Global Change Impacts on Biodiversity and their Implications for Species Conservation

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ERKLÄRUNG

Hiermit versichere ich, dass ich für die Anfertigung der vorliegenden Dissertation keine anderen als die angegebenen Hilfsmittel genutzt habe, und dass die Ergebnisse anderer Beteiligter sowie die inhaltlich und wörtlich aus anderen Werken entnommenen Stellen und Zitate als solche gekennzeichnet sind. Die Arbeit hat in gleicher oder ähnlicher Form noch keiner anderen Prüfungsbehörde vorgelegen oder wurde von dieser als Teil einer Prüfungsleistung angenommen.

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Katharina J. Filz

„ It seems to me that the natural world is the greatest source of excitement,
the greatest source of visual beauty,
the greatest source of intellectual interest.
It is the greatest source of so much in life that makes life worth living.“

− David Attenborough

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PRELIMINARY REMARKS

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The work was performed under the supervision of PROF. DR. THOMAS SCHMITT, who was substantially involved in all aspects of the thesis, i.e. planning of the studies, data analyses and writing of the manuscripts. This thesis consists of an introduction giving a general overview about the scientific background and the aims of the thesis and two sections written as scientific papers reporting the findings of the project. Parts of this thesis are already published or submitted for publication as listed in the following. A statement that clarifies the contributions of the authors or other persons to the collection and analyses of data or the preparation of manuscripts is given at the beginning of each manuscript.

Table 1 Articles contributing to this thesis with all authors and current publication status.

Part	Published in or submitted to	Status
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I.3	**Katharina J. Filz** & Thomas Schmitt. Untersuchung der Arealdynamik des Kurzschwänzigen Bläulings (*Cupido argiades*, Pallas 1771) unter Klimawandelbedingungen mittels Artverbreitungsmodellen – *Abhandlungen der Delattinia* 38, 215-228 (2012).	published
I.4	**Katharina J. Filz**, Thomas Schmitt & Stefan Lötters. Niche evolution in a host-parasite system: answers from Ecological Niche Models	unpublished
I.5	Stefan Lötters, **Katharina J. Filz**, Norman Wagner, Benedikt Schmidt, Jason R. Rohr, Rick A. Releya, Christoph Emmerling, Carsten Brühl & Michael Veith. Climate change and the 'pesticide-phenology problem' in amphibians – boon or bane?	unpublished
II.1	**Katharina J. Filz**, David Jänicke, Thomas Schmitt, Miriam Frede & Matthias Weitzel. Untersuchung zur Bestandsentwicklung der Tagfalterzönosen auf Kalkmagerrasen im Saar-Mosel Gebiet - *Mainzer Naturwissenschaftliches Archiv* 50, 383-397 (2013).	published
II.2	**Katharina J. Filz**, Jan O. Engler, Johannes Stoffels, Matthias Weitzel & Thomas Schmitt. Missing the target? A critical view on butterfly conservation efforts on calcareous grasslands – *Biodiversity and Conservation* 22, 2223–2241 (2013).	published
II.3	**Katharina J. Filz**, Thomas Schmitt & Jan O. Engler. How fine is fine-scale? – Validating the use of fine-scale bioclimatic data in species distribution models to forecast abundance patterns in butterflies – *European Journal of Entomology* 110 (2): 311–317 (2013).	published
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INTRODUCTION

I. Biodiversity and climate change

Anthropogenic climate change is predicted to become a major threat to biodiversity in the 21st century (SALA et al. 2000, STEFFEN 2004, THOMAS et al. 2004, see also Fig. 1). Since the beginning of the industrial revolution in the 1850s, changes in climate have become unequivocal (IPCC 2007). Widespread temperature increases have been documented all over the globe accompanied by rising sea levels (CAZENAVE & NEREM 2004), shrinking sea ice extents (CORRELL et al. 2004) and melting mountain glaciers (PAUL et al. 2004) consistent with warming. During the 20th century, the global average annual surface temperature has increased by 0.6-0.7°C with most severe temperature changes at higher latitudes (IPCC 2007). Following the 4th assessment of the IPCC, average temperatures in the northern hemisphere during the second half of the 20th century are likely the highest in at least the past 1300 years. During the same time span, the amount of cold days and nights as well as frosts has declined. On average, night-time daily minimum air temperatures over land increased by about 0.2°C per decade between 1950 and 1993. This is about twice the rate of increase in day-time daily maximum air temperatures (0.1°C per decade) lengthening the freeze-free season in many mid- and high latitude regions (HOUGHTON et al. 2001). Moreover, observational evidence is arising that worldwide extreme events such as heat waves, droughts, heavy precipitation events, cyclone activities and extreme high sea levels have become more frequent.

Climate has shown considerable variability during the earth's history (GANOPOLSKI & RAHMSDORF 2001, RAHMSDORF 2002, ROYER et al. 2004). Changes in the climate system occur as a result of a combination of internal variability and external factors (e.g. natural and anthropogenic impacts). HOUGHTON et al. (2001) compared the influence of external factors on climate using the concept of radiative forcing (i.e. the influence certain factors have in altering the balance of incoming and outgoing energy in the Earth-atmosphere system). Positive radiative forcing tends to increase global temperatures whereas negative radiative forcing tends to cool the surface. Natural factors like volcanic eruptions or changes in solar irradiance can cause positive radiative forcing. However, the rate in which climate has changed over the last decades can not be explained by natural factors alone (IPCC 2007). Since the 1750s the concentrations of atmospheric greenhouse gases (e.g. carbon dioxide, methane, nitrous oxide) and sulphate aerosols have significantly increased due to massive anthropogenic emissions mainly resulting from fossil fuel burning and

land use changes (SUESS 1955, BAZZAZ 1990). The human impact on the composition of the atmosphere during the industrial era has lead to a positive radiative forcing changing climate at rates unique in Earth's history (HOUGHTON et al. 2001, PHILIPONA et al. 2004).

Human activities will continue to influence climate in the future. As indicated by different emission scenarios (based on the Special Report on Emission Scenarios, SRES) developed by the Intergovernmental Panel on Climate Change (IPCC), the dominant influence of increasing or persistent greenhouse gases and aerosols in the atmosphere is expected to drive climate change in the upcoming decades. Further increases in average annual surface temperatures by 1.4-5.5°C until 2100 are predicted, thereby exceeding the rate of temperature increase during the 20th century (IPCC 2007). Temperature increases are expected to be most pronounced in middle and higher latitudes accompanied by reduced intra-annual and diurnal temperature ranges over most land areas (HOUGHTON et al. 2001). Globally, the amount of annual rainfall will increase during the 21st century. Several models predict large scale shifts in precipitation patterns with strong year to year variability leading regionally to prolonged summer droughts or heavy precipitation events. An increase in extreme phenomena and cyclone intensities is expected to lead to severe impacts on society and environments.

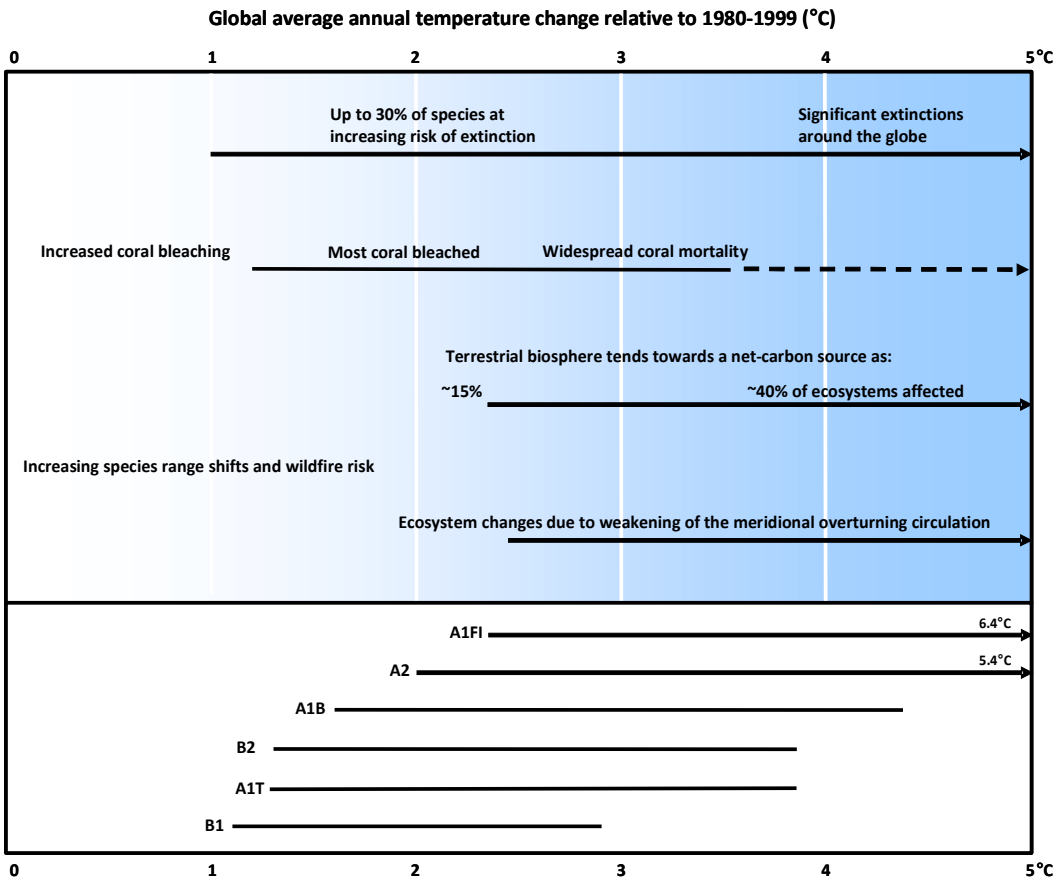

Fig. 1 Changes in natural systems relative to increases in global average annual temperatures (above) predicted by the respective climate change scenarios released by the IPCC (below). Modified after HOUGHTON et al. 2001.

Climate change impact on biological environments is a late-breaking, but not a new topic. Already in 1917, GRINNELL first observed the role of climatic thresholds in constraining range boundaries of species. Observations of range shifts driven by climatic changes in several bird, butterfly and plant species date back to the 18th century (reviewed in PARMESAN 2006). Based on historical records dating back to 1760, KAISLA (1962) has shown range shifts of several moth species in Finland documenting southward contractions during cold climatic conditions and northward range expansion in warmer decades. Since the beginning of the 20th, century researches have observed changes in phenology of insects according to warmer spring temperatures and northward expansions of ranges to areas not being occupied prior to this due to unsuitable climatic conditions (THOMAS et al. 2001 a, PARMESAN & YOHE 2003, VISSER & BOTH 2005, CHEN et al. 2011, DIAMOND et al. 2011). A burst of scientific papers has followed in the last decades documenting the direct and indirect impacts of anthropogenic climate change on every continent, ocean and almost all taxonomic groups (PARMESAN 2000, PARMESAN & YOHE 2003, PARMESAN 2006, IPCC 2007, FODEN et al. 2008, THOMAS et al. 2010).

However, species and ecosystems are not equally at risk when facing changing climates (DEVICTOR et al 2012). Given their high number and diversity, potential climate change impacts and species responses vary significantly and are difficult to predict (Fig. 2). Climatic vulnerability, i.e. to which extent a species or ecosystem is affected, heavily depends on both intrinsic (species biology, ecological specialization, genetic diversity) and extrinsic (e.g. rate, magnitude and nature of climate change, competition, trophic relationships, additional stressors) factors (FODEN et al 2008, DAWSON et al. 2011). Species climatic responses are closely linked to their ecological niche. Following the definition by HUTCHINSON (1957, 1978), in modern niche theory (PETERSON et al. 2011), a species' fundamental niche is defined by the abiotic environmental conditions under which the respective species can persist in the absence of biotic interactions. Its realized niche, or potential distribution, is considered to be a part of its fundamental niche, however taking into account biotic interactions. A species potential distribution has not always to be completely congruent with its realized distribution for example due to dispersal limitations. This implies that a species' adaptation potential to changing environments can go beyond conditions observed within its current range (PETERSON et al. 2011). That means, under climate change a species might persist in areas where environmental factors do not exceed its physiological constraints and where it does not suffer from competitors, predators or pathogens, maybe not suitable or accessible today.

In this aspect, poikilothermic taxa as insects, amphibians and reptiles are suggested to be more directly affected by climate warming than homoiothermic ones (DENNIS 1993, GUTIERREZ et al. 2008, BLAUSTEIN et al. 2010). By affecting the thermal tolerances of these species, going in line with activity patterns or reproduction success, climate change might directly result in changes in

local abundances, widespread range shifts, phenological responses or even local extinctions (THOMAS et al. 2004, ARAÚJO et al. 2006, VISSER & BOTH 2005, PARMESAN 2006, CHUINE 2010, DIAMOND et al. 2011). Examples are manifold. According to SINERVO et al. (2010), 20% of all lizard species might be threatened by extinction in 2080 being driven out of their thermal niche. Globally, substantial decreases in species abundances and a reduction of species richness is predicted for chelonian species (IHLOW et al. 2012). Recent studies of British butterflies suggest that approximately half of the recent population-level extinctions are likely to be caused by climate change (THOMAS et al. 2006). Especially in warmer climates like the Mediterranean area, a serious loss of butterfly diversity is expected due to species already reaching their climatic maxima (WARREN et al. 2001). Unsurprisingly, first entire species extinctions attributed to global warming appeared in mountain restricted species, not able to cope with temperature increases or to adjust their ranges (PARMESAN 2006).

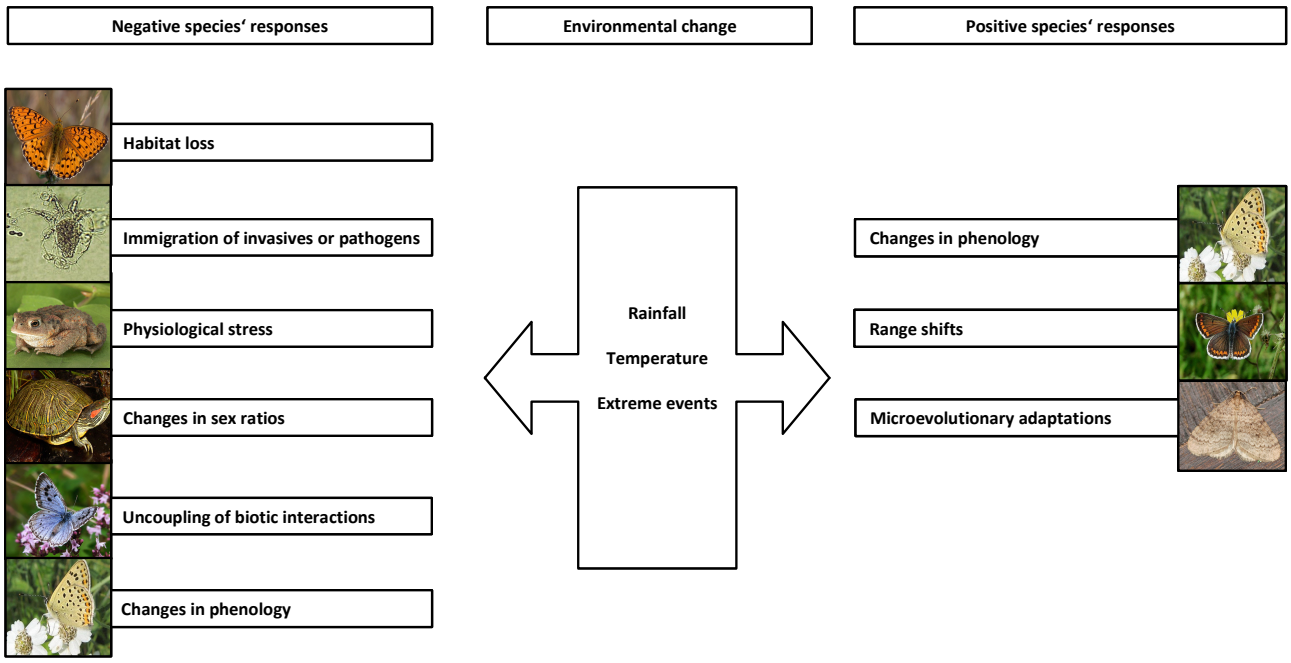

Fig. 2 Potential positive and negative impacts of increasing annual surface temperatures, variations in rainfall patterns and an increase in the frequency of extreme events; exemplary a selected species is given for which impacts are proven (from top to bottom and left to right: *Argynnis adippe, Batrachochytrium dendrobatidis, Bufo bufo, Trachemys scripta, Maculinea arion, Lycaena tityrus, Aricia agestis, Operophtera brumata*).

Direct observations, experiments or mechanistic models have shown that some species have the capability to cope with climate change due to phenotypic plasticity (e.g. acclimatization, developmental adjustments) or microevolutionary adaptations (FRANKS et al. 2007, VISSER 2008, PHILLIMORE et al. 2010, SOMERO 2010, HILL et al. 2011). In most cases, evolutionary adaptations are not expressed by the evolution of new phenotypes, but rather a higher predominance of already existing heat-tolerant genotypes (PARMESAN 2006). Each adaptation process has constraints, limiting a species' ability to keep up with certain magnitudes of climate change (VISSER 2008). Hence, for

most of the species, it seems more likely to trace climatic changes by shifting their distributions, rather than adapting *in situ* (PARMESAN 2006, THOMAS 2010).

Climate changes have profound impacts on species distributions. Observations show that range shifts do not occur at random, but directed by regional changes in the climate (PARMESAN & YOHE 2003, THOMAS 2010), i.e. species adjust their ranges in response to spatial shifts of their suitable climates. Migratory species are expected to cope with year-to-year variations in climate more easily as they are capable to alter their timing and destination of migration (PARMESAN et al. 1999). In more sedentary wildlife, rapid reactions are less likely. The geographic ranges of many species have shifted polewards or to higher elevations associated with global warming over time (WARREN et al. 2001, PARMESAN 2006, WILSON et al. 2007, THOMAS 2010, CHEN et al. 2011, DEVICTOR et al. 2012). Geographical range shifts occur at population levels and express positive colonization rates at one range boundary, often coupled with extinctions at the other (PARMESAN et al. 1999). Meta-analysis of range boundary changes in the Northern Hemisphere revealed averaged changes of 6.1 km per decade northward or 6.1 m per decade upward (PARMESAN & YOHE 2003). In the most extreme cases, the southern range boundary contracted congruent with range expansions at the northern edge (PARMESAN 2006). Thus, observations in the Sooty copper (*Lycaena tityrus*) reported severe range contractions in Spain since 1920 and symmetrically the establishment of several successful breeding populations in the Baltic states (PARMESAN et al. 1999). Range expansions might be facilitated by local evolutionary adaptations as recognized in the Brown argus (*Aricia agestis*). In this species, warming did not initially cause range expansions, but a rapid evolution of a broader diet enabling the butterfly to shift its current range northward (THOMAS et al. 2001 a).

Range shifts or expansions are largely trait dependent, i.e. species responses to changing climates highly differ with regard to dispersal abilities, diapausing or habitat specialization (WARREN et al. 2001, PARMESAN 2006, TOBIN et al. 2008). Under the hypothesis that climate is the major factor limiting a species' distribution, in particular warm-habitat dwellers are expected to respond positively to global warming with rapid range expansions especially in mobile habitat generalists. Changes in species abundances thereby often match changes in distribution size (WARREN et al. 2001). As a result, communities have become increasingly dominated by mobile, thermophilic species inhabiting wider countrysides (WARREN et al. 2001, DEVICTOR et al. 2012).

Especially in mountain regions, rapid range shifts of species consistent with an uphill shift in isotherms have been observed (PARMESAN 2006). WILSON et al. (2007) attributed the more rapid responses of butterfly species to climate change in cooler latitudes and in mountain regions compared to lowland landscapes to rather intact habitats and steeper temperature gradients within short distances. In some cases range shifts have lead to local increases in species richness at higher

elevations or latitudes, but often go in line with the extinction of cold-adapted species or high-elevation specialists (WILSON et al. 2007, OHLEMÜLLER et al. 2008).

Comparative observations showing range retractions at low latitudes or low elevations are relatively scarce (PARMESAN 2006, THOMAS et al. 2006). Given that widespread climate-driven biodiversity losses are predicted (THOMAS et al. 2004), reasons for the lack of knowledge regarding range retractions do not become immediately obvious. JACKSON & SAX (2010) attributed this knowledge gap to sampling biases as decline rates might be underestimated due to locally restricted distributions of species, coarse-scale measures or the failure to attribute range retractions to climate. However, retreating distributions have been observed for several taxa including butterflies and frogs (Thomas et al. 2006, THOMAS 2010, TRAUTMANN et al. 2012). Exemplary, PARMESAN (1996) documented more than 40% of the populations of Edith's checkerspot butterfly (*Euphydryas editha*) being extinct in elevations from 0-2400 m throughout its range, whereas only 15% declined at higher elevations (2400-3500 m). In southern France, populations of the cold-habitat dweller *Parnassius apollo* declined remarkably at elevations below 850 m, but remained stable on plateaus higher than 900 m (DESCIMON et al. 2006). Local range retractions can even lead to regional population declines and potentially to extinction events as shown for harlequin frogs (*Atelopus* ssp.) in the tropics (RON et al. 2003, POUNDS et al. 2006).

Beyond individual fates, climate change should also affect species interactions and the composition of communities. As mentioned above, DEVICTOR et al. (2012) postulated severe shifts in community composition in European butterflies towards an increasing presence of thermophilic species as shown by changes in their community temperature indices. The occurrence of wide-ranging generalists has increased at the expense of specialized and sedentary species whose range expansions or shifts have been hindered by habitat loss or fragmentation (FILZ et al. 2013). Assemblages of closely interacting species are suspected to be most vulnerable to climate change. Predator-prey, plant-insect or host-parasite interactions have been disrupted when species respond differently to warming (PARMESAN 2006). Species differ in their physiological tolerances and life history traits. These underlie different climatic forcings possibly driving species' life cycles in asynchrony. The persistence of closely interacting species highly depends on climatic conditions matching the thermal niche of both species groups (SETTELE & KÜHN 2009). In this aspect, greatest declines were recorded in myrmecophilic butterflies, i.e. species depending in their development on host ants, as *Maculinea* butterflies. THOMAS et al. (2009) traced back the potential extinction of the Large Blue (*Maculinea arion*) in the UK during the second half of the 20th century to climatic changes.

Most observations involve alterations of species' phenologies tightly linking the appearance of species and seasonal climates. Several studies indicate a lengthening of the growing season

particularly in higher latitudes congruent with temperature increases (MENZEL et al. 2006). This also implies for the earlier appearance of several insect or bird species as well as an advanced breeding in amphibians (CAREY et al. 2003, PARMESAN 2006). According to a cross-taxonomic study of PARMESAN & YOHE (2003), 59% of 1598 species studied exhibited changes in their phenologies. Further analysis of phenological responses resulted in estimates of an averaged earlier appearance of 2.3 days per decade (PARMESAN & YOHE 2003). Especially butterflies show a high correlation between dates of first appearance and warming spring temperatures (ROY & SPARKS 2000, STEFANESCU et al. 2003, CHEN et al. 2011). In Britain, most butterfly species have significantly advanced their appearance during the last 30 years (DIAMOND et al. 2011). In this aspect, species' ecological traits as larval diet breadth or overwintering stages are likely to influence species phenology (DIAMOND et al. 2011). Thereby, the potential disruption of trophic interactions in herbivorous insects and their host plants, pollinators and flowering plants or parasites and their hosts might be more crucial than individual changes in timing alone (VISSER & BOTH 2005). In Britain, the orange-tip butterfly *Anthocharis cardamines* has accurately tracked the phenological shifts of its host plant (SPARKS & YATES 1997), but in general an increasing asynchrony can be observed (VISSER & BOTH 2005). Field studies already revealed trophic mismatches between insects and their nectar sources leading either to range shifts (as shown in *Euphydryas editha*, SINGER et al. 1979) or to population crashes (THOMAS et al. 1996, HAGEN et al. 2010). According to VAN NOUHUYS & LEI (2004), an increased host-parasitoid synchrony between the wasp *Cotesia melitaerum* and the butterfly *Melitaea cinxia* consistent with warmer spring temperatures has lead to population declines in the butterfly due to intensified parasite infestation. Furthermore, shifts in sex ratios as a consequence of altered parasite infestation have been observed in this protandrous butterfly.

Also amphibian breeding has advanced (BLAUSTEIN et al. 2001, CAREY et al. 2003). Ecophysiological studies revealed a close link between reproduction success and both night-time and day-time temperatures (BEEBEE 1995). In the United States, an earlier initiation of calling and breeding by one to three weeks per decade was reported (GIBBS & BRIESCH 2001), thus matching results from Germany and Great Britain (BEEBEE 1995, READING 1998, MÜNCH 2001). Phenological responses can have important implications for reproduction success, population persistence, individual fitness und community composition (READING 1998, VISSER & BOTH 2005, MØLLER et al. 2008, MILLER-RUSHING et al. 2010). TRAUTMANN et al. (2012) summarized positive and negative impacts of phenological changes on German amphibian populations. The authors acknowledge population benefits from earlier breeding due to a prolonged time to grow and store energy before hibernation. However, increased mortality rates resulting from sudden temperature drops and potential asynchronization with food resources might counteract the advantage of an earlier metamorphosis.

Climate change has proven to be a major driver of biological invasions and the spread of pest species. A multitude of pathways, mainly human-mediated, serves to introduce species to new environments, often followed by adverse impacts on native ecosystems, anthropogenic health and values (LOWE et al. 2000, PIMENTEL et al. 2005). Successful establishment of populations at the receiving location necessitates a good match of the habitat requirements of a non-native species with the biotic and abiotic parameters found in the new environment (BOMFORD et al. 2009). Thereby, climate represents an important factor for invasion success (HAYES & BARRY 2008). Climate change is suggested to promote biological invasions and the distribution of pest species by facilitating range shifts, disturbing native ecosystems and creating potentially new niches (HELLMANN et al. 2008, DIEZ et al. 2012, TRAUTMANN et al. 2012). Already in recent times under relatively 'mild' climatic changes, a magnitude of studies reveals severe range expansions of invasive and pest species with considerable impacts on humans and ecosystems (FICETOLA et al. 2007, 2009, RÖDDER et al. 2009, RÖDDER & LÖTTERS 2010, BIDINGER et al. 2012). BATTISTI et al. (2005) reported a significant northward range expansion of the Pine processionary moth (*Thaumetopoea pityocampa*) since the 1970s, probably associated with warmer winters. Evolutionary adaptations in pest species as shortened life cycles or increased population abundances are suggested to even enhance negative impacts on native ecosystems (LOGAN et al. 2003, reviewed in PARMESAN 2006).

Climate-driven dispersal or human-mediated introductions are also suspected to indirectly promote population declines by facilitating the spread of infectious diseases (PARMESAN & MARTENS 2006, DOBSON 2009, FISHER et al. 2009, ROHR et al. 2011). Globally, environmental factors play a crucial role in the emergence and spread of pathogens and infectious diseases. High mortality rates in larvae of the Western toad (*Bufo boreas*) have been traced back to a cause-and-effect chain of El Niño/Southern Oscillation phenomena and the spread of the fungus *Saprolegnia ferax* (KIESECKER et al. 2001). Infectious diseases such as amphibian chytridiomycosis, caused by the fungus *Batrachochytrium dedrobatidis* (*Bd*) play an increasing role driving amphibian populations towards extinction (STUART et al. 2004, FODEN et al. 2008, FISHER et al. 2009). Outputs from the *Bd* Global Mapping Project have shown that the presence of *Bd* is significantly associated with environmental variables such as temperature and annual precipitation, thus closing the link between the emergence of *Bd*, climate change and global amphibian declines (FISHER et al. 2009). Moreover, the vulnerability of a species strongly depends on its individual fitness and immunological response, which in amphibians is strongly driven by extrinsic factors (RÖDDER et al. 2008, RIBAS et al. 2009). READING (2007) supposed a lower immunity in common toads (*Bufo bufo*) as a consequence of increasing temperatures.

Observations of climate change impacts on species and ecosystems have lead to alarming

predictions about the future of the Earth's biodiversity that require immediate action and strategic conservation planning. However, population declines should be interpreted with care. In terrestrial ecosystems land use is suspected to have large impacts on biodiversity (SALA et al. 2000, PIMM & RAVEN 2000). Many population and species declines can be attributed to habitat destruction, fragmentation, land use changes or overexploitation (VITOUSEK et al. 1997, FAHRIG 2003). However, globally worst impacts on natural ecosystems are not caused by land use alone, but can be traced back to a combination of land use and climate change (TRAVIS 2003, OPDAM & WASCHER 2004, JELTSCH et al. 2010, MANTYKA-PRINGLE et al. 2012). Interactions between these factors and their impacts on ecosystems still represent large uncertainties and might even intensify environmental threats to biodiversity.

II. Land use and species distributions

Besides changes in the climatic system, human activities altering landscape and habitat structures strongly influence global biodiversity (VITOUSEK et al. 1997, MANTYKA-PRINGLE et al. 2012). Habitat loss is acknowledged to be one of the greatest threats to flora and fauna. Globally, natural habitats fall victim to destruction, fragmentation and over-exploitation of natural resources (FAHRIG 2003). Roads, motorways, railways, intensive agriculture and urban development are breaking the landscape into small and isolate fragments often unable to support high levels of biodiversity (EAA 2011). For some species, they even lack to provide a minimum area to support a viable population (DOVER & SETTELE 2009).

Fragmentation, reduction and isolation with their concomitant impacts on species and communities in terms of habitat size, quality and connectivity, today are the most obvious effects of land use changes (ARAÚJO et al. 2006, DOVER & SETTELE 2009). However, the European perspective in agriculture and land use has also demonstrated positive effects of land use on biodiversity. Europe is one of the most intensively used continents on the globe and affected by a long tradition of anthropogenic agriculture (POTT 1998). Whilst human activities often have adverse impacts on species and ecosystems, across Europe extensive land use has also created landscape structures that favor the persistence of many species such as butterflies. Traditional management practices like sheep herding have shaped European country sides for hundreds of years, and it may be suspected that some butterfly species would have become extinct if these practices discontinued (ASHER et al. 2001). THOMAS (1991) traced back the dependency of butterflies on traditional management practices to the generation of widespread, open habitats containing different and mainly early successional stages. These patches provide favorable, i.e. warm, microclimatic conditions even in generally cooler climates. As a result, traditional landscapes have developed into species-rich habitats harboring unique species assemblages with different ecological and biogeographical

characteristics (VARGA 2003, SCHMITT & RÁKOSY 2007). However, despite the high ecological and cultural conservation value, these habitats are currently at risk of being lost (WENZEL et al. 2006, FILZ et al. 2013).

The presence of suitable habitats is without question a prerequisite for species occurrence. Suitable habitat is defined specifically for a respective species by means of quality, size and isolation (DENNIS & EALES 1997, LIZÉE et al. 2011). A patch or an arrangement of patches must provide resources (e.g. host plants, nectar sources, microclimate, shelter, overwintering) to complete a butterflies life cycle (WALLISDEVRIES & VAN SWAAY 2006). Excluding seasonal migrations, DENNIS & SHREEVE (1996) indicated possible scenarios of resource accessibility where (i) one habitat patch provides all resources needed, (ii) several patches containing a single resource with partial overlap creating a core area of completely resourced habitat and (iii) several isolated patches containing a single resource. The last case requires individuals to cross, even daily, unsuitable landscapes to gain resources. A sufficient mobility of a species is a prerequisite for such a scenario (WENZEL et al. 2006).

In large unfragmented habitat patches, natural stochastic processes of habitat perturbations and creation are likely to provide all resources needed to maintain long-term population stability. According to THOMAS et al. (2001 b), habitat quality was the predominant factor determining the occurrence of *Melitaea cinxia, Polyommatus bellargus* and *Thymelicus acteon* in Britain, whereas patch size and isolation had less effects. Also in *Maculinea arion,* habitat quality could be identified as fundamental factor (WALLISDEVRIES 2004). In both cases, the inferior role of patch isolation can be traced back to high quality habitats producing larger populations with a higher amount of dispersing individuals (JOHNSON 2004). In these cases, a sufficient habitat quality seems to counterbalance isolation effects.

Habitat accessibility or connectivity is an important factor determining if habitat patches can become occupied and hence if species can permanently persist. However, connectivity is highly species specific and landscape structures that represent barriers for one species might still retain connectivity for another (BAGUETTE & VAN DYCK 2007, DOVER & SETTELE 2009). Strongest barriers for all species are likely to be large parts of non-habitat or physical features as deep valleys or steep ridges that species can not physically pass. Most barrier effects have species specific variability. Thus, a hedgerow has shown to be a severe barrier for dispersal in *Polyommatus bellargus* (WOIDWOD & THOMAS 1993) or *Ephydryas aurinia* (WARREN 1994), whereas one kilometer of woodland has been bridged by the grassland species *Maculinea arion* (PAULER-FÜRSTE et al. 1996). The vegetation structures of the habitat-surrounding areas hence represent major dispersal limiting factors in many species (FISCHER & FIEDLER 2000). In general, it might be expected that generalist or specialist species react in different ways to landscape fragmentation (FILZ et al. 2013). Habitat

specialists or species depending on biotic interactions (e.g. mutualists, parasitoids) are suspected to be most vulnerable to habitat loss and isolation. Migratory species are likely to have less difficulties to move through hostile landscapes than species with closed population structures or poor dispersal capabilities. Moreover, species exploiting multiple host plants will probably be more successful in immigrating different habitat patches than monophagous species (ZIMMERMAN et al. 2005, WENZEL et al. 2006, FILZ et al. 2013). Several studies demonstrated that butterfly species with low diet breadth and poor dispersal abilities experienced significantly more severe negative impacts than mobile and polyphagous species in fragmented semi-natural grasslands in south-western Germany (WENZEL et al. 2006, FILZ et al. 2013). On the other hand, adaptations in flight behavior have been observed in *Proclossiana eunomia*, which tend to fly faster and more linear over unsuitable landscape patches (SCHTICKZELLE 2006, 2007). The author claimed that fragmented landscapes would select for specializations in dispersal behaviors minimizing costs. Dispersal costs highly differ between species and the landscape structures to pass. KARLSON & WIKLUND (2005) found a significantly lower fecundity and longevity in the two woodland species *Pararge aegeria* and *Aphantopus hyperantus* in high temperature regimes. Consequently, these species are expected to have much higher costs when dispersing through open landscapes than through shady habitats. The other way round, open habitat species as *Coenonympha pamphilus* and *Hipparchia semele* are shown to experience a reduction in fecundity at temperatures more favorable for woodland species. In this aspect, a dependency on weather conditions could be recognized in *Plebejus argus* that exploited different habitat structures in relation to sunshine or cloud cover (DENNIS & SPARKS 2006). The high costs of dispersal might lead to a species tolerating non-optimum conditions within a habitat patch instead of crossing unsuitable landscapes (DOVER & SETTELE 2009).

Dispersal activities and habitat accessibility is additionally dependent on geographic factors arranging habitat patches within the landscape. Large distances between habitat patches reduce colonization rates and dispersal events (MACARTHUR & WILSON 1967, LOMOLINO & BROWN 2009). In this aspect, landscape heterogeneity, i.e. the variety and spatial arrangement of habitat patches usable as stepping stones, rather than the pure distance between habitats is expected to promote or restrict species' migration (CHARDON et al. 2003, MCRAE et al. 2008, RICHARDSON 2012). ÖCKINGER & SMITH (2006) stated that butterfly richness was highest in landscapes with a high overall proportion of grasslands compared to landscapes with a smaller portion of grasslands. However, in human mediated landscapes, areas suitable as habitats or stepping stones continuously become lost and often are not replaced by new ones. WITH (1997) stated that connectivity between patches is severely threatened after a critical threshold of 59% of habitat loss. As a result of a landscape matrix becoming more and more hostile and impermeable for many species, habitat isolation and fragmentation continuously increase with devastating impacts on biodiversity

(HABEL et al. 2012, FILZ et al. 2013).

The isolation of habitats generally increases the risk of adverse impacts leading potentially to species extinction including inbreeding depression (NIEMINEN et al. 2001, HABEL & SCHMITT 2012). SCHMITT & SEITZ (2002) observed in strongly isolated populations of *Polyommatus coridon* in western Germany a significant lower gene flow than in populations with low levels of fragmentation. On the other hand, increasing habitat fragmentation might also lead to advanced rates of genetic divergence between populations as shown for *Proclossiana eunomia* in Belgium (VANDEWOESTIJNE & BAGUETTE 2004). Isolated habitats force species communities to change and adapt fast to environmental changes with populations potentially differentiating rapidly from each other.

Patch size clearly is an important factor influencing biodiversity. Following the theory of island biogeography of MACARTHUR & WILSON (1967), larger patches tend to have higher immigration rates and host more species than smaller ones. On large habitat patches, stable source populations are more likely to establish whereas populations on smaller patches might experience higher extinction risks (REMEŠ 2000). Consequently, communities of small habitat patches generally are characterized by high turn over rates (TSCHARNTKE et al. 2002, FILZ et al. 2013). Model results derived by KINDVALL & PETERSSON (2000) suggested that reproduction of species on smaller patches would not counterbalance emigration rates. Hence populations are forced to rely on immigration to maintain stability, a situation classically described as sink population. Especially in scenarios of growing landscape fragmentation, sink populations are expected to be more at risk of becoming extinct than source populations (WITH 1997, DOVER & SETTELE 2009). Moreover, smaller habitat patches are suggested to be more susceptible to environmental impacts due to their higher proportion of edges, i.e. areas where two adjacent habitat types join up. Habitat edges are characterized by different microclimates (temperature, humidity, wind velocity etc.) than core areas so that many species avoid edges as habitats. These different conditions are also enhanced by successful species invasions from adjacent patches. As a consequence, edges often inhabit different species communities than core areas. Species like *Euphydryas maturna* or *Lopinga achine* actually depend on habitat edges as main habitat (BERGMAN 2001, WAHLBERG 2001). However, impacts of pesticides that are applied at surrounding crop fields affect edges and even core areas of smaller habitats. These edge-effects are found to severely reduce species fitness and survival and are expected to be more pronounced in smaller patches than in larger ones. Large habitats encompass a higher amount of core area that is not affected by edge-effects. Negative impacts of surrounding areas also highly dependent on patch geometry. Linear habitat patches are completely determined by edge-effects whereas more compact shapes provide more core areas that buffer negative impacts. In circular shaped habitats, the proportion of edges is reduced to a

minimum (DENYS & TSCHARNTKE 2002).

Patch size can hardly be distinguished from habitat quality as larger patches are likely to be more heterogeneous and hence provide more resources (TSCHARNTKE et al. 2002). The habitat-heterogeneity hypothesis claims that larger habitats include a greater variety of habitat types supporting different communities of species (TEWS et al. 2004). A high habitat heterogeneity should therefore foster high degrees of species specialization. Moreover, topographical and structural variation within the landscape tend to buffer against stochastic extinction events due to environmental disturbances (PE'ER et al. 2004, 2006, DOVER & SETTELE 2009). However, a reduction in patch size often goes in line with alterations in habitat characteristics. Changes in soil conditions, decreasing humidity or changes in plant growth or richness have been documented as consequences of reductions in patch size (TSCHARNTKE et al. 2002). Especially small and isolated patches are subsequently at risk to underlie subtle changes in the habitat structures leading to a homogenization of habitat characteristics (DOVER & SETTELE 2009). In this aspect, agricultural improvements going in line with severe nitrogen immissions (BARTHOLMESS et al. 2011) as well as the abandonment of traditional farming systems (VAN SWAAY 2002, LUOTO et al. 2003, WENZEL et al. 2006, SCHMITT & RÁKOSY 2007) are considered to be main threats to vegetation richness and characteristic habitat structures (e.g. vegetation height, microclimates). As a result, climate change and intensive agriculture lead to habitats continuously merging with their surrounding landscape. In Switzerland, almost 100% of wetlands have vanished over the past 150 years (HONEGGER 1982), and up to 87% up *Molinia* meadows and *Juniperus* heathlands disappeared in southern Germany (KAPFER 1993). Especially habitat types originating from traditional, extensive agriculture and hence depending on management are currently at risk of being lost, followed by a severe decline in ecological and functional diversity (WENZEL et al. 2006, FILZ et al. 2013). Similar trends are observed globally and can be predicted for the future leading locally to extinctions on species and population levels (JELTSCH et al. 2010).

III. Species conservation in times of global change

Europe is currently undergoing an inimitable period of environmental changes. Researchers, conservationists, policymakers and stakeholders, both governmental and non-governmental, have developed numerous monitoring and actions plans at different scales for ecosystem and species conservation. Resources in conservation usually are scarce so that a strategic focus and a definition of priorities is required. Hence, several questions arise concerning subjects and instruments of conservation. The margin of conservation efforts stretches from 'laissez faire' to drastic anthropogenic interventions. As global change impacts are supposed to be highly species' specific, a one-size-fits-all conservation approach risks failure (DAWSON et al. 2011).

Species-level conservation usually tends to be focused on rare and/or endangered species (GASTON & FULLER 2007). The general goal behind this approach is the idea to protect the greatest proportion of the 'original' species assemblage as possible giving priority to those species with low abundances or small geographic range sizes. However, in the last decades, this conservation strategy was questioned by numerous studies attracting notice to the conservation of keystone, umbrella or indicator species (ROBERGE & ANGELSTAM 2004, MAES & VANDYCK 2005, KOTLIAR et al. 2006, ROWLAND et al. 2006, for discussion see SEDON & LEECH 2008). The advantage of this assumption is that a greater biodiversity might be preserved on the long-term than under a strict focus on endangered species. Moreover, GASTON & FULLER (2007) recommended an extension of current conservation approaches focusing only on endangered species in the future. They stated that even currently common and widespread species might also merit protection, facing pressure under future climate and land use change with attendant consequences for several ecosystem functions.

Although much attention has been paid to impacts at the species' level, analyses concerning entire entities of biodiversity are sparse (MACE et al. 2000). Species-directed conservation strategies commonly neglect impacts on distinct assemblages of species or ecological processes within communities and ecosystems. It becomes evident that effective conservation strategies need to mitigate global change impacts on ecosystems as a whole. Therefore, conservation strategies must strive not only to protect species, but also to conserve natural communities and the distinctive ecosystem that supports them. Conservation plans aiming at entire entities have been developed for example by the World Wide Fund for Nature (WWF) by classifying the world into marine, terrestrial and freshwater ecoregions; each defined as relatively large units of land or water containing a distinct assemblage of natural communities that share a majority of species, ecological dynamics and environmental conditions (GROVES et al. 2000, OLSON et al. 2001). They aim to function as coarse-scale conservation units, which conserve representative examples of the world's biomes in each realm where they occur based on exceptional levels of species richness or endemism and extraordinary ecological or evolutionary phenomena in the distinct region (DINERSTEIN et al. 1995, OLSON & DINERSTEIN 1998, OLSON & DINERSTEIN 2002).

The empirical foundation of functional or trait-based risk assessments and conservation efforts is now beginning to appear (FODEN et al. 2008, WILLIAMS et al. 2008, THOMAS et al. 2011). These assessments aim to identify traits that make species susceptible to global change including for example species at higher trophic levels, with long generation times, poor dispersal abilities or low reproductive output (WENZEL et al. 2006, ARAÚJO et al. 2006, CHIN et al. 2010). Especially range size is acknowledged to be correlated with extinction risk as large ranges may buffer against habitat loss or fragmentation (DAWSON et al. 2011). However, paleoecological data and long-term observations justify concerns that, on the long-term, mitigation rates may stay behind the predicted

rates of land use and climate change in the coming decades (JACKSON & OVERPECK 2000).

These observations rise challenges for conservationists that can mainly be grouped in three categories: (i) the prevention of habitat loss, (ii) habitat management and (iii) the mitigation of problems associated with habitat isolation and fragmentation. Already THOMAS et al. (2001 b) highlighted the importance of habitat management to retain suitable habitats for species persistence. Since the Middle Ages, human activities have created open, structure-rich habitats (POTT 1998), today representing characteristic landscape elements in Europe. Many studies believe them to be 'hotspots' of biodiversity in Europe with high conservation value (VAN SWAAY 2002, SCHMITT & RÁKOSY 2007). However, in the light of agricultural intensification (e.g. monocultures, fertilization, pesticide input), these habitats continuously retract and disappear. Reductions in size, changes in climate, plant richness, vegetation growth, productivity and structural richness mainly result from adverse impacts of adjacent patches or changes in management practices (BALMER & ERHARDT 2000, WENZEL et al. 2006). That means, species depending on specific habitat structures may suffer from hedge trimming, from the removal or the abandonment of pasturing or coppicing. Prevalent conservation efforts are geared to counteract negative habitat dynamics, loss or isolation and to provide a sufficient habitat quality and connectivity (BALMER & ERHARDT 2000, BOURN & THOMAS 2002). However, the ongoing species declines in many European countries indicate that more emphasis should be placed on the management and integration of habitats in human-mediated landscapes (TSCHARNTKE et al. 2002, LUOTO et al. 2003, VAN SWAAY 2002, SAMWAYS 2007).

Already during the 1970s and 1980s, the SLOSS (**s**ingle-**l**arge-**o**r-**s**everal-**s**mall) debate addressed the issue if species were best protected by conserving several small habitat fragments or a single large one (DIAMOND 1975, QUINN & HARRISON 1988). One fifth of Germany is currently covered with protected areas (EAA 2011). These are complemented by more than 40,000 very small reserves (i.e. 'natural monuments') many of them encompassing an area of some hundreds of square meters only. This mosaic of small-scale reserves clearly contradicts the hypothesis of a general superiority of large reserves towards smaller ones. However, it might be expected that in human-dominated landscapes sufficient area is only available for small or medium-sized reserves, and maximum species protection might not be guaranteed by strictly focusing on large ones (VAN SWAAY 2002, DOVER & SETTELE 2009). Hence, several authors suggest an intermediate approach of spreading small-scale reserves over an area possibly encompassing a wide range of habitat types close enough to enable species dispersal. Complex habitat networks are shown to support more species due to a wider array of habitat types and to reduce the relative importance of habitat quality of single habitat patches. As a result, this approach is supposed to maximize beta diversity and simultaneously reduce extinction risk of area sensitive species (TSCHARNTKE et al. 2002, DOVER & SETTELE 2009). In the case of butterflies, TSCHARNTKE et al. (2002) observed remarkably higher

species richness and abundance rates on a group of smaller fragments. Only focusing on endangered species, all species known from the study area could be found in a network of smaller habitats compared to only 60% on one large habitat patch. However, the same study revealed a considerable dependence of highly specialized species (e.g. monophagous species) on large habitats due to a higher plant heterogeneity. Small habitat patches might also not be able to provide the minimum area needed to support populations of species requiring widespread habitats (WENZEL et al. 2006).

The establishment of corridors, hereby has been proven to be a sustainable solution to allow species to disperse between habitat patches with low costs in purpose to maintain gene flow. However, landscape connectivity may already be maintained by developing stepping stones for mobile species like various butterflies. In many cases, this approach is expected to be a more appropriate response to landscape fragmentation as it avoids numerous practical problems involved in creating continuous corridors like landowner resistance, high costs or interferences with infrastructures (DOVER & SETTELE 2009). SAMWAYS (2007) proposed six basic components to retain healthy populations within fragmented human-dominated landscapes: (i) the maintenance of source populations, (ii) the protection of high landscape heterogeneity, (iii) a reduction of contrasts between patches, (iv) the introduction of land management, (v) the simulation of natural habitat conditions and disturbances and (vi) the connection of high quality patches. Although these principles give a general guidance for policymakers and landowners, effective species conservation always demands for a specific assessment of the given factors. Species might respond specifically to different landscape configurations or dependent from the geographic location, thus making generalizations difficult, even more as specific responses of species and landscapes to climatic changes have to be increasingly taken into account (FODEN et al. 2008, THOMAS et al. 2011).

Today, networks of protected areas represent the most prevalent and valuable conservation strategy (BRUNER et al. 2001). The majority, however, has been established only with regard to current patterns of biodiversity mainly neglecting the increasing threat of anthropogenic global change (GASTON et al. 2008, HANNAH et al. 2007). Changes in climate and land use question their effectiveness in the future. Species' responses to climate change are expected to significantly alter current spatial patterns of biodiversity. Especially shifts in species' ranges to keep up with suitable climates might potentially displace their future distributions outside of protected areas (BURNS et al. 2003, HOLE et al. 2009). Modeling studies predict substantial turn-over rates in many protected areas in the future, raising the concern of increasing extinction rates (ARAÚJO et al. 2011). Already now, legally protected sites continue to be lost due to changes in microhabitat climates or land use impacts from adjacent patches (FILZ et al. 2013). Periodic assessments regarding the efficiency of protected areas are required to maintain the possibility for the inhabiting species to cope with global change. Moreover, mitigation efforts as dynamic buffer zones around protected areas or the

establishment of corridors between habitats might be complementary strategies, although cost and benefits are currently under debate (HADDAD & BAUM 1999, PASCUAL-HORTAL & SAURA 2006).

To date, conservation plans are largely based on a quite narrow methodological base. Conservation approaches including the re-design of protected area networks or the establishment of new sites heavily draw on empirical niche models, experiments or monitoring data. However, the reliance of policymakers or conservationists on a single approach increases the risk of failures. Each methodological approach provides useful, but often incomplete information on exposure and reactions of species to global change. Complementary methods are available, and the integration of multiple approaches is required to provide more comprehensive and robust information about species and ecosystems as well as their potential responses to global change (Fig. 3). Niche models based on presence records and environmental variables provide useful tools for exposure assessments, direct observations - including long-term monitoring data - assess all aspects of actual vulnerability and recent species' responses (e.g. range shifts, changes in phenology) (ARAÚJO et al. 2005, PARMESAN 2006, THOMAS et al. 2010). These can be extended by paleoecological records to encompass a broader range of climate and landscape variability (JACKSON & OVERPECK 2000). Additionally, mechanistic or ecophysiological models can be used to assess species-specific vulnerability and adaptive capacity based on species traits (KEITH et al. 2008, BUCKLEY et al. 2010, KEARNEY et al. 2010a,b). Experimental observations produce direct information on species' constraints and can be used to supplement modeling approaches (AUTUMN et al. 2002, KEARNEY & PORTER 2009). The combined information might facilitate the integration of species adaptation capabilities to maximize conservation efforts at minimum costs (DAWSON et al. 2011).

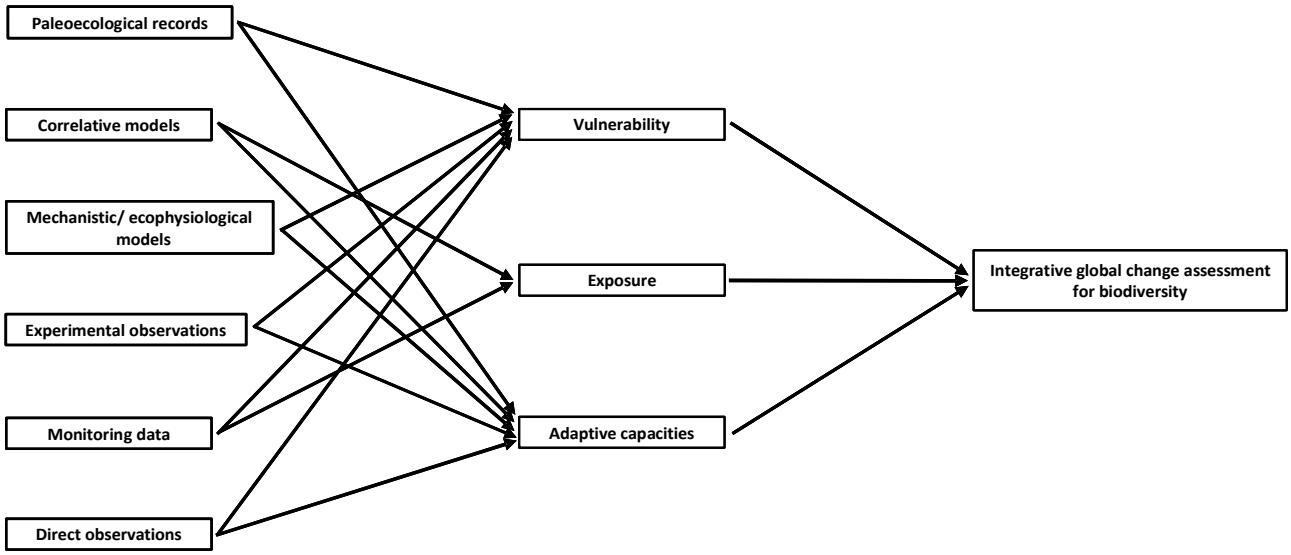

Fig. 3 An integrated global change assessment for biodiversity is based on multiple approaches giving evidence about exposure, vulnerability and adaptive capacities of the respective species or ecosystem. Modified after DAWSON et al. 2011.

In every ecosystem or community, some species may require specific conservation efforts. An improved understanding of threats resulting from global change to species and ecosystems as well as of their natural mitigation capabilities has to be the foundation of sustainable conservation strategies (FODEN et al. 2008, THOMAS et al. 2011). Depending on their specific susceptibility to climate and habitat change, those species and ecosystems with lowest exposure or highest adaptation capacity will need minimal intervention. On the other hand, costly and labor-intensive management activities as the maintenance of characteristic habitat structures, the interruption of natural succession or the restoration of biotic interactions might be able to buffer worst impacts on species with specific ecological requirements (SUTHERLAND & HILL 1995). Most intensive mitigation strategies include the translocation or *ex situ* conservation of endangered species. Despite the high risk of potentially negative ecological, evolutionary and economic impacts (SANDLER 2010) as well as ethical concerns (RICHARDSON et al. 2009, MINTEER & COLLINS 2010), these strategies are and might be even more necessary in the future to encounter global change.

IV. Objectives

In this thesis, the impacts of climate and land use changes on butterflies, and also amphibians and reptiles, and their concomitant implications for species conservation were studied. Poikilothermic animals are expected to be among the most sensitive taxa under global change due to niche constraints (BLAUSTEIN et al. 2010). Moreover, the study species exhibit a wide range of functional traits in terms of habitat requirements, phenologies, food resources and dispersal abilities making them suitable indicators for environmental change (DIAMOND et al. 2011, DEVICTOR et al. 2012). As a result, all species groups studied have been used in numerous pioneering studies in global change biology building a solid background of comprehensive investigations to draw comparisons over different temporal and geographic scales (BEEBEE 1995, PARMESAN & YOHE 2003, THOMAS et al. 2004, WENZEL et al. 2006, HILL et al. 2011).

The work generally aimed at identifying impacts of climate and land use changes on species and ecosystems in order to gain a differentiated view on species conservation at different scales. We selected a 'top-down approach', first evaluating environmental impacts on entire ecosystems going down to the identification of responses at the species level. Within nine individual studies, we tested hypotheses regarding (i) spatial range shifts of individual species and species assemblages, (ii) trait dependent individual responses of species, (iii) disruptions of biotic interactions, (iv) alterations of species' phenologies, (v) genetic isolation in course of landscape fragmentation and vi) the appropriateness and long-term efficiency of conservation strategies. Based on an integrative approach relying on field observations and modeling techniques, my observations identify the nature and magnitude of changes in natural systems and draw a picture of the current stage of

species conservation.

The studies summarized in **Part I** aim at identifying global change impacts on habitat and population dynamics. Commonly, conservationists target their actions on rare, endangered and vulnerable species due to scarce resources and high expenditure of time (GASTON & FULLER 2007). However, these species-directed conservation strategies commonly neglect impacts on distinct assemblages of species, ecological processes within communities and ecosystems and ecosystem services. The ecoregion classification of the Word Wide Fund for Nature (WWF) is a pragmatic approach to identify distinct assemblages of natural communities that share a multitude of species, ecological dynamics and environmental conditions within the same realm (OLSON et al. 2001). We assessed future changes in the extent of each terrestrial ecoregion under different climate change scenarios to give an estimate how environmental changes will affect natural systems on the ecosystem-level. Therefore, we extended previous correlative modeling techniques and developed a statistical model that accounts not only for climatic variables alone, but also for non-climate determinants throughout the addition of autoregressive error terms. Our results intend to support conservation plans aiming at whole entities so that, in the long run, a greater proportion of biodiversity might be preserved than under a strict focus on endangered species.

It is crucial to identify not only declines in species abundances, but also traits that make species susceptible to environmental changes to develop efficient and long-term conservation strategies (FODEN et al. 2008, WILLIAMS et al. 2008, HOF et al. 2011, THOMAS et al. 2011). Therefore, results of present butterfly surveys were compared with historical data to observe population developments and changes in community composition. In cooperation with the Helmholtz Center for Environmental Research, Leipzig (UFZ), we calculated the community temperature index (CTI) for each butterfly community in each year to demonstrate the importance of climate change in affecting butterfly communities. The CTI is acknowledged by the pan-European framework supporting the Convention on Biological Diversity (CBD) to be a good indicator of climate change impacts on biodiversity. Based on species specific temperature indices, it reflects the relative composition of heat-loving versus cold-adapted species in local communities of a given taxonomic group (DEVICTOR et al. 2012). Based on these data, we were able to analyse how butterflies differing in distribution patterns, dispersal abilities and habitat specialization have responded specifically to recent climate change and concomitant habitat changes during the last decades, to point the way to a more trait-based conservation strategy. This study is published in the *European Journal of Entomology* 110 (4), 633–642 (2013).

Climate change has profound impacts on species distributions with species adjusting their distribution to suitable climates (WARREN et al. 2001, PARMESAN 2006, WILSON et al. 2007, THOMAS 2010, CHEN et al. 2011, DEVICTOR et al. 2012). During the last decades expansive range shifts have

been observed in the Short-tailed blue (*Cupido argiade*s) at its northernmost range border in Germany (S. CASPARI, pers. comm.). Thereby, the magnitude of year-to-year shifts exceeds expectations and scientific predictions, and experts suggest this thermophilic species to be a 'winner' under climate change. Correlative species distribution models (SDMs) have emerged as powerful tools to address ecological and evolutionary questions (ARAÚJO et al. 2005, 2011, RÖDDER et al. 2009, KEARNEY et al. 2010a, PETERSON et al. 2011, IHLOW et al. 2012). Based on presence records of *Cupido argiades,* aiming to represent its fundamental niche to a maximum, we assessed the species' potential distribution under different climate change scenarios of the IPCC. We evaluated the susceptibility of a currently common and widespread species, which is commonly neglected in species conservation, to adverse impacts of climate change. The results have been published in *Abhandlungen der Delattinia* 38, 215-228 (2012).

Climate-driven alterations in species phenologies result in an earlier appearance of several insect or bird species as well as an advanced breeding in amphibians (CAREY et al. 2003, PARMESAN 2006). Concomitant to warmer spring temperatures a prolonged growing season of crops and hence an advanced application of fertilizers and pesticides might be expected, both with serious consequences for species inhabiting agricultural landscapes (MENZEL et al. 2006, TUBIELLO et al. 2007, BRÜHL et al. 2013). We hypothesize that symmetrical shifts in amphibian phenology and pesticide applications, here referred to as 'pesticide-phenology problem', lead to acute toxic effects and increased malformation rates in both adults and larvae, significantly decreasing the fitness of individuals and populations (Brühl et al. 2011, 2013). Species declines in agricultural landscapes remain an acute problem, unfortunately often neglected when setting conservation priorities that might even be aggravated in the future by a combination of external stressors, which may not cause problems when considered alone.

Disruptions of biotic interactions as parasite-host-relations are often hold responsible for local species extinctions as both species underlie different climatic forcing possibly driving species' life cycles in asynchrony (see SETTELE & KÜHN 2009 for *Maculinea arion*). We evaluated niche dynamics in the host-parasite-relationship of *Maculinea* butterflies and *Myrmica* ants. Range overlap and niche similarity of all species was assessed. This is the first approach to determine an evolutionary arms race between hosts and parasites based on environmental niche models, potentially forcing the butterflies to alternative host exploitation on the one hand and short-time niche adaptations on the other hand to minimize local selective pressure resulting from host escapes.

Part II summarizes studies developed to assess global change impacts on species and ecosystems, which have a high conservation value and are in course of being lost due to climate or land use changes. We focus on the evaluation of current conservation and management strategies to

uncover possible caveats and improvement opportunities.

Periodic assessments of protected areas are crucial to maintain their purpose and efficiency under global change (HOLE et al. 2009, ARAÚJO et al. 2011). In the first study of this section, we evaluated population trends and community compositions on six protected calcareous grasslands by intensively re-investigating butterfly communities after a 40-year time period (*Mainzer Naturwissenschaftliches Archiv* 50, 383-397 (2013)). In a second study, we compared the observed changes in butterfly diversity and community structure with data derived from butterfly surveys in vineyard fallows within the same time period to gain a direct comparison of butterfly community development in protected versus unprotected areas. For a sustainable conservation management, it is necessary to achieve sufficient knowledge about the factors driving population development. We considered a species specific vulnerability due to ecological traits and conducted species distribution and landscape connectivity models to analyze spatial factors as habitat connectivity, geographical integration and management. In this approach, we combine observations on both, the macro- and the microscale to assess the appropriateness of recent conservation efforts. The results have been published in *Biodiversity and Conservation* 22, 2223–2241 (2013).

In recent conservation activities, species abundances, i.e. whether a species can be classified as rare, often are considered useful indicators for endangerment (BUNDESAMT FÜR NATURSCHUTZ 1998). However, assessing species abundances still remains labor-intensive and often costly as it relies on field surveys. Species occurrence is acknowledged to be well predictable by correlative species distribution models (ELITH & LEATHWICK 2009). Thus, the predictive power of SDMs to assess abundances of species is well recognized for vertebrates (PEARCE & FERRIER 2001, VAN DERWAL et al. 2009). Therefore, we evaluated the application of these models to predict the spatial abundance of butterflies in relation to environmental predictors intending to significantly facilitate local conservation efforts. This study has been published in the *European Journal of Entomology* 110 (2), 311–317 (2013).

Multiple studies have already been conducted assessing impacts of climate change on biodiversity (BEAUMONT et al. 2011, DAWSON et al. 2011). Policy, science and society bear responsibility for species already rare or endangered as well as for species having the core area of their distribution within the respective country (STEINICKE et al. 2002). In the last study we summarized potential impacts of climate change on amphibians and reptiles listed as endangered or potentially endangered in Germany, with means of giving decision support to policymakers and stakeholders in terms of species conservation. This bookchapter is part of the *Statusreport „Klimawandel und Biodiversität – Folgen für Deutschland* edited by Stribrny B, Krohmer B, Schaller M, published by the Wissenschaftliche Buchgesellschaft Darmstadt.

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Part I: Climate and Landscape Impacts on Habitat and Population Dynamics

Novel modeling algorithms reveal dramatic climate-driven changes in broad-scale spatial patterns of biodiversity

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Anthropogenic climate change will alter the Earth's ecosystems. However, our knowledge about climate-driven responses of entire biodiversity entities still remains scarce and is rarely incorporated in current conservation schemes. Applying the ecoregion classification of the World Wide Fund for Nature (WWF), we use a novel modeling approach to address qualitative macroecological changes in ecoregion composition and extend under future climatic conditions. Here we show that tropical and boreal forests, as well as tundra, taiga and desert ecoregions are most likely to shift to alternative ecoregion types. We further demonstrate that the expansion and location of these ecoregions will alter geographically across all continents. Several of the biologically most unique ecoregions of the world are expected to get under severe pressure in the coming decades. Given the high conservation priority of these ecoregions, an intensification and even repriorisation of conservation efforts is required to cope with future climate change impacts on biodiversity.

Biodiversity patterns are heterogeneously distributed over the globe. Major differences occur in the distribution of biological variation as some areas inhabit a renowned biological diversity whereas others almost appear devoid of life. These broad-scale biodiversity patterns are well described (*1*), especially as associated ecosystem goods and services are substantial for human well-being and require sustainable use. However, they continue to alter as anthropogenic changes dominate and transform natural systems. Given the highly uneven distribution of biodiversity and threats, multiple integrated research approaches today provide useful information about the current and future status of the Earth's biodiversity to determine potential responses to global change (*2*). The identification of biodiversity's exposure and sensitivity to environmental changes goes in hand with severe concerns about the future development of species and ecosystems, as several independent studies have linked major changes in biodiversity to global change (*3,4*). Besides habitat destruction, fragmentation, overexploitation and biological invasions, global warming is identified as a major threat to biodiversity in the 21st century (*5-7*). Drawing evidence from recent observations climate change impacts already have serious consequences on macro- und microecological scales (*8*). The disruption of ecological communities and processes might even enhance, as especially increases of greenhouse gas emissions might drive climate changes above current rates in the coming decades (*9*).

In the light of current biodiversity losses, mitigating impacts of global change will require immediate action and consistent conservation planning (*2*). However, although much attention has been paid to impacts on the species level, analyses concerning entire biodiversity entities are largely missing (*10-12*). Due to scarce resources and high expenditure of time, commonly conservationists target their actions on rare, endangered and vulnerable species. However, these species-directed

conservation strategies often neglect impacts on distinct assemblages of species or ecological processes within communities and ecosystems. It becomes evident that effective conservation strategies need to mitigate the impacts of climate change on ecosystems at whole. Therefore, conservation strategies must strive not only to protect species, but also to conserve natural communities and the distinctive ecosystem supporting them. Accordingly, profound knowledge about the global distribution of life and the identification of areas with exceptional biodiversity is a precondition for effective *in situ* conservation planning.

The pragmatic approach of the World Wide Fund for Nature (WWF) to create a global map of biodiversity with sufficient biogeographic resolution, reflecting the complex distribution of floral and faunal communities, resulted in the creation of 867 terrestrial, 426 freshwater and 232 marine ecoregions (*13-15*). Terrestrial ecoregions are defined as relatively large units of land containing a distinct assemblage of natural communities that share the majority of their species, ecological dynamics and environmental conditions (*13*,*16*). They aim to function as coarse-scale conservation units, which conserve representative examples of the world's biomes in each realm where they occur, based on exceptional levels of species richness or endemism and extraordinary ecological or evolutionary phenomena in the distinct region (*17,18*).

Climate change impacts are unevenly distributed over space and time and are rarely adequately incorporated in current conservation schemes (*19*). Although considerable adaptability exists across natural ecosystems, many ecoregions might be under substantial climatic stress by 2100 given the current rate of warming, variabilities in precipitation patterns and frequencies of extreme events (*3,19*). Spatial shifts as well as changes in species composition or ecosystem dynamics might be the consequences, thus leading to changes in the unique characteristics of distinct ecoregions. As a result, the experience of extreme climates might even direct the repriorization of conservation efforts on the long run.

The impacts of climate change on ecosystems strongly depend on (i) its nature and magnitude and (ii) the individual composition and hence adaptability within the distinct ecoregion. Conventional climate risk assessments strongly focus on impacts of changing climates, but neglect biologically distinct factors which might have important implications for climatic adaptability in ecoregions (*3,19*). Therefore, a more comprehensive, multi-dimensional approach combining climatic and ecoregion-specific biotic factors to address the exposure and sensitivity of ecoregions to current and future anthropogenic threats might significantly enhance conservation priorities.

We employ an adaptation of a newly developed dynamic species distribution model, PLMMRF (Probit Linear Model with Markov Random Fields), based on an ensemble of four General Circulation Models (GCM) under the A1b, A2a and B1 Emission Scenarios (SRES) released by the IPCC for 2050 and 2080 to estimate changes in the spatial distribution of ecoregions under climate

change. This model uses a multinomial extension of the probit regression model that allows the regression of a categorical response variable. Moreover, it allows for the specification of spatially autocorrelated latent variables to account for non-climatic sources of spatial contagion in ecoregion classification.

Projected changes in mean annual temperature predict an unambiguous warming trend of 1.1-6.4°C depending on the respective SRES scenario by 2100 (*9*). Accordingly, our model results predict severe area changes in almost all observed terrestrial ecoregions (Fig. 1). Strong area losses are predicted for tropical and subtropical moist and dry broadleaf forests, boreal forests, taiga and tundra ecoregions, whereas gains in range size for xeric and desert ecoregions are revealed. The most stable ecoregions are found in Europe, the northern Amazon basin, the Congo basin, south-eastern Asia and the Malaysian archipelago.

The observed changes in the northern hemisphere might largely be traced back to alterations in the Arctic Oscillation (AO). Over most of the past century, the Arctic Oscillation alternated between its positive and negative phases (*20*). A positive phase of the AO is defined as a period of below normal Arctic sea-level-pressure, enhanced surface westerlies in the north Atlantic, warmer and wetter than normal conditions in northern Europe and northern America, but colder than normal conditions in Africa and exceptional dry Mediterranean climates. In contrast, negative phases are characterized by higher than normal atmospheric pressure over the Arctic followed by weak surface westerlies, colder as normal condition in Europe and northern America, wet climates in the Mediterranean and warmer than normal conditions in Africa (*21*).

The predicted increasingly positive direction of the AO in the upcoming decades (*19*) might well explain an expansion of forest ecoregions across large parts of Eurasia, especially at the actual northern and southern range boundaries of forests. With higher than normal atmospheric pressure over the Atlantic, strong westerlies push warm and humid air masses towards Eurasia. As a result, range retractions of tundra and alpine ecoregions might also be attributed to higher than normal temperatures in much of northern America and northern Eurasia. In the southern Mediterranean basin, severe droughts might lead to small-scale desertification on the Iberian peninsula and large-scale range shifts of desert ecoregions towards higher latitudes in northern Africa for the same reasons. On the other hand, the stronger westerlies might cause more humid conditions in the northern Mediterranean, explaining the loss of the typical Mediterranean climate type all over the Mediterranean basin. A concomitant cooling in northern Africa and Arabia might inhibit widespread desertification at the southern edge of the Saharo-Arabian desert, but on the contrary may go in line with large-scale ecoregion changes from desert to savannah biomes in the northern Sahel, southern Sahara and at the Arabian Peninsula.

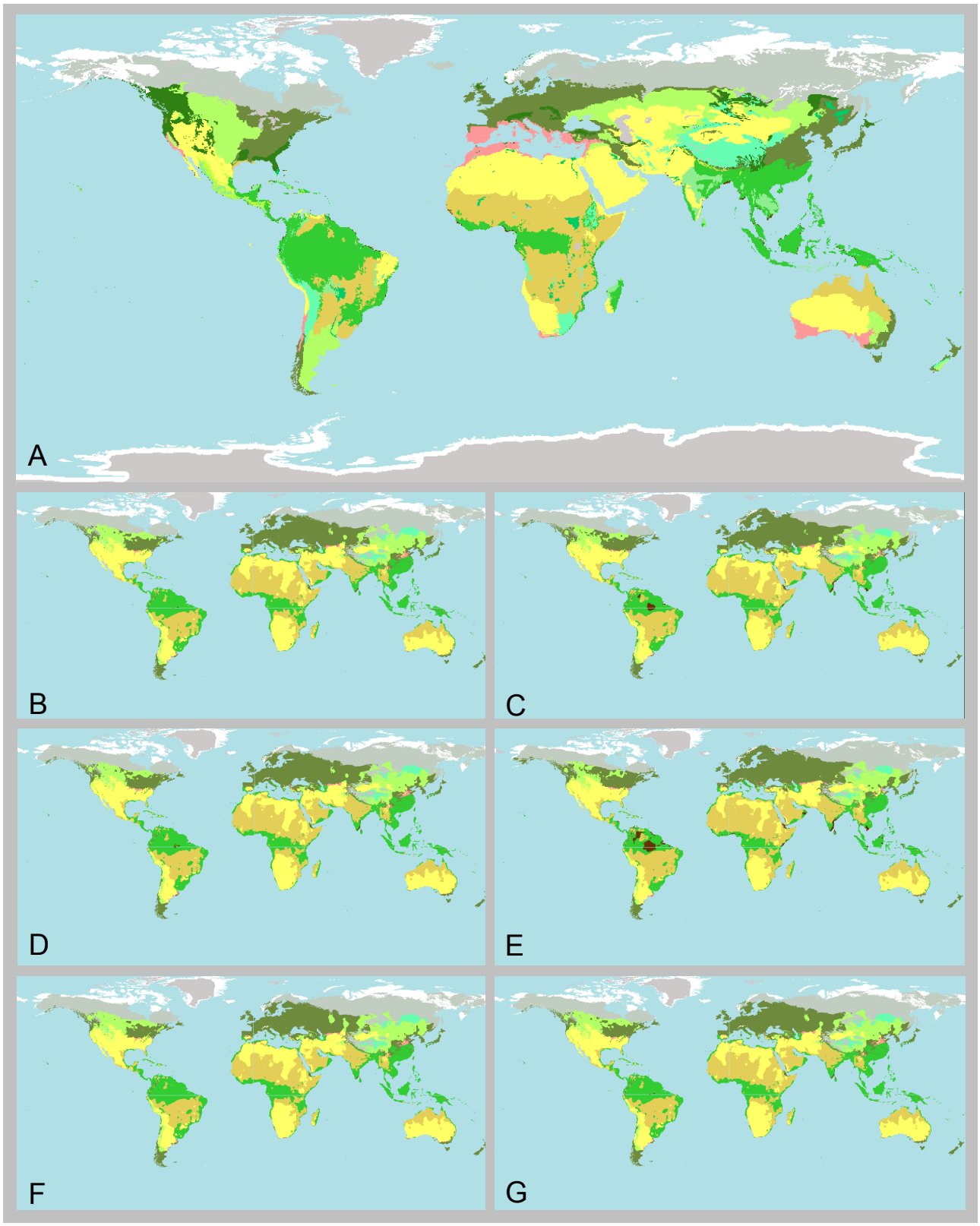

Fig. 1. Global spatial distribution of terrestrial ecoregions (A) Current climate (B) IPCC scenario A1b for 2050, (C) IPCC scenario A1b for 2080, (D) IPCC scenario A2a for 2050, (E) IPCC scenario A2a for 2080, (F) IPCC scenario B1 for 2050, (G) IPCC scenario B1 for 2080. Similar ecoregion types were combined to biomes for better presentability.

Although strong trade winds prevail in the subtropics and tropics under positive AO conditions, precipitation might be reduced in parts of southern America. In this context, advances of savannahs into the region of the southern Sahara might be of special importance as Sahara dust transfer to southern America might decrease during the rainy season in northern hemisphere summer. This goes in line with strong savannah advances in southern Amazonia, as the area is most affected by reduced rainfall during the rainy season in the southern Sahara region when dust production and transport is suppressed in this area responsible for the dust supply of southern Amazonia. Consequently, the rain forests of northern Amazonia might not be seriously affected as the northern regions of the Sahara will remain deserts.

Also on the Indian subcontinent, predominant north-easterly trade winds might be expected to cause a replacement of humid ecoregions by dry savannahs and shrub lands. In general, an expansion of desert ecoregions can be observed on all continents apart from central Asia and northern Africa. According to the Millennium ecosystem assessment of the United Nations (*22*), the most vulnerable ecoregions for desertification under climate change can be found in the Sahel, southern Africa, southern Asia, Australia northern and southern America as well as southern Europe. The results of our model mostly support the vulnerability assessment also showing increasing desertification in the above mentioned regions with the exception of central Asia and northern Africa. However, all regions predicted by PLMMRF to be suffering from desertification also match predictions of the IPCC to experience severe temperature increases and droughts under climate change (*9*). Besides, these findings might also be attributed to severe erosion processes caused by the overexploitation of the affected landscapes (*22*). This might also largely explain the almost complete conversion of the territory of the United States into deserts. This severe large-scale desertification process might also be explained by the considerably stronger westerlies, getting rather dry after passing the Rocky Mountains and inhibiting the influx of southern winds from the Golf of Mexico actually transporting humid air masses to the central and eastern regions of the USA. Hence, northern America maybe might represent one of the world-wide most affected regions by global change, if our model holds true.

All model predictions revealed largely similar results under the different SRES scenarios. However, present-day CO_2 rates have almost reached the upper limit of the presented SRES emission scenarios (*9*), thus making B1 predictions rather unlikely. Our results strongly suggest that several of the biologically most unique ecoregions of the world will get under severe pressure in the coming decades. Multiple previous studies have revealed alarming predictions about the potential future of biodiversity, and present-day conservation efforts might be insufficient for the preservation of many of the observed ecoregions (*2,3,8*). However, assessing climate change impacts is a multifaceted problem, and predictions and conservation priorities are often focused one-sided. With our novel

modeling technique, we pave the way for a multi-dimensional assessment of exposure and vulnerability of large-scale ecosystems including not only climatic but also biotic factors for the first time. This approach enables scientists and conservation planners to access a more robust foundation with accurate information about both, extrinsic and intrinsic factors driving ecoregion responses to climate change. There is little doubt that a repriorization of conservation efforts is required to cope with future climate change impacts on biodiversity.

Methods In order to model the distribution and turnover of ecoregions we must first draw inference about the climatic and non-climatic determinants of their boundaries. The ecological literature is abound with examples of applications of species distribution models (SDMs) (*23,24*), a class of models designed with the purpose in mind of deriving relationships between the environment and the occurrence of species. Whilst these models have demonstrated great utility in areas as disparate as the planning of protected areas for conservation (*25,26*) and assessing the vulnerability of species to climate change (*6*), they are designed for a data type that exhibits very different properties than the distribution of ecoregions: the occurrence of a single species is a dichotomous variable, that is, a species is either 'present' or 'absent' at a particular location. The ecoregion data is instead polychotomous, where each location is categorized to one of the 837 possible WWF ecoregion classifications.

One possible method to model such data would be to create one separate dataset for each ecoregion classification, such that each cell in each dataset contains a 'presence' or 'absence' value for the respective ecoregion, and utilize the standard modeling techniques. Such methods have been applied in the context of land-use modeling before (*27-31*) but they exhibit a number of serious statistical deficiencies when applied to polychotomous data. Firstly, by modeling each category separately then we are making an implicit assumption that the probability of assignment of a cell as belong to one category is independent of the probability of assignment of the cell to another category. Secondly, this independence results in the undesirable property that, in any particular location, the sum of the probabilities of assignment to each category in not guaranteed to equal one. To address such deficiencies there has been an increased interest in the use of multinomial regression models to model land-use change (*32-34*). These regression models extended the binomial case (otherwise known as 'logistic regression') to handle polychotomous data explicitly. Multinomial regression models rely on the definition of a set of indicant variables for each category and location such that that the indicant variable for category *c* at location *i*, y_{ic}, is some function of the set of predictor variables at that location (given here by the row vector $x_{i\circ}$), a set of regression coefficients for category *c*, β_c, and an error term, Φ_{ic}.

Under a standard multinomial regression model, the only determinants of the ecoregion classification is the environmental predictor variables. However, the WWF ecoregion classification exercise takes into account many criteria (*13*) such as endemism, extraordinary ecological or evolutionary phenomena, and species richness, that may be only partly determined by climatic factors. To take into account these non-climatic effects we allow our indicant variable error term, Φ_{ic}, to follow a spatially autoregressive error process. In other words, the value of Φ_{ic} is dependent upon the values of the indicant error term at other locations. In order to define our autoregressive error term we must introduce an n x n neighborhood weights matrix, **w**, which describes the spatial relationship between the n different locations. One simple specification of a neighborhood neighborhood is to set each element, w_{ij}, equal to one if the cells i and j lie adjacent in the cardinal directions and zero otherwise. In this study, we also give diagonal neighbors a weight of $2^{-½}$. We then use a particular parametrization of the Conditional Auto-Regressive (CAR) model (*35,36*) to define the following distribution of Φ_{ic}:

$$\Phi_{ic} \sim \text{Normal}\left(\frac{\alpha_c}{w_{i+}}\sum_{j\neq i} w_{ij}\Phi_{jc}, \frac{1}{\lambda_c w_{i+}}\right)$$

where w_{i+} is the sum of the entire neighborhood weights for cell i. The parameter α_c controls the strength of spatial autocorrelation in the indicant error terms with values close to one produces very strong spatial association, with ecoregions of type c tending to appear in clusters, and values close to zero tending towards independence. Technically it is possible for α_c to take negative values as low as -1 to induce negative spatial association and make nearby values of Φ_{ic} be highly dissimilar but the CAR model can become quite poorly behaved in this region of parameter space and such effects may not scale monotonically for values of α_c lower than zero (*37*). For this reason, we only consider values above zero for α_c in this study. The parameter λ_c controls the degree to which the non-climatic process dominate the distribution, with larger values increasing this effect.

We apply a multinomial probit sub-model (*38,39*) to describe the link between the set of indicant variables and the observed ecoregion classification at location i. Here we define the following distribution for each indicant variable:

$$y_{ic} \sim \text{Normal}\left(\mathbf{x}_{io}\boldsymbol{\beta}_c + \Phi_{ic}, 1\right)$$

The observed ecoregion classification at cell i is then considered to be the category that has the largest indicant value at that location. The multinomial probit model has an advantage in that it is

relatively easy to parameterise from the data using Bayesian methods of inference (*39*).

Once we have parametrized our model from the WWF ecosystem classification data we then use the distribution of values for Φ_{ic} and $\boldsymbol{\beta}_c$, drawn using Gibbs sampling methods, to calculate the respective probabilities of the different possible classifications for each location under different scenarios of climate change. For each sample of Φ_{ic} and $\boldsymbol{\beta}_c$ we simulate a new indicant variable, l_{ic}, such that

$$l_{ic} \sim \text{Normal}\left(\mathbf{z}_{i\circ}\boldsymbol{\beta}_c + \Phi_{ic}, 1\right)$$

where $\mathbf{z}_{i\circ}$ is a row vector containing the predicted environmental conditions at location i. The proportion of indicant variables of category c that have the highest value under the different simulations can then be used as an estimate of the probability that location i will be categorized as ecoregion c under a future climate.

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A question of adaptability - Climate change lowers trait diversity in butterfly communities in south-western Germany

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Abstract. During the last century, invertebrate diversity has rapidly declined throughout Europe. Various reasons for this decrease have been discussed including human induced factors like climate change. Temperature changes alter distributions and occurrences of butterflies determining habitat conditions at different scales. We evaluated changes in butterfly community compositions at nine fallow grounds in south-western Germany between 1973, 1986, 2010 and 2012 using Pollard's transect technique. To demonstrate the importance of climatic changes in affecting butterfly communities, we calculated the community temperature index (CTI) for each butterfly community in each year. Although slightly increasing, CTI-values did not match the temperature trends of the study region. Moreover, a reduction of CTI standard deviations along time reflects a severe loss of cold- and warm-adapted species due to their inability to cope with temperature and land use induced habitat changes. Results of our butterfly surveys underline the severe decline in species richness and striking changes in the composition of the observed butterfly communities. This trend was most pronounced with regard to habitat specialists mirroring a depletion in trait diversity. Our results suggest that, in course of large-scale anthropogenic changes, habitat degradation at smaller scales will continuously lead to a replacement of habitat specialists by ubiquitous species.

Key words. Species decline, community composition change, habitat specialisation, functional groups, community temperature index, fallows

INTRODUCTION

In the past decades, a multitude of studies has documented a broad-scale species decline explained by various reasons. However, all studies expressed a major concern about the future of biodiversity (Sala et al., 2000; Gaston & Fuller, 2007; Beaumont et al., 2011; Dawson et al., 2011). Overall, climate change and landscape changes leading to habitat destruction and fragmentation have been identified as major threats to biodiversity in the 21st century (Thomas et al., 2004a; Dover & Settele, 2009). Therefore, the accurate identification of such emerging threats is crucial to develop appropriate *in situ* management and conservation strategies (Mantyka-Pringle et al., 2012).

Butterflies are known to respond quickly to a number of environmental parameters and are therefore recognized as a suitable umbrella group in insect conservation (Rákosy & Schmitt, 2011). The ongoing decline of many butterfly species across all parts of Europe (León-Cortés et al., 2000; Maes & Van Dyck, 2001; Van Swaay et al., 2011) highlights the need to identify environmental factors influencing species diversity and characteristic habitats for contemporary conservation action.

Insect diversity and butterfly species richness are closely related to certain habitat characteristics. In agricultural dominated landscapes, human activities have created a characteristic mosaic of open habitats, forests and floodplains (Schmitt & Rákosy, 2007) offering suitable habitats for a multitude of species. However, the abandonment and replacement of traditional farming and landscape management systems, ensuring their survival for hundreds of years, is particularly deleterious for these taxa (Warren, 1997; Wenzel et al., 2006; Schmitt & Rákosy, 2007). Two frequently observed biological changes following anthropogenic activities or climate changes are species loss and biotic homogenization over time (Wenzel et al., 2006; Gillette et al., 2012). Besides habitat loss, a reduction in habitat size and fragmentation as well as changes in climatic habitat conditions are counted among the major threats for diversity. The degree in which habitats become increasingly unsuitable for butterfly species due to changing microclimatic conditions is still under debate. In contrast to broad-scale climatic impacts on biodiversity, small-scale impacts influencing habitat associations are hardly understood. A better understanding of these small-scale effects would fundamentally improve the ecological understanding of natural communities, especially those harbouring specialized species with narrow physical tolerances. Moreover, it would enhance the development of conservation efforts maintaining species diversity under climate change.

In Europe, semi-natural grasslands (e.g. as old fallow grounds) today are considered important habitats in cultivated landscapes (Van Swaay, 2002). These habitats are usually characterised by a higher plant diversity and more favourable (often warmer) climatic conditions than the surroundings. Hence, they provide retreats for many taxa and host an important diversity of plants

and animals differing from those inhabiting intensively cultivated farmland. This value is especially meaningful for the conservation of insect diversity (Wenzel et al., 2006). However, conservation activities may be misleading as little is known about the within-habitat dynamics influencing local species diversity and community compositions.

In the present study, we compare contemporary (2010, 2012) butterfly communities to historical (1973, 1986) assemblages on vineyard fallows in south-western Germany. During the time period studied, temperature in the study region has increased by approximately one degree Celsius, but also showed considerable annual variability. To demonstrate the importance of climatic changes in affecting butterfly communities, we calculated the community temperature index (CTI) for each butterfly community in each year. The CTI is acknowledged to be a good indicator of climate change impacts on biodiversity by the pan-European framework supporting the Convention on Biological Diversity. Based on species specific temperature indices, it reflects the relative composition of heat-loving versus cold-adapted species in local communities of a given taxonomic group (Devictor et al., 2012). Due to the observed temperature increase, an increase in CTI values as an indicator for community shifts towards more heat-loving species might be expected. In butterfly species, CTI-values show a strong correlation with the two-year moving temperature average so that annual variations might be more pronuounced than the overall trend (Wiemers et al. 2012).

Besides a rich fauna, vineyard fallows are acknowledged to hold a high functional diversity. We analysed how butterflies differing in distribution patterns, dispersal abilities and habitat specialisation have responded specifically to recent climate change expecting not only a decrease in species richness, but especially in functional diversity. The loss of less thermophilic butterflies or range contractions of species reaching their distribution edge in Germany might lead to depleted communities. Necessarily, the results of this case study might not be generalized globally, but may stimulate a discussion about small-scale impacts on local community compositions and its implications for species conservation.

MATERIAL AND METHODS

Study region

Our study area, the vicinity of Trier, is located in south-western Germany near to the border with France and Luxembourg (see Figure 1). The area is characterized by a long tradition of human settlement and anthropogenic land-use. Since Roman times, landscape characteristics were transformed leading to an increase in open habitats. The growing structural diversity in habitats encompassing residential areas, arable fields, vineyards, meadows, forests and flood plains fostered

species diversity. Today, a multitude of natural and semi-natural habitats provide a retreat for many rare and endangered species.

However, changes in the climatic conditions and land-use patterns during the 20th century have had severe negative impacts on the quantity and quality of the respective habitat types. The intensification of farming activities, anthropogenic loads of nutrients, the failure of extensive management and a changing climate have driven the loss and fragmentation of certain habitats, potentially leading to a decline of species diversity.

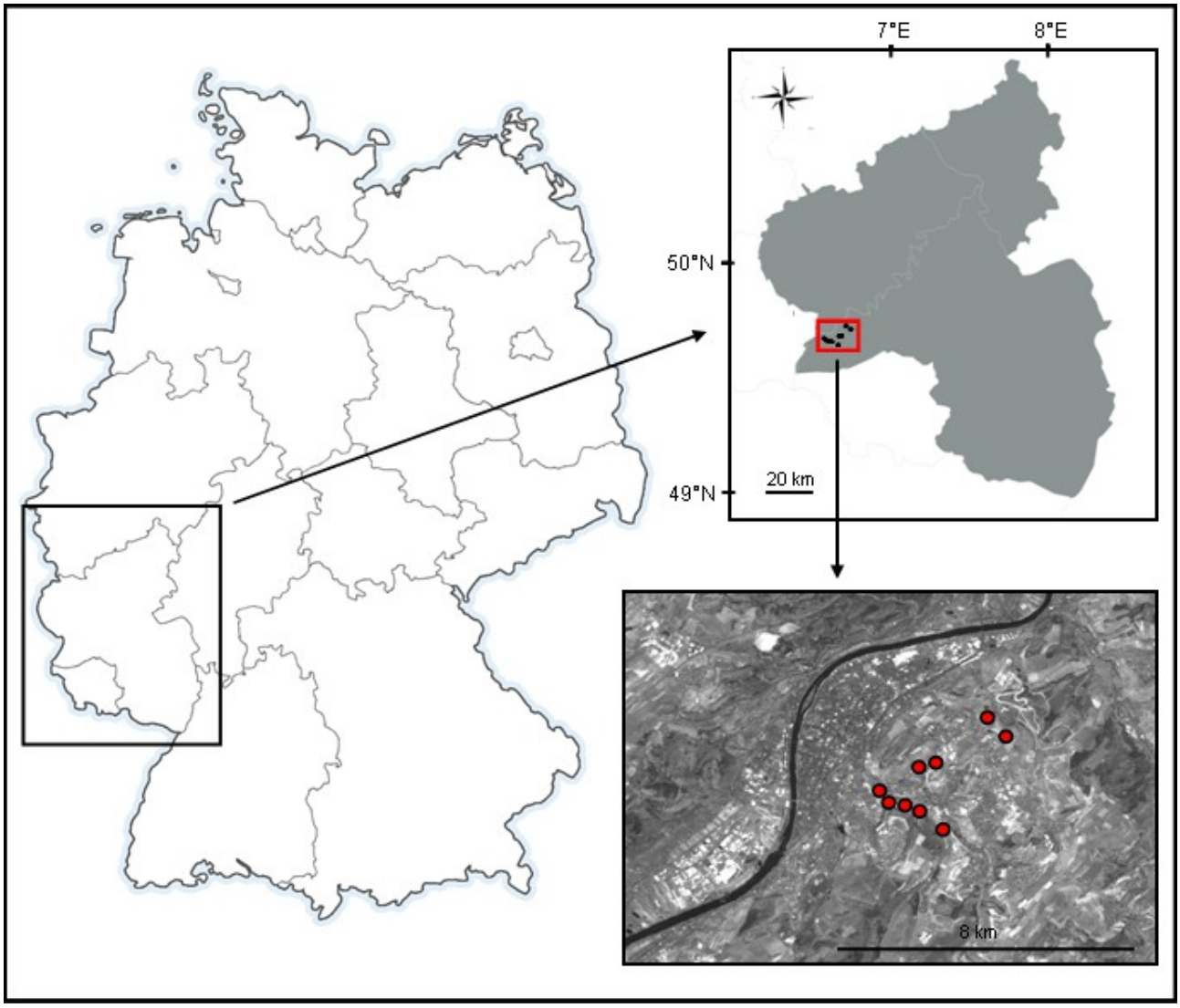

Fig. 1 Location of the study sites within Germany and Rhineland-Palatinate, respectively. Circles indicate the location of transects near the city of Trier (left: Tiergarten I, Tiergarten II, Tiergarten III, Hill, Kernscheid; centre: Brettenbach I, Brettenbach II; right: Avelertal II, Avelertal III)

Study sites

Nine xerothermic vineyard and grassland fallows were selected for butterfly surveys. Old fallows are considered to hold a considerably high species richness and act as important retreats for rare and endangered species in cultivated landscapes. All patches were surrounded by intensively cultivated farmland (mostly vineyards), hay meadows and housing areas and hence suffering from a high degree of fragmentation. Minimum distance between patches was 200 m (Brettenbach I; Brettenbach II). In the other cases, geographic distances were on average 1.6 km. A spatial autocorrelation among patches could be excluded, i.e. no influence of spatial distance on species composition could be revealed by calculating turn over rates between all study patches (Kruskal-Wallis-test p_{same}=0.88, see S1).

All study patches were structurally young fallows in 1973 and were abandoned from agricultural use for more than fifty years now. The vegetation was dominated by perennial bunch grasses, a variety of thermophilic flowering herbs and few interspersed hedge structures composed of *Rosa* ssp., *Rubus* ssp., *Cytisus scoparius* and some *Crataegus monogyna.* Vegetation height varied throughout the year, but on average did not exceed 80 cm. With the exception of one transect (Hill), geological conditions and microclimatic factors prevent the vegetation of converting into secondary forests. The vegetal characteristics of three fallows have been maintained by occasional extensive sheep pasturing once or twice a year, whereas six fallows were left abandoned.

The studied vineyard fallows stretched across a total area of 34.5 ha. Patch size varied between 2.7 ha (Kernscheid) and 5.8 ha (Brettenbach I). In 1973, one transect of varying length (432-1430 m) was established per patch. These transects were re-established and re-investigated in 1986, 2010 and 2012 in cooperation with the initial observer (M. Weitzel). In 2010 and 2012 butterfly surveys were performed at all study sites whereas in 1986 only three transects could be reinvestigated.

Data acquisition

We applied the method developed for the UK Butterfly Monitoring Scheme (Pollard & Yates, 1993) to derive species presence/absence as well as abundance data from field surveys at ten locations in south-western Germany. Standardized butterfly counts were performed along fixed transects. Each butterfly seen within 5 m ahead and 2.5 m on each side of the observer was counted. Individuals were either counted by sight or captured with a butterfly net for closer determination. Transect counts were performed several times throughout the year during the peak flight period of the butterfly species known from this area to avoid misinterpretation of extreme abundances or zero abundances that can arise from singular surveys and variations in generation numbers in certain butterfly species. Each transect was visited every ten days (if weather conditions permitted) from

April to October for a time period correspondent to its length. The observations were conducted between 10:00 am and 5:00 pm under suitable weather conditions (Pollard & Yates, 1993; Settele et al., 1999), i.e. temperature above 17°C, wind less than six on the scale of Beaufort and no rain (Van Swaay et al., 2008). Variations due to weather and time of day were counterbalanced by randomising the butterfly surveys. Each transect walk was kept along with a description of weather conditions and recent management activities.

Field work was similar in all observation years. Bias in data acquisition was minimized, conducting butterfly surveys throughout the same time period each year using congruent transects as well as identical field methods. The number of transect walks was comparable each year and varied between 109 walks in 2010 and 96 walks in 2012. Only in 1986 a smaller number of walks was performed corresponding to a smaller number of study sites surveyed (i.e. three transects).

Classification of butterflies

The recorded butterflies were classified into functional groups defined by their dispersal behaviour, habitat requirements, larval food plant specialisation and global distribution patterns.

We used the classification of Bink (1992) for the analysis of dispersal abilities. However, due to easier manageability, the nine dispersal classes were condensed to three new ones: poor dispersers (class 1-3), medium dispersers (class 4-6) and good dispersers (class 7-9). For general habitat requirements, we used the classification of Reinhardt & Thust (1988) to distinguish between ubiquitous, mesophilic, hygrophilic and xerothermophilic species. Caterpillars, respective to their food plant use, were classified as monophagous (only one plant genus), oligophagous (only plants of one family) and polyphagous (several plant families) (Ebert & Rennwald, 1991). Distribution patterns for Central Europe were obtained from Kudrna et al. (2011). We classified a butterfly species as Mediterranean if their distribution area includes southern Iberia, southern Italy or Greece. The distribution areas of continental species usually exclude these regions and do not reach the lowland areas along the coast of the Atlantic or the British Isles. A species was classified as a Mediterranean-continental species if their distribution area includes at least one of the areas typical for the Mediterranean species, but also extends to the continental parts of Eurasia.

Leptidea sinapis and *L. reali* were treated as a sibling species complex in this study because the split into these two species was still unknown in 1973. Nomenclature of butterflies follows Gaedike & Heinicke (1999).

Statistical analysis

We constructed a data matrix for each observation year containing the number of observed individuals for each species. To exclude outliers due to unsuitable conditions (e.g. weather), the mean number of species counts per month was transformed on the value for 1000 m transect length and summed up to an annual value. Differences in species composition between study years and sites were evaluated using univariate und multivariate statistics. Tests among study sites and observation years were done by Kruskal-Wallis Tests and Cochran-Q-tests.

Turn-over rates were estimated to identify changes in the observed communities between the observation years. This rate was calculated as the number of species recorded in only one of the observation years divided by the total number of species observed during both observation years. As similarity coefficient we calculated Jaccard's index by dividing the number of species recorded on the respective patches by the number of species recorded on each single patch. Moreover, a hierarchical cluster analyses was conducted based on presence-absence data of each transect to test for similarities between the butterfly assemblages in the different study years. All statistics were calculated using PAST 2.17b (O. Hammer, Geological Museum of Copenhagen), SPSS 15.0 and Microsoft Excel 2010.

Community temperature indices (CTI)

For each butterfly species, a Species Temperature Index (STI) was obtained from the European distribution data from Kudrna (2002) and the climate data as used by Settele et al. (2008). The STI is the long-term average temperature experienced by individuals of that species over its range. Species which are predominantly distributed in warmer areas of Europe (e.g. Mediterranean species) therefore have a higher STI value than more northerly distributed species. For each study patch and every year, a Community Temperature Index (CTI) was calculated as the average of each individual’s STI present in the assemblage. A higher CTI would thus reflect a higher proportion of species with high STI.

Results

Species decline

During the field surveys in 1973, 1986, 2010 and 2012 significantly different numbers of species and individuals could be detected on all patches (Kruskal-Wallis-Test, $p_{same}<0.01$) accompanied by severe changes in community composition. In 2010, 21 species, i.e. 36%, could not be recorded formerly present in 1973. In contrast, species numbers were only slightly different in 2010 and

2012. The proportion of species recorded newly in each study year was low ranging between three species in 2010 and four species in 2012. In all cases, the amount of newly appearing species did not compensate for the recorded species losses.

Turnover rates were high on all study patches ranging from 15% (2010-2012) to 33% (1973-2012). Moreover, Jaccard's similarity index, with on average 0.61, suggests community composition changes over time. No influence of grazing activities could be recognized as species richness and community composition between grazed and non grazed patches did not differ.

Cluster analysis based on presence-absence data revealed severe changes in community composition between the early and the late observations (Fig. 2). A considerably higher degree of similarity in the community composition of the years 2010 and 2012 in contrast to the year 1973 becomes obvious. Observations of 1986 hold an intermediate position as one transect still shows a close relationship to the observations in 1973, whereas two transects already resemble the younger observations in 2010 and 2012.

Presence-absence data for all species including the number of transects with the respective species being present in each observation year are given in Table 1.

Table 1 Presence-absence data of all butterfly species recorded on vineyard fallows in south-western Germany. Numbers indicate the number of study sites with the species being present in the respective study year including their species specific functional traits (D1: sedentary, D2: medium, D3: migrant; P1: monophagous, P2: oligophagous, P3: polyphagous; H1: xerothermophilic, H2: mesophilic, H3: hygrophilic, H4: ubiquitous; A1: mediterranean, A2: continental, A3: continental-mediterranean, A4: migrant). Note that the number of surveyed transects varied between the study years: 1973: eight; 1986: three; 2010/12: nine.

	1973	1986	2010	2012	Traits
Hesperidae					
Erynnis tages (L., 1758)	7	3	0	0	D1 P2 H1 A1
Carcharodus alceae (Esp., 1780)	7	3	0	1	D2 P2 H1 A1
Spialia sertorius (Hoff., 1804)	6	0	0	0	D1 P1 H1 A1
Pyrgus malvae (L., 1758)	8	3	6	6	D1 P2 H2 A1
Carterocephalus palaemon (Pal., 1771)	3	0	0	0	D1 P2 H2 A2
Thymelicus lineola (O., 1808)	8	3	6	8	D2 P2 H2 A2
Thymelicus sylvestris (Poda, 1761)	5	3	7	8	D1 P2 H2 A1
Ochlodes sylvanus (Esp., 1778)	8	3	4	1	D2 P3 H4 A1
Papilionidae					
Papilio machaon L., 1758	8	3	7	3	D2 P3 H2 A1
Pieridae					
Leptidea sinapis (L., 1758)/ *reali* Reiss, 1989	8	3	9	6	D2 P2 H2 A1
Anthocharis cardamines (L., 1758)	8	3	9	2	D2 P2 H2 A3
Aporia crataegi (L., 1758)	6	1	6	0	D2 P2 H2 A1
Pieris brassicae (L., 1758)	8	3	4	4	D3 P3 H4 A1
Pieris rapae (L., 1758)	8	3	9	9	D2 P3 H4 A1
Pieris napi (L., 1758)	8	3	7	9	D2 P3 H4 A1
Colias croceus (Fourc, 1785)	2	2	0	0	D3 P2 H4 A4
Colias hyale (L., 1758)	8	3	6	7	D2 P2 H2 A2

Gonepteryx rhamni (L., 1758)	8	3	8	4	D2 P2 H2 A1
Lycaenidae					
Hamearis lucina (L., 1758)	5	1	0	0	D1 P1 H2 A2
Lycaena phlaeas (L., 1761)	8	3	6	4	D2 P1 H2 A1
Lycaena dispar (Haw., 1803)	0	0	1	1	D2 P1 H3 A2
Lycaena tityrus (Poda, 1761)	8	2	3	3	D1 P1 H2 A3
Lycaena hippothoe (L., 1761)	1	0	0	0	D1 P1 H3 A2
Thecla betulae (L., 1758)	8	1	1	1	D1 P1 H2 A2
Neozephyrus quercus (L., 1758)	3	1	0	0	D1 P1 H1 A3
Callophrys rubi (L., 1758)	8	3	5	1	D2 P3 H2 A1
Satyrium w-album (Knoch, 1782)	3	0	0	0	D1 P1 H2 A2
Satyrium pruni (L., 1758)	8	3	0	0	D1 P1 H1 A2
Cupido minimus (Fues., 1775)	4	1	0	0	D1 P1 H1 A3
Cupido argiades (Pallas, 1771)	0	0	3	7	D2 P2 H1 A2
Celastrina argiolus (L., 1758)	8	3	1	2	D2 P3 H2 A3
Aricia agestis ([Den. & Schiff.], 1775)	0	2	8	5	D2 P3 H1 A1
Polyommatus semiargus (Rott., 1775)	7	2	7	4	D2 P1 H2 A1
Polyommatus icarus (Rott., 1775)	8	3	8	5	D2 P2 H4 A1
Polyommatus coridon (Poda, 1761)	4	0	0	0	D2 P1 H1 A1
Nymphalidae					
Argynnis paphia (L., 1758)	5	1	1	0	D2 P1 H2 A3
Argynnis aglaja (L., 1758)	7	1	4	0	D1 P1 H2 A1
Argynnis adippe ([Den. & Schiff.], 1775)	0	1	0	0	D2 P1 H2 A3
Issoria lathonia (L., 1758)	4	1	7	5	D2 P1 H2 A1
Brentis ino (Rott., 1775)	2	0	0	0	D1 P2 H3 A2
Brenthis daphne (Berg., 1780)	0	0	0	1	D1 P1 H1 A1
Boloria selene ([Den. & Schiff.], 1775)	8	1	0	0	D1 P1 H3 A2
Boloria dia (L., 1767)	0	1	0	2	D2 P1 H1 A2
Vanessa atalanta (L., 1758)	8	1	6	8	D3 P1 H4 A4
Vanessa cardui (L., 1758)	8	1	1	2	D3 P3 H4 A4
Inachis io (L., 1758)	8	1	9	3	D2 P3 H4 A3
Aglais urticae (L., 1758)	8	1	8	5	D2 P1 H4 A1
Polygonia c-album (L., 1758)	8	1	5	5	D2 P3 H2 A1
Araschnia levana (L., 1758)	8	1	6	4	D2 P1 H2 A2
Nymphalis polychloros (L., 1758)	3	1	0	0	D2 P3 H2 A3
Melitaea cinxia (L., 1758)	3	0	2	1	D1 P1 H2 A3
Melitaea diamina (Lang, 1789)	6	1	0	0	D1 P1 H3 A2
Melitaea athalia (Rott., 1775)	7	1	2	0	D1 P3 H2 A3
Limentis populi (L., 1758)	2	0	0	0	D1 P1 H2 A2
Limentis camilla (L., 1764)	6	1	0	0	D1 P1 H2 A2
Apatura iris (L., 1764)	1	0	1	0	D1 P1 H2 A2
Pararge aegeria (L., 1758)	8	3	1	0	D2 P2 H2 A1
Lasiommata megera (L., 1767)	7	3	3	0	D2 P2 H2 A1
Coenonympha arcania (L., 1761)	8	3	5	0	D1 P3 H2 A3
Coenonympha pamphilus (L., 1758)	8	3	8	7	D1 P3 H2 A1
Pyronia tithonus (L., 1771)	8	3	9	8	D1 P2 H1 A3
Aphantopus hyperantus (L., 1758)	8	3	8	7	D1 P3 H2 A2
Maniola jurtina (L., 1758)	8	3	9	9	D2 P3 H4 A1
Erebia medusa ([Den. & Schiff.], 1775)	7	0	0	0	D1 P3 H2 A2
Melanargia galathea (L., 1758)	8	2	9	8	D1 P2 H2 A1
Species number	59	52	43	38	

Community composition changes

All functional groups were redetected in 1986, 2010 and 2012. However, species declines were accompanied by significant changes within the composition of each functional group (Fig. 3). The highest proportion of species recorded in 1973 had mesophilic, monophagous and/or sedentary characteristics. In 2010/12, the majority of species showed mesophilic, polyphagous and/or mobile species traits. The strongest negative developments were observed in butterfly species with high functional specialization ($p<0.05$), i.e. in 2010/12 community composition exhibited a significantly higher proportion of generalist species than in 1973. Consequently, strong decrease rates occurred in sedentary species. Butterfly species with poor dispersal abilities declined by 64%, whereas mobile and migrant species showed only moderate declines. Moreover, hydrophilic and mesophilic species exhibited high decrease rates exceeding those of xerothermophilic and ubiquitous species. Especially moist-habitat dwellers declined remarkably by 75%. Monophagous species decreased considerably more than polyphagous and oligophagous species. Hence, half of the butterfly species with high larval food plant specialisation recorded in 1973 were not redetected in 2010 and 2012.
Analyses regarding the affiliation of the newly appearing species to the observed functional groups produced no clear results. New species belonging to all functional groups were detected in 2010/12 with a majority of mobile and xerothermophilic species.

Community temperature index

We found a slight, but significant increase in CTI-values between 1973 and 2012 (Kruskal-Wallis-Anova, psame< 0.05), indicating a proportional increase of thermophilic species within butterfly communities (Fig. 4). In parallel, annual mean temperature increased from 9.2°C to 10°C in the observation years. However, standard deviation of CTI-values contracted remarkably. Since 1970, the temperature in the Trier region increased underlying broad annual variations (German Weather Service (DWD)). No temporal trend matching the recorded temperature increase could be recognized over the time period studied. Neither the annual temperature values nor the climatic trend over time could be accurately represented by the CTI-values (Fig. 5). A summary of all CTI-values and their corresponding standard deviations for each butterfly community monitored between 1973 and 2012 is given in Table 2.

Table 2 Summary of CTI-values and standard deviation for each butterfly community monitored between 1973 and 2012. CTI-values are calculated based on species numbers on the respective transect in each study year.

Transect	1973	1986	2010	2012
Tiergarten I	8.933 (± 0.824)	-	9.049 (± 0.77)	9.169 (± 0.875)
Tiergarten II	8.789 (± 0.94)	9.188 (± 0.833)	9.037 (± 0.812)	9.065 (± 0.739)
Tiergarten III	8.945 (± 0.869)	-	9.001 (± 0.782)	9.000 (± 0.684)
Hill	8.880 (± 0.872)	9.054 (± 0.725)	9.015 (± 0.723)	9.284 (± 0.881)
Kernscheid	8.916 (± 0.828)	-	9.047 (± 0.739)	9.052 (± 0.776)
Brettenbach I	8.912 (± 0.787)	-	8.979 (± 0.759)	9.090 (± 0.766)
Brettenbach II	8.868 (± 0.71)	-	9.054 (± 0.773)	9.208 (± 0.719)
Avelertal II	-	-	9.030 (± 0.736)	9.004 (± 0.789)
Avelertal III	8.972 (± 0.856)	8.998 (± 0.833)	8.928 (± 0.721)	9.151 (± 0.817)
Total	**8.904 (± 0.952)**	**9.069 (± 0.833)**	**9.013 (± 0.707)**	**9.108 (± 0.781)**

Discussion

Butterfly diversity declined dramatically in the region of Trier between 1973 and 2012. These results match anterior observations from Britain, Belgium, Switzerland, and the Czech Republic (Lepidopterologen-Arbeitsgruppe, 1987; Benes & Kuras, 1998; Maes & Van Dyck, 2001; Thomas et al., 2004b, Kadlec et al., 2008) and apparently represent parts of a trans-European phenomenon of biodiversity loss. The observed species decline was most pronounced with regard to species with high functional specialization, i.e. habitat generalists showed less severe decrease rates compared to habitat specialists.

Open grasslands are habitats with relatively warm microclimates (Dennis, 1993). Under a scenario of climate change, an increase of thermophilic species often originating from Mediterranean regions might be expected. It is also likely that hygrophilic and cold-adapted species might show highest vulnerability to increasing habitat temperatures. CTI-values show a slight upward trend reflecting a proportional increase of heat-loving species in butterfly communities since the 1970s. However, the increase in CTI-values did not match the climatic trend over time. We found neither a correlation between CTI-values and the annual mean temperature nor between the CTI and the moving temperature average of the ongoing and the previous year which appeared plausible especially in univoltine butterfly species (Wiemers et al. 2012). Although a complete match of annual mean temperatures and CTI-values might not be expected due to latitude-dependent differences in land-sea distribution across Europe, our results indicate a considerable reduction in both, warm and cold adapted species in the study region, which is also shown by a contraction in the standard deviation of the CTI-values. Although the decrease of cold-habitat dwellers was more pronounced in our study area, species favouring high temperatures also declined at dramatic rates. Our results suggest an inability of both functional groups to cope with temperature changes. Hence, changes in climate (at the macro- and at the microscale) seem to have become a strong selective pressure on both thermophilic and cold-adapted species leading to severe species losses in both functional groups.

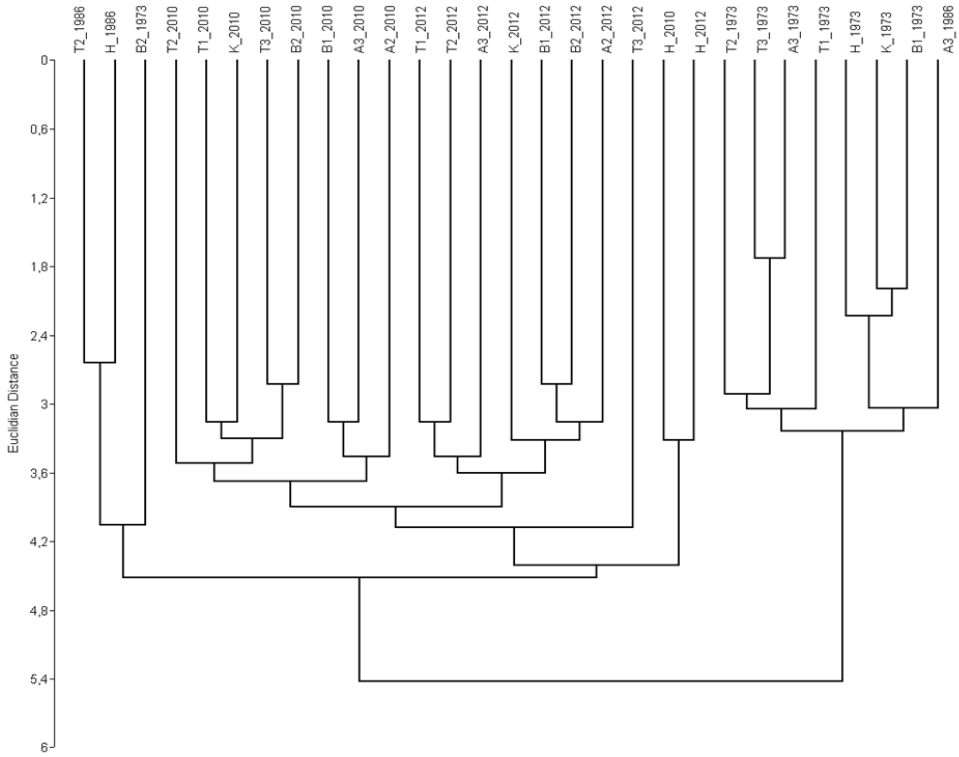

Fig. 2 Cluster analysis based on presence-absence data reflecting the degree of similarity between the butterfly assemblages at the observed transects in the years 1973, 1986, 2010 and 2012 (T1: Tiergarten I, T2: Tiergarten II, T3: Tiergarten III, H: Hill, K: Kernscheid, B1: Brettenbach I, B2: Brettenbach II, A2: Avelertal II, A3: Avelertal III)

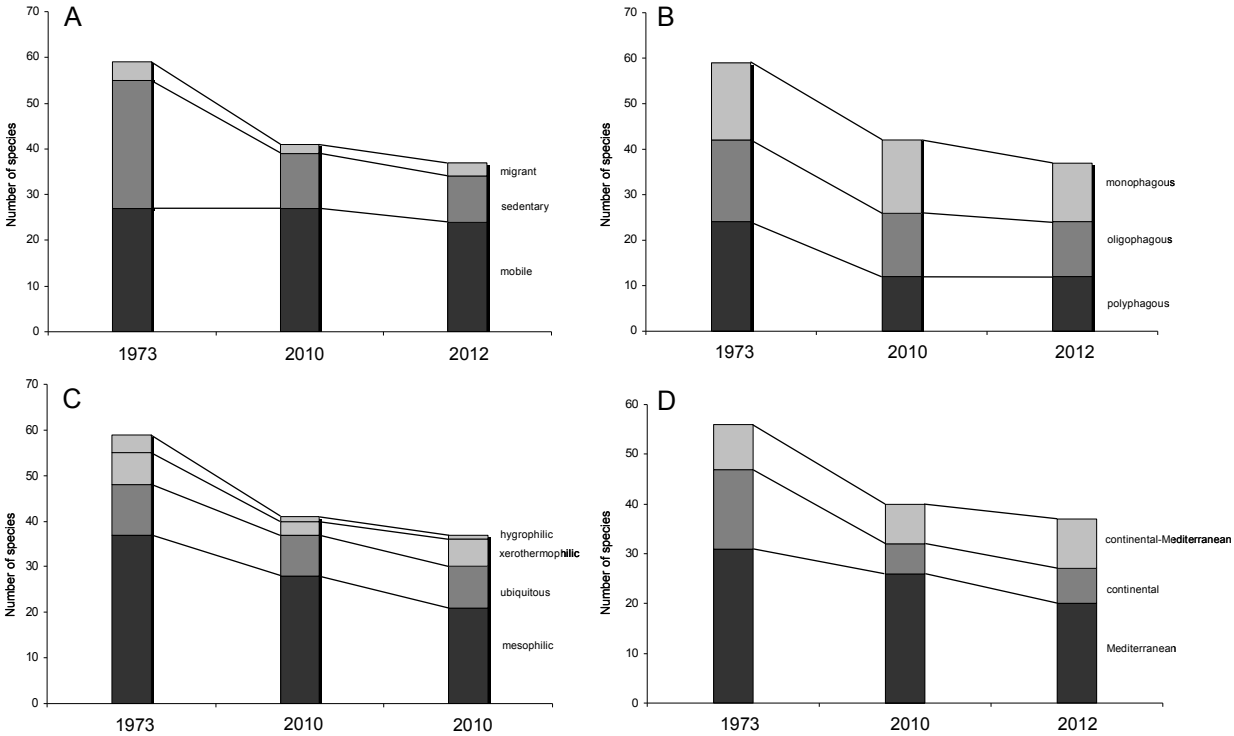

Fig. 3 Community composition changes between the study years with regard to the respective functional traits studied: A) dispersal, B) larval food plant specialisation, C) habitat requirements, D) global distribution patterns.

At the macroscale, local distributions of species can be explained by their thermal environments (Gillingham et al., 2012). Species reaching their range margins are known to be very sensitive to environmental disturbances (Parmesan et al., 1999; Oliver et al., 2009). Therefore, these taxa might be strongly affected by changing climates including newly appearing temperature extremes. We assume that especially increasing winter temperatures and stronger temperature variability during the cold season represent important triggers for the serious decline of the number of cold-adapted species in our study region. Hence, transgressions of their climatic tolerances in recent times might be one reason for the observed local extinction of species belonging to this functional group.

At the microscale, vegetation and habitat structures (e.g. short turf, immature soil, single hedge structures) are often correlated with microclimatic variations and seem to play a major role in determining species occurrence. There is a large body of evidence showing that variations in vegetation height and density generate major microclimatic differences (Schneider & Eugster, 2005; Suggitt et al., 2011).

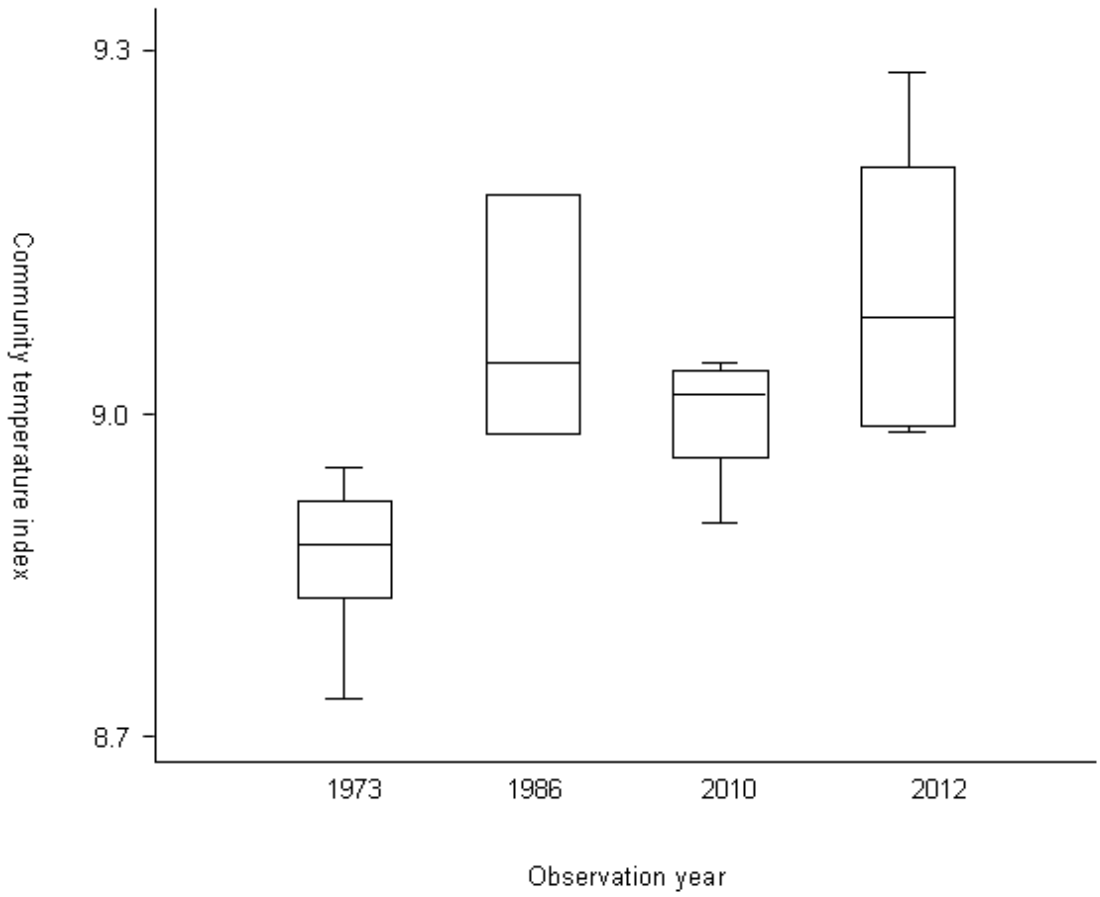

Fig. 4 Range of community temperature indices mirroring the proportion of heat and cold loving species in each observation year. The calculation was based on species numbers at each transect, respectively. CTI-values of 1986 are based on only three fallows and thus lack representativeness.

For open habitats, Thomas (1983) demonstrated that short turf can generate about 8°C higher surface temperatures than tall turfs. In the light of growing eutrophication, growth capacities of plants are strongly enhanced (Bartolomess et al., 2011), especially when combined with an increase in temperatures and precipitation. A gain in biomass possibly remarkably deteriorates the microclimatic conditions close to the ground. Currently, microclimatic cooling might not be outweighed by large-scale global warming. Consequently, conditions for larval development of thermophilic species might decrease for the short term, preventing successful reproduction and thus maybe even occurrence of these species. This also might explain the paradoxical situation of warm-loving species getting rare in a warming environment.

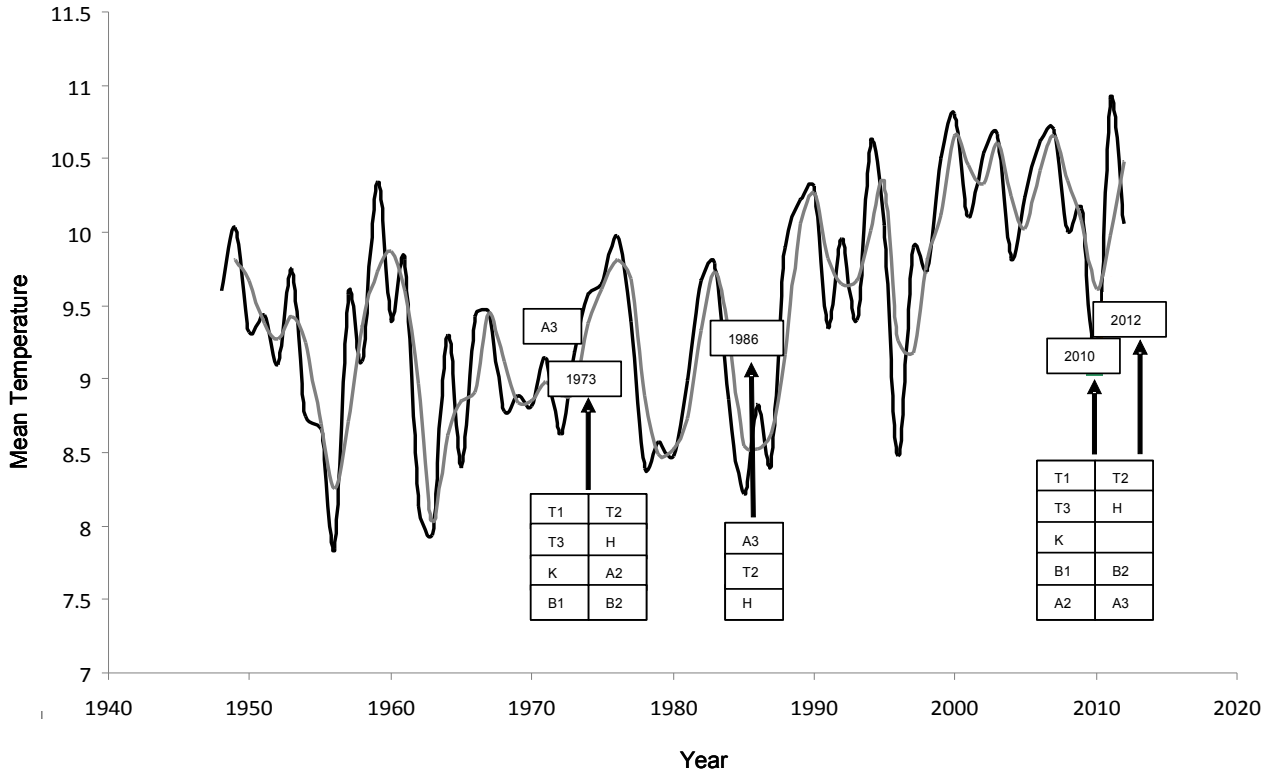

Fig. 5 Variability of mean temperatures for the time period 1948-2012 in the study region. The black line indicates the annual mean temperature measured at Trier Petrisberg, the grey line the two-year moving average temperature. Calculated CTI-values for the observed transects in the respective study year do not match the average temperatures of the running or the previous year nor the general temperature increase (T1: Tiergarten I, T2: Tiergarten II, T3: Tiergarten III, H: Hill, K: Kernscheid, B1: Brettenbach I, B2: Brettenbach II,, A2: Avelertal II, A3: Avelertal III).

Besides microclimatic conditions, the predominant influence of nitrogen on open habitats might also explain small-scale changes in vegetation patterns leading to a replacement of a divers flowering vegetation by nitrophyts (e.g. *Rubus* spec., *Cirsium arvense, Cirsium vulgare*). Many open habitats suffer from a reduction of plant diversity and hence a loss of nectar as well as larval food plants, especially pressing habitat specialists (Van Swaay, 2002). Hence, the dramatic decline

of monophagous species might be the result of substantial changes in vegetation composition over time, disrupting this direct biotic interaction due to agricultural abandonment and eutrophication.

Ecosystem engineers like grazing mammals are expected to positively influence plant diversity, regulate vegetation growth and increase structural heterogeneity in open habitats as many conservation efforts involve mowing and grazing strategies (Römermann et al., 2009; Drobnik et al., 2011). However, additional nutrition impact due to feces might favour the growth potential of competitive nitrophilic plant species. As a result of trampling effects, grazed habitats are also more likely to hold smaller populations and in combination with habitat fragmentation to accelerate species loss (Bogich et al., 2011). We found neither positive nor additional negative effects of grazing activities on butterfly communities in our study. Grazing impacts in the study area differ considerably from year to year due to variabilities in intensity, timing and duration with long periods for vegetation recovery in between. We presume that environmental factors like slope, insolation and geological conditions have predominant influence on vegetation development as there was no significant difference in species richness or species composition between grazed or non grazed patches (Mann-Whitney-Test $p>0.05$). Consequently, contrary to Settele et al. (2009) in our case a compensation of habitat degradation by grazing activities seems unlikely.

A decrease in habitat quality necessarily affects species with low dispersal capacities. As shown by Filz et al. (2013), semi-natural grasslands frequently miss sufficient connectivity facilitating emigration or habitat shifts. In agricultural landscapes, distances between suitable habitats continuously increase, frequently exceeding dispersal capacities of butterflies (Ouin et al., 2004). As a result of a reduced accessibility of non-adjacent patches, populations are restricted to small habitat fragments being particularly vulnerable for microhabitat changes (Thomas, 2000; Dover & Settele, 2009).

The observed ongoing species decline induced by severe changes in habitat quality will consequently result in an entire rearrangement of trait diversity in German butterflies (c.f. Kadlec et al., 2009). Our results indicate impacts of several extrinsic factors as climate and habitat changes which are difficult to distinguish and are likely to operate in combination. Both factors seem to influence butterfly diversity at different scales partly in opposing directions (Warren et al., 2001). Generally, functional groups mirroring high habitat specialisation are locally at high risk of being lost and being replaced by ubiquists. However, most of these functional groups have been identified as particularly important for species conservation purposes (Henle et al., 2004). Hence, our results do not only reflect a depletion in trait diversity of butterfly communities, but also point the way to a more trait-based approach in species conservation.

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SUPPLEMENTARY MATERIAL

S1 Turn over rates calculated to identify differences between the observed communities on the different transects due to spatial autocorrelation. Transects were classified with regard to their spatial distance to each other (T1: Tiergarten I, T2: Tiergarten II, T3: Tiergarten III, H: Hill, K: Kernscheid, B1: Brettenbach I, B2: Brettenbach II, A2: Avelertal II, A3: Avelertal III).

< 1km		1-2km		2-3km		> 3km	
Transects	**Turn over**	**Transects**	**Turn over**	**Transects**	**Turn over**	**Transects**	**Turn over**
A2/A3	0.1935	B1/H	0.3696	A2/B1	0.2222	A2/H	0.375
B1/B2	0.234	B1/T1	0.1852	A2/B2	0.3673	A2/K	0.2857
H/T3	0.4419	B1/T2	0.283	A3/B1	0.1667	A2/T1	0.2143
T1/T2	0.2182	B1/T3	0.2245	A3/B2	0.2727	A2/T2	0.3091
T2/T3	0.2	B2/H	0.3415	B1/K	0.2592	A2/T3	0.2941
		B2/T1	0.2653	B2/K	0.2653	A3/H	0.3148
		B2/T2	0.3333	K/T1	0.1786	A3/K	0.2258
		B2/T3	0.1818			A3/T1	0.1613
		H/K	0.4167			A3/T2	0.2131
		H/T1	0.3125			A3/T3	0.2281
		H/T2	0.4894				
		K/T2	0.2				
		K/T3	0.1765				
		T1/T3	0.1373				

Untersuchung der Arealdynamik des Kurzschwänzigen Bläulings (*Cupido argiades*, Pallas 1771) unter Klimawandelbedingungen mit Artverbreitungsmodellen in Europa

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Author contributions: KJF and TS developed the idea and designed the study, KJF collected occurrence records for *C. argiades,* computed the species distribution models and wrote the manuscript with significant contributions of TS.

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Titel: Climate change impacts on the range dynamics of the short-tailed blue (*Cupido argiades*, PALLAS 1771) in Europe

Kurzfassung: Der Klimawandel hat weltweit gravierende Auswirkungen auf die Biodiversität. Besonders wechselwarme Taxa wie Reptilien, Amphibien oder Insekten sind von Veränderungen in Temperatur- und Niederschlagsverhältnissen stark betroffen. Der Kurzschwänzige Bläuling (*Cupido argiades*) ist eine thermophile Offenlandart, deren rezentes Verbreitungsgebiet weite Teile Europas umfasst und die in ganz Deutschland Ausbreitungstendenzen zeigt. Artverbreitungsmodelle prognostizieren jedoch unter verschiedenen Klimaszenarien (A2a, A1b) des IPCC gravierende Arealverluste über die nächsten Jahrzehnte und eine deutliche Verlagerung klimatisch geeigneter Habitate in Richtung Nordosteuropa und in die Höhenlagen der mitteleuropäischen Gebirgszüge. Folglich ist anzunehmen, dass die aktuell starke Ausbreitung der Art im Saarland und in Rheinland-Pfalz nur vorübergehenden Charakter besitzt. Unsere Studie verdeutlicht somit, dass Veränderungen klimatischer Faktoren wie der jährlichen Temperaturspanne sowie der durchschnittlichen Temperaturen und Niederschlagsmengen der Sommer- und Wintermonate entgegen den allgemeinen Erwartungen in den kommenden Jahrzehnten direkten negativen Einfluss auf das Vorkommen einer rezent weitverbreiteten Art haben könnten.

Abstract: Biodiversity is globally suffering from severe impacts of climate change. Temperature increases and variations in precipitation patterns may especially affect poikilothermic taxa as reptiles, amphibians and insects. Current ranges of the short-tailed blue (*Cupido argiades*) encompass large portions of Europe, and range expansions have been documented at its range border in south-western Germany. However, species distribution models predict a severe habitat loss, and a shift of potentially suitable habitats towards north-eastern Europe and higher altitudes under several IPCC scenarios (A1b, A2a) in the forthcoming decades. Consequently, the currently observed range dynamics in south-western Germany are possibly a temporarily occurring phenomenon. Hence, the model predictions demonstrate that, contrary to expectations, variations in climatic parameters as annual temperature, temperature range and precipitation patterns have long-term negative impacts on the occurrence of a recently widely distributed and dispersing species.

Résumé: Le changement climatique affecte la biodiversité à l'échelle mondiale. La hausse des températures et les changements de précipitations influencent particulièrement les animaux poïkilothermes comme les reptiles, les amphibiens et les insectes. L'Azuré du trèfle (*Cupido argiades*) est largement répandu dans toute l'Europe et est en train de se propager rapidement en Allemagne. Cependant, les pronostics concernant sa propagation pour les années 2050 et 2080

prévoient des pertes d'habitat et un déplacement de ces habitats potentiellement appropriés vers le nord-est de l'Europe et aux altitudes plus hautes. Ainsi, la présence de l'Azuré du trèfle en Rhénanie-Palatinat et en Sarre est probablement seulement temporaire. Nos résultats démontrent que, contrairement aux attentes, des changements climatiques, portant sur la température annuelle ou les températures moyennes ainsi que sur le niveau des précipitations des mois d'été et d'hiver, peuvent influencer négativement la propagation et la présence d'une espèce actuellement largement répandue.

Schlüsselbegriffe: Artverbreitung, Arealverschiebung, Kontinentalität, anthropogener Wandel, Nischenmodell, MAXENT

Keywords: species range, range shift, continentality, anthropogenic change, species distribution model, MAXENT

1. Einleitung

Der anthropogen bedingte Globale Wandel hat weltweit zu Veränderungen und Verschiebungen von Biodiversitätsmustern geführt, die sowohl direkt als auch indirekt die Verbreitung von Arten beeinflussen (PARMESAN et al. 1999). Die durchschnittliche globale Jahrestemperatur ist seit den 1950er Jahren kontinuierlich gestiegen und ein weiterer Temperaturanstieg wird bis 2100 prognostiziert (IPCC 2007). Es wird angenommen, dass wechselwarme Taxa, wie Amphibien, Reptilien und Insekten, besonders vom Klimawandel betroffen sein werden (FODEN et al. 2008, SETTELE et al. 2008, THOMAS et al. 2011). Erste Studien zeigen bereits weltweit großräumige Habitatverluste, temperaturbedingten physiologischen Stress sowie gravierende Rückgänge in der Artenvielfalt auf der regionalen Ebene, verbunden mit Veränderungen in der Zusammensetzung der Zönosen der genannten Taxa (THOMAS et al. 2004a,b, 2006, DIAMOND et al 2011, PÖYRY et al. 2011).
Die steigende Sorge über die potenziellen Auswirkungen des Klimawandels auf die Biodiversität haben in den vergangenen Jahrzehnten zum vermehrten Einsatz von Artverbreitungsmodellen (Species distribution models, SDMs) geführt (ARAÚJO et al. 2005, SETTELE et al. 2008). Diese haben sich heute für die räumliche Interpolation ökologischer *in situ* Beobachtungen als wichtiges Werkzeug etabliert. Hierbei werden, unter Einbeziehung von georeferenzierten Fundpunkten einer Art sowie Topographie, Klima- und Fernerkundungsdaten, räumliche Vorhersagen zur Wahrscheinlichkeit des Vorkommens einer Art getroffen. So können potenzielle Arealveränderungen, biologische Invasionen oder Extinktionsprozesse unter verschiedenen Klimawandelszenarien vorhergesagt werden (RÖDDER et al. 2009, CHING CHEN et al. 2011, IHLOW et al. 2012).
Die vom Intergovernmental Panel on Climate Change (IPCC) für dieses Jahrhundert prognostizierten Veränderungen in Temperatur- und Niederschlagsverhältnissen lassen gravierende Auswirkungen auf die Verbreitungsmuster vieler Arten erwarten. In Abhängigkeit von ihrer Konkurrenzstärke und ihrer Spezialisierung reagieren einzelne Taxa sehr unterschiedlich auf Klimaveränderungen. In vielen Fällen wird die Ausbreitung einer Art trotz einer Verbesserung der klimatischen Gegebenheiten in einem Gebiet durch die arteigene Dispersionsfähigkeit, Habitatzerstörung und -fragmentierung sowie geographische Barrieren begrenzt. Sofern genügend Zeit für die Kolonisierung bisher nicht besiedelter Bereiche zur Verfügung stand, wurden bereits (schwerpunktmäßig in den gemäßigten Breiten) Arealexpansionen in einem breiten Artenspektrum (Vögel, Schmetterlinge, Libellen) zu den Polen oder in größere Höhenlagen nachgewiesen (PARMESAN et al. 1999, PARMESAN & YOHE 2003). Diese Expansionen werden bisher weitgehend in Verbindung mit den steigenden durchschnittlichen Jahrestemperaturen gesehen.
Der Kurzschwänzige Bläuling (*Cupido argiades*) zeigte von 1950 bis 1990 einen bislang

unerklärlichen Rückgang seiner Vorkommen und Deutschland, so dass Populationen der Art Ende des letzten Jahrhunderts nur vereinzelt und stark disjunkt anzutreffen waren, fast ausschließlich in Teilen der Oberrheinebene nördlich des Kaiserstuhls (EBERT & RENNWALD 1991; SETTELE et al. 2009). Seit Beginn der 1990er Jahre zeigt diese polyvoltine und dispersionsfreudige Art jedoch einen starken Ausbreitungstrend. Dies wurde meist im Zusammenhang mit der klimatischen Erwärmung gesehen, kann jedoch nur bedingt durch diesen erklärt werden, da sich die Ausbreitung des Bläulings auch in vergleichsweise kühlen Jahren ungebremst fortsetzt. Auf Basis der bekannten Klimanische des Bläulings haben wir in dieser Studie deshalb Artverbreitungsmodelle erstellt, um sein potenzielles Areal in den Jahren 2050 und 2080 unter verschiedenen Klimawandelszenarien des IPCC (A1b, A2a) zu skizzieren und die Arealdynamik der Art zu diskutieren und vor allem die mögliche Dynamik dieser Art im Saarland und seinen angrenzenden Gebieten genauer zu beleuchten.

2. Material und Methoden

2.1. *Cupido argiades* (PALLAS, 1771)

Der Kurzschwänzige Bläuling (*Cupido argiades*) ist die zweitkleinste Bläulingsart in Deutschland, die sich von anderen heimischen Bläulingsarten deutlich durch die Flügelzipfel und die beiden kräftigen organgefarbenen Randmale auf der Unterseite der Hinterflügel unterscheidet. Diese Wärme liebende Art ist im Sinne von WEIDEMANN (1986) ein Verschiedenbiotopbewohner, der gebüschreiche Strukturen in extensiv genutztem Grünland sowie Bereiche der offenen Kulturlandschaft wie Böschungen, Brachen und Ruderalflächen bevorzugt. Er zeigt eine gewisse Präferenz für feuchte Standorte, ist jedoch auch in trockenen Bereichen bis 1.000 Meter Höhe zu finden (SETTELE et al. 1999).

Sein rezentes Verbreitungsgebiet erstreckt sich vom Norden Spaniens über Mittel,- Süd-, und Osteuropa bis nach Asien und Japan. Im Norden ist die Art vereinzelt im Süden von Schweden und Finnland zu finden. Sie fehlt weitgehend den Gebieten mit mediterranem Klima, also weiten Teilen Iberiens und Italiens, dem Süden der Balkanhalbinsel und der Türkei (TOLMAN & LEWINGTON 1998). In Deutschland sind Populationen aus der Oberrheinebene, Bayern, Hessen, Sachsen, Brandenburg und Sachsens-Anhalt sowie neuerdings aus dem Saarland und Rheinland-Pfalz bekannt (Tabelle 1). Oft wird angenommen, dass sich die Art, als Folge einiger überdurchschnittlich warmer Jahre, stark ausbreiten konnte und Bundesländer besiedelte, aus denen Nachweise lange Zeit fehlten (SETTELE et al. 2009). Vor allem das Extremjahr 2003 scheint eine besondere Schlüsselbedeutung in diesem Prozess zu haben. In diesem Jahr stellte die Art ihre Ökologie regelrecht um und wurde an ihren

Abb. 1: Ein Weibchen des Kurzschwänzigen Bläulings (*Cupido argiades*) bei der charakteristischen Eiablage in ein noch nicht aufgeblühtes Blütenköpfchen des Rotklees (*Trifolium pratense*; Foto: H. Petrischak, Birzberg/Fechingen, 20.08.2010)

Vorkommen in Baden-Württemberg, an denen sie bis dahin weitgehend eine sesshafte und biotoptreue Art dargestellt hatte, zu einem ausgesprochenen r-Strategen, der sich überall zu reproduzieren versuchte und ein stark ausgeweitetes Spektrum an Eiablagepflanzen nutze. Ein Zusammenhang mit der Extremwitterung in 2003 muss angenommen werden, da die Art in ihrem Verhalten in den kühleren Folgejahren deutlich unauffälliger war (pers. Mitt. J. Hensele & E. Rennwald über S. Caspari).

Tab. 1: Verbreitung von *C. argiades* in den Bundesländern Deutschlands, inklusive Rote-Liste-Status und Status nach BArtSchV.

	AV	RL		§D
Deutschland	+	V	Reinhardt & Bolz (2011)	N
SH	E	-	Kolligs (2003)	
HH	-			
MV	x	0	Wachlin et al. (1993)	
NI	+	=	Lobenstein (1986)	
ST	+	0	Grosser (1993)	
BE	-			
BB	+	1	Gelbrecht & Weidlich (1992)	
SN	+	R	Reinhardt (2007)	
TH	+	0	Thust et al. (2006)	
HE	E	D	Kristal & Brockmann (1996)	
NW	+	0	LÖLF (1988)	
RP	+	G	Schmidt (2010)	
SL	+	G	Caspari & Ulrich (2008)	
BW	+	V	Ebert et al. (2005)	
BY	+	0	Bolz &Geyer (2003)	

Aktualität der Vorkommen (AV)

-: kein Vorkommen

o: ausgestorben

x: Fundmeldung 1946-1980

+: Fundmeldung nach 1980

E: Einzelfund(e) nach 1980

Rote-Liste Eistufung (RL)

-: nicht gefährdet

0: ausgestroben

1: vom Aussterben bedroht

2: stark gefährdet

V: Vorwarnliste

D: Daten defizitär

R: seltene Art mit begrenztem Vorkommen

G: Status unbekannt, Gefährdung anzunehmen

=: nicht bewertet

Rechtliche Aspekte (§D)

N: in BArtSchV nicht aufgeführt

2.2. Fundpunkte und Klimadaten

Georeferenzierte Funddaten für die vorliegende Studie wurden aus der Global Biodiversity Information Facility (GBIF, http://data.gbif.org), dem Wanderfaltermonitoring (N. HIRNEISEN, pers. Mitteilung) und dem Tagfaltermonitoring Deutschland (S. CASPARI, pers. Mitteilung) sowie LUCHTANOV & LUCHTANOV (1994) entnommen und räumlich gefiltert, um Autokorrelationen zwischen den Punkten zu vermeiden. Insgesamt flossen 1.680 Fundpunkte aus dem rezenten Areal von
C. argiades in die Studie ein.

Um die Klimanische der Art abzubilden, wurden aktuelle Klimadaten in Form von Bioclim-Variablen mit einer Auflösung von 30 arc-Sekunden (entspricht in Europa einer Kantenlänge der Raster von etwa 900 m) für das rezente Verbreitungsgebiet von *C. argiades* von der WorldClim-Datenbank bezogen. Die 19 verwendeten Bioclim-Variablen repräsentieren klimatische Mittelwerte für den Zeitraum zwischen 1950 und 2000 (HIJMANS et al. 2005) und haben sich bereits innerhalb zahlreicher Modellierungsstudien bewährt (BEAUMONT et al. 2005). Da die räumliche Autokorrelation der 19 Bioclim-Variablen, d.h. die gegenseitige Beeinflussung der Datenwerte durch die Distanz der Werte zueinander, die Modellqualität beeinflussen kann, wurde mit Hilfe einer Pearson-Korrelation eine Auswahl an Klimavariablen getroffen. Die Korrelation misst den Grad des linearen Zusammenhangs zwischen zwei Variablen, wobei im Falle von deutlichen Autokorrelationen ($r^2>0,75$) nachfolgend nur die jeweils die Biologie der Art besser abbildende Variable verwendet wurde. Für unser Modell wurden insgesamt neun Variablen mit ökologischer Bedeutung für das Vorkommen von Tagfaltern ausgewählt. Der endgültige Datensatz beinhaltete die Klimavariablen 'jährliche Mitteltemperatur' (bio1), 'jährliche Temperaturspanne' (bio7), 'mittlere Temperatur des wärmsten Quartals' (bio 10), 'mittlere Temperatur des kältesten Quartals' (bio 11), 'jährlicher Niederschlag' (bio12), 'Niederschlag des feuchtesten Quartals' (bio16), 'Niederschlag des trockensten Quartals' (bio17), 'Niederschlag des wärmsten Quartals' (bio18), 'Niederschlag des kältesten Quartals' (bio19).

Klimadaten für die Jahre 2050 und 2080 wurden mit einer Auflösung von 2,5 arc-Minuten über das globale Klimamodell (GCM, general circulation model) 'HadCM3' (Hadley Centre Coupled Model, version 3) des Hadley Center in Großbritannien bezogen. Die gleichen Bioclim-Variablen wurden verwendet, um Artverbreitungsmodelle für die Klimaszenarien (SRES) A1b und A2a zu erstellen. Grundsätzliche Annahmen des Szenariums A1b sind ein mittlerer Anstieg der CO_2-Emissionen bis 2100 bei einem maximalen Energiebedarf, rasches Bevölkerungswachstum, zunehmende kulturelle

und soziale Interaktion, schnelles Wirtschaftswachstum und Entwicklung neuer, effizienterer Technologien sowie ein ausbalancierter Verbrauch aller zur Verfügung stehenden Energieressourcen. Die globale Durchschnittstemperatur steigt in diesem Szenario um rund 2,8°C (1,7-4,4°C) bis 2100. Im Gegensatz dazu setzt Szenarion A2a eine sehr heterogene Welt mit stetigen Bevölkerungswachstum und großen regionalen Unterschieden in Wirtschaft und Entwicklung voraus. Im Vergleich zu anderen Szenarien-Familien schreiten das Pro-Kopf-Wirtschaftswachstum und technologische Fortschritte langsamer voran. Die globale Durchschnittstemperatur steigt in diesem Szenario um rund 3,4°C (2,0-5,4°C) bis 2100 (IPCC 2007).

2.3. Artverbreitungsmodelle

Aktuelle mathematische Algorithmen zur Berechnung von Artverbreitungsmodellen greifen den empirischen Zusammenhang zwischen georeferenzierten Fundpunkten einer Art und den Umweltvariablen am Fundort auf, um die Klimanische einer Art zu quantifizieren und in den geographischen Raum zu projizieren. Wir haben uns für einen Maximum-Entropy-Ansatz entschieden und mit dem Programm Maxent Version 3.3.3.v auf Basis der gewählten Klimavariablen und georeferenzierten Präsensangaben des Bläulings Verbreitungsmodelle für die gewünschten Zeiträume erstellt (für eine detaillierte Beschreibung des Modellalgorithmus siehe PHILLIPS et al. 2006, ELITH et al. 2011). 25% der Fundpunkte wurden bei jeder Modellierung als Testdaten genutzt, um in einem weiteren Rechenschritt die Qualität des Modells zu bemessen (PHILLIPS et al. 2006). Diese wurde über den AUC-Wert (Area under the receiver operation characteristic curve) bestimmt. Dieser Wert variiert nach der Klassifikation von SWETS (1988) zwischen 0,5 (keine Vorhersagekraft des Modells) und 1,0 (sehr gute Vorhersagekraft des Modells) und definiert die Fehlerrate des Algorithmus. Die Software liefert als Resultat eine Karte, die die Wahrscheinlichkeit für das potenzielle Vorkommen der Art in einem bestimmten Gebiet darstellt. Die relative Eignung jeder Rasterzelle als Habitat wird dabei mit Werten zwischen 0 und 1 dargestellt. Eine potenzielle Habitateignung wurde für *C. argiades* ab einem berechneten Schwellenwert von 0,002 angenommen.

3. Ergebnisse

Unter rezenten klimatischen Bedingungen bilden die Modellergebnisse die heutige bekannte Verbreitung von *C. argiades* gut ab (Abbildung 1). Die modellierte Arealgrenze umfasst weitestgehend alle in Europa rezent bekannten Vorkommen des Bläulings. Weiterhin decken sich die vorhergesagten Gebiete mit hoher klimatischer Habitateignung in Nordspanien, Frankreich, dem Alpenvorraum, dem Balkan und Osteuropa mit bekannten Vorkommen der Art in diesen Regionen.

Besonders hohe Maxent-Werte treten in der Schweiz und in Österreich nördlich des Alpenhauptkamms sowie am südlichen Alpenrand im Tessin, in Norditalien, Österreich und Slowenien auf. In Deutschland liegt der Verbreitungsschwerpunkt der Art in Baden-Württemberg (Oberrheinische Tiefebene), Bayern und Hessen sowie in Sachsen und Niedersachsen. In Rheinland-Pfalz und dem Saarland erreicht der Bläuling zur Zeit potenziell seine nordwestliche Arealgrenze. Diese Modellergebnisse decken sich sehr gut mit dem bekannten Verbreitungsgebiet der Art, die in diesen Regionen zur Zeit eine Grenze kontinuierlicher Verbreitung mit starken Populationen erreicht.

Das Modell hat mit einem AUC-Wert von 0,942 nach der Definition von SWETS (1988) exzellente Vorhersagekraft. Den größten Erklärungsanteil für die rezente und zukünftige Verbreitung von *C. argiades* hatten die Klimavariablen 'jährliche Temperaturspanne' (bio7), 'mittlere Temperatur des kältesten Quartals' (bio 11), 'Niederschlag des trockensten Quartals' (bio17) und 'Niederschlag des wärmsten Quartals' (bio18). Obwohl aus einigen Regionen keine georeferenzierten Fundpunkte in das Modell einfließen konnten, wird die Art weitestgehend flächendeckend in ihrem Areal vorhergesagt. Darüber hinaus werden einige potenzielle Verbreitungsgebiete angezeigt, aus denen zur Zeit kein Artnachweis vorliegt (z.B. Apenninen, Dänemark).

Die potenzielle Verbreitung der Art verändert sich in allen berechneten Szenarien unter alleiniger Berücksichtung klimatischer Parameter in der Zukunft stark. Projiziert man das unter rezenten Klimabedingungen entwickelte Modell auf die Klimawandelszenarien A1b und A2a für die Jahre 2030, 2050 und 2080, zeigt sich, dass die Gesamtfläche des europäischen Verbreitungsgebiets tendenziell abnimmt und sich zudem deutlich in nordöstlicher Richtung verschiebt (Abbildung 1). Außerdem wird eine Verlagerung günstiger Habitate in höhere Lagen prognostiziert. Bereits für 2030 sagen die Modelle eine Reduktion der Vorkommen von *C. argiades* in Spanien und Frankreich auf die Höhenlagen der Pyrenäen, der Vogesen, der Alpen und des Zentralmassivs voraus. Zudem wird auf der Balkanhalbinsel und am Südalpenrand ein deutlicher Verlust heute potenziell günstiger Regionen wahrscheinlich.

Gebiete mit bester klimatischer Eignung werden für das Jahr 2030 für beide untersuchten Klimawandelszenarien am nördlichen Alpenrand vorhergesagt. Eine Arealerweiterung ist jedoch in Belgien, im Süden Skandinaviens, im nördlichen Polen und im Baltikum potenziell möglich. Zunehmend günstige Habitatbedingungen prognostizieren die Modelle zudem im Erzgebirge, dem Böhmerwald, in den Sudenten, auf der Böhmisch-Mährischen Höhe und in den Karpaten. Auch in der Mitte Deutschlands werden von den Modellen zunehmend Habitate als klimatisch günstig ausgewiesen. Hier zeigen die Modelle weiterhin günstige klimatische Voraussetzungen für ein zusammenhängendes Areal von *C. argiades* in Bayern, Teilen Baden-Württembergs, Hessen,

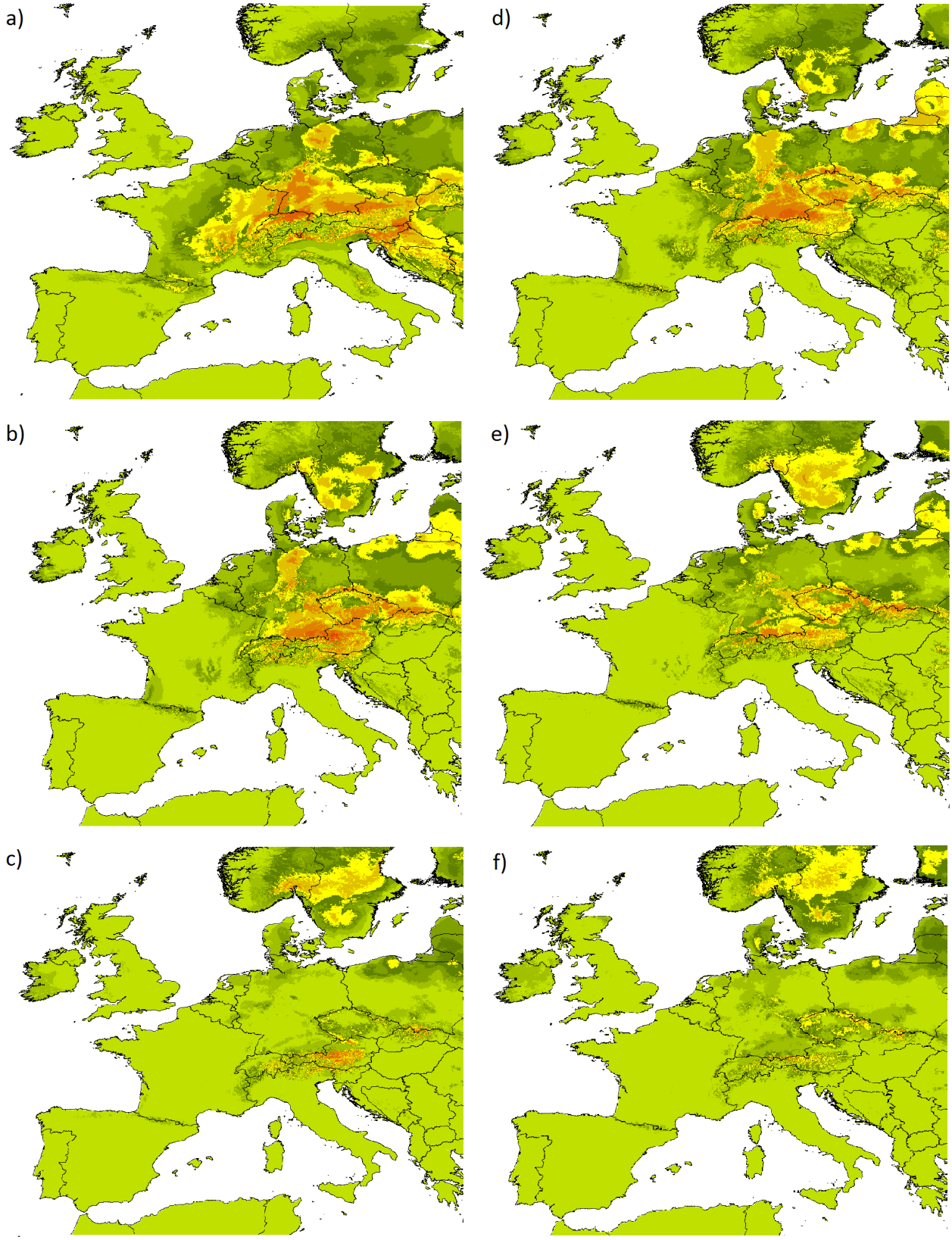

Abb. 1: Potenzielle Verbreitung von *Cupido argiades* unter alleiniger Berücksichtigung klimatischer Parameter in Europa: a) heute, b) 2050 A2a-Szenario, c) 2080 A2a-Szenario, d) 2030 A1b-Szenario, e) 2050 A1b-Szenario, f) 2080 A1b-Szenario. Wärmere Farben indizieren eine höhere klimatische Habitateignung.

Thüringen, Sachsen und Niedersachsen. Jedoch verschiebt sich die Arealgrenze der Art innerhalb Deutschlands auch nach Osten. Folglich sind im Jahr 2030 im Saarland und in Rheinland-Pfalz voraussichtlich nur noch wenige Standorte klimatisch für den Bläuling geeignet.

Bei der Betrachtung der beiden Zukunftsszenarien im Jahr 2050 macht sich erneut ein deutlicher Verlust potenzieller Habitate am südlichen und westlichen Arealrand von *C. argiades* bemerkbar. Im Szenario A1b sind der zu erwartende Arealverlust und die Verlagerung günstiger Habitate nach Norden noch eindeutiger als unter den A2a-Annahmen. Weite Teile Südskandinaviens und des Baltikums werden als potenziell günstige Habitate vorhergesagt, während in Südeuropa unter beiden Szenarien nur noch disjunkte Restareale in den Pyrenäen und in den Gebirgen der Balkanhalbinsel zu finden sind. Auch in Ostmitteleuropa wird ein Rückzug potenzieller Vorkommen des Bläulings in höhere Lagen des Erzgebirges, des Böhmerwaldes, der Sudeten, der Böhmisch-Mährischen Höhe und der Karpaten wahrscheinlich.

Weiterhin werden Gebiete im nördlichen Alpenraum als Regionen mit höchster klimatischer Habitateignung prognostiziert. Die Vorhersagen für Deutschland weichen jedoch zwischen den beiden Zukunftsszenarien stark voneinander ab. Beide Modelle weisen das Voralpenland, Teile des Oberrheingrabens, den Schwarzwald, den Harz, den Thüringer Wald, das Fichtelgebirge, den Bayrischen Wald sowie vereinzelte Regionen Mitteldeutschlands als klimatisch günstige Habitate aus. Im A1b-Szenarion beschränkt sich die Verbreitung des Bläulings nördlich der Donau jedoch auf einige wenige Höhenlagen, während ein großer Arealverlust im Tiefland vorhergesagt wird. Unter A2a-Annahmen bleiben hingegen, unabhängig von der Topographie, großflächig weite Teile des für 2030 prognostizierten Areals in Norddeutschland, Hessen, Bayern und Sachsen erhalten. Im Saarland und in Rheinland-Pfalz werden nur vereinzelte Habitate in Eifel und Hunsrück als klimatisch günstig ausgewiesen.

Die Projektionen der beiden Zukunftsszenarien für das Jahr 2080 unterscheiden sich nicht erheblich. Die prognostizierte Kerngebiete des Areals von *C. argiades* in Europa liegen im südöstlichen Skandinavien, Südfinnland, dem Baltikum, dem östlichen Alpenraum, dem Erzgebirge, den Sudeten, dem Zelezné Gebirge (zentraler Teil der Böhmisch-Mährischen Höhe) und der Tatra. Die höchste klimatische Habitateignung wird dabei für Gebiete im östlichen Alpenraum und den Karpaten vorhergesagt. Rezente Habitateignungen in Süd-, West- und Südosteuropa dürften unter diesen Szenarien vollständig erlöschen. Auch in Deutschland sind voraussichtlich im Jahr 2080 nur noch vereinzelte Reliktpopulationen im Alpenvorland, dem Erzgebirge, dem Harz und dem Thüringer Wald zu finden. Alle Zukunftsmodelle weisen mit AUC Werten zwischen 0,941 und 0,942 exzellente Vorhersagekraft auf.

4. Diskussion

Der Vergleich der prognostizierten Verbreitung unter rezenten klimatischen Bedingungen mit der realen Verbreitung von *C. argiades* zeigt, dass die errechneten Artverbreitungsmodelle für den Untersuchungsraum realistische Annahmen bezogen auf die zukünftigen Verbreitungsmuster machen. Einzig wenige Gebiete, aus denen wenige bis keine georeferenzierten Fundpunkte für das Modell zur Verfügung standen, wurden unzureichend wiedergegeben (zum Beispiel Teile des Karpatenbeckens). Das Fehlen einer Art in Regionen, die das Modell als potenziell günstige Habitate einstuft, kann generell durch den negativen Einfluss von biotischen Interaktionen, eine limitierende Ausbreitungsfähigkeit oder das Fehlen geeigneter Mikrohabitate erklärt werden (SOBERÓN & PETERSON 2005, SOBERÓN 2007, BROOKER et al. 2006), wobei die beiden letztgenannten wohl für *C. argiades* ausgeschlossen werden können.

Cupido argiades zeigt aktuell in der Südhälfte Deutschlands eine weitgehend flächendeckende Verbreitung, was auch von unserem Modell fast deckungsgleich vorausgesagt wird. Über die vergangenen Jahre wurden immer wieder regionale Ausbreitungswellen, jedoch auch Rückgänge der Art festgestellt (SETTELE et al. 2009), wobei jedoch die Phasen vor und nach 2003 differenziert gesehen werden müssen. Vor diesem Zeitpunkt sind beispielsweise die Fundstellen der Art im Oberrheingraben seit 1980 deutlich zurückgegangen, während gleichzeitig eine Ausbreitungstendenz in östlicher Richtung festzustellen war (EBERT 1991). Seit dem Hitzejahr 2003 kam es jedoch ausschließlich zu Ausbreitungen (S. CASPARI, schriftl. Mitt.). *C. argiades* ist nach der Klassifikation von BINK (1992) ein Binnenwanderer, der regelmäßig Wanderflüge über kurze bis mittlere Distanzen unternimmt. Das ökologische Verhalten der Art während dieser Ausbreitungswellen wird derzeit näher untersucht.

Der Falter ist ein thermophiler Offenlandbewohner, der jedoch keine speziellen Ansprüche an sein Habitat stellt; er fliegt in offenem Grasland, lichten Wäldern sowie auf Ruderalstellen (SETTELE et al. 1999). Erste Beobachtungen zeigen, dass die Art während der expansiven Phase der Ausbreitung ihre Habitate opportunistisch wählt, während in der sich anschließenden stationären Phase eine deutlich selektivere Habitatwahl dominiert (pers. Mitt. J. HENSLE durch S. CASPARI). Im Zuge der (Re-)Kolonisierung neuer Habitate scheint der Bläuling schrittweise die für ihn günstigen Habitate zu besiedeln. Bisher sind kaum Vorkommen außerhalb des prognostizierten Vorkommens in Deutschland bekannt, was auf eine klimatische Limitierung in diesen Bereichen schließen lässt. Gründe für die Rückgänge oder das bisherige Fehlen der Art in weiten Teilen Deutschlands können auf Basis der klimatischen Einnischung und der Mobilität des Falters nicht benannt werden. Jedoch können der Einfluss biotischer Interaktionen sowie unterschiedlicher Landschaftsparameter nicht ausgeschlossen werden. Letzteres ließe sich in einem weiteren Schritt durch die Verschneidung der

Artverbreitungsmodelle mit Landschaftsvariablen untersuchen (HUWYLER et al. 2012).
Bemerkenswert ist die Zusammensetzung der Klimavariablen, die den höchsten Erklärungsgehalt im Modell besitzen. Diese klimatischen Faktoren beeinflussen das Vorkommen von Tagfaltern sowohl direkt wie auch indirekt (DENNIS 1993). So haben hohe Sommerniederschläge meist einen deutlich negativen Einfluss auf das Vorkommen von Tagfalterarten, während gleichzeitig oft eine ökologische Abhängigkeit von den Temperaturen im wärmsten und kältesten Quartal besteht (SETTELE et al. 1999). Im vorliegenden Fall weisen neben den genannten Klimaparametern auch die jährliche Temperaturspanne sowie die Winterniederschläge hohen Einfluss auf die Artverbreitung auf.
Die rezente Verbreitung von *C. argiades* umfasst in weiten Teilen Regionen mit kontinentalen Klimaten, d.h. mit trocken-kalten Wintern und trocken-heißen Sommern. In Regionen mit kühlem und stark atlantisch geprägtem Klima sowie in Winterregenklimaten kommt die Art rezent nur auf Sonderstandorten vor. Da Deutschland zur Zeit eine Übergangsregion zwischen atlantisch und kontinental geprägten Klimaten darstellt, ist hier aktuell das Vorkommen des Bläulings regional möglich. Auch die Ergebnisse der Modellierungen unter zukünftigen Klimaszenarien zeigen eine hohe Übereinstimmung der prognostizierten Verbreitung von *C. argiades* mit den dann kontinental geprägten Gebieten Europas. Ein möglicher zukünftiger Rückzug der Art aus dem Westen Europas, und in diesem Zusammenhang auch weitgehend aus dem Saarland und angrenzenden Regionen, dürfte zu einem großen Teil in der zunehmenden Atlantisierung des Klimas begründet sein, was sich durch die überdurchschnittlich milden Winter der letzten Jahre deutlich abzeichnet.
Betrachtet man die Zukunftsmodelle, so wird ab 2030 unter beiden Klimaszenarien eine deutliche Verlagerung des Habitats in Richtung Nordosten und in höhere Lagen erkennbar. Dem IPCC (2007) zufolge ist es wahrscheinlich, dass der Klimawandel in Deutschland zu steigenden Jahresdurchschnittstemperaturen und in Folge auch zu heißeren, trockeneren Sommern führt. Zudem werden auch höhere Durchschnittstemperaturen in den Wintermonaten sowie verstärkte Winterregenfälle prognostiziert. Generell kann vor allem durch die Verringerung der jährlichen Temperaturamplitude von einer 'Atlantisierung' des Klimas in West- und Mitteleuropa ausgegangen werden.
Aus den Modellen ist abzuleiten, dass die Veränderung in der jährlichen Temperaturspanne sowie die erhöhten Temperaturen und Niederschlagsmengen in den Wintermonaten zu einem weitgehenden Erlöschen der Populationen von *C. argiades* in diesen Regionen führen könnten. Andererseits ist jedoch eine Etablierung der Art in Südskandinavien und dem Baltikum nicht unwahrscheinlich, zumal dort schon rezent Einzelfunde nachgewiesen wurden (TOLMAN & LEWINGTON 1998). Im Laufe der Zeit ist dem Modell zu Folge jedoch auch dort ein Rückzug der Art in kontinental geprägte Regionen südöstlich der Skanden, ins nördliche Baltikum und nach

Südfinnland zu erwarten.

Für Mittel- und Osteuropa prognostizieren unsere Modelle, dass zukünftig lediglich noch vereinzelt Populationen in den kalt-gemäßigten Höhenlagen der Alpen, der östlichen Mittelgebirge und der Tatra auftreten werden. Vorkommen von *C. argiades* sind aktuell bis 1.000 m Höhe bekannt (TOLMAN & LEWINGTON 1998). Höhenlagen deutlich oberhalb dieser Marke werden wahrscheinlich auch in Zukunft nicht von der Art besiedelt werden. Es ist anzunehmen, dass eine vertikale Verbreitungsgrenze auch zukünftig durch klimatische Limitierungen bestehen bleiben wird. Das derzeit stark zunehmende und gehäufte Auftreten des Kurzschwänzigen Bläulings im Saarland und den angrenzenden Regionen könnte somit nur eine Art "Gastspiel" sein, das schon in den nächsten Jahrzehnten auch aus klimatischen Gründen in unserer Region zu Ende gehen könnte.

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Niche evolution in a host-parasite system: answers from ecological niche models

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Abstract

A strong host-parasite association has developed in *Maculinea* butterflies and *Myrmica* ants. Thereby, sufficient overlap in their ecological niches is a prerequisite for efficient host exploitation. Environmental niche models revealed considerable niche dynamics in the observed parasite-host relation. In the majority of butterfly species, niche overlap with host ants was lower than expected at random, indicating an evasive niche shift in the hosts to minimize infestation risk. Locally, high selective pressure on butterfly species might be counterbalanced by alternative host use. In contrast, in the assumed autapomorphic *Maculinea rebeli*, considerably higher niche overlap values were observed. This goes in line with a recent ecological niche shift in this butterfly species. The observed changes in habitat requirements may be interpreted as an evolutionary response to previous evasive niche shifts in its host ants now potentially adapting to their niches. Our results indicate an evolutionary arms race between *Maculinea* butterflies and *Myrmica* ants, potentially forcing the butterflies to alternative host exploitation on the one hand and short-time niche adaptations on the other hand to minimize local selective pressure resulting from host escapes.

Keywords: Myrmecophily, *Maculinea*, niche similarity, range overlap, ENMtools, Lycaenidae, Maxent, *Myrmica*

Introduction

Multiple biotic interactions have evolved between butterflies and other species. Common examples include relationships of lycaenid butterflies with ants (Fiedler, 1991; Fiedler *et al*., 1996). Communication mechanisms such as chemical or acoustic mimicry and camouflage are suggested to play a major role in mediating these systems (DeVries *et al*., 1993; Akino *et al*., 1999). Most of these interactions are suggested to be mutualistic as butterfly larvae retrieve protection against their natural enemies from ants and provide nutrition in return. However, a complex form of social parasitism has developed from these mutualistic systems in the Palearctic butterfly genus *Maculinea* (Thomas & Settele, 2004; Thomas *et al*., 2005).

As shown in Table 1, myrmecophilic behaviour is described for six *Maculinea* species, being parasites of different *Myrmica* ants (Thomas *et al*., 1989; Wynhoff, 1998; Jansen *et al*., 2011). Early larval stages are mono- or oligophagous feeders on buds of flowers (*Gentiana, Origanum*, *Sanguisorba*, *Thymus*), which flower in midsummer only (Thomas *et al*., 1998; Settele *et al*., 1999). Molting to the final instar, caterpillars are adopted by ants, apparently mimicking their larvae, as pointed out by Akino *et al*. (1999). Henceforth, caterpillars live underground as social parasites in *Myrmica* colonies until pupation for up to two years (Witek *et al*., 2006). They are either being actively fed via regurgitation ('cuckoo-feeding') or prey on the ant brood (Elmes & Thomas, 1992; Thomas & Wardlaw, 1992). With the aim to avoid being attacked by the ants, butterfly larvae biosynthesize cuticular hydrocarbon profiles similar to their hosts (Akino *et al*., 1999). Still in the early 2000s a strong host specificity was expected (Thomas *et al*., 2005), because this kind of chemical mimicry requires highly specific signals. Therefore, it has long been assumed that each *Maculinea* species parasitizes on a particular *Myrmica* species, perhaps even in the framework of co-evolutionary relationships (Elmes *et al*., 2002; Thomas *et al*., 2005). However, recent field studies have brought to light that host exploitation by *Maculinea* seems more variable (Als *et al.*, 2004; Sielezniew & Stankiewicz, 2004; Tartally *et al*., 2008) than previously expected; i.e. although all *Maculinea* species prefer particular ant species, they are also able to switch hosts. Apparent host shifts have been documented for all parasitic *Maculinea* species, but caterpillar survival rates are highest in their preferred hosts, suggesting that primary (or main) and secondary hosts do exist (Als *et al*., 2001; Jansen *et al*., 2011). However, to date mechanisms driving host shifts or multiple host use at one locality still remain poorly understood.

A high degree of niche overlap between hosts and parasites seems a prerequisite for efficient host exploitation. However, parasitic myrmecophily represents an important selective pressure potentially driving the ecology and evolution of ant hosts (Janzen, 1980; Thompson, 2005). Butterflies are intimately associated to ants as these provide shelter and food for butterfly larvae,

main factors crucial for their survival. Hereby, depending on the intensity of parasitism, butterfly larvae might be extremely harmful to host ants, considerably reducing their fitness and survival rates (Kaltz & Shykoff, 1998; Nash *et al*., 2008). Especially in the case of *Maculinea* with more than one parasite species relying on a single host species for survival, critical damages of the host might occur. As a result, different mechanisms have evolved to reduce the risk of being attacked in most host-parasite relations. This includes host specific responses that activate evolutionary pathways which also might considerably alter a species niche (Ridley, 2004). In response, parasite species continuously try to develop ways to overcome these defence barriers or niche shifts to maximize the efficiency of host exploitation (Kaltz & Shykoff, 1998; Dybdahl & Storfer, 2003). This is the basis of the co-evolution theory proposed by Ehrlich and Raven (1964).

We here use *Maculinea* butterflies and *Myrmica* ants as a test system to evaluate niche dynamics in a parasite-host relation. Regarding their climatic niches, four of five *Maculinea* species show preferences for hygrophilic habitats. Only *Maculinea rebeli* is a thermophilc dry-habitat dweller (Settele *et al*., 1999). These different habitat requirements match quite well the current discussion about the intra- and interspecific taxonomy of the genus *Maculinea* (Fric *et al*., 2007; Balletto *et al*., 2010). Some authors discuss *Maculinea rebeli* as a sister species of *M. alcon*, whereas others only expect it to be a different ecotype within the same species (Als *et al.*, 2001; Jansen *et al*., 2011; Sielezniew *et al*., 2012). In both cases, a relatively recent shift in the species' ecological niche from moist to dry habitats can be suspected.

Table 1 Associations of *Maculinea* parasites with their *Myrmica* host species: X= main host, (X)= secondary host

	Myrmica rubra	*Myrmica ruginodis*	*Myrmica scabrinodis*	*Myrmica sabuleti*	*Myrmica schencki*
Maculinea alcon	X	X	X		
Maculinea arion			(X)	X	(X)
Maculinea nausithous	X	(X)	X		
Maculinea rebeli		(X)		X	X
Maculinea teleius	X	(X)	X	(X)	

Over the last decade, environmental niche models (ENMs) have emerged as powerful tools to address ecological and evolutionary questions (Rödder *et al*., 2009; Araújo *et al*., 2011; Habel *et al*., 2010, 2011). Climatic parameters recorded at occurrence sites of a species are aggregated to uncover the 'climatic niche' of this species (Soberon & Nakamura, 2009; Franklin, 2009; Araújo & Peterson, 2012). Based on this climatic niche, ENMs aim to predict the 'likelihood' of a species' potential distribution across different geographic and temporal scales (Franklin, 2009; Elith *et al*., 2006; Peterson *et al*., 2011).

Ecological modelling thus far has not been applied to butterfly social parasitism. Given the hypothesis that selective pressure fostering the development of pathways to avoid parasite

infestation might alter species' niches, we here test for niche similarities between *Maculinea* butterflies and *Myrmica* ants. We developed ENMs of associated parasitic butterflies and their host ant species (1) to assess the similarities between their climatic niches and (2) to identify the amount of range overlap, especially with regard to niche differences between the closely related species *M. rebeli* and *M. alcon*. Here, the probably young autapomorphy of *M. rebeli* might be seen in congruence with a recent ecological niche shift of this species. As a consequence, host ants might not have experienced enough time to respond to the new selective pressure by shifting their niches. Therefore, we expect a larger niche overlap in *M. rebeli* and its host ants than in the other *Maculinea* butterflies, that gave their host ants more time for evasive niche shifts.

Methods

We conducted correlative environmental niche models, thereby using presence-only (versus absence) records and grid-based climate surfaces for all butterfly, ant and host plant species. The distribution of *Maculinea* butterflies is acknowledged to be mainly limited by the presence of their host plants (Munguira & Martín, 1999; Thomas & Elmes, 2001; Jansen *et al*., 2011). Consequently, habitat suitability maps of butterflies were pruned with the predicted distribution of the respective host plant. Subsequently, spatial range overlap and niche similarity between hosts and parasites were assessed.

Species records

Occurrence data of butterfly and ant species were obtained from the Global Biodiversity Information Facility (Gbif; http://data.gbif.org, accessed November 2012). In order to mirror a species' entire current distributions over geographic space, additional records were taken from the literature and supplemented by own georeferenced observations (A. Tartally, pers. comm.). As the distribution of *M. arionides* was represented by less than 30 records, assumptions for ENM building (see below) were violated (e.g. Peterson *et al*., 2011) so that this species was excluded from our study. All available records were geo-referenced with DIVA-GIS 7.5.0 (Hijmans *et al*., 2002). To reduce effects of spatial autocorrelation, all records were filtered and duplicate records per grid cell were removed. In total, we incorporated 5,512 unique distributional records for the five remaining butterfly species, 35,799 records for the host plants and 8,455 records for the ant species in this study. The intra- and intergeneric taxonomy of *Maculinea* butterflies is under current debate, especially the species status of *Maculinea rebeli* (Fric *et al*., 2007; Balletto *et al*., 2010). However, this taxonomic status has no further implication on our ecological analysis.

Climate data

Climatic information for current climates was derived from the WorldClim database (version 1.4, http://www.worldclim.org; Hijmans *et al*., 2005). The database provides climatic variables based on interpolations of the climate conditions of the time period 1950-2000 with a spatial resolution of 30 arc seconds (Hijmans *et al*., 2005). For ENM building, we used 19 'bioclim' variables derived from the monthly temperature and rainfall values in order to generate variables with higher biological relevance. These are widely used in ecological modelling as they are meant to outperform monthly climate values since they are independent of latitudinal variation (Busby, 1991; Beaumont, 2005) (Supplement S1).

Table 2 Bioclims applied for modelling the associated butterfly, plant and ant species. Climatic variables with highest explanative power are given in bold and underlined.

Taxon assessed	Bioclim variables
Maculinea alcon	bio1, bio2, **bio3**, **bio4**, bio5, bio6, bio7, bio8, bio9, **bio10**, bio11
Maculinea arion	bio1, **bio3**, **bio4**, bio5, bio7, bio10, bio11, bio12, **bio18**
Maculinea nausithous	**bio1**, **bio3**, bio4, bio6, bio7, bio10, bio11, bio12, **bio18**
Maculinea rebeli	bio1, bio2, **bio3**, **bio4**, bio5, bio6, bio7, bio10, bio11, bio12, **bio18**
Maculinea teleius	bio1, **bio2**, bio3, bio4, bio5, bio6, bio7, **bio10**, bio11, bio12, **bio18**
Myrmica rubra	**bio1**, **bio2**, **bio6**, bio9, bio12, bio15
Myrmica ruginodis	bio2, **bio3**, bio6, **bio7**, bio8, **bio9**
Myrmica sabuleti	**bio1**, bio3, **bio6**, **bio7**, bio8, bio9
Myrmica scabrinodis	**bio3**, bio5, **bio6**, **bio7**, bio8, bio9
Myrmica schencki	bio1, **bio3**, bio5, **bio6**, bio8, **bio9**, bio15
Gentiana cruciata	**bio1**, **bio5**, bio6, bio12, **bio16**, bio17
Gentiana asclepiadea	**bio1**, **bio3**, bio4, bio5, bio6, bio12, bio15, **bio16**, bio17
Gentiana pneumonathe	**bio4**, bio6, bio7, **bio9**, **bio11**, bio14, bio17
Saguisorba officinalis	bio1, bio3, **bio4**, bio7, bio9, **bio10**, bio11, bio12, bio16, **bio17**
Origanum vulgare	bio4, bio6, **bio7**, bio9, bio11, **bio15**, bio17, **bio19**

Multicolinearity of climatic data and the inclusion of biologically less important variables can inflate the ENM performance (e.g. Heikkinen *et al*., 2006). We therefore applied a jackknifing approach as implemented in Maxent (see below) to choose a subset of five to six bioclim variables for each species (Table 2). These variables are supposed to have high importance for model fitting following Phillips *et al*. (2006).

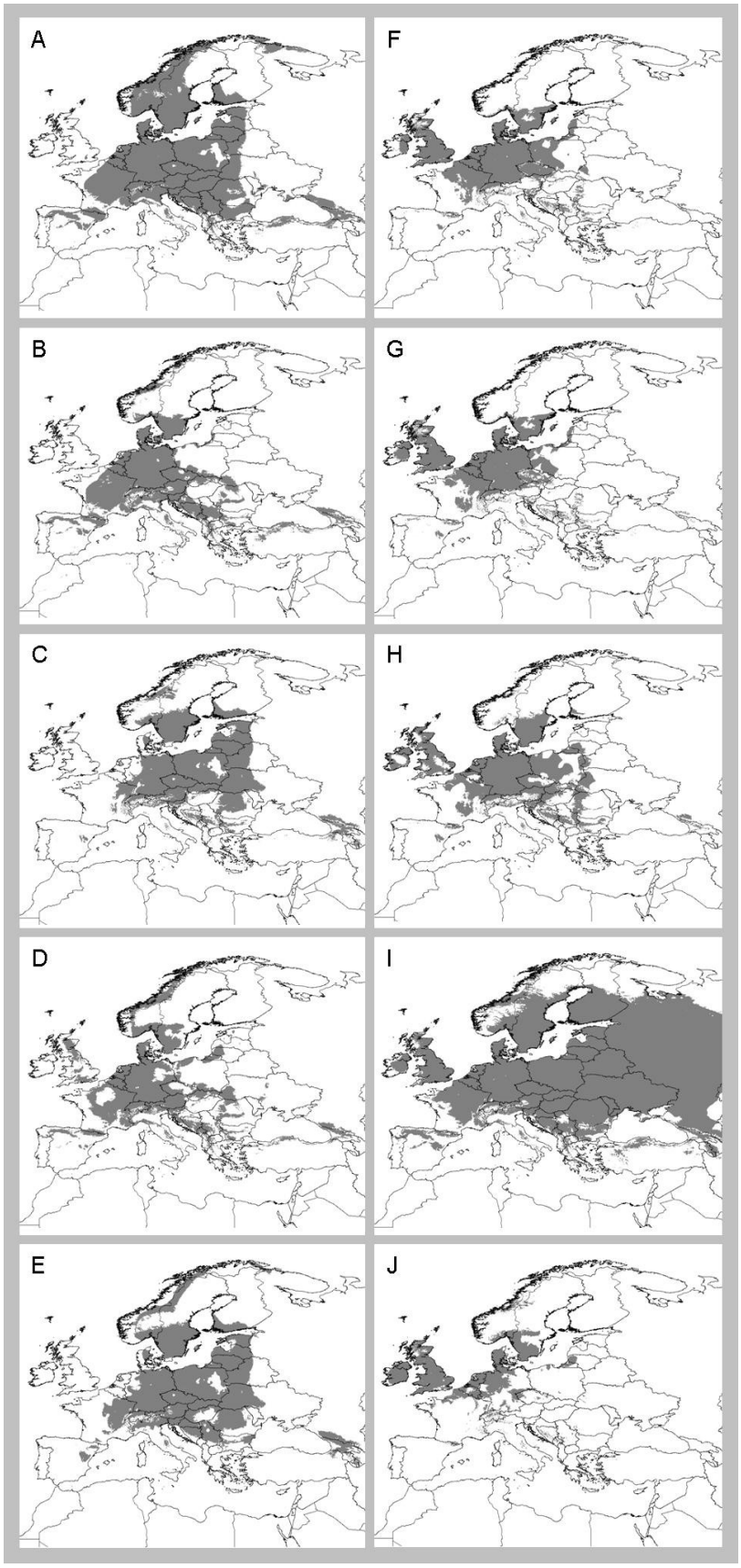

Fig. 1 Environmental niche models of *Maculinea* butterflies and *Myrmica* ants using the Bioclim algorithm. Potential distributions of butterfly species were subsequently pruned with model predictions of their respective host plants (A: *Maculinea arion*, B: *Maculinea alcon*, C: *Maculinea nausithous*, D: *Maculinea rebeli*, E: *Maculinea teleius*, F: *Myrmica sabuleti*, G: *Myrmica scabrinodis*, H: *Myrmica schencki*, I: *Myrmica rubra*, J: *Myrmica ruginodis*)

Environmental Niche Models

Models for butterflies and ants were computed in DIVA-GIS 7.5.0 using the Bioclim algorithm (Busby, 1991). Bioclim predictions are based on the similarity of climates at points on a geographical grid to the climatic profile of the study species. That means, the climatic parameters at each grid point are compared with the climatic profile of a species to estimate whether the climate at a given location is potentially suitable (Busby, 1991). Modelling results were displayed in a continuous map in DIVA-GIS 7.5.0 indexing six types of predicted habitat suitability: areas outside the 0–100 percentile climatic envelope of a species are considered unsuitable, areas within the 0–2.5 percentile have a 'low' climatic suitability, those within the 2.5–5 percentile a 'medium', those within the 5–10 percentile a 'high', those within the 10–20 percentile a 'very high' and cells within the 20–100 percentile an 'excellent' climatic suitability (Hijmans *et al*., 2005).

Potential distributions of host plant species were estimated using Maxent 3.3.3k, a machine learning algorithm based on the principles of maximum entropy (Phillips *et al*., 2006; Phillips & Dudík, 2008; Elith *et al*., 2011). Maxent is a presence-only/background method (Peterson *et al*., 2011), which is considered especially suitable when the number of records is low. We ran Maxent under standard settings, i.e. randomly splitting the dataset into 70% training and a 30% testing subsets using a bootstrap approach, with 10,000 background points and 100 replicate runs to average model output. A non-fixed threshold for identifying suitable areas as suggested by Morán-Ordóñez *et al*. (2012) was used, setting the 'equate entropy of thresholded and original distributions logistic threshold' as presence/absence threshold. Model accuracy was tested calculating the 'area under the receiver operation characteristic curve' (AUC) as implemented in Maxent and DIVA-GIS. Following the classification of Swets (1988) and Araújo *et al*. (2005), AUC values range between 0.5 for models with no predictive ability and 1.0 for models giving perfect predictions with values > 0.9 describing a 'very good', > 0.8 'good' and > 0.7 'useable' discrimination ability of the model, and allow to assess the ability of the model to differentiate between species records and background data (Phillips *et al*., 2006). Maxent output was displayed in logistic format classifying the area of interest by means of the predicted environmental suitability from 0 (unsuitable conditions) to 1 (optimal conditions) and subsequently mapped with DIVA-GIS 7.5.0.

Habitat suitability predictions of host plants were used to prune butterfly predictions in DIVA-GIS 7.5.0. Subsequently, all suitability maps were reclassified and set to a similar threshold.

Range overlap

In purpose to quantify potential distribution overlap between the parasites and their hosts, we measured the range overlap predicted by different ENMs as implemented in ENMtools 1.4 (Warren

et al., 2008, 2010). Based on a user selected presence/absence threshold, this metric estimates the amount of overlap from raster grids ranging from 0 (no overlap) to 1 (complete overlap). We acknowledge that the occurrence of *Maculinea* is mainly driven by the presence of their host plant. Hence, we pruned their predicted potential distribution based on the occurrence of the particular host plant in DIVA-GIS. Subsequently, we reclassified all ENMs and selected a similar presence/absence threshold of 0.0001 before estimating range overlaps between parasites and hosts. All calculated range overlaps are given in Supplement S2.

Niche overlap metrics

To compare the climatic niches of butterflies and ants derived from the ENMs, we calculated Schoeners's D as recently suggested for ENM comparisons implemented in ENMtools 1.4 (Warren *et al*., 2008, 2010). This metric is acknowledged to be a standard parameter to measure the proportional similarity of the observed niches making them comparable to a percentage overlap (Kohn & Riggs, 1982; Rödder & Engler, 2011). It describes the degree of similarity of potential distributions by comparing corresponding values per cell of two grids and ranges linearly from 0 (no similarity) to 1 (two grids are identical). We computed the proportion of niche overlap between all species as proposed by Warren *et al*. (2008, 2010). To facilitate the interpretation of results, we subsequently condensed the output into five classes as suggested by Rödder & Engler (2011): 0-0.2 = no or very limited overlap, 0.2-0.4 = low overlap, 0.4-0.6 = moderate overlap, 0.6-0.8 = high overlap, 0.8-1.0 = very high overlap. Differences in niche overlap were tested using univariate statistics.

Results

ENMs performed 'good' to 'excellent' according to Swets (1988) with all species modelled within this study receiving AUC values > 0.7. Variable contribution automatically calculated by Maxent highly differed across species. In all taxa, the majority of variables with highest explanative power for the prediction of species distribution was temperature related. In *Myrmica* species, not a single precipitation-related variable was found among the three bioclimatic variables with highest model contribution. Highest explanative power for potential butterfly distribution was found in 'isothermality' (bio3), 'temperature seasonality' (bio4) and 'precipitation of warmest quarter' (bio18). Variables with maximum explanative power for ant species comprised 'minimum temperature of the coldest month' (bio6), 'temperature annual range' (bio7) and 'isothermality' (bio3). However, no particular dominance in model contribution was recognized for a single variable in plant species (Table 2).

Model predictions well explained the known geographical ranges of the observed species. Figure 1 displays the potential distribution of *Maculinea* butterflies and *Myrmica* ants under current climate. All butterfly species achieved high range overlap scores with all *Myrmica* species studied. No differences in the amount of range overlap between main or secondary hosts and the respective parasitic butterfly could be found. Moreover, similarly high overlap scores were recognized between butterflies and *Myrmica* species not exploited as hosts (Fig. 2; Table 3).

Table 3 Niche overlap in terms of Schoener's index (*D*) between parasites, hosts and non-hosts. Schoener' s D describes the degree of similarity of potential distributions by comparing corresponding values per cell of two grids and ranges linearly from 0 (no similarity) to 1 (two grids are identical).

SPECIES	*Maculinea arion*	*Maculinea nausithous*	*Maculinea rebeli*	*Maculinea teleius*	*Myrmica rubra*	*Myrmica ruginodis*	*Myrmica sabuleti*	*Myrmica scabrinodis*	*Myrmica schencki*	*Maculinea alcon*
Maculinea arion		0.469	0.408	0.572	0.374	0.142	0.318	0.277	0.383	0.446
Maculinea nausithous			0.481	0.807	0.266	0.166	0.432	0.367	0.549	0.479
Maculinea rebeli				0.430	0.214	0.334	0.556	0.508	0.620	0.714
Maculinea teleius					0.299	0.141	0.392	0.327	0.502	0.474
Myrmica rubra						0.106	0.194	0.175	0.224	0.211
Myrmica ruginodis							0.449	0.470	0.401	0.248
Myrmica sabuleti								0.854	0.701	0.556
Myrmica scabrinodis									0.649	0.512
Myrmica schencki										0.586
Maculinea alcon										

Niche overlaps between models based on the D statistics of Warren *et al*. (2008) show that the niches of hosts and parasites differ considerably. In all *Maculinea* species, with the exception of *M. rebeli*, niches of parasites and main hosts were not found to be more similar compared to niches of secondary hosts or non-hosts. Univariate statistics revealed a significant difference of niche overlap scores between both, main or secondary hosts, and ant species not exploited as hosts (Mann-Whitney-Test $p<0.05$), excluding *M. rebeli*. However, no significant difference was found comparing niche overlap scores of main and secondary hosts (Mann-Whitney-Test $p>0.05$). In *M. rebeli*, highest niche overlap was found with its main hosts. Additionally, compared with its closest relative *M. alcon*, an inverted host exploitation was observed (Fig. 3).

Discussion

All parasites essentially depend on the presence of their host species. This is also the case for *Maculinea* butterflies and their *Myrmica* host ants. Even though, niches of both species groups were not congruent. In fact, niches between hosts and parasites differ even more than expected at random. The lack of niche overlap might be interpreted as an evolutionary escape of the ants to avoid the butterfly's niche in terms of minimizing infestation risk (Ridley, 2004). This assumption is further supported by lower amounts of niche overlap for host ant species compared to non-hosts. The low infestation rates even of main hosts might therefore be explained by the rather limited ecological niche overlap as parasite infestations presumably are restricted to the few habitats where the ecological niches of hosts and parasites overlap. The major part of the host ant's habitats might not be suitable for butterflies due to niche constraints, thus relieving pressure from the host species. Consequently, only a small portion of ant colonies currently is infected by butterfly larvae (Elmes *et al*., 1998), thus significantly minimizing costs in the host species.

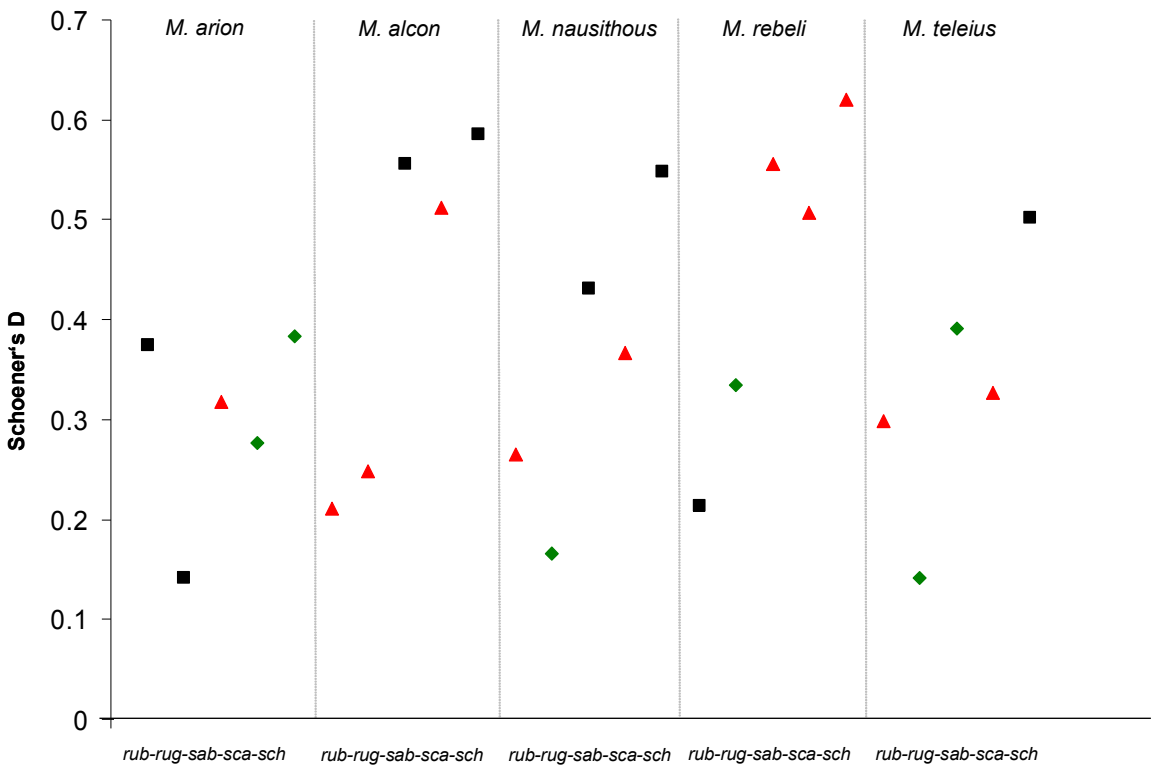

Fig. 2 Niche overlap in terms of Schoener's index (D) between *Maculinea* butterflies and their main hosts (▲), secondary hosts (◆) and non-hosts (■). Higher values of Schoener's D indicate higher amounts of niche overlap. Abbreviations: rub: *Myrmica rubra*, rug: *Myrmica ruginodis*, sab: *Myrmica sabuleti*, sca: *Myrmica scabrinodis*, sch: *Myrmica schencki*.

On the other hand, the limited niche overlap imposes considerable pressure on *Maculinea* (Kaltz & Shykoff, 1998; Ridley, 2004). The high dependency of the butterfly species on *Myrmica* ants for their larval development restricts these species to a small number of habitats. This goes in line with the pronounced rarity of these species and might explain the necessity of a high potential to shift to alternative hosts (Munguira & Martín, 1999; Settele *et al*., 2002; Thomas & Settele, 2004; IUCN, 2007; Van Swaay *et al*., 2011). Host exploitation in *Maculinea* is, even locally, rather flexible and obviously not determined by niche constraints (Tartally *et al*., 2008). The observed pattern in niche overlap indicates no preference between main and secondary host species, but tolerates a high flexibility in host exploitation. Even multiple host exploitation can be tolerated as larvae of several *Maculinea* species were found in a single ant colony (Tartally & Varga, 2008).

This situation appears rather inverted with regard to *M. rebeli*. This species shows considerably higher niche overlap scores with its host ants than with its non-hosts. In contrast to its closest relative *M. alcon*, this species has changed its habitat requirements from moist to xerothermophilic conditions (Munguira & Martín, 1999). As *M. rebeli* is the only *Maculinea* species with clear xerothermophilic habitat requirements, this trait should be interpreted as an autapomorphism while the use of humid habitats might be plesiomorphic. The recent emergence of this assumed niche shift is well supported by the proportionally higher amount of niche overlap with its host ants compared to the other *Maculinea* species. We assume, that *M. rebeli* has caught up with previous evasive niche shifts in its host ants, hence now maximizing host exploitation still not giving the affected host ants the necessary time for evolutionary escape reactions. More stable populations and a lower degree of endangerment of *M. rebeli* might also be seen as a result of a more beneficial host-parasite relation for this butterfly species (Sielezniew *et al*., 2012; Thomas *et al*., 2013).

Our results indicate a co-evolutionary arms-race between *Maculinea* butterflies and *Myrmica* ants (Foitzik *et al*., 2003; Nash *et al*., 2008) revealing long-time evasive niche shifts in host ants potentially forcing *Maculinea* butterflies to alternative host exploitation on the one hand and short-time niche adaptations on the other hand. In general, a lower niche plasticity can be recognized in the butterflies reducing selective pressure on *Myrmica* by minimizing niche overlap. Evolutionary evasion and adaptation are crucial elements in predator-prey or host-parasite relations, a process that might in the future proceed in *M. rebeli*, the only *Maculinea* species currently leading in this contest.

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Supplement

S1 Bioclimatic variables derived from monthly temperature and rainfall values in order to generate biologically more meaningful variables for model predictions.

Bio1 = Annual mean temperature

Bio2 = Mean diurnal range (mean of monthly (maximum temperature - minimum temperature))

Bio3 = Isothermality (Bio2/Bio7) (* 100)

Bio4 = Temperature seasonality (standard deviation *100)

Bio5 = Maximum temperature of warmest month

Bio6 = Minimum temperature of coldest month

Bio7 = Temperature annual range (Bio5-Bio6)

Bio8 = Mean temperature of wettest quarter

Bio9 = Mean temperature of driest quarter

Bio10 = Mean temperature of warmest quarter

Bio11 = Mean temperature of coldest quarter

Bio12 = Annual precipitation

Bio13 = Precipitation of wettest month

Bio14 = Precipitation of driest month

Bio15 = Precipitation seasonality (coefficient of variation)

Bio16 = Precipitation of wettest quarter

Bio17 = Precipitation of driest quarter

Bio18 = Precipitation of warmest quarter

Bio19 = Precipitation of coldest quarter

S2 Range overlap between *Maculinea* butterflies and *Myrmica* ants. This metric estimates the amount of overlap from raster grids of model predictions ranging from 0 (no overlap) to 1 (complete overlap).

SPECIES	*Myrmica schencki*	*Maculinea alcon*	*Maculinea arion*	*Maculinea nausithous*	*Maculinea rebeli*	*Maculinea teleius*	*Myrmica rubra*	*Myrmica ruginodis*	*Myrmica sabuleti*	*Myrmica scabrinodis*
Myrmica schencki	1	0.61	0.85	0.64	0.62	0.71	0.97	0.80	0.80	0.79
Maculinea alcon	0.61	1	0.95	0.54	0.74	0.64	0.88	0.51	0.66	0.64
Maculinea arion	0.85	0.95	1	0.89	0.90	0.90	0.73	0.62	0.80	0.74
Maculinea nausithous	0.64	0.54	0.89	1	0.56	0.97	0.98	0.39	0.57	0.52
Maculinea rebeli	0.62	0.74	0.90	0.56	1	0.61	0.93	0.66	0.63	0.61
Maculinea teleius	0.71	0.64	0.90	0.97	0.61	1	0.92	0.40	0.62	0.56
Myrmica rubra	0.97	0.88	0.73	0.98	0.93	0.92	1	0.91	0.95	0.92
Myrmica ruginodis	0.80	0.51	0.62	0.39	0.66	0.40	0.91	1	0.79	0.77
Myrmica sabuleti	0.80	0.66	0.80	0.57	0.63	0.62	0.95	0.79	1	0.91
Myrmica scabrinodis	0.79	0.64	0.74	0.52	0.61	0.56	0.92	0.77	0.91	1

Climate change and the 'pesticide-phenology problem' in amphibians – boon or bane?

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Pesticides and amphibian decline

To scientists and conservationists it is unequivocal that worldwide amphibians are declining at alarming rates which is suggested to parallel past mass extinctions; more than one third of the almost 7,000 known species is threatened with extinction (Stuart *et al.,* 2004; Wake & Vredenburg, 2008). Various reasons are debated and it is suggested that many of them interact (Collins & Storfer, 2003). We need (i) to better understand the processes and (ii) to identify the problems, so that adequate responses can be given (Mendelson *et al.,* 2006; Gascon *et al.,* 2012).

One problem, frogs, toads and newts in the agrarian landscape are confronted with, is pesticide usage (Sparling *et al*., 2001; Mann *et al*., 2009; Brühl *et al.,* 2011). Numerous of these agrochemicals are known to directly or indirectly affect these animals (Sparling *et al.,* 2001). Damages include acute toxic effects and increased malformation rates at environmentally relevant concentrations as well as teratogenic and genotoxic effects have already been observed at sublethal concentrations (Hayes *et al.*, 2006). Although, especially embryonic and larval stages are considered sensitive to insecticides, herbicides and fungicides, it is suggested that contaminations can affect all amphibian life stages and that even very short contacts can be fatal (Relyea, 2005; Dinehart *et al.,* 2009; Brühl *et al.,* 2011, 2013). Problems may go beyond damage or death of individuals and may cause local population declines (Relyea *et al*., 2005).

For instance, taking amphibians from temperate North America and Europe, where many agrochemicals are being used throughout the year, the following scenarios can be reality. Adult mass migration via fields in early or late spring to ponds for reproduction can collide with overspaying; likewise, the same can happen during juvenile mass emergence in early summer (Brühl *et al.,* 2013). Especially, the last mentioned can have dramatic consequences beyond the 'individual', as the fate of juveniles has a significantly large influence on population dynamics (Schmidt, 2011). High amounts of eggs and tadpoles developing from early spring into summer in small water bodies on or near fields can be easily exposed to high pesticide concentrations due to surface water runoff (Brown & van Beinum, 2009) or drift (Davidson *et al.,* 2002; Davidson, 2004). As effects of pesticides are linked to the annual life cycle, we refer to this as the 'pesticide-phenology problem' in amphibians. It may contribute to population declines at the local scale (Sparling *et al*., 2001; Brühl *et al*., 2013).

Some amphibians respond to climate change

Amphibians are poikilothermic life forms with a thin water-permeable skin. Their activity is strongly dependent from temperature and humidity and different effects from anthropogenic climate change have been proposed. Despite geographic range shifts and others (Carey & Alexander, 2003;

Araújo *et al.,* 2006), some species have been observed to undergo phenological changes. Shifts in annual activity patterns may be independent from climate zones (Todd *et al.,* 2011), but we here refer to amphibians from the temperate zone only, as these have been studied in detail. Their yearly breeding activity takes place from early spring to late summer. In response to warmer winter and spring temperatures, some frogs, toads and newts have been found to breed earlier for up to about one month, as for instance observed in England and Germany (Beebee, 1995; Münch, 1998; Reading *et al.,* 2003). However, neither all species nor all populations of a given species show 'preterm' breeding activity but remain 'stable' (Beebee, 1995; Blaustein *et al.,* 2001; Gibbs & Breisch, 2001). Eventually, there are amphibians in which reproductive periods do start earlier but then slow-down so that metamorphosis takes place seasonally unchanged (Reading & Clarke, 1999; Scott *et al.,* 2008).

Earlier amphibian breeding activity coherently with temperature increase is considered disadvantageous. Larval food availability is more limited and sudden temperature drops are stronger and more common, leading to reduced growth and fitness of larvae. As a causality of this, individual survival and reproductive success are weakened and favor populations declines (Blaustein *et al.,* 2001; Reading *et al.,* 2003; Scott *et al.,* 2008).

Linking causalities in simple scenarios

Climate change will affect agriculture. For instance, with moderate warming (up to 3°C) in the temperate zone and adaptations in cultivation practice, crop production is predicted to benefit. Especially, with warmer winters at higher latitudes, crop production will start earlier to best exploit ripeness of fruit. Start might be in late winter/early spring accompanied by an earlier and more frequent use of pesticides. Mild winters may alternatively result in the increase of seed launch before winter accompanied by higher pesticide applications in autumn (IPCC, 2007; Tubiello *et al.,* 2007; Kattwinkel *et al.,* 2011).

Linking this to the preterm class of amphibians the following assumptions for the temperate zone can be made. If shifts in phenology and pesticide applications are symmetrical, pesticide effects on amphibians early in the year may not change (Fig. 1A and B, D and E). But a higher impact later in the year through an additional application in autumn (winter seed) is expectable. This should increase the portion of the adult population potentially contaminated, as many frog, toad and newt species migrate to their breeding pond already before overwintering (Fig. 1B). However, this should not affect the most sensitive early year larval stages and emerging juveniles that largely influence population dynamics (see above). Therefore, it may be expected that the 'pesticide-phenology problem' generally remains unchanged. It can be followed that in preterm amphibians negative

impacts from climate change alone, i.e. directly on amphibians or their natural environment, remain the only problem in the context discussed here. Interestingly, even positive effects on the 'pesticide-phenology problem' have been suggested, that is that faster development due to warmer climate may decrease the risk of contamination effects.

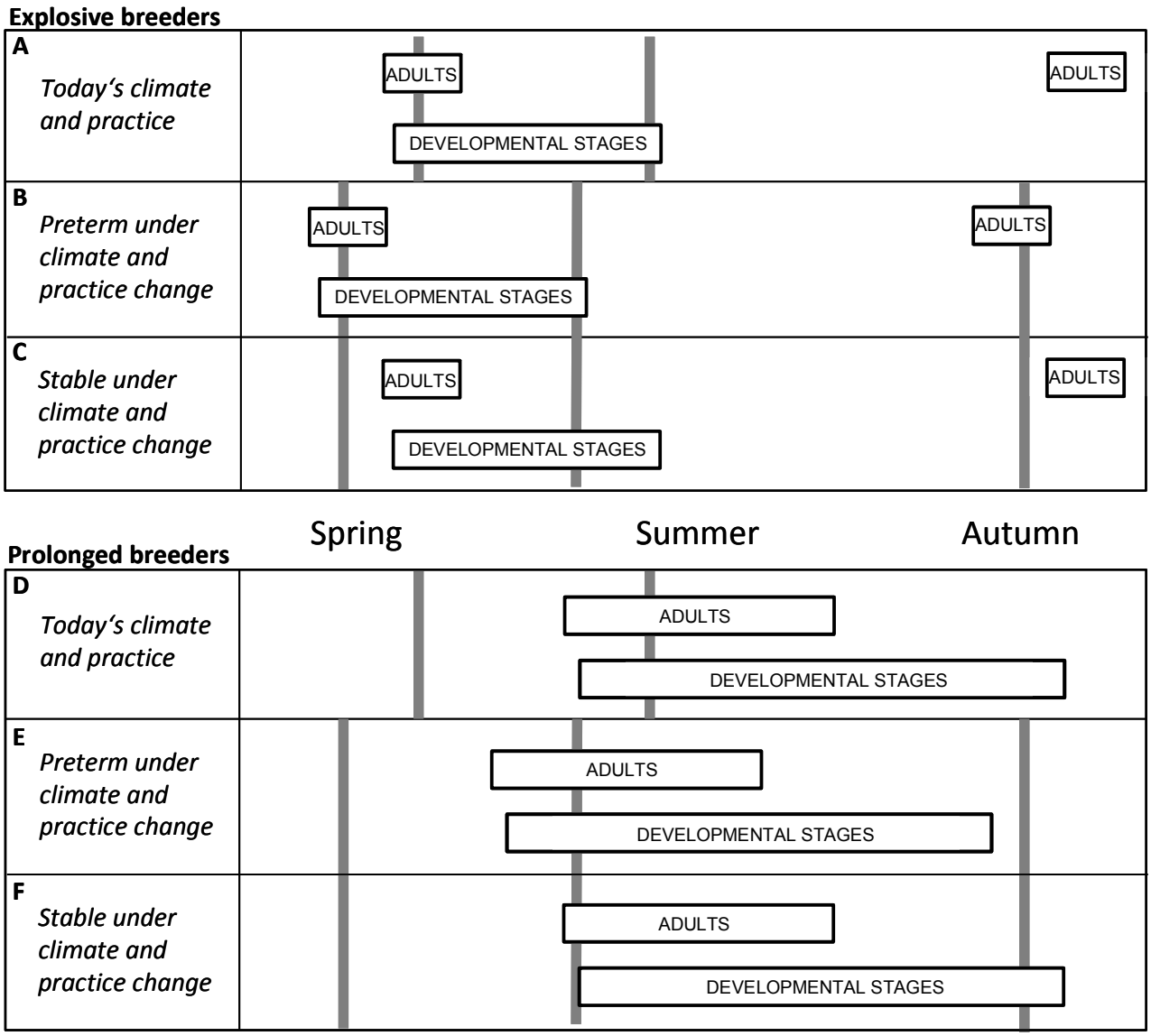

Fig. 1 Three schematic scenarios each for explosive and prolonged breeding amphibians from the temperate zone, showing the appearance of most adults and developmental stages (eggs, larvae, juveniles) on fields and breeding ponds nearby throughout their annual life cycle. In this example, gray bars indicate the application of a non-defined herbicide which is applied twice under current climate and ternary under climate change.

How about stable amphibians? These may have to cope little with direct effects from climate change or those on their natural environment, at least less than preterm species. However, we here advocate that for stable frogs, toads and newts in fact the situation can be another. When occurring in the anthropogenic landscape they hypothetically can suffer from human activities when such

operations are adjusted to climate change. This includes that pesticides are sprayed earlier and longer, revealing an asymmetry of phenology and pesticide applications. However, not only negative but also positive effects are thinkable – boon or bane. Under these circumstances the 'pesticide-phenology problem' in stable amphibians requires particular attention.

We put this into light, keeping at the case of temperate zone amphibian species. Their reproductive strategies and phenologies differ remarkably among species (Wells, 2007). So called explosive breeders involve amphibians accumulating in masses for a relatively short time period mainly in early spring; juveniles mostly emerge in early summer. Examples of explosive breeders which have stable populations are the European common frog (*Rana temporaria*) or the North American western toad (*Anaxyrus boreas*) (Beebee, 1995; Blaustein *et al.,* 2001). Other amphibians show prolonged breeding activity and are asynchronously present at their breeding places, usually from late spring on, such as the Spring peeper (*Pseudacris crucifer*) or the Green frog (*Rana clamitans*) in North America (Blaustein *et al.,* 2001; Gibbs & Breisch, 2001).

Figure 1C and F illustrate the potential contamination of stable amphibians with a non-defined herbicide which is applied twice under current climate but ternary under climate change. In this example, explosive breeders do benefit: only their developmental stages experience contact once. In contrast, under today's climate and likewise being preterm under climate change their reproductive adults and both early and late developmental stages may suffer from herbicide applications (cf. Fig. 1A, B). In stable prolonged breeders there is no such benefit in our example. Portions of the adult population as well as early and late developmental stages are exposed to the risk of contamination. These results in a higher risk of contamination compared to preterm or today's populations (cf. Fig. 1D, E).

A message

Certainly, given the magnitude of insecticides, herbicides and fungicides and their varying use, our scenarios and flowcharts are over-simplified. Also new agrarian practices (including genetically manipulated plants accompanied by new herbicide technologies; Lopez *et al*., 2012; Wagner *et al*., 2013 a,b; Böll *et al*., 2013), additional co-stressors (habitat change, diseases, biotic interaction etc.; Kiesecker, 2002; Relyea, 2003; Rohr *et al*., 2008) and direct effects of climate change (e.g. decreased contamination due to faster larval development) are neglected here. Nevertheless, we regard our 'equations' clear enough to underpin that, under the assumption of symmetrical shifts in amphibian phenology and pesticide applications, the 'pesticide-phenology problem' in stable amphibians needs reconsideration. As concrete answers to boon or bane cannot be given at the current state of knowledge, an immense research field opens here involving field observations and tests, modeling and so on.

In addition to the highlighted research needs, another quintessence can be drawn here. Amphibian decline remains to be an acute problem, as for instance the IUCN Red List status of many species has shifted towards a worse category within last three decades (Stuart *et al.,* 2008). Seeking for solutions also means uncovering the complexity of causalities. We here suggest that linking aspects, which may not cause problems when standing alone (i.e. stable prolonged breeding under climate change) with other aspects may reveal new problems contributing to the worldwide amphibian decline.

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Part II: Implications for Conservation Efforts

Untersuchungen zur Bestandsentwicklung der Tagfalterzönosen auf Kalkmagerrasen im Saar-Mosel-Gebiet

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Author contributions: TS and KJF designed the project; MW, MF, KJF and DJ performed butterfly surveys in 1972, 2001, 2010 and 2012 respectively; KJF conducted the statistical analyses and lead the writing of the manuscript with significant contributions of TS.

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Kurzfassung Kalkmagerrasen gehören auf Grund ihrer einzigartigen Tier- und Pflanzenvielfalt zu den gemäß der Flora-Fauna-Habitat-Richtlinie geschützten Biotopen und sind bedeutende Habitate für den Tagfalterschutz. In den Jahren 1972, 2001, 2011 und 2012 wurden die Tagfalterzönosen von sechs teils als Naturschutzgebiete ausgewiesenen Kalkmagerrasen standardisiert untersucht und alle Tagfalterarten semi-quantitativ erfasst. Die meisten Arten wiesen über diesen Zeitraum einen starken Rückgang auf, und viele von ihnen fehlten in den letzten Untersuchungsjahren vollständig. Besonders hervorzuheben ist der Verlust vieler hochgradig spezialisierter Arten, die als Charakterarten für diesen Habitattyp gelten. Auch die Bestandsentwicklung vieler Rote-Liste-Arten ist deutlich negativ. Auf Grund unserer Ergebnisse ist zu befürchten, dass dieser Habitattyp nicht nur als Rückzugsgebiet seltener und großräumig bedrohter Arten verloren geht, sondern dass die angewandten Schutzkonzepte in Frage gestellt werden müssen.

Abstract Calcareous grasslands contain a renowned biological diversity. Consequently, many of these habitats are protected as nature reserves and are integrated in the Natura 2000 network of the European Union. Today, these grasslands are considered to be one of the most important habitat types for insect conservation. During the years 1972, 2001, 2011 and 2012, we conducted standardized transect walks on six partly legally protected calcareous grasslands to assess local butterfly occurrences and abundances. We detected a severe decline in species richness during the last forty years, with many species completely missing in 2012. Highest vulnerability and severest decrease rates were observed in highly specialized species, which are commonly used as umbrella species for this habitat type. Moreover, especially Red List species are declining at alarming rates. On the long term, our results suggest that the decrease in habitat quality leads to a severe habitat loss for endangered species and question the appropriateness of prevalent conservation strategies for nature reserves.

Key words Habitat quality, habitat destruction, connectivity, species extinction, species turnover, habitat specialist, Red List, nature reserve

1. Einleitung

Kalkmagerrasen beherbergen eine einzigartige Vielfalt an Tieren und Pflanzen. Sie stellen in ansonsten vom Menschen stark genutzten und überformten Landschaften wichtige Rückzugsgebiete für seltene und hoch spezialisierte Arten dar (VAN SWAAY 2002). Viele von ihnen stehen auf Grund ihrer Seltenheit auf zahlreichen Roten Listen oder unter dem Schutz der Fauna-Flora-Habitat Richtlinie (VAN HELSDINGEN et al. 1996). Besonders bedeutsam sind Magerrasen als Habitate einer vielfältigen Schmetterlingsfauna: 274, d.h. 48 % der 576 europäischen Tagfalterarten, leben auf Kalkmagerrasen, und bedeutende Populationen großräumig bedrohter Arten sind noch heute in diesen Habitaten zu finden (VAN SWAAY 2002, VAN SWAAY et al. 2011). Daher wurden diese schützenswerten Biotope in den vergangenen Jahrzehnten zunehmend als Naturschutzgebiete ausgewiesen und spielen eine entscheidende Rolle für den Erhalt der Insektenfauna (VAN SWAAY 2002, WALLISDEVRIES et al. 2002).

Seit den 1970er Jahren ist auch eine deutliche Zunahme an Ausweisungen in Rheinland-Pfalz zu verzeichnen (JUNGBLUTH 1985, JUNGBLUTH et al. 1987, 1989, 1995). Dennoch haben die rheinland-pfälzischen Kalkmagerrasen (trotz teilweise intensiver Pflegemaßnahmen) deutliche Flächenrückgänge sowie hohe Qualitätsverluste im Rahmen der Intensivierung der Landwirtschaft und aus Aufforstung oder Nutzungsaufgabe resultierenden Sukzessionsprozessen erfahren (WENZEL et al. 2006, FILZ et al. 2013). All diese Prozesse führen zum Verlust des offenen, aber strukturreichen Habitatcharakters. Es entstehen vermehrt stark isolierte und fragmentierte Flächen mit weitgehend homogenisierter Vegetationsstruktur, die einen dramatischen Verlust an Biodiversität zu verzeichnen haben (VAN SWAAY 2002, WENZEL et al. 2006, FILZ et al. 2013).

Viele Tagfalterarten sind in Europa stark vom Rückgang betroffen und einige sind sogar lokal vom Aussterben bedroht (VAN SWAAY et al. 2011). Die Gründe hierfür sind vielfältig, werden jedoch vornehmlich in Klima- und Landnutzungsveränderungen gesehen (THOMAS et al. 2004, PARMESAN 2006, DOVER & SETTELE 2009). Die Verluste wichtiger Habitatstrukturen, wie sie auch auf Kalkmagerrasen vorgefunden werden, treten dabei zunehmend in den Vordergrund (BALMER & ERHARDT 2000, VAN SWAAY 2002, SCHMITT & RÁKOSY 2007). Tagfalter gehören unter den Invertebraten zu den am besten untersuchten Gruppen (EBERT & RENNWALD 1991). Dennoch sind viele ökologische Zusammenhänge noch nicht abschließend geklärt. Die langfristige Erhebung von Bestandsdaten ist daher von großer Bedeutung, um die großräumigen Auswirkungen verschiedener Umweltparameter zu ermitteln, Bestandstrends zu erfassen und die Ergebnisse in Schutzkonzepte umzusetzen.

Im Rahmen diese Studie wurden die Bestandsentwicklungen der Tagfalterzönosen von sechs mehrheitlich als Naturschutzgebiete ausgewiesenen Kalkmagerrasen untersucht. In zeitlichen Abständen

von 29, zehn und einem Jahr(en) wurden standardisierte Transektbegehungen durchgeführt und hierbei semiquantitativ die Populationen sämtlicher Tagfalterarten dieser Gebiete erfasst. Neben einem langfristigen Bestandstrend geben die ermittelten Daten zudem Auskunft über den Einfluss externer Umweltfaktoren auf Tagfalterpopulationen innerhalb gepflegter und geschützter Kalkmagerrasen sowie über die Wirksamkeit der diese Habitate erhaltenden Pflege- und Schutzkonzepte.

2. Methodik

2.1 Untersuchungsgebiete

Bei den Untersuchungsgebieten handelt es sich um sechs mehrheitlich als Naturschutzgebiete gesetzlich geschützte Kalkmagerrasen (Mesobromion erecti) im Saar-Mosel-Gau (Abb. 1 und Tab. 1). Alle Flächen liegen auf strukturell alte Magerrasen, die schon seit über vierzig Jahren Bestand haben. Diese Gebiete zeichnen sich durch ihren Reichtum an xerothermophilen Magerrasenarten unter den Tagfaltern wie den Magerrasen-Perlmutterfalter (*Boloria dia*), den Silbergrünen Bläuling (*Polyommatus coridon*) und den Mattscheckigen Braun-Dickkopffalter (*Thymelicus acteon*) aus. Zudem sind auch Bewohner wärmebegünstigter Gebüsch- und Saumstrukturen in diesen Gebieten häufig anzutreffen. Besonders für viele seltene und hoch spezialisierte Arten stellen diese Habitate wertvolle Rückzugsgebiete dar.

Der Strukturreichtum der Vegetation ist für die Habitatqualität und den Erhalt der Tagfalterdiversität von großer Bedeutung. Um die Magerrasen vor Sukzession zu schützen und eine Vielfalt verschiedener Vegetationsstadien zu gewährleisten, werden jährlich auf vier Flächen Pflegemaßnahmen in Form von Streifenmahd und gelegentlichen Entbuschungseinsätzen durchgeführt. Inwieweit diese jedoch einen Ausgleich für negative Umwelteinflüsse benachbarter, oft intensiv landwirtschaftlich genutzter Flächen schaffen können, erscheint jedoch fraglich (vgl. Filz et al. 2013).

Tabelle 1: Geographische Lage der sechs Untersuchungsflächen in Rheinland-Pfalz (NSG: Naturschutzgebiet)

Untersuchungsfläche	Landkreis	Geographische lage
NSG 'Kelterdell/Kuckuckslay' bei Echternacherbrück	Eifelkreis Bitburg-Prüm	49.818183°N, 6.432411°O
NSG 'Eiderberg' bei Freudenburg	Trier-Saarburg	49.54875°N, 6.537786°O
Igel	Trier-Saarburg	49.71°N, 6.548056°O
Kelsen	Trier-Saarburg	49.574472°N, 6.486431°O
NSG 'Nitteler Fels' bei Nittel	Trier-Saarburg	49.656581°N, 6.4542°O
NSG 'Perfeist' bei Wasserliesch	Trier-Saarburg	49.696117°N, 6.527064°O

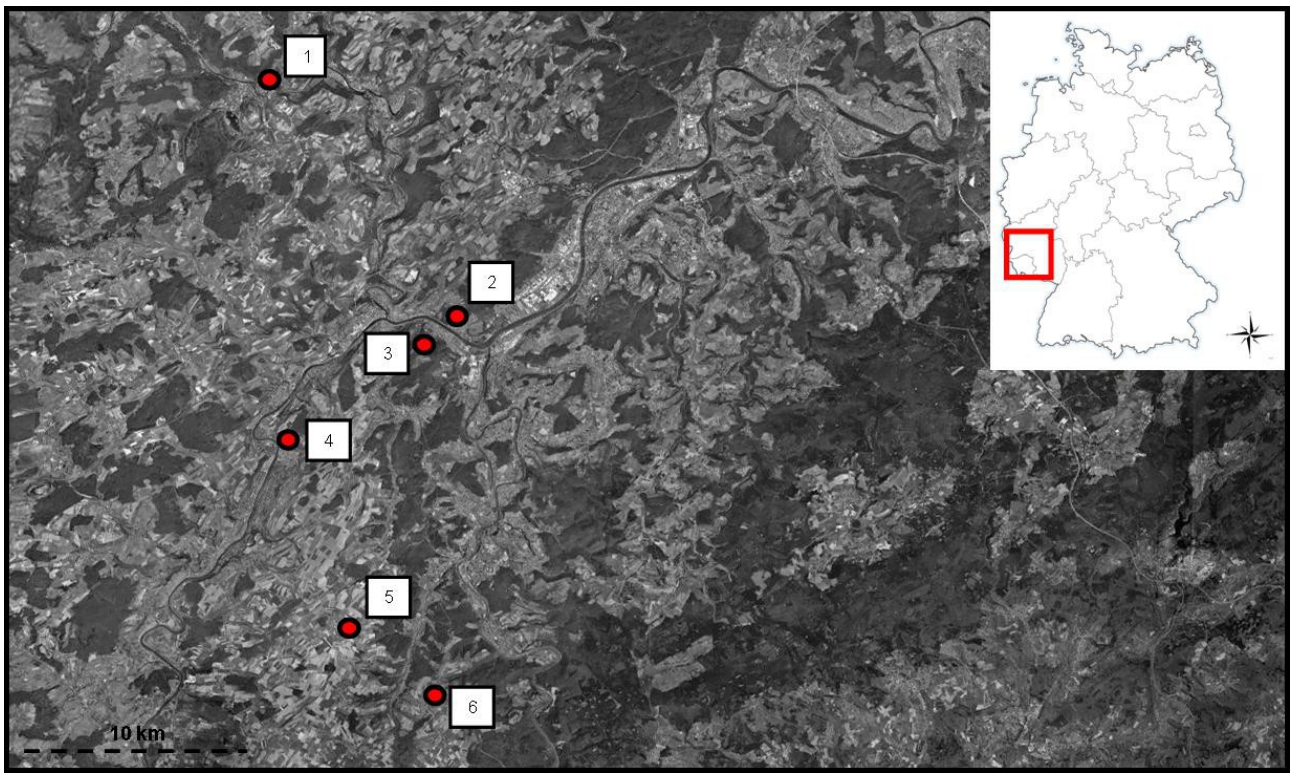

Abb. 1: Lage der Untersuchungsgebiete im Saar-Mosel-Gebiet (1: Echternacherbrück, 2: Igel, 3: Wasserliesch, 4: Nittel, 5: Kelsen, 6: Eiderberg bei Freudenburg).

2.2 Erfassungsmethode

Im Jahr 1972 wurden die Tagfalterzönosen der beschriebenen Kalkmagerrasen erstmalig untersucht. Insgesamt wurden zu diesem Zweck elf Linientransekte unterschiedlicher Länge eingerichtet, wobei die später von POLLARD & YATES (1993) beschriebene Methode eingesetzt wurde. Diese Transekte wurden bei günstiger Witterung zwischen März und Oktober alle zehn Tage in randomisierter Reihenfolge begangen. Als Tage mit günstiger Witterung wurden, wie später auch von SETTELE et al. (1999) vorgeschlagen, sonnenreiche Tage ohne Niederschlag und mit nur geringem Windaufkommen definiert. Während jeder Begehung wurden sämtliche Tagfalterarten auf einer Breite und Höhe von 5m registriert. Schwieriger zu bestimmende Arten wurden mit Hilfe eines Schmetterlingsnetzes gefangen und nach Bestimmung freigelassen. Alle Transekte wurden in den Jahren 2001, 2011 und 2012 mit der gleichen Methode und Intensität erneut bearbeitet. Bei diesen Bearbeitungen wurden zusätzlich zur Erfassung der Arten auch Angaben zu ihrer Häufigkeit aufgenommen.

2.3 Klassifizierungen der Tagfalterarten in funktionale Gruppen

Die erfassten Tagfalterarten wurden gemäß ihrer Habitatansprüche, ihres Ausbreitungspotenzials, ihrer Larvalökologie und ihres Gefährdungsgrades klassifiziert. Die Klassi-fizierung gemäß des

Habitatanspruchs erfolgte nach REINHARDT & THUST (1988) in vier Klassen: i) mesophile, ii) xerothermophile, iii) hygrophile und iv) ubiquitäre Arten. Das Dispersionspotenzial der Arten wurde nach BINK (1992) modifiziert nach WENZEL et al. (2006) in drei Klassen unterteilt: i) standorttreue, ii) mobile und iii) wandernde Arten. Des Weiteren wurde die Angaben in EBERT & RENNWALD (1991) genutzt, um sämtliche Tagfalterarten anhand der Anzahl ihrer Raupenfraßpflanzen einzustufen. Arten, deren Raupen Fraßpflanzen ausschließlich einer Gattung nutzen, wurden als monophag klassifiziert. Falter, deren Raupen Fraßpflanzen einer bzw. mehrerer Pflanzenfamilien nutzen, wurden als oligo- bzw. polyphag eingestuft. Zur Klassifizierung der erfassten Tagfalter nach ihrem Gefährdungsgrad wurde die Rote Liste Rheinland-Pfalz (SCHMIDT 2010) herangezogen.

2.4 Vergleiche der Tagfalterzönosen

Die Bestandsentwicklungen der unterschiedlichen Tagfalterzönosen wurden durch statistische Vergleiche der erfassten Bestände innerhalb der einzelnen Untersuchungsjahre ermittelt. Für jede Art wurde zuvor aus den gemittelten Monatszählwerten ein Jahreswert gebildet. Für die statistischen Analysen wurden alle Individuenzahlen auf 1000m Transektlänge normiert. Vergleiche zwischen den Untersuchungsjahren, den einzelnen Transekten und den funktionalen Gruppen wurden mit einem Kruskal-Wallis-Test bzw. einer Clusteranalyse durchgeführt. Darüber hinaus wurden der Arten-Turnover sowie der Jaccard-Index als Maße für Ähnlichkeiten bzw. Unterschiede in der Zusammensetzung der erfassten Zönosen berechnet. Bezüglich weiterer Details zu diesen statistischen Analysen siehe auch FILZ et al. (2013).

3. Ergebnisse

Im Jahr 1972 wurden insgesamt 70 Tagfalterarten nachgewiesen (vgl. Tafel 1). Diese Zahl sank in den Jahren 2001, 2011 und 2012 signifikant auf 47, 52 bzw. 30 Arten ab (Kruskal-Wallis-Test, $p<0,05$). Die Zahl der innerhalb dieses Zeitraumes neu erfassten Arten konnte den beobachteten Verlust bei weitem nicht ausgleichen. So konnten 2012 insgesamt 40 Tagfalterarten, die noch 1972 auf den Transekten erfasst wurden, nicht mehr nachgewiesen werden. Im Gegenzug wurden bis einschließlich 2012 nur drei neue Arten festgestellt (*Lycaena dispar*, *Boloria dia*, *Euphydryas aurinia*). Mit diesen Zahlen lässt sich auch der relativ hohe Arten-Turnover von durchschnittlich 24% erklären.

2001 betrug die Gesamtindividuenzahl 2.234 Tiere. Zehn Jahre später wurden mit 5.680 Individuen mehr als doppelt so viele registriert. 2012 wurden jedoch wiederum nur 2.720 Falter gezählte. Aus dem Jahr 1972 existieren keine Individuenzahlen. Eine Liste aller in den jeweiligen Jahren erfassten Tagfalterarten inklusive der gezählten Individuen ist in Tabelle 2 für jeden der sechs Standorte

dargestellt.

Tabelle 2: Beobachtete Tagfalterarten einschließlich ihrer Individuenzahlen auf den untersuchten Kalkmagerrasen. Da für das Jahr 1972 keine Individuenzahlen vorlagen, gilt: + = Art anwesend, - = Art abwesend.

	Echternacher-brück			Eiderberg				Igel				Kelsen				Nittel				Wasserliesch				Gesamtüberblick			
	1972	2001	2011	1972	2001	2011	2012	1972	2001	2011	2012	1972	2001	2011	2012	1972	2001	2011	2012	1972	2001	2011	2012	1972	2001	2011	2012
Hesperiidae																											
S. sertorius	+			+	1	1		+		1		+				+				+	3	1		+	+	+	-
P. malvae	+		2	+		7	4	+	2	2	4	+				+	2	2		+	3	3	4	+	+	+	+
P. serratulae	+			-				-				-				-				-				+	-	-	-
C. alceae	-			-				-				-				+				-				+	-	-	-
E. tages	+			+	2	5		+				+		1		+	1	2		+	7	1		+	+	+	-
C. palaemon	+	1		+				-				-				+				+				+	+	-	-
T. sylvestris	+	1	37	+	1	8		+	7	12	2	+	2	1		+	2	3	11	+	3	25		+	+	+	+
T. lineola	+		18	+		4		+	2	3		+		1		+		4		+	2	41		+	+	+	-
T. acteon	+	1		-				-				-				+				+	3			+	+	-	-
H. comma	-			+				-				-				-		2		-				+	-	+	-
O. sylvanus	+	2	1	+	5			+	1			+				+		3		+	4	2		+	+	+	-
Papilionidae																											
P. machaon	+	7	3	+	4	6		+	1	3		+				+		1		+	3	1		+	+	+	-
Pieridae																											
L. sinapis/reali	+	1	5	+	21	29	24	+		7	11	+	1	9	14	+	2	10	18	+	11	13	9	+	+	+	+
C. hyale	+		10	+	2	3		+		3		+		1		+				+				+	+	+	-
C. alfacariensis	+		2	+				+				-				+				+				+	-	+	-
C. croceus	+			+				-				-				+				-				+	-	-	-
G. rhamni	+		5	+	6	10	10	+		5	5	+		2	2	+		4	6	+		10	6	+	+	+	+
A. crataegi	+	1	2	+	4	1		+	3			-				+	3			+	5	3		+	+	+	-
P. brassicae	+	3	3	+	21	13	19	+	5	5	8	+	2	15	19	+	5	6	25	+	2	4	18	+	+	+	+
P. rapae	+	7	42	+	28	125		+	5	35		+	44	142		+	4	34		+	2	24	3	+	+	+	+
P. napi	+		5	+		29		+	1	6		+	3	26	5	+	1	7		+		6	1	+	+	+	+
P_daplidice	-			-				-				-				+				-				+	-	-	-
A. cardamines	+		2	+		12		+		1	23	+			18	+	1	2		+	1	2	2	+	+	+	+
Lycaenidae																											
L. dispar	-			-				-	1			-				-				-				-	+	-	-
L. phlaeas	+			+		1		+		2		+		1		+		1		+				+	-	+	-
L. tityrus	+		3	+				+				+				+				+		1		+	-	+	-
T. betulae	+			+		1		+	1	2		+				+				+				+	+	+	-
N. quercus	+			+				-				-				+				+				+	-	-	-
S. ilicis	+			-				+				-				+				+				+	-	-	-
S. pruni	+		2	+	1			+		5		+				+				+		1		+	+	+	-
S. acaciae	+			-				+				-				+				-				+	-	-	-
C. rubi	+	1	1	+		32	16	+		1		+		1		+		13	19	+		21	4	+	+	+	+
C. minimus	+		1	+	15	95	5	+	3	1	8	+		22	23	+	3	14	23	+	6	82	12	+	+	+	+
C. argiolus	+			+		2	1	+	1			+				+		1		+		1		+	+	+	+
M. arion	+			-				+				-				+				-				+	-	-	-
A. agestis	+		10	+		7		+		7	6	+		11		+		4		+		7		+	-	+	+
C. semiargus	+		2	+		14		+	2	4		+		7		+	1	8		+	1	6		+	+	+	-
P. coridon	+	21		+	48	278	101	+	14	27	45	+		3	19	+	34	137	53	+	43	231	155	+	+	+	+
P. bellargus	-			-				-				-				+				-	1			+	+	-	-
P. icarus	+	33	25	+	55	15	3	+	10	9	11	+	6	27	11	+	12	4	22	+	18	10	14	+	+	+	+
H. lucina	+			+				+								+				+				+	-	-	-
Nymphalidae																											
A. paphia	+			+		2	18	+		3		+				+		3	5	+		4	21	+	-	+	+
A. aglaja	+		1	+	1	51		+		11		+				+		11		+		42		+	+	+	-

	Echternacher-brück			Eiderberg				Igel				Kelsen				Nittel			Wasserliesch				Gesamtüberblick			
I. lathonia	+		1	+	1	7		+		1		+		1		+			2		+			+	+	+	-
B. selene	+			+		2		+				+				+					+			+	-	+	-
B. euphrosyne	+			+				-				-				+					+			+	-	-	-
B. dia	-		2	-		24	30	-			1	-			2	-	1	16	24	-	11	15	29	-	+	+	+
V. atalanta	+			+	1	3	8	+			7	+			5	+	1	1	4	+		2	1	+	+	+	+
V. cardui	+	1		+	2			+	1	1		+	4			+				+				+	+	+	-
I. io	+			+	2	4		+	2	1	12	+	1	1	25	+	1	1	2	+	1			+	+	+	+
N. urticae	+	1	7	+	1	40	16	+	4	7	15	+	6	11	29	+		1	16	+	3	2	3	+	+	+	+
N. polychloros	+			+				-				-			24	+				+				+	-	-	+
N. c-album	+			+		3		+		1		+			19	+				+		1		+	-	+	+
A. levana	+	1		+		4		+	4	2		+				+		1		+				+	+	+	-
M. cinxia	+	2		+				+				+				+				+				+	+	-	-
M. diamina	-			+	1			-				-				-				+				+	+	-	-
M. athalia	+			+		10		+				+				+		1		+				+	-	+	-
M. aurelia	+		2	-	5	114	108	-			16	-			26	+		4	28	-	1	26	79	+	+	+	+
E. aurinia	-			-				-				-				-		1		-				-	-	+	-
L. populi	+			-				-				-				-				-				+	-	-	-
L. camilla	+			+				+				-				+				+				+	-	-	-
A. iris	+			+				+				-				+		1		+				+	-	+	-
P. aegeria	+			+	1	6	3	+		2		+				+		2		+		3		+	+	+	+
L. megera	+	3	2	+	7	15	16	+	5	7		+	6	4		+	9	4		+			3	+	+	+	+
L. maera	-		1	-				+				-				-				-				+	-	+	-
C. pamphilus	+	21	58	+	14	46	26	+	9	29	7	+	10	24	16	+	12	21	56	+	6	81	72	+	+	+	+
C. arcania	+	5	6	+	48	80	76	-	10	27	43	-		8		+	18	9		+	49	169	79	+	+	+	+
A. hyperanthus	+	8	2	+	24	48	8	+	14	21	12	+		5	3	+	2	29	3	+	28	59	15	+	+	+	+
M. jurtina	+	102	100	+	217	441	83	+	47	159	67	+	23	65	25	+	3	69	41	+	123	182	42	+	+	+	+
M. tithonus	+	39	14	+	44	42	29	+	61	113	36	+	25	44	11	+	8	10	19	+	158	103	63	+	+	+	+
E. medusa	+			+	7			-				-				+				+				+	+	-	-
H. semele	+			+				-				-				-				-				+	-	-	-
M. galathea	+	88	57	+	148	349	85	+	33	184	173	+	7	17	48	+	50	75	73	+	83	388	92	+	+	+	+
Gesamtarten-zahl	64	27	34	59	36	43	22	53	29	37	21	44	15	26	20	64	30	41	19	58	31	37	23	70	47	52	30

Clusteranalysen basierend auf Präsenz-Absenz-Daten zeigen eine dramatische Umstrukturierung der Zönosen zwischen 1972 und den drei Aufnahmejahren ab 2001. Insgesamt weisen die beiden witterungsmäßig vergleichsweise ungünstigen Jahre 2001 und 2012 eine etwas größere Ähnlichkeit in ihrer Artenzusammensetzungen zueinander auf als zum witterungsmäßig günstigeren Jahr 2011.

Mit diesen Veränderungen geht auch ein gravierender Wandel in der strukturellen Zusammensetzung der Zönosen einher: Hoch spezialisierte Arten, wie standorttreue, thermophile oder monophage Arten, sind in besonderem Ausmaß vom Artenschwund betroffen. Für diese Arten wurden für die Jahre 2001 und 2011 schon deutliche Verluste nachgewiesen, sie sanken jedoch 2012 auf einen neuen Tiefstand. Die Anzahl standorttreuer Arten nahm auf allen Flächen kontinuierlich von 35 Arten im Jahr 1972 auf zehn Arten im Jahr 2012 ab. Der Verlust betrug bis 2001 im Durchschnitt 37%, schwächte sich allerdings bis 2011 leicht ab. Weiterhin konnten nur rund 50% der als mobil eingestuften Arten des Jahres 1972 auch im Jahr 2012 registriert werden. Die Zahl der Wanderfalter wird hierbei vernachlässigt, da deren Auftreten als stochastisch angesehen werden muss.

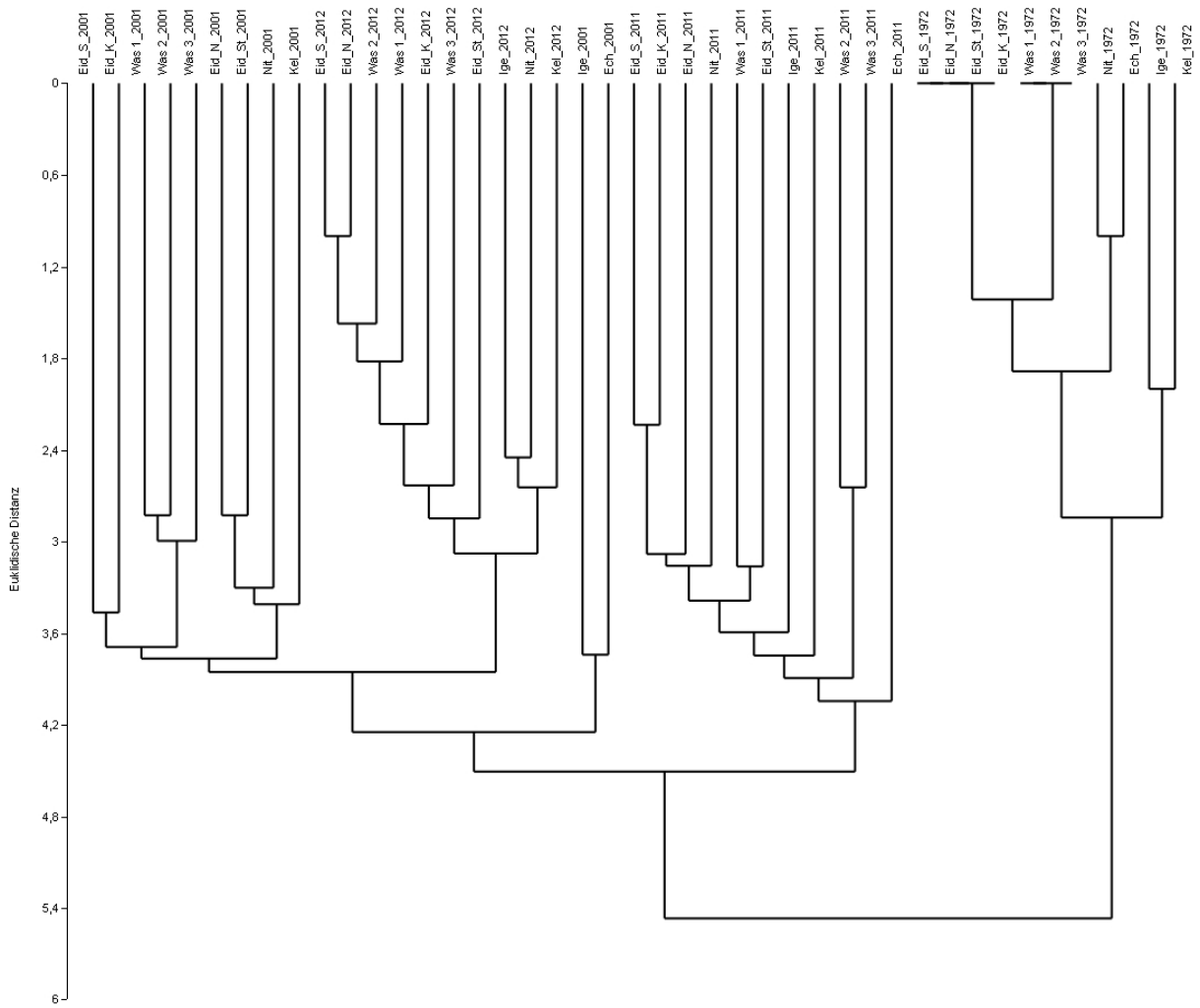

Abb. 2: Clusteranalyse der jeweils 1972, 2001, 2011 und 2012 untersuchten Transekte (Ech: Echternacherbrück, Eid: Eiderberg bei Freudenburg, Ige: Igel, Kel: Kelsen, Nit: Nittel, Was: Wasserliesch). Als Distanzmaß wurde die Euklidische Distanz verwendet.

Einen ähnlich starken Rückgang wie die standorttreuen Arten erfuhren die xerothermophilen Arten, deren Anzahl von 1972 bis 2012 um 68% auf sechs Arten sank. Mesophile, hygrophile und ubiquitäre Arten gingen im gleichen Zeitraum ebenfalls um 45% bis 50% zurück. Den stärksten Rückgang erfuhren monophage Arten, deren Anzahl insgesamt um 77% von 26 auf sechs Arten abnahm. Ebenfalls fiel im Jahr 2012 die Zahl oligophager Arten von 23 auf zehn sowie die Anzahl polyphager Arten von 21 auf 14. Insgesamt ist somit der Artenrückgang von 1972 bis 2001 als ebenso stark wie derjenige von 2001 bis 2012 einzustufen.

Tabelle 3: Klassifizierung der erfassten Tagfalterarten und deren prozentualer Anteil an der Tagfalterzönose im jeweiligen Untersuchungsjahr

	1972	2001	2011	2012
Phagie				
monophag	26	15	17	6
	(37%)	(32%)	(34%)	(20%)
oligophag	23	17	18	10
	(33%)	(36%)	(35%)	(33%)
polyphag	21	15	17	14
	(30%)	(32%)	(33%)	(47%)
Thermophilie				
xerothermophil	19	10	11	6
	(27%)	(21%)	(21%)	(20%)
mesophil	38	25	29	19
	(54%)	(53%)	(56%)	(63%)
hygrophil	2	2	2	1
	(3%)	(4%)	(4%)	(3%)
Ubiquisten	11	10	10	6
	(16%)	(21%)	(19%)	(20%)
Ausbreitungsfähigkeit				
standorttreu	35	20	21	10
	(50%)	(43%)	(40%)	(33%)
mobil	31	24	28	18
	(44%)	(51%)	(54%)	(60%)
wandernd	4	3	3	2
	(6%)	(6%)	(6%)	(7%)
Rote-Liste				
-	44	36	40	24
	(63%)	(77%)	(77%)	(80%)
Vorwarnliste	11	4	7	4
	(16%)	(9%)	(13%)	(13%)
defiziär	1	1	1	1
	(1%)	(2%)	(2%)	(3%)
gefährdet	10	6	2	1
	(14%)	(13%)	(4%)	(3%)
stark gefährdet	4	0	1	0
	(6%)	(0%)	(2%)	(0%)

Besonders hervorzuheben ist die starke Abnahme der durch ihre hohe Spezialisierung in Rheinland-Pfalz als gefährdet eingestufter Arten. Unter den in 1972 nachgewiesenen Tagfalterarten befanden sich 14 Arten, die in der aktuellen Roten Liste von Rheinland-Pfalz (SCHMIDT 2010) in den Kategorien 'gefährdet' und 'stark gefährdet' aufgeführt sind. 2001 sank diese Zahl auf sechs, 2011 weiter auf drei Arten. 2012 wurde mit nur noch einer gefährdeten Rote Liste-Art innerhalb der Naturschutzgebiete ein vorläufiger Tiefstand erreicht. Alle Werte sind in Tabelle 3 zusammengefasst.

4. Diskussion und Ausblick

Insgesamt ist die Bilanz dieser langfristigen Untersuchung sehr ernüchternd: Eine große Zahl an Tagfalterarten ist in den letzten 40 Jahren in den hier untersuchten Kalkmagerrasen der Region Trier nicht mehr nachgewiesen worden. Bei vielen dieser Arten ist zu befürchten, dass sie in den Untersuchungsgebieten definitiv ausgestorben sind. Hiermit zeigen auch diese mehrheitlich als Schutzgebiete ausgewiesenen Bereiche kleinräumig und gestützt auf solide Untersuchungen denselben negativen Trend, der für große Bereiche Europas generell festgestellt wurde (Benes & Kuras 1998, Léon-Cortéz et al. 1999, Maes & Van Dyck 2001, van Swaay et al. 2011).

Tafel 1: Eine Auswahl der in den Untersuchungsflächen nachgewiesenen Tagfalterarten: Weißklee-Gelbling (*Colias hyale*) bei Kernscheid, Trier, aufgenommen 21.05.2010 (Foto: K. Filz); Kleiner Würfel-Dickkopffalter (*Pyrgus malvae*) im Brettenbachtal bei Trier, aufgenommen 18.04.2010 (Foto: K. Filz); Tagpfauenauge (*Inachis io*) in Stâna de Vale, Apusenigebirge Rumänien, aufgenommen am 12.08.2010 (Foto: T. Schmitt); Wegerich-Scheckenfalter (*Melitaea cinxia*) in Slavnik, Südslowenien, aufgenommen am 29.05.2009 (Foto: T. Schmitt); Nierenfleck-Zipfelfalter (*Thecla betulae*) im Avelertal bei Trier. Aufgenommen am 09.08.2009 (Foto: T. Schmitt); Großer Feuerfalter (*Lycaena dispar*) in Velem, Westungarn, aufgenommen am 12.08.2012 (Foto: T. Schmitt) (Reihenfolge der Fotos von links nach rechts und oben nach unten).

Dass es sich bei diesem Trend nicht um zufällige Ergebnisse einiger Jahre handelt, zeigen die Resultate für die beiden aufeinander folgenden Jahre 2011 und 2012, von denen ersteres ein vergleichsweise günstiges Jahr für Tagfalter darstellte, letzteres ein recht ungünstiges, ebenso wie 2001. Dies führte wohl für einige Arten zu einem gemeinsamen Absinken der Individuenzahlen in diesen beiden ungünstigen Jahren unter die Nachweisschwelle auf den Transekten, was eine Erklärung für die relative Ähnlichkeit der Zönosen darstellen könnte. Es fällt jedoch auf, dass gerade einige der so genannten wertstellenden Arten, die 2001 noch nachgewiesen werden konnten, sowohl 2011 als auch 2012 nicht mehr registriert wurden.

Besonders bedenklich ist, dass die Arten, welche nicht mehr nachgewiesen werden konnten oder zumindest sehr deutliche Rückgangstendenzen zeigten, mehrheitlich diejenigen Taxa umfassen, welche wegen ihrer hohen Habitatspezifizität diejenigen Organismen darstellen, welche gerade durch die Ausweisung und Pflege von Naturschutzgebieten in besonderem Maße unterstützt werden sollten. Vorrangig betrifft dies die Arten der Roten Liste, welche in den meisten Fällen über den Untersuchungszeitraum dramatisch abnahmen. Es muss folglich in Frage gestellt werden, ob die bisher durchgeführten Konzepte im Arten- und Biotopschutz in ausreichendem Maße die gesetzten Ziele erreichen können.

Hierbei scheinen tierischen Organismen höhere Anforderungen an die Schutzkonzepte von hochwertigen Habitaten zu stellen als Pflanzen. So konnte RUTHSATZ (2012) keine wesentlichen Veränderungen in der Florenzusammensetzung ausgewählter Kalkmagerrasen im Westen von Rheinland-Pfalz feststellen. Sie konstatiert, dass die Luftstickstoffeinträge (vergl. BARTHOLMESS et al. 2011) auf diesen besonderen Standorten wohl keinen oder nur vergleichsweise geringen Einfluss auf die Artenzusammensetzungen der Pflanzengesellschaften besitzen. Diese Depositionen sollten jedoch Einfluss auf die jährliche Biomasseproduktion haben, und somit das Mikroklima für Wärme liebende Tagfalterarten nachteilig beeinflussen. Es ist folglich nicht ausreichend, Habitattypen unter Schutz zu stellen ohne ihre Pflege durch regelmäßige Qualitätsmonitorings der wertstellenden Arten zu überprüfen. In der Entwicklung geeigneter Pflegekonzepte, um zum einen dieser mikroklimatischen Verschlechterung entgegen zu wirken, hiermit jedoch nicht die Blütenhorizonte, die Pflanzenvielfalt und den Strukturreichtum von Flächen nachhaltig nachteilig zu beeinträchtigen, besteht noch erheblicher Forschungsbedarf.

Bei genauerer Analyse der auf unseren Untersuchungsflächen vom Rückgang besonders betroffenen Arten lassen sich zwei ökologisch-biogeographische Gruppen ausmachen, für deren Rückgang voraussichtlich unterschiedliche Gründe verantwortlich sind.

Arten wie *Erebia medusa*, *Hesperia comma* und *Boloria selene* gehören einer Gruppe an, die zum einen magere Habitate benötigen, zum anderen aber auch eine eher kontinentale Verbreitung aufweisen (TOLMAN & LEWINGTON 1998, SETTELE et al. 1999, TSHIKOLOVETS 2011). Für diese Arten

wirken vermutlich zwei unterschiedliche Ursachen an ihrem Rückgang mit: Ihre Habitate werden weniger und die klimatischen Bedingungen verschlechtern sich für sie, bedingt durch die zunehmende Atlantisierung des Klimas und vor allem durch die zunehmend warmen Winter. Hierdurch ziehen sich solche Arten zunehmend in die höheren Bereiche der Mittelgebirge zurück, im Trierer Raum also in den Hunsrück und die Eifel. Für diese auch aus Gründen des klimatischen Wandels aussterbenden Arten lassen sich durch gezielte Pflegemaßnahmen nur bedingt Erfolge erzielen; allenfalls kann hierdurch ihr Aussterben verzögert werden (vergl. HABEL et al. 2011).

Die zweite Gruppe umfasst Wärme liebende Habitatspezialisten, welche meist mediterraner Herkunft sind (DE LATTIN 1957), wie beispielsweise *Spialia sertorius*, *Thymelicus acteon* und *Colias alfacariensis*. Obwohl man auf Grund der Klimaerwärmung eher positive Tendenzen für diese Gruppe erwarten sollte (SETTELE et al. 2008), nehmen auch ihre Vertreter sehr stark ab. Dies kann zum einen durch die oben beschriebenen mikroklimatischen Verschlechterungen bedingt sein, zum anderen scheinen vor allem diejenigen Arten aus dieser Gruppe besonders betroffen zu sein, bei denen davon ausgegangen wird, dass sie intakte Metapopulationsstrukturen benötigen (HANSKI 1999). Brechen diese zusammen, dann ist das Aussterben in den verbleibenden Habitatfragmenten nur eine Frage der Zeit, ein Prozess, der mit den von uns beobachteten Rückgängen große Ähnlichkeit aufweist. Zusätzlich können genetsche Effekte bei diesen Aussterbeprozessen eine nicht unerhebliche Rolle spielen. Vor allem genetisch diverse Arten, die auf einen Austausch zwischen Habitaten angewiesen sind, können genetisch degenerieren, was den Prozess des Aussterbens zusätzlich antreiben kann (HABEL & SCHMITT 2012) und was zu recht abrupten Aussterbefällen führen kann, wie exemplarisch für das plötzliche Verschwinden von *Chazara briseis* in Böhmen beschrieben (KADLEC et al. 2010).

Um also die biologische Vielfalt in Rheinland-Pfalz zu bewahren, wird es nicht ausreichend sein, kleine Landschaftsbestandteile in Naturschutzgebieten zu schützen, denn in diesen werden diejenigen Arten, deretwegen diese eingerichtet wurden, zu einem nicht unerheblichen Teil über die Zeit erodieren und verschwinden (FILZ et al. 2013). Dies wird die einzelnen Arten unterschiedlich stark betreffen. Arten wie *Melitaea aurelia* scheinen sich besonders gut in isolierten Habitaten zu halten, wobei auch ihre einfache genetische Struktur einen Beitrag hierzu leisten dürfte (HABEL et al. 2009). Ganz anders scheint dieses jedoch für genetisch komplexere Arten wie beispielsweise *Thymelicus acteon* auszusehen (LOUY et al. 2007), für die auch in unserem Untersuchungsgebiet ein gravierender Rückgang festzustellen war.

Die Bewahrung des Artenreichtums unserer Region dürfte also nur durch eine Defragmentierung unserer Landschaft erreicht werden können, durch die ein Austausch zwischen den erhaltenen hochwertigen Habitatinseln wieder ermöglicht oder zumindest erleichtert wird. Ein solcher Austausch könnte beispielsweise durch die Verbesserung der Permeabilität der Landschaft entlang des Mosel-

korridors geschaffen werden, wodurch zum einen eine Erhöhung der Vernetzung zwischen den hier untersuchten Habitaten in Nittel, Wasserliesch und Igel erreicht, und darüber hinaus ihre Anbindung an die bedeutenden Kalkmagerrasenvorkommen Nordostlothringens gewährleistet werden könnte. Auch für die heute stark isolierten Flächen in Freudenburg und Kelsen besteht die Möglichkeit, sie durch vergleichbare Aktivitäten in einen Biotopverbund mit vergleichbaren Flächen im angrenzenden Kalkgebiet des westlichen Saarlandes einzubeziehen.
Für ein solches Vernetzungskonzept würde es sich zum Beispiel anbieten, Straßenränder und Verkehrsinseln nicht mehr intensiv zu mähen, sondern nur noch soweit es die Verkehrssicherheit erfordert. Auch kleine unproduktive Bereiche in der Landschaft wie gelegentliche Brachen und Ödlandflächen sollten erhalten und gefördert werden, um sie als Trittsteine zwischen den ökologisch deutlich höherwertigen Naturschutzgebieten zu nutzen. Hierdurch muss die historisch gewachsene vielfältige Landschaftsstruktur unseres Raumes erhalten und vor der Überprägung durch Intensivlandwirtschaft bewart werden. Unbedingt vermieden werden muss eine „Vermaisung“ der Landschaft, wie diese schon in weiten Bereichen vor allem Norddeutschland stark vorangeschritten ist. Die notwendige Förderung regenerativer Energien darf nicht dazu führen, dass die Ressourcen einer biologisch vielfältigen Landschaft in diesem Zuge zerstört werden.

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Missing the target? A critical view on butterfly conservation efforts on calcareous grasslands in south-western Germany

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Abstract

Butterflies are strongly declining on grassland habitats of Central Europe. Therefore, the success of conservation measures on high quality grassland habitats is controversially discussed. We compared the changes in butterfly diversity and community structure on six managed calcareous grasslands with eight unmanaged vineyard fallows. We obtained strong losses of species diversity and remarkable shifts of community compositions on both habitat types. However, the changes on vineyard fallows were only slightly more severe but more stochastic than on the calcareous grasslands. The shifts in community composition with respect to functional species traits were rather similar between the two different grassland types so that complex butterfly communities evolved into generalist-dominated ones. Connectivity was higher among vineyard fallows than among calcareous grasslands. Consequently, conservation measures on calcareous grasslands only partly archived their goal to maintain the high species diversity and functional complexity still observed in the 1970s. The negative impacts of eutrophication and monotonisation of the landscape as well as climate change are affecting all habitats, independently from management concepts. Therefore, management on conservation sites can buffer against these effects, but is not sufficient for a full compensation.

Keywords biodiversity loss**,** community composition change, global change, habitat fragmentation, Circuitscape, landscape resistance

Introduction

Europe is undergoing a continuous period of invertebrate decline (Van Swaay et al. 2011). In particular, the loss of typical habitats like semi-natural grasslands due to intensive agriculture and urban development has been particularly dramatic for butterfly species (Bourn and Thomas 2002; Van Swaay 2002; Wenzel et al. 2006). In this aspect, calcareous grasslands of south-western Europe are considered to be one of the most important habitat types for insect conservation (Van Swaay 2002; WallisDeVries et al. 2002). These habitats contain a renowned biological diversity (Varga and Rákosy 2007) including a variety of species listed under the habitat directive of the Bern Convention (Van Helsdingen et al. 1996). 274 (i.e. 48%) of the 576 butterfly species reported as native in Europe occur on calcareous grasslands. Moreover, from the 71 species considered threatened in the same area, 37 (i.e. 52%) can be found in theses habitats (Van Swaay 2002). Consequently, many calcareous grasslands are protected as nature reserves and are integrated in the Natura 2000 network of the European Union (Van Swaay et al. 2011). However, even such legally protected sites degrade in quality and are still losing species despite protection. As a result, many specialised and rare species are now threatened or already extinct (Warren 1997; Wenzel et al. 2006).

Many European countries are experiencing similar population declines. The Netherlands have lost over 24% of its butterfly fauna (Wynhoff and Van Swaay 1995) and 30% of the indigenous species became extinct in Flanders during the 20th century (Maes and Van Dyck, 2001). In Britain, nearly nine percent of the resident butterfly species have gone extinct (Warren 1997) and in Moravia (Czech Republic) Benes and Kuras (1998) recorded a general loss of butterflies by 60% during the same time period. The decline of butterflies has caused an increasing concern in Western Europe and the subsequent implementation of conservation activities for Lepidoptera and other wildlife (Thomas 1995; Van Swaay and Warren 2006; Van Swaay et al. 2011).

The prevalent conservation strategy has been to designate threatened habitat types as nature reserves. The habitat types most deserving protection have been identified by the conservation value of the habitat itself and/or by the presence of a great number of rare and endangered species. Until today, such biodiversity assessments have been the major tool in conservation planning and implementation. However, this strategy has had the negative effect of frequently creating small habitat patches isolated by unsuitable, unprotected landscape, which prevents the inter-patch exchange of species. Moreover, small habitat patches may lack the possibility to buffer large- and meso-scale environmental effects (for a discussion see Hof et al. 2011). Habitats are lost due to diverse land-use changes, which do not necessarily stop at the margin of protected areas, but also changes subtly the characteristics of semi-natural grasslands (Dover and Settele 2009). The negative

impacts of nutrient and pesticide loads as well as climatic changes influence the habitat structure as well as microclimatic conditions (Parmesan 2006, Bartholmess et al. 2011). Frequently, a loss of plant diversity and changes in plant communities is followed by butterfly declines, and especially species with high specialisation on particular food plants might be affected (e.g. Warren et al. 2001, Polus et al. 2007).

Besides the impacts of agricultural improvements on adjacent patches, abandonment is considered to be one major threat to semi-natural habitats (Van Swaay 2002). As many butterfly species depend on the preservation of habitats created by extensive human land-use activities, habitat management is considered to play a crucial role for the practical conservation of threatened species (Warren 1993 a,b). Many species are restricted in their local distribution to these often small and fragmented remnants making them susceptible for any change in habitat quality (Dover and Settele 2009). As a consequence, today species conservation is more than ever a question of protecting habitats in a changing environment, but also to retain species diversity within small and fragmented habitats.

However, the lack of habitat quality and habitat connectivity has led to decreasing numbers of butterfly species not only in legally protected semi-natural habitats, but even more severely in unprotected agricultural areas (Dover and Settele 2009). In the latter, remnants of pre-industrial human land-use (e.g. as fallow grounds) are considered to belong to the most species rich habitats in these areas (Schmitt and Rákosy 2007). These fallows act as retreats as well as stepping stones for many specialised taxa, consequently turning into habitats with high conservation value (Weibull 2000; Schmitt and Rákosy 2007; Schmitt et al. 2008; Lizée et al. 2011). Agricultural areas adjacent to fallow grounds affect population dynamics and community structures within these habitats. Additionally, the ongoing loss of stepping stones reduces overall habitat area and landscape connectivity. Hence, patch size and isolation, as well as missing management activities often favour the vulnerability of this habitat type to environmental effects. Consequently, the decline of butterfly species should proceed even faster in cultivated landscapes than in protected areas.

In this study, we aim to identify the mechanisms responsible for the vulnerability of butterfly species and their habitats using the examples of calcareous grasslands and fallow grounds. We intensively re-investigated butterfly communities after a 40-year time period within a defined region of south-western Germany in both managed and legally protected as well as unmanaged grasslands. Regarding the location, geographical integration and management activities of the different grasslands, we evaluate the connectivity of specific habitat types in the landscape and discuss the possible impacts of recent land-use changes and local global warming on the stability of functional trait diversity in butterfly communities. In particular, we assess whether and how butterfly species richness and community composition in managed versus unmanaged grasslands have changed over the last decades and discuss the appropriateness of conservation strategies for nature reserves.

Material and methods

Study sites

Our study area is located at the south-western border of Germany (Fig. 1a). The vicinity of Trier is characterized by a long tradition of human settlement. Anthropogenic land-use created a manifold mosaic of habitat types ranging from vineyards, agricultural fields, fallows, flower rich meadows, woodlands, rivers and floodplains to several semi-natural habitats like calcareous grasslands. Today, traditional farming systems and semi-natural habitats, which ensured the survival of a diversity of species for thousands of years, are replaced by intensively cultivated agricultural areas. Since the middle of the 20th century, land-use changes have caused serious consequences for the conservation of these traditional habitats as their quality and quantity have declined. Habitats are being lost due to intensive agricultural usage, anthropogenic loads of nutrients and the failure of extensive management, which lead to advanced succession and final loss of these habitats (Burggraaff and Kleefeld 1998).

Calcareous grasslands

For our study, we selected six calcareous grasslands. During the last 40 years, the patches remained as grassland and five of them are preserved as nature reserves. Calcareous grasslands rank among the most species-rich habitats in Europe (Van Swaay 2002, Varga and Rákosy 2007) and are classified as highly endangered in the Red List of endangered habitat types in Rhineland-Palatinate. A strong decline of these habitats has already been observed during the last decades in our study area (Bielefeld 1985; Wenzel et al. 2006; M. Weitzel own observations.) and even legally protected sites continue to decline (Wenzel et al. 2006).

The phytocoenosis of the study sites can be described as *Mesobromion erecti* dominated by flowering herbs and grasses (e.g. *Bromus erectus*, many Orchidaceae), interspersed with single stands of shrubs (e.g. C*rataegus monogyna, Prunus spinosa*) or small trees. Vegetation varied in height throughout the year, but in general was, corresponding to the dominating plant species, less than 30 cm high. In four reserves, structural characteristics were preserved by tending strategies (mowing and clearing). Like most semi-natural habitats, the patches were highly fragmented and under external pressure from agricultural intensification and changing land-use. The degree of isolation, calculated using the formula of Power (1972), varied between 78.8% (Echternacherbrück) and 99.9% (Kelsen). The isolation of the investigated habitats can be explained by natural limiting factors like the geological condition, microclimatic factors or by anthropogenic fragmentation.

In total, the study sites extended over 136 ha, which represent a considerable proportion of the 752 ha of calcareous grasslands known in Rhineland-Palatinate (Klein et al. 2001). The minimum

geographic distance between patches was 3 km between Igel and Wasserliesch. Distances exceeded 10 km in the other cases. Spatial autocorrelation among sites could be excluded.

Patch size varies considerably from 1.5 ha (Kelsen) to 68 ha (Echternacherbrück). Depending on the total size of the reserve, one to four transects per patch (transect length 40-385 m) were established in 1972. All transects were re-established and re-investigated in 2011 in cooperation with the initial observer (M. Weitzel).

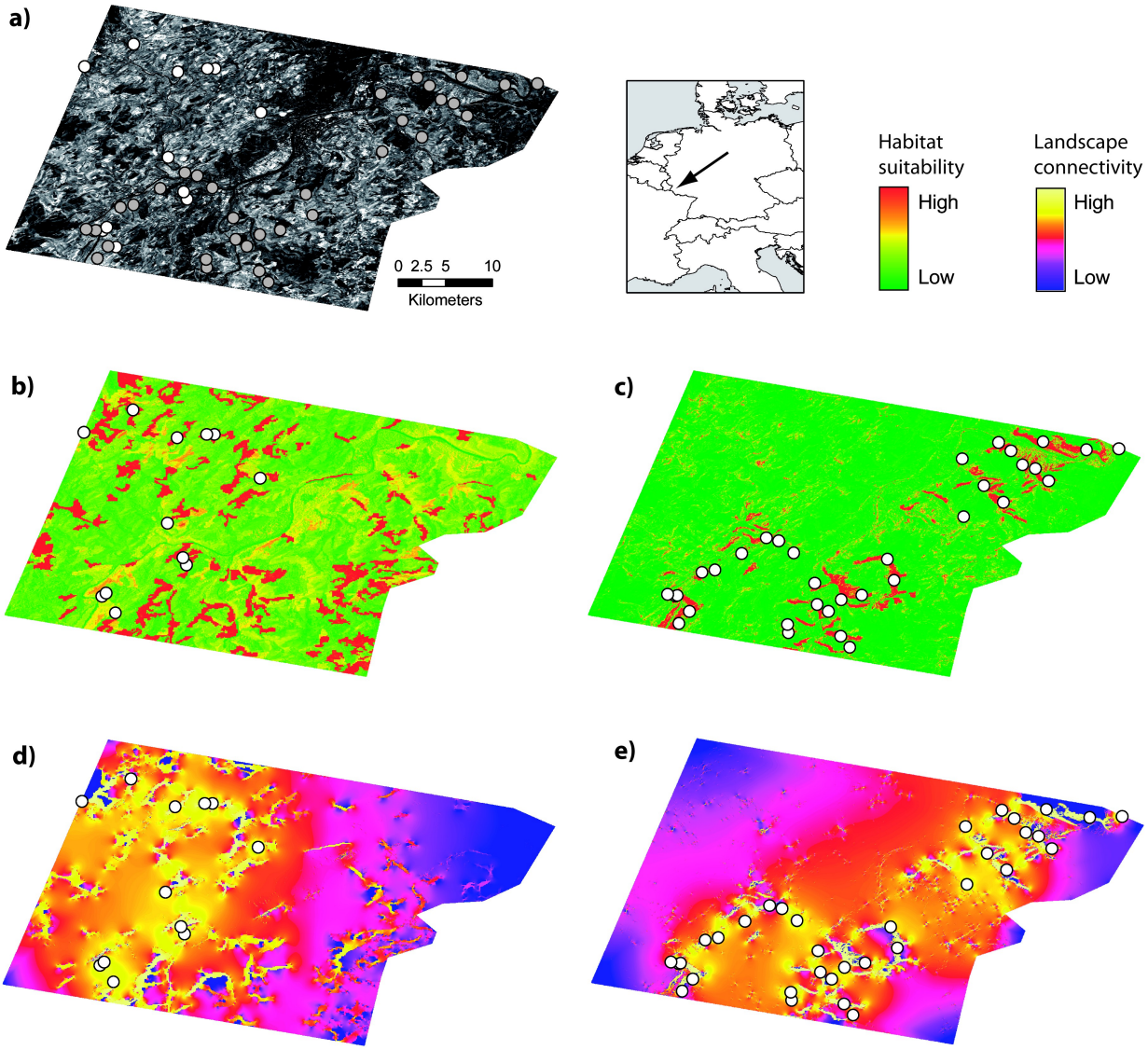

Fig. 1 Location of the study area near Trier in south-western Germany (**a**). *White circles* indicate locations of selected calcareous grasslands and *grey circles* represent vineyard fallows used for connectivity modelling respectively. Habitat suitability maps based on the locations of both habitat types were generated (**b** calcareous grasslands; **c** vineyard fallows) and used for connectivity models (**d** calcareous grasslands; **e** vineyard fallows).

Vineyard fallows

Eight xerothermic vineyard fallows were selected for field surveys. Theses patches were structurally young fallows in 1973 and have been abandoned from agricultural use for at least fifty years. Old fallows are considered to hold a significantly higher species richness and heterogeneity and host more Red Data Book species than earlier stages (Balmer and Erhardt 2000). Vegetation height varied throughout the year, but on average did not exceed 80 cm. The vegetation was dominated by perennial bunch grasses, a variety of thermophilic flowering herbs as *Onobrychis viciifolia*, *Daucus carota*, *Centaurea* ssp., *Medicago* ssp., *Vicia* spp, *Rumex* ssp. and few interspersed hedge structures composed of *Rosa* ssp., *Rubus* ssp*., Cytisus scoparius* and C*rataegus monogyna.* Geological conditions and microclimatic factors prevent the vegetation of converting into secondary forests. Moreover, structural characteristics have been maintained by occasional extensive sheep pasturing. All patches suffer from a high degree of fragmentation as well as external pressure from adjacent intensively cultivated farmland (mostly vineyards), hay meadows and housing areas. Minimum distance between patches was 200 m (Brettenbach I; Brettenbach II). In the other cases, geographic distances were on average 1.6 km. A spatial autocorrelation among patches could be excluded. Patch size varied between 2.7 ha (Kernscheid) and 5.8 ha (Brettenbach I). In total, the studied vineyard fallows extended over 34.5 ha. In 1973, one transect of varying length (432-1430 m) was established per patch. The transects were re-established and re-investigated in 2010 in cooperation with the initial observer (M. Weitzel).

Field sampling design

In both grassland types, data were taken from standardized transect counts along fixed transects. The structure of this monitoring was similar to that described by Pollard and Yates (1993). Each butterfly seen within an observation radius of 5 m ahead and 2.5 m on each side of the observer was counted. Individuals were either identified and counted by sight or captured with a butterfly net for closer determination to species level. If possible, each transect was visited every ten days from April to October for a time period appropriate to their length. The observations were conducted randomly between 10:00 am and 5:00 pm if weather conditions permitted (Pollard and Yates 1993; Settele et al. 1999), i.e. temperature above 17°C, wind less than six Beaufort and no rain (Van Swaay et al. 2008). Variations due to weather and time of day were counterbalanced by randomising the visits. Records were kept along with descriptions of weather conditions and recent management activities. In total, 105 transect walks were performed in 2011 and a similar amount in 1972 on calcareous grasslands. 136 transect walks were conducted in 1973 and 109 in 2010 on vineyard fallows. To obtain unbiased data, observations were conducted throughout the same time period each year using identical transects as well as field methods.

Classification of butterfly species

We categorized all butterfly species regarding their national conservation status and classified them into functional groups defined by habitat requirements, dispersal behaviour, larval food plant specialisation and global distribution.

We used the classification of Bink (1992) for the analysis of dispersal abilities. For increasing the statistical power, the nine dispersal classes were condensed to three: sedentary species (class 1-3), mobile species (class 4-6) and migrants (class 7-9). We used the classification of Reinhardt and Thust (1988) for general habitat requirements to distinguish between ubiquitous, mesophilic, hygrophilic and xerothermophilic species. Caterpillars were classified, respective to their food plant use, as monophagous, oligophagous and polyphagous (Ebert and Rennwald 1991). Global distribution data were obtained from Kudrna (2002). We classified butterfly species as Mediterranean if their distribution area includes southern Iberia, southern Italy or Greece, i.e. ensuring their survival in Mediterranean glacial refugia. The distribution areas of continental species usually exclude these regions and do not reach the lowland areas along the coast of the Atlantic or the British Isles. These species usually survived in the last glacial period in extra-Mediterranean and/or more eastern refugia. Species were classified as Mediterranean-continental species if their distribution areas include at least one of the areas typical for the Mediterranean species, but also extend to the continental parts of Eurasia. The classification of each species is given in Table 1.

The categorisation of endangerment was taken from the respective Red Data Book for Rhineland-Palatinate (Schmidt 2010) and the national law of wildlife conservation (BArtSchV §1). Due to taxonomic revisions within the investigated time period, *Leptidea sinapis* and *L. reali* were treated as a sibling species complex in this study. The nomenclature of butterflies follows Gaedike & Heinicke (1999).

Statistical analysis

For each study patch, we constructed a data matrix containing the presence-absence data of all recorded butterflies. Species estimate accuracy was calculated computing expected species accumulation curves (sample-based rarefaction curves) and incidence-based richness estimators (Chao1, Chao2, ICE, first-order jackknife, Michaelis-Menten) using EstimateS Win 8.00.

Differences in species composition between the study years were evaluated for each study patch. Tests among study sites and observation years were done by Wilcoxon tests, Cochran Q tests and χ^2 tests for heterogeneity in SPSS 15.0. We also performed separate statistical calculations for each functional group using Cochran-Q-tests to analyse community shifts between the observation years.

Turn-over rates were estimated for both grassland types to identify the changes of the faunas between the two observation years in Microsoft Excel 2003. It was calculated as the number of species recorded in only one of the observation years divided by the total number of species observed during both observation years. Comparisons of the similarity of the community structures were made using the Sørensen similarity index. It was calculated on the basis of presence/absence data as the number of shared species divided by the number of species in the two samples, respectively.

Table 1 Presence-absence data of all butterfly species recorded on six calcareous grasslands and on eight vineyard fallows with the number of study sites with the species being present in 1972/73 and 2010/11 including their species specific functional traits (D1: sedentary, D2: medium, D3: migrant; P1: monophagous, P2: oligophagous, P3: polyphagous; H1: xerothermophilic, H2: mesophilic, H3: hygrophilic, H4: ubiquitous; A1: Mediterranean, A2: continental, A3: continental-Mediterranean, A4: migrant)

	Calcareous grasslands		**Vineyard fallows**		
	1972	**2011**	**1973**	**2010**	**Traits**
Hesperidae					
Erynnis tages (L., 1758)	6	4	7	0	D1 P2 H1 A1
Carcharodus alceae (Esp., 1780)	1	0	7	0	D2 P2 H1 A1
Spialia sertorius (Hoff., 1804)	6	3	6	0	D1 P1 H1 A1
Pyrgus malvae (L., 1758)	6	5	8	5	D1 P2 H2 A1
Pyrgus serratulae (Ram., 1839)	1	0	0	0	D1 P1 H1 A3
Carterocephalus palaemon (Pal., 1771)	4	0	3	0	D1 P2 H2 A2
Thymelicus lineola (O., 1808)	6	6	8	6	D2 P2 H2 A2
Thymelicus sylvestris (Poda, 1761)	6	6	5	6	D1 P2 H2 A1
Thymelicus acteon (Rott., 1775)	3	0	0	0	D1 P2 H1 A1
Hesperia comma (L., 1758)	1	1	0	0	D1 P2 H2 A3
Ochlodes sylvanus (Esp., 1778)	6	3	8	4	D2 P3 H4 A1
Papilionidae					
Papilio machaon L., 1758	6	5	8	6	D2 P3 H2 A1
Pieridae					
Leptidea sinapis (L., 1758)/ *reali* Reiss, 1989	6	6	8	8	D2 P2 H2 A1
Anthocharis cardamines (L., 1758)	6	5	8	8	D2 P2 H2 A3
Aporia crataegi (L., 1758)	5	3	6	5	D2 P2 H2 A1
Pieris brassicae (L., 1758)	6	6	8	3	D3 P3 H4 A1
Pieris rapae (L., 1758)	6	6	8	8	D2 P3 H4 A1
Pieris napi (L., 1758)	6	6	8	6	D2 P3 H4 A1
Pontia daplidice (L., 1758)	1	0	0	0	D2 P3 H1 A1
Colias croceus (Fourc, 1785)	3	0	2	0	D3 P2 H4 A4
Colias hyale (L., 1758)	6	4	8	6	D2 P2 H2 A2
Colias alfacariensis (Rib., 1905)	5	1	0	0	D2 P2 H1 A1
Gonepteryx rhamni (L., 1758)	6	6	8	7	D2 P2 H2 A1
Lycaenidae					
Hamearis lucina (L., 1758)	5	0	5	0	D1 P1 H2 A2
Lycaena phlaeas (L., 1761)	6	4	8	6	D2 P1 H2 A1
Lycaena dispar (Haw., 1803)	0	0	0	1	D2 P1 H3 A2
Lycaena tityrus (Poda, 1761)	6	2	8	3	D1 P1 H2 A3
Lycaena hippothoe (L., 1761)	0	0	1	0	D1 P1 H3 A2
Thecla betulae (L., 1758)	6	2	8	1	D1 P1 H2 A2

Neozephyrus quercus (L., 1758)	4	0	3	0	D1 P1 H1 A3
Satyrium ilicis (Esp., 1779)	4	0	0	0	D1 P1 H1 A3
Callophrys rubi (L., 1758)	6	6	8	5	D2 P3 H2 A1
Satyrium w-album (Knoch, 1782)	0	0	3	0	D1 P1 H2 A2
Satyrium pruni (L., 1758)	6	3	8	0	D1 P1 H1 A2
Satyrium acaciae (Fab., 1787)	3	0	0	0	D1 P1 H1 A3
Cupido minimus (Fues., 1775)	6	6	4	0	D1 P1 H1 A3
Cupido argiades (Pallas, 1771)	0	0	0	2	D2 P2 H1 A2
Celastrina argiolus (L., 1758)	6	3	8	1	D2 P3 H2 A3
Maculinea arion (L., 1758)	3	0	0	0	D1 P2 H1 A3
Aricia agestis ([Den. & Schiff.], 1775)	6	6	0	7	D2 P3 H1 A1
Polyommatus semiargus (Rott., 1775)	6	6	7	7	D2 P1 H2 A1
Polyommatus icarus (Rott., 1775)	6	6	8	7	D2 P2 H4 A1
Polyommatus coridon (Poda, 1761)	6	5	4	0	D2 P1 H1 A1
Polyommatus bellargus (Rott., 1775)	1	0	0	0	D1 P2 H1 A1
Nymphalidae					
Argynnis paphia (L., 1758)	6	4	8	1	D2 P1 H2 A3
Argynnis aglaja (L., 1758)	6	5	7	3	D1 P1 H2 A1
Issoria lathonia (L., 1758)	6	5	4	6	D2 P1 H2 A1
Brentis ino (Rott., 1775)	0	0	2	0	D1 P2 H3 A2
Boloria selene ([Den. & Schiff.], 1775)	6	1	8	0	D1 P1 H3 A2
Boloria euphrosyne (L., 1758)	4	0	0	0	D1 P1 H2 A3
Boloria dia (L., 1767)	0	4	0	0	D2 P1 H1 A2
Vanessa atalanta (L., 1758)	6	3	8	5	D3 P1 H4 A4
Vanessa cardui (L., 1758)	6	1	8	0	D3 P3 H4 A4
Inachis io (L., 1758)	6	4	8	8	D2 P3 H4 A3
Aglais urticae (L., 1758)	6	6	8	7	D2 P1 H4 A1
Polygonia c-album (L., 1758)	6	3	8	4	D2 P3 H2 A1
Araschnia levana (L., 1758)	6	3	8	5	D2 P1 H2 A2
Nymphalis polychloros (L., 1758)	4	0	3	0	D2 P3 H2 A3
Euphydryas aurinia (Rott., 1775)	0	1	0	0	D1 P2 H3 A3
Melitea cinxia (L., 1758)	6	0	3	1	D1 P1 H2 A3
Melitea diamina (Lang, 1789)	2	0	6	0	D1 P1 H3 A2
Melitea athalia (Rott., 1775)	6	3	7	2	D1 P3 H2 A3
Melitea aurelia (Nick., 1850)	2	1	0	0	D1 P3 H1 A2
Limentis populi (L., 1758)	1	0	2	0	D1 P1 H2 A2
Limentis camilla (L., 1764)	5	0	6	0	D1 P1 H2 A2
Apatura iris (L., 1764)	5	1	1	0	D1 P1 H2 A2
Pararge aegeria (L., 1758)	6	4	8	1	D2 P2 H2 A1
Lasiommata megera (L., 1767)	6	5	7	3	D2 P2 H2 A1
Lasiommata maera (L., 1758)	1	1	0	0	D1 P2 H1 A3
Coenonympha arcania (L., 1761)	4	6	8	5	D1 P3 H2 A3
Coenonympha pamphilus (L., 1758)	6	6	8	7	D1 P3 H2 A1
Pyronia tithonus (L., 1771)	6	6	8	8	D1 P2 H1 A3
Aphantopus hyperantus (L., 1758)	6	6	8	7	D1 P3 H2 A2
Maniola jurtina (L., 1758)	6	6	8	8	D2 P3 H4 A1
Erebia medusa ([Den. & Schiff.], 1775)	4	0	7	0	D1 P3 H2 A2
Hipparchia semele (L., 1758)	2	0	0	0	D2 P3 H1 A1
Melanargia galathea (L., 1758)	6	6	8	8	D1 P2 H2 A1
Species number	70	52	59	41	

Independently from changes in absolute species composition, we evaluated changes in relative functional trait diversity by using PCA in combination with linear discriminant analysis (LDA) in SPSS. We calculated relative proportions for the functional trait classes separately for each site and time slice. In consequence, each trait (Dispersal: 3 classes; Foodplant use: 3 classes; Habitat: 4 classes, Distribution: 4 classes) was summed to one on each site. This information was thereafter transformed via PCA into a multivariate scenopoetic trait space by taking principal components that exceeds the value of one after conducting a varimax rotation. Group discrimination (i.e. taking year as grouping variable) was tested thereafter using cross-validated LDA.
To test for differences in parallelism of the community shifts between calcareous grasslands and the vineyard fallows, we performed a circular ANOVA using the *circular* package in R (Jammalamadaka and SenGupta 2001, R development core team 2010), where the directions of each vector connecting the two observation years in the PCA-space were used as dependent factor.

Resistance surface modeling

To infer patterns of habitat fragmentation in both habitat types, we combine an environmental niche model with a habitat connectivity model using fine-scale environmental GIS-layers as predictors for model building. The environmental layers comprise four different vegetation indices based on multispectral ASTER (Advanced Space Borne Thermal Emission and Reflection Radiometer) data in 30 m resolution (NDVI, NDWI, soil-brightness, vegetation-greenness) as well as topography information derived from the ASTER global digital elevation map of the same resolution (altitude, slope, aspect). Further, we used categorical CORINE landcover data of 2006 (available through: eea.europe.com) with a resolution of 100 m. The Normalized Different Vegetation Index (NDVI), developed by Rouse et al. (1974), is a simple vegetation index for remotely sensed data that quantifies the density of plant growth on earth, and so provides information about vegetation biomass (Jensen 2007). The calculation of the Normalized Difference Water Index (NDWI), introduced by Gao (1996), provides information about the vegetation water content and allows assessments to be made of changes in plant biomass and water stress of vegetation.

Suitable satellite data for the purpose of a study like this need to have a sufficient spectral resolution to ensure a spectral discrimination of different land cover types. Furthermore, a high spatial resolution is required to accurately depict small landscape structures. The ASTER multispectral imager onboard NASA's Terra satellite is largely compliant with these requirements. ASTER has three separate imaging subsystems which cover the visible and near infrared (VNIR), the shortwave infrared (SWIR) and the thermal infrared (TIR) spectral ranges with 3, 6 and 5 spectral bands with

spatial resolutions of 15 m, 30 m and 90 m (Yamaguchi et al. 1999; Abrams 2000). In this study, one ASTER scene (acquisition date: June 26, 2001), covering the northern and central parts of Rhineland-Palatinate was selected for analysis.

ASTER spectral bands 1-4, primarily designed for assessing vegetation properties, were selected. From the especially narrow band in the 2-2.5 µm range, conceptualized mainly for the purpose of surface soil and mineral mapping (Yamagushi et al. 1998), a single broad bandwidth channel centered at 2.2 µm was synthesized by averaging channel 5-7, thereby prioritizing improved signal-to-noise ratio versus spectral resolution considered less important for the study purpose. No Thermal bands were used in this study.

Since remote sensing data with medium spatial resolution has only been of limited use for the identification of species compositions (Wulder 1998), the reduced spatial resolution of the ASTER channels in the SWIR Range (i.e. 4 and the synthesized channel 5) has been adjusted to match the 15 m pixel size of the visible and near-infrared bands (1-3). The data fusion was performed with a local correlation approach that preserves the spectral characteristics of the low resolution input and transfers the textural properties of the high resolution reference to the ASTER-SWIR channels (Hill et al. 1999).

The ASTER-scene was calibrated by converting the original digital numbers to absolute reflectance values for each pixel based on ASTER calibration functions (Yamaguchi et al. 1999; Arai and Tonooka 2005) and full radiative transfer modeling (AtCPro©; Hill and Sturm 1991; Hill and Mehl 2003) based on the 5S Code by Tanré et al. (1990). As the terrain of the study area is mountainous, the removal of topographic effects is important prior to the analysis of landscape structures. On the basis of the AtCpro© model, terms describing illumination can be approximated by the integration of a digital elevation model and finally compensated for each raster cell of the dataset. In addition to the radiometric correction, the data preprocessing comprised a precise georectification. The resulting ortho-projected datasets were referenced to the national Gauss-Krüger coordinate system with sub-pixel accuracy and later projected onto the classical WGS reference system using ArcGIS 9.3, thereby fulfilling all requirements for an efficient integration of external geodata.

The Tasseled Cap Transformation, first presented in 1976 by R.J. Kauth and G.S. Thomas, could be described as a guided and scaled linear transformation, which transforms the input satellite data into three (or four) bands of known characteristics. A Tasseled Cap Transformation was applied to the ASTER scene, and three thematic bands representing: soil-brightness, vegetation-greenness and soil- and vegetation-wetness were derived. Within the study extend (Fig. 1a), georeferenced locations of the respective habitat type were set by visual inspection of aerophotos (using Google Earth) and during several field surveys resulting in 12 and 34 locations for either habitat type, respectively.

Environmental niche models were computed using Maxent 3.3.3k, a machine learning algorithm based on the principles of maximum entropy (Phillips et al. 2006; Phillips et al. 2008; Elith et al. 2011). Maxent has frequently outperformed other approaches, especially when the number of georeferenced locations is scarce (e.g. Hernandez et al. 2006; Elith et al. 2006; Wisz et al. 2008). Thus, this algorithm became the method of choice. We used the standard settings, randomly splitting the dataset into a 70% training and a 30% testing subset and using a bootstrap approach between 100 different replicate runs to average model output. Variable importance was assessed by jackknifing the training datasets. The output was scaled in a logistic format. Despite recent criticisms (Lobo et al. 2008; Jiménez-Valverde 2011), but in lack of other alternatives (e.g. Baldwin 2009), AUC statistics (Swets 1988; Fielding and Bell 1997) were used, as implemented in Maxent, to validate model performance. As threshold for identifying areas of low suitability probability, we used the non-fixed equal training sensitivity and specificity threshold as previously recommended (Liu et al. 2005). Connectivity between study sites in either habitat was assessed depending on habitat specific suitability maps within a connectivity model.

Here, we used the program Circuitscape vers. 3.4.1 (McRae and Beier 2007; McRae et al. 2008), which calculates pairwise resistance values between a defined set of locations (here: habitat specific study sites). Circuitscape is based on circuit theory recently adapted from electrical engineering for the solution of landscape ecological problems (McRae et al. 2008). By incorporating multiple pathways, Circuitscape reproduces connectivity between sites more accurate and with higher biological relevance than more classical approaches like isolation-by-distance models or least cost path models (McRae and Beier 2007).

Prior to analysis, habitat suitability maps as derived from Maxent models were retransformed by multiplication of each probability by 10000 and again saved as integer value, to reduce calculation time derived from long decimals, but without loss of information (Brad McRae pers. comm.). Further, values below the previously defined absence threshold were set to the defined positive minimum integer value (i.e. setting to a value of 1) indicating highest resistance in those areas. Generally, the habitat suitability map acts as conductance surface for the connectivity model. This means that the higher the resistance, the lower the value is. Circuitscape was run in four-node mode to safe computing time. For comparison of resistance values, we used the site location used to build the resistance surfaces because they cover the entire study extent. Depending on the difference of absolute location numbers, we get 561 pairwise comparisons for fallow grounds and 66 pairwise comparisons for calcareous grasslands.

To avoid misleading conclusions by comparing an unbalanced study design (i.e. 561 vs. 66 records), we resample the higher number of fallow ground comparisons in a bootstrap approach with 1000 iterations. For each iteration, we selected just as many records randomly as records were available

for the smaller group (i.e. 66 records). Using this subset of fallow ground records, we subtracted the resistances of the fallow grounds by those from the calcareous grasslands. Repeating this procedure for each iteration, we get a distribution of the mean difference between both groups. According to Nakagawa and Cuthill (2007), this effect size is superior for comparing groups outside of a classical null-hypothesis-significance-testing approach. A significant difference is unlikely if the 95% confidence interval of the distribution of this effect size includes zero.

Results

Species decline

During the field surveys in the 1970s and 2010/11, significantly different numbers of species (Cochran-Q-Test, all $p<0.001$) were observed on calcareous grasslands as well as on vineyard fallows. In both habitat types, a remarkable loss of species and changes in community structures were detected. However, neither the absolute number nor the proportion of species loss was considerably different between managed and semi-natural grasslands. After 40 years, 18 species have disappeared in vineyard fallows, i.e. 31%. Similarly, 17 species, i.e. 25%, were not redetected on calcareous grasslands after the same time period. 53% of the species lost were identical in both grassland types. Turnover rates were high on all study patches indicating a shift in community composition over time. No major difference in the average species turnover rates was detected between semi-natural grasslands (i.e. 26%) and fallow grounds (i.e. 35%). Moreover, Sørensen similarity index demonstrates community composition changes over time, on average 74% on calcareous grasslands and 63% on vineyard fallows. The proportion of species recorded newly was low and no major differences in the absolute number or proportion of such species were detected between the two grassland types. In all cases, the amount of newly appearing species did not balance the recorded species losses. The number of observed species for each transect in 2010/11 ranged from 80% to 97% of the species numbers predicted by species richness estimators. Presence-absence data for all species are given in Table 1.

Degradation of functional groups

Analysis of changes in community composition regarding the observed functional groups produced comparable results for vineyard fallows and semi-natural grasslands. In both habitat types, all functional groups were re-detected in 2010/11, with the exception of hygrophilic species. The latter had disappeared from a similar amount of semi-natural grasslands and fallows in 2010/11. Moreover, species declines accompanied by significant changes within the composition of each functional group were recorded in both habitat types (Cochran-Q-test, $p<0.01$). Losses of species

numbers with similar traits were also comparable. In this aspect, butterfly species with high functional specialization showed the strongest negative impacts. In 2010/11, community composition exhibited a significantly higher proportion of generalist species in both habitat types (Cochran-Q-test, $p<0.01$).

Regarding specific species traits, the strongest decline was apparent in sedentary species, independently from habitat type. Butterflies with poor dispersal abilities showed a highly significant decline of 60% (Cochran-Q-test, $p<0.01$) on vineyard fallows and 37% (Cochran-Q-test, $p<0.01$) on calcareous grasslands, respectively. Medium and good dispersers declined considerably less. Besides, monophagous species showed a significant decline in both habitat types (Cochran-Q-test, $p<0.05$) exceeding those of oligo- and polyphagous species. Xerothermophilic and mesophilic species exhibited high decrease rates. In combination, both groups had a comparable amount of decline on both grassland types. However, considerably different species decrease rates were calculated for each single trait: xerothermophilic species decreased slightly more on fallows, whereas mesophilic taxa decreased remarkably more on calcareous grasslands. In a similar way, species declines were documented for all distribution categories, with highest decrease rates of Mediterranean species on calcareous grasslands and of continental species on vineyard fallows.

Concerning the conservation state of the observed butterfly species, following the German national law of wildlife conservation (Bundesartenschutzverordnung §1), species listed as "highly protected" declined significantly and species listed as "strictly protected" were lost completely on calcareous grasslands. Only slightly higher losses were recorded for the protected species in vineyard fallows. Taking into account the categories of the Red Data Book of Rhineland-Palatinate, especially those categories, indicating the highest conservation demand, shrank significantly by 70 to 75% on calcareous grasslands (Cochran-Q-test, $p<0.01$). On vineyard fallows, the number of species also declined in all categories of the Red Data Book, but less severe compared to the declines on calcareous grasslands. However, the overall number of endangered and/or protected species was lower on vineyard fallows than on calcareous grasslands in the early 1970s.

Changes in relative trait diversity

The first three principal components of the PCA explained 86.2% of the entire variance (Tab. 2). The obtained factor loadings strongly support the above described rearrangements of the assignments to the different species traits. The first two components, separated in a calcareous grassland and the vineyard fallow part in Figure 2, support a stronger shift and a more stochastic change of community compositions on the vineyard fallows. However, this result could not be assured statistically as between group differences in the circular ANOVA becomes non-significant ($F = 0.038$, $df = 1$, $p = 0.8487$). LDA using the time frame as grouping variable leads into a

complete differentiation between the groups.

Table 2 Factor loadings as well as Eigenvalues and cumulative explained variance in % for each of the three Principal components (PC) extracted. Bold values indicate most significant correlations for a single PC. Underlined values highlight highest loadings without a clear significant contribution to a single PC (D1: sedentary, D2: medium, D3: migrant; P1: monophagous, P2: oligophagous, P3: polyphagous; H1: xerothermophilic, H2: mesophilic, H3: hygrophilic, H4: ubiquitous; A1: mediterranean, A2: continental, A3: continental-mediterranean, A4: migrant).

	PC1	PC2	PC3
D1	**0.85**	0.31	-0.24
D2	**-0.75**	-0.53	0.26
D3	-0.06	**0.93**	-0.17
P1	**0.70**	0.62	-0.15
P2	-0.28	**-0.87**	0.21
P3	**-0.88**	-0.11	0.03
H1	0.57	-0.21	**-0.77**
H2	0.02	-0.17	**0.86**
H3	<u>0.57</u>	<u>0.57</u>	0.33
H4	**-0.96**	0.13	0.07
A1	-0.54	**-0.79**	0.06
A2	**0.72**	0.50	0.27
A3	0.02	0.58	<u>-0.62</u>
A4	0.15	**0.93**	0.05
Eigenvalue	5.03	4.90	2.13
Cum %	35.93	70.94	86.16

Connectivity modelling

Environmental niche models provide good to excellent results depending on AUC inference (AUC: 0.893 +- 0.037 on calcareous grasslands, Fig. 1b; 0.977 +- 0.006 on vineyard fallows, Fig. 1c). CORINE Landcover information was by far the most delimiting factor for model construction for both habitat types followed by topographical and multispectral information (Tab. 3). The threshold that cuts areas with low habitat suitability was 0.3969 for calcareous grasslands and 0.185 for vineyard fallows. Consequently, mean connectivity (Fig. 1d/e) differs significantly between both habitat types indicating a generally better connectivity between vineyard fallows than between calcareous grasslands (mean difference: -0.172, 95% CI = -0.319 - -0.034, p = 0.004).

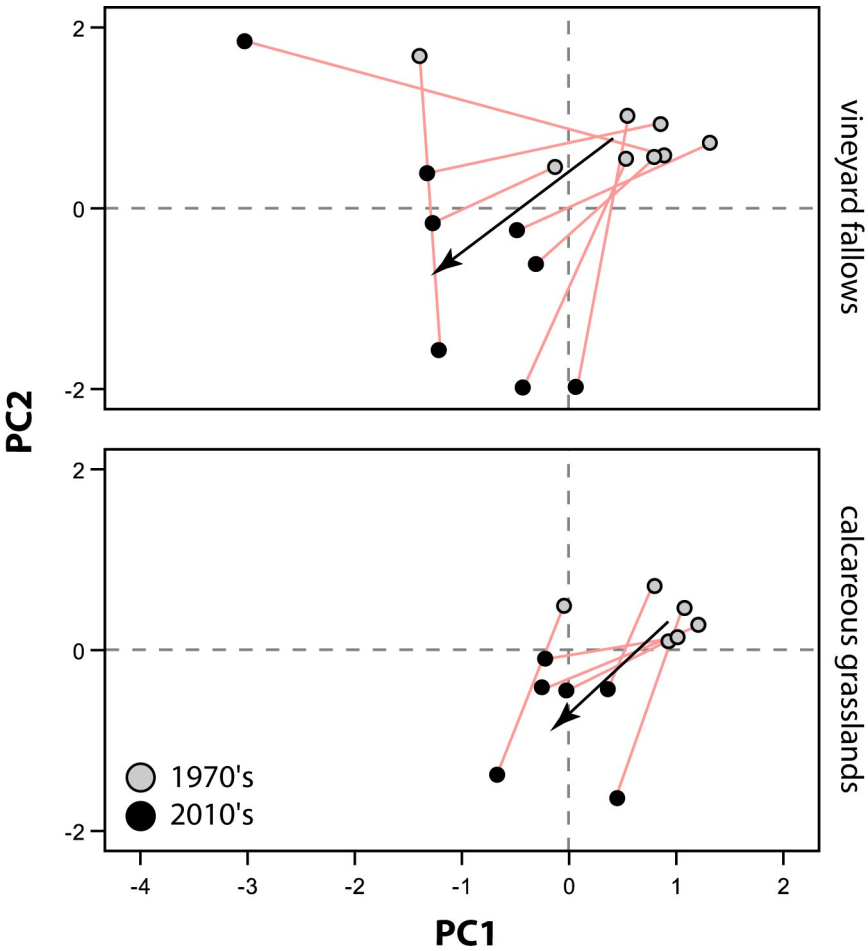

Fig. 2 Trait space spanned by the first two principal components for either vineyard fallows (upper panel) and calcareous grasslands (lower panel), respectively. Grey circles represent sites from the first surveys in the 1970s, black circles from the second surveys in 2010/11. Arrows indicate the mean change within trait space.

Table 3 Percentage of the importance of predictor variables used for constructing environmental niche models of calcareous grasslands and vineyard fallows respectively. The higher the value, the larger is the importance of the respective environmental variable for the model construction.

	Calcareous grasslands	Vineyard fallows
Altitude	2.0	1.6
Aspect	9.7	17.2
Brightness	9.9	1.3
Landuse	72.2	40.3
Greenness	1.1	2.3
NDVI	2.5	6.4
NDWI	0.2	5.2
Slope	2.4	25.7

Discussion

Butterflies have declined remarkably in the region of Trier, both on unmanaged vineyard fallows, but also on managed calcareous grasslands. However, the latter showed considerably higher numbers of species (including rare species) than the vineyard fallows in the 1970s. Nevertheless, the observed species decline was stronger on the fallows than on the calcareous grasslands, and also the turn-over rates were higher on the former. Furthermore, the development of the butterfly communities was much more at random than at the calcareous grasslands, which showed more directed changes of their communities.

These results suggest that the applied management strategies on the observed calcareous grasslands (mowing, sheep pasturing, cutting of shrubs and little trees) had, at least some, success in preserving the previously existing diverse butterfly communities as well as rare and habitat specific species (cf. Balmer and Erhardt 2000). This goes in line with results obtained from Carinthia (Austria), demonstrating the direct positive effects of calcareous grassland management measures on the population development of several habitat specific butterfly species (Rákosy and Schmitt 2011).

Nevertheless, the conservation success is not as high as desired: A considerable number of target species (e.g. *Glaucopsyche alexis*, *Maculinea arion*, *Hipparchia semele*) disappeared from all study sites, and the rate of species loss at calcareous grasslands was, in general, only gradually lower than at the unmanaged vineyard fallows. Thus, the applied management strategies were not able to preserve the *status quo* of the 1970s on the calcareous grasslands, but simply prevented natural succession in a mostly similar way. Therefore, these measures only archived that community shifts on these sites were somewhat less severe and more in parallel than on vineyard fallows, which showed much more arbitrary and stochastic community shifts. Consequently, the management concepts applied at these calcareous grasslands were not able to outweigh the complex external impacts affecting these habitats (e.g. influences from adjacent areas, nutrient loads, changing climate), but had the capability to buffer these negative influences to some extent.

In contrast, the community shifts at the studied vineyard fallows were much more dynamic, reflecting habitat characteristics and the unbuffered effects resulting from large and meso-scale environmental changes over the last few decades. Turn-over rates were considerably higher at the vineyard fallows fostering their stochasticity in community evolution. The higher habitat connectivity of the vineyard fallows compared to the highly isolated calcareous grasslands might reinforce these turn-over dynamics. Consequently, the missing connectivity among calcareous grassland makes that arbitrary losses of species cannot be compensated by immigration within short time. Furthermore, gene flow among these isolated populations will be strongly hampered or even

completely blocked so that populations might also disappear due to the degradation of their gene pools (cf. Habel and Schmitt 2012).

In spite of the notable differences between the managed calcareous grasslands and the unmanaged vineyard fