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Terrestrial and Aquatic Invertebrates as Bioindicators for Environmental Monitoring, with Particular Reference to Mountain Ecosystems

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ABSTRACT / The use of terrestrial and aquatic invertebrates as a management tool for monitoring change in ecosystems is reviewed and critically evaluated. Their suitability and value for assessing a range of environmental problems from pollution impacts, through habitat evaluation for conservation to the long-term degradation and recovery of ecosystems, is critically discussed. Guidelines are provided for the choice of appropriate bioindicators. Examples of the use of a broad spectrum of invertebrates to assess a variety of environmental problems are summarized. The particular potential of invertebrates for monitoring montane ecosystems is highlighted.

A bioindicator can be defined as ''a species or group of species that readily reflects the abiotic or biotic state of an environment, represents the impact of environmental change on a habitat, community, or ecosystem, or is indicative of the diversity of a subset of taxa, or of the wholesale diversity, within an area'' (McGeoch 1998). The principles and ranges of applications for the use of invertebrate bioindicators as tools for environmental management within mountain environments are similar to those pertaining generally. This paper focuses primarily, therefore, on the common problems and issues arising from the use of aquatic (i.e., freshwater) and terrestrial invertebrates as bioindicators before suggesting some more specific uses within mountain environments. The ideas presented originate from an international workshop (Global Mountain Biodiversity Assessment–DIVERSITAS programme) organized by the Austrian Academy of Sciences to review critically the range of options for monitoring long-term impacts of environmental change in mountain habitats using invertebrates and to provide realistic guidelines for their use.

There is a strong relationship between human activities and disturbance of the environment. Recognition of this connection, and the need to protect human health and recreation, fisheries production, and industrial/agricultural systems, led to the early development of water quality regulations and monitoring methods. Early efforts include river and stream eutrophication typology (Sprobiensystem of Kolkwitz and Marsson 1909) and lake eutrophication typology (Thienemann 1921). The utility of invertebrates for assessing environmental conditions in aquatic ecosystems has thus long been recognized (Cairns and Pratt 1993), and this has spawned a variety of biological monitoring tools that use aquatic invertebrates (Hellawell 1986, Rosenberg and Resh 1993). These monitoring methods recognized that different invertebrate taxa tolerate organic pollution to a lesser or greater extent and that their differing responses can be used to indicate water quality. For example, in rivers, invertebrate groups such as larvae of Plecoptera and Ephemeroptera were shown to be pollution intolerant, whereas other taxa, such as tubificid worms and particular species of chironomid midge larvae, survived under deoxygenated conditions verging on anoxia. Modern assessment protocols still rely on such indicator species or assemblages and detailed knowledge of pollution responses, but they now also often involve sophisticated transformation or statistical analyses of data. Protocols continue to be developed and refined, especially for wetland and large river invertebrates. Aquatic invertebrates have, therefore, repeatedly shown their utility in evaluating aquatic resources. The beauty of this approach is the ease with which it can be

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applied and communicated, and the responsiveness of the indicator invertebrates.

By contrast, Rosenberg and others (1986) noted that the effective use of invertebrates in monitoring and assessment of the terrestrial environment was less developed than for aquatic environments, and this still appears to be the case almost 20 years later. It is not clear, however, why this difference developed, but a key factor may be the absence of specific regulations for terrestrial environments, and the lesser need to assess compliance. In any event, the utility of terrestrial invertebrates as bioindicators will presumably come to match that of aquatic invertebrates in future because terrestrial invertebrates exhibit many of the characteristics that make aquatic invertebrates such valuable bioindicators.

The concept of bioindication has, within the past 25 years, been broadened and expanded to address emerging ecological issues related to conservation assessment and landscape management. A plethora of papers has suggested how an increasingly wide range of invertebrates might be used to indicate environmental trends, impacts, and change or the ecological value of sites (see Rosenberg and Resh 1993, Dallinger 1994, Paoletti and Bressan 1996, van Straalen 1998, Jonsson and Jonsell 1999, Cortet and others 1999, Moritz and others 2001, Reyers and others 2000, Norden and Appelqvist 2001, Taylor and Doran 2001, Mac Nally and others 2002 for summaries). Many of the suggestions are vague, impractical, or unworkable and little energy has been invested in evaluating, defining, and testing their appropriateness and applicability as workable bioindicator systems.

The purpose of this paper, therefore, is to 1) examine how and which invertebrates might prove useful as bioindicators, 2) identify criteria for the selection of useful bioindicator systems, and 3) evaluate the use of these systems across a wide range of potential applications, particularly within montane environments.

How Can Invertebrates Be Used as Indicators?

Invertebrates can indicate changes in the environment through their responses at different levels of organization, ranging from the individual animal to the total invertebrate community. The appropriateness of the level chosen to indicate a changing environment depends on the particular factor(s) that are thought to be acting. Responses to single pollutants may be picked up by changes in individual animals or species populations, whereas long-term forest degradation, or the conservation value of particular sites, may be better indicated by changes in the whole invertebrate community. It is a question of choosing the right indicators for each specific purpose. This necessitates that the initial problem be clearly delineated and defined, that suitable bioindicator organisms be selected using rigorous criteria, and that the predicted response of the bioindicator taxa be clear and well tested (McGeoch 1998, Pearson 1994). Because knowledge for individual species and species assemblages is often incomplete, and environmental stress often involves several concurrent factors at varying levels, monitoring programs frequently rely on the responses of more than one indicator to increase the accuracy of their assessments.

