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Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms

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Abstract

Rigorous and widely applicable indicators of biodiversity are needed to monitor the responses of ecosystems to global change and design effective conservation schemes. Among the potential indicators of biodiversity, those based on the functional traits of species and communities are interesting because they can be generalized to similar habitats and can be assessed by relatively rapid field assessment across eco-regions. Functional traits, however, have as yet been rarely considered in current common monitoring schemes. Moreover, standardized procedures of trait measurement and analyses have almost exclusively been developed for plants but different approaches have been used for different groups of organisms.

Here we review approaches using functional traits as biodiversity indicators focussing not on plants as usual but particularly on animal groups that are commonly considered in different biodiversity monitoring schemes (benthic invertebrates, collembolans, above ground insects and birds). Further, we introduce a new framework based on functional traits indices and illustrate it using case studies where the traits of these organisms can help monitoring the response of biodiversity to different land use change drivers. We propose and test standard procedures to integrate different components of functional traits into biodiversity monitoring schemes across trophic levels and disciplines. We suggest that the development of indicators using functional traits could complement, rather than replace, the existent biodiversity monitoring. In this way, the comparison of the effect of land use changes on biodiversity is facilitated and is expected to positively influence conservation management practices.

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Keywords

Bioindicators; birds; carabids; collembola; functional diversity; macroinvertebrates; community weighted mean trait; standardized biodiversity monitoring


Abbreviations

mT          mean Trait per community

FD          Functional Diversity

LU          Landscape Unit


Introduction

Globally, the proportion of land that has been transformed or degraded by humans is estimated to range between 40-50 % since 1945 (Daily 1995). Much of this land use transformation has led to a decline in ecosystem quality, i.e. naturalness, and the erosion of biological diversity. Biodiversity loss is a growing concern that has moved from the scientific community to public awareness and the political arena. In 2010, more than 190 nations worldwide will be called to present their progress in biodiversity conservation at the 10th Conference of Parties of the Convention on Biological Diversity (Balmford et al. 2005; Mace and Baillie 2007). Consensus and commitment to biodiversity conservation, however, cannot be achieved and translated into management planning unless reliable ways to monitor biodiversity have been developed (Noss 1990; Mace and Baillie 2007). The identification of widely applicable indicators of biodiversity is crucial for effective monitoring schemes.

Various methodologies are adopted for monitoring different aspects of biodiversity and practically it is impossible to assess all aspects of biodiversity in an ecosystem. In theory, a number of different indicators, providing information on genes,

species or populations, and ecosystems or any combination thereof are needed for a relevant, albeit relative, evaluation of biological diversity (Niemi and MacDonald 2004; de Bello et al. 2010). The term indicator  of biodiversity, in this sense, is used for any measurable single or composite variable that can help to estimate and monitor a particular component of biodiversity (Teder et al. 2007). Standardized indicators, i.e. for which a methodology and data exist, are therefore essential for all types of biodiversity monitoring (e.g. Green et al. 2005) and different initiatives have attempted to produce lists of minimum sets of indicators of biodiversity to monitor the pace of biodiversity loss and assess the result of restoration and conservation policies (e.g. Streamlining European 2010 Biodiversity Indicators; EEA 2007).

In general however, biodiversity, have been often estimated using a simple index, i.e. species richness (i.e. the number of species; Levrel 2007) or other indices based on the taxonomical composition of communities and ecosystem under study (such as the Simpson index or the presence of red-list species). However biodiversity need not be restricted to taxonomical components such as numbers of species, but should also include functional components of communities (Noss 1990; de Bello et al. 2010), which reflect important structural properties of communities (Moretti et al. 2009).  For example, taxonomical  indicators assign an equal functional weight to all species, for which there is no clear justification (Levrel 2007). Functional traits, i.e. the characteristics of organisms with demonstrable links to the organism's fitness, have a long tradition in ecological studies, especially with regard to plants (Cornelissen et al. 2003). Their possible application have, nevertheless, been investigated through a dozen of papers in freshwater and marine ecology (e.g., Statzner et al. 2001; Bonada et al. 2006; Diaz et al. 2008; for freshwater environment and e.g., Bremner et al. 2006; Mouillot et al. 2006; for marine or transitional environments). In freshwater

environments, Charvet et al. (1998) showed, for example, that effluents from a wastewater treatment plant significantly changed the trait composition of benthic invertebrate communities in a small stream. Similar investigations at the European scale showed significant differences in the trait composition between communities impacted by sewage and natural reference communities for different countries (Statzner et al. 2001). However this concept is yet a neglected component in biodiversity monitoring programmes in most ecosystems (Feld et al. 2009).

Traits can be an effective tool in many monitoring studies because, beside capturing key dimensions of biodiversity not taken into account by other purely taxonomical indices, they can be relatively easy to estimate once they have been defined and standard methodologies have been established (Hodgson et al. 2005; Gaucherand and Lavorel 2007). The presence, abundance and diversity of a given set of functional traits (e.g., morphological, ecophysiological and life history characteristics) could be used for estimating particular components of biodiversity (de Bello et al. 2010) and form together what we will call "functional indicators of biodiversity". The advantages of including functional indicators in biodiversity monitoring are numerous. As the ecosystem processes that are measured do not rely on a specific set of species, functional indicators can allow further comparison of biodiversity among regions with different biogeography (Statzner et al. 2001; Hodgson et al. 2005). Hodgson et al. (2005) for example demonstrated how simple plant traits (e.g. leaf characteristics and plant height) could be used as indicators for biodiversity conservation in different European grasslands. Abandoned grasslands (i.e. dominated by tall species) often host a lower number of plant species due to competitive displacements (Pärtel et al. 1996; Lepš 2006). Consequently, it has been shown that the diversity of higher trophic levels (e.g. phytophages, predators) is decreased (Usher 1992). Similarly, canopy architecture

has been used as one of the most important indicators for biodiversity of different trophic groups in Swiss grasslands (Schwab et al. 2002). Further, Moretti and Legg (2009) describe a method to assess functional response to disturbance by combining plant and animal traits and suggest new challenging opportunities for comparing traits across trophic levels. Finally functional indicators can also greatly improve predicting the functions or services provided by an ecosystem as they are proxies for the rate, or relative importance, of particular processes (Diaz et al. 2007; de Bello et al. this issue).

In this study we explore concepts, methods and possible applications of functional traits as bioindicators in organisms other than plants. Four case studies were selected based on the traits of freshwater benthic invertebrates, soil fauna, above-ground insects and urban birds. The organism groups selected are widely used in large-scale monitoring because of their indication potential (e.g. Breure et al. 2005). These four groups of organisms can therefore be considered to represent some key components of biodiversity monitoring that could not be captured by focussing on plants alone in terms of e.g., their life histories and dispersal potential. We first review possible approaches for defining and analyzing functional traits as indicators in these organisms and allowing generalization beyond specific taxa and regions. We then propose a standardized procedure for including trait data into biodiversity assessments and evaluate which type of metrics has the greatest potential as indicators of the response of biodiversity to land use intensification.

Functional trait indicators across trophic levels: a historical perspective

Freshwater indicators

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The Index of Biotic Integrity (IBI; Karr 1981) was a first step toward preserving most of the ecological information into a new synthetic expression beyond usual indices (biotic index, species richness). This index aimed to assess the biotic integrity of fish communities in North America and was composed of 12 metrics or biological measures representing some aspects of the composition, function (e.g., the proportion of specific feeding types) or other characteristics (e.g., the proportion of individuals with disease). The use of numerous metrics, each reflecting a different aspect of the community, was supposed to provide a comprehensive view of the status of biodiversity with respect to multiple environmental stressors (e.g., pollution, physical habitat modification, acidification and eutrophication). Multimetric indices were further developed for other organism groups (e.g. benthic macroinvertebrates) and became the national standard for river assessment and monitoring in the U.S.A. (Karr 1999). Since 2000, the development and application of multimetric assessment systems has been increasingly acknowledged in Europe (e.g., FAME consortium 2005; Hering et al. 2006; Pont et al. 2006). Some metrics are based on sound concepts of ecology and are a priori predictive (e.g. functional feeding groups and their composition along the river continuum) whereas most structural metrics are based on generalizations drawn from empirical observations (see Bonada et al. 2006). The advantage of traits over traditional assessment and monitoring of rivers in Europe has been demonstrated by Dolédec et al. (1999), Usseglio-Polatera and Beisel (2002) and Statzner et al. (2001; 2005). Besides their applicability in large biogeographic areas, most traits are predictably affected by various types of human impact (e.g., Dolédec et al. 2006; Feld and Hering 2007; Dolédec and Statzner 2008).

