Ecology of millipedes (Diplopoda) in the context of global change

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Abstract

Current knowledge on the effects of climate, food quality and land cover on millipedes is reviewed, to explore the potential responses of this arthropod group to global change. Climate warming could result in higher rates of population growth and have a positive effect on the abundance of some temperate species. The generality of this finding is evaluated in relation to the life history and current distribution of species. At low latitudes, interactions with more severe droughts are likely and could affect the composition of millipede communities. Elevated atmospheric CO_2 and changes in plant community composition are expected to alter leaf litter quality, a major determinant of millipede fertility. This could significantly influence population growth rates, but the warming effect will be probably more important for decades. Land cover changes, mainly due to deforestation in the tropics and land abandonment in Europe, are critical to habitat specialists and could override any other effect of global change. At the landscape scale, habitat heterogeneity seems to be a good option for millipede conservation, even at the cost of some fragmentation.

Keywords: abundance, diversity, climate change, food quality, habitat loss

1. Introduction

The IPCC (Intergovernmental Panel on Climate Change) fourth assessment report indicates that considerable climate changes are occurring due to the increase in greenhouse gas concentrations in the atmosphere (IPCC 2007a). Depending on the emission scenarios, global average temperature is predicted to increase by 1.8 to 4.0 °C at the end of this century. Warming is expected to be greatest at high northern latitudes. Increases in the amount of precipitations are very likely at high latitudes, while decreases are likely in most subtropical regions. In Europe, precipitations should increase in winter, but more severe summer drought is expected in the Mediterranean region. These climate changes are modifying the composition of plant communities (IPCC 2007b and references therein). Other environmental changes resulting from human activities occur over large areas, such as land use changes and nitrogen deposition.

All those changes have already affected and will increasingly affect animal species, especially poikilotherms that feed on plant materials, such as millipedes. The challenge is to predict their potential responses to this global environmental change. The aim of this paper is to review our knowledge on the effects of climate, food quality and land cover on millipedes, and to identify what is relevant in terms of their responses to global change. The review has

a European bias, but, as the change is global, much can be learnt from other areas in the world. Therefore, this paper is an opportunity to highlight gaps, i.e. topics and geographical areas on which more research is needed.

2. Direct effects of climate change on millipedes

Responses to temperature rise have been much less studied in millipedes than in insects. The few existing studies are based either on the examination of large-scale patterns in nature or on the experimental study of small-scale population dynamics.

2.1. Observed changes in distributions: a fingerprint of climate warming?

Difficulties in interpreting large-scale patterns are clearly illustrated with a recent study on the poleward expansion of animals (Hickling et al. 2006). The distributions of many species that reach the northern margin of their range in Great Britain were compared at a 25-year interval. The northern range margin was defined as the mean latitude of the ten most northerly occupied 10-km grid squares. Over 25 years, the mean northward shift of millipedes was 74 km for six southern species (Tab. 1). Although the consistency of trends across many taxa does suggest there is range expansion driven by climate warming (Parmesan 2006), this interpretation is not necessarily correct for all taxa. There may be alternative explanations for millipedes, e.g. a collecting artefact, because a number of grid squares were poorly explored in the first collecting period (P. Lee, pers. comm.). It is necessary to identify the processes involved before we conclude that these observations are linked to climate warming.

Tab. 1   Northward shift (in km) at the range margins of six millipede species, which was observed in Great Britain over 25 years. The list of species selected by Hickling et al. (2006) was kindly provided by P. Lee (pers. comm.).

Species	Shift (in km)
Glomeris marginata (Villers, 1789)	11
Cylindroiulus caeruleocinctus (Wood, 1864)	119
Leptoiulus belgicus (Latzel, 1884)	48
Brachychaeteuma melanops Brade-Birks, 1918	75
Chordeuma proximum Ribaut, 1913	70
Polydesmus coriaceus gallicus (Latzel, 1884)	119
Mean	74

A prerequisite for poleward expansion is dispersal or at least human-mediated transport. Although dispersal ability is generally considered to be low in millipedes, that is not true of all species. Wandering is widespread in this group (Hopkin & Read 1992). Many species have been shown to colonise post-mining rehabilitation sites in various geographical areas (Dunger & Voigtländer 2009, Tajovský 2001, Redi et al. 2005), which can only be explained by dispersal. However, in Hickling's et al. (2006) data, the expansion rate of millipedes – up to 4.8 km yr^{-1} – would have been higher than in carabids and butterflies. Assuming that they have migrated northwards in Britain, such a high expansion rate is not easy to explain at present.

2.2. Ecophysiological responses to climate warming

To understand the effects of warming on millipedes, an important step is to determine their ecophysiological responses to temperature in terms of population growth rate. In insects, those responses are not always positive (Bale et al. 2002). A laboratory study was performed to assess the effects of elevated temperatures on the life-history traits of the polydesmid *Polydesmus angustus* Latzel, 1884 (David & Gillon 2009). Individuals were reared throughout their life cycle under two seasonal regimes of temperature, which differed by 3.3 °C on average. This corresponded to the temperature difference between the Atlantic climate of the Paris region – where the animals came from – and the Mediterranean climate of southern France, at the edge of the species' range (Kime 1990).
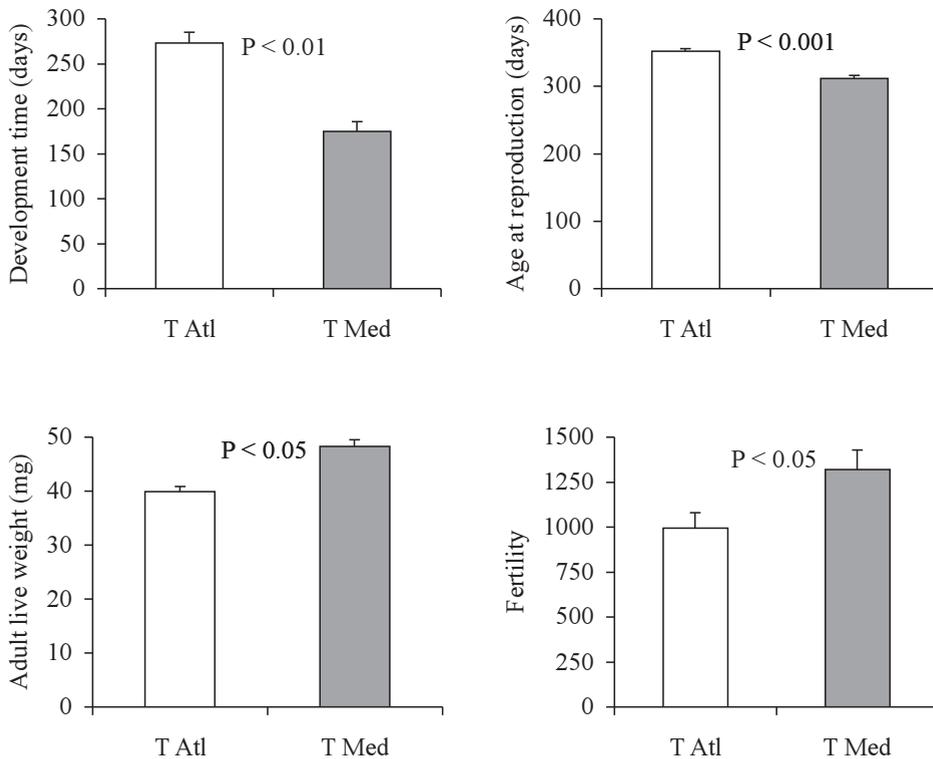

