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► To cite this version:

Annegret Nicolai, Armelle Ansart. Conservation at a slow pace: terrestrial gastropods facing fast-changing climate. *Conservation Physiology*, 2017, 5 (1), pp.cox007. 10.1093/conphys/cox007 . hal-01510690

HAL Id: hal-01510690

<https://univ-rennes.hal.science/hal-01510690>

Submitted on 20 Jun 2018

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Conservation at a slow pace: terrestrial gastropods facing fast-changing climate

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The climate is changing rapidly, and terrestrial ectotherms are expected to be particularly vulnerable to changes in temperature and water regime, but also to an increase in extreme weather events in temperate regions. Physiological responses of terrestrial gastropods to climate change are poorly studied. This is surprising, because they are of biodiversity significance among litter-dwelling species, playing important roles in ecosystem function, with numerous species being listed as endangered and requiring efficient conservation management. Through a summary of our ecophysiological work on snail and slug species, we gained some insights into physiological and behavioural responses to climate change that we can organize into the following four threat categories. (i) Winter temperature and snow cover. Terrestrial gastropods use different strategies to survive sub-zero temperatures in buffered refuges, such as the litter or the soil. Absence of the insulating snow cover exposes species to high variability in temperature. The extent of specific cold tolerance might influence the potential of local extinction, but also of invasion. (ii) Drought and high temperature. Physiological responses involve high-cost processes that protect against heat and dehydration. Some species decrease activity periods, thereby reducing foraging and reproduction time. Related costs and physiological limits are expected to increase mortality. (iii) Extreme events. Although some terrestrial gastropod communities can have a good resilience to fire, storms and flooding, an increase in the frequency of those events might lead to community impoverishment. (iv) Habitat loss and fragmentation. Given that terrestrial gastropods are poorly mobile, landscape alteration generally results in an increased risk of local extinction, but responses are highly variable between species, requiring studies at the population level. There is a great need for studies involving non-invasive methods on the plasticity of physiological and behavioural responses and the ability for local adaptation, considering the spatiotemporally heterogeneous climatic landscape, to allow efficient management of ecosystems and conservation of biodiversity.

Key words: Cold tolerance, dispersal, drought resistance, extreme events, habitat alteration, species at risk

Editor: Steven Cooke

Received 30 September 2016; Revised 26 December 2016; Editorial Decision 14 January 2017; accepted 9 February 2017

Cite as: Nicolai A, Ansart A (2017) Conservation at a slow pace: terrestrial gastropods facing fast-changing climate. *Conserv Physiol* 5(1): cox007; doi:10.1093/conphys/cox007.

Introduction

Climate is one of the most important drivers of species' distribution and abundance. Over the last decades, the earth's climate has irrefutably warmed. For the coming century, global

mean surface temperature is projected to increase by ~1°C, for the most optimistic scenario, to ~3.7°C, for the least optimistic one. The global precipitation regime is expected to change, increasing the contrast between seasons and between wet and dry regions (Meehl *et al.*, 2007). In temperate regions, snow

cover and snow events will decrease, and extreme events, such as heat waves and drought, heavy precipitation and storms, are expected to occur more often (Stocker *et al.*, 2013). Rapid variation of climate is expected to alter species' life-history traits (for example, phenology, Fabina *et al.*, 2010) and biotic interactions (e.g. Wernegreen, 2012), which might lead to range contractions or even extinctions (Thomas *et al.*, 2004, 2006).

Terrestrial ectothermic organisms may be particularly affected by modifications of local climate conditions, because body temperature and, subsequently, basic physiological functions, depend on environmental temperature (Gillooly *et al.*, 2001; Deutsch *et al.*, 2008). Among ectotherms, terrestrial gastropods (i.e. land snails and slugs) are particularly prone to climate change for the following reasons. First, their activity and physiology are highly sensitive to local temperatures (Cameron, 1970; Bailey, 1975), and many species enter a state of dormancy (aestivation and/or hibernation) when conditions are unfavourable for activity (e.g. Heller and Ittiel, 1990; Iglesias *et al.*, 1996). Second, their moist skin and the secretion of a mucus trail for locomotion make them particularly sensitive to low hygrometric conditions (e.g. Young and Port, 1989). Third, moreover, their proverbial slowness and high cost of movement strongly limit their ability to escape a hostile environment actively (Denny, 1980). Although widely used as witnesses of previous climate changes (Goodfriend, 1992), terrestrial gastropods have so far received little attention regarding the potential impact of current rapid climate change on their distribution, compared with other taxa. This is surprising for the following reasons. First, with ~24 000 described species, inhabiting a large range of habitats, terrestrial gastropods are one of the most diverse group of land animals (Lydeard *et al.*, 2004), playing a primordial role in ecosystem functioning specifically by aiding in decomposition, nutrient cycling and soil-building processes (Mason, 1970a, b; Jennings and Barkham, 1979; Prather *et al.*, 2013), providing food and essential nutrients to wildlife (South, 1980; Churchfield, 1984; Frest and

Johannes, 1995; Martin, 2000; Nyffeler and Symondson, 2001), and determining plant community structure (Hulme, 1996; Peters, 2007). Second, 1105 species worldwide appear on the IUCN red list as extinct, critically endangered, endangered or vulnerable (www.iucnredlist.org), and many more are listed regionally and nationally (Fig. 1A). Third, many species are serious pests that lead to crop damage and pesticide spreading (Barker, 2002) as well as negative impacts on natural habitats and native biodiversity (Cowie, 2011). Fourth, some gastropods are pathogen vectors (Rowley *et al.*, 1987; Graeff-Teixeira, 2007).

Models of future distribution of gastropod species tend to predict range shifts and an increase of diversity with latitude and altitude. These models are based on climate projections that predict higher temperatures and more precipitation at high latitudes and altitudes compared with low latitudes and altitudes, where climate is expected to become drier (Willis *et al.*, 2006; Müller *et al.*, 2009; Hof, 2011; Beltramino *et al.*, 2015). Although such models have a general interest, their reliability is limited. For example, most of the critically endangered species live on islands (Oceania) or in Europe and North America, where the climate change will largely interact with anthropogenic pressures (Fig. 1B and C; Gibson *et al.*, 2009). In fact, it has been demonstrated that climate change could push gastropod species to the brink of extinction, e.g. *Rhachistia aldabrae* was believed to be extinct (Gerlach, 2007), but a few specimens were rediscovered in 2014 (Amla, 2014). Modifications in species' distribution and abundance without a northward shift of the range were also reported (Baur and Baur, 1993, 2013; Peltanova *et al.*, 2012; Pearce and Paustian, 2013).

Conservation management plans aim to protect ecosystems and biodiversity, but they often lack approaches that take the ecological impacts of climate change into account, as well as specific organism responses and interactions. Furthermore, conservation strategies typically target the ecological integrity of large areas, a scale inadequate for taxa

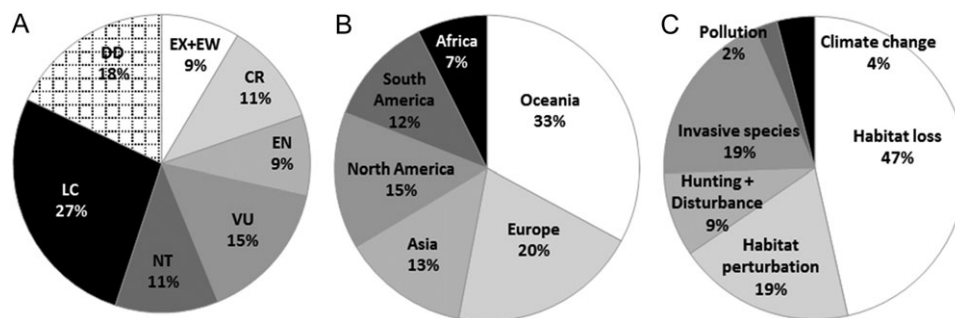


Figure 1: Terrestrial gastropods on the IUCN Red List of Threatened Species™ (IUCN, 2016). (A) Global distribution of assessed terrestrial gastropods ($n = 2070$) in the red list categories Abbreviations: CR, critically endangered; DD, data deficient; EN, endangered; EX+EW, extinct and extinct in the wild; LC, least concern; NT, near threatened; and VU, vulnerable. (B) Geographical origin of terrestrial gastropods in the CR category ($n = 283$). (C) Threats ($n = 2153$) encountered in all red list categories for assessed terrestrial gastropods ($n = 2070$). One species can face more than one threat.

such as terrestrial gastropods, which are constrained by low mobility or thermal barriers within the habitat. The lack of knowledge on organisms' responses to climate change and on how effects of extreme weather events can be mitigated by adequate habitat management is striking. There is a crucial need to incorporate physiological and behavioural specific traits into projection of ecological effects of climate change (Deutsch *et al.*, 2008) when conceiving management or restoration plans of protected areas (Evans *et al.*, 2015). For example, the Committee of Status of Endangered Wildlife in Canada (COSEWIC) identified droughts and absence of snow (Augsburger, 2013) as ongoing threats in all of the species at-risk assessments of terrestrial gastropods (14 species; see www.sararegistry.gc.ca for species status reports). However, none of them could clearly identify the scope and severity of climate change impact because specific physiological and behavioural knowledge is lacking. Only partial knowledge on thermal tolerance of model organisms (e.g. Staikou, 1999; see also Table 1 and Fig. 2) is available.

Currently, the threats of climate change are documented in only 87 of 283 critically endangered terrestrial gastropods worldwide (Fig. 1C; IUCN, 2016). Although habitat loss and perturbation, invasive species and pollution may increase the impact of climate change, in many of the remaining species the impact of the threats of climate change are unknown. In the threat calculation for a species at-risk assessment, 'climate change' is divided into different threat categories illustrating effects on species (for complete information on these categories, see Salafsky *et al.*, 2008 and <http://cmp-openstandards.org/using-os/tools/classification-beta-v-2-0>). These categories are not always evident to differentiate. For example, 'changes in temperature regimes' (threat 11.3) and 'changes in precipitation

and hydrological regimes' (threat 11.4) are, in general, closely linked. Here, we gathered some aspects of terrestrial gastropod physiology and species' strategies, including our own research work, which may provide a perspective for increasing the understanding of potential impacts of climate change and a gaining integration of species traits in conservation management. We address the following four main climate change threats, critical for terrestrial gastropods: (i) winter temperature and snow cover; (ii) drought and high temperature; (iii) extreme events; and (iv) habitat loss and fragmentation.