Based on the ideas of Southwood (1977), Townsend and Hildrew (1994) developed the habitat templet concept for river ecosystems. The concept relies on

predicting general ecological response (in terms of size, reproduction, dispersal, physiology, i.e., biological traits) of aquatic organisms to habitat disturbance, thus potentially adding strength if used for river assessment and monitoring. This strength was picked up by Charvet et al. (1998), who proposed a first river assessment and monitoring tool to discriminate conditions up- and downstream of a power plant effluent using biological traits. An overview of the traits of European benthic macroinvertebrate genera is provided by Usseglio-Polatera (2000) and Statzner et al. (2007).

Although mostly developed for macroinvertebrates of European running waters, other biota have been given concern. For example, Pont et al. (2006) applied fish traits (e.g., reproduction, migration) for river assessment at the European scale.


Soil indicators


Since the early 1960s (e.g. Volz 1962) soil organisms have been used as indicators in applied ecological studies (Faber 1991; Breure et al. 2005), particularly for soil quality assessment purposes in managed ecosystems (e.g. microorganisms: Kennedy 1999; protozoans: Foissner 1999; nematodes: Yeates and Bongers 1999; enchytraeids: Graefe and Schmelz 1999; earthworms: Paoletti 1999; mites: Behan-Pelletier 1999; collembolans: Van Straalen 1998). Excepting microorganisms, soil indicator groups have mainly been applied based on taxonomic identification (Breure et al. 2005). Yet, in recent decades, a more functional approach has been developed using organisms' traits and functional groups, particularly with regard to soil fauna.

With regard to nematodes, a predominance of trait indicators has been typically applied to soil quality evaluation, mainly life-history traits such as "maturity index" (MI)

(Bongers 1990; Bongers and Bongers 1998; Yeates and Bongers 1999). MI is considered to be an ecological measure of disturbance based on ranking taxa according to their dominant life strategy along a colonizer-persister (c-p) scale, i.e., from r strategists (colonizers) to K strategists (persisters). Low c-p values are assigned to nematode families that have a short life-cycle, high colonization ability and are tolerant to disturbances. Hence, a high MI indicates a nematode fauna that is associated with more stable environmental conditions.

Life-history traits based on this r-K continuum, as well as on life-forms (i.e. traits related to taxa vertical distribution in soils), were also considered for enchytraeids (e.g., Jänsch et al. 2005), earthworms (e.g., Römbke et al. 2005) and mites (e.g., Zaitsev et al. 2002). Life-history traits have been useful to soil ecologists in measuring the impact of stressors and management practices, suggesting an easier functional interpretation in relation to land-use disturbance (Siepel 1995). Another functional approach that has been widely used among soil fauna is based on the trophic groups to which the different taxa belongs (e.g. Bongers and Bongers 1998; Nahmani et al. 2006). All these functional approaches are especially relevant considering their potential at regional and national scales, such as for the soil ecological classification frameworks developed in Europe during the 1990s (e.g. BISQ, Schouten et al. 1997; BBSK, Römbke et al. 1997).

Among soil fauna, collembolans have great potential for use in integrated biodiversity monitoring schemes (Siepel 1995; Van Straalen et al 2008). Despite their abundance, diversity and functional role in soils (Hopkin, 1997; Wolters 2001), a trait-based approach was not explicitly used for indication purposes until recently. Only a few attempts, particularly addressing traits of dispersal and colonization ability, have been made to assess the effects of land-use disturbance (Lindberg and Bengtsson 2005;

Ponge et al. 2006). However, collembolan species display a wide variation in life-history traits (Hopkin 1997), which could provide a functional and more insightful tool for assessing the effects of land-use disturbance on collembolan diversity, particularly in dynamic landscapes (Lindberg and Bengtsson 2005; Van Straalen et al. 2008).

Collembolan life-forms have already been included in Parisi's 'Qualità Biologica del Suolo' (QBS) (Parisi 2001), a soil quality index based on an eco-morphological range of arthropods edaphic adaptations for assessment of land-use sustainability. Yet, the present state of knowledge concerning the impact of disturbance on life-history traits and functional diversity of collembolans remains limited, partly due to a lack of empirical data for many species (Lindberg and Bengtsson 2005; Van Straalen et al. 2008).

Above ground insects as indicators

Terrestrial arthropod diversity has long been used as an indicator of environmental change, for example, termites, beetles, bees, butterflies, true bugs and hoverflies have all been used as indicators of changing land-use (Lawton et al. 1998; Hendrickx et al. 2007). Moreover, some insect taxa (e.g. butterflies and beetles) covary with other taxa and can, sometimes, be used as a surrogate measure for changes in other trophic levels (Oliver and Beattie 1996; Lawton et al. 1998; Billeter et al. 2008). Insects have many advantages as indicators. They are numerous and diverse, but can be sampled relatively easily and often passively with traps. Specific habitat or resource requirements make them responsive to environmental change (Steffan-Dewenter and Tscharntke 2000, Moretti and Legg 2009). Despite high diversity and small size they can be identified to species by specialists or morphospecies by trained non-specialists who, using the

concept of recognizable taxonomic units (RTU), can provide an accurate proxy of species diversity (Oliver and Beattie 1996).

The use of trait-based indicators for above ground insects is a relatively uncommon, but growing, approach. Traits, such as trophic level, diet breadth, dispersal power, voltinism, and body size, have been used to understand the response of insects to disturbance or habitat structure (Didham et al. 1998; Steffan-Dewenter and Tscharntke 2000; Driscoll and Weir 2005; Schweiger et al. 2005). More recent examples examined the relationship between bee and predatory arthropod traits and incidence of fire and flooding, respectively (Lambeets et al. 2008; Moretti et al. 2009). Ground beetles (Carabidae) are often used as indicators because they are taxonomically and functionally diverse, widely-distributed and abundant, well studied, and are sensitive to habitat heterogeneity and land-use within individual countries (Vanbergen et al. 2005). Moreover, there is evidence that ground beetle assemblages from different regions respond in a comparable way to the same environmental factors (Schweiger et al. 2005). Historically, most ground beetle studies have focused on taxonomic diversity, but a few studies have considered the response of ground beetle traits to land-use or landscape heterogeneity (Driscoll and Weir 2005; Pizzolotto 2009).

Bird as indicators

Birds are a good model for indicators because they react rapidly and markedly to environmental changes (Gregory et al. 2005). They are comparatively easy to survey, their ecology is known and the limits of the census methods are established. The species-specific ecological requirements of birds allow assessment of their responses to modifications of landscape structures. For these reasons birds are often chosen as

indicators of habitat quality (e.g. Revaz et al. 2008; Douglas et al. 2009). But only recently, the response and redundancy of bird functional traits to environmental changes is receiving attention as a way to generalize patterns in biodiversity response across regions (e.g. Petchey et al. 2007). Bird traits have been used to assess the functional response to different kinds of ecosystem change, from structure alteration (Cooch and Ricklefs 1994), to landscape fragmentation (Barbaro and van Halder 2009), land use intensity (Flynn et al. 2009) and climate changes (Jiguet et al. 2007). The most commonly traits used are both life-history and autoecological attributes such as body size, trophic guild, dispersal power, feeding and nesting strategy, and migration behaviour.

