Conservation of European environments: The Spheciformes wasps as biodiversity indicators (Hymenoptera: Apoidea: Ampulicidae, Sphecidae and Crabronidae)

SEVERIANO F. GAYUBO, JOSÉ A. GONZÁLEZ, JOSEP D. ASÍS, & JOSÉ TORMOS

Área de Zoología, Facultad de Biología, Universidad de Salamanca, Salamanca, Spain

(Accepted 18 March 2005)

Abstract
The aim of this work is to propose the use of the Spheciformes wasps (Hymenoptera: Apoidea: Ampulicidae, Sphecidae and Crabronidae) as indicators of European biodiversity. One advantage of studying this group of insects lies in the regulating effects that such wasps have on other insect populations. We discuss the applicability of seven criteria, taken from the literature, to use the Spheciformes wasps as an indicator group, with respect to which parameters this group offers guarantees of being good indicators of biodiversity, both for predicting the diversity of other groups of animals and for all the species of a given area.

Keywords: Biodiversity indicators, European environments, Spheciformes

Introduction
In view of the current “biodiversity crisis”, studies investigating this issue explore one of the greatest challenges ever faced by humankind: how to analyse the current benefits of environmental manipulation and future costs of environmental harm (Tilman 2000; Weddell 2002; Wilson 2002). Although faunistic and floristic inventories are in marked decline (García-Valdecasas et al. 2000; Krell 2000; McNeely 2002), making inventories of diversity is considered to be a basic need (e.g. Cotterill 1995; Stork et al. 1996; Lawton et al. 1998; Peterson et al. 2002), since with current knowledge it would be necessary to generalize and make important decisions for the conservation of biological diversity using only some groups of organisms, mainly vertebrates and vascular plants (Noss 1990; Stork et al. 1996; Halffter 1998; Purvis and Hector 2000). Despite this, it has been shown that the diversity patterns in these groups do not always correspond to those of entomological groups (Reid 1998).
Bioindicators

The use of indicators in any biodiversity study involves indirect information about other groups, obtained from the direct information collected about the indicator group (Noss 1990; McGeoch and Chown 1998). However, their use is justified when it is difficult to collect such information in a direct and satisfactory way or when it involves a methodological improvement and a saving of time and economic resources (Reid et al. 1993; Favila and Halffter 1997; McGeoch 1998; Feinsinger 2001).

The term “biological indicator” was originally used in aquatic systems and referred to the detection and monitoring of changes in biota to reflect changes in the environment. When applied later to terrestrial systems, the meaning of the term “bioindicator” has expanded to encompass a broad variety of applications (McGeoch 1998):

1. Environmental indicators: a species or group of species, readily observable and quantifiable, that respond in a predictable way to any disturbance or change in the state of the environment (e.g. Paoletti 1999; Andersen et al. 2002; Sieren and Fischer 2002).

2. Ecological indicators: indicator taxa often used to demonstrate the effects of environmental changes (such as the alteration and fragmentation of the habitat or climate change) in biotic systems (e.g. Perfecto and Vandermeer 1996; Lawton et al. 1998; Przybylski 2002).

3. Biodiversity indicators: a group of taxa, or functional group, whose diversity reflects some measure of diversity (species richness, level of endemism) of other higher taxa in a habitat or landscape (e.g. Kitching 1996; Williams and Gaston 1998).

The use of insects as biodiversity indicators

Insects are the group of macroorganisms with the greatest adaptive plasticity, which has allowed them to colonize all habitats and made them the most diversified group of animals on the planet. They occupy nearly all terrestrial environments at proportions far higher than any other group of organisms as regards both abundance and richness. Also, they form a crucial part of the trophic chains of such environments.

The collection, mapping, and study of insect diversity are of increasing interest (e.g. Kremen et al. 1993; Gaston et al. 1996; Canovai et al. 2000; Campos and Fernández 2002). It is necessary to know the location of the sites with the greatest number of species and to know whether these sites also harbour rare, endemic or, from the point of view of systematics, singular species (Kerr 1997; Howard et al. 1998; New 1999a; Lobo and Martín-Piera 2002).

