

In: Gastropods: Diversity, Habitat and Genetics ISBN: 978-1-61324-695-5
Editors: Andrea Bianchi and Jamie Fields ©2011 Nova Science Publishers, Inc.

Chapter 7

**EUROPEAN TERRESTRIAL GASTROPOD
DISTRIBUTION. HOW MAY CLIMATE
CHANGE AFFECT THEIR DIVERSITY AND
CURRENT DISTRIBUTION**

Anouschka R. Hof

Landscape Ecology Group, Department of Ecology and Environmental
Science, Umeå University, Umeå, Sweden

ABSTRACT

It is expected that ongoing climate change may have significant direct effects on the geographic distribution of species. Especially ectothermic species, such as terrestrial gastropods, may be affected considerably by alterations in temperature and precipitation regimes. In addition to these direct impacts, climate change can have a large impact on species communities and habitat structure as well. Since terrestrial gastropods are also sensitive to alterations in habitat structure and species interactions, it is expected that a further changing climate will affect terrestrial gastropods in ways difficult to anticipate.

While experimental studies are useful and necessary to predict the impact of a future warming climate on single species, predictive modelling approaches can provide us with a better understanding of the impact of climate change on a larger number of species, on a wider geographical scale. I used species distribution modelling to assess the geographic distribution of

nearly 100 terrestrial gastropods (order *Stylommatophora*) under emission scenarios A and B, of the HADCM3 projection, for the year 2080.

The results show that most terrestrial gastropods will likely shift their geographic distribution range north-eastwards. It is thus expected that the gastropod diversity in Fennoscandia and North-western Russia will increase, whilst species diversity in the Mediterranean regions is likely going to decrease. Predicted range shifts of terrestrial gastropods will alter regional species diversity and abundance, which can have far reaching consequences for agricultural management. In addition, predators of macro-invertebrate prey might be affected by changes in terrestrial gastropod abundances, which needs to be taken into account in conservation planning.

INTRODUCTION

Changes in the climate have led to shifts in species' distribution ranges in the past [Bennett, 1997; Parmesan *et al.*, 1999; Walther *et al.*, 2002], and may well have been the cause for a number of species extinctions and range contractions [Crowley & North, 1988; Pounds *et al.*, 1999]. Climate change has also been recognised as one of the main drivers behind possible future extinctions [Markham, 1996; Thomas *et al.*, 2004]. Indeed, species range contractions initiated by climate change are already occurring globally [Thomas *et al.*, 2006]. The predicted impact of climate change is thought to be large scale and capable of affecting entire ecosystems, since the geographic distribution of terrestrial ecosystems is mainly shaped by climatic factors such as temperature and precipitation [Woodward, 1987].

Especially ectothermic species, such as terrestrial gastropods, may be affected considerably by alterations in temperature and precipitation regimes [Deutsch *et al.*, 2008; Aragón *et al.*, 2010; Aubret & Shine, 2010]. Physiologically, ectotherms strongly depend on heterogeneity of the ambient temperature to regulate their body temperature [Deutsch *et al.*, 2008; Kearney *et al.*, 2009; Aubret & Shine, 2010]. In addition, the metabolic rate, growth, reproduction, and activity of ectotherms increase with temperature [Crawford-Sidebotham, 1972; Gillooly *et al.*, 2001]. It is therefore not surprising that it has been shown that the performance and abundance of gastropods may be affected by climate change. The abundance of land snails for instance, decreased due to higher temperatures according to a study by Baur & Baur [1993]. Elevated CO₂ levels on the other hand, did not seem to significantly affect snail abundance in a study by Ledergerber *et al.* [1997]. Besides that, it is well known that the activity and behaviour of slugs is related to weather conditions [Webley, 1964]. Higher

temperatures and more humidity will generally increase their activity [Crawford-Sidebotham, 1972]. Crawford-Sidebotham [1972] found for instance that an increase of 2°C in temperature, and an increase in relative humidity from 90% to 100%, led to a clear increase in the number of active slugs. In many cases, the number of active slugs doubled. Even the most conservative climate change scenarios predict an increase of around 2°C in large parts of Europe [IPCC, 2001]. This rise in temperature, together with the regionally predicted increase in precipitation, is thus likely to cause terrestrial ectotherms, like slugs and snails, to be more active in large parts of Europe than is momentarily the case. This consequently gives rise to concerns with regard to pest management in agricultural landscapes.

One way a species may respond to climate change is by adaptation to its new environmental circumstances [Davis & Shaw, 2001; Parmesan, 2006; Aubret & Shine, 2010]. Another way frequently adopted by species is by tracking their climatic envelope [Parmesan *et al.*, 1999; Parmesan, 2006], and it is therefore expected that ongoing climate change may have significant direct effects on the geographic distribution of species. Although many studies investigate the impact of future climate change on species distributions, the number of studies on terrestrial gastropods is limited. This is surprising since gastropods can become an economical pest, causing crop damage in agricultural landscapes [e.g. Glen *et al.*, 1990; Frank, 1998; Barker, 2002]. For economical reasons it is important to know in which regions the number of agricultural pest species might increase or decrease. It is further highly valuable to get a better understanding of future species distributions for the purpose of nature conservation.