The Individual Animal Level Response

Individual animals may serve as short-term bioindicators of particular environmental conditions, where a response to a particular environmental stress can be demonstrated in their physiology or behavior. For example, in stream-dwelling mayflies and stoneflies, the rate of respiration (physiology) fails to compensate for falling oxygen levels within the water, and this may be coupled with more rapid movement of body parts involved with gas exchange (behavior) (Eriksen and others 1996). Similarly, some aquatic midge larvae display avoidance behavior when confronted with sediments contaminated by heavy metals above certain concentrations. Other examples include the bioaccumulation of toxins (e.g., Kovats and Ciborowski 1989, Cain and others 1992, Standley and Sweeney 1995), development of biomarkers (e.g., Maycock and others 2003), or morphological deformities (fluctuating asymmetry or FA). FA refers to the phenomenon that when some animals are subjected to environmental stresses, they show increased levels of asymmetry in their body shape and size, usually measured either side of a bilateral line. The distortion can be measured quantitatively and expressed as an index for a species population. This index may increase with increasing stress levels and thus serve as a simple way in which to monitor the impact of a wide range of known environmental stress factors. The concept of FA has been widely applied as a stress indicator in both aquatic and terrestrial ecosystems (e.g., Clarke 1993, Lenat 1993, Rabitsch 1997, Groenendijk and others 1998, Tessier and others 2000) involving pollution by pesticides, fertilizers, PCBs, aluminum, heavy metals, and thermal stress, but with varying degrees of success.

The Species Population-Level Response

Responses here involve changes that are apparent only when observing multiple individuals (populations) of single species in response to an external factor. Such factors may induce changes in population density as a result of effects on invertebrate performance that enhance or reduce rates of recruitment/mortality. There may also be changes in the ''quality'' of the individual animals, either in the short term through detrimental impacts on growth and development (see later) or in the long term through genetic selection (Frati and others 1992). Species-level responses are most easy to interpret when they are linked to single clearly defined factors, particularly physical or chemical features of their environment. The distribution of particular monophagous species of herbivorous insect on their host plants, for example, serves as a sensitive indicator of changing environmental temperatures (Hodkinson and Bird 1998). Insects shift their distribution relatively rapidly *within* the broader geographical range of their plant, and this is most readily observed among arctic/alpine species along latitudinal or altitudinal gradients that serve as proxies for a changing climate (Whittaker and Tribe 1996, Randall 1982). Similarly, among soil animals, certain earthworm species, particularly *Lumbricus* spp., are good bioindicators of soil pH and several soil arthropods, particularly Collembola, snails and isopod species are known to suffer mortality at known threshold levels of soil contaminants, especially heavy metals (Cortet and others 1999, van Straalen 1998). Population genetic structure of mayflies (Benton and Guttman 1990), caddisflies (Benton and Guttman 1992), and amphipods (Duan and others 2000) have been observed to change in response to heavy metal exposure. Here the direct linkage between the bioindicator species population and the strength of the external factor is recognized and exploited.

The Community-Level Response

Monitoring community-level responses is complex in that it involves integrating the responses of numerous species populations. However, the community response provides a valuable perspective with regard to the biological magnitude of changes. There is generally little question that a community response is significant because it reflects changes for multiple species, whereas indicator species responses involve only one species, and many other species are potentially unaffected. In addition, in a world with complex sources of disturbance, the multispecies approach makes use of more biological monitoring tools (i.e., species).

Communities possess several attributes useful for bioindication. These include the number of species present (species richness), the relative abundances of the different species, and the presence of ''important'' species. These important species may be Keystone species, in the ecological sense, that is, species having several other species depending upon them for their existence and where removing them would instantly eradicate several other species (Mills and others 1993). The important species may also include rare, relict, endemic, or endangered taxa of conservation significance.

Invertebrates within any given habitat are generally taxonomically diverse, and it may be unrealistic to expect the simple bioindicator organism–environmental factor relationships that are observed at the species level to be repeated at the community level. Because of the sheer number of species present, it becomes increasing difficult to establish precise and well-understood causal relationships between external factors and the composition of entire communities. Community composition is thus more usually used to bioindicate broader aspects of habitat quality and more general changes within the habitat such as degradation and recovery following stress or disturbance. Nevertheless, examples of the effective use of whole invertebrate communities for biomonitoring do exist. The relatively easy-to-sample and species-poor (50–100 species are commonly collected in a single visit to a unimpaired site) communities of running water ecosystems, for example, are reasonably well understood and the predictable response of the whole community to organic pollution, as mentioned earlier, forms the basis of water quality assessment. More frequently, however, it is necessary to work with subsets of taxa that can be shown to act as proxies for the whole community. For example, in running water ecosystems, the subset of Ephemeroptera, Plecoptera, and Trichoptera are commonly monitored together as a single richness variable–EPT Index (Resh and Jackson 1993). Together, this represents a group that can be identified reliably, is ecologically important, and contains many pollution-sensitive species. This subset reflects a common response to pollution observed over many years of monitoring, and excludes some of the more taxonomically challenging groups (i.e., chironomid midges and oligochaete worms).

