

D

**DISCUSSION OF METHODOLOGICAL
LIMITATIONS**

D.1 Limitations of species distribution models and future projections

General suitability of species distribution projections

Species distribution models (Guisan & Zimmermann 2000) are widely used in assessing possible future distribution patterns. They correlate current environmental conditions with observed presences/absences (or only presences) of single species. Species distribution models are based on the assumption that a species occupies all areas with a suitable environment, i.e. the species fills its so called fundamental niche. In reality, species realize only parts of their fundamental niches and thus are rarely in equilibrium with their environment. This may be caused by several reasons, e.g. biotic interactions or dispersal ability may restrict the niche filling or slow it down in a changing environment.

Though the approach of species distribution models is purely correlative and does not imply causality, species distributions can usually be described well enough to draw some useful conclusions. Based on the assumption that the relation between environment and species distribution holds in a changing environment, distribution models are used to project the potential impacts on species distribution and biodiversity corresponding to climate and land use change scenarios.

Species distribution models are validated by comparing the fit between the modelled distribution, based on current environmental conditions, and the observed distribution. Such validation helps estimating the model reliability and uncover sources and patterns of discrepancy between modelled and real species distribution. Having assessed the modelling errors, it is possible to make a careful and sound interpretation of the results.

The most important causes of modelling errors for species distribution models are as follows:

- **Data quality:** A low sampling effort, due to low accessibility or inconspicuousness of species, underestimates the true species distribution and truncates environmental niches. Data should cover the whole range of a species and thus the full niche of species, otherwise tolerance to environmental conditions may be misjudged (Kadmon et al. 2003).
- **Data resolution:** Data resolution may not be appropriate to capture environmental conditions that are experienced by organisms (Pearson & Dawson 2003). Mean climatic conditions taken over a larger area may not reflect the local climatic conditions experienced in a species' microhabitat. For example conditions in mountains and peat bogs may change substantially

within short distances due to variations in local topography and land-form (Trivedi et al. 2008).

- **Modelling algorithm:** Choice of modelling algorithm affects prediction error (Pearson et al. 2006). Some methods may give a better fit to nonlinear data, but are subject to over-fitting (Randin et al. 2006) (i.e. they may describe calibration data well but are useless for temporal or spatial projections). To reduce the influence of the chosen technique on the modelling results Araujo & New (2007) suggested to combine the results of many different (good) models by ensemble forecasting. Ensemble methods are surely appropriate in the absence of detailed ecological knowledge of the species modelled. However, for species with known ecological requirements, model results can be judged according to their sensibility. Using ensemble methods and average across all results (including insensible models) would lead to worse instead of better model results.
- **Species' ecology:** Model performance may be influenced in a variety of ways by species characteristics (McPherson & Jetz 2007). Range characteristics resemble the ecological niche of a species in space. Species with clumped distribution and narrow niches have a good predictability; results for range size itself were ambiguous and may even be an statistical artefact (for discussion see: Hernandez et al. 2006). Species of higher trophic levels are expected to be modelled least well, since they strongly depend on other species (Huntley et al. 2004). A high temporal or spatial mobility (e.g. good dispersal, migratory behaviour) may lead to reduced detectability or misjudgement of habitat preferences (Pulliam 2000). Low performance of inconspicuousness or scarce species is opposed by a good performance of large and easily detectable species (Seoane et al. 2005).
- **Intraspecific variation:** In species distribution models (and usually in dynamic models as well) it is assumed that species are not differentiated and do not have phenotypic or behavioural plasticity. Ignoring the adaptation to local conditions leads to overestimation of the environmental niche (Harte et al. 2004).
- **Evolutionary adaptation:** Usually, both types of modelling approaches ignore the ability of species for (micro-)evolutionary changes, i.e. species can adapt to novel conditions only within the limits of their genetically predetermined potential. However, it was shown that species have the evolutionary potential to adapt to novel environmental conditions (Thomas et al. 2001). This will underestimate the potential environmental niche in the future.
- **Lacking parameters:** Limited knowledge on environmental conditions influencing species distribution seriously reduces modelling performance (Barry & Elith 2006). Inclusion of land use increased model performance on small scale (Luoto et al. 2007) as well as large scale (Pompe et al. 2008). The influence of biotic interactions (e.g. competition, facilitation, diseases, prey) are generally ignored in species distribution models though they are assumed

to play a large role in shaping species distribution. Recent applications are promising at least to describe simple interactions (Heikkinen et al. 2007, Schweiger et al. in press).

- **Changing biotic and environmental interactions.** Species distribution models based on correlations between current distribution environment may be invalidated by uncoupling and rearrangement of biotic interactions (see above) or the appearance of unprecedented environmental conditions (e.g. CO₂ fertilization of plants). For example, increased environmental CO₂ may lead to increased stomatal conductance and hence to less evapotranspiration and subsequently higher soil water availability than can be assumed from purely climatic conditions. Ignoring this can largely affect species distribution models (Rickebusch et al. 2008).

This list makes clear that biodiversity models are not able to replicate all the complex patterns of reality and are valid only under its simplifying assumptions. The extent of this limitation might question the usefulness of such models. However, the aim of such modelling procedures is not to capture the full complexity of the systems but to gain a better understanding of the basic patterns and underlying natural processes. The simplifications allow us to reduce the complexity of the real world to a level that can be handled with the available techniques and knowledge. It is better to achieve some limited knowledge, even with imperfect methods and the related uncertainties, than to remain in complete ignorance.

Hence predictive species distribution models cannot forecast the future but are able to give potential reactions of species under environment change scenarios, which may help in deriving appropriate policy recommendations.

Approaches used in the present atlas

We used generalised linear models (GLMs) to relate climatic variables to species distributional data using a binomial error structure, which means that we need both reliable presence and absence data and to assess the full climatic niche of a species. It would hence be best if both northern and southern range margins are at least to some extent defined by climate and not solely by other factors such as e.g. geographical borders. To ensure high quality models we excluded countries with low levels of sampling and highly uneven coverage.