It is particularly interesting to assess functional trait response in urban birds. Urban areas are the fastest growing land-use type worldwide (United Nations 2000). The urban matrix represents a heterogeneous environment that is adopted frequently to suit changing human needs. Plant and animal communities living in urban landscapes are influenced by urban-specific processes, such as fragmentation, management of the urban green and high anthropogenic pressure (e.g. Shochat et al. 2006). Bird community composition strongly modified by the structure related to urban green (see Clergeau et al. 2001 for review). As a general pattern, bird species richness and diversity decrease with increasing level of urbanization along a rural to urban gradient but individual numbers may increase (e.g. Clergeau et al. 2006; McKinney 2006). Considering urban green gradients within cities, rather than out-vs-inside gradients, species diversity, community composition and functional structure are expected to be positively affected by the amount and the structural heterogeneity of the urban green (e.g. Shochat et al. 2006; Sorace and Gustin 2008).

Metrics for functional trait indicators

The approach by Moretti et al. (2009) to define functional traits as indicators of biotic communities is applied here as a way to generalize and include functional traits into biodiversity indication. This approach, derived from studies on plants (Diaz et al. 2007) has the potential for application at different trophic levels and gives relatively simple and intuitive indices based on functional traits of species.

From the taxonomic point of view, two indices are commonly considered in biodiversity monitoring schemes and in ecological studies. These are the number of species (species richness), and other indices that also consider species abundance, such as Simpson's diversity (Simpson 1949). The Simpson index is defined as 1 minus Simpson dominance (D) where:

$$(1) \ D = \sum_{i=1}^{S} p_i^2$$

with S being the number of species in the community, and $p_i$ the proportion of the i-th species in a sample (i.e. $p_i = N_i / N$ and $N = \sum N_i$. where, Ni is the number of individuals of the i-th species). The index can be calculated after log-transformation of the number of individuals of each species to reduce the effect of dominant species (Moretti et al. 2009).

Likewise, two main types of functional trait indices can be used for biodiversity monitoring (Diaz et al. 2007; Lavorel et al. 2008). First, the mean trait value per community (mT) can be calculated for each species trait as the average of trait values in the community, weighted by the relative abundance of the species carrying each value. This metric is often understood as defining the dominant functional attribute in a community or the proportion of a given functional group (functional groups can generally indicate group of species that either has a similar set of traits, or that share

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similar resources, in this case these groups are generally defined as "guilds"; see glossary paper in the same issue). Second, the range of trait values within the community can be expressed through various indices, among which functional diversity is increasingly used (Lepš et al. 2006; Petchey and Gaston 2006).

Both mT and FD can be calculated for different species traits in each community. The mT is calculated as an average for a given trait weighted by species abundance, according to Garnier et al. (2004):

$$(2) \quad mT = \sum_{i=1}^{S} p_i x_i$$

where $x_i$ is the trait value of the i-th species. For binary traits $x_i$ can be either zero or one. Categorical traits are treated as binary traits and for each category the relative abundance of a particular group (or modality) is calculated by the index. In freshwater ecology, since the information on traits generally includes expert knowledge and various literature sources, authors have used a "fuzzy coding" approach to quantify traits (Chevenet et al. 1994). This coding consists in assigning, for each taxon, an affinity (ak) to each category (1≤ k ≤ h) of a given trait. An affinity score of "0" indicates no affinity of the taxon whereas an affinity score of "3" indicates a high affinity of the taxon for a given trait category. For example, the final maximal body size of a genus was described as falling into seven length categories (Appendix 1). If all the individuals of a genus fell in one size category, affinity of that species was scored "3". If most individuals fell into one size category but a few lay in a neighbouring category, the genus would score "2" and "1" for the two categories respectively. Here, we further treated this information as frequency distributions (ak/sum(ak) with sum(ak)=1, see Bady et al. 2005).

Functional diversity (FD) was calculated for different species traits and using the Rao index of diversity (Rao 1982; Lepš et al. 2006) as:

$$(3) \quad FD = \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij} \, p_i \, p_j$$

where $d_{ij}$ expresses the dissimilarity between each pair of species i and j according to their trait values (Pavoine & Dolédec 2005). Thus the FD index equals the sum of the dissimilarity in trait space among all possible pairs of species, weighted by the product of the species' relative abundances. The parameter $d_{ij}$ varies between 0 (two species have exactly the same trait values) and 1 (the two species have completely different trait values). For example, in the case of binary traits, when the species have the same trait value then $d_{ij} = 0$; when they have different values then $d_{ij} = 1$. Note, that the Rao index is a generalization of a Simpson index of diversity because if $d_{ij} = 1$ for any pair of species (i.e. each pair of species is completely different), then FD is equal to the Simpson index of diversity SD (1) (see Rao 1982 for details). In natural communities, however, the Simpson index and the Rao FD can vary independently (de Bello et al. 2006), therefore the Rao index does not produce necessarily correlated indices of species and functional diversity (as, for example, Petchey et al. 2007).

The quantification of an ecosystem's biodiversity from a functional traits point of view can proceed following three steps. First, the environmental gradient for which indicators are needed has to be defined. This could be represented by a gradient of increased human pressure, such as land use changes and intensification. Second, the response of taxonomic and functional indicators to this gradient needs to be assessed. Different models can be applied according to the type of design and ecological hypothesis underlying the response of the organism to this gradient. Third, the relationship between species and functional diversity needs to be assessed to account for the overlap between the taxonomic and functional components. In the next section we use four case studies to explore this framework.

Case studies


Benthic macroinvertebrates


Benthic macroinvertebrates were sampled in 75 sites across southern Sweden, the Netherlands, Germany, and western and central Poland. Five land cover types (forest, grass/shrubs, pasture, crop land, and urban settlement) and ten hydromorphological variables (shade, density and width of riparian woody vegetation, proportion of riprap at site, number of logs and debris dams at site, number of dam structures upstream, stagnation at site, and meandering/straightened river course) were recorded at each site to quantify two environmental gradients: land use/cover and hydromorphology. All samples were taken according to a standard multi-habitat sampling protocol using a handned (mesh: 500 µm, sampling area: 1.25 m$^2$; for details on sampling and sample processing see Feld and Hering 2007).

The overall taxon list comprised 240 benthic macroinvertebrate species or genera. We used a trait by taxon matrix comprising 11 traits (maximal body size, life cycle duration, number of reproduction cycles per year, aquatic stages, reproduction type, dissemination strategy, resistance form, respiration types, locomotion, food and feeding habits) subdivided into 62 fuzzy coded trait categories (see Appendix 1 for details). Simpson diversity, mT for each single trait and overall FD based on 11 traits (expressed as arithmetic mean of the 11 FD values) were calculated. Here, the mT metric reflects the relative abundance of functionally different genera from their trait categories (Appendix 1). We applied Principal Components Analysis (PCA) to land cover and hydromorphological variables respectively to derive the degree of environmental impact at each site. The first PCA axes explained 64 % of the total

variance of land cover data and 73 % of the total variance of hydromorphological data respectively. As a result, only first site scores were used to define environmental stress at each site. The relationships between Simpson diversity, trait/functional diversity and environmental stress were quantified using Pearson's correlation coefficients.

Species and functional diversity were positively correlated with each other ($r = 0.441$, $p < 0.001$) but neither Simpson index (taxonomic diversity) nor functional diversity (FD) were correlated with environmental pressure gradients (Table 2). On the contrary, the proportion of various functional groups (as summarized by the mT) responded significantly to the environmental stressors considered (Table 2). For instance, the proportion of multivoltine organisms significantly increased with the proportion of crop in the floodplain (and decreased in the forested floodplains).

Both increasing and intensified agricultural land use (crops) often cause surface erosion and the entry of fine sediments and organic material into the river channel. This fine material (fine sand, silt, mud) should promote, for instance, deposit feeders or species that live on muddy substrata. Deposit feeders significantly decreased with increasing floodplain forest area, while the correlation with crop land was insignificant. We also tested the relation of mud-dwelling species proportion to land use. The correlation of % mud dwellers to % land use was $r = -0.411$ ($p < 0.001$) for forest and $r = 0.300$ ($p < 0.001$) for crop land in the floodplain.

In summary, we found Simpson and functional diversity (FD) to remain relatively stable along environmental stress gradients in lowland rivers of Central Europe, even in the presence of severe hydromorphological and land use impact. The results imply that it is the community mean trait values (mT) of various traits that measurably respond to environmental gradients rather than the overall community

diversity. We conclude that community diversity measures are likely to be less useful for the assessment and monitoring of environmental stress in river ecosystems.


Soil collembola


Replacing autochthonous forests by exotic Eucalypus globulus plantations has been an important land use change pressure on soil biodiversity (Sousa et al. 1997, 2000). In this case study, data collected in 16 forested areas in Portugal, separated into 8 groups of contiguous sites (comparing, at each group, one or more stands of autochthonous tree species and one or more plantations of E. globulus) were considered (see Table 3). At each site 16 soil cores were taken following a nested design (see details in Sousa et al. 1997, 2000). In each core, the organic horizon was separated from the mineral soil layer. In the laboratory, collembolans from each horizon of each sample were extracted using a Tulgren funnel. Traits considered were morphological characteristics connected to the adaptation of each collembolan species to the soil environment, namely the ocelli, furca, antenna, pigmentation and the presence of hairs and scales (Appendix 2). These individual traits were combined to create the "Life-form" trait used in all calculations; it was the sum of all the scores from each individual trait, being comprised between 2 (minimum, indicating a species with higher adaptation to the surface layers) and 18 (maximum, indicating a species with higher adaptation to deep soil layers). All the analyses in this example were undertaken at the site level, pooling all the samples from each site. Simpson index, mT and FD were calculated for each site using the methods described above. The mT values were compared within each pair of matching sites using a t-test.

The comparison of forest types (autochthonous forest vs. eucalypt plantation from the same area) showed that the eucalypt plantation led to a generalized impoverishment in the taxonomic diversity of Collembola together with significant changes in community composition (Sousa et al. 1997, 2000). Moreover, species present in the upper soil layers (with some exceptions) were generally most affected by the exotic plantation. The decrease of species diversity in collembolans under E. globulus stands was accompanied by a similar trend of functional diversity values (Table 3). In fact both parameters presented a strong and positive correlation ($r = 0.85$, $p<0.001$) although in most comparisons functional diversity suffered a larger decrease than taxonomic diversity. This decrease was more evident in the upper soil layer when compared to the mineral horizon (data not shown). Regarding the mean trait community, despite the absence of significant differences between pairs of corresponding sites, the shift to the exotic trees led to a general increase of the mT values. Since higher trait values correspond to species more adapted to mineral soil layers, this shift led to a change in the functional composition of the community, namely to an increase in the representation of eu- and hemi-edaphic species, and the decrease of litter dwelling species (with the exception of Lousã sites). These findings indicate a general change in the quality and structure of the organic horizon originated by the exotic plantations. Collembolan life-form traits gave this response trend. Presumably, therefore, the use of more trait types (e.g. feeding, habitat width related traits, and ecophysiological tolerance traits) could provide a finer analysis of the community composition at the functional level and could help to understand better the reasons behind the observed response.

Data from a pan-European landscape-scale survey of ground beetles were used to compare the relative performance of taxonomic (activity density and species richness) and functional measures (FD, mT) of diversity along two gradients in landscape structure (habitat composition and landscape heterogeneity). Twenty-four landscape areas were selected comprising six 1 km$^2$ landscape units (LU) sited in each of four European countries (Finland, France, Ireland and Scotland). Landscape structure was quantified in GIS (ArcView 3.1), using remotely sensed land cover data (fused Landsat 7 ETM+ & IRS-1C image), following the CORINE (Level 3) biotopes classification (EEA). Using FRAGSTATS (McGarigal et al. 2002) a measure of landscape composition (percentage cover of all forest classes) and heterogeneity (habitat richness: count of all habitat classes excluding aquatic and artificial surfaces) was calculated for each LU. Forest percentage cover was the chosen measure of landscape composition because it is the dominant perennial habitat across these regions offering refuges for carabids in contemporary agricultural landscapes (Petit and Usher 1998). Habitat richness was the chosen measure of landscape heterogeneity because it represented the accumulation of ecological niches.

Carabid beetle assemblages were sampled with pitfall traps on a systematic grid of 16 sampling plots, 200m apart, in each LU giving a total of 96 sampling plots per country (details in Vanbergen et al. 2005). Trait information was available for 117 out of the 124 species collected and this subset forms the basis of this analysis. Traits used were morphological proxies of body size (body length, elytra and pronotum size), activity and dispersal power (leg femora, tibia, metatarsus size and winglessness), colour variation (leg and body), sensory structures (body pubescence, eye and antenna

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size), and association with anthropogenic habitat (Appendix 3). These traits were used to calculate mT and FD (total and morphological and colour traits separately) as detailed above. Species richness was estimated by rarefaction (Coleman method standardized to 250 individuals) curves (Estimate-S 8.00) because of large differences in beetle densities among countries (Gotelli and Colwell 2001). Taxonomic (activity density and rarefied species richness) and functional (FD and mT) data were log and arcsine square-root transformed, respectively.

The country of origin was often a significant predictor of both taxonomic and functional diversity (Table 4a), and the trait dominance of the assemblages (Table 4b), indicating turnover in individuals and species among geographical regions. This effect of geographical region was controlled for when testing for relationships between taxonomic and functional diversity and landscape structure (heterogeneity and composition). The response of most taxonomic and functional parameters was generally consistent across geographical regions; local species pools had an effect only on FDmorph (Table 4a: Forest × Country) and on a single mT (Pronotum height: Forest × Country $F_{3, 16} = 3.71$ $p = 0.0337$ (not shown)) and this was controlled when testing for the main effects of landscape structure. Both measures of taxonomic diversity (activity density and species richness) of ground beetles were positively correlated with increasing landscape heterogeneity (habitat richness) in the landscapes (Table 4a), while landscape heterogeneity predicted taxonomic diversity, functional diversity and mean community trait value were more strongly correlated with landscape composition (forest cover).

There was a significant positive correlation between species richness and FDcolour (Pearson correlation coefficient 0.63352, $p = 0.0009$) but FDmorph was unrelated (-0.01029, $p = 0.9620$) (not shown). Activity density was unrelated to either

FDmorph (-0.29180, p = 0.1665) or FDcolour (0.24268, p = 0.2532) (not shown). FDmorph and FDcolour were positively and negatively correlated with forest cover, respectively (Table 4a); these inverse relationships explaining a lack of detectable effects when all traits were pooled (Table 4a: FDtotal).

The mT of these assemblages shifted along the gradient of forest cover with 67% and 22% of the traits related positively and negatively respectively to increasing forest cover (Table 4b, Fig.1). Increasing forest cover in the landscape led to a shift in the mT. Species with larger body size, longer legs, larger eyes and longer antennas and darker in colour dominate the more forested landscapes (Table 4b, Fig.1). Assemblages in open landscapes were dominated by species covered with pubescence, paler in colour and fully winged species (Table 4b, Fig.1). In summary, the example of ground beetles shows that both taxonomic and functional descriptors of diversity conveyed complementary information about the response of this group to landscape structure. Taxonomic diversity was enhanced by the addition of niches in landscapes of high habitat richness, whereas functional diversity and the mean community trait value was influenced by the shift in landscape composition from forested to open, agricultural landscapes.

Urban birds

The case study on urban birds was carried out in three Swiss cities (i.e. Zurich, Lucerne and Lugano). In each city 32 census points (total 96) were selected along a gradient of impervious area (buildings and sealed surfaces) within cities. Birds were assessed visually and acoustically by point count method (Bibby et al. 1992) within a 50 m radius, six mornings between April 15 and June 13, 2007 during 15 minutes (order of

locations was switched). Nesting, visiting, and migrating individuals were counted and considered equally in the analyses (Fontana 2008). We assessed the ecological and functional response of the bird community by selecting 8 species traits (Bezzel 1993; Maumary et al. 2007). Partial Redundancy Analyses (pRDA) was used to test the multivariate response of bird species diversity (D) and trait composition (mT and FD) to urbanization, while city identity was used as co-variable. Species-specific nesting habitats and feeding guilds (see Appendix 4) were used as model traits in this study. The number of individuals was log-transformed to reduce the influence of extreme values. Urbanization was described using two main factors sampled in a radius of 50 m around the bird count points: the proportion of surface that was covered by impervious area (Impervious Area), and the percentage cover of trees and bushes (Bush&Tree).

Partial RDA on the community mT and FD resulted in urbanization explaining a significant amount of variance (12.5%; P <0.0001) in trait composition (biplot not shown). Increasing asphalted and built area enhanced bird nesting in buildings, while negatively affected tree and bush nesting communities (Table 5a). This rising coverage also increased the FD of traits related to nesting habitats while it reduced the FD related to feeding (Table 5b). Simpson species diversity (SD) of birds was positively linearly related to functional diversity (FD) ($R^2_{adj}$ = 0.1048, P = 0.0008) and to the percentage cover of bushes and trees (Bush&Tree) ($R^2_{adj}$ = 0.1996, P = 0.0069).

Discussion

One of the most important, but yet unresolved, issue to build sound indicator systems is the standardization of monitoring schemes across organisms and disciplines (see e.g. Cornelissen et al. 2003; de Bello et al. 2010). In this context the complementarity of

taxonomical and functional indicators has the potential to lead to an improved system of biodiversity monitoring, especially in very diverse animal communities (Moretti et al. 2009) and across trophical guilds trying to combine plants and animals (Moretti and Legg, 2009).

In our study, we deliberately chose examples of animals that are widely used as indicators for different ecosystem types and different monitoring schemes (Bongers 1990; Siepel 1995; EASAC 2005; Gregory et al. 2005; Douglas et al. 2009) and show that simple functional metrics (e.g. mT and FD) can be applied in different contexts. Our main goal was to assess to what extent animal traits measurements could efficiently complement the traditional use of more taxonomical measurements in the assessment of the current ecological state of biodiversity. We show (see Table 1 for a summary) that taxonomical and functional components of diversity respond differently to land use changes and that, although they can be partially related to each other, they do largely cover different facets of diversity. In this sense we suggest that the development of indicators using functional traits could expand, rather than replace, the existent biodiversity monitoring schemes.

Large and accessible databases of traits are accumulating for plants and animals (e.g. Vieira et al. 2006; Kleyer et al. 2008), despite this, the use of species-specific traits as reliable indicator tools is not yet widely applied in current monitoring schemes of the biodiversity, especially with respect to animal groups. As previously demonstrated for plants (e.g. Lavorel et al. 2008), we show here that, in general, averaged trait values over a community (mT) and functional diversity metrics can respond strongly to environmental changes (Table 1), and are therefore promising as biodiversity indicators. In the benthic invertebrates' case study, for example, we found a low level response of species diversity despite the large changes in species composition (taxon richness

ranged between 5 and 37 taxa per sample in our case study; see also Bady et al. 2005). By combining different indicators, and including functional trait metrics, such as the dominant functional groups in the community, we could better determine the changes in community structure that has, potentially, key consequences in the functioning of these ecosystems. Voltinism and the proportion of deposit feeders seem to be indicative of land use impact in European lowland rivers. As such relationships can be derived from ecological theory (e.g., from the Habitat Templet Concept, Townsend and Hildrew 1994), traits provide a means for both prediction-based assessment and predictive modelling of community changes along environmental gradients.

In all the other examples (Table 1), the mean trait value in a community was always an important indicator of community response to land use modification, both in terms of land use intensity and landscape structure. This suggest that this facet of community composition, which reflects the dominant type of organisms in biological communities (Garnier et al. 2004; Lavorel et al. 2008), can be particularly useful to understand the response of ecosystems and different trophic levels to changes in environmental conditions. In most of the case studies considered, species diversity and FD were correlated significantly ($p<0.05$), even if the covariation was sometimes week (low R). The Rao index of FD is a mathematical generalization of the Simpson index, where the Simpson index is the upper limit for its values (de Bello et al. 2009). Consequently, purely mathematically, we cannot expect that these two values will be completely independent. However, the degree to which they are related to each other depends mostly on properties of the data set and on the biological communities considered (unlike other indices where a strong positive correlation with species diversity results by the mathematical properties of the indices; Petchey and Gaston 2006). An important issue is how the variability of the Simpson index compares with

the variability of the functional diversity index. In our case studies (except for the soil one, see above), low correlation values, together with different responses of species diversity and FD to land use gradients, suggest that these two dimensions can indicate largely independent components of diversity (Pavoine and Dolédec 2005; de Bello et al. 2006; Moretti et al. 2009).

These cases studies suggest, overall, that both the mT and FD metrics have important potential as to complement present indicators of biodiversity. First, while taxonomical indicators (such as a list of taxa) cannot be easily extrapolated and applied to different regions, traits and functional groups can generalise across regions (Statzner et al. 2001; Hodgson et al. 2005; Pont et al. 2006). This is further justified by the example on Carabids showing very weak different effects of land use on traits in different regions (lack of strong effects of land use x country Table 4a). Thus, indicators that provide consistent measures of biological condition across regions are valuable tools for both research and management (Carlisle and Hawkins, 2008). Comparisons across bioclimatic regions, however, should be interpreted carefully (Moretti et al. 2009). Second, such as the soft traits for plants, some morphological traits (e.g. body or organ size, colour and shape) often do not require strong specific taxonomical knowledge or specific biological expertise and equipment and could, therefore, provide a less expensive solution for biodiversity monitoring by shortly trained personnel. Third, these functional metrics underlie a number of ecosystem functions that can link biodiversity responses of communities to the delivery of different ecosystem services (Diaz et al. 2007). Of the mT and FD metrics, probably the most useful remains the mT since it responds better to environmental gradients and is easier to estimate than FD, which requires greater experience. Finally, simple functional metrics do have a more direct link to changes in the ecosystem because, if well selected, functional traits are

directly coupled to the fitness of the animal. They might therefore give better predictions of ecosystem response than taxonomical indicators alone (Cornelissen et al. 2003).

As for all indicators of biodiversity, we could foresee some limitations to the use of these functional metrics. We should indeed be aware that this approach does not for example take the rare species or the species with a particular conservation priority into account. Using functional indicators alone, therefore, could lead to a non-optimal conclusion on biodiversity indication. For example in a conservation perspective, the use of the functional metrics alone would not be suitable to highlight the importance of red listed species, which means that we may loose some information on an important aspect of biodiversity. However, most of indices based on species diversity, as currently applied in various standardized monitoring schemes (e.g. the number of species), present the same limitation. Although in some cases, the functional indicator approach could represent a cost-effective monitoring alternative, we don't propose here to replace taxonomical indicators by functional indicators but rather to combine both methods to improve the biodiversity assessment.

Conclusions

We propose standard indicators that can help integrate monitoring of biodiversity via functional traits assessment across trophic levels and disciplines. In particular, we propose that different studies are defined and compared as in Table 1 to assess to what extent and in which conditions functional traits measurements could efficiently complement the common use of more taxonomical measurements in the assessment of the current ecological state of biodiversity. In general, we ask for more background

knowledge on patterns of variation of the proposed indices to serve as benchmarks for future observed variations when monitoring the effect of a land use change.

To conclude, and as a step forward to the general criteria mentioned by Balmford et al. (2005) in the establishment of indicators of biodiversity and ecosystem services, we propose the following criteria for selecting good functional indicators:

- A precise definition of the indication goals
- A precise definition of the environmental factors that might drive the change in biodiversity
- A precise definition of the trait or combination of traits, carefully selected according the driver of change in place.
- If possible, available traits database ready to use
- Functional indicators have to be appropriate for comparative investigations and estimations
- The developed functional indicator should be easy to measure.

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Running head: Functional traits as indicators of biodiversity

Table 1: Summary of the results for the 4 case studies (i.e. 4 organism types): response of species diversity (richness or Simpson), functional

diversity (Rao) and community mean traits (or % of different functional groups) metrics to different environmental changes

| Organism type | Environmental gradient | Response of indices to environment | | | Species vs. functional diversity |
|---|---|---|---|---|---|
| | | Species diversity (Richness or Simpson) | Functional diversity (FD with Rao index) | Community mean trait (mT) | |
| River benthic invertebrates (GER) | Land use intensity | Non linear (difference only among extremes) | Non linear (difference only among extremes) | Yes (linear for aquatic stages, reproduction, dispersion) | Yes – weak linear relationship |
| Soil fauna (PT) | Native vs. exotic forest stands | Yes (general decrease of species diversity in exotic stands) | Yes (Similar pattern as Simpson index, but in most cases more pronounced decreases) | Yes (for life-form trait). Shift to the exotic led to an increase in the representation of eu- and hemi-edaphic species, and a decrease in litter dwelling species | Yes -linear relationship (expected since traits are also used for species identification) |
| Terrestrial insects (EU) | Landscape heterogeneity and composition | Yes –positive linear relationship with landscape heterogeneity | Yes FDcolour negatively and FD morph positively related to landscape composition | Yes (for all traits) with landscape composition | Yes -linear relationship between FDcolour and species richness, but not for activity density |
| Birds (CH) | Urbanization | Yes -linear relationship | Yes -linear relationship | Yes - linear relationship | Yes – weak linear relationship |

Table 2: Correlation of land use and hydromorphological degradation, selected traits (mT metrics), Simpson index and Functional Diversity (FD) for benthic macroinvertebrates. PCA 1 axes (sample scores) represent land use and hydromorphological gradients.

| Diversity measure | x | Environmental gradients | r | p |
|---|---|---|---|---|
| Simpson index | | PCA 1 land use | 0.047 | 0.654 |
| Simpson index | | PCA 1 hydromorphology | 0.088 | 0.404 |
| FD | | PCA 1 land use | 0.140 | 0.181 |
| FD | | PCA 1 hydromorphology | 0.089 | 0.394 |

| mT category (metrics) | x | Environmental gradients and parameters | | |
|---|---|---|---|---|
| multivoltine species | | PCA1 land use | -0.383 | <0.001 |
| multivoltine species | | PCA 1 hydromorphology | -0.400 | <0.001 |
| multivoltine species | | % Forest land cover | -0.389 | <0.001 |
| multivoltine species | | % Crop land use | 0.230 | 0.006 |
| mud preferences | | PCA1 land use | -0.418 | <0.001 |
| mud preferences | | PCA1 hydromorphology | -0.271 | <0.001 |
| mud preferences | | % Forest land cover | -0.411 | <0.001 |
| mud preferences | | % Crop land use | 0.300 | <0.001 |
| deposit-feeders | | PCA1 land use | -0.209 | 0.012 |
| deposit feeder | | PCA1 hydromorphology | -0.157 | 0.061 |
| deposit feeder | | % Forest land cover | -0.188 | 0.024 |
| deposit feeder | | % Crop land use | -0.091 | 0.280 |

Table 3: Summary of the results obtained for the 8 Collembola case studies. Information is given for each forest stand. Comparisons should be analysed between the autochthonous and exotic stand at each case study

| Case study / author | Tree species | Sp richness | Simpson | | Functional diversity | | Mean trait per community | | Habitat Diff (3) |
|---|---|---|---|---|---|---|---|---|---|
| | | | Values | % change (1) | Values | % change (1) | mT | % change (2) | |
| **Cercal** | **Q. suber** | 59 | 0,911 | | 0,235 | | 0,219 | | |
| Gama et al (1991) | **E. globulus** | 39 | 0,834 | 8,42 | 0,225 | 4,21 | 0,284 | 29,68 | Some |
| **Almeirim** | **Q. suber** | 19 | 0,805 | | 0,239 | | 0,442 | | |
| Sousa et al (1997) | **E. globulus** | 21 | 0,648 | 19,51 | 0,174 | 27,26 | 0,509 | 15,16 | Some |
| **Monchique 1** | **Q. suber 1** | 47 | 0,629 | | 0,111 | | 0,285 | | |
| Barrocas et al (1998) | **E. globulus 1** | 19 | 0,576 | 8,49 | 0,064 | 42,09 | 0,547 | 91,93 | Marked |
| | **E. globulus 2** | 21 | 0,568 | 9,64 | 0,067 | 39,71 | 0,510 | 78,95 | Marked |
| | **E. globulus 3** | 23 | 0,858 | -36,41 | 0,160 | -44,63 | 0,513 | 80,00 | Few |
| **Monchique 2** | **Q. suber 2** | 46 | 0,651 | | 0,120 | | 0,334 | | |
| Barrocas et al (1998) | **E. globulus 1** | 19 | 0,576 | 11,66 | 0,064 | 46,44 | 0,547 | 63,77 | Marked |
| | **E. globulus 2** | 21 | 0,568 | 12,77 | 0,067 | 44,24 | 0,510 | 52,69 | Marked |
| | **E. globulus 3** | 23 | 0,858 | -31,68 | 0,160 | -33,77 | 0,513 | 53,59 | Few |
| **Monchique 3** | **Q. canariensis** | 45 | 0,852 | | 0,166 | | 0,285 | | |
| Barrocas et al (1998) | **E. globulus 1** | 19 | 0,576 | 32,46 | 0,064 | 61,30 | 0,547 | 91,93 | Marked |
| | **E. globulus 2** | 21 | 0,568 | 33,31 | 0,067 | 59,71 | 0,510 | 78,95 | Marked |
| | **E. globulus 3** | 23 | 0,858 | -0,68 | 0,160 | 3,34 | 0,513 | 80,00 | Few |
| **Idanha** | **Q. ilex** | 43 | 0,863 | | 0,201 | | 0,242 | | |
| Sousa et al (1994) | **E. globulus** | 26 | 0,773 | 10,44 | 0,209 | -3,70 | 0,410 | 69,42 | Marked |
| **Sever** | **P. pinaster** | 46 | 0,787 | | 0,214 | | 0,182 | | |
| Sousa et al (2000) | **E. globulus** | 41 | 0,708 | 9,96 | 0,153 | 28,61 | 0,235 | 29,12 | Few |
| **Lousã** | **P. pinaster** | 37 | 0,603 | | 0,083 | | 0,264 | | |
| Gama et al (1994) | **E. globulus** | 40 | 0,845 | -40,08 | 0,192 | -130,53 | 0,248 | -6,06 | Few |

(1) Positive values indicate a decrease in Simpson or Functional diversity values when shifting to Eucalyptus
(2) Positive values indicate na increase in mT values when shifting to Eucalyptus
(3) Habitat differences were evaluated taking into account vegetation cover, structure of the organic horizon and soil parameters

Table 4 a: Results of GLMMs (proc glimmix SAS v9.0) showing the influence of region (Country), landscape heterogeneity (habitat richness) and composition (% cover forest) on the taxonomic and functional diversity of ground beetle assemblages (Carabidae) sampled from 24 $1km^2$ landscape units (LU) situated in four European countries. AIC = goodness of fit; MPE = multiple parameter estimates; ndf = numerator degrees of freedom, ddf = denominator degrees of freedom. FDtotal includes all traits; FDmorph = morphological traits only; FDcolour = colour variation only.

| | AIC | Fixed effects | Random estimate ± SE | Slope | ndf, ddf | F | p |
|---|---|---|---|---|---|---|---|
| Taxonomic diversity | | | LU(Country) | | | | |
| Activity density | 28.31 | Country | 0.05714 ± 0.03708 | MPE | 3,19 | 13.40 | <0.0001 |
| | | Habitat richness | | 0.08240 | 1,19 | 5.03 | 0.0370 |
| Species richness | -34.20 | Habitat richness | 0.003567 ± 0.002151 | 0.02849 | 1,22 | 15.76 | 0.0006 |
| Functional diversity | | | | | | | |
| FDtotal | 19.22 | Country | 0.04380 ± 0.02770 | MPE | 3,20 | 3.05 | 0.0525 |
| FDmorph | 18.69 | Country | 0.005225±0.003695 | MPE | 3,16 | 1.88 | 0.1740 |
| | | Forest | | 0.003837 | 1,16 | 5.75 | 0.0290 |
| | | Forest × Country | | MPE | 3,16 | 3.78 | 0.0318 |
| FDcolour | 12.07 | Country | 0.01790 ± 0.01162 | MPE | 3,19 | 3.31 | 0.0421 |
| | | Forest | | -0.00251 | 1,19 | 4.99 | 0.0378 |

Table 4 b: Results of GLMMs (proc glimmix SAS v9.0) showing the influence of region (Country) and landscape composition (% cover forest) on the dominance of traits (mT) of ground beetle assemblages (Carabidae) sampled from 24 1km$^2$ landscape units (LU) situated in four European countries. AIC = goodness of fit; MPE = multiple parameter estimates; ndf = numerator degrees of freedom, ddf =denominator degrees of freedom.

| Trait (mT) | Random estimate ± SE | | Fixed effects | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | AIC | LU(Country) | Country | | | | % Forest | | | |
| | | | Slope | ndf, ddf | F | P | Slope | ndf, ddf | F | p |
| Body Length | -37.70 | 0.001304 ± 0.000846 | MPE | 3,19 | 8.80 | 0.0007 | 0.001527 | 1,19 | 25.28 | <.0001 |
| Elytra width | -38.81 | 0.001230 ± 0.000798 | MPE | 3,19 | 8.18 | 0.0011 | 0.001425 | 1,19 | 23.33 | 0.0001 |
| Elytra length | -35.32 | 0.001478 ±0.000959 | MPE | 3,19 | 8.43 | 0.0009 | 0.001540 | 1,19 | 22.67 | 0.0001 |
| Femora length | -31.06 | 0.001850 ± 0.001200 | MPE | 3,19 | 8.30 | 0.0010 | 0.001853 | 1,19 | 26.23 | <.0001 |
| Femora width | -24.50 | 0.002612 ± 0.001695 | MPE | 3,19 | 5.75 | 0.0057 | 0.001384 | 1,19 | 10.37 | 0.0045 |
| Tibia length | -35.97 | 0.001428 ± 0.000927 | MPE | 3,19 | 10.88 | 0.0002 | 0.001802 | 1,19 | 32.12 | <.0001 |
| Pronotum height | -4.48 | 0.001228 ±0.000868 | MPE | 3,16 | 4.79 | 0.0144 | 0.002519 | 1,16 | 9.65 | 0.0068 |
| Pronotum length | -28.80 | 0.002083 ± 0.001352 | MPE | 3,19 | 8.42 | 0.0009 | 0.001709 | 1,19 | 19.79 | 0.0003 |
| Metatarsus length | -38.15 | 0.001274 ± 0.000826 | MPE | 3,19 | 13.49 | <.0001 | 0.001676 | 1,19 | 31.15 | <.0001 |
| Eye diameter | -38.70 | 0.001237 ± 0.000803 | MPE | 3,19 | 6.41 | 0.0035 | 0.001246 | 1,19 | 17.73 | 0.0005 |
| Antenna length | -41.38 | 0.001074 ± 0.000697 | MPE | 3,19 | 6.68 | 0.0029 | 0.001604 | 1,19 | 33.82 | <.0001 |
| Black legs | 5.12 | 0.02163 ± 0.01368 | MPE | 3,20 | 5.26 | 0.0077 | - | - | - | - |
| Pale legs | 3.65 | 0.02011 ± 0.01272 | MPE | 3,20 | 5.63 | 0.0058 | - | - | - | - |
| Black body | -9.45 | 0.008571 ± 0.00516 | - | - | - | - | 0.002688 | 1,22 | 13.83 | 0.0012 |
| Wing form | -2.26 | 0.01188 ± 0.007166 | - | - | - | - | -0.00360 | 1,22 | 17.86 | 0.0003 |
| Anthropic | 13.91 | 0.02478 ± 0.01495 | - | - | - | - | -0.00497 | 1,22 | 16.39 | 0.0005 |
| Pubescence | -26.73 | 0.002323 ± 0.001507 | MPE | 3,19 | 3.64 | 0.0315 | -0.00121 | 1,19 | 8.86 | 0.0078 |
| Pale body | -16.91 | 0.003894 ± 0.002526 | MPE | 3,19 | 26.30 | <.0001 | -0.00253 | 1,19 | 23.27 | 0.0001 |

1  Table 5 a,b: Linear regressions between bird traits of nesting habitats and feeding

2  guilds (see Appendix 4) and urbanization factors, i.e. asphalted and built area

3  (Impervious Area) and percentage cover of bushes and trees (Bush&Tree) for (a)

4  Community weight mean of single traits (mT) and (b) FD of trait groups. Only

5  significant results are given (P-value < 0.05; Coef = coefficient of regression; $R^2_{adj}$ =

6  adjusted R squared).

7

8  a) mT

| Trait group | Trait | Urbanization factor | Coef | P-value | $R^2_{adj}$ |
|---|---|---|---|---|---|
| Nesting habitat | NestBuilding | ImperviousArea | 0.222 | 0.0017 | 0.3149 |
| | | Bush&Tree | - 0.250 | 0.0130 | |
| | NestTree | ImperviousArea | - 0.120 | 0.0011 | 0.1025 |
| | NestCavity | Bush&Tree | 0.108 | 0.0511 | 0.0800 |
| | NestBush | ImperviousArea | - 0.068 | 0.0385 | 0.2701 |
| | | Bush&Tree | 0.144 | 0.0027 | |
| | NestGround | Bush&Tree | 0.048 | 0.0200 | 0.0897 |
| Feeding guild | LargeCarnivore | - | - | n.s. | 0.0072 |
| | Insectivore | Bush&Tree | 0.342 | 0.0005 | 0.1811 |
| | Granivore | Bush&Tree | - 0.348 | 0.0005 | 0.1930 |

9

10  b) FD

| Trait group | Urbanization factor | Coef | P-value | $R^2_{adj}$ |
|---|---|---|---|---|
| Nesting habitat | Bush&Tree | 0.094 | 0.0001 | 0.3218 |
| Feeding guild | Bush&Tree | - 0.097 | 0.0013 | 0.1935 |

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19    Figure 1

20    Mean traits (mT) of ground beetle (Carabidae) assemblages negatively (A) and

21    positively (B) correlated with increasing forest cover in 24 1km$^2$ landscape units (LU)

22    situated in four European countries.

23
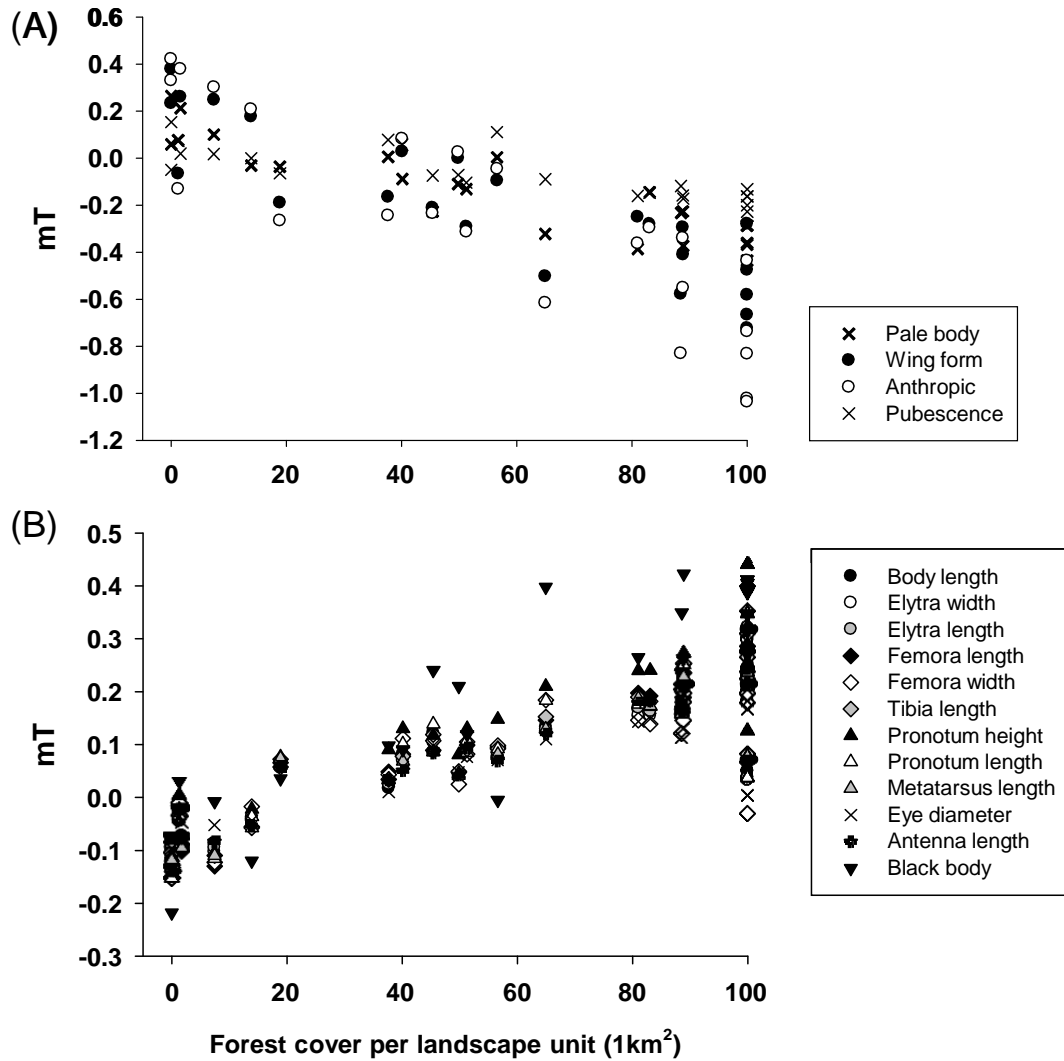
Appendix 1:

Benthic macroinvertebrate traits and trait modalities.

| Traits | No. of categories | Categories |
|---|---|---|
| Maximal body size | 7 | ≤ 0.25 cm, > 0.25–0.5 cm, > 0.5–1 cm, > 1–2 cm, > 2–4 cm, > 4–8 cm, > 8 cm |
| Life cycle duration | 2 | ≤ 1 year, > 1 year |
| Potential number of reproduction cycles per year | 3 | < 1, 1, > 1 |
| Aquatic stages | 4 | egg, larva, nymph, imago |
| Reproduction | 8 | ovoviviparity, isolated free eggs, isolated cemented eggs, cemented or fixed clutches, free clutches, clutches in vegetation (endophytic), terrestrial clutches, asexual reproduction |
| Dissemination | 4 | aquatic passive, aquatic active, aerial passive, aerial active |
| Resistance form | 5 | eggs/statoblasts/gemmules, cocoons, cells against desiccation, diapause or dormancy, none |
| Respiration | 4 | tegument, gill, plastron, spiracle (aerial) |
| Locomotion and substrate relation | 8 | flier, surface swimmer, swimmer, crawler, burrower (epibenthic), interstitial (endobenthic), temporarily attached, permanently attached |
| Food | 9 | fine sediment + microorganisms, detritus < 1 mm, plant detritus ≥ 1 mm, living macrophytes, dead animals > 1 mm, living microinvertebrates, living macroinvertebrates, vertebrates |
| Feeding habits | 8 | absorber, deposit feeder, shredder, scraper, filter feeder, piercer (plant or animal), predator (carver/engulfer/swallower), parasite/parasitoid |

Appendix 2:

Collembolan species traits and trait modalities. Traits considered were morphological characteristics connected to the adaptation of each collembolan species to the soil environment, namely number of ocelli, furca length, antenna length, pigmentation and the presence of hairs and scales. . A composite life-form trait was calculated by adding individual trait scores and used in calculations.

| Trait | Codification |
|---|---|
| Ocelli | 0+0 ocelli = 4 |
| | 1+1 – 2+2 ocelli = 3 |
| | 3+3 – 4+4 ocelli = 2 |
| | 5+5 – 6+6 ocelli =1 |
| | 7+7 – 8+8 ocelli = 0 |
| Antenna length | $0 < X \leq 0.5$ body length = 4 |
| | 0.5 body length $< X \leq 1$ body length = 2 |
| | $X > 1$ body length = 0 |
| Furca | Absent = 4 |
| | Reduced/short = 2 |
| | Fully developed = 0 |
| Hairs/Scales | Absent = 2 |
| | Present = 0 |
| Pigmentation | Absent (white colour) = 4 |
| | Coloured but not patterns = 2 |
| | Coloured and with patterns = 0 |

Appendix  3:

Traits of carabids (117 species collected from 24 landscapes in four European countries) used in the calculation of FD and mT.

| Trait group | Trait | Definition |
|---|---|---|
| Morphology | Wing form | 0 = wingless,  0.5 = brachypterous,  1.0 = macropterous |
| | Body pubescence | 0 = glabrous,  1 = pubescent |
| | Body length | Continuous (scaled between 0-1) |
| | Elytra  width | Continuous (scaled between 0-1) |
| | Elytra length | Continuous (scaled between 0-1) |
| | Femora length | Continuous (scaled between 0-1) |
| | Femora  width | Continuous (scaled between 0-1) |
| | Tibae length | Continuous (scaled between 0-1) |
| | Metatarsus length | Continuous (scaled between 0-1) |
| | Pronotum height | Continuous (scaled between 0-1) |
| | Pronotum length | Continuous (scaled between 0-1) |
| | Eye diameter | Continuous (scaled between 0-1) |
| | Antennae length | Continuous (scaled between 0-1) |
| Colouration | Body black | 0 = other, 1 = black |
| | Body pale | 0 = other, 1 = pale |
| | Legs black | 0 = other, 1 = black |
| | Legs Pale | 0 = other, 1 = pale |
| Habitat | Anthropic | 0  = natural habitat only, 1 = associated  with humans |

Running head: Functional traits as indicators of biodiversity

Appendix 4:

Description of the bird nesting and feeding traits and categories. Traits were described

for each species according published sources (Bezzel 1993; Maumary et al. 2007)

nominal value that range from 0 to 1 to describe better the attribute to the species. For

each trait we calculated the community weighted mean trait (mT) and functional

diversity (FD) to assess the impact of the urbanization on bird communities (see

Methods).

| Trait group | Trait | Description | Type |
| --- | --- | --- | --- |
| Nesting habitats | NestBuilding | Nest on / in buildings | continuous |
| | NestTree | Nest on trees | continuous |
| | NestCavity | Nest in natural cavities and nest-boxes | continuous |
| | NestBush | Nest on bushes | continuous |
| | NestGround | Nest on the ground | continuous |
| Feeding guild | LargeCarnivore | All vertebrates | continuous |
| | Insectivore | All invertebrates | continuous |
| | Granivore | All vegetal diet (buds, leaves, seeds) | continuous |