This is clearly the point at which problems can arise. How representative is the chosen subset? How does one know? Choice of the species subset can be based on some combination of taxonomic or functional group criteria as well as responses to disturbance. Manageable taxonomic subsets, which may embrace genera, families, or higher groupings, should ideally be chosen on the basis that they are representative of the whole community and the group can be shown to respond sensitively to the factor affecting the whole community. Often, however, individual taxonomic specialists promote the virtues of their own particular specialist group with scant regard to cross-referencing their findings to the residual taxa. A single experimental demonstration of a negative impact of a disturbance on a given taxon does not necessarily make that taxon a reliable indicator. A consistent, repeatable response to that disturbance is necessary to establish the efficacy of the taxon as a bioindicator. The problems may be compounded by the fact that there is often little consistency in the measured responses by two different taxonomic groups to the same external factor (e.g., Heino and others 2003b). In other instances, however, similar responses are observed in taxonomically divergent groups such as birds and butterflies (Blair 1999). Passy and others (2004) observed generally similar responses among fish, macroinvertebrates, and algae across numerous streams, but suggested that each taxonomic group responds to a distinct combination of environmental factors. Sometimes relationships can be counterintuitive, such as the inverse relationship between species richness of gall-forming insects and plant diversity in tropical rain forest (Cuevas-Reyes and others 2003). These problems may be particularly acute where invertebrates are being used to indicate the conservation value of natural habitats or to indicate longer-term changes occurring within those habitats. The value of particular groups can, however, be enhanced by a knowledge of the habitat fidelity and specificity of the member species, which aid interpretation and prediction (McGeoch and others 2002).

One possible way around this problem of varying responses within taxonomic groupings is to use selected functional groups or guilds of organisms rather than taxonomic entities (Rawer-Jost and others 2000). A functional group or guild is defined as a set of taxonomically unrelated species that perform similar functions within the community (Simberloff and Dayan 1991). This, if used in a targeted manner, can focus the effect of an external factor onto an ecological process and those species that are most likely to respond to it. Examples might include the response of lichen-feeding invertebrates to sulfur dioxide pollution (acidification) or soil fungus-feeding communities responding to changes in the quality and quantity of available leaf litter after ecosystem disturbance (decomposition). However, in a biomonitoring study of anthropogenic disturbance in tropical forests, broad-feeding guilds were weaker discriminators than selected-target taxa within the guild (Basset and others 2004). Similarly, biometrics describing trophic or feeding functional structure have not been strong indicators for stream macroinvertebrates (Barbour and others 1999, Carlisle and Clements 1999). However, an alternative approach is being actively explored that combines food and feeding habits with a wide variety of other biological traits such as body size, fecundity, voltinism, development time, and vagility to describe functional community structure relative to a habitat template (Poff 1997, Statzner and others 2004). This approach shows better promise for detecting changes in community structure in response to habitat modification and pollution (Charvet and others 1998, 2000, Dolédec and others 1999, Gayrud and others 2003).

One of the problems of using invertebrate communities or guilds as bioindicators is that such assemblages are subject to natural stochastic variation in addition to the independent deterministic changes resulting from pollution or disturbance, particularly over the long term. It may be necessary, therefore, to establish the natural range of variation for the indicator community before its use in bioindication: good bioindicators will respond more sensitively to the deterministic forces than to the stochastic ones.

What Can Invertebrates Bioindicate?

McGeoch (1998) divided bioindicators into environmental indicators (changes in physicochemical environment), ecological indicators (impacts of factors on ecosystems), and biodiversity indicators (habitat assessment for conservation). This framework is, however, a little fuzzy with some conceptual overlap between categories, and here we have categorized instead the impacting factors or the habitat properties rather than their bioindicators. Broadly speaking, bioindicators can be used to indicate 1) a changing physical environment; 2) a changing chemical environment, particularly with respect to various forms of pollution; 3) the comparative quality or conservation value of habitat; and 4) changes in the ecological status of the habitat with respect to time and place. These may (1, 2, 4) or may not (3 and sometimes 4) involve external impacts on the habitat.

Changing Physical Environment

Relative to studies on the chemical environment, studies on the physical environment in terrestrial habitats are few, mainly investigating responses to temperature. The response to a changing physical environment embraces raised or lowered environmental temperatures (mean, range, and frequency of extremes) and patterns of precipitation and drought, together with associated phenomena such as the frequency of freeze–thaw cycles and the persistence of snow/ice cover on both landscape and wider geographical scales. It also embraces changes in UVB exposure associated with ozone depletion and more localized and obscure effects such as changes in soil properties associated with compaction by skiing (Kopeszki and Trockner 1994). By contrast with terrestrial ecosystems, the effects of the primary physical parameters, especially current, substrate type, depth, and temperature, on invertebrates are much more widely understood in aquatic ecosystems (Allan 1995).