In addition to possible shifts in species' distribution ranges following changing temperature and precipitation regimes, climate change can have a large impact on species communities and habitat structure. Next to the sensitivity of terrestrial gastropods to weather conditions, they are also sensitive to alterations in habitat structure and species interactions. Increased levels of predation pressure by invertebrate feeders like carabids, might for instance severely affect the abundance of terrestrial gastropods [Symondson *et al.*, 1996]. Experimental setups in order to investigate the impact of changes in the climate (e.g. elevated CO₂ and temperature) have shown that it is difficult to predict the consequences of climate change on terrestrial gastropods [Bezemer & Knight, 2001]. Likely, future climate change related changes in species composition, vegetation cover and land-use further affect terrestrial gastropods in ways difficult to anticipate.

Nonetheless, due to the availability of future climate projections, like the downscaled general circulation models CGCM2, developed by the 'Canadian Centre for Climate Modelling and Analysis', and HadCM3, developed by the

Hadley Centre, it becomes increasingly possible to assess the impact of future climate change on species distributions by using modelling algorithms like MaxEnt [Phillips *et al.*, 2006]. Although concerns about the reliability of such modelling algorithms exist [Davis *et al.*, 1998; Beale *et al.*, 2008], mainly because of their assumption that the distribution of species is largely shaped by climatological conditions, it is generally thought that these models can provide useful information when used carefully [Pearson & Dawson, 2003; Araújo *et al.*, 2005a]. Furthermore, while experimental studies are useful and necessary to predict the impact of a future warming climate on single species, predictive modelling approaches can provide us with a better understanding of the general impact of climate change on a larger number of species, on a wider geographical scale. I used species distribution modelling to assess the geographic distribution of terrestrial gastropods (order *Stylommatophora*) in future climatologic situations.

METHODS

Occurrence data (mean $n=131$, $se=16$, $min=31$, $max=976$) for 99 terrestrial gastropods in Europe were obtained for the period 01-01-2000 until 01-01-2010 from the data portal of the Global Biodiversity Information Facility [<http://data.gbif.org>]. Unfortunately, species occurrence data from the Iberian Peninsula and the Russia Federation were largely lacking, biasing the database to some extent. The climate projection for 2080 used in this study was the downscaled general circulation model (GCM) HADCM3, developed by the Hadley Centre, under emission scenarios A2 (business as usual) and B2 (local solutions to economic, social, and environmental sustainability will be adopted) [<http://www.worldclim.org/futdown.htm>, Nakicenovic *et al.*, 2000]. The environmental variables used in the models consisted of elevation data, and the nineteen bioclimatic variables derived from recent (1950–2000) monthly temperature and rainfall values. These data are described and available online at WorldClim [<http://www.worldclim.org/futdown.htm> (developed by Hijmans *et al.*, 2005)]. The 10 arc-minutes scale was used to work at.

I used the maximum entropy method (MaxEnt), developed by Phillips *et al.* [2006], to predict the distribution ranges of the terrestrial gastropods in 2080. MaxEnt has shown to be one of the best performing modelling algorithms in predicting species distributions [e.g. Elith *et al.*, 2006; Hijmans & Graham, 2006; Wisz *et al.*, 2008]. The method calculates the probability distribution of maximum entropy, taking a certain number of environmental variables into account, in order

to estimate a probability distribution for a species in a particular area [Phillips *et al.*, 2006; Elith *et al.*, 2011]. I used the default convergence threshold (10^{-6}) and maximum number of iterations (500) values. Hinge features were applied, as is recommended by Phillips & Dudík (2008). The expected distribution range of a species was limited to areas in which the generated models predicted a suitability >0.1 on a scale of 0–1 [Phillips *et al.*, 2006]. The threshold of 0.1 was chosen by means of the receiver operating characteristic (ROC) plot based approach [Cantor *et al.*, 1999; Liu *et al.*, 2005], based upon 10% of the species investigated. Species richness of *Stylommatophora* was based upon the total number of species predicted to be present per grid cell. The future species richness was estimated for two scenarios; (a) worst case scenario (WCS): no dispersal ability, the species concerned is only able to persist in areas where its predicted current and potential future range overlap, and (b) best case scenario (BCS): full dispersal ability, the species concerned is able to reach its full potential extent of occurrence.

The accuracy of the models generated by MaxEnt was assessed by using the area under the curve (AUC) of a ROC plot [Hanley & Mcneil, 1982; Phillips *et al.*, 2006]. Models with an $AUC > 0.75$ are deemed suitable [Elith *et al.*, 2006]. Furthermore, I set 30% of the occurrence data aside as ‘test’ data, by means of randomized partition, in order to compare the AUC of these models with the AUC from 70% models.

RESULTS

In total 99 species, representing 53 genera from 25 families, of the order *Stylommatophora* were assessed. Of these, three species, the narrow-mouthed whorl snail (*Vertigo angustior*, Jeffreys 1830), *Vertigo geyeri* (Lindholm 1925), and the Des Moulin’s Snail (*Vertigo moulinsiana*, Dupuy 1849) were assessed as lower risk/ conservation dependent by the IUCN Red List of Threatened Species (<http://www.iucnredlist.org/>). The AUC of the 70% models was on average 0.993 ($se < 0.001$), with a minimum of 0.980. The AUC of the 30% test models was on average 0.991 ($se = 0.001$), with a minimum of 0.945, which was well above the required AUC value of 0.750 [Elith *et al.*, 2006]. Table 1 shows the mean predicted current range sizes, the mean potential range sizes assuming full dispersal ability, and the number of winners (species that acquire a larger distribution range over time) and losers (species that are left with a smaller distribution range in future) for each genus.