With the above in mind, all programmes addressing biodiversity should present inventories of insect fauna (and perhaps of all invertebrates) as priority components (Hawksworth and Ritchie 1993; Kim 1993; New 1999a), the evaluation and cataloguing of species of different insect groups being essential in the first stages of studies aimed at fostering environmental protection (Howard et al. 1998). However, the reports made of the fauna of sites of community importance proposed (pursuant to Council Directive 92/43/EEC) to form part of the European ecological network NATURA 2000 mainly address vertebrates, and fail to take into account insects (and arthropods in general), which constitute more than 90% of the species present in most terrestrial biotopes (Kremen et al. 1993; Finnamore 1996; Speight et al. 1999). As a result, the work of entomologists should be included in these tasks, since...
insects are considered to be the most relevant animals as biological indicators, both in terrestrial and freshwater systems. The interest in acquiring knowledge about entomological diversity is further increased if its importance in agriculture-related issues is considered, as is the case with the control of harmful insects or crop pollination (Hill 1997).

The size of the problem, the lack of available data, and the huge number of species have made it necessary to restrict the field of study and give priority to groups of insects that, playing a primary ecological role, exert a significant effect on the diversity of other organisms and that are subject to the danger of extinction when they occupy a high level in the trophic chain (Fisher 1998; New 1999a, 1999b).

Currently, studies are being undertaken to demonstrate the possible value of certain taxa as indicators, in order to predict the richness of other taxa. Thus, analysing the validity of some groups of insects as indicators in biogeographical and ecological studies in the Neotropical Region, Brown (1991, 1997) obtained a higher evaluation for ants and certain taxa of butterflies (Heliconiini, Ithominae). Kremen (1994) studied the butterflies of Madagascar as target taxa in biological inventories. Beccaloni and Gaston (1995) demonstrated the appropriateness of the Ithomiinae (Nymphalidae) as indicators of the diversity of all the Lepidoptera inhabiting neotropical forests. Pearson and Cassola (1992) and Carroll and Pearson (1998) demonstrated that with the diversity of tiger beetles (Coleoptera: Cicindelidae) that of butterflies is predicted on a very broad scale.

In this sense, in most European countries research into the biodiversity of different groups of Hymenoptera Aculeata is gaining importance; according to Ulrich (1999), this group would include some 2660 expected species for Europe. This number is a serious underestimate, since according to the authors of the present work that number of aculeates would be found in the Iberian Peninsula alone.

Proposal for Spheciformes as biodiversity indicators

Choice of a group as a biodiversity indicator should be based on well-defined criteria aimed at collecting scientifically rigorous results that will increase the efficiency of available funding and time; moreover, the use of such a group should guarantee reliability in the presentation of the results in any generalization established (Pearson 1994; Brown 1997; McGeoch and Chown 1998).

In order to use a given group as a diversity indicator with any degree of guarantee, mainly the criteria described by Pearson (1994) should be fulfilled:

1. A well-known and stable taxonomy.
2. A satisfactorily known natural history.
3. Ease in sampling, observation, and handling of the populations.
4. The taxa of the upper range of the group should have a wide geographical distribution and should be present in the greatest number of habitats possible.
5. The taxa of the lower range should be specialized and sensitive to habitat changes.
6. Patterns of biodiversity reflected in other taxa, related or related.
7. Potential economic importance.

The Spheciformes wasps fulfil these seven criteria, as may be seen from the following arguments.
1. A well-known and stable taxonomy

Since 1802, when Latreille used the term “Sphegimae”, many studies have been carried out on this group of Hymenoptera and a huge body of information has been compiled. Apart from the pioneering work of the 19th century, modern classification is due to Kohl (1896), who defined the “Gattungsgruppen” (subfamilies) and the “Untergruppen” (tribes) of today’s Spheciformes.