The southern range margins of many Mediterranean species (e.g. *Danaus chrysippus*, *Gegenes nostradamus*, *Leptotes pirithous*, *Libythea celtis*, *Tomares ballus* see Figs. D.1.1-D.1.5) are, however, often limited by the geographical borders of Europe and not necessarily by climate. Here, future projections may be treated with caution; since extrapolations to future warmer and dryer climates might be overly pessimistic in some cases as such species' potential performance in such climates (e.g. species that also occur in North Africa) was not included in model parameterisation.



Figure D.1.1: Actual distribution and modelled present climatic niche of *Danaus chrysippus*



Figure D.1.2: Actual distribution and modelled present climatic niche of *Gegeres nostradamus*

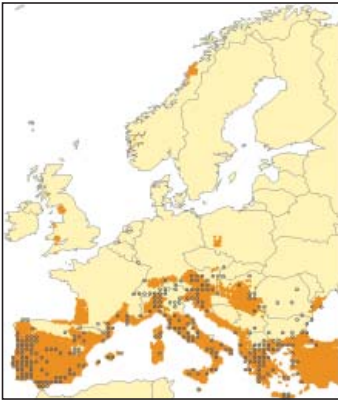


Figure D.1.3: Actual distribution and modelled present climatic niche of *Leptotes pirithous*

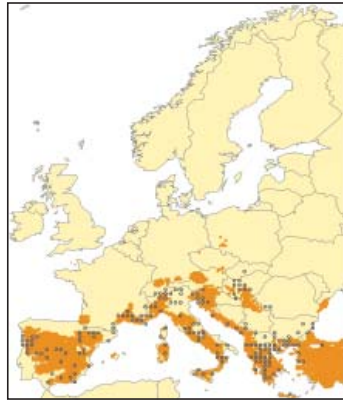


Figure D.1.4: Actual distribution and modelled present climatic niche of *Libythea celtis*



Figure D.1.5: Actual distribution and modelled present climatic niche of *Tomares ballus*

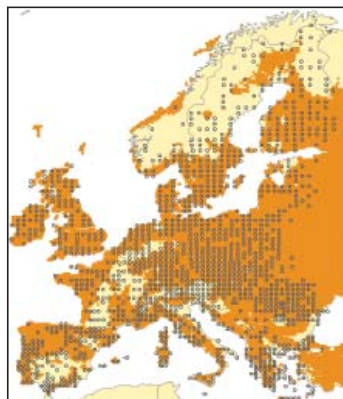


Figure D.1.6: Actual distribution and modelled present climatic niche of *Vanessa cardui*

Vanessa cardui (Fig. D.1.6) for example, is even more difficult, as this species seems to survive the winter only in South Mediterranean regions while populations might vanish there in summer, depending on re-migrants from the North. Here it would be most important to model the future overwintering area. Unfortunately this area seems to be situated mostly outside Europe, and little is known on this (apart from the Canaries where this species can be found all year round). It therefore is of limited use to model the total area where this species can be found, because this is the whole of Europe.

Within this atlas we present ecological niche models based on climatic variables. It is crucial to note that the depicted current and future climatic niches do not represent predictions of future species distributions but are projected distributions of the potentially suitable **climate space** for the species. Of course there are many more factors that determine whether a species is actually able to occupy the potentially suitable climate spaces, including landscape structure, habitat quality, resource availability or predation and parasitic pressures and the dispersal ability of a species. However, as applied at the coarse scale across the whole of Europe, climate is usually best suited to explain such large scale distributional patterns (Thuiller et al. 2004). This is supported by the generally high accuracy of our models (i.e. high AUC values for most species). However, there are exceptions such as *Lycena belle* (Fig. D.1.7), *Coenonympha oedippus* (Fig. D.1.8), and *Euphydryas maturna* (Fig. D.1.9), whose distributions are tied closely to particular habitat conditions. Such local habitats with specific structural and microclimatic conditions are averaged out at the resolution used in this analysis and thus do not contribute to model development. In these cases where habitat and microclimatic conditions are much more important determinants of species' distributions, large scale bioclimatic niche models often fail to adequately describe and consequently to project future species distributions. We address these concerns by taking AUC values into account when assessing species risk (see section B4).

A high temporal or spatial mobility (e.g. good dispersal, migratory behaviour, invasive species) may lead to misjudgement of habitat preferences. This means that results for species like *Vanessa cardui* (Fig. D.1.14), *Vanessa atalanta* (Fig. D.1.10) or *Cacyreus marshalli* (Fig. D.1.11) have to be treated with caution. In many such cases it would be much better to only include the range of permanent populations (e.g. in *Colias croceus*, Fig. D.1.12; and *Lampides boeticus*, Fig. D.1.13). Unfortunately, this is a rather difficult task which might be tackled in the future, because it is often not known whether records represent permanent populations.

Another example is *Boloria titania* (Fig. D.1.15), where the model was not able to predict the occurrence of this species in the Baltic States. The inclusion of constraints of the larval host plant *Polygonum bistorta* in the process of model development results in much better models (Schweiger et al. in press). This shows that including other essential abiotic and biotic environmental factors can help to improve model accuracy, but in most cases we lack crucial information about the multitude of species interactions that may add to the effects of climate. Consequently, to be consistent across the species, we relied solely on climatic variables in the current atlas.