Table 1. Mean current predicted and future potential range sizes (assuming full dispersal ability) and the number of ‘losers’ and ‘winners’ for the different genera of *Stylommatophora*.

Genus	Mean range size 2000 (1000km²)	mean range size 2080 (1000km²)	Number of losers	Number of winners
<i>Abida</i>	4.69	5.13	0	1
<i>Acanthinula</i>	13.23	27.88	0	1
<i>Aegopinella</i>	5.12	13.64	0	2
<i>Arianta</i>	7.15	9.71	0	1
<i>Arion</i>	5.34	6.72	5	7
<i>Boettgerilla</i>	6.93	9.03	0	1
<i>Candidula</i>	3.69	8.03	0	3
<i>Ceciloides</i>	4.74	8.70	0	1
<i>Cepaea</i>	4.80	9.63	0	3
<i>Cernuella</i>	3.49	4.27	0	1
<i>Chondrina</i>	3.48	5.94	0	1
<i>Ciliella</i>	1.70	2.11	0	1
<i>Clausilia</i>	8.57	14.88	0	3
<i>Cochlicella</i>	4.21	14.13	0	1
<i>Cochlicopa</i>	13.53	23.42	0	2
<i>Cochlodina</i>	6.88	16.83	0	1
<i>Columella</i>	13.66	26.05	0	2
<i>Cornu</i>	2.69	3.91	0	1
<i>Deroceras</i>	6.57	9.16	1	3
<i>Discus</i>	6.65	11.44	1	1
<i>Euconulus</i>	10.43	21.24	0	3
<i>Euomphalia</i>	12.36	25.77	0	1
<i>Fruticicola</i>	9.90	21.22	0	1
<i>Granaria</i>	2.60	3.88	0	1
<i>Helicella</i>	5.83	7.38	0	1
<i>Helicigona</i>	7.80	21.78	0	1
<i>Helicodonta</i>	5.53	4.45	1	0
<i>Helix</i>	4.57	5.78	0	1
<i>Hygromia</i>	4.21	13.43	0	1
<i>Lauria</i>	3.83	3.38	1	0
<i>Limax</i>	8.39	14.71	1	1
<i>Macrogastera</i>	9.60	24.30	0	2
<i>Malacolimax</i>	10.85	22.30	0	1
<i>Monacha</i>	2.77	4.48	1	1
<i>Monachoides</i>	7.04	4.90	1	0
<i>Morlina</i>	2.65	3.72	0	1

Table 1. (continued)

Genus	Mean range size 2000 (1000km ²)	mean range size 2080 (1000km ²)	Number of losers	Number of winners
<i>Nesovitrea</i>	8.81	17.56	0	2
<i>Oxychilus</i>	4.81	5.63	1	2
<i>Oxyloma</i>	7.34	23.02	0	1
<i>Phenacolimax</i>	3.58	4.24	0	1
<i>Punctum</i>	9.55	23.83	0	1
<i>Pupilla</i>	5.77	14.30	0	2
<i>Pyramidula</i>	4.00	4.21	0	1
<i>Solatopupa</i>	2.19	4.94	0	1
<i>Succinea</i>	5.66	6.72	0	1
<i>Tandonia</i>	1.45	1.99	0	1
<i>Trochulus</i>	2.23	3.11	0	1
<i>Truncatellina</i>	3.97	5.79	1	1
<i>Vallonia</i>	9.45	23.37	0	3
<i>Vertigo</i>	10.42	20.76	0	9
<i>Vitrea</i>	4.76	6.53	0	3
<i>Vitrina</i>	8.27	19.48	0	1
<i>Zonitoides</i>	6.68	16.41	0	1
Total	6.74	12.50	14	85

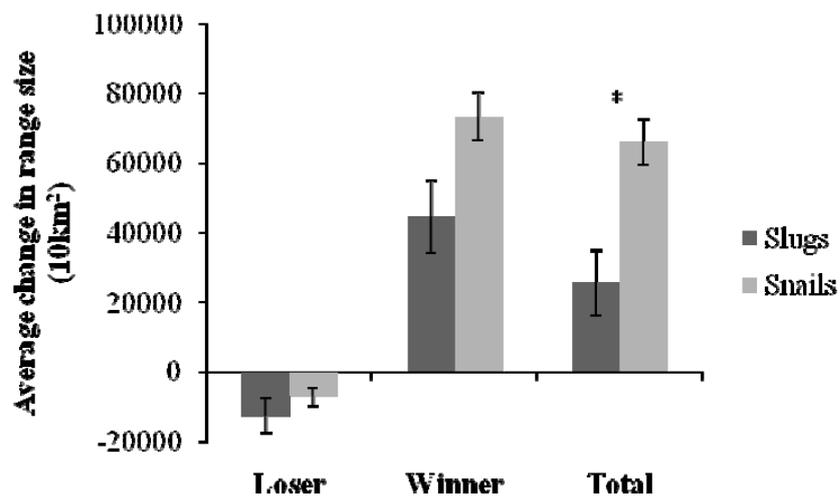


Figure 1. Mean range contraction/ expansion of losers and winners amongst slugs and snails, * denotes a significant difference.

When assuming full dispersal ability, only 14 out of the 99 species assessed were expected to contract their future distribution range with on average 9964 10km² (se= 2776). The remaining 85 species, including the three species assessed as lower risk/ conservation dependent by the IUCN Red List of Threatened Species, were expected to expand their range with on average 68636 10km² (se= 5981). Slugs were in general more often expected to contract their range than snails, 33% versus 9% (Pearson $\chi^2=8.086$, df=1, p=0.040). Although slugs seemed to lose on average more area than snails amongst the losers, and gain on average less area amongst the winners, these difference were not significant (Losers: Mann-Whitney U=18.000, df=13, p=0.406, Winners: Mann-Whitney U =386.000, df=84, p=0.188, Figure 1). However, when the total predicted change in range size was considered, slugs did on average gain less area than snails (Mann-Whitney U=502.000, df=98, p=0.007, Figure 1). Especially a relatively large number (n=5) of the 12 species of the roundback slugs (*Arionidae*) family were expected to contract their future range (Table 1).

Figure 2a shows the predicted species richness of *Stylommatophora* throughout Europe in 2000. MaxEnt predicted that Western Europe (Denmark, The Netherlands, Belgium, Luxemburg, parts of Germany, France, and the United Kingdom) has a high species richness (> 75 species) at present. Northern and Eastern Europe, and large parts of the Iberian Peninsula were expected to have a low species richness (< 25 species). It was predicted that by 2080 the species richness will in general be higher in large parts of Europe than in 2000, assuming full dispersal ability (Figure 3). The climatic envelop of most species will have shifted in a north-eastern direction (Figure 2b). Consequently, species richness will likely be highest in Northern and Western Europe. Whilst both Denmark and The Netherlands probably contain their high species richness in 2080, the number of *Stylommatophora* predicted to be present in future in countries like Belgium, France and the United Kingdom, but also in the Mediterranean region, was noticeably lower than at present. On the other hand, large parts of Fennoscandia, especially the Southern part of Sweden, and Russia, may be invaded by a large number of species in future. However, when no dispersal ability was assumed, most parts of Europe might experience a decrease in the number of *Stylommatophora* species present. Only Denmark and The Netherlands likely maintain their high species richness (Figure 2c).

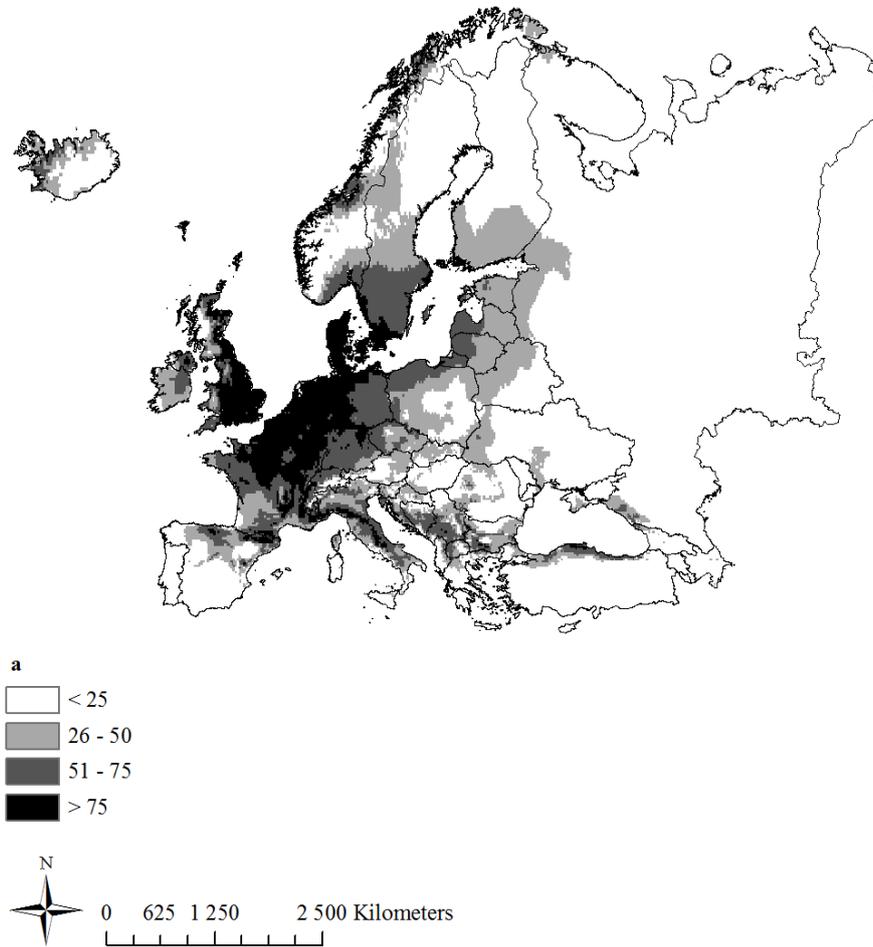


Figure 2. (continued)

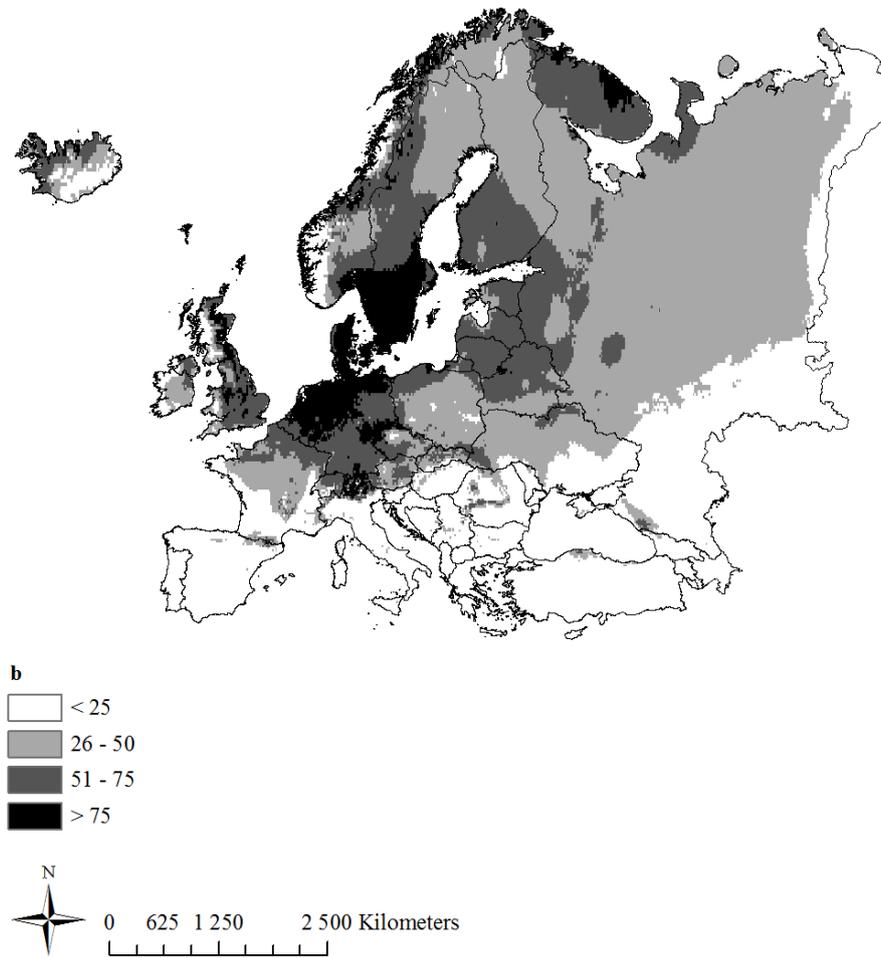


Figure 2. (continued)