Fig. 1   Effects of two seasonal temperature regimes (T Atl: Atlantic temperatures; T Med: Mediterranean temperatures) on the development time, age at first reproduction, adult live weight and fertility of female *Polydesmus angustus* reared in the laboratory (redrawn from David & Gillon 2009).

Polydesmus angustus was positively affected by the 3.3 °C rise (Fig. 1). Development was faster, with a larger proportion of individuals that reached the adult stage before the winter. This resulted in earlier reproduction in spring, because adult females are in postdiapause quiescence in late winter and start laying eggs as soon as temperature conditions improve (David et al. 2003). At Mediterranean temperatures, reproduction started in April, 1.3 months earlier than at Atlantic temperatures. There was no trade-off between development rate and adult body weight; females that developed at elevated temperatures even emerged with higher live weights. These positive effects of temperature on growth may result from a greater microbial development in leaf litter and/or a better exploitation of food by millipedes. The larger body size of females at elevated temperatures resulted in higher fertility, which is the rule in macroarthropods (Sutton et al. 1984, David 1992). Finally, survival was not significantly affected by warming.

Overall, the temperature rise resulted in a higher population growth rate, which indicates that the impact of warming will be positive over large parts of the species' range (David & Gillon 2009). All other things being equal, the abundance of *P. angustus* should tend to increase in established populations. From a metapopulation viewpoint, these populations could function as sources, from which individuals could disperse (Hanski 2005). This is consistent with signs of the species' expansion in Europe since the end of the 20th century (Meidell & Enghoff 1993).

2.3. Problems of generalisation

To what extent can we extrapolate this positive effect of warming to other millipedes? Results from earlier laboratory studies suggest that another polydesmid, *Polydesmus inconstans* Latzel, 1884, also benefits from elevated temperatures (Snider 1981a, 1981b). However, the response to warming is likely to vary with the life-history characteristics of species. Nondiapausing species that can breed throughout the year, like the paradoxosomatid *Oxidus gracilis* (C. L. Koch, 1847) (Causey 1943), should also respond positively to warming. In contrast, species that need a period of chilling to terminate winter diapause, resume development and reproduce, like the xystodesmid *Parafontaria laminata armigera* Verhoeff, 1936 (Fujiyama 1996), may be affected negatively by warming. Similarly, species that overwinter for long periods without feeding may be affected negatively by warming, which may accelerate the exhaustion of metabolic reserves. For example, the spirostreptid *Orthoporus ornatus* (Girard, 1853) overwinters for about eight months of dry season and moults prior to emergence from the soil (Crawford et al. 1987). During that prolonged dormancy, the species uses its fat reserves, the consumption of which increases with temperature (Wooten & Crawford 1974).

Spatial considerations are also important. Cold-adapted species that live close to summits, e.g. the endemic *Pyreneosoma* spp. (Haplobainosomatidae) that occur at an altitude of about 2000 m in the Pyrenees (Mauries 1974), are potentially threatened by the reduction of their habitat due to climate warming. In widespread species like *P. angustus*, populations that already live at the warmer edge of the species' range may be affected negatively by warming. Studies in which insect species were monitored repeatedly throughout their range have shown that the proportion of extinct populations was greater at low latitudes (Parmesan 2006). No such data exist for millipedes, but the effects of drought may be important in this respect.

2.4. Possible interactions with drought

Elevated temperatures increase evapotranspiration and make regional climates increasingly dependent on rainfall. As more severe summer drought is likely at low latitudes (IPCC 2007a), this may have demographic consequences in animals.

Most millipede species easily cope with normal, annual periods of dryness using both behavioural and physiological mechanisms. Few species are active and forage during the dry season, even in temperate zones. The basic behaviour is to take refuge in cavities or to burrow into the soil (Lewis 1974, Bailey & Kovaliski 1993, Dangerfield 1998). Physiological adaptations allow millipedes to survive those conditions for weeks or months (Crawford 1979, Hopkin & Read 1992, Wright & Westh 2006). Quite often, dry periods are spent moulting. For example, the wood-feeding spirobolid *Narceus americanus* (Beauvois, 1817) burrows into logs in late summer, seals the entrance and moults. O'Neill (1969) showed that this is a response to desiccation, which may protect the species during the dry season.