There are many different methodological approaches to develop ecological niche models and ways to deal with issues such as host-plant constraints (Guisan &

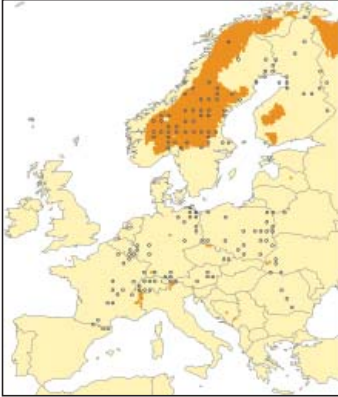


Figure D.1.7: Actual distribution and modelled present climatic niche of *Lycaena helle*

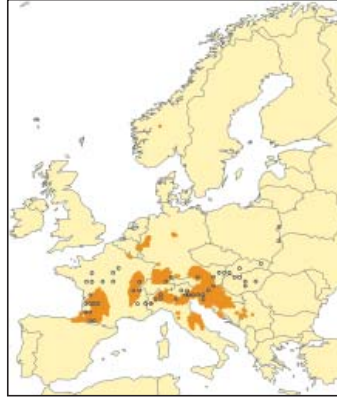


Figure D.1.8: Actual distribution and modelled present climatic niche of *Coenonympha oedippus*



Figure D.1.9: Actual distribution and modelled present climatic niche of *Euphydryas maturna*



Figure D.1.10: Actual distribution and modelled present climatic niche of *Vanessa atalanta*



Figure D.1.11: Actual distribution and modelled present climatic niche of *Cacyreus marshalli*

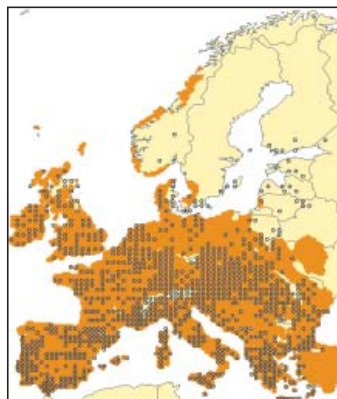


Figure D.1.12: Actual distribution and modelled present climatic niche of *Colias croceus*



Figure D.1.13: Actual distribution and modelled present climatic niche of *Lampides boeticus*



Figure D.1.14: Actual distribution and modelled present climatic niche of *Euphydryas cynthia*

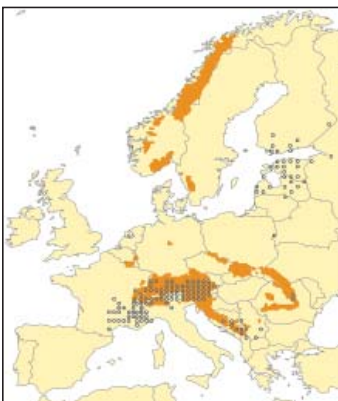


Figure D.1.15: Actual distribution and modelled present climatic niche of *Boloria titania*

Zimmermann 2000, Elith et al. 2006, Heikkinen et al. 2006, Thuiller et al. 2008). We used GLMs despite the fact that they did not always provide the best model fit for the current distribution. However, their clear and simple mathematical formulation allows highly accurate extrapolations into new environmental space (Elith et al. 2006, Kühn et al. in press).

There are also many ways to evaluate model accuracy. The most commonly accepted measures are Cohen's Kappa (Cohen 1960) and AUC (Hanley & McNeil 1982). Both measure the agreement between observed and modelled occurrence (threshold dependent occurrence for Kappa and threshold independent occurrence probability for AUC) and depend on four cases of agreement: cases where actual occurrences were modelled correctly (right presence) or incorrectly (false absence) and cases where actual absences were modelled correctly (right absences) or incorrectly (false presences). Unfortunately, all four cases are weighted equally, which may result in extraordinarily high accuracy values when accuracy is dominated by just one of the four cases (Lobo et al. 2008). For instance, a number of species like *Lycaena helle* (Fig. D.1.7) and *Coenonympha oedippus* (Fig. D.1.8), or *Euphydryas cynthia* (Fig. D.1.14) and *Boloria titania* (Fig. D.1.15) and many others (as listed in table D.1.3) have a very restricted distribution with a high number of absences and a low number of presences.

The model was able to predict most of the absences correctly (right absence rate) but not many of the presences (false absence rate). As a consequence, the models give high AUC values because of the dominating effect of the right absences. However, for ecological niche modelling, the false absence rate is of most interest since it shows how well the model fits the actual occurrence, while false presences can easily be a consequence of other interacting limiting factors. To take this into account, we provide false absence rates as well as other values for all modelled species in a table in Appendix 1 and the most extreme cases in Tables D.1.1-4.

Table D.1.1: 38 European butterflies with the highest AUC values (AUC > 0.95):
(incl. overall risk categories with full and without dispersal)