Winter temperature and snow cover

Climate warming includes changes of mean temperature with the effect of delaying the cold season, but also increasing the variability of temperature in the litter and upper soil layers as a result of the absence of snow, especially in autumn and spring when temperatures fluctuate around 0°C (Augsburger, 2013). Delaying the winter season might have an impact on phenology of terrestrial gastropods. Winter dormancy is triggered by photoperiod and temperature (Bailey, 1981; Jeppesen, 1977), and reproduction is possible at suitable temperatures with decreasing photoperiod (Nicolai *et al.*, 2010). Terrestrial gastropods that change phenology by later entry into dormancy and/or autumn reproduction are susceptible to be exposed to below-zero temperatures and/or have reduced energy reserves for winter survival, respectively. Given that winter survival increases with size in many terrestrial gastropod species (in *Cepaea nemoralis*, Oosterhoff, 1977; in *Arianta arbustorum*, Terhivuo, 1978; Baur and Baur, 1991), juveniles from autumn reproduction might be particularly vulnerable, especially if they do not reach the crucial shell size

Table 1: Comparison of cold tolerance strategies in three species of European Helicidae

Parameter	<i>Helix pomatia</i>	<i>Cornu aspersum</i>	<i>Cepaea nemoralis</i>
Annual cycle	Hibernation: 5–6 months Aestivation: few days	Hibernation/aestivation: highly variable across Europe (6–0 months)	Hibernation: 5–6 months Aestivation: few days
Shell breadth	30–50 mm	25–40 mm	18–25 mm
Cold-tolerance processes	T _c = −2°C (activity) T _c = −6°C (dormancy) LT ₅₀ = −10°C (2 h exposure)	T _c = −3°C (activity) T _c = −5°C (dormancy) LT ₅₀ = −10°C (2 h exposure)	T _c = −4°C (activity) LT ₅₀ = −10°C (2 h exposure in activity) T _c = LLT = −10°C (dormancy)
Cold-tolerance strategy	Partly freeze tolerant	Partly freeze tolerant	Partly freeze tolerant (activity) Freeze avoidant (dormancy)
Distribution	South-Eastern Europe to England and Scandinavia	North Africa to North Western Europe (The Netherlands, England) and eastwards to the Rhine Valley	Central Europe from Mediterranean to England and eastwards to Poland
Status	Protected in Europe (Appendix III, Bern Convention)	Invasive in North and South America, Australia, South Africa and New Zealand	Invasive in North America
References	Nietzke (1970); Lind (1988); Kerney and Cameron (1999); Nicolai <i>et al.</i> (2005, 2011, 2012a, 2015); Ansart <i>et al.</i> (2014); personal observation A.N.	Kerney and Cameron (1999); Ansart <i>et al.</i> (2001, 2002, 2010, 2014); Nicolai <i>et al.</i> (2005); personal observations A.A. and A.N.	Kerney and Cameron (1999); Ansart <i>et al.</i> (2014); personal observations A.A. and A.N.

Abbreviations: LT₅₀, lethal temperature for 50% of individuals; LLT, absolute lower lethal temperature; T_c, temperature of crystallization.

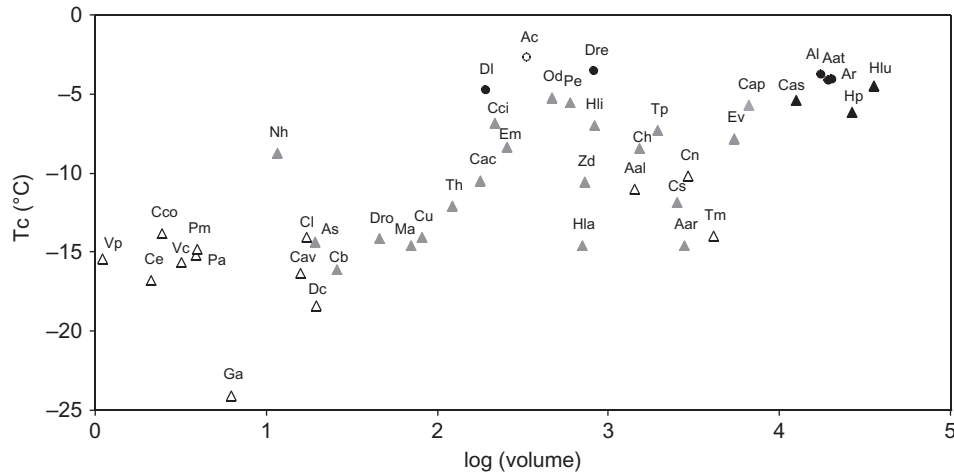


Figure 2: Relationships between the temperature of crystallization (T_c) and the volume of 43 species of slugs and snails. Triangles indicate shelled species and circles slugs. White symbols indicate freeze-intolerant species, black symbols partly freeze-tolerant or freeze-tolerant species and grey symbols indicate species with unknown cold-tolerance strategy. Data are from Ansart *et al.* (2014) and personal observations A.A. except for species DI and Ac (Storey *et al.*, 2007), Dre (Cook, 2004), Al, Aat and Ar (Slotsbo *et al.*, 2012), Aal (Riddle, 1981), Dc and Ga (Riddle and Miller, 1988), Cav (Košťál *et al.*, 2013), Vp (Schmid, 1988) and Aar (Stöver, 1973), Tm (Franke, 1985). Sample size ranges from five to 110 individuals depending on species. Only T_c values obtained during the cold season have been considered. Volume was estimated as the mean between the volume of a cone and that of an ellipsoid for shelled snails (see Ansart *et al.*, 2014) and as the volume of a cylinder for slugs. Mean size estimations were extracted from Welter-Schultes (2012), Kerney and Cameron (1999) and Rowson *et al.* (2014) for European species and from Pilsbry (1940, 1948) for American species. Abbreviations: Aal, *Anguispira alternata*; Aar, *Arianta arbustorum*; Aat, *Arion ater*; Ac, *Arion circumscriptus*; Al, *Arion 'lusitanicus' = vulgaris* (invader); Ar, *Arion rufus*; As, *Abida secale*; Cac, *Cochlicella acuta*; Cap, *Cantareus apertus*; Cas, *Cornu aspersum*; Cav, *Chondrina avenacea*; Cb, *Clausilia bidentata*; Cci, *Ciliella ciliata*; Cco, *Columella columella*; Ce, *Columella edentula*; Ch, *Cepaea hortensis*; Cl, *Cochlicopa lubrica*; Cn, *Cepaea nemoralis*; Cs, *Cepaea sylvatica*; Cu, *Candidula unifasciata*; Dc, *Discus cronkhitei*; DI, *Deroceras laeve*; Dre, *Deroceras reticulatum*; Dro, *Discus rotundatus*; Em, *Ena montana*; Ev, *Eobania vermiculata*; Ga, *Gastrocopta armifera*; Hla, *Helicigona lapicida*; Hli, *Hygromia limbata*; Hlu, *Helix lucorum*; Hp, *Helix pomatia*; Ma, *Macrogastra attenuata*; Nh, *Nesovitrea hammonis*; Od, *Oxychilus draparnaudi*; Pa, *Pupilla alpicola*; Pe, *Pomatias elegans*; Pm, *Pupilla muscorum*; Th, *Trochulus hispidus*; Tp, *Theba pisana*; Vc, *Vallonia costata*; Vp, *Vallonia perspectiva*; Wm, *Triodopsis (Webbhelix) multilineata*; and Zd, *Zebrina detrita*.

below which they are unable to hibernate (Biannic and Daguzan, 1993). The length of dormancy is also important for genital tract maturation and gamete genesis, assuring the success of future reproduction (Bonnefoy-Claudet and Deray, 1984; Gomot and Gomot, 1991). When dormancy of *C. nemoralis* was reduced from 5–6 to 3 months, no spring reproduction occurred, and the albumen gland had increased by only 36% of its initial dry mass compared with 91% increase after 5 months (unpublished data A.N. for Annegret Nicolai). Although some species have a highly variable length of dormancy depending on the geographical origin of the population, other species need a long dormancy period, such as the Roman snail *Helix pomatia* (Lind, 1988) dormancy period. For example, hibernation in *C. aspersum* lasts >7 months in Scotland (Crook, 1980), 6 months in Wales (Bailey, 1981), ~5 months in North-Western France (Lorvelec and Daguzan, 1990) and 4 months in North-Western Spain (Iglesias *et al.*, 1996), whereas some Mediterranean populations do not hibernate (Madec, 1989). Changing phenology has consequences for population dynamics because of the possibility of higher winter mortality, low juvenile winter survival from autumn reproduction and reduced spring reproduction.

Survival to sub-zero temperatures is partly related to behaviour, such as the ability to occupy buffered microsites (Heller

and Dolev, 1994; Nicolai *et al.*, 2011) and the orientation of the apex in the hibernation position (Carney, 1966; Terhivuo, 1978; Baur and Baur 1991). At a physiological level, winter mortality can be caused by insufficient energy reserves to endure long periods of inactivity (Storey and Storey, 1990, 2004; Bailey and Lazaridou-Dimitriadou, 1991; Heller and Dolev, 1994; Pakay *et al.*, 2002) and by a low ability to tolerate the exposure to sub-zero temperatures. Cold hardiness strategy is thus crucial for the maintenance and development of a species in a cold-constrained habitat (Bale and Walters, 2001; Pither, 2003; Bale and Hayward, 2010; Chown *et al.*, 2010). There are currently two main categories of physiological responses to sub-zero temperatures, freeze avoidance and freeze tolerance, although many intermediate response strategies are possible. Freeze-tolerant organisms generally have a poor ability to supercool (i.e. the ability to maintain body fluids at a liquid state below the freezing point), between -5 and -10°C , allowing slow freezing of tissues and thus sufficient time to implement protection mechanisms. In some snail species, ice nucleating agents decrease the supercooling ability (e.g. gut bacteria; Ansart *et al.*, 2010; Nicolai *et al.*, 2015). On the contrary, in freeze-avoidant organisms, for which ice formation in tissues is lethal, the supercooling ability will be enhanced, often in association with the synthesis of large amount of antifreeze substances (for more

information on these strategies, see, for example, Ramløv, 2000; Zachariassen and Kristiansen, 2000; Block, 2003).

Winter mortality as a result extreme cold temperatures appears to be a key factor in shaping the distribution and abundance of land gastropods (Pfenninger, 2004; Horsák *et al.*, 2013; Horsák and Chytrý, 2014). Terrestrial gastropods are largely present in regions with harsh cold seasons; in northwest Europe, 35 species are recorded above the Arctic Circle and 44 species can be found at altitudes higher than 2000 m (Kerney *et al.*, 1983; Kerney and Cameron, 1999), and in Canada, ~30 species live at high altitudes in the Rocky Mountains and in arctic provinces (Grimm *et al.*, 2009; Forsyth RG pers. communication).

Cold tolerance strategies are still poorly known within the group of terrestrial gastropods, but all strategies from freezing avoidance to tolerance can be encountered. Some species have a short generation time, and only eggs will persist during winter (e.g. the slug *Lehmannia marginata*; Cook and Radford, 1988). For all studied species, eggs are killed by ice formation but can supercool more or less depending on the species [temperature of crystallization (T_c) = -3.9 to -14.7°C in 34 different species; T_c is the temperature at which body fluids start to freeze; unpublished data A.A. and A.N. for the two authors). In species for which adults hibernate, the comparison of 31 terrestrial European snails from 13 different families revealed a strong phylogenetic constraint on the T_c , highly dependent on both water mass and water content (see Fig. 2; Ansart *et al.*, 2014). The cold hardiness strategy has been extensively studied for only few species; all small species with high supercooling ability are freezing avoidant, in contrast to large snail species, which can supercool poorly but tolerate freezing of body fluids to some extent (from a few hours to a few days). All slug species, particularly sensitive to inoculative freezing, appear to be freezing tolerant (Fig. 2). Even if knowledge is still too scarce to conclude undoubtedly, only the smallest species seem able to survive extreme cold temperatures during winter. This hypothesis is supported by several studies offering evidence that land snail communities are less diverse at high altitudes and latitudes, where small taxa become more frequent (Hausdorf and Hennig, 2003; Nekola *et al.*, 2013; Baur *et al.*, 2014; Horsák and Chytrý, 2014; Schmera and Baur, 2014; Forsyth and Oldham, 2016). With climate warming, we would expect the gastropod community to become richer in bigger species, with consequences for competition, trophic webs, vegetation grazing and soil dynamics.