The question is whether those seasonal adaptations will be sufficient to withstand more severe droughts due to climate change. The least tolerant species could be negatively affected. After exceptional droughts in temperate forests, Chordeumatida suffered significant population declines (David 1990, Geoffroy & Celerier 1996), which is in line with their low desiccation resistance in laboratory experiments (Haacker 1968, Meyer & Eisenbeis 1985). For more tolerant species, predictions are more difficult. In Greece, first-stadium juveniles of the glomerid *Glomeris balcanica* Verhoeff, 1906 die in large numbers during their first summer (Iatrou & Stamou 1991), which might worsen in particularly hot and dry years. However, drought may affect resistant species through other, non-lethal demographic processes. In general, behaviours that maintain survivorship under harsh conditions are costly in terms of growth and reproduction, because they hamper access to energetic resources (David 1996, Dangerfield 1998). So far no studies have assessed these costs in terms of population growth.

Nevertheless, latitudinal patterns of abundance indicate that the impacts of drought are likely to interact with the positive effects of warming on millipedes. A number of species that are widespread in western Europe occur as far south as the Mediterranean region, which is warm with a dry summer. Their abundance in this region is closely associated with their desiccation resistance measured in the laboratory by Haacker (1968). Thus, the poorly resistant *P. angustus* is not very abundant in the Mediterranean region, except in some humid forests. In drier forest soils, it is outnumbered by two more resistant species, the julid *Cylindroiulus caeruleocinctus* (Wood, 1864) and the glomerid *Glomeris marginata* (Villers, 1789), the abundances of which peak at their southern range margins (David 1996). These latitudinal patterns, while confirming that warming has positive effects on millipedes, suggest that the composition of southern communities is strongly influenced by the seasonal drought.

3. Effects of changes in food quality on millipedes

3.1. The food of saprophages

Millipedes are typically saprophages, which feed on decomposing plant material, mainly leaves, wood or both (Hopkin & Read 1992). This protein-poor diet is a major constraint on all saprophagous macroarthropods, which prefer leaf litter comparatively rich in nitrogen, with a low C:N ratio (Dunger 1958, Pobozsny 1978). The decrease in C:N ratio during

decomposition may partly explain why dead leaves of many plant species become more palatable when ageing (Kheirallah 1973, David & Gillon 2002). Occasionally, millipedes also feed on higher quality food, such as fallen fruits, mammalian faeces and even dead invertebrates, which are very rich in nutrients (Hoffman & Payne 1969, Dangerfield & Telford 1996). The presence of plant defences against herbivores (secondary compounds, toughness) is another characteristic of litter that is important to millipedes. Deterrent factors must be eliminated for litter to become palatable, irrespective of its nutritive value (Sakwa 1974, Carcamo et al. 2000). Fungal colonisation may increase the palatability of litter not only because fungi concentrate easily assimilable nutrients, but also because of their effects on deterrent factors (Kukor & Martin 1987).

3.2. Global change and leaf litter quality

Two factors can potentially alter litter quality in the context of global change: elevated atmospheric CO_2 concentrations and changes in plant community composition. Experiments on the short-term effects of elevated atmospheric CO_2 on plants indicate that chemical changes are much less marked in leaf litter than in green plant material. However, the litter N content decreases slightly – by 7 % on average – with a concomitant increase in C:N ratio (Norby et al. 2001). This corresponds to an overall decrease in food quality for millipedes. The effects of elevated CO_2 on the physical and chemical defences of plants are less clear (Wardle 2002).

On the other hand, global warming is progressively changing the composition of plant communities (IPCC 2007b and references therein). This may have a greater influence on litter quality, because (1) differences in nutrients and deterrent factors between plant species are markedly greater than intraspecific variations due to elevated CO_2 (Norby et al. 2001); and (2) changes in the composition of a litter mixture can significantly affect its overall quality, due to interactions between component species (Hättenschwiler et al. 2005). However, there is much uncertainty about the rate of changes in plant communities at continental scale (Neilson et al. 2005). Moreover, global warming may promote plant species with better or poorer litter quality for millipedes (Wardle 2002). Whereas Mediterranean tree species are expanding northwards in temperate Europe, which results in litter of lower quality, deciduous tree species are invading coniferous forests at higher latitudes, which may improve litter quality.

3.3. Responses of millipedes to food quality changes

Food quality is an important factor in millipede demography, mainly through its effects on growth and reproduction (Striganova & Prishutova 1990, David & Celerier 1997). When Blower (1974) reared the julid *Ophyiulus pilosus* (Newport, 1842) from egg to maturity on dead sycamore leaves alone, adult females did not lay eggs. On dissection, only half-sized eggs were found, which was probably due to a nutrient deficiency. Female *P. angustus* that were reared from egg to maturity on a mixture of leaf litter did reproduce, but their fertility was very low (David & Celerier 1997). When a pinch of yeast was added monthly to the leaf litter, female fertility was 4.3 times as high and similar to the fertility of adult females from the field.

Since low-quality food has negative effects on demography, the question is whether these effects can offset the positive influence of warming on the population growth rate. David &