Several authors have suggested that invertebrates can serve as useful bioindicators of current and past temperature changes (e.g., Parsons 1991, Kopeszki and Trockner 1994, Danks 1992, Brodersen and Anderson 2002, Coope and Lehmdahl 1996, Hogg and Williams 1996, Hodkinson and others 1999, Hodkinson and Bird 1998, Bird and Hodkinson 1999, Bale and others 2002) in both terrestrial and aquatic environments. The confirmatory criteria are generally changes in species distribution and abundance over medium to long time scales. More recently, measurements of FA have shown increased levels of developmental asymmetry resulting most probably from thermal stresses experienced by aquatic invertebrates over shorter developmental time scales. This suggests that sublethal traits such as FA within populations of selected species may prove useful, indicating more subtle changes in the thermal environment (Savage and Hogarth 1999, Hogg and others 2001, Mpho and others 2002). The general significance of FA in biomonitoring is discussed separately later.

Invertebrates may also prove useful in indicating factors linked to precipitation, such as soil moisture. Several species of Collembola, oligochaete worms, and Diptera larvae show declining abundance with reduced soil moisture (Convey and others 2003, Briones and others 1997).

Many, but not all, invertebrates appear directly sensitive to varying levels of UV radiation (e.g., Kiffney and others 1997, Kelley and others 2003, Tank and others 2003). The direct effects of exposure, for example, among zooplankton, are well documented and include behavioral modification and increased mortality levels, dependent on species (e.g., Hader and others 1998). More subtle responses, with bioindication potential, occur among leaf beetles (Chrysomelidae) that exist as different polymorphic forms with different reflectivity of UV radiation (Mikhailov 2001). In several species, the proportion of UV-tolerant forms increases with altitude and parallels the trend in incident radiation. This corresponds with the relationship between pigment color in zooplankton and UV exposure (Tartarotti and others 2001).

Changing Chemical Environment

Invertebrates have been suggested as bioindicators of a range of chemical changes occurring in aquatic and terrestrial environments. These can involve a single chemical parameter such as pH, the concentration of a single heavy metal pollutant such as cadmium, or excess amounts of plant nutrients, especially nitrogen and phosphorus (Brodersen and Andersen 2002). A direct relationship can be established between the concentration of the chemical and the performance of one or more indicator species. For example, the mayfly *Hexagenia* has served as a sentinel organism in the Great Lakes and large rivers of North America, indicating when eutrophication resulted in lethal anoxic conditions beginning in the 1950s, and the rebirth of these ecosystems (Fremling 1991, Krieger and others 1996). *Hexagenia* tusks in the lake beds provide a view of human impacts looking back over the last 300 years (Renoldson and Hamilton 1993). More frequently, however, chemical changes may involve a cocktail of chemical effects that combine several compounds simultaneously. Here it becomes exceedingly difficult to unravel the independent effects of each compound on the individual species, and often the invertebrate community or some subset thereof is used to indicate some general measure of ecosystem ''health'' or level of pollution such as ''water quality.'' Much work also remains to be done on the synergistic effects of chemicals and the manner in which this affects invertebrate responses (Belden and Lydy 2001). Clements and others (2002) recently demonstrated how a combination of descriptive and experimental approaches help to focus arguments when faced with multiple causal factors. Table 1 gives a selective list of examples where chemical changes occurring in aquatic and terrestrial ecosystems have been suggested as systems that can be monitored using invertebrate bioindicators. Sublethal effects of stress associated with several forms of pollution have also been documented, showing changes in the levels of FA in several species of aquatic and terrestrial invertebrate (see later).

Habitat Quality and Conservation Value

At the simplest level, a basic inventory of the ecologically important species that might be affected by a planned development may be considered when drawing up a statutory Environmental Impact Assessment for a given site. The bioindicator may be merely the number of rare, local, or endangered species (Rosenberg and others 1986). However, one of the main basic problems of conservation biology is to establish the relative value and importance of the ecological com-

Table 1. Selected recent and specific examples to illustrate the range of chemical factors in aquatic and terrestrial environments that have potential for being biomonitored by invertebrates

Chemical/pollutant	Invertebrate group	Reference
Aquatic		
pH/acidification	General lotic invertebrates	Clenaghan and others 1998, Larsen and others 1996
	Lentic invertebrates	Lonergan and Rasmussen 1996
	Lentic chironomids	Mousavi 2002
Nitrogen and phosphorus	Lotic insects with pathogenic microorganisms	Lemly 2000, Lemly and King 2000
	Lentic chironomids	Brodersen and Lindegaard 1997
Heavy metals	Lentic *Chaoborus*	Croteau and others 2002
	Lotic nematodes and ciliates	Fenske and Gunther 2001
	Benthic invertebrates	Grumiaux and others 2000, Nelson 2000, Cain and others 1992
	Caddisflies	Aizawa and others 1994
Organic toxicants	Lotic nematodes and ciliates	Fenske and Gunther 2001
	Cladocera	Baldwin and others 2001, Guilhermino and others 2000
	Benthic invertebrates	Grumiaux and others 2000
Pesticides	Benthie invertebrates	Fulton and Key 2001
	Lentic zooplankton	Kreutzweiser and Faber 1999
	Dragonflies	Takamura and others 1991
Coal mine runoff	Trichoptera	Fernandez-Alaez and others 2002
Terrestrial		
pH/acidification	Soil microarthropods	van Straalen 1998
Heavy/trace metals	Several soil invertebrates	Cortet and others 1999, van Straalen 1998, Dallinger 1994
	Sarcophagid flies	Bartosova and others 1997
Air pollution/ acid deposition	Several invertebrates	Saldiva and Bohm 1998
	Spiders	Horvath and others 2001
	Collembola	Kopeszki 1997, Steiner 1995
	Cryptostigmatic mites	Sterner 1995
	Day flying Lepidoptera	Kozlov and others 1996
Nitrogen inputs	Collembola	Kopeszki 1997
Pesticides	Collembola	Frampton 1997
	Soil microarthropods	Trublayevich and Semenova 1994
	Various soil invertebrates	Cortet and others 1999
Asbestos	Sarcophagid flies	Bartosova and others 1997