Under global warming, climatologists predict a decrease of snow events and a thinning of snow cover. Snow cover plays a very important buffer role. When present, soil temperature is perfectly constant near 0°C , i.e. above the freezing point of the fluids of living organisms. If absent, high variation of temperature can be a real threat for species survival and considerably modify future distribution predictions. In *Chondrina clienta* and *Balea perversa*, two

sympatric species with different cold tolerance capacities, survival was significantly higher in snow-covered microsites compared with exposed ones, at 90 vs. 79% and 100 vs. 88%, respectively (Baur and Baur, 1991). In recent years, we have compared cold tolerance in three Helicidae species: the large edible snails *Cornu aspersum* (brown garden snail) and *Helix pomatia* (Roman Snail), and the smaller *C. nemoralis* (grove snail), revealing that closely related species within the same family can have very different responses to climate change (Table 1). *Cornu aspersum* and *C. nemoralis* are invasive in some parts of the world, owing in particular to the development of human-related traffic. In some places, they are considered to be an agricultural pest (e.g. in USA and Canada, Ansart *et al.*, 2009; Cowie *et al.*, 2009). On the contrary, *H. pomatia* was common in many parts of Europe until the end of the 20th century (Nietzke, 1970), but habitat loss through agriculture and urbanization diminished important populations in some parts of Europe, such as Germany. As consequence, the species has been protected in Europe since 2002 (Appendix III of the Bern Convention). We found that the three species are partly freezing tolerant in activity, because they can bear body freezing (but only for a very short time (Table 1)). During the winter, while *H. pomatia*, partly freezing tolerant, relies on permanent snow cover for winter survival, *C. nemoralis*, freeze-avoidant with a higher supercooling capacity, can survive longer periods of frost. *Cepaea nemoralis* would then be less vulnerable than *H. pomatia* to high variations in winter temperature, which are expected to occur more frequently at high latitudes when snow cover is absent (Augsburger, 2013). Different geographical populations show slight variations in cold hardiness processes, but an adaptive and/or plastic response to local climate is difficult to prove because differences in individual size and water compartment interfered with environmental conditions (Ansart and Vernon, 2004; Nicolai *et al.*, 2005, 2012a; Gaitan-Espitia *et al.*, 2013). The loss of snow cover is the major threat of climate change in temperate regions, because it directly affects winter survival and indirectly affects reproductive success in some bigger terrestrial gastropods (data for smaller gastropod species are lacking).

Drought and high temperature

Temperature has a fundamental impact on physiological processes that determines the performance of ectotherms relative to temperature (Angilletta, 2009). Thermal performance curves (Gillooly *et al.*, 2001), which describe this relationship, are asymmetric for most ectotherms, and upward shifts of global temperature bring organisms much closer to critical limits, leading to the risk of local extinction, especially for species that cannot rapidly shift their distribution (Dillon *et al.*, 2010), such as terrestrial gastropods.

As a consequence of their soft and permeable integument, air breathing and mode of locomotion, land gastropods are particularly sensitive to desiccation (Machin, 1964). Body

temperature regulation is mainly achieved by the active research of a buffered microhabitat and metabolic down-regulation (daily torpor or aestivation). Although many scientists have been interested in the upper thermal limit and adaptations to heat of intertidal species, which endure daily highly variable ecological conditions (e.g. Marshall and McQuaid, 2011), far fewer have studied precisely heat resistance and the underlining mechanisms in land snails and slugs. At the community level, whereas the surface-to-volume ratio of globular shells would be more beneficial for facing dehydration in high-temperature conditions (Ansart *et al.*, 2014), oblong and thick shells would prevent desiccation and facilitate access to sheltered microhabitats (Giokas *et al.*, 2005). Lacking a shell, slug species are supposed to be much more sensitive to heat stress (Thompson *et al.*, 2006).

Usually, snails can cope with drought periods in the summer. Although *H. pomatia* aestivates for a short period, *C. aspersum* can endure several months in the Mediterranean region (Table 1), and snails of semiarid to arid regions are inactive for the whole year except for a few rainy days (e.g. 6–12 days/year in *Cristataria genezarethana*; Heller and Dolev, 1994). Mortality in snails from semiarid to arid regions is usually low; 5% in *Cristataria genezarethana* (Heller and Dolev, 1994) and 14% in *Rhagada convicta* (Johnson and Black, 1991), whereas *H. pomatia* in a continental climate has a mortality rate that varies between age classes from 6 to 20% (Starodubtseva and Dedkov, 2003). However, during a drought of 1 month immediately after arousal from hibernation when snails had to recover from winter fasting, mortality was up to 70% in *H. pomatia* in Germany (Nicolai *et al.*, 2011). Richardson (1974) observed direct lethal effect of high temperatures in a sand-dune population of *C. nemoralis*. For the same species, Chang and Emlen (1993) showed that repartition of the individuals in the landscape was strongly constrained by high temperatures and low humidity. Linked to urban development, subsequent increase in the soil temperature near Basel (Switzerland) might have triggered the extinction of several populations of the land snail *Arianta arbustorum*, mainly explained by the limited heat resistance of eggs (Baur and Baur, 1993). In the same species, it has also been demonstrated that the sperm length was reduced at higher temperatures, thereby affecting reproductive success (Minoretti *et al.*, 2013). In the African species *Achatina fulica* and *Macrochlamys indica*, a longer aestivation was related to a weaker viability of allosperm stored in the spermatheca, a longer gestation period because of the time necessary to meet energy needs, and a reduced number of eggs per brood (Raut and Ghose, 1982).

For species inhabiting arid regions, being active for very short periods and requiring several years to reach maturity (e.g. Yom-Tov, 1971; Heller and Dolev, 1994; Arad *et al.*, 1995), longer droughts can have important consequences on population dynamics, as for the endangered Corsica snail *Tyrrhenaria ceratina*, for which activity periods are

extremely short in spring and autumn depending on humidity (Charrier *et al.*, 2013).

Heat tolerance is diverse among terrestrial gastropods (e.g. Riddle, 1990). Given that most species spend drought periods hidden in a buffered shelter, with their shell aperture closed with an epiphragm, costs associated with aestivation are also the production of chemical compounds that allow for maintenance of cell function. The Mediterranean species *Xeropicta derbentina* is particularly well adapted to high temperatures, with individuals enduring hot hours of the day agglutinated on the top of vegetation. In this species, calcium cells playing a role in osmoregulation (Dittbrenner *et al.*, 2009; Scheil *et al.*, 2011), heat shock proteins and antioxidant defences (Troschinski *et al.*, 2014) have been shown to be implicated in heat tolerance. In the less heat-adapted species *H. pomatia*, we observed via a metabolomic fingerprinting method an increase of polyols, such as myo-inositol and glycerol, and sugars, such as maltose, that might protect the cell against dehydration (Nicolai *et al.*, 2011). Moreover, cholesterol was found in high concentration, which is responsible for the maintenance of membrane fluidity at high temperatures (Robertson and Hazel, 1997). The high concentration of succinid acid indicated the use of an anaerobic mollusc-specific glycolytic pathway that produces more energy than fermentation (Livingstone, 1991) also observed in some slugs during freezing (Storey *et al.*, 2007). These compounds implied a stress reaction to a prolonged drought, with an unusual timing involving high costs.

We can also expect different selective intra-specific effects of climatic pressures on land gastropods. Individuals with light-coloured shells have been suggested to tolerate solar radiation and heat better (e.g. *C. nemoralis*, Richardson, 1974; *C. aspersum*, Lecompte and Madec, 1998; *Cepaea vindobonensis*, Staikou, 1999; *Theba pisana*, Johnson, 2011). In *C. nemoralis*, for which shell polymorphism has been much studied, the higher frequency of light shells in open habitats compared with dark ones (Özgo, 2005) has been related to differences in mortality (Tilling, 1983), activity (Chang, 1991) and behavioural thermoregulation (Jones, 1982) in relationship with the opioid system (Kavaliers, 1992).

Extreme events

Flood

If floods are a normal and important element of biodiversity maintenance in certain ecosystems (Ilg *et al.*, 2009), they can also directly or indirectly threaten terrestrial soil faunas, for several reasons, as follows: (i) air breathing becomes impossible; (ii) water intrudes into body compartments (swelling); (iii) individuals can uncontrollably be displaced and/or (iv) be contaminated by toxic substances from the water; and (v) environmental conditions can be impacted by flooding (Plum, 2005). Abundances and biomass of soil invertebrates are immediately reduced by flooding. The effect is generally reversible and is normally compensated during the next soil

dry period, but flooding events that are too frequent can prevent communities from recovering and affect the environmental conditions more harshly (Plum, 2005).

There have been few studies concerned with the effects of flooding on land gastropod communities or species. Along a gradient of flood frequency in Danubian floodplain forests, Čejka *et al.* (2008) found that land snail communities were less rich, with lower abundance, when floods were frequent, compared with other sites. When confronted by flooding, slugs and snails actively migrate, but their ability to move is insufficient to escape brutal inundation. They can be transported passively, thereby colonizing new habitats (by water itself, driftwood, or large animals; Dahl *et al.*, 1993; Özgo *et al.*, 2015). They can avoid drowning by climbing onto emerging substrates or floating vegetation or by using air-filled cavities in the soil (Dahl *et al.*, 1993).

Flood impacts on land gastropods can be difficult to generalize. Some terrestrial gastropods, such as *C. nemoralis*, might be able to survive sudden hypoxic conditions for several hours. Active adults of *C. nemoralis* were exposed to N₂ for 15 h and tested for long-term survival; all snails survived and reproduced (unpublished data A.N.). Antioxidant defences have been shown to be highly implicated in tolerance to hypoxia/anoxia occurring during dormancy periods in *C. aspersum* (Welker *et al.*, 2016) and *H. pomatia* (Nowakowska *et al.*, 2015). Given that the majority of gastropod species spend some time with low metabolism, we could expect such a tolerance to be highly shared among the taxon.

In the North American snail *Anguispira kochi* the main threat for the Canadian range is increased risk of flooding of the habitat (COSEWIC, *in press*). The water level of Lake Erie has been high for a few years owing to higher precipitation, which increases the impact of storms, completely immersing smaller islands and eroding the habitat. Population maintenance in stochastically flooded occurrence sites might depend on the population density, dispersal capacity in the fragmented landscape and the spatiotemporal pattern of the occurrences of storms and flooding, but also on hypoxia tolerance.

Storms and hurricanes

Species respond in different ways to large-scale habitat modifications attributable to storms and hurricanes with respect to population density, absolute spatial variability or relative spatial variability (Bloch and Willig, 2006). Storms can change the pattern of spatial organization of the gastropod community through cross-scale interactions between local species demographics and human-shaped landscape configuration of patches (Willig *et al.*, 2007). In tropical forests, gaps in the canopy triggered by hurricanes are thought to enhance mortality of gastropods by desiccation stress, mostly affecting eggs and young stages. At the same time, the deposition of organic matter on the soil provides supplementary food resources and humid microhabitat. In two endangered

Hawaiian tree species, *Achatinella mustelina* and *Achatinella sowerbyana*, between-tree movements might be mostly passive, occurring during violent wind storms (Hall and Hadfield, 2009). This results in heterogeneous responses of species, with some being favoured by such events in contrast to others, and some exhibiting variable trends (Bloch and Willig, 2006).