Gillon (2009) compared the effects of elevated temperatures and reduced litter quality on the life-history traits of *P. angustus*. In the above-mentioned experiment, millipedes were reared under each temperature regime on two types of leaf litter: Atlantic leaf litter and Mediterranean leaf litter, which was poorer in nitrogen. This choice made it possible to explore the effects of a higher C:N ratio in the food, while simulating the ultimate stage of litter changes associated with a 3.3 °C rise in temperature. All components of the population growth rate were affected negatively by the switch from Atlantic to Mediterranean leaf litter, and deteriorating food conditions amply offset the effects of warming. When both treatments were applied in *P. angustus*, there were no significant changes in development rate, survival, adult live weight, and age at first reproduction (Fig. 2). Fertility was more responsive to food quality than to warming and decreased significantly when both factors were combined (Fig. 2). Therefore, from an ecophysiological point of view, a reduction in litter quality can offset the positive effects of warming on saprophages (David & Gillon 2009).
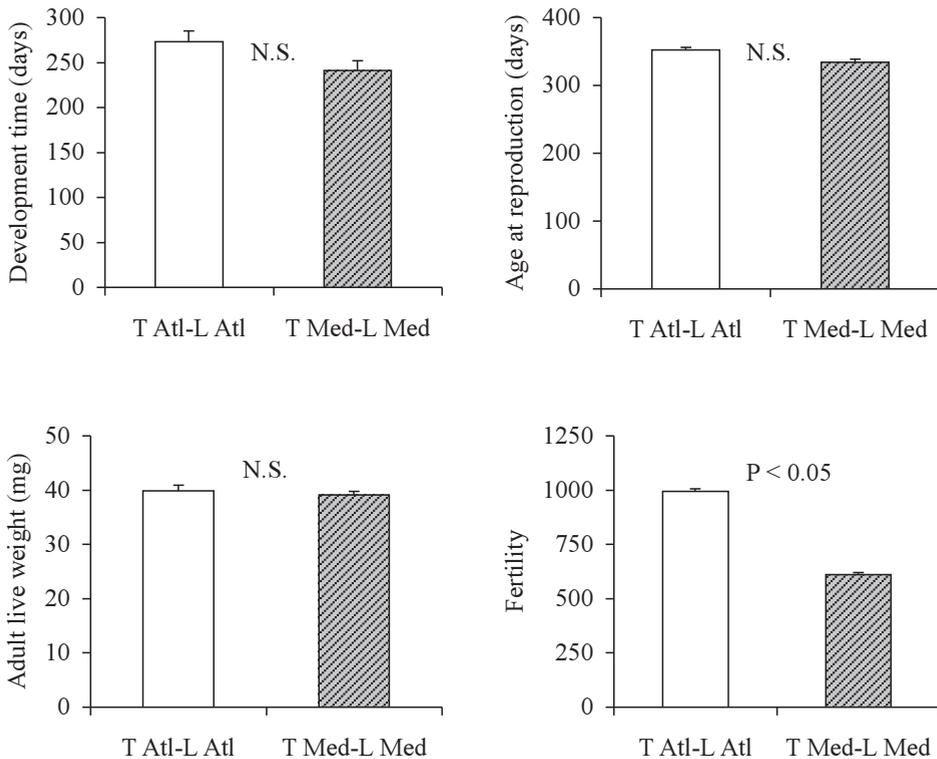

Fig. 2   Combined effects of elevated temperatures (T Med vs. T Atl) and reduced litter quality (L Med vs. L Atl) on the development time, age at first reproduction, adult live weight and fertility of female *Polydesmus angustus* reared in the laboratory (redrawn from David & Gillon 2009).

However, such a drastic change in leaf litter as that simulated in this experiment is unlikely to occur in the near future. The replacement of plant species by new migrants from the south may require decades or centuries, especially in forests (Neilson et al. 2005). If changes in leaf litter composition lag behind climate warming, temperate millipedes should retain the opportunity of feeding on high-quality plant species. In addition, the potential effects of elevated atmospheric CO_2 on high-quality leaf litter should not affect N concentration to the same degree as in this experiment (Norby et al. 2001). These considerations suggest that temperate millipedes are likely to be favoured by climate warming, even in areas where litter quality tends to deteriorate.

4. Effects of land cover changes on millipedes

4.1. Importance of land use for habitat specialists

Although climate plus physical and chemical properties of the soil largely determine millipede distributions (Haacker 1968, Kime & Wauthy 1984), land use is equally important. It is important at the site scale, where land cover and the level of disturbance are major site characteristics for these arthropods (e.g. Serra et al. 1996), and at the landscape scale, where land use determines the level of spatial heterogeneity among sites (Dauber et al. 2005). Management practices that alter microhabitats within sites also influence communities (Topp et al. 2006).

In temperate, tropical or mountain areas, specialist millipede species are clearly associated with land cover, such as forest, grassland, or mixed habitats with scattered trees and shrubs (Pedroli-Christen 1993, Kime 2004, Hamer et al. 2006, Lee 2006). Within those habitats, some species have a further specialisation on microhabitats, especially in forests (O'Neill 1967, Geoffroy 1981, Enghoff 1992). Although self-evident, it should be emphasised that habitat loss is critical to habitat specialists and can override the positive effects of climate warming. For example, in Great Britain, although many butterflies were predicted to thrive because of ameliorating climatic conditions, there was range reduction for a number of species at the end of the 20th century (Warren et al. 2001). Habitat specialists were much more affected than habitat generalists, which suggests that habitat loss played a prominent role. There have been no such studies for millipedes, but there is no doubt that they are also affected by habitat loss.

4.2 Tropical deforestation as a case in point

Deforestation is likely to be critical to forest specialists, especially in tropical zones. Millipede communities in old-growth forests are often rich in species, possibly in relation to the high diversity of tree leaf litter. The immediate impact of deforestation on soil macroarthropods is strongly negative (Mathieu et al. 2004), just as in temperate forests (Paquin & Coderre 1997). Forest specialists are eliminated and do not reinvade sites subsequently used as grassland.

The replacement of old-growth forests by managed, low-diversity tree plantations does not restore the original habitats. In tropical plantations of eucalypt, rubber, cocoa, etc. millipede abundance may remain high but species richness may be markedly reduced. For example, in Ivory Coast, Bourdanne (1997) compared millipede communities in a humid tropical forest and three nearby plantations. Out of 31 species found in the forest, seven were absent from

plantations, and a further five had their population density strongly lowered. In contrast, only three species had systematically higher population densities in plantations – with an outbreak of the spirostreptid *Aulonopygus aculeatus* Attems, 1914. Overall, even taking into account a few species found only in plantations, total millipede richness decreased by 8 to 13 species depending on the plantation, i.e. by 26 to 42 % in comparison with the old-growth forest.

Can tropical secondary forests on abandoned lands, which are more diversified than plantations, provide suitable habitats for all old-growth forest specialists? It is doubtful, according to data obtained for ants and dung beetles (Bihn et al. 2008, Gardner et al. 2008), but different taxa may show different responses to changes in habitat. There are little data for millipedes, mainly from young or very young secondary forests (e.g. Nakamura et al. 2003). This hinders comparisons with old-growth forests because millipede communities are known to change considerably with the age of regenerating forest sites (Redi et al. 2005).

4.3. Habitat heterogeneity and biodiversity

Other species are open-habitat specialists and the extension of closed-canopy woodland in Europe, due to the abandonment of extensive grazing and coppicing, also affects millipede diversity. Julids such as *Cylindroiulus arborum* Verhoeff, 1928, which typically occurs in open woodland in central Europe (Spitzer et al. 2008), and *Ommatoiulus rutilans* (C. L. Koch, 1847), which typically occurs in grazed grassland in western Europe (David et al. 1999), are negatively affected by habitat closure.

Fine scale studies in habitat mosaics have shown that the composition of millipede communities changes with land cover over very short distances (Dunger & Steinmetzger 1981, David et al. 1999). This results in a high overall species richness (γ-diversity) at the landscape scale, because mosaics contain typical species of each habitat patch – grassland, woodland, shrubland – and, possibly, ecotonal species specialised on edges (David et al. 1999, Tracz 2000). Presumably, a degree of land cover heterogeneity is more favourable to millipede diversity than uniform habitats covering large areas, as in many arthropod groups (Tews et al. 2004). In Hungary, Baldi (2008) found that millipede species richness in nature reserves was more dependent on land cover heterogenity than on reserve size.

4.4. Heterogeneity vs fragmentation

On the other hand, an excess of habitat heterogeneity may turn into fragmentation, which could be detrimental to biodiversity (Tews et al. 2004). On theoretical grounds, highly fragmented habitats are generally considered to increase the risk of extinction, especially for species that lack dispersal ability (Hansky 2005). In empirical studies, however, the effects of fragmentation on arthropods are highly variable across taxa and across studies (Ewers & Didham 2006). At what point does habitat heterogeneity become fragmentation for millipedes? The only experimental data available are from a eucalypt forest in Australia, where a large area was clearcut to be planted to pines, except on forest remnants of different sizes. Over a 9-year period following clearing, paradoxosomatids (*Somethus* sp.) were not affected by fragmentation and dalodesmids (*Gephyrodesmus* sp.) became more abundant, especially in the smaller remnants (Baker 1998) (Fig. 3). The mechanisms driving these changes in abundance are unclear, but the results illustrate that there is little evidence for negative effects of fragmentation on millipedes. This is confirmed by the fact that, in Poland, normally abundant and rich communities have been described on lake islets only a few

hectares in area (Wytwer & Zalewski 2005). Likewise, in South Africa, a large number of forest specialists – including large-bodied species – occupy remnants < 1 km² (Hamer & Slotow 2000).

Although conservation issues are beyond the scope of this paper, these data suggest that a number of specialist millipede species with shrinking habitats can survive in relatively small conservation areas, especially if these are not too isolated. Of course, this will not be a cure for all ills. Small remnants may preserve faunal richness at given sites (α-diversity), but if species turnover is high among sites (β-diversity), many species may remain threatened. That is the case in areas with large numbers of site endemics, like Madagascar, South Africa and certain oceanic islands (Enghoff 1992, Wesener 2005, Hamer et al. 2006).
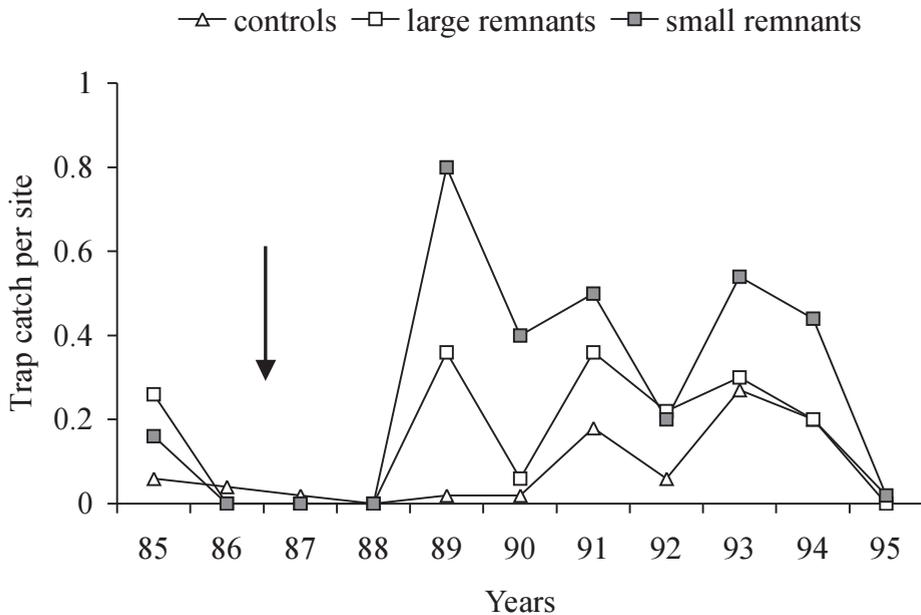

Fig. 3   Numbers of *Gephyrodesmus* sp. trapped in a eucalypt forest (controls) and in large (3 ha) and small (0.25 ha) forest remnants surrounded by an area clearcut for pine plantation. The arrow indicates the time of clearcutting and replanting (redrawn from Baker 1998).

5. Conclusions

In terms of impacts of global change on millipedes, this review suggests some tentative conclusions': (1) climate warming could have a positive effect on the abundance of some temperate species; (2) the warming effect could be offset by a drastic reduction of leaf litter quality, but this is unlikely in the near future; (3) land cover changes, mainly due to deforestation in the tropics and land abandonment in Europe, could override any other factor for habitat specialists; and (4) landscape heterogeneity could be a good option for millipede conservation, even at the cost of some fragmentation.

However, this review inevitably leaves questions unanswered for several reasons. The main reason is the paucity of data in millipede ecology. Most conclusions are based on short-term studies involving a handful of species. Little is known about the physiological ecology of most species, i.e. how they respond to abiotic factors in terms of population growth. To improve our knowledge, we need ecophysiological studies over broader geographical ranges, including species with different ecologies and life histories.

We also need studies involving other environmental factors. Only a few components of global change have been mentioned here, whereas all components interact in the real world. For example, the ecological consequences of nitrogen deposition may strongly interact with those of CO_2 enrichment in terrestrial ecosystems (Wardle 2002). The frequency of extreme events (heat wave, drought, fire…) may also have direct and indirect effects on millipedes, even though soil arthropods are better protected than their aboveground counterparts.

Finally, little is known about the significance of biotic interactions in field communities under global change, i.e., to what extent the responses of populations are influenced by competition, predation and mutualistic interactions. Biotic interactions are rarely considered in millipede ecology, despite growing evidence of the demographic impacts of parasitism and predation (Baker 1985a, 1985b, Krooss & Schaefer 1998, McKillup et al. 1988). As the parasites, predators and pathogens of millipedes also respond to the current environmental change, both ecophysiology and biotic interaction studies are necessary to fully understand the effects of global change in the field.

6. References

Bailey, P. T. & J. Kovaliski (1993): Summer quiescent behaviour of the millipede *Ommatoiulus moreleti* (Julida: Julidae). – Journal of Zoology (London) **231**: 523–532.

Baker, G. H. (1985a): Parasites of the millipede *Ommatoiulus moreletii* (Lucas) (Diplopoda: Iulidae) in Portugal, and their potential as biological control agents in Australia. – Australian Journal of Zoology **33**: 23–32.

Baker, G. H. (1985b): Predators of *Ommatoiulus moreletii* (Lucas) (Diplopoda: Iulidae) in Portugal and Australia. – Journal of the Australian Entomological Society **24**: 247–252.

Baker, G. H. (1998): Recognising and responding to the influences of agriculture and other land-use practices on soil fauna in Australia. – Applied Soil Ecology **9**: 303–310.

Baldi, A. (2008): Habitat heterogeneity overrides the species-area relationship. – Journal of Biogeography **35**: 675–681.

Bale, J. S., G. J. Masters, I. D. Hodkinson, C. Awmack, T. M. Bezemer, V. K. Brown et al. (2002): Herbivory in global climate change research: direct effects of rising temperatures on insect herbivores. – Global Change Biology **8**: 1–16.

Bihn, O. H., M. Verhaagh, M. Brandle & R. Brandl (2008): Do secondary forests act as refuges for old growth forest animals? Recovery of ant diversity in the Atlantic forest of Brazil. – Biological Conservation **141**: 733–743.

Blower, J. G. (1974): Food consumption and growth in a laboratory population of *Ophyiulus pilosus* (Newport). – Symposia of the Zoological Society of London **32**: 527–551.

Bourdanne, D. K. (1997): Influence de l'anthropisation sur le peuplement en diplopodes de la région d'Abidjan, Cote d'Ivoire (Diplopoda). – Entomologica Scandinavica Supplement **51**: 245–249.

Carcamo, H. A., T. A. Abe, C. E. Prescott, F. B. Holl & C. P. Chanway (2000): Influence of millipedes on litter decomposition, N mineralization, and microbial communities in a coastal forest in British Columbia, Canada. – Canadian Journal of Forest Research **30**: 817–826.

Causey, N. B. (1943): Studies on the life history and the ecology of the hothouse millipede, *Orthomorpha gracilis* (C.L. Koch, 1847). – American Midland Naturalist **29**: 670–682.

Crawford, C. S. (1979): Desert millipedes: a rationale for their distribution. – In: Camatini, M. (ed.): Myriapod Biology. – Academic Press, London: 171–181.

Crawford, C. S., K. Bercovitz & M. R. Warburg (1987): Regional environments, life-history patterns, and habitat use of Spirostreptid millipedes in arid regions. – Zoological Journal of the Linnean Society **89**: 63–88.

Dangerfield, J. M. (1998): Biology and ecology of millipedes in the Kalahari. – Transactions of the Royal Society of South Africa **53**: 183–194.

Dangerfield, J. M. & S. R. Telford (1996): The ecology of savanna millipedes in Southern Africa. – Memoires du Museum National d'Histoire Naturelle **169**: 617–625.

Dauber, J., T. Purtauf, A. Allspach, J. Frisch, K. Voigtländer & V. Wolters (2005): Local vs. landscape controls on diversity: a test using surface-dwelling soil macroinvertebrates of differing mobility. – Global Ecology and Biogeography **14**: 213–221.

David, J. F. (1990): Comparison of the diplopod communities before and after an exceptional drought in the Forest of Orleans (France). – In: Minelli, A. (ed.): Proceedings of the 7th International Congress of Myriapodology. – Brill, Leiden: 209–218.

David, J. F. (1992): Some questions about the evolution of life-history traits in Diplopoda. – Berichte des Naturwissenschaftlich-Medizinischen Vereins in Innsbruck Supplementum **10**: 143–152.

David, J. F. (1996): The diplopod community of a Mediterranean oak forest in southern France: ecological and evolutionary interest. – Memoires du Museum National d'Histoire Naturelle **169**: 627–634.

David, J. F. & M. L. Celerier (1997): Effects of yeast on the growth and reproduction of the saprophagous millipede *Polydesmus angustus* (Diplopoda, Polydesmidae). – Biology and Fertility of Soils **24**: 66–69.

David, J. F. & D. Gillon (2002): Annual feeding rate of the millipede *Glomeris marginata* on holm oak (*Quercus ilex*) leaf litter under Mediterranean conditions – Pedobiologia **46**: 42–52.

David, J. F. & D. Gillon (2009): Combined effects of elevated temperatures and reduced leaf litter quality on the life-history parameters of a saprophagous macroarthropod. – Global Change Biology **15**: 156–165.

David, J. F., J. J. Geoffroy & M. L. Celerier (2003): First evidence for photoperiodic regulation of the life cycle in a millipede species, *Polydesmus angustus* (Diplopoda, Polydesmidae). – Journal of Zoology (London) **260**: 111–116.

David, J. F., S. Devernay, G. Loucougaray & E. Le Floc'h (1999): Belowground biodiversity in a Mediterranean landscape: relationships between saprophagous macroarthropod communities and vegetation structure. – Biodiversity and Conservation **8**: 753–767.

Dunger, W. (1958): Uber die Zersetzung der Laubstreu durch die Boden-Makrofauna im Auenwald. – Zoologische Jahrbücher, Abteilung für Systematik Ökologie und Geographie der Tiere **86**: 139–180.