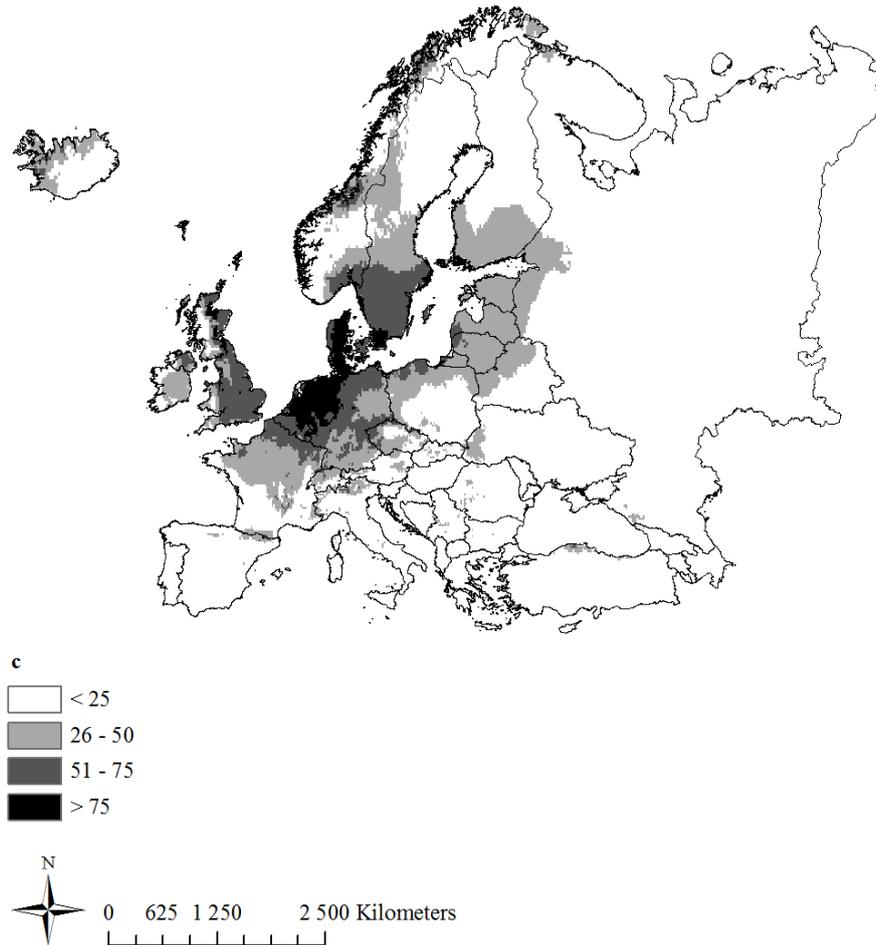


Figure 2. Predicted species richness of *Stylommatophora* throughout Europe in a) 2000, b) best case scenario 2080: full dispersal ability, the species concerned is able to reach its full potential extent of occurrence, and c) worst case scenario 2080: no dispersal ability, the species concerned is only able to persist in areas where its predicted current and potential future range overlap.

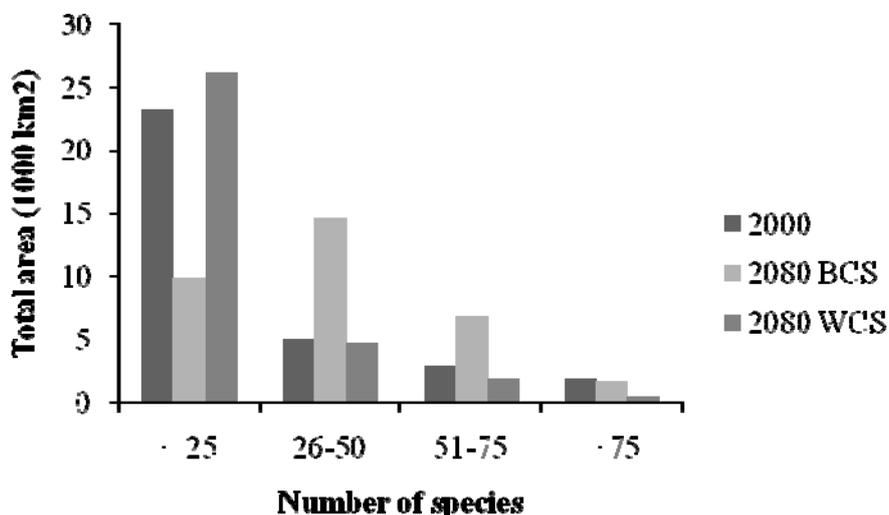


Figure 3. Total area in 1000 km² per species richness category for 2000, 2080 best case scenario (full dispersal ability), and 2080 worst case scenario (no dispersal ability)

CONCLUSION

The results show that most terrestrial gastropods are likely to expand their geographic distribution range and shift it north-eastwards. It is thus expected that the terrestrial gastropod diversity in Fennoscandia and North-western Russia will increase, whilst species diversity in the Mediterranean regions is likely going to decrease. Future climatic conditions are predicted to become favourable in a larger part of Europe for the three species of a high conservation concern (the narrow-mouthed whorl snail, *Vertigo geyeri*, and the Des Moulin's Snail) as well, which is proficient for their preservation. However, an accurate prediction of the future distribution range of a species is not only highly valuable for its conservation; it might be valuable for the sake of the conservation of other species as well. Since habitat availability for a species correlates with population size through local abundance [Borregaard & Rahbek, 2010], changes in the distribution range might be used as a surrogate for species abundance [Thomas *et al.*, 2004; Araújo *et al.*, 2005b], and an increased abundance of terrestrial gastropods might be beneficial for a range of invertebrate-feeders, such as carabids, and mammals like hedgehogs (*Erinaceus* sp.) and badgers (*Meles meles*).

It is not surprising that a relatively larger number of slugs were predicted to contract their range, and on average to a larger extent, than snails. Slugs are not protected against unfavourable environmental conditions by a shell, like snails are, their activity is thus to a larger extent dependent on microclimatic conditions [Crawford-Sidebotham, 1972]. However, both slugs and snails are generally regarded as pest species in arable dominated agricultural landscapes [e.g. Glen *et al.*, 1990; Frank, 1998; Barker, 2002]. Although my results show that a larger number of slug species are likely going to be more severely negatively affected by future climate change than snail species, both slugs and snails in general were predicted to increase their total distribution range, which might thus negatively affect agricultural practices. An increasing abundance of terrestrial gastropods in large parts of Europe might be highly detrimental for the current pest management. Increased levels of molluscicides and biological pest management, e.g. adapted cultivation techniques [Symondson *et al.*, 1996; Hollingsworth *et al.*, 2002], might be necessary to decrease potential damages in arable crops caused by slugs and snails.