Bohart and Menke (1976) collated a large part of the data known about taxonomy, phylogeny, natural history and geographic distribution. The taxonomic data are complete and include identification keys up to the level of genus and check-lists of all the described species. Later, studies continued exhaustively, taxonomic reviews having been made of less well-known genera at world-wide level.

After the work of Bohart and Menke (1976), this group of wasps was considered by most authors to be monophyletic. Recently, Melo (1999) has demonstrated that it constitutes a paraphyletic group formed by three families (Ampulicidae, Sphecidae and Crabronidae), using the term “Spheciformes”—previously proposed by Brothers (1975)—for the denomination of the overall group.

Regarding studies on this group of hymenopterans in Europe, the degree of taxonomic knowledge is extraordinary and has allowed the compilation of Red Lists that relate certain species with different categories, ranging from rare to those considered to be extinct (Day 1991; Schmid-Egger et al. 1995, 1996; Archer 1998). This would to a certain extent make it equal to the taxonomic information available concerning some groups of vertebrates, at least in northern countries.

2. A satisfactorily known natural history

Within the Hymenoptera Aculeata, the Spheciformes colonize and exploit different habitats and reach a vast degree of diversification owing to the varied nature of their behaviour and morphology. In Europe, most species undergo a winter diapause in the pre-pupa stage. The males usually emerge before the females, which, after copulation, begin their nesting activity (nest construction, provisioning and oviposition). The females are predators and capture other insects (or in certain cases spiders) to feed their larvae. The nests are built in the ground, in wood or in galleries in plants, or are made of mud (in exceptional cases plant fibres are also used). In these nests, prey are stored in separate cells, where an egg of the female hymenopteran is also laid.

The biology of the members of the group is well known and there are many papers and reviews available (Evans 1966; Krombein 1967; Iwata 1976; Evans and O’Neill 1988; O’Neill 2001).

3. Ease of sampling, observation, and handling of the populations

The classic method used to capture Spheciformes has been the insect net. More recently, yellow pan traps and trap-nesting have been incorporated into the arsenal (e.g. Trojan et al. 1994; Skibinska 1995; Tscharntke et al. 1998) together with Malaise traps (e.g. Sorg and Cölln 1992; Shlyakhtenok 1995; Gayubo et al. 2000), with satisfactory results. These four capture methods can be used in a complementary fashion (Harris 1982; Schmid-Egger 1992). In this way it has been possible to perform an easy and very representative capture of Spheciformes from a given area.
Taking into account the results of other authors (Pearson and Cassola 1992; Favila and Halffter 1997), it seems that insect capture using the above methods does not endanger their conservation.

4. The taxa of the upper range of the group should have a wide geographical distribution and should be present in the greatest number of habitats possible

The three families of Spheciformes are cosmopolitan and encompass more than 8000 species and about 250 genera (Gauld and Bolton 1988; Finnamore 1993).

The continental areas with the greatest number of endemic genera are South Africa, Australia and South America. The deserts of south-western USA also harbour some endemic forms and the drier areas of the Palaearctic Region, such as N Africa or SE Russia, display a high number of their own elements, at both genus and species level (Bohart and Menke 1976).

In light of the above, it is possible to distinguish two main components in the Spheciformes fauna of Europe: temperate and Mediterranean (Barbier 1999). Many dominant species are common in both simultaneously. They undoubtedly originated from temperate climates and have become adapted to local regimes of temperature, humidity and day length. These species are usually common members of universal genera, whose distribution covers both the Old World and the rest of the planet (Day 1991).

Finally, certain genera show a disjoint distribution; outstanding among these are Chalybion Dahlbom, with two species in the New World and many in the Old World; Ancistromma Fox, with a high number in North America and some in the west of the Palaearctic Region, and Plenoculus Fox, with many species in North America, one in SW Russia, and one in the Iberian Peninsula (Bohart and Menke 1976).

5. The taxa of the lower range should be specialized and sensitive to habitat changes

Owing to the complex biology of their species, the Spheciformes are considered crucial insects in all terrestrial ecosystems (Gauld and Bolton 1988; Gauld et al. 1990; Day 1991; LaSalle and Gauld 1993). The complexity shown by these insects, together with the lower genetic diversity that characterizes Hymenoptera with respect to other orders (Unruh and Messing 1993), make them particularly sensitive to certain forms of environmental damage, although they are able to exist in small isolated populations (Day 1991). This is why the Hymenoptera are particularly important biological indicators, apart from the intrinsic interest of their complex models of behaviour. Furthermore, many species profit from zones of ecotone in ecological successions and zones in which, owing to the natural conditions or human interference, there are areas appropriate for nesting (Duelli et al. 1990; Shlyakhtenok 2000; Kirby 2001). Certain species coexist very well with humans, human agricultural practices and techniques, and in built-up areas, and indeed their absence can be seen as an indicator of the poverty of a given environment (Day 1991; Kirby 2001). In this sense, the Spheciformes form a group that can be used to delimit potential areas of protection, in which not only such “natural” (well-conserved) zones should be included but also other surrounding areas, thereby making biodiversity conservation compatible with the continuance of traditional customs.

6. Patterns of biodiversity reflected in other taxa, related or not

Considering the importance of the predatory behaviour for paedotrophic purposes and in view of the amount of prey captured, the Spheciformes may be good indicators of the
diversity of other groups of arthropods, such as spiders, and insects of the orders Orthoptera, Hemiptera, Diptera (Cyclorrhapha), and Lepidoptera (O’Neill 2001). Likewise, they can be indicators of the availability of potential prey in a given area for certain threatened species of birds, such as the red-legged partridge (*Alectoris rufa* L.) or the lesser kestrel (*Falco naumanni* Fleischer), species which in the fledgling stage follow an entomophagous diet mainly based on the capture of Orthoptera and in which changes in agricultural practices have led to the disappearance of uncultivated land from much of the arable landscape and, consequently, to a reduction in nesting cover and chick food (Tucker and Heath 1994; BirdLife International 2000).

Regarding their natural enemies, the Spheciformes are a group to be considered as indicators of the diversity of parasitoids belonging to different families of hymenopterans and dipterans. The different substrates used, together with the broad variety of nesting strategies employed by representatives of this group, mean that some parasitoids are different from both the taxonomic and behavioural point of view. These natural enemies oviposit or larviposit: (a) on paedotrophic material, (b) on the total content of the cell, or (c) on the mature larva, pre-pupa or pupa of the host. They can be encompassed within four biological types; namely (1) inquilines: the egg of the parasitoid is deposited on or close to the egg of the host, rapidly hatches, and the larva feeds first on the egg of the host and then on the rest of the contents of the cell (e.g. Gasteruptiidae: *Gasteruption*, species of Chrysididae); (2) metaparasitoids: the host larva is attacked in its different stages (e.g. Ichneumonidae, Chalcidoidea, Chrysididae); (3) orthoparasitoids: only the pre-pupa or pupa of the host are susceptible to attack (e.g. Chrysididae, Mutillidae); and (4) cleptoparasitoids: only the paedotrophic material is consumed (e.g. Diptera).

As a conclusion to this section, it may be said that in view of the relationship of prey groups and parasitoid groups with the structure and state of the environment (Lawton 1983; Andow 1991; Duelli et al. 1999), the Spheciformes can be considered as environmental and ecological indicators, and offer guarantees of being good indicators of sustainability in a given landscape or changes in the general diversity of a territory due to the impact of human activity.

7. Potential economic importance

Although the Spheciformes cannot be considered a group of economic importance, since they are not used in biological control, the regulating effects they exert on other insect populations that may cause plagues (e.g. aphids) are interesting; this is the case of individuals of several genera, above all belonging to the subfamily Pemphredoninae (O’Neill 2001).

This paper only proposes Spheciformes as an indicator group, but it would be appropriate, if one considers the economic point of view, to complete this type of study with phylogenetically related groups of proven economic importance. This is the case for certain families of wild bees, which are important pollinators, and whose taxonomy is well established. Duelli and Obrist (1998) have shown a high correlation between the number of species and the overall species richness for these groups.

In any case, this criterion is less important than the previous ones for defining a given group as a biodiversity indicator (Speight et al. 1999).

To conclude, after the work of Pearson (1994), McGeech (1998) expanded to 15 the obvious criteria that any group proposed as a biodiversity indicator must fulfil. Most of them (12) ... “may be, or usually are, possible to determine before the selection of a
potential bioindicator”, while the remaining three ... “are usually only assessable after testing the suitability of the selected potential bioindicator”.

Some of these criteria are of a practical nature (costs deriving from research, time, funding, and human resources) while others are a result of those considered to be essential. Regarding the proposal of Spheciformes as a biodiversity indicator group, stress should be placed on criterion 1: “Cost efficient and effective”. It is clear that the results obtained are highly satisfactory, with relatively low budgets, which is sufficiently well-demonstrated by the many projects carried out even with minimal funding.

Acknowledgements

We sincerely thank Dr Gonzalo Halffter (Instituto de Ecología A. C., Veracruz, Mexico) and Dr Michael E. Archer (York St John College of the University of Leeds, UK) for critical reading of the manuscript. Financial support for this paper was provided from the Ministerio de Ciencia y Tecnología (Spain), project REN2001-1737/GLO.

References

Andersen AN, Hoffmann BD, Muller WJ, Griffiths AD. 2002. Using ants as bioindicators in land management: simplifying assessment of ant community responses. Journal of Applied Ecology 39(1):8–17.

Andow DA. 1991. Vegetational diversity and arthropod population response. Annual Review of Entomology 36:561–586.

Archer ME. 1998. Threatened wasps, ants and bees (Hymenoptera: Aculeata) in Watsonian Yorkshire: a Red Data Book. York: PLACE Research Centre and York St John College of the University of Leeds. 68 p.

Barbier Y. 1999. Comparaison de deux unités géographiques pour l’étude de la biogéographie des Crabroniens et des Sphecines en France, Belgique et Grand-Duché de Luxembourg (Hymenoptera: Sphecidae). Annales de la Société Entomologique de France (N.S.) 35(Suppl):268–273.

Beccaloni GW, Gaston KJ. 1995. Predicting the species richness of Neotropical forest butterflies: Ithomiinae (Lepidoptera: Nymphalidae) as indicators. Biological Conservation 71:77–86.

BirdLife International. 2000. Threatened birds of the world. Barcelona: BirdLife International and Lynx Edicions. 852 p.

Bohart RM, Menke AS. 1976. Sphecid wasps of the world, a generic revision. Berkeley: University of California Press. 695 p.

Brothers DJ. 1975. Phylogeny and classification of the aculeate Hymenoptera, with special reference to the Mutillidae. University of Kansas Science Bulletin 50:483–648.

Brown KS Jr. 1991. Conservation of Neotropical environments: insects as indicators. In: Collins NM, Thomas JA, editors. The conservation of insects and their habitats. London: Academic Press. p 349–404.

Brown KS Jr. 1997. Diversity, disturbance, and sustainable use of Neotropical forests: insects as indicators for conservation monitoring. Journal of Insect Conservation 1:25–42.

Campos DF, Fernández F. 2002. El Proyecto “Diversidad de Insectos en Colombia”. In: Costa C, Vanin SA, Lobo JM, Melic A, editors. Proyecto de Red Iberoamericana de Biogeografia y Entomología Sistemática PrIBES 2002. Zaragoza: Sociedad Entomológica Aragonesa (SEA) and CYTED. p 297–300. (m3m-Monografias Tercer Milenio; 2).

