

Conversion of natural vegetation into agroecosystems and agriculture intensification, have profound impact on soil communities because they involve changes within the primary determinants of soil biodiversity, e.g. vegetation and soil microclimate [39,124] (Fig. 8). As stated by Decaëns and Jiménez [39], agricultural intensification impacts on soil animal diversity fits well within the Huston's dynamic equilibrium model [67]. According to Huston, community diversity is driven by the productivity level and the perturbation rate of the considered ecosystem (Fig. 8). The maximum diversity is observed in systems where equilibrium exists between both factors, whereas local species extinctions may occur by lack of demographic recuperation when perturbations increase or by competitive exclusion when productivity increases.

Disturbance associated with land management practices are extremely diverse, going from decrease in refuges or trophic resources in case of firewood harvesting ([59,97]) or modifications of soil microclimate following periodic fires ([25,34,41,55]), to high mortality of soil fauna consequently to tillage or use of pesticides ([37,38,41,45,46,84,110,116]). System carrying capacity for soil fauna is generally highly increased in medium intensified systems, e.g. sowed pastures. Earthworms particularly take advantage of these suitable condition to rapidly dominate communities [9,38,41, 70,84]. Conversely to pastures, many tilled systems are characterised by a decrease in organic matter levels, which leads to a weak potential of population growth and higher probability of extinction process when disturbances are increased by practices [39].

Land use changes and agricultural intensification also generate severe habitat degradation or destruction for soil biota. In many cases, soil compaction is reported to have negative impact on soil fauna [8]. Examples include: the reduction in soil macrofaunal biomass associated with regular movement of workers in Indian tea plantations [114]; the impact of sheep and goats compacting soil on South African subterranean herpetofauna [10]; or the detrimental effects on soil macrofauna of large logging equipment, tractors and other vehicles [108]. Soil erosion is another severe pro-

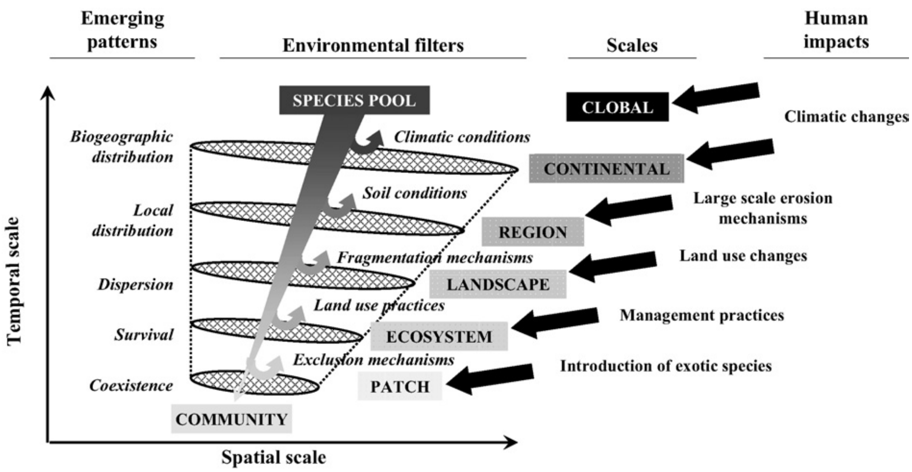

Fig. 8. The species pool hypothesis or how environmental factors act as filters that determine the composition and diversity of communities from a large scale species pool (after [1]).

blem associated with agriculture in many corners of the globe [72], leading to a total destruction of soil biota habitats.

At larger scales, impacts of land use modifications and agricultural intensification may be observed from the landscape to the global levels. As an example, over 50,000 different pesticide products, representing well over two million metric tons are used each year [66], with non-target impacts extending beyond the local scale via bioaccumulation processes along the whole soil food web and eliminating natural predator insects of certain pests [26,36,66,111,128]. Although the subject has been little documented in the literature for soil biota, natural habitat fragmentation and landscape structure have been shown to be important for both macroinvertebrate density and diversity [31,32,61].

6.3. Atmospheric CO_2 levels and climate change

Climate change, increasing atmospheric CO_2 levels, and the resulting changes in rainfall patterns, soil temperatures, and plant performances are predicted to alter soil fauna through different modalities according to the considered scale [118]. Hence, the geographical distribution of soil species is likely to be indirectly influenced through changes in vegetation distribution [58, 124,129]. Ecosystem-level effects of elevated CO_2 are expected to be indirect rather than direct because most soils have higher CO_2 concentrations than surrounding air due to root respiration. Indirect effects on soil biota may occur from changes in plant metabolism, resulting in modification of litter quality and reallocation of C and N [85,124]. Although still largely misunderstood, responses of soil fauna are likely to be different among ecosystems. Swift et al. [118] suggest for example that cold-limited arctic ecosystems are particularly sensitive to global warming, while nutrient limited temperate grasslands are susceptible to CO_2 increase and N-depositions.