In the case of the endangered species *T. ceratina*, climate change increased wind speed and changed wind direction at the locality, thereby allowing storms that erode the coastal habitat at an increasing frequency (Charrier *et al.*, 2013). The highest abundance of the species was measured on the marine terrace ridge immediately behind the beach, probably related to the vegetation community providing food and shelter. Parts of the ridge are eroded by storms, thereby affecting the population size. Retreat to lower parts of the sand savannah behind the dunes, which are usually not affected by storms, seems to be negated by the presence of a lower gravel-soil layer in the sand. This layer originates from the construction of the urban zone bordering the habitat and interferes with deep burrowing behaviour (up to 50 cm deep) related to dormancy periods.

Fire

Fire can result from long droughts that might increase in frequency and duration, especially in Mediterranean to continental and temperate climate. Fire can directly affect the survival of terrestrial gastropods (Nekola, 2002; Bros *et al.*, 2011) or indirectly by reducing the wood, litter and mulch layer on the soil surface (Bellido, 1987). Fire reduces and modifies organic substrates and residues that are sources of nutrients, buffering and sheltering; it changes microclimate, such as heating of bare soil and increasing soil evaporation (reviewed by Saestedt and Ramundo, 1990; Knapp *et al.*, 2009). In the tall grass prairie in Manitoba, the gastropod community was impoverished a few years after fire; unburned prairie hosted more aquatic and terrestrial species than burned prairie (unpublished data A.N.). In Mediterranean regions, Santos *et al.* (2009) showed that 4 years after the perturbation, the gastropod community was dominated by xerophilous species, whereas forest species dominated in unburned sites. Recolonization of burnt patches by terrestrial gastropods depends on their survival in microsites within the habitat (Kiss and Magnin, 2003, 2006). Severely burnt patches display a higher pH, possibly attractive to gastropods (Hylander, 2011). Post-fire management can increase post-fire survival by restoring the humus-litter layer and providing moist microhabitat (Bros *et al.*, 2011). Even if resilience of gastropod communities to fire events is high, a long time is required to return to the initial state (Kiss and Magnin, 2006), whatever the post-fire management type (see Bros *et al.*, 2011). It is expected that an increased frequency of fire and a loss of microsites as refugia within the habitat, triggered by the combined effect of climate change and human impact, will weaken their sustainability and consequently affect litter decomposition and nutrient cycling.

Habitat loss and fragmentation

Interacting with human-driven changes in land use, climate change is expected to affect landscape structure (Opdam and Wascher, 2004; Vos *et al.*, 2008). Habitat loss and habitat fragmentation are two distinct processes, even though they are often confounded in experimental and field studies, because they generally occur together (McGarigal and Cushman, 2002; Fahrig, 2003). Habitat loss generally has a negative effect on biodiversity, directly by impacting species richness, population abundance, species distribution and genetic diversity, and indirectly by affecting species interactions and population growth rate (for a review, see Fahrig, 2003).

Few examples document the effect of climate change-induced habitat loss on gastropod species, independently of fragmentation. In Lake Erie islands (North America), habitat loss results from the disruption of natural erosion–deposition cycles owing to changes in the frequency and intensity of precipitation and storms and to the human activity of sand mining. This disruption affects the habitat of the endangered species *Allogona profunda* (COSEWIC, 2014). A comparable situation is described for the Corsica snail *T. ceratina* (see section ‘Storms and hurricanes’; Charrier *et al.*, 2013).

Habitat loss can drive species to occupy suboptimal patches, leading to reduced fitness. For example, a change in resource availability, and thereby energy and types of nutrients provided, can impact reproduction and egg quality in *C. aspersum* (Nicolai *et al.*, 2012b), such as egg shell thickness, which can also lead to secondary effects on heat tolerance (Nicolai *et al.*, 2013).

Models have highlighted the existence of an extinction threshold in habitat availability, below which the population size does not allow its maintenance (e.g. Flather and Bevers, 2002). Moreover, the existence of such a threshold has also been theoretically highlighted for the fixation time of selectively neutral genotypes by genetic drift (Ezard and Travis, 2006). Both thresholds are affected by habitat shape and spatial correlation (Ezard and Travis, 2006), supporting the necessity to study habitat loss and fragmentation simultaneously when considering the impact of climate change on local populations.

The consequences of fragmentation *per se* are more diverse and less clear than those of habitat loss (Robinson *et al.*, 1992; Harrison and Bruna, 1999), with negative impacts involving a reduction of the population size, edge effects and reduced flow between patches, intensifying isolation, thereby decreasing genetic diversity and increasing inbreeding rate, leading eventually to the extinction of local population (Fahrig, 2003 and references therein). Positive impacts of habitat fragmentation on population maintenance have also been demonstrated, such as the persistence of inter-specific interactions (predator–prey relationship, competition); heterogeneity of patch conditions can also avoid simultaneous extinction of a whole population (Fahrig, 2003). Moreover, the matrix quality can considerably

influence the impact of habitat fragmentation on biodiversity (Franklin and Lindenmayer, 2009). Taxa with low mobility, such as terrestrial gastropods, are supposed to be particularly sensitive to habitat fragmentation. Although dispersal in minute gastropods is mainly passive (wind, water, animal, mainly birds and human transport; e.g. Dörge *et al.*, 1999; Aubry *et al.*, 2006; Özgo *et al.*, 2015; Simonová *et al.*, 2016), active dispersal is expected to play an important role at a local scale (Aubry *et al.*, 2006). Active dispersal is known to be a highly variable trait, within and among populations, as a response to cost–benefit balance, depending on the species traits and environmental context and with potential consequences on population dynamics (Bonte *et al.*, 2012; Clobert *et al.*, 2012). This variability of active dispersal depends on climatic conditions (Hall and Hadfield, 2009; Dahirel *et al.*, 2014), species (see Kramarenko, 2014 and references therein) and individual size (Baur and Baur, 1988; Honek and Martinkova, 2011), age and/or reproductive status (Tomiyama and Nakane, 1993; Dahirel *et al.*, 2014) and habitat exploitation (sedentary vs. nomadic species, Murphy, 2002; Edworthy *et al.*, 2012; specialist vs. generalist species, Kappes *et al.*, 2009; Dahirel *et al.*, 2015). As an illustration, in the minute European land snail *Punctum pygmaeum* (shell breadth approximately 1.2–1.5 mm), the mean distance travelled over a 12 h period is 47 mm (Baur and Baur, 1988), whereas in the large Australian *Hedleyella falconeri* (shell breadth approximately 90–100 mm), individuals moved 9 m on average per night (Murphy, 2002), and in the endangered *Allogona townsendiana*, displacement during 3 years was 32.2 m (Edworthy *et al.*, 2012).

Fragmentation can alter gastropod dispersal cost in two ways: directly, as the cost for crossing hostile matrix is increased, and indirectly, as movements of vector species, such as mammals, can also be affected by landscape structure changes (Kappes *et al.*, 2009). Moreover, alteration of the habitat and its consequences (reduced resources, higher density, microclimatic changes and community modification) can modify the dispersal behaviour of species. In general, fragmentation is negatively correlated with emigration propensity (Bonte *et al.*, 2006; Schtickzelle *et al.*, 2006). If a boundary-crossing avoidance behaviour has effectively been observed in gastropods (Baur and Baur, 1988; Giokas and Mylonas, 2004), in some species, such as the brown garden snail *C. aspersum*, exploration increased with higher fragmentation on an urbanization gradient (Dahirel *et al.*, 2016). In the endangered Canadian species *A. townsendiana*, the individual home-range area was highly variable (from 18.4 to 404.4 m²), depending on habitat quality; in habitats where stinging nettle (food source and shelter) and coarse woody debris (reproduction sites) were present, the home range was significantly smaller (Edworthy *et al.*, 2012). In a comparative analysis (20 European Helicoidea species), Dahirel *et al.* (2015) showed that several traits linked to mobility were phylogenetically constrained (e.g. locomotion speed), whereas others were independent of phylogeny (e.g. exploration propensity, path sinuosity).

Several field or experimental studies gave interesting insights into the consequences of fragmentation for gastropod species. In small conservation forests, litter mollusc species assemblages depended not only on local environmental variables but also on surrounding landscapes, with open fields having a negative impact on species richness and composition (Götmark *et al.*, 2008), somehow counterbalancing the conclusion from Cameron and Pokryszko (2004); gastropod faunas can survive in very small fragments of suitable habitat. Moreover, connectivity of habitat patches has been shown to be important for maintaining a diversity of taxa with low dispersal ability, such as gastropods (Knop *et al.*, 2011). In an experimentally fragmented grassland, a 3 year survey of six land snail species allowed the demonstration of a significant impact of fragmentation on all species, but with specific differences in population size reduction, extinction rate and recolonization probability (Stoll *et al.*, 2009). Species with a larger body (more mobile), longer activity period and short generation time were less susceptible to fragmentation. The fragment size was negatively correlated with the extinction rate and positively correlated with the recolonization probability, highlighting the importance of edge effects, affecting both the composition of vegetation and microclimatic conditions on the edge zone (Stoll *et al.*, 2009). In the same experimental system, the reduced density of herbivores (mainly gastropods) and the vegetation shifts in the fragments decreased the grazing intensity to *Trifolium repens* seedlings, thereby amplifying the modification of the habitat quality (Ledergerber *et al.*, 2002). In deciduous forests, fragmentation affected more forest-specialized than euryecious and matrix species, with main effects being generated by edge effects on environmental conditions (Kappes *et al.*, 2009).

Facing rapid changes of their habitat, some species have proved a high evolvability of some traits, such as *C. nemoralis*. In the British Isles and The Netherlands, large-scale habitat changes (opening and warming) triggered a rapid adaptive change in shell morph frequencies; lighter and unbanded shells were more frequent, which could be advantageous against insolation and predators compared with darker and banded shells (Ozgo and Schilthuizen, 2012; Cameron and Cook, 2013; Schilthuizen, 2013). Responses to habitat loss and fragmentation appear then as an idiosyncratic trait, highlighting the necessity to conduct studies at the population level. Fast adaptation might confer some ability to maintain a population in unstable and rapidly changing habitat for some species (Ozgo, 2011), but it remains difficult, if not impossible, to generalize responses.

Perspectives

Molluscs are the taxon with the highest number of extinctions; 42% of the 693 recorded extinctions of animal species since the year 1500 were molluscs, and 99% of them were terrestrial and freshwater species (Lydeard *et al.*, 2004). As a result of a general bias in both public and scientific interest

for vertebrate extinctions, the conservation status of gastropod species is poorly known and biodiversity management generally not intended to promote their maintenance (Régnier *et al.*, 2008, 2015).

To understand how a species will be affected by climate change, we need to know responses at different organizational levels: species-specific physiological and behavioural processes, population responses and distribution of species in the climatic heterogeneous landscape. In most endangered gastropods, studies are scarce and sensitivity traits (physiological and behavioural) and their evolvability unknown. Without this knowledge, we are unable to assess species' status that will be the basis for species' recovery strategies, integrated in conservation strategies of ecosystems.

Experimental manipulation of environmental conditions in the field (temperature and/or rainfall; Sternberg, 2000) or in climate chambers (temperature and/or CO₂; Bezemer and Knight, 2001) has confirmed the difficulty in drawing a general picture of organisms' responses. In general, physiological studies, involving metabolomic fingerprinting, survival or performance analysis in different climatic conditions (methods used in studies of Table 1; for more, see Madliger and Love, 2015), are highly invasive, making them unsuitable for endangered and protected species. As numerous physiological processes are phylogenetically constrained, an ideal situation would be to approximate the responses of endangered species by those of a common, phylogenetically close species. However, our example of cold tolerance in three Helicidae species showed that they differ in life-history strategy, behavioural responses and physiological processes. Therefore, species-specific studies at the population level and the development of non-invasive methods (e.g. heart rate to measure thermal performance; Marshall and McQuaid, 2011; Han *et al.*, 2013) are required to understand the physiological responses to climate change of rare and endangered species.