page	Species	Risk categ. full disp	Risk categ. no disp	AUC
372	<i>Boloria chariclea</i> (SCHNEIDER, 1794)	HHHR	HHHR	1
410	<i>Euphydryas iduna</i> (DALMAN, 1816)	HHHR	HHHR	1
286	<i>Plebejus aquilo</i> (BOISDUVAL, 1832)	HHHR	HHHR	1
82	<i>Pyrgus warrenensis</i> (VERITY, 1928)	R	HR	0.99
112	<i>Parnassius phoebus</i> (FABRICIUS, 1793)	LR	HR	0.99
170	<i>Colias becla</i> LEFEBVRE, 1836	HHHR	HHHR	0.99
284	<i>Plebejus glandon</i> (PRUNNER, 1798)	R	HHR	0.99
514	<i>Erebia eriphyle</i> (FREYER, 1836)	LR	HR	0.99
530	<i>Erebia disa</i> (BECKLIN, 1791)	HHHR	HHHR	0.99
546	<i>Erebia tyndarus</i> (ESPER, 1781)	R	HR	0.99
614	<i>Oeneis glacialis</i> (MOLL, 1785)	R	HR	0.99
34	<i>Erynnis marlyoi</i> (BOISDUVAL, 1834)	HR	HHHR	0.98
158	<i>Pontia callidice</i> (HÜBNER, 1800)	R	HR	0.98
194	<i>Lycæna ottomana</i> (LEFEBVRE, 1830)	LR	HHR	0.98
288	<i>Plebejus orbitulus</i> (PRUNNER, 1798)	LR	LR	0.98
312	<i>Polyommatus nivescens</i> (KEFERSTEIN, 1851)	HHHR	HHHR	0.98
412	<i>Euphydryas Cynthia</i> ([SCHIFFERMÜLLER], 1775)	R	HR	0.98
414	<i>Euphydryas intermedia</i> (MENETRIES, 1859)	R	HHR	0.98
458	<i>Apatura metis</i> (FREYER, 1829)	LR	HHR	0.98
522	<i>Erebia melampus</i> (FUSSL, 1775)	LR	R	0.98
536	<i>Erebia pluto</i> (PRUNNER, 1798)	R	HR	0.98
554	<i>Erebia montana</i> (PRUNNER, 1798)	R	HR	0.98
574	<i>Melanargia arge</i> (SULZER, 1776)	LR	HR	0.98
598	<i>Hipparchia fatua</i> (FREYER, 1845)	LR	HR	0.98
612	<i>Oeneis norna</i> (BECKLIN, 1791)	HHHR	HHHR	0.98
134	<i>Zegris eupheme</i> (ESPER, 1805)	HHHR	HHHR	0.97
336	<i>Polyommatus dolus</i> (HÜBNER, 1823)	LR	HHHR	0.97
486	<i>Coenonympha gardetta</i> (PRUNNER, 1798)	LR	HR	0.97
528	<i>Erebia embla</i> (BECKLIN, 1791)	R	R	0.97
64	<i>Pyrgus centaureae</i> (RAMBUR, 1840)	R	R	0.96
100	<i>Gegens pumilio</i> (HOFFMANSEGG, 1804)	LR	HR	0.96
136	<i>Euchloe belemia</i> (ESPER, 1798)	HHR	HHHR	0.96
162	<i>Colias phicomone</i> (ESPER, 1780)	LR	HR	0.96
302	<i>Aricia anteros</i> (FREYER, 1838)	HR	HHHR	0.96
380	<i>Boloria frigga</i> (BECKLIN, 1791)	R	R	0.96
436	<i>Melitæa varia</i> (MEYER-DÜR, 1851)	LR	HHR	0.96
540	<i>Erebia mnestra</i> (ESPER, 1805)	R	HHR	0.96
616	<i>Oeneis jutta</i> (HÜBNER, 1806)	LR	R	0.96

Table D.1.2: 34 European butterflies with the highest Kappa values (> 0.54): (incl. overall risk categories with full and without dispersal)

page	Species	Risk categ. full disp	Risk categ. no disp	Kappa
286	<i>Plebejus aquilo</i> (BOISDUVAL, 1832)	HHHR	HHHR	0.78
170	<i>Colias hecla</i> LEFEBVRE, 1836	HHHR	HHHR	0.77
372	<i>Boloria chariclea</i> (SCHNEIDER, 1794)	HHHR	HHHR	0.73
530	<i>Erebia disa</i> (BECKLIN, 1791)	HHHR	HHHR	0.72
64	<i>Pyrgus centaureae</i> (RAMBUR, 1840)	R	R	0.71
528	<i>Erebia embla</i> (BECKLIN, 1791)	R	R	0.70
616	<i>Oeneis jutta</i> (HÜBNER, 1806)	LR	R	0.68
164	<i>Colias palaeno</i> (LINNAEUS, 1758)	R	R	0.66
364	<i>Boloria eunomia</i> (ESPER, 1799)	LR	LR	0.64
410	<i>Euphydryas iduma</i> (DALMAN, 1816)	HHHR	HHHR	0.64
514	<i>Erebia eriphyle</i> (FREYER, 1836)	LR	HR	0.64
288	<i>Plebejus orbitulus</i> (PRUNNER, 1798)	LR	LR	0.64
380	<i>Boloria frigga</i> (BECKLIN, 1791)	R	R	0.64
112	<i>Parnassius phoebus</i> (FABRICIUS, 1793)	LR	HR	0.63
282	<i>Plebejus optilete</i> (KNOCH, 1781)	R	R	0.63
284	<i>Plebejus glandon</i> (PRUNNER, 1798)	R	HHR	0.63
564	<i>Erebia pandrose</i> (BORKHAUSEN, 1788)	LR	LR	0.62
374	<i>Boloria freija</i> (BECKLIN, 1791)	HR	HR	0.62
158	<i>Pontia callidice</i> (HÜBNER, 1800)	R	HR	0.61
384	<i>Boloria aquilonaris</i> (STICHEL, 1908)	R	R	0.60
184	<i>Gonepteryx cleopatra</i> (LINNAEUS, 1767)	LR	HR	0.60
192	<i>Lycæna virgaureae</i> (LINNAEUS, 1758)	LR	HR	0.60
614	<i>Oeneis glacialis</i> (MOLL, 1785)	R	HR	0.59
88	<i>Carterocephalus silvicolus</i> (MEIGEN, 1829)	LR	HR	0.59
358	<i>Brenthis ino</i> (ROTTEMBERG, 1775)	R	HR	0.59
554	<i>Erebia montana</i> (PRUNNER, 1798)	R	HR	0.58
502	<i>Aphantopus hyperantus</i> (LINNAEUS, 1758)	LR	HR	0.58
612	<i>Oeneis norna</i> (BECKLIN, 1791)	HHHR	HHHR	0.58
408	<i>Araschnia levana</i> (LINNAEUS, 1758)	LR	HR	0.58
484	<i>Coenonympha glycerion</i> (BORKHAUSEN, 1788)	LR	R	0.57
486	<i>Coenonympha gardetta</i> (PRUNNER, 1798)	LR	HR	0.57
510	<i>Erebia ligea</i> (LINNAEUS, 1758)	LR	R	0.55
162	<i>Colias phicomone</i> (ESPER, 1780)	LR	HR	0.55
498	<i>Pyronia cecilia</i> (VALLANTIN, 1894)	R	HHHR	0.55