Dunger, W. & K. Steinmetzger (1981): Ökologische Untersuchungen an Diplopoden einer Rasen-Wald-Catena im Thüringer Kalkgebiet. – Zoologische Jahrbücher, Abteilung für Systematik Ökologie und Geographie der Tiere **108**: 519–533.

Dunger, W. & K. Voigtländer (2009): Soil fauna (Lumbricidae, Collembola, Diplopoda and Chilopoda) as indicators of soil eco-subsystem development in post-mining sites of eastern Germany – a review. – Soil Organisms **81**(1): 1–51.

Enghoff, H. (1992): Macaronesian millipedes (Diplopoda) with emphasis on endemic species swarms on Madeira and the Canary Islands. – Biological Journal of the Linnean Society **46**: 153–161.

Ewers, R. M. & R. K. Didham (2006): Confounding factors in the detection of species responses to habitat fragmentation. – Biological Reviews of the Cambridge Philosophical Society **81**: 117–142.

Fujiyama, S. (1996): Annual thermoperiod regulating an eight-year life-cycle of a periodical diplopod, *Parafontaria laminata armigera* Verhoeff (Diplopoda). – Pedobiologia **40**: 541–547.

Gardner, T. A., M. I. M. Hernandez, J. Barlow & C. A. Perez (2008): Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. – Journal of Applied Ecology **45**: 883–893.

Geoffroy, J. J. (1981): Modalités de la coexistence de deux diplopodes, *Cylindroiulus punctatus* (Leach) et *Cylindroiulus nitidus* (Verhoeff) dans un écosystème forestier du Bassin parisien. – Acta Oecologica, Oecologia Generalis **2**: 227–243.

Geoffroy, J. J. & M. L. Celerier (1996): Cycles d'activité comparés de populations de diplopodes édaphiques dans un écosystème forestier tempéré. – Memoires du Museum National d'Histoire Naturelle **169**: 533–554.

Haacker, U. (1968): Deskriptive, experimentelle und vergleichende Untersuchungen zur Autökologie rhein-mainischer Diplopoden. – Oecologia (Berlin) **1**: 87–129.

Hamer, M. L. & R. H. Slotow (2000): Patterns of distribution and speciation in the genus *Doratogonus* (Diplopoda: Spirostreptidae). – Fragmenta Faunistica Supplement **43**: 295–311.

Hamer, M. L., R. H. Slotow & S. Lovell (2006): The South African savanna millipede (Diplopoda) fauna: taxonomic diversity, endemism, spatial and temporal effects on conservation assessments. – Norwegian Journal of Entomology **53**: 321–334.

Hanski, I. (2005): The Shrinking World: Ecological Consequences of Habitat Loss. – International Ecology Institute, Oldendorf/Luhe: 307 pp.

Hättenschwiler, S., A. V. Tiunov & S. Scheu (2005): Biodiversity and litter decomposition in terrestrial ecosystems. – Annual Review of Ecology Evolution and Systematics **36**: 191–218.

Hickling, R., D. B. Roy, J. K. Hill, R. Fox & C. D. Thomas (2006): The distributions of a wide range of taxonomic groups are expanding polewards. – Global Change Biology **12**: 450–455.

Hoffman, R. L. & J. A. Payne (1969): Diplopods as carnivores. – Ecology **50**: 1096–1098.

Hopkin, S. P. & H. J. Read (1992): The Biology of Millipedes. – Oxford University Press, Oxford: 233 pp.

Iatrou, G. D. & G. P. Stamou (1991): The life cycle and spatial distribution of *Glomeris balcanica* (Diplopoda: Glomeridae) in an evergreen-sclerophyllous formation in northern Greece. – Pedobiologia **35**: 1–10.

IPCC (2007a): Climate Change 2007: the Physical Science Basis. – Cambridge University Press, Cambridge: 996 pp.

IPCC (2007b): Climate Change 2007: Impacts, Adaptation and Vulnerability. – Cambridge University Press, Cambridge: 976 pp.

Kheirallah, A .M. (1973): Food preferences of the hothouse millipede *Orthomorpha gracilis* (Koch) and the Isopod *Leptotrichus panzeri* (Aud. and Sav.)*. – Bulletin de la Societe Entomologique d'Egypte **57**: 371–377.

Kime, R. D. (1990): A Provisional Atlas of European Myriapods. Part 1. – European Invertebrate Survey, Luxembourg: 109 pp.

Kime, R. D. (2004): The Belgian millipede fauna (Diplopoda). – Bulletin de l'Institut Royal de Sciences Naturelles de Belgique, Entomologie **74**: 35–68.

Kime, R. D. & G. Wauthy (1984): Aspects of relationships between millepedes, soil texture and temperature in deciduous forests. – Pedobiologia **26**: 387–402.

Krooss, S. & M. Schaefer (1998): How predacious are predators? A study on *Ocypus similis*, a rove beetle of cereal fields. – Annals of Applied Biology **133**: 1–16.

Kukor, J. J. & M. M. Martin (1987): Nutritional ecology of fungus-feeding arthropods. – In: Slansky, F. & J. G. Rodriguez (eds): Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates. – Wiley, New York: 791–814.

Lee, P. (2006): Atlas of the Millipedes (Diplopoda) of Britain and Ireland. – Pensoft, Sofia: 216 pp.

Lewis, J. G. E. (1974): The ecology of centipedes and millipedes in northern Nigeria. – Symposia of the Zoological Society of London **32**: 423–431.

Mathieu, J., J. P. Rossi, P. Mora, P. Lavelle, P. E. Da S.-Martins, C. Rouland et al. (2005): Recovery of soil macrofauna communities after forest clearance in eastern Amazonia, Brazil. – Conservation Biology **19**: 1598–1605.

Mauries, J. P. (1974): *Pyreneosoma bessoni* n. sp. Diagnose, synonymie et répartition du genre endémique Pyrénéen *Pyreneosoma* Mauriès, 1959 (Diplopoda, Craspedosomoidea, Haplobainosomidae). – Bulletin de la Société d'Histoire Naturelle de Toulouse **110**: 47–54.