Habitat alteration drives species to migrate to suitable habitat. Given that most of the critically endangered species are on islands (Fig. 1 and, e.g. COSEWIC, 2014, in press), habitat is limited. Moreover, human-driven habitat loss and fragmentation through intensified urbanization, agriculture and forestry, dramatically increases the impact of climate change at the population level. Especially for endangered species, living in restricted habitat (such as protected areas or habitat remnants), dispersal or migration being largely negated by habitat loss and fragmentation, studies on the impact of habitat alteration are still scarce, but greatly needed.

Recently, several authors pointed to the necessity of integrating physiological and behavioural traits in an interacting environment to avoid false predictions (Helmuth, 2009; Kearney *et al.*, 2009; Chapperton and Seuront, 2011; Huey *et al.*, 2012; Twomey *et al.*, 2012). Historical impacts of climate change and anthropogenic pressure on population size

or on habitat structure combined with density-dependant population maintenance processes, such as reproduction and dispersal, should be considered to develop dynamic conservation models in changing landscape. Providing a thermally heterogeneous landscape may be a key component of conservation of terrestrial species under climate change. However, the complexity of the thermal landscape as perceived by an organism is difficult to infer from average temperatures recorded by weather stations, so many studies are simplified to take only one landscape factor into account, e.g. topography (Sears *et al.*, 2011). Anthropogenic activity influences these landscape parameters, but is often largely ignored in large-scale models. The link between habitat choice and physiology is poorly known for all but a few species (Angilletta, 2009). Genetic diversity, phenotypic plasticity and evolvability of traits seem to be essential elements to a complete understanding of how a species will face climate change (Marshall *et al.*, 2010; Donnelly *et al.*, 2012; Huey *et al.*, 2012; Merilä and Hendry, 2014; Schilthuizen and Kellermann, 2014). Integrative approaches should consider spatiotemporal heterogeneity of climate at local scales over a species' range and the capacity of species to respond to climate variations through plasticity of traits or adaptation.

Understanding the spatiotemporal effect of climate change on gastropod species would require a precise knowledge of specific physiological processes, behavioural responses and their plasticity in combination with genetic adaptation at different organizational scales, from individual to species. This objective seems reachable for some well-studied model species, such as the brown garden snail *C. aspersum* or the grove snail *C. nemoralis*, with a panel of studies conducted worldwide, from phylogeographic history (e.g. Davison and Clarke, 2000; Guiller *et al.*, 2012) to physiological (see Table 1) and behavioural traits (e.g. Jaremovic and Rollo, 1979; Dahirel *et al.*, 2014). Extrapolation to other species, particularly to endangered ones, remains limited, and a minimal knowledge of basic physiological processes in species at risk is urgently needed to determine adequate conservation strategies.

In parallel, as most terrestrial gastropods are part of a diverse mulch and litter community that is essential in all ecosystems to ensure soil fertility (Swift *et al.*, 1979), it is necessary to develop a functional approach to understand the effect of climate change in the soil system. The need for the preservation of soil functions, via the conservation of species in the litter community and the ecosystems they occupy, is still too often underestimated.

Acknowledgements

We thank the reviewers, particularly T. A. Pearce, for their constructive comments, and Valérie Briand, University Rennes 1, for her help with the literature search.

References

- Amla H (2014) Living to fight another day – “extinct” Aldabra snail re-discovered in Seychelles. Seychelles News Agency, August 30, Category Environment-Species, <http://www.seychellesnewsagency.com/articles/1256/Living+to+fight+another+day++extinct+Aldabra+snail+re-discovered+in+Seychelles>.
- Angilletta MJ (2009) *Thermal Adaptation: a Theoretical and Empirical Synthesis*. Oxford University Press Inc., New York.
- Ansart A, Vernon P (2004) Cold hardiness abilities vary with the size of the land snail *Cornu aspersum*. *Comp Biochem Physiol A Mol Integr Physiol* 139: 205–211.
- Ansart A, Vernon P, Daguzan J (2001) Freezing tolerance versus freezing susceptibility in the land snail *Helix aspersa* (Gastropoda: Helicidae). *Cryo Letters* 22: 183–190.
- Ansart A, Vernon P, Daguzan J (2002) Elements of cold hardiness in a littoral population of the land snail *Helix aspersa* (Gastropoda, Pulmonata). *J Comp Physiol B* 172: 619–625.
- Ansart A, Madec L, Guiller A (2009) Cabi invasive species compendium: *Cornu aspersum* (common snail). <http://www.cabi.org/isc/datasheet/26821>.
- Ansart A, Nicolai A, Vernon P, Madec L (2010) Do ice nucleating agents limit the supercooling ability of the land snail *Cornu aspersum*? *Cryo Letters* 31: 329–340.
- Ansart A, Guiller A, Moine O, Martin M-C, Madec L (2014) Is cold hardiness size-constrained? A comparative approach in land snails. *Evol Ecol* 28: 471–493.
- Arad Z, Goldenberg S, Heller J (1995) Water balance and resistance to desiccation in rock-dwelling snails. *Int J Biometeorol* 38: 78–83.
- Aubry S, Labaune C, Magnin F, Roche P, Kiss L (2006) Active and passive dispersal of an invading land snail in mediterranean France. *J Anim Ecol* 75: 802–813.
- Augsburger CK (2013) Reconstructing patterns of temperature, phenology, and frost damage over 124 years: spring damage risk is increasing. *Ecology* 94: 41–50.
- Bailey SER (1975) The seasonal and daily patterns of locomotor activity in the snail *Helix aspersa* Müller, and their relation to environmental variables. *J Mollus Stud* 41: 415–428.
- Bailey SER (1981) Circannual and circadian rhythms in the snail *Helix aspersa* Müller and the photoperiodic control of annual activity and reproduction. *J Comp Physiol* 142: 89–94.
- Bailey SER, Lazaridou-Dimitriadou M (1991) Inverse temperature acclimation of heart rate in hibernating land snails. *J Comp Physiol* 160B: 677–681.
- Bale JS, Hayward SAL (2010) Insect overwintering in a changing climate. *J Exp Biol* 213: 980–994.
- Bale JS, Walters KFA (2001) Overwintering biology as a guide to the establishment potential of non-native arthropods in the UK. In D

- Atkinson, M Thorndyke, eds, *Environment and Animal Development: Genes, Life Histories and Plasticity*. BIOS Scientific Publishers Ltd, Oxford, pp 343–354.
- Barker GM (2002) *Molluscs as Crop Pests*. CABI Publishing, Wallingford.
- Baur A, Baur B (1988) Individual movement patterns of the minute land snail *Punctum pygmaeum* (Draparnaud) (Pulmonata: Endodontidae). *Veliger* 30: 372–376.
- Baur A, Baur B (1991) The effect of hibernation position on winter survival of the rock-dwelling land snails *Chondrina clienta* and *Balea perversa* on Öland, Sweden. *J Mollus Stud* 57: 331–336.
- Baur B, Baur A (1993) Climatic warming due to thermal radiation from an urban area as possible cause for the local extinction of a land snail. *J Appl Ecol* 30: 333–340.
- Baur B, Baur A (2013) Snails keep the pace: shift in upper elevation limit on mountain slopes as a response to climate warming. *Can J Zool* 91: 596–599.
- Baur B, Meier T, Baur A, Schmera D (2014) Terrestrial gastropod diversity in an alpine region: disentangling effects of elevation, area, geometric constraints, habitat type and land-use intensity. *Ecography* 37: 390–401.
- Bellido A (1987) Field experiment about direct effect of a heathland prescribed fire on microarthropod community. *Revue Ecologie et Biologie du Sol* 24: 603–633.
- Beltramino AA, Vogler RE, Gutiérrez Gregoric DE, Rumi A (2015) Impact of climate change on the distribution of a giant land snail from South America: predicting future trends for setting conservation priorities on native malacofauna. *Clim Change* 131: 621–633.
- Bezemer TM, Knight KJ (2001) Unpredictable responses of garden snail (*Helix aspersa*) populations to climate change. *Acta Oecol* 22: 201–208.
- Biannic M, Daguzan J (1993) Cold-hardiness and freezing in the land snail *Helix aspersa* Müller (Gastropoda, Pulmonata). *Comp Biochem Physiol A* 104: 503–506.
- Bloch CP, Willig MR (2006) Context-dependence of long-term responses of terrestrial gastropod populations to large-scale disturbance. *J Tropical Ecol* 22: 111–122.
- Block W (2003) Water or ice? - The challenge for invertebrate cold survival. *Sci Prog* 86: 77–101.
- Bonnefoy-Claudet R, Deray A (1984) Influence de la durée d'hibernation sur l'activité reproductrice de l'escargot *Helix aspersa* Müller. *Comptes Rendus des Séances de la Société de Biologie et de ses Filiales* 178: 442–449.
- Bonte D, Borre JV, Lens L, Maelfait J-P (2006) Geographical variation in wolf spider dispersal behaviour is related to landscape structure. *Anim Behav* 72: 655–662.
- Bonte D, Van Dyck H, Bullock JM, Coulon A, Delgado M, Gibbs M, Lehouck V, Matthysen E, Mustin K, Saastamoinen M et al. (2012) Costs of dispersal. *Biol Rev* 87: 290–312.
- Bros V, Moreno-Rueda G, Santos X (2011) Does postfire management affect the recovery of Mediterranean communities? The case study of terrestrial gastropods. *For Ecol Manage* 261: 611–619.
- Cameron RAD (1970) The effect of temperature on the activity of three species of helixid snail (Mollusca: Gastropoda). *J Zool* 162: 303–315.
- Cameron RAD, Cook LM (2013) Temporal morph frequency changes in sand-dune populations of *Cepaea nemoralis* (L.). *Biol J Linnean Soc* 108: 315–322.
- Cameron RAD, Pokryszko BM (2004) Land mollusc faunas of Białowieża forest (Poland), and the character and survival of forest faunas in the north European plain. *J Mollus Stud* 70: 149–164.
- Carney WP (1966) Mortality and aperture orientation in *Allogona ptychophora* during winter hibernation in Montana. *Nautilus*, 79: 134–136.
- Čejka T, Horsák M, Nemethová D (2008) The composition and richness of Danubian floodplain forest land snail faunas in relation to forest type and flood frequency. *J Mollus Stud* 74: 37–45.
- Chang HW (1991) Activity and weight loss in relation to solar radiation in the polymorphic land snail *Cepaea nemoralis*. *J Zool* 225: 213–225.
- Chang H-W, Emlen JM (1993) Seasonal variation of microhabitat distribution of the polymorphic land snail *Cepaea nemoralis*. *Oecologia* 93: 501–507.
- Chappon C, Seuront L (2011) Space-time variability in environmental thermal properties and snail thermoregulatory behavior. *Funct Ecol* 25: 1040–1050.
- Charrier M, Nicolai A, Dabard M-P, Crave A (2013) Plan National d'Action en faveur d'Hélix de Corse *Tyrrhenaria ceratina*. Ministère de l'Écologie, du Développement Durable et de l'Énergie, Paris, France, 91 pp.
- Chown SL, Hoffmann AA, Kristensen TN, Angilletta MJ Jr, Stenseth NC, Pertoldi C (2010) Adapting to climate change: a perspective from evolutionary physiology. *Clim Res* 43: 3–15.
- Churchfield S (1984) Dietary separation in three species of shrew inhabiting water-cress beds. *J Zool* 204: 211–228.
- Clobert J, Baguette M, Benton TG, Bullock JM (2012). *Dispersal Ecology and Evolution*. Oxford University Press, Oxford, UK.
- Cook A, Radford DJ (1988) The comparative ecology of four sympatric limacid slug species in Northern Ireland. *Malacologia* 28: 131–146.
- Cook RT (2004) The tolerance of the field slug *Deroceras reticulatum* to freezing temperatures. *Cryo Letters* 25: 187–194.
- COSEWIC (Committee on the Status of Endangered Wildlife in Canada) (2014) Writers: Foster R, Alan H, Oldham MJ, Nicolai A. Status Report on the Broad-banded Forestsnail *Allogona profunda*. Committee on the Status of Endangered Wildlife in Canada, Ottawa, xi + 53 pp.

- COSEWIC (Committee on the Status of Endangered Wildlife in Canada) (in press) Writers: Nicolai A, Ovaska K. Status Report on the Banded Tigersnail *Anguispira kochi*. Committee on the Status of Endangered Wildlife in Canada, Ottawa.
- Cowie RH (2011) Snails and slugs. In D Simberloff, M Rejmanek, eds. *Encyclopedia of Biological Invasions*. University of California Press, Berkeley, pp 634–643.
- Cowie RH, Dillon RT, Robinson DG, Smith JW (2009) Alien non-marine snails and slugs of priority quarantine importance in the United States: a preliminary risk assessment. *Am Malacol Bull* 27: 113–132.
- Crook SJ (1980) Studies on the ecological genetics in *Helix aspersa* Müller. PhD thesis, University of Manchester, Manchester, UK.
- Dahirel M, Ansart A, Madec L (2014) Stage- and weather-dependent dispersal in the brown garden snail *Cornu aspersum*. *Popul Ecol* 56: 227–237.
- Dahirel M, Olivier E, Guiller A, Martin M-C, Madec L, Ansart A (2015) Movement propensity and ability correlate with ecological specialization in European land snails: comparative analysis of a dispersal syndrome. *J Anim Ecol* 84: 228–238.
- Dahirel M, Séguret A, Ansart A, Madec L (2016) Dispersal-related traits of the snail *Cornu aspersum* along an urbanisation gradient: maintenance of mobility across life stages despite high costs. *Urban Ecosyst* 19: 1–13.
- Dahl A, Klemm M, Weis M (1993). *Untersuchung der Land-Gehäusaueschnecken im Rahmen des Pflege- und Entwicklungsplanes für die Fischerhuder Wümmeniederung*. Report for Biologische Station im Kreis Osterholz (BIOS), Tübingen, Germany.
- Davison A, Clarke B (2000) History or current selection? A molecular analysis of area effects in the land snail *Cepaea nemoralis*. *Proc Biol Sci* 267: 1399–1405.
- Denny M (1980) Locomotion: the cost of gastropod crawling. *Science* 208: 1288–1290.
- Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *Proc Natl Acad Sci USA* 105: 6668–6672.
- Dillon ME, Wang G, Huey RB (2010) Global metabolic impacts of recent climate warming. *Nature* 467: 704–707.
- Dittbrenner N, Lazzara R, Köhler H-R, Mazzia C, Capowiez Y, Triebkorn R (2009) Heat tolerance in Mediterranean land snails: histopathology after exposure to different temperature regimes. *J Mollus Stud* 75: 9–18.
- Donnelly A, Caffarra A, Kelleher CT, O'Neill BF, Diskin E, Pletsers A, Proctor H, Stirnemann R, O'Halloran J, Peñuelas J et al. (2012) Surviving in a warmer world: environmental and genetic responses. *Clim Res* 53: 245–262.
- Dörge N, Walther C, Beinlich B, Plachter H (1999) The significance of passive transport for dispersal in terrestrial snails (Gastropoda, Pulmonata). *Zeitschrift für Ökologie und Naturschutz* 8: 1–10.
- Edworthy AB, Steensma KMM, Zandberg HM, Lilley PL (2012) Dispersal, home-range size, and habitat use of an endangered land snail, the Oregon forestsnail (*Allogona townsendiana*). *Can J Zool* 90: 875–884.
- Evans TG, Diamond SE, Kelly MW (2015) Mechanistic species distribution modelling as a link between physiology and conservation. *Conserv Physiol* 3: cov056; doi:10.1093/conphys/cov056.
- Ezard THG, Travis MJM (2006) The impact of habitat loss and fragmentation on genetic drift and fixation time. *Oikos* 114: 367–375.
- Fabina NS, Abbott KC, Gilman RT (2010) Sensitivity of plant–pollinator–herbivore communities to changes in phenology. *Ecol Model* 221: 453–458.
- Fahrig L (2003) Effects of habitat fragmentation on biodiversity. *Ann Rev Ecol Syst* 34: 487–515.
- Flather CH, Bevers M (2002) Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. *Am Nat* 159: 40–56.
- Forsyth RG, Oldham MJ (2016) Terrestrial molluscs from the Ontario far north. *Check List* 12: 1881.
- Franke TG (1985) Winter adaptations of a land snail, *Triodopsis multilineata* (Gastropoda, Polygyridae). 22nd annual meeting abstracts, *Cryobiology*, 22: 606
- Franklin JF, Lindenmayer DB (2009) Importance of matrix habitats in maintaining biological diversity. *Proc Natl Acad Sci USA* 106: 349–350.
- Frest TJ, Johannes EJ (1995) Interior Columbia Basin mollusk species of special concern. Deixis Consultants, Seattle, WA. Prepared for the US Department of Agriculture, Forest Service; US Department of the Interior, Bureau of Land Management, Upper Columbia River Basin Ecosystem Management Project. 274 pp + appendices.
- Gaitan-Espitia JD, Arias MB, Lardies MA, Nespolo RF (2013) Variation in thermal sensitivity and thermal tolerances in an invasive species across a climatic gradient: lessons from the land snail *Cornu aspersum*. *PLoS One* 8: e70662.
- Gerlach J (2007) Short-term climate change and the extinction of the snail *Rhachistia aldabrae* (Gastropoda: Pulmonata). *Biol Lett* 3: 581–584.
- Gibson SY, Van der Marel RC, Starzomski BM (2009) Climate change and conservation of leading-edge peripheral populations. *Conserv Biol* 23: 1369–1373.
- Gillooly JF, Brown JH, West GB, Savage VM, Charnov EL (2001) Effects of size and temperature on metabolic rate. *Science* 293: 2248–2251.
- Giokas S, Mylonas M (2004) Dispersal patterns and population structure of the land snail *Albinaria caerulea* (Pulmonata, Clausiliidae). *J Molluscan Stud* 70: 107–116
- Giokas S, Pafilis P, Valakos E (2005) Ecological and physiological adaptations of the land snail *Albinaria caerulea* (Pulmonata: Clausiliidae). *J Mollus Stud* 71: 15–23.

- Gomot P, Gomot L (1991) Length of hibernation and the brain's influence on temperature-induced spermatogenic DNA synthesis in *Helix aspersa*. *Comp Biochem Physiol A* 100: 689–692.
- Goodfriend GA (1992) The use of land snail shells in paleoenvironmental reconstruction. *Quat Sci Rev* 11: 665–685.
- Götmark F, Von Proschwitz T, Franc N (2008) Are small sedentary species affected by habitat fragmentation? Local vs. landscape factors predicting species richness and composition of land molluscs in Swedish conservation forests. *J Biogeogr* 35: 1062–1076.
- Graeff-Teixeira C (2007) Expansion of *Achatina fulica* in Brazil and potential increased risk for angiostrongyliasis. *Trans R Soc Trop Med Hyg* 101: 743–744.
- Grimm FW, Forsyth RG, Schueler FW, Karstad A (2009) *Identifying Land Snails and Slugs in Canada: Introduced Species and Native Genera*. Canadian Food Inspection Agency, Ottawa, 168 pp.
- Guiller A, Martin M-C, Hiraux C, Madec L (2012) Tracing the invasion of the Mediterranean land snail *Cornu aspersum aspersum* becoming an agricultural and garden pest in areas recently introduced. *PLoS One* 7: e49674.
- Hall KT, Hadfield MG (2009) Application of harmonic radar technology to monitor tree snail dispersal. *Invertebr Biol* 128: 9–15.
- Han G-D, Zhang S, Marshall DJ, Ke C-H, Dong Y-W (2013) Metabolic energy sensors (AMPK and SIRT1), protein carbonylation and cardiac failure as biomarkers of thermal stress in an intertidal limpet: linking energetic allocation with environmental temperature during aerial emersion. *J Exp Biol* 216: 3273–3282.
- Harrison S, Bruna E (1999) Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography* 22: 225–232.
- Hausdorf B, Hennig C (2003) Nestedness of north-west European land snail ranges as a consequence of differential immigration from Pleistocene glacial refuges. *Oecologia* 135: 102–109.
- Heller J, Dolev A (1994) Biology and population dynamics of a crevice-dwelling land snail, *Cristataria genezarethana* (Clausiliidae). *J Mollus Stud* 60: 33–46.
- Heller J, Ittli H (1990) Natural history and population dynamics of the land snail *Helix texta* in Israel (Pulmonata: Helicidae). *J Mollus Stud* 56: 189–204.
- Helmuth B (2009) From cells to coastlines: how can we use physiology to forecast the impacts of climate change? *J Exp Biol* 212: 753–760.
- Hof AR (2011) European terrestrial gastropod distribution. How may climate change affect their diversity and current distribution. In AM Bianchi, JN Fields, eds, *Gastropods: Diversity, habitat and genetics*. Nova Science Publishers Inc., Hauppauge, USA, pp 165–182.
- Honek A, Martinkova Z (2011) Body size and the colonisation of cereal crops by the invasive slug *Arion lusitanicus*. *Ann Appl Biol* 158: 79–86.
- Horsák M, Chytrý M (2014) Unimodal latitudinal pattern of land-snail species richness across northern Eurasian lowlands. *PLoS One* 9: e104035.
- Horsák M, Chytrý M, Axmanová I (2013) Exceptionally poor land snail fauna of central Yakutia (NE Russia): climatic and habitat determinants of species richness. *Polar Biol* 36: 185–191.
- Huey RB, Kearney MR, Krockenberger A, Holtum JAM, Jess M, Williams SE (2012) Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Philos Trans R Soc Lond B Biol Sci* 367: 1665–1679.
- Hulme PE (1996) Herbivores and the performance of grassland plants: a comparison of arthropod, mollusc and rodent herbivory. *J Ecol* 84: 43–51.
- Hylander K (2011) The response of land snail assemblages below aspens to forest fire and clear-cutting in Fennoscandian boreal forests. *For Ecol Manage*, 261: 1811–1819
- Iglesias J, Santos M, Castillejo J (1996) Annual activity cycles of the land snail *Helix aspersa* Müller in natural populations in north western Spain. *J Mollus Stud* 62: 495–505.
- Ilg C, Foeckler F, Deichner O, Henle K (2009) Extreme flood events favour floodplain mollusc diversity. *Hydrobiologia* 321: 63–73.
- IUCN (2016) The IUCN Red List of Threatened Species. Version 2016-1. <http://www.iucnredlist.org>.
- Jaremovic R, Rollo D (1979) Tree climbing by the snail *Cepaea nemoralis* (L.): a possible method for regulating temperature and hydration. *Can J Zool* 57: 1010–1014.
- Jennings TJ, Barkham JP (1979) Litter decomposition by slugs in mixed deciduous woodland. *Holarct Ecol* 2: 21–29.
- Jeppesen LL (1977) Photoperiodic control of hibernation in *Helix pomatia* L. (Gastropoda; Pulmonata). *Behav Processes* 2: 373–382.
- Johnson MS (2011) Thirty-four years of climatic selection in the land snail *Theba pisana*. *Heredity* 106: 741–748.
- Johnson M, Black R (1991) Growth, survivorship, and population size in the land snail *Rhagada convicta* Cox, 1870 (Pulmonata: Camaenidae) from a semiarid environment in Western Australia. *J Mollus Stud* 57: 367–374.
- Jones JS (1982) Genetic differences in individual behaviour associated with shell polymorphism in the snail *Cepaea nemoralis*. *Nature* 298: 749–750.
- Kappes H, Jordaens K, Hendrickx F, Maelfait J-P, Lens L, Backeljau T (2009) Response of snails and slugs to fragmentation of lowland forests in NW Germany. *Landscape Ecol* 24: 685–697.
- Kavaliers M (1992) Opioid systems, behavioral thermoregulation and shell polymorphism in the land snail, *Cepaea nemoralis*. *J Comp Physiol B* 162: 172–178.
- Kearney M, Shine R, Porter WP (2009) The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *Proc Natl Acad Sci USA* 106: 3835–3840.
- Kerney MP, Cameron RAD (1999) *Guide des Escargots et Limaces d'Europe*. Delachaux et Niestlé, Paris, 370 pp.