While the expected species richness in 2080 was expected to be higher in many regions throughout Europe when full dispersal ability was assumed, terrestrial gastropods, such as the *Stylommatophora*, are slow moving species and might not reach their future potential distribution range. Terrestrial snails are for instance able to disperse up to only a few meters per year in environmentally hospitable conditions [Baur, 1988; Welter-Schultes, 1998]. Furthermore, it is thought that active dispersal of terrestrial snails over large distance does not generally occur [Hausdorf, 2000]. It is therefore questionable whether species will be able to reach their full potential extent of occurrence in future. On the other hand, it is known from past experience that by means of passive dispersal species are able to colonize large areas [Hausdorf, 2000]. Terrestrial gastropods are for instance intentionally or unintentionally introduced to new areas by mankind [Ibáñez *et al.*, 1997; Welter-Schultes, 1998]. Additionally, terrestrial snails are also able to colonize new, environmentally suitable, regions by means of areal dispersal [Vagvolgyi, 1975]. Therefore, the figures depicting the predicted future species richness should be interpreted with some care.

Although great care has been taken when assessing the distribution ranges of the species considered, their current and future distribution ranges have solely been based upon climatological conditions. Since biotic factors and active and passive dispersal may also be important in shaping the (future) distribution of terrestrial gastropods [Suominen, 1999; Hausdorf, 2000; Kappes *et al.*, 2009], the generated predicted species distribution ranges depict their potential fundamental climate niche, rather than their potential realized niche. Furthermore, as

occurrence data for large parts of the Iberian Peninsula and North-western Russia were lacking, the distribution range of slugs and snails within these parts of Europe, and thus the species richness in these areas, might have been underestimated. Nevertheless, the results give a good indication of where we might expect to find climatological suitable and less suitable areas for terrestrial gastropods throughout Europe, aiding conservation management and pest control.

REFERENCES

- Aragón, P., Rodríguez, M., Olalla Tárrega, M. & Lobo, J. (2010). Predicted impact of climate change on threatened terrestrial vertebrates in central Spain highlights differences between endotherms and ectotherms. *Animal Conservation*, *13*, 363-373.
- Araújo, M., Pearson, R., Thuiller, W. & Erhard, M. (2005a). Validation of species–climate impact models under climate change. *Global change biology*, *11*, 1504-1513.
- Araújo, M., Whittaker, R., Ladle, R. & Erhard, M. (2005b). Reducing uncertainty in projections of extinction risk from climate change. *Global Ecology and Biogeography*, *14*, 529-538.
- Aubret, F. & Shine, R. (2010). Thermal plasticity in young snakes: how will climate change affect the thermoregulatory tactics of ectotherms? *The Journal of experimental biology*, *213*, 242-248.
- Barker, G. M. (2002) *Molluscs as crop pests*. Wallingford: CAB International.
- Baur, B. (1988). Microgeographical variation in shell size of the land snail *Chondrina clienta*. *Biological Journal of the Linnean Society*, *35*, 247-259.
- 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. *Journal of Applied Ecology*, *30*, 333-340.
- Beale, C., Lennon, J. & Gimona, A. (2008). Opening the climate envelope reveals no macroscale associations with climate in European birds. *Proceedings of the National Academy of Sciences*, *105*, 14908-14912.
- Bennett, K. D. (1997). *Evolution and ecology: the pace of life*. Cambridge: Cambridge University Press.
- Bezemer, T. M. & Knight, K. J. (2001). Unpredictable responses of garden snail (*Helix aspersa*) populations to climate change. *Acta Oecologica*, *22*, 201-208.
- Borregaard, M. & Rahbek, C. (2010). Causality of the relationship between geographic distribution and species abundance. *The Quarterly review of biology*, *85*, 3-25.

- Cantor, S. B., Sun, C. C., Tortolero-Luna, G., Richards-Kortum, R. & Follen, M. (1999). A Comparison of C/B Ratios from Studies Using Receiver Operating Characteristic Curve Analysis. *Journal of Clinical Epidemiology*, 52, 885-892.
- Crawford-Sidebotham, T. (1972). The influence of weather upon the activity of slugs. *Oecologia*, 9, 141-154.
- Crowley, T. J. & North, G. R. (1988). Abrupt climate change and extinction events in earth history. *Science*, 240, 996-1002.
- Davis, A. J., Jenkinson, L. S., Lawton, J. H., Shorrocks, B. & Wood, S. (1998). Making mistakes when predicting shifts in species range in response to global warming. *Nature*, 391, 783-786.
- Davis, M. B. & Shaw, R. G. (2001). Range shifts and adaptive responses to Quaternary climate change. *Science*, 292, 673-679.
- Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C. & Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences*, 105, 6668-6672.
- Elith, J., Graham, C., Anderson, R., Dudík, M., Ferrier, S., Guisan, A., Hijmans, R., Huettmann, F., Leathwick, J. & Lehmann, A. (2006). Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, 29, 129-151.
- Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E. & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distributions*, 17, 43-57.
- Frank, T. (1998). Slug damage and numbers of the slug pests, *Arion lusitanicus* and *Deroceras reticulatum*, in oilseed rape grown beside sown wildflower strips. *Agriculture, Ecosystems & Environment*, 67, 67-78.
- Gillooly, J. F., Brown, J. H., West, G. B., Savage, V. M. & Charnov, E. L. (2001). Effects of size and temperature on metabolic rate. *Science*, 293, 2248-2251.
- Glen, D., Jones, H. & Fieldsend, J. (1990). Damage to oilseed rape seedlings by the field slug *Deroceras reticulatum* in relation to glucosinolate concentration. *Annals of Applied Biology*, 117, 197-207.
- Hanley, J. & Mcneil, B. (1982). The meaning and use of the area under a receiver operating characteristic (ROC) curve. *Radiology*, 143, 29-36.
- Hausdorf, B. (2000). Biogeography of the Limacoidea sensu lato (*Gastropoda: Stylommatophora*): vicariance events and long distance dispersal. *Journal of Biogeography*, 27, 379-390.