munities inhabiting a range of habitats. This is often a precursor to the selection of unique or representative areas to achieve stated conservation strategy objectives. Areas may vary in size from small local reserves to major fragments of habitat such as regional forests (Statzner and others 2001). Furthermore, additional factors including habitat seasonality (Euliss 2002) and ecotone effects (Boscaini and others 2000) may complicate the issue.

Clearly it is impractical to collect full comparative inventories of every species present in all areas, and a measure of subsampling using selected taxa is required. Subsampling needs to reflect as accurately as possible the trends that would be likely to occur in a full data set, taking into account the important criteria for community subset sampling and evaluation listed previously. Generally, evaluation will be made on the basis of a single set of samples and will not necessarily involve repeated measurement over time (monitoring).

Table 2 illustrates the diversity of invertebrate taxa that have been suggested as good bioindicators of habitat quality. Most of them are relatively untested, and formal protocols for their use as indicators are not in place. They often represent the work of a single specialist, and although the results describe meaningful trends within the chosen taxon, it is often not always clear how reflective the results are of the whole community and whether the taxon represents the best biodiversity indicator for that particular community. It may be that favored invertebrate groups, such as butterflies, are given higher subjective weighting than

Table 2. Selected recent examples of the suggested use of indicator invertebrates for evaluating habitats for biodiversity, condition, and structure

Habitat	Invertebrate group	Reference
Terrestrial		
General (habitat continuity)	Fungivorous beetles	Sverdrup-Thygeson 2001
General (quality)	Spiders	Riecken 1999, Paoletti and Hassall 1999
	Diptera	Frouz 1999
	Coccinellid beetles	Iperti 1999
	Syrphid flies	Haslett 1997b, Sommaggio 1999
	Staphylinid beetles	Bohac 1999
	Cryptostigmatic mites	Behan-Pelletier 1999
	Rare beetles	Franc 1994
	Tiger beetles	Pearson and Cassola 1992
	Butterflies	Brown and Freitas 2000
Landscape and habitat features	Lepidoptera, spiders, carabid beetles	Jeanneret and others 2003
Agroecosystems	Heteropterous bugs	Fauvel 1999
	Ants	Peck and others 1998
	General invertebrates	Buchs and others 2003
Savanna grassland	Dung beetles	McGeoch and others 2002
Grassland	Collembola	Greenslade 1997
Forest	Fungivorous insects	Jonsell and Nordlander 2002
Boreal forest	Coleoptera	Jonsson and Jonsell 1999
Rangeland	Ants	Andersen and others 2004
Aquatic		
Aquatic ecosystems (general)	Interstitial invertebrates	Claret and others 1999
	General invertebrates	Charvet and others 1998
River (typology)	Lotic invertebrates	Cayrou and others 2000
Stream (habitat integrity)	Benthic invertebrates	Buffagni and Comin 2000
Stream (morphological integrity)	Benthic invertebrates	Jansen and others 2000
Lakes	Chironomid midges	Brodersen and Lindegaard 1999
Ponds	Odonata and Trichoptera	Briers and Biggs 2003
Streams	Plecoptera	Helesic 2001
Headwater streams	Macron vertebrates	Heino and others 2003a
Rivers	Benthic invertebrates	Lang 2000
Seasonal and temporary wetlands	Aquatic invertebrates	Euliss and others 2002
Freshwater littoral	Macroinvertebrates	White and Irvine 2003

their less aesthetically attractive community consorts such as, for example, the ants. The latter may be, for example, less well studied but better indicators of comparative biodiversity. Furthermore, where the same habitat units have been assessed using different subsets of invertebrate taxa, there is often surprisingly little commonality in the results obtained (McGeoch 1998, Reyers and others 2000), although in others the level of congruence may be high (Saetersdal and others 2003).

Another major problem is taxonomic comparability among samples from spatially dispersed areas. The more samples taken from a wider area, the more likely it is that the level of taxon overlap, particularly at the species level, will decline. This raises the question of whether it is more appropriate to work at the species level or whether it is better to work at a higher taxon level, with all the loss of species-specific information that this entails. There is clearly a trade-off between the number of taxa that can be ''captured,'' the taxonomic level at which one operates, and the land area needed to conserve biodiversity as defined by the criteria used. The application of the concept of complementarity defined by Reyers and others (2000) offers one way in which the assessment of biodiversity can be optimized when choosing reserve areas.