- Kerney MP, Cameron RAD, Jungbluth JH (1983). Die Landschnecken Nord- und Mitteleuropas. Parey, Hamburg.
- Kiss L, Magnin F (2003) The impact of fire on some Mediterranean land snail communities and patterns of post-fire recolonization. *J Mollus Stud* 69: 43–53.
- Kiss L, Magnin F (2006) High resilience of Mediterranean land snail communities to wildfires. *Biodivers Conserv* 15: 2925–2944.
- Knapp EE, Estes BL, Skinner CE (2009) Ecological effects of prescribed fire season: a literature review and synthesis for managers. United States Department of Agriculture General Technical Report PSW-GTR-224, Washington, USA.
- Knop E, Herzog F, Schmid B (2011) Effect of connectivity between restoration meadows on invertebrates with contrasting dispersal abilities. *Restorat Ecol* 19: 151–159.
- Košťál V, Rozsypal J, Pavel P, Zahradníčková H, Šimek P (2013) Physiological and biochemical responses to cold and drought in the rock-dwelling pulmonate snail, *Chondrina avenacea*. *J Comp Physiol B* 183: 749–761.
- Kramarenko S (2014) Active and passive dispersal of terrestrial mollusks: a review. *Ruthenica* 24: 1–14.
- Lecompte O, Madec L (1998) Température et plasticité du chromatisme de la coquille chez le mollusque pulmoné *Helix aspersa*. *Comptes Rendus de l'Académie des Sciences – Series III – Sciences de la Vie* 321: 649–654.
- Ledergerber S, Dolt C, Zschokke S, Baur B (2002) Effects of experimental small-scale grassland fragmentation on the extent of grazing damage in *Trifolium repens* seedlings. *Acta Oecol* 23: 329–336.
- Lind H (1988) The behaviour of *Helix pomatia* in a natural habitat. *Videnskabelige meddelelser fra Dansk Naturhistorisk Forening* 147: 67–92.
- Livingstone DR (1991) Origins and evolution of pathways of anaerobic metabolism in the animal kingdom. *Am Zool* 31: 522–534.
- Lorvelec O, Daguzan J (1990) Etude, en conditions climatiques naturelles, de la variation saisonnière de l'activité locomotrice chez l'escargot *Helix aspersa* Müller. In Régulation des Cycles Saisonniers chez les Invertébrés, Les Colloques de l'INRA N°52, ed. INRA, Paris, France, pp 52–64.
- Lydeard C, Cowie RH, Ponder WF, Bogan AE, Bouchet P, Clark SA, Cummings KS, Frest TJ, Gargominy O, Herbert DG (2004) The global decline of nonmarine mollusks. *BioScience* 54: 321–330.
- McGarigal K, Cushman SA (2002) Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecol Appl* 12: 335–345.
- Machin J (1964) The evaporation of water from *Helix aspersa*. 1. The nature of the evaporative surface. *J Exp Biol* 41: 759–769.
- Madec L (1989). Etude de la différenciation de quelques populations géographiquement séparées de l'espèce *Helix aspersa* Müller (Mollusque Gastéropode Pulmoné): aspects morphologiques, ecophysiologiques et biochimiques. Thèse de Doctorat, Université Rennes 1, Rennes, France, 380 pp.
- Madliger CL, Love OP (2015) The power of physiology in changing landscapes: considerations for the continued integration of conservation and physiology. *Integr Comp Biol* 55: 545–553.
- Marshall DJ, McQuaid CD (2011) Warming reduces metabolic rate in marine snails: adaptation to fluctuating high temperatures challenges the metabolic theory of ecology. *Proc Biol Sci* 278: 281–288.
- Marshall DJ, McQuaid CD, Williams GA (2010) Non-climatic thermal adaptation: implications for species' responses to climate warming. *Biol Lett* 6: 669–673.
- Martin SM (2000) Terrestrial snails and slugs (Mollusca: Gastropoda) of Maine. *Northeast Nat* 7: 33–88.
- Mason CF (1970a) Food, feeding rates and assimilation in woodland snails. *Oecologia* 4: 358–373.
- Mason CF (1970b) Snail populations, beech litter production, and the role of snails in litter decomposition. *Oecologia* 5: 215–239.
- Meehl, GA, Stocker TF, Collins WD, Friedlingstein P, Gaye AT, Gregory JM, Kitoh A, Knutti R, Murphy JM, Noda A *et al.* (2007) Global climate projections. In S Solomon, D Qin, M Manning, Z Chen, M Marquis, KB Averyt, M Tignor, HL Miller, eds, *Climate Change 2007: the Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK and New York, NY, USA, pp 749–844.
- Merilä J, Hendry AP (2014) Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evol Appl* 7: 1–14.
- Minoretti N, Stoll P, Baur B (2013) Heritability of sperm length and adult shell size in the land snail *Arianta arbustorum* (Linnaeus, 1758). *J Mollus Stud* 79: 218–224.
- Müller J, Bässler C, Strätz C, Klöcking B, Brandl R (2009) Molluscs and climate warming in a low mountain range national park. *Malacologia* 51: 89–109.
- Murphy MJ (2002) Observations on the behaviour of the Australian land snail *Hedleyella falconeri* (Grey, 1834) (Pulmonata: Caryodidae) using the spool-and-line tracking technique. *Mollus Res* 22: 149–164.
- Nekola JC (2002) Effects of fire management on the richness and abundance of central North American grassland land snail faunas. *Anim Biodivers Conserv* 25: 53–66.
- Nekola JC, Barker GM, Cameron RAD, Pokryszko PM (2013) Latitudinal variation of body size in land snail populations and communities. In F Smith, K Lyons, eds, *Animal Body Size: Linking Pattern and Process across Space, Time and Taxonomic Group*. University of Chicago Press, Chicago, IL, USA, pp 62–82.
- Nicolai A, Vernon P, Lee M, Ansart A, Charrier M (2005) Supercooling ability in two populations of the land snail *Helix pomatia* (Gastropoda: Helicidae) and ice-nucleating activity of gut bacteria. *Cryobiology* 50: 48–57.

- Nicolai A, Filser J, Briand V, Charrier M (2010) Seasonally contrasting life history strategies in the land snail *Cornu aspersum*: physiological and ecological implications. *Can J Zool* 88: 995–1002.
- Nicolai A, Filser J, Lenz R, Bertrand C, Charrier M (2011) Adjustment of metabolite composition in the haemolymph to seasonal variations in the land snail *Helix pomatia*. *J Comp Physiol B* 181: 457–466.
- Nicolai A, Filser J, Lenz R, Bertrand C, Charrier M (2012a) Quantitative assessment of haemolymph metabolites in respect to the physiological state in two populations of the land snail *Helix pomatia*. *Physiol Biochem Zool* 85: 274–284.
- Nicolai A, Filser J, Lenz R, Briand V, Charrier M (2012b) The composition of body storage compounds influences egg quality and the reproductive investment in the land snail *Cornu aspersum*. *Can J Zool* 90: 1161–1170.
- Nicolai A, Vernon P, Lenz R, Le Lannic J, Briand V, Charrier M (2013) Well wrapped eggs: effects of egg shell structure on heat resistance and hatchling mass in the invasive land snail *Cornu aspersum*. *J Exp Zool A* 319: 63–73.
- Nicolai A, Rouland-Lefèvre C, Ansart A, Filser J, Lenz R, Pando A, Charrier M (2015) Seasonal dynamic of the bacterial gut community in three populations of the endangered land snail *Helix pomatia*. *Malacologia* 59: 177–190.
- Nietzke G (1970) *Die Weinbergschnecke*. 2. Auflage. Verlag Eugen Ulmer, Stuttgart.
- Nowakowska A, Rogalska J, Caputa M (2015) Adaptability of antioxidant defence system in *Helix pomatia* snails: effect of forced aestivation during early spring. *J Mollus Stud* 82: 205–207.
- Nyffeler M, Symondson WOP (2001) Spiders and harvestmen as gastropod predators. *Ecol Entomol* 26: 617–628.
- Oosterhoff LM (1977) Variation in growth rate as an ecological factor in the land snail *Cepaea nemoralis* (L.). *Neth J Zool* 27: 1–132.
- Opdam P, Wascher D (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biol Conserv* 117: 285–297.
- Ozgo M (2005) *Cepaea nemoralis* (L.) in southeastern Poland: association of morph frequencies with habitat. *J Mollus Stud* 71: 93–103.
- Ozgo M (2011) Rapid evolution in unstable habitats: a success story of the polymorphic land snail *Cepaea nemoralis*. *Biol J Linn Soc* 102: 251–262.
- Ozgo M, Schilthuizen M (2012) Evolutionary change in *Cepaea nemoralis* shell colour over 43 years. *Global Change Biol* 18: 74–81.
- Ozgo M, Örstan A, Kirschenstein M, Cameron R (2015) Dispersal of land snails by sea storms. *J Mollus Stud* 82: 341–343.
- Pakay JL, Withers PC, Hobbs AA, Guppy M (2002) In vivo downregulation of protein synthesis in the snail *Helix aspersa* during estivation. *Am J Physiol Regul Integr Comp Physiol* 283: R197–R204.
- Pearce TA, Paustian ME (2013) Are temperate land snails susceptible to climate change through reduced altitudinal ranges? A Pennsylvania example. *Am Malacol Bull* 31: 213–224.
- Peltanova A, Petrusek A, Kment P, Jurickova L (2012) A fast snail's pace: colonization of central Europe by Mediterranean gastropods. *Biol Invas* 14: 759–764.
- Peters HA (2007) The significance of small herbivores in structuring annual grassland. *J Veg Sci* 18: 175–182.
- Pfenninger M (2004) Comparative analysis of range sizes in Helicidae (Pulmonata, Gastropoda). *Evol Ecol Res* 6: 359–376.
- Pilsbry HA (1940) *Land Mollusca of North America (North of Mexico)*. Vol. I, Part 2. The Academy of Natural Sciences of Philadelphia, Monograph 3 (1113pp)
- Pilsbry HA (1948) *Land Mollusca of North America*. Vol II, Part 2. Wickersham Printing Company, Lancaster, pp XLVII + 521–1113.
- Pither J (2003) Climate tolerance and interspecific variation in geographic range size. *Proc Biol Sci* 270: 475–481.
- Plum N (2005) Terrestrial invertebrates in flooded grassland: a literature review. *Wetlands* 25: 721–737.
- Prather CM, Pelini SL, Laws A, Rivest E, Woltz M, Bloch CP, Del Toro I, Ho C-K, Kominoski J, Newbold TAS et al. (2013) Invertebrates, ecosystem services and climate change. *Biol Rev* 88: 327–348.
- Ramløv H (2000) Aspects of natural cold tolerance in ectothermic animals. *Hum Reprod* 15: 24–26.
- Raut SK, Ghose KC (1982) Viability of sperm in aestivating *Achatina fulica* Bodwich and *Macrochlamys indica* Godwin-Austen. *J Mollus Stud* 48: 84–86.
- Régnier C, Fontaine B, Bouchet P (2008) Not Knowing, not recording, not listing: numerous unnoticed mollusk extinctions. *Conserv Biol* 23: 1214–1221.
- Régnier C, Achaz G, Lambert A, Cowie RH, Bouchet P, Fontaine B (2015) Mass extinction in poorly known taxa. *Proc Natl Acad Sci USA* 112: 7761–7766.
- Richardson AMM (1974) Differential climatic selection in natural population of land snail *Cepaea nemoralis*. *Nature* 247: 572–573.
- Riddle WA (1981) Cold hardiness in the woodland snail, *Anguispira alternata* (Say) (Eendodontidae). *J Therm Biol* 6: 117–120.
- Riddle WA (1990) High temperature tolerance in three species of land snails. *J Therm Biol* 15: 119–124.
- Riddle WA, Miller VJ (1988) Cold-hardiness in several species of land snails. *J Therm Biol* 13: 163–167.
- Robertson JC, Hazel JR (1997) Membrane constraints to physiological function at different temperatures: does cholesterol stabilize membranes at elevated temperatures? In CM Woods, DG McDonald, eds, *Global Warming: Implications for Freshwater and Marine Fish*. Cambridge University Press, Cambridge, pp 25–49.

- Robinson GR, Holt RD, Gaines MS, Hamburg SP, Johnson ML, Fitch HS, Martinko EA (1992) Diverse and contrasting effects of habitat fragmentation. *Science* 257: 524–526.
- Rowley MA, Loker ES, Pagels JF, Montali RJ (1987) Terrestrial gastropod hosts of *Parelaphostrongylus tenuis* at the National Zoological Park's Conservation and Research Center, Virginia. *J Parasitol* 73: 1084–1089.
- Rowson B, Turner J, Anderson R, Symondson B (2014) *Slugs of Britain and Ireland*. FSC Publications, Telford, iv+136 pp.
- Saestedt TR, Ramundo RA (1990) The influence of fire on below-ground processes of tallgrass prairie. In SL Collins, LL Wallace, eds, *Fire in North American Tall Grass Prairies*. University of Oklahoma Press, Norman, pp 99–117.
- Salafsky N, Salzer D, Stattersfield AJ, Hilton-Taylor C, Neugarten R, Butchart SHM, Collen BEN, Cox N, Master LL, O'Connor S (2008) A standard lexicon for biodiversity conservation: unified classifications of threats and actions. *Conserv Biol* 22: 897–911.
- Santos X, Bros V, Miño À (2009) Recolonization of a burned Mediterranean area by terrestrial gastropods. *Biodivers Conserv* 18: 3153–3165.
- Scheil AE, Köhler H-R, Trieborsk R (2011) Heat tolerance and recovery in Mediterranean land snails after pre-exposure in the field. *J Mollus Stud* 77: 165–174.
- Schilthuizen M (2013) Rapid, habitat-related evolution of land snail colour morphs on reclaimed land. *Heredity* 110: 247–252.
- Schilthuizen M, Kellermann V (2014) Contemporary climate change and terrestrial invertebrates: evolutionary versus plastic changes. *Evol Appl* 7: 56–67.
- Schmera D, Baur B (2014) Gastropod communities in alpine grasslands are characterized by high beta diversity. *Commun Ecol* 15: 246–255.
- Schmid WD (1988) Supercooling and freezing in winter dormant animals. In RW Pfeifer, ed, *Tested Studies of Laboratory Teaching*. Proceedings of the 9th Workshop/Conference of the ABLE, 193–203.
- Schtickzelle N, Mennechez G, Baguette M, Mennechez G (2006) Dispersal depression with habitat fragmentation in the bog fritillary butterfly. *Ecology* 87: 1057–1065.
- Sears MW, Raskin E, Angilletta MJ (2011) The world is not flat: defining relevant thermal landscapes in the context of climate change. *Integr Comp Biol* 51: 666–675.
- Simonová J, Simon OP, Kapic S, Nehasil L, Horsák M (2016) Medium-sized forest snails survive passage through birds' digestive tract and adhere strongly to birds' legs: more evidence for passive dispersal mechanisms. *J Mollus Stud* 82: 422–426.
- Slotsbo S, Hansen LM, Jordaens K, Backeljau T, Malmendal A, Nielsen NC, Holmstrup M (2012) Cold tolerance and freeze-induced glucose accumulation in three terrestrial slugs. *Comp Biochem Physiol A Mol Integr Physiol* 161: 443–449.
- South A (1980) A technique for the assessment of predation by birds and mammals on the slug *Deroceras reticulatum* (Müller) (Pulmonata: Limacidae). *J Conchol* 30: 229–234.
- Staikou AE (1999) Shell temperature, activity and resistance to desiccation in the polymorphic land snail *Cepaea vindobonensis*. *J Mollus Stud* 65: 171–184.
- Starodubtseva e.g. Dedkov VP (2003) Возрастное распределение, выживаемость и смертность виноградной улитки *Helix pomatia* L. в экосистемах Калининградской области [The age distribution, survival and mortality of *Helix pomatia* L. in ecosystems of the Kaliningrad region]. Theoretical and Applied Aspects of Ecology: Jubilee collection of scientific papers, Kaliningrad State University, Kaliningrad, pp 121–132.
- Sternberg M (2000) Terrestrial gastropods and experimental climate change: a field study in a calcareous grassland. *Ecol Res* 15: 73–81.
- Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (2013) IPCC, 2013: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY, USA, 1535 pp.
- Stoll P, Oggier P, Baur B (2009) Population dynamics of six land snail species in experimentally fragmented grassland. *J Anim Ecol* 78: 236–246.
- Storey KB, Storey JM (1990) Metabolic rate depression and biochemical adaptation in anaerobiosis, hibernation and estivation. *Quat Rev Biol* 65: 145–174.
- Storey KB, Storey JM (2004) Metabolic rate depression in animals: transcriptional and translational controls. *Biol Rev* 79: 207–233.
- Storey KB, Storey JM, Churchill TA (2007) Freezing and anoxia tolerance of slugs: a metabolic perspective. *J Comp Physiol B* 177: 833–840.
- Stöver H (1973) Cold-resistance and freezing in *Arianta arborustorum* L. (Pulmonata). In W Wieser, ed, *Effects of Temperature on Ectothermic Animals*. Springer, Berlin, pp 281–290.
- Swift MJ, Heal OW, Anderson JM (1979) *Decomposition in Terrestrial Ecosystems*. Blackwell Scientific Publications, Oxford, UK.
- Terhivuo J (1978) Growth, reproduction and hibernation of *Arianta arbustorum* (L.) (Gastropoda, Helicidae) in southern Finland. *Ann Zool Fennici* 15: 8–16.
- Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger A, Hannah L et al. (2004) Extinction risk from climate change. *Nature* 427: 145–148.
- Thomas CD, Franco AMA, Hill JK (2006) Range retractions and extinction in the face of climate warming. *Trends Ecol Evol* 21: 415–416.
- Thompson JM, Appel AG, Sibley JL, Keever GJ, Foshee WG III (2006) Comparative water relations of three sympatric terrestrial slugs

- (Stylommatophora: Agriolimacidae, Limacidae and Philomycidae). *J Alabama Acad Sci* 77: 181–192.
- Tilling SM (1983) An experimental investigation of the behaviour and mortality of artificial and natural morphs of *Cepaea nemoralis* (L.). *Biol J Linn Soc* 19: 35–50.
- Tomiyama K, Nakane M (1993) Dispersal patterns of the giant african snail, *Achatina fulica* (Ferussac)(Stylommatophora: Achatinidae), equipped with a radio-transmitter. *J Mollus Stud* 59: 315–322.
- Troschinski S, Dieterich A, Kraus S, Triebkorn R, Köhler H-R (2014) Antioxidant defence and stress protein induction following heat stress in the Mediterranean snail *Xeropicta derbentina*. *J Exp Biol* 217: 4399–4405.
- Twomey M, Brodte E, Jacob U, Brose U, Crowe TP, Emmerson MC (2012) Idiosyncratic species effects confound size-based predictions of responses to climate change. *Philos Trans R Soc Lond B Biol Sci* 367: 2971–2978.
- Vos CC, Berry P, Opdam P, Baveco H, Nijhof B, O'Hanley J, Bell C, Kuipers H (2008) Adapting landscapes to climate change: examples of climate-proof ecosystem networks and priority adaptation zones. *J Appl Ecol* 45: 1722–1731.
- Welker AF, Moreira DC, Hermes-Lima M (2016) Roles of catalase and glutathione peroxidase in the tolerance of a pulmonate gastropod to anoxia and reoxygenation. *J Comp Physiol B* 186: 553–568.
- Welter-Schultes FW (2012) *European Non-Marine Molluscs, a Guide for Species Identification*. Planet Poster Editions, Göttingen, 679 pp.
- Wernegreen JJ (2012) Mutualism meltdown in insects: bacteria constrain thermal adaptation. *Curr Opin Microbiol* 15: 255–262.
- Willig MR, Bloch CP, Brokaw N, Higgins C, Thompson J, Zimmermann CR (2007) Cross-scale responses of biodiversity to hurricane and anthropogenic disturbance in a tropical forest. *Ecosystems* 10: 824–838.
- Willis JC, Bohan DA, Choi YH, Conrad KF, Semenov MA (2006) Use of an individual-based model to forecast the effect of climate change on the dynamics, abundance and geographical range of the pest slug *Deroceras reticulatum* in the UK. *Global Change Biol* 12: 1643–1657.
- Yom-Tov Y (1971) The biology of two desert snails *Trochoidea* (*Xerocrassa*) *seetzeni* and *Sphincterochila boissieri*. *Isr J Zool* 20: 231–248.
- Young AG, Port GR (1989) The effect of microclimate on slug activity in the field. In IF Henderson, ed, *Slugs and Snails in World Agriculture*. Vol 41, British Crop Protection Council Monograph, Alton, UK, pp 263–269.
- Zachariassen KE, Kristiansen E (2000) Ice nucleation and antinucleation in nature. *Cryobiology* 41: 257–279.