Table D.1.3: 44 European butterflies with the highest percentage of false absences (> 0.55): (incl. overall risk categories with full and without dispersal)

page	Species	Risk categ. full disp	Risk categ. no disp	false abs
256	<i>Scolitantides bavius</i> (EVERSMANN, 1832)	HR	HHR	0.90
386	<i>Boloria graeca</i> (STAUDINGER, 1870)	PR	PR	0.84
542	<i>Erebia epistygne</i> (HÜBNER, 1819)	HHHR	HHHR	0.83
44	<i>Carcharodus baeticus</i> (RAMBUR, 1840)	LR	HR	0.82
302	<i>Aricia anteros</i> (FREYER, 1838)	HR	HHHR	0.81
46	<i>Spialia phlomidis</i> (HERRICH-SCHÄFFER, 1845)	HR	HHHR	0.80
334	<i>Polyommatus ripartii</i> (FREYER, 1830)	PR	PR	0.80
480	<i>Coenonympha rhodopensis</i> ELWES, 1900	LR	HHHR	0.79
544	<i>Erebia ottomana</i> (HERRICH-SCHÄFFER, 1847)	LR	HR	0.79
202	<i>Lycena candens</i> (HERRICH-SCHÄFFER, 1844)	LR	HHR	0.78
174	<i>Colias chrysotheme</i> (ESPER, 1780)	HR	HHHR	0.75
240	<i>Cupido osiris</i> (MEIGEN, 1829)	LR	HHHR	0.75
188	<i>Lycena helle</i> ([SCHIFFERMÜLLER], 1775)	LR	LR	0.72
558	<i>Erebia melas</i> (HERBST, 1796)	LR	HR	0.71
212	<i>Tomares ballus</i> (FABRICIUS, 1787)	HHHR	HHHR	0.71
58	<i>Pyrgus sidae</i> (ESPER, 1782)	R	HHHR	0.70
594	<i>Hipparchia volgensis</i> (MAZOCHIN-PORSHNYAKOV, 1952)	LR	HHR	0.69
108	<i>Zerynthia cerisyi</i> (GODART, 1822)	LR	LR	0.69
124	<i>Leptidea duponcheli</i> (STAUDINGER, 1871)	PR	PR	0.69
332	<i>Polyommatus admetus</i> (ESPER, 1785)	R	HHHR	0.67
290	<i>Plebejus sephirus</i> (FRIVALDSZKY, 1835)	LR	HHR	0.67
148	<i>Pieris mannii</i> (MAYER, 1851)	LR	HHR	0.66
38	<i>Carcharodus lavatherae</i> (ESPER, 1783)	PR	PR	0.64
478	<i>Coenonympha oedippus</i> (FABRICIUS, 1787)	LR	R	0.63
492	<i>Coenonympha leander</i> (ESPER, 1784)	R	HHHR	0.63
336	<i>Polyommatus dolus</i> (HÜBNER, 1823)	LR	HHHR	0.63
194	<i>Lycena ottomana</i> (LEFEBVRE, 1830)	LR	HHR	0.62
216	<i>Callophrys avis</i> CHAPMAN, 1909	LR	HHHR	0.62
412	<i>Euphydryas Cynthia</i> ([SCHIFFERMÜLLER], 1775)	R	HR	0.62
100	<i>Gegenes pumilio</i> (HOFFMANSEGG, 1804)	LR	HR	0.62
602	<i>Hipparchia senthes</i> (FRUHSTORFER, 1908)	R	HHR	0.61
560	<i>Erebia oeme</i> (ESPER, 1805)	LR	R	0.61
416	<i>Euphydryas maturna</i> (LINNAEUS, 1758)	LR	LR	0.60
552	<i>Erebia styx</i> (FREYER, 1834)	R	HR	0.60
548	<i>Erebia cassioides</i> (REINER & HOHENWARTH, 1792) (species complex)	R	R	0.60
338	<i>Polyommatus damon</i> ([SCHIFFERMÜLLER], 1775)	R	HHR	0.60
572	<i>Melanargia larissa</i> (ESPER, 1784)	LR	HHR	0.59

page	Species	Risk categ. full disp	Risk categ. no disp	false abs
246	<i>Cupido alcetas</i> (HOFFMANSEGG, 1804)	LR	HR	0.58
120	<i>Papilio alexanor</i> ESPER, 1799	LR	HHR	0.57
368	<i>Boloria titania</i> (ESPER, 1793)	LR	R	0.57
436	<i>Melitaea varia</i> (MEYER-DÜR, 1851)	LR	HHR	0.56
182	<i>Gonepteryx farinosa</i> ZELLER, 1847	LR	HR	0.56
566	<i>Melanargia russiae</i> (ESPER, 1784)	LR	HHHR	0.56
136	<i>Euchloe belemia</i> (ESPER, 1798)	HHR	HHHR	0.56

Table D.1.4: 36 European butterflies with the highest percentage of false presences (> 0.39): (incl. overall risk categories with full and without dispersal)