A further suggested use of invertebrates is in the assessment of habitat continuity in which the presence of certain species is used to bioindicate long-term stability or unchangeability within the habitat over time (Norden and Appelqvist 2001). Indicator taxa such as land snails and certain fungus-feeding beetles associated with persistent forest fungi have been suggested as indicating such long-term stability within woodland (Norden and Appelqvist 2001, Sverdrup-Thygeson 2001).

Table 3. Selected recent examples of the suggested use of invertebrates as indicators of habitat management, degradation, restoration, and improvement

Change indicated	Invertebrate group	Reference
Grassland topsoil removal	Carabid beetles	Sieren and Fischer 2002
Land management practice	Ants	Andersen and others 2002
	Dispersing insects	Mora and others 2004
Extent of logging	Spiders	Willett 2001
	Dung beetles	Davis and others 2001
	Stream macroinvertebrates	Bojsen and Jacobsen, 2003
Mining disturbance in savanna	Grasshoppers	Andersen and others 2001
General ecosystem health	Many invertebrates	Hilty and Merenlender 2000
Landscape/ecosystem sustainability	Many invertebrates	Paoletti 1999b
	Soil invertebrates	Duelli and others 1999
	Earthworms	Paoletti 1999a
Impact of genetically modified crops	Invertebrates	Haughton and others 2003
Soil management	Soil invertebrates	Enami and others 1999
Change in general habitat quality	Bees and wasps	Tscharntke and 1998
Forest restoration	General invertebrate community	Jansen 1997
Farming impacts	Protozoa	Foissner 1997
Forest degradation	Tiger beetles	Rodriguez and others 1998
	Various insects and nematodes	Lawton and others 1998
Sheep grazing	Several insect groups	Gibson and others 1992
Grassland management	Coleoptera and Orthoptera	Jonas and others 2002
Pollutant effects on forest	Scolytid beetles	Grodzki 1997
Forest disturbance	Butterflies	Hamer and others 1997
	Moths (Arctiidae and Notodontidae)	Summerville and others 2004
Forest management	Mycetophilid flies	Okland 1994
	Forest floor invertebrates	Schowalter and others 2003
	Longicorn beetles	Maeto and others 2002
Grassland habitat disturbance	Hemiptera Auchenorrhyncha	Nickel and Hildebrandt 2003
Urbanization	Carabid beetles	Sustek 1992
Habitat fragmentation	Ants, Coleoptera, Arenaea, Diptera, other Hymenoptera	Gibb and Hochuli 2002
Water quality/habitat integrity	Benthic invertebrates	Kashian and Burton 2000
Stream restoration	Bethic invertebrates	Muotka and others 2002

Habitat Change, Degradation, and Recovery

Ecological change, through the process of succession and species change (community assembly in modern parlance), is a natural trend that occurs over time after the creation of new habitat. It may also take place after catastrophic loss of soil and vegetation cover through natural disturbance. Many habitats, however, have been subjected, through a variety of agencies, to nonnatural alteration. These agencies of change often involve negative human impacts such as land use modification, pollutant input, agricultural practices, etc., often leading to habitat degradation and reduced biodiversity. Relaxation of these imposed stresses, particularly when accompanied by active restoration programs, leads to habitat recovery and improved biodiversity. Biomonitoring may also include forward-looking assessments aimed at predicting landscape or ecosystem sustainability (Paoletti 1999b). Some invertebrate taxa are more sensitive to these changes than others and, when used sensibly as part of a monitoring program over time, can mirror and thereby bioindicate the processes of change. As in the case of biodiversity assessment, there are many suggested indicator taxa of habitat change, but again their comparative suitability often remains untested (Table 3). A suitable single biomonitor species will respond sensitively to the changes taking place but will have sufficient resilience not to go extinct, that is, broad tolerance. It is, however, the changing species balance within a wider community that often serves better to indicate change. The well-tried example of organic pollution effects in lotic ecosystems again illustrates this principle well. As pollution gradually increases, the invertebrate community shifts from one dominated by stoneflies, mayflies, and caddisflies to one in which chironomid midges and tubificid worms predominate. Remove the stress and the previous community balance is restored. Similar species replacement takes place during succession.

Which Organisms and Measures are the Most Useful and Why?

The advantages of including biological monitoring and evaluation systems over those that rely only on physical and/or chemical data have already been clearly stated (Hellawell 1986, Rosenberg and Resh 1993). Put succinctly, living organisms occupy their habitat continuously and experience the stresses, changes, or modifications taking place therein. Their response integrates the cumulative effects of environmental change over time, and they may be sensitive to several different stresses simultaneously. This includes pulsed inputs of pollutants or pulsed disturbances that may not be picked up by spot chemical monitoring, although again the impact of pulsed disturbance may vary among communities (Collier and Quinn 2003). Biological organisms are, nevertheless, good long-term indicators of ecosystem health, and biological monitoring allows us to focus, at least initially, on environmental changes that elicit significant biological responses. Having established that organisms serve a useful function as biomonitors, how do we decide which are the best groups of organisms to use?