Canovai R, Giannotti P, Giannetti S, Loni A, Raspi A, Santini L, Dellacasa M, Generan M, Pagliano G, Strumia F, Scaramozzino PL, Zuffi M, Baldacchini NE, Puglisi L, Battesti MJ, Brocard E. 2000. Biodiversità: compilazione delle specie dell’entomofauna e dei piccoli vertebrati della Corsica e della Toscana Marittima. In: Strumia F, editor. Progetto INTERREG II Toscana-Corsica. L’attività scientifica delle Università di Pisa e Corte. Pisa: European Union and Edizioni ETS. p 75–86.

Carroll SS, Pearson DL. 1998. Spatial modeling of butterfly species diversity using tiger beetles as a bioindicator taxon. Ecological Applications 8:531–543.

Cotterill FPD. 1995. Systematics, biological knowledge and environmental conservation. Biodiversity and Conservation 4:183–205.

Day MC. 1991. Towards the conservation of aculeate Hymenoptera in Europe. Strasbourg: Council of Europe. 80 p. (Nature and Environment Series; 51).
LaSalle J, Gauld ID. 1993. Hymenoptera: their diversity, and their impact on the diversity of other organisms. In: LaSalle J, Gauld ID, editors. Hymenoptera and biodiversity. Wallingford (UK): CAB International and The Natural History Museum. p 1–26.

Lawton JH. 1983. Plant architecture and the diversity of phytophagous insects. Annual Review of Entomology 28:23–39.

Lawton JH, Bignell DE, Bolton B, Bloemers GF, Eggleton P, Hammond PM, Hodda M, Holt RD, Larsen TB, Mawdsley NA, Stork NE, Srivastava DS, Watt AD. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391:72–76.

Lobo JM, Martín-Piera F. 2002. Searching for a predictive model for species richness of Iberian dung beetle based on spatial and environmental variables. Conservation Biology 16:158–173.

McGeoch MA. 1998. The selection, testing and application of terrestrial insects as bioindicators. Biological Review 73:181–201.

McGeoch MA, Chown SL. 1998. Scaling up the value of bioindicators. Trends in Ecology and Evolution 13:46–47.

McNeely JA. 2002. The role of taxonomy in conserving biodiversity. Journal of Nature Conservation (Jena) 10(3):145–153.

Melo GAR. 1999. Phylogenetic relationships and classification of the major lineages of Apoidea (Hymenoptera), with emphasis on the crabronid wasps. Scientific Papers, Natural History Museum, The University of Kansas 14:1–55.

New TR. 1999a. Limits to species focusing in insect conservation. Annals of the Entomological Society of America 92:853–860.

New TR. 1999b. Entomology and nature conservation. European Journal of Entomology 96:11–17.

Noss RF. 1990. Indicators for monitoring biodiversity: a hierarchical approach. Conservation Biology 4:355–364.

O’Neill KM. 2001. Solitary wasps: behavior and natural history. Ithaca (NY): Cornell University Press. 406 p.

Paoletti MG. 1999. Using bioindicators based on biodiversity to assess landscape sustainability. Agriculture, Ecosystems and Environment 74:1–18.

Pearson DL. 1994. Selecting indicator taxa for the quantitative assessment of biodiversity. Philosophical Transactions of the Royal Society of London, Series B 345:75–79.

Pearson DL, Cassola F. 1992. World-wide species richness patterns of tiger beetles (Coleoptera: Cicindelidae): indicator taxon for biodiversity and conservation studies. Conservation Biology 6:376–391.

Perfecto I, Vandermeer J. 1996. Microclimatic changes and the indirect loss of ant diversity in a tropical agroecosystem. Oecologia 108:577–582.

Peterson AT, Ortega-Huerta MA, Bartley J, Sánchez-Cordero V, Soberón JM, Buddemeier RH, Stockwell RB. 2002. Future projections for Mexican faunas under global climate change scenarios. Nature 416:626–629.

Przybylski Z. 2002. Future research on possibility of using potato beetle (Leptinotarsa decemlineata Say) as a bioindicator of soil polluted by lead. Journal of Plant Protection Research 42(1):53–56.