page	Species	Risk categ. full disp	Risk categ. no disp	false pres
318	<i>Polyommatus icarus</i> (ROTTEMBURG, 1775)	PR	PR	0.76
186	<i>Lycæna phlæas</i> (LINNÆUS, 1761)	PR	PR	0.73
144	<i>Pieris brassicae</i> (LINNÆUS, 1758)	PR	PR	0.66
150	<i>Pieris rapae</i> (LINNÆUS, 1758)	PR	PR	0.66
154	<i>Pieris napi</i> (LINNÆUS, 1758)	PR	PR	0.65
466	<i>Pararge aegeria</i> (LINNÆUS, 1758)	PR	PR	0.64
388	<i>Vanessa atalanta</i> (LINNÆUS, 1758)	PR	PR	0.62
494	<i>Coenonympha pamphilus</i> (LINNÆUS, 1758)	PR	PR	0.58
248	<i>Celastrina argiolus</i> (LINNÆUS, 1758)	PR	PR	0.54
504	<i>Maniola jurtina</i> (LINNÆUS, 1758)	PR	PR	0.54
118	<i>Papilio machaon</i> LINNÆUS, 1758	PR	PR	0.54
214	<i>Callophrys rubi</i> (LINNÆUS, 1758)	PR	PR	0.54
142	<i>Aporia crataegi</i> (LINNÆUS, 1758)	PR	PR	0.52
66	<i>Pyrgus malvae</i> (LINNÆUS, 1758) (species complex)	PR	PR	0.52
390	<i>Vanessa cardui</i> (LINNÆUS, 1758)	PR	PR	0.51
32	<i>Erynnis tages</i> (LINNÆUS, 1758)	PR	PR	0.50
396	<i>Nymphalis c-album</i> (LINNÆUS, 1758)	LR	LR	0.49
296	<i>Aricia agestis</i> ([SCHIFFERMÜLLER], 1775)	PR	PR	0.48
402	<i>Nymphalis polychloros</i> (LINNÆUS, 1758)	PR	PR	0.47
98	<i>Ochlodes sylvanus</i> (ESPER, 1777)	PR	PR	0.47
122	<i>Leptidea sinapis</i> (LINNÆUS, 1758) & <i>Leptidea reali</i> REISSINGER, 1990 (species complex)	PR	PR	0.47
366	<i>Boloria euphrosyne</i> (LINNÆUS, 1758)	PR	PR	0.46
276	<i>Plebejus argus</i> (LINNÆUS, 1758)	PR	PR	0.46
168	<i>Colias croceus</i> (GEOFFROY, 1785)	LR	LR	0.45
262	<i>Glaucopsyche alexis</i> (PODA, 1761)	PR	PR	0.45
90	<i>Thymelicus lineola</i> (OCHSENHEIMER, 1806)	PR	PR	0.45

page	Species	Risk categ. full disp	Risk categ. no disp	false pres
180	<i>Gonepteryx rhamni</i> (LINNAEUS, 1758)	PR	PR	0.44
352	<i>Argynnis niobe</i> (LINNAEUS, 1758)	PR	PR	0.43
468	<i>Lasiommata megera</i> (LINNAEUS, 1767)	PR	PR	0.43
238	<i>Cupido minimus</i> (FUESSLY, 1775)	LR	R	0.42
422	<i>Melitaea cinxia</i> (LINNAEUS, 1758)	PR	PR	0.41
208	<i>Favonius quercus</i> (LINNAEUS, 1758)	PR	PR	0.41
324	<i>Polyommatus bellargus</i> (ROTTEMBURG, 1775)	PR	PR	0.41
392	<i>Aglais io</i> (LINNAEUS, 1758)	LR	R	0.40
36	<i>Carcharodus alceae</i> (ESPER, 1870)	PR	PR	0.40
348	<i>Argynnis aglaja</i> (LINNAEUS, 1758)	LR	R	0.40

D.2 Interaction of taxonomic status and modelling results

A special problem in niche modelling is presented by sister species or sibling species. They typically occupy very similar niches because they originated from the same ancestors, but are normally allopatric in distribution (no overlap in their areas). If we take the present distribution of just one of such a pair, we are bound to experience problems in the modelling, as the niche model will encompass the entire distribution of the climate space which may be occupied by the sister species. This leads to rather poor modelling results. If the distribution of these species is pooled, the model fits are normally much better.

Within this atlas we repeatedly came across this problem. The selection of some species was already affected, for example when some of the sister species had a very limited distribution (below our threshold of 20 UTM grids) and thus have been excluded from our analysis. However, their climate space might have been modelled through the other sister or sibling species.

We have selected the following examples to illustrate some of the effects:

First we have a more detailed look at the *Euchloe ausonia* complex. The maps and results presented in part C.2 include *Euchloe ausonia* (s.str.), *Euchloe crameri*, and *Euchloe simplonia*. If we differentiate between the results for the complex and the two three included here, we can see substantial differences in the output. These are summarized in table D.2.1 and also presented as maps (Figures D.2.1-4).

The results suggest that *E. ausonia* (s.str.) would suffer much less from climate change and under all scenarios would gain in climate space assuming full dispersal. In contrast, the climate space of *E. crameri* and *E. simplonia* would decrease under nearly all scenarios. The models for the three species together lies in between these results. Although there are large areas of false presences, these are compensated by right presences and right absences in *E. crameri* and *E. ausonia*.

Table D.2.1: Results of climate modelling for the *Euchloe ausonia* complex and *Euchloe ausonia* (in the strict sense), *Euchloe crameri* and *Euchloe simpplonia* separately

		<i>Euchloe ausonia</i> complex		<i>Euchloe ausonia</i> s.str.		<i>Euchloe crameri</i>		<i>Euchloe simpplonia</i>	
Presently occupied grid cells	AUC	4483		2392		4174		529	
		0.85		0.90		0.84		0.91	
		Full dispersal	No dispersal	Full dispersal	No dispersal	Full dispersal	No dispersal	Full dispersal	No dispersal
2050	SEDG	742 (16.55%)	-802 (-17.89%)	804 (33.61%)	-283 (-11.83%)	-571 (-13.68%)	-1986 (-47.58%)	-10 (-1.89%)	-329 (-62.19%)
	BAMBU	-91 (-2.03%)	-1080 (-24.09%)	778 (32.53%)	-232 (-9.7%)	-1436 (-34.4%)	-2201 (-52.73%)	61 (11.53%)	-301 (-56.9%)
	GRAS	586 (13.07%)	-1029 (-22.95%)	1026 (42.89%)	-296 (-12.37%)	-1142 (-27.36%)	-2389 (-57.24%)	-92 (-17.39%)	-358 (-67.67%)
2080	SEDG	338 (7.54%)	-1439 (-32.1%)	1760 (73.58%)	-419 (-17.52%)	-2045 (-48.99%)	-2897 (-69.41%)	-187 (-35.35%)	-443 (-83.74%)
	BAMBU	-327 (-7.29%)	-2058 (-45.91%)	1783 (74.54%)	-626 (-26.17%)	-2492 (-59.7%)	-3478 (-83.33%)	-113 (-21.36%)	-402 (-75.99%)
	GRAS	-265 (-5.91%)	-2472 (-55.14%)	2771 (115.84%)	-787 (-32.9%)	-2936 (-70.34%)	-4001 (-95.86%)	-255 (-44.42%)	-446 (-84.31%)