7. Current status of soil animals in conservation policies

Giller [53] stressed the conspicuous lack of attention paid to soil biota by conservation biologists, and described the soil community as “the poor man’s tropical rain forest”. This opinion was recently followed by Wolters [129], who considered the lack of conservation ecology approaches for soil biota as a major shortcoming of soil science. Paradoxically, soil habitats and their communities are not likely to be restored easily [85, 124].

When surveying the contents of major conservation biology journals ([16,48,74]), we found that papers dealing with soil fauna only represented 8% of the papers dedicated to animal taxa (Figs. 9, 10). The most addressed soil taxa was ants with 239 papers, a number far below that of papers dedicated to vertebrate groups. A similar trend was found when looking at soil animals in the red lists of the IUCN [69]. Less than 100 species are considered threatened to any degree, and soil animals only represent about 1% of the total number of listed species (Fig. 11). Only eight soil animal species have CITES protection world-wide (i.e. three scorpions, four tarantulas and one lucanid beetle [28]). This point constitutes a real paradox if we consider the high number of species that can be found in insect fairs in many European countries.

As a consequence, soil animals are not taken into account in preliminary biodiversity surveys that are undertaken for protected area planning. At the local scale, impact studies necessary prior to the establishment of any kind of infrastructure do not consider soil taxa (Gioia pers. observation). This is also the case when similar studies are needed to define the place and shape of natural parks and reserves (e.g. in Uganda [64]). This is still obvious when biodiversity spatial patterns are addressed for the identification of proprietary conservation areas at larger scales (e.g. biodiversity hotspots; [94]). Many impact studies particularly lay emphasis on higher plants, vertebrates and, among invertebrates, on butterflies and to a lesser extend on moths.

In few cases are soil organisms used in impact studies which result in significant decisions at the local

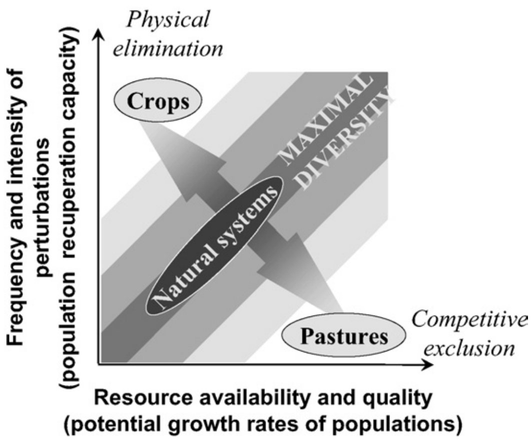

Fig. 9. The Huston’s model of diversity driving factors at the community level [67].

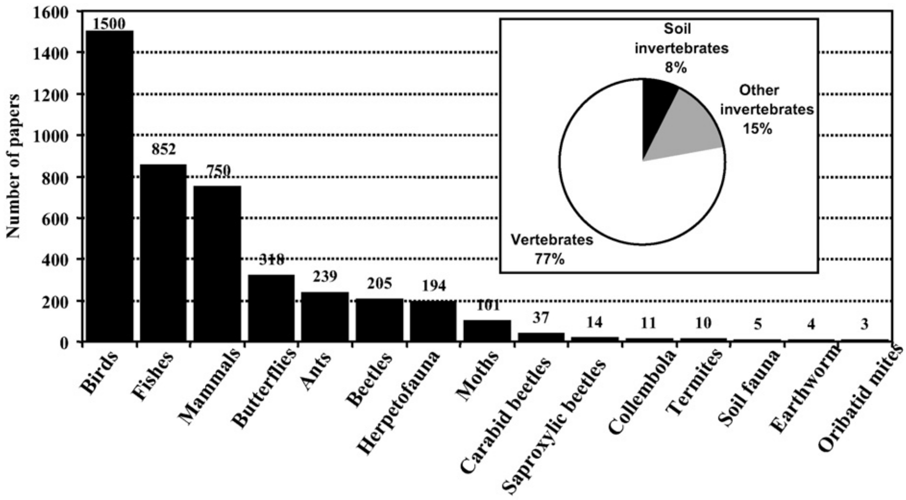

Fig. 10. Number of papers published in three biological conservation journals according to the considered taxa (data from [16,48,74]).

scale. In France for example, the discovery of the beetle *O. eremita*, registered in 1979 and 1992 in annex II of the Bern Convention "Habitats" Directive, during entomological surveys prior to a road construction justified the suspension of engineering works over more than 3 years. Taking into account this species while redefining land organisation significantly orientated management decisions at different scales. For example, the conservation of individual old hollow trees and the maintenance of hedgerow networks as ecological corridors. These protection actions obviously helped at conserving populations of *O. eremita*, but were also considered beneficial for a number of species associated with temperate hedgerows, including a number of plants, saproxylic invertebrates and fungi, nocturnal birds, bats and other small-mammals.

8. Conclusion and perspectives

The multiple values of soil animals presented in this paper provide good arguments to justify concerns about decreasing soil biodiversity. Hence, soil biodiversity ensures the multiplicity of the ecological, environmental and instrumental functions of soil animals in a wide variety of environmental conditions [129]. Policy makers, the public, and national and international trade and economic organisations have yet to realise that soil biodiversity is linked to the visible aboveground compartments of ecosystems, and contributes to ecosystem services and goods that drive economics and benefit humanity [85,124].

As pointed out by Bengtsson et al. [12,13], the relationships between biodiversity and ecosystem function-

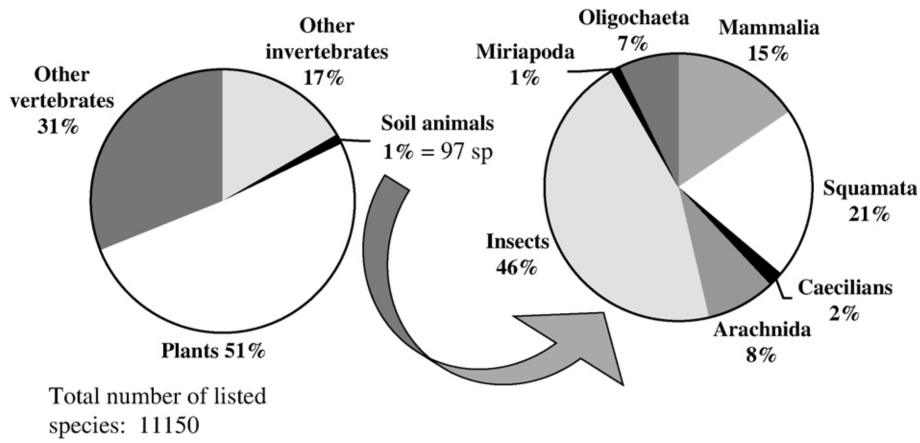

Fig. 11. Relative contribution of soil fauna in the IUCN Red Lists of threatened species (a), and relative representation of the major taxa within the threatened soil animal species (data from [69]).

ing, far from being simple, appears to be system-specific, taxa-specific and process-specific in the light of our current knowledge. In soil while the number of functional groups of animals is important, the number of species per se does not affect primary productivity [115]. Even if the functional importance of soil biodiversity still lacks sufficient studies to be clearly understood [127], its conservation is vital as an insurance against unpredictable or expected environmental changes that may impair ecosystem functioning in the future [13]. Yet evidence suggests that the destruction of soil and its biota would result in cascading effects on ecosystem biodiversity and functioning, thus impairing their capacity at maintaining ecosystem services [85, 124]. In other terms, the application of the so-called "precautionary principle" suggests to consider the conservation of soil biodiversity in planning and policy making.

We propose the following questions and some related research perspectives as main challenges for future soil ecology research:

- How many species in the soil and which functions do they assume? Soil ecologists need to develop strategies to increase the number of taxonomists and systematists working with soil taxa, as they are presently very few [85,124]. They also need to better understand the basic functions assumed by these organisms, especially for poorly studied taxa.
- How much soil biodiversity is enough to maintain the integrity of ecosystem functioning? Studies of the relationships between soil fauna diversity and major ecosystem functions are particularly needed, especially at the landscape level. Functional classification of soil animals may help us to estimate how functional redundancy is important in soil, and whether species loss will have significant functional consequences to the ecosystem. The relationships between biota above and below the soil interface, and how changes in one compartment may alter the functioning of the other should also receive more attention.
- Which tools should be used to evaluate the economic and social values of species and biodiversity? How can we evaluate the importance of biodiversity for local to global markets?
- How can we identify "important" species on which we should concentrate our conservation efforts? For this, we will need to identify which species or taxa are more vulnerable to extinction mechanisms, which are important for local biodiversity maintenance (keystone species), which are providing significant ecosystems goods or services (regulating species), or are sufficiently charismatic to be used as umbrella species by conservation biologists. We also need to identify strategic habitats for conservation below ground biodiversity hot spots or ecosystems that sustain key ecosystem services at the landscape scale (keystone ecosystems).
- How can we transfer our scientific knowledge to the public, policy deciders and soil users? Protection and conservation of soil biota will necessitate and justify more education on the role of "subsurface" habitat biodiversity and how they are linked to aboveground organisms [85,124]. Elementary biology curricula should include more comprehensive approaches to understand how ecosystem functions are sustained by biotic interactions, and how the relationships between biota and the complex physico-chemical soil environment are important to regulate key processes like nutrient cycling and organic matter decomposition.

Finally, the "option value" of soil animals, which refers to their potential to provide an economic benefit to human society at some point in the future [106] should also be considered in further studies. This future value is hard to predict, since it may be based on products or processes that are as yet unimaginable. To date, no attempt has been made to address this topic for soil fauna. Though, the option values of soil animals are likely to be huge, given the very fragmentary knowledge we have regarding their taxonomy, biology and ecology, and their potential use in agriculture and bioremediation.

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