Purvis A, Hector A. 2000. Getting the measure of biodiversity. Nature 405:212–219.

Reid WV. 1998. Biodiversity hotspots. Trends in Ecology and Evolution 13:275–280.

Reid WV, McNeely JA, Tunstall DB, Bryant DA, Winograd M. 1993. Biodiversity indicators for policy-makers. Washington: WRI-UICN-UNEP. 42 p.

Schmid-Egger C. 1992. Malaisefallen versus Handfang—Der Vergleich zweier Methoden zur Erfassung von Stichlingen (Hymenoptera, Aculeata). Verhandlungen Westdeutscher Entomologentag Düsseldorf 1992:195–201.

Schmid-Egger C, Risch S, Niehuis O. 1995. Die Wildbienen und Wespen in Rheinland-Pfalz (Hymenoptera, Aculeata). Verbreitung, Ökologie und Gefährdungssituation. Fauna und Flora in Rheinland-Pfalz, Beiheft 16:1–296.

Shlyakhtenok AS. 1995. Distribution of spider and digger wasps (Hymenoptera, Pompilidae, Sphecidae) in a mossy pine forest (Pinetum pleurosum) in the Berezinsky Biosphere Reserve. Fragmenta Faunistica 38:191–195.

Shlyakhtenok AS. 2000. Effectiveness of Malaise traps for collection of wasps (Hymenoptera: Aculeata). Pakistan Journal of Zoology 32(1):45–47.

Sieren E, Fischer FP. 2002. Evaluation of measures for enlargement, renaturation and development of a dry grassland biotope by analyzing differences in the carabid fauna (Coleoptera). Acta Oecologica 23(1):1–12.

Skibinska E. 1995. Sphecidae (Aculeata) of subcontinental pine forest stands (Peucedano-Pinetum) of various ages in Puszcza Białowieska. Fragmenta Faunistica 38:420–433.
Sorg M, Cölln K. 1992. Die Grabwespen (Hymenoptera, Sphecidae) von Gönnersdorf (Kr. Daun). Beiträge zur Insektenfauna der Eifeldörfer VI. Dendrocopos 19:126–142.

Speight MR, Hunter MD, Watt AD. 1999. Ecology of insects: concepts and applications. Oxford: Blackwell Science. 350 p.

Stork NE, Samways MJ, Eeley HAC. 1996. Inventorying and monitoring biodiversity. Trends in Ecology and Evolution 11:39–40.

Tilman D. 2000. Causes, consequences and ethics of biodiversity. Nature 405:208–211.

Trojan P, Bankowska R, Chudzicka E, Pilipiuk I, Skibinska E, Sterzynska M, Wytwer J. 1994. Secondary succession of fauna in the pine forests of Puszcza Bialowieska. Fragmenta Faunistica 37:1–104.

Tscharntke T, Gathmann A, Steffan-Dewenter I. 1998. Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. Journal of Applied Ecology 35:708–719.

Tucker GM, Heath MF. 1994. Birds in Europe: their conservation status. Cambridge: BirdLife International. 600 p. (BirdLife Conservation Series; 3).

Ulrich W. 1999. The number of species of Hymenoptera in Europe and assessment of the total number of Hymenoptera in the world. Polskie Pismo Entomologiczne 68:151–164.

Unruh TR, Messing RH. 1993. Intraspecific biodiversity in Hymenoptera, implications for conservation and biological control. In: LaSalle J, Gauld ID, editors. Hymenoptera and biodiversity. Wallingford (UK): CAB International and The Natural History Museum. p 27–52.

Weddell BJ. 2002. Conserving living natural resources: in the context of a changing world. Cambridge: Cambridge University Press. 400 p.

Williams PH, Gaston KJ. 1998. Biodiversity indicators: graphical techniques, smoothing and searching for what makes relationships work. Ecography 21:551–560.

Wilson EO. 2002. The future of life. New York: Alfred A. Knopf Editor and Random House. 229 p.