(s.str.). In the *E. ausonia* complex and in *E. simplonia* there are less false presences but more false absences. This leads to the effect that the AUC values are rather similar in all cases.

Few false absences

In many instances we come across sister species that can be modelled quite well independently from each other, with little overlap between the derived climate niches. A good example is *Scolitantides baton* and *Scolitantides vicrama*, (Table D.2.2. and Figures D.2.5 & 6). Here the models show differences in climate requirements which suggests different evolutionary histories for the two species.

Similar in terms of output statistics are the sister species *Lycaena hippothoe* and *Lycaena candens* (Table D.2.3; Figures D.2.7-8). However the map of the absolute distribution is very different between the two species and the distribution points of *L. candens* are to a large extent included in the climate space of *L. hippothoe*. This contributes to the large number of false presences which in general lead to the low AUC. The climate space model of *L. candens* is relatively poor if we look at right presences as well as false absences and the high AUC is due to the many right absences across Europe. Here a combination of both species would clearly lead to an improvement of the climate models and highlights the “disadvantage” of the separate modelling of sister species which we can observe in several other cases. Two other examples of sister species are shown below: a) *Spialia sertorius* and *Spialia orbifer* (Table D.2.4; Figures D.2.9-10); and b) *Hipparchia semele* and *Hipparchia senthes* (Table D.2.5; Figures D.2.11-12).

Table D.2.2: Results of climate modelling for the sister species *Scolitantides baton* and *Scolitantides vicrama*

		<i>Scolitantides baton</i>		<i>Scolitantides vicrama</i>	
Presently occupied grid cells		2643		5393	
AUC		0.83		0.85	
		Full dispersal	No dispersal	Full dispersal	No dispersal
2050	SEDG	-226 (-8.55%)	-1037 (-39.24%)	2985 (55.35%)	-353 (-6.55%)
	BAMBU	15 (0.57%)	-964 (-36.47%)	383 (7.1%)	-1599 (-29.65%)
	GRAS	-401 (-15.17%)	-1295 (-49%)	1968 (36.49%)	-962 (-17.84%)
2080	SEDG	-81 (-3.06%)	-1179 (-44.61%)	2198 (40.76%)	-1457 (-27.02%)
	BAMBU	-88 (-3.33%)	-1433 (-54.22%)	309 (5.73%)	-2974 (-55.15%)
	GRAS	-847 (-32.05%)	-2209 (-83.58%)	2622 (48.62%)	-3135 (-58.13%)

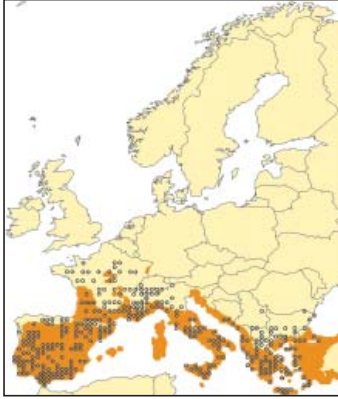


Figure D.2.1: Actual distribution and modelled present climatic niche of the *Euchloe ausonia* complex

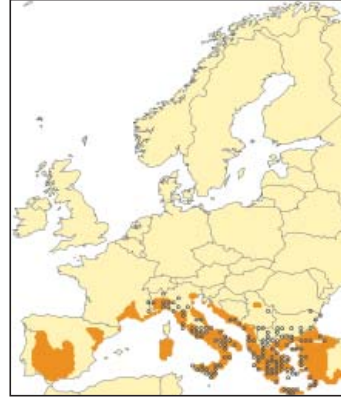


Figure D.2.2: Actual distribution and modelled present climatic niche of *Euchloe ausonia* (in the strict sense)



Figure D.2.3: Actual distribution and modelled present climatic niche of *Euchloe crameri*

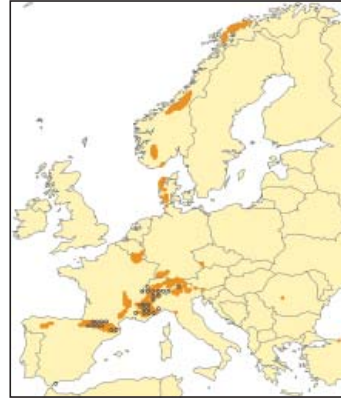


Figure D.2.4: Actual distribution and modelled present climatic niche of *Euchloe simplonia*

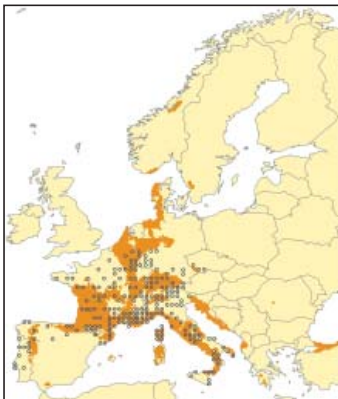


Figure D.2.5: Actual distribution and modelled present climatic niche of *Scolitantides baton*