Why Use Invertebrates?

Invertebrates are abundant medium-sized organisms that, as a generality, have growth rates and population turnover times lying midway between those of microorganisms and higher plants and animals. Invertebrates also have effective active and passive dispersal mechanisms that often allow wide dissemination and rapid recolonization of disturbed habitats (Hodkinson and others 2002). Because of their slow population turnover times and slower dispersal, plants are relatively less responsive indicators of change. At the opposite extreme, microorganisms, with their very rapid responses to changing environmental conditions, tend to fluctuate more wildly and be less stable indicators of longer-term trends. Finally, there is evidence that invertebrate responses are also indicative of changes in ecosystem function (Wallace and others 1996). Having thus established that invertebrates probably have the better overall potential to serve as good bioindicators, the problem then is choosing which organisms or subsets of communities to use. As has already been shown, a multitude of different aquatic and terrestrial invertebrates from protozoa, oligochaete and nematode worms, isopods, microcrustacea, Collembola, mites, spiders, and insects have all been suggested as bioindicators. Which of them, however, is the best or most appropriate for a particular situation remains a question for debate.

Selection of Bioindicator Organisms

Before choosing a suitable bioindicator system, it is first necessary to define clearly the objectives and endpoints of the study (McGeoch 1998). This should include a statement of exactly what it is intended to measure, how it will be measured, and why. It needs to take into account the nature of the problem, whether it is a response to a single pollutant at a restricted site or an attempt to compare biodiversity over a broader area. The spatial and temporal scales over which the study is conducted require special consideration. Lack of precision at this stage will result in inappropriate bioindicators being chosen and results that are difficult to interpret. Only after the groundwork has been established can a suitable indicator system be selected to support the strict protocols necessary. Sometimes taxa that are good bioindicators on one spatial scale may lose their reliability at higher or lower scales, raising questions about how stable their measured response is (Allen and others 1999). Similarly, different groups of organisms display contrasting responses on temporal scales. Response times in microorganisms can be a matter of hours; those in trees and larger vertebrates are measured in years. Clearly, the best bioindicators show consistent responses over a wide range of spatial and temporal scales.

The criteria for the selection of bioindicator organisms were detailed by Hellawell (1986), Pearson (1994), McGeoch (1998), Cortet and others (1999), and Hilty and Merenlender (2000). The appropriateness of particular criteria depends on the nature and scale of the problem addressed.

The prime generic criteria are as follows:

1. Higher and/or lower taxa chosen have well-known and stable taxonomy, with ease of identification emphasized.
2. Biology of organisms is well known, particularly in response to stress factors or to changes in habitat properties of interest.
3. Organisms are abundant, straightforwardly surveyed, and easily manipulated.
4. Higher and lower taxa chosen are distributed on a scale that matches the spatial and temporal requirements of the study.
5. The chosen taxon or groups of taxa are representative of the whole community, or, if not, then their responses are strongly correlated with a known stress factor.

In addition, a number of other issues should be considered. These include the economic significance or aesthetic appeal of the biomonitoring group chosen and the logistics and cost of biomonitoring and evaluation compared with alternative methodologies. The ideal system is inexpensive, simple, easy to implement, quick, reliable, and easily understood by nonprofessionals. This ideal clearly is hardly ever achievable, and any biomonitoring system is a compromise between precision and cost. There is, nevertheless, an inherent danger that chosen indicator systems can become overcomplicated relative to the problems being addressed. It is important, therefore, that the methodology be optimized for the parameters being used (Rabeni and Wang 2001, Bailey and others 2001).

Taxonomic Challenges

One of the main problems in using invertebrates as bioindicators is the sheer number and range of species that potentially could be used. This inevitably leads to problems of species identification. Taxa differ markedly in the ease with which they can be identified by nonspecialists, and some of the taxa suggested for biomonitoring can only be reliably identified by taxonomic specialists. Thus, a group of invertebrates may be shown to be excellent indicators, but their widespread and regular use could be precluded by taxonomic difficulties. One way around this problem is to analyze quantitatively the levels of predictability achieved using successively higher levels of taxonomic resolution (Rabeni and Wang 2001, Bailey and others 2001). It may be, for example, that genera have the same predictive power as species. If this is the case, then it is unnecessary to identify the animals down to species (Lenat and Resh 2001). For aquatic invertebrates, professional and volunteer monitoring programs often rely on higher taxa, whereas others rely on species-based protocols (e.g., Carter and Resh 2002, Engel and Voshell 2002). A confounding factor in resolving this controversy may be the limited information that is available for the vast majority of aquatic and terrestrial species. For example, quantitative observations of responses to complex environmental stresses are rarely available, and the general applicability of observations is often unknown because levels of genetic variation within and among populations are unclear, and the plasticity of responses to environmental stress is largely untested. Even so, invertebrates clearly offer an important source of information concerning environmental conditions.