McKillup, S. C., P. G. Allen & M. A. Skewes (1988): The natural decline of an introduced species following its initial increase in abundance; an explanation for *Ommatoiulus moreletii* in Australia. – Oecologia **77**: 339–342.

Meidell, B. & H. Enghoff (1993): *Polydesmus angustus* Latzel, 1884 – et for Danmark nyt tusindben (Diplopoda, Polydesmida, Polydesmidae). – Entomologiske Meddelelser **61**: 83–84.

Meyer, E. & G. Eisenbeis (1985): Water relations in millipedes from some alpine habitat types (Central Alps, Tyrol) (Diplopoda). – Bijdragen tot de Dierkunde **55**: 131–142.

Nakamura, A., H. Proctor & C. P. Catterall (2003): Using soil and litter arthropods to assess the state of rainforest restoration. – Ecological Management and Restoration **4** (Suppl.): 20–28.

Neilson, R. P., L. F. Pitelka, A. M. Solomon, R. Nathan, G. F. Midgley, J. M. V. Fragoso et al. (2005): Forecasting regional to global plant migration in response to climate change. – BioScience **55**: 749–759.

Norby, R. J., M. F. Cotrufo, P. Ineson, E. O'Neill & J. G. Canadell (2001): Elevated CO_2, litter chemistry, and decomposition: a synthesis. – Oecologia **127**: 153–165.

O'Neill, R. V. (1967): Niche segregation in seven species of Diplopods. – Ecology **48**: 983.

O'Neill, R. V. (1969): Adaptive responses to desiccation in the millipede, *Narceus americanus* (Beauvois). – American Midland Naturalist **81**: 578–583.

Paquin, P. & D. Coderre (1997): Deforestation and fire impact on edaphic insect larvae and other macroarthropods. – Environmental Entomology **26**: 21–30.

Parmesan, C. (2006): Ecological and evolutionary responses to recent climate change. – Annual Review of Ecology Evolution and Systematics **37**: 637–669.

Pedroli-Christen, A. (1993): Faunistique des mille-pattes de Suisse (Diplopoda). – Documenta Faunistica Helvetiae **14**: 1–167.

Pobozsny, M. (1978): Nahrungsansprüche einiger Diplopoden- und Isopoden-Arten in mesophilen Laubwäldern Ungarns. – Acta Zoologica Academiae Scientiarum Hungaricae **24**: 397–406.

Redi, B. H., R. J. Van Aarde & T. D. Wassenaar (2005): Coastal dune forest development and the regeneration of millipede communities. – Restoration Ecology **13**: 284–291.

Sakwa, W. N. (1974): A consideration of the chemical basis of food preference in millipedes. – Symposia of the Zoological Society of London **32**: 329–346.

Serra, A., M. C. Vicente & E. Mateos (1996): Etude des communautés de myriapodes (Chilopoda et Diplopoda) des forêts prépyrénéennes (Huesca, Espagne). – Memoires du Museum National d'Histoire Naturelle **169**: 187–204.

Snider, R. M. (1981a): Growth and survival of *Polydesmus inconstans* (Diplopoda: Polydesmidae) at constant temperatures. – Pedobiologia **22**: 345–353.

Snider, R. M. (1981b): The reproductive biology of *Polydesmus inconstans* (Diplopoda: Polydesmidae) at constant temperatures. – Pedobiologia **22**: 354–365.

Spitzer, L., M. Konvicka, J. Benes, R. Tropek, I. H. Tuf & J. Tufová (2008): Does closure of traditionally managed open woodlands threaten epigeic invertebrates? Effects of coppicing and high deer densities. – Biological Conservation **141**: 827–837.

Striganova, B. R. & Z. G. Prishutova (1990): Food requirements of diplopods in the dry steppe subzone of the USSR. – Pedobiologia **34**: 37–41.

Sutton, S. L., M. Hassall, R. Willows, R. C. Davis, A. Grundy & K. D. Sunderland (1984): Life histories of terrestrial Isopods: a study of intra- and interspecific variation. – Symposia of the Zoological Society of London **53**: 269–294.

Tajovský, K. (2001): Colonization of colliery spoil heaps by millipedes (Diplopoda) and terrestrial isopods (Oniscidea) in the Sokolov region, Czech Republic. – Restoration Ecology **9**: 365–369.

Tews, J., U. Brose, V. Grimm, K. Tielbörger, M. C. Wichmann, M. Schwager et al. (2004): Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. – Journal of Biogeography **31**: 79–92.

Topp, W., H. Kappes, J. Kulfan & P. Zach (2006): Distribution pattern of woodlice (Isopoda) and millipedes (Diplopoda) in four primeval forests of the western Carpathians (Central Slovakia). – Soil Biology & Biochemistry **38**: 43–50.

Tracz, H. (2000): The Diplopoda and Chilopoda of selected ecotones in northwestern Poland. – Fragmenta Faunistica Supplement **43**: 351–360.

Wardle, D. A. (2002): Communities and Ecosystems. – Princeton University Press, Princeton: 392 pp.

Warren, M. S., J. K. Hill, J. A. Thomas, J. Asher, R. Fox, B. Huntley et al. (2001): Rapid responses of British butterflies to opposing forces of climate and habitat change. – Nature **414**: 65–69.

Wesener, T. (2005): Giant-pill millipede diversity on Madagascar (Diplopoda: Sphaerotheriida). – Peckiana **4**: 189–193.

Wooten, R. C. & C. S. Crawford (1974): Respiratory metabolism of the desert millipede *Orthoporus ornatus* (Girard) (Diplopoda). – Oecologia (Berlin) **17**: 179–186.

Wright, J. C. & P. Westh (2006): Water vapour absorption in the penicillate millipede *Polyxenus lagurus* (Diplopoda: Penicillata: Polyxenida): microcalorimetric analysis of uptake kinetics. – Journal of Experimental Biology **209**: 2486–2494.

Wytwer, J. & M. Zalewski (2005): The role of island size and isolation in diversity of Myriapoda. – Peckiana **4**: 195–208.