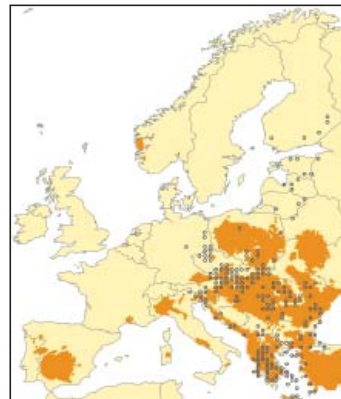


Figure D.2.6: Actual distribution and modelled present climatic niche of *Scolitantides vicrama*

Table D.2.3: Results of climate modelling for the sister species *Lycaena hippothoe* and *Lycaena candens*

		<i>Lycaena hippothoe</i>		<i>Lycaena candens</i>	
Presently occupied grid cells		14109		657	
AUC		0.85		0.86	
		Full dispersal	No dispersal	Full dispersal	No dispersal
2050	SEDG	-4111 (-29.14%)	-5600 (-39.69%)	192 (29.22%)	-289 (-43.99%)
	BAMBU	-3282 (-23.26%)	-4839 (-34.3%)	-161 (-24.51%)	-376 (-57.23%)
	GRAS	-4808 (-34.08%)	-6020 (-42.67%)	-75 (-11.42%)	-414 (-63.01%)
2080	SEDG	-5935 (-42.07%)	-7427 (-52.64%)	70 (10.65%)	-343 (-52.21%)
	BAMBU	-6505 (-46.11%)	-8317 (-58.95%)	-391 (-59.51%)	-564 (-85.84%)
	GRAS	-8606 (-61%)	-9862 (-69.9%)	-394 (-59.97%)	-624 (-94.98%)

Table D.2.4: Results of climate modelling for the sister species *Spialia sertorius* and *Spialia orbifer*

		<i>Spialia sertorius</i>		<i>Spialia orbifer</i>	
Presently occupied grid cells		6768		2728	
AUC		0.77		0.89	
		Full dispersal	No dispersal	Full dispersal	No dispersal
2050	SEDG	-426 (-6.29%)	-1771 (-26.17%)	2229 (81.71%)	-341 (-12.5%)
	BAMBU	-331 (-4.89%)	-1755 (-25.93%)	528 (19.35%)	-987 (-36.18%)
	GRAS	-1114 (-16.46%)	-2425 (-35.83%)	1211 (44.39%)	-976 (-35.78%)
2080	SEDG	-553 (-8.17%)	-2424 (-35.82%)	1025 (37.57%)	-1188 (-43.55%)
	BAMBU	-1006 (-14.86%)	-3188 (-47.1%)	-59 (-2.16%)	-1848 (-67.74%)
	GRAS	-2218 (-32.77%)	-4639 (-68.54%)	1443 (52.9%)	-2000 (-73.31%)

Table D.2.5: Results of climate modelling for the sister species *Hipparchia semele* and *Hipparchia senthes*

		<i>Hipparchia semele</i>		<i>Hipparchia senthes</i>	
Presently occupied grid cells		13833		840	
AUC		0.79		0.94	
		Full dispersal	No dispersal	Full dispersal	No dispersal
2050	SEDG	-2284 (-16.51%)	-3095 (-22.37%)	-62 (-7.38%)	-350 (-41.67%)
	BAMBU	-3269 (-23.63%)	-4031 (-29.14%)	-2 (-0.24%)	-293 (-34.88%)
	GRAS	-3564 (-25.76%)	-4405 (-31.84%)	-85 (-10.12%)	-386 (-45.95%)
2080	SEDG	-5233 (-37.83%)	-6024 (-43.55%)	207 (24.64%)	-421 (-50.12%)
	BAMBU	-6634 (-47.96%)	-7748 (-56.01%)	-280 (-33.33%)	-631 (-75.12%)
	GRAS	-8424 (-60.9%)	-9748 (-70.47%)	-444 (-52.86%)	-767 (-91.31%)



Figure D.2.7: Actual distribution and modelled present climatic niche of *Lycaena hippothoe*



Figure D.2.8: Actual distribution and modelled present climatic niche of *Lycaena candens*



Figure D.2.9: Actual distribution and modelled present climatic niche of *Spialia sertorius*

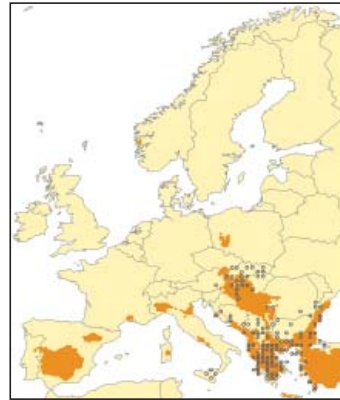


Figure D.2.10: Actual distribution and modelled present climatic niche of *Spialia orbifer*

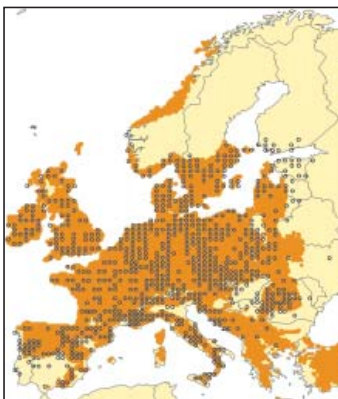


Figure D.2.11: Actual distribution and modelled present climatic niche of *Hipparchia semele*

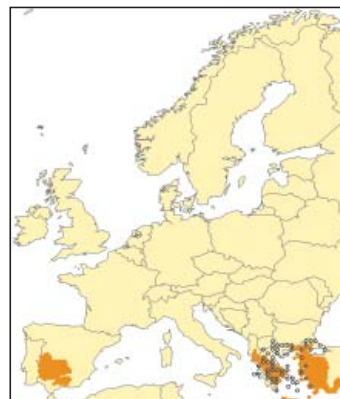


Figure D.2.12: Actual distribution and modelled present climatic niche of *Hipparchia senthes*