Measures of Invertebrate Responses

As indicated above, invertebrates can be used to assess environmental stress using a variety of individual, population, and community measures. The choice of measure(s) remains controversial and subject to intense analysis. For example, there have been numerous articles written on the strengths and weakness of multimetric and multivariate measures of invertebrate responses in streams (Gerritsen 1995, Norris 1995, Renoldson and others 1997). Similarly, FA has been criticized, and attempts have thus been made to develop a more refined and robust methodology (Leung and Forbes 1997, Leung and others 2000, Bjorksten and others 2000, Lens and others 2002). In the end, each approach has strengths and weaknesses. The challenge is to incorporate this information in the process of developing and modifying monitoring protocols.

Specific Use of Bioindicators in Mountain Areas

Mountain landscapes represent steep gradients for a wide range of environmental parameters, particularly temperature, precipitation, UV radiation, atmospheric gas concentrations, and so on. This is reflected in the adaptations and distributions of varying types of organisms and ecological communities that occupy different positions along these gradients, both in terrestrial and aquatic ecosystems. Many of the environmental factors that affect the organisms are multifaceted and interlinked. For example, precipitation can fall as rain or snow. The rain can run off to form streams and river ecosystems; the snow may remain, either seasonally or permanently, creating unique snowbed environments. Precipitation interacts with temperature through snow insulation effects and thermal buffering of environmental temperatures within moist terrestrial and aquatic habitats. The harsh environmental conditions combined with the isolated and fragmented nature of many alpine areas means that they serve as a focal point for microevolution and adaptation in particular groups of organisms (Haslett 1997a) and contribute to their unique biodiversity. The combination of relatively specialized species and naturally harsh conditions makes animal communities at high altitude especially vulnerable to environmental disturbance, particularly anthropogenic pollution and changing climate. This vulnerability often gives alpine areas high conservation significance. Alpine environments and their invertebrate communities are generally subject to less direct pollution and disturbance relative to many of the surrounding low-elevation areas because agricultural, industrial, and residential development is far less intense. However, environmental degradation from anthropogenic activities is still common in alpine areas. For example, they have been subjected to intensive land use, including forest harvest and management, livestock and dairy production, mining, and most recently, recreation, for hundreds, if not thousands of years. In addition, aerial dispersion and deposition results in significant exposure to a wide range of gaseous and/or particulate pollutants. Increased deposition of nitrogen, for example, tends to occur in areas of high precipitation (Morecroft and Woodward 1996).

Invertebrate communities are distributed along these steep altitudinal gradients in relation to their particular environmental tolerances and respond accordingly when environment conditions change. However, despite their clear potential, there are few well-established invertebrate biomonitoring systems that are commonly and widely used to monitor change in montane environments, especially among terrestrial invertebrates.

Mountain communities may potentially respond to disturbance in different ways. For example, species richness and diversity will most probably decrease in response to many types of chemical pollution. By contrast, warming, additional precipitation, or increased nutrient loading within limits is likely to produce overall increases in species richness and diversity. This may, however, be accompanied by the loss of true alpine species as the environment becomes more benign and species immigration and establishment from lower elevations takes place. True alpine species cannot shift their ranges upwards above the tops of mountains. There also may be a temporal component that needs to be considered in assessing a response. For example, an alpine site may experience a rapid drop in species richness as temperature thresholds are exceeded, but then experience a long-term gain in species richness as soils and vegetation change and mature, and as immigration brings new invertebrate species to the site. The research challenge is to identify the range of expected responses to defined impacts.

Nevertheless, selected invertebrates, if used judiciously as outlined previously, can act as good *in situ* biomonitors for a wide range of environmental factors that impinge upon mountain ecosystems. They have high potential for monitoring physical and chemical changes within the environment, they can bioindicate differences in the patterns of biodiversity across the landscape, and they can be expected to respond to deteriorating or improving habitat quality linked to changing patterns of land use. Range shifts in mountain dwelling species in response to changing temperatures appear to provide particularly good biological indications of climate warming. Several species, such as the spittle bug *Neophilaenus lineatus* as noted earlier (Whittaker and Tribe 1996), exhibit rapid, often year-to-year variation in their upper altitudinal limit in response to changing mean temperatures.

Often the relative time scales of change can be important. Herbivorous invertebrate species frequently respond more sensitively to changing temperatures over shorter time scales than their host plant. For example, the three congeneric species of jumping plant louse living on fireweed (*Chamerion angustifolium*) in North America each have characteristic altitudinal distributions within the much broader altitudinal distribution of their host and might be expected to respond to rising temperatures in different ways. The high-altitude species, *Craspedolepta schwarzi*, might vanish as suitable alpine habitats disappear. The two lower-altitude species, *C. nebulosa* and *C. subpunctata*, might be expected to exhibit an upwards extension of their overlapping ranges, but with *C. nebulosa* always occupying a slightly higher elevation than *C. subpunctata* (Hodkinson and Bird 1998, Bird and Hodkinson 1999). Similar altitudinal changes in species distributions in response to temperature are likely to occur among invertebrates occupying mountain streams where temperature also affects dissolved oxygen availability (Devan and Mucina 1986, Jacobsen and others 2003). Although these examples illustrate the potential of mountain dwelling invertebrates as bioindicators, rigorous and fully tested protocols with wide applicability remain to be developed.

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