- Hijmans, R., Cameron, S., Parra, J., Jones, P. & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, 25, 1965-1978.
- Hijmans, R. & Graham, C. (2006). The ability of climate envelope models to predict the effect of climate change on species distributions. *Global change biology*, 12, 2272-2281.
- Hollingsworth, R. G., Armstrong, J. W. & Campbell, E. (2002). Pest Control: Caffeine as a repellent for slugs and snails. *Nature*, 417, 915-916.
- Ibáñez, M., Alonso, M. R., Henri' Quez, F. & Valido, M. J. (1997). Distribution of land snails (*Mollusca, Gastropoda, Pulmonata*) on the island of Gran Canaria (Canary Islands) in relation to protected natural areas. *Biodiversity and Conservation*, 6, 627-632.
- IPCC (2001). Climate Change 2001: Impacts, Adaptation, and Vulnerability. *Contribution of Working Group II to Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press.
- 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 Ecology*, 24, 685-697.
- Kearney, M., Shine, R. & Porter, W. P. (2009). The potential for behavioral thermoregulation to buffer "cold-blooded" animals against climate warming. *Proceedings of the National Academy of Sciences*, 106, 3835-3840.
- Ledergerber, S., Thommen, G. & Baur, B. (1997). Grazing damage to plants and gastropod and grasshopper densities in a CO₂-enrichment experiment on calcareous grassland. *Acta Oecologica*, 18, 255-261.
- Liu, C., Berry, P., Dawson, T. & Pearson, R. (2005). Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*, 28, 385-393.
- Markham, A. (1996). Potential impacts of climate change on ecosystems: a review of implications for Policymakers and conservation biologists. *Climate Research*, 6, 179-191.
- Nakicenovic, N., Alcamo, J., Davis, G., De Vries, B., Fenhann, J., Gaffin, S., Gregory, K., Grubler, A., Jung, T. Y., Kram, T., La Rovere, E. L., Michaelis, L., Mori, S., Morita, T., Pepper, W., Pitcher, H. M., Price, L., Riahi, K., Roehrl, A., Rogner, H.-H., Sankovski, A., Schlesinger, M., Shukla, P., Smith, S. J., Swart, R., Van Rooijen, S., Victor, N. & Dadi, Z. (2000). *Special Report on Emissions Scenarios : a special report of Working Group III of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press.

- Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, 37, 637-669.
- Parmesan, C., Ryrholm, N., Stefanescu, C., Hill, J. K., Thomas, C. D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W. J., Thomas, J. A. & Warren, M. (1999). Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, 399, 579-583.
- Pearson, R. & Dawson, T. (2003). Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, 12, 361-371.
- Phillips, S., Anderson, R. & Schapire, R. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190, 231-259.
- Pounds, J. A., Fogden, M. P. L. & Campbell, J. H. (1999). Biological response to climate change on a tropical mountain. *Nature*, 398, 611-615.
- Suominen, O. (1999). Impact of cervid browsing and grazing on the terrestrial gastropod fauna in the boreal forests of Fennoscandia. *Ecography*, 22, 651-658.
- Symondson, W., Glen, D., Wiltshire, C., Langdon, C. & Liddell, J. (1996). Effects of cultivation techniques and methods of straw disposal on predation by *Pterostichus melanarius* (Coleoptera: Carabidae) upon slugs (Gastropoda: Pulmonata) in an arable field. *Journal of Applied Ecology*, 33, 741-753.
- Thomas, C., Cameron, A., Green, R., Bakkenes, M., Beaumont, L., Collingham, Y., Erasmus, B., Ferreira De Siqueira, M., Grainger, A. & Hannah, L. (2004). Extinction risk from climate change. *Nature*, 427, 145-148.
- Thomas, C., Franco, A. & Hill, J. (2006). Range retractions and extinction in the face of climate warming. *Trends in Ecology & Evolution*, 21, 415-416.
- Vagvolgyi, J. (1975). Body size, aerial dispersal, and origin of the Pacific land snail fauna. *Systematic Zoology*, 24, 465-488.
- Walther, G., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T., Fromentin, J., Hoegh-Guldberg, O. & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, 416, 389-395.
- Webley, D. (1964). Slug activity in relation to weather. *Annals of Applied Biology*, 53, 407-414.
- Welter-Schultes, F. (1998). Human-dispersed land snails in Crete, with special reference to *Albinaria* (Gastropoda: Clausiliidae). *Biologia Gallo-Hellenica*, 24, 83-106.
- Wisz, M., Hijmans, R., Li, J., Peterson, A., Graham, C. & Guisan, A. (2008). Effects of sample size on the performance of species distribution models. *Diversity and Distributions—a Journal of Biological Invasions and Biodiversity*, 14, 763–773.

Woodward, F. (1987). Climate and plant distribution at global and local scales.
Vegetatio, 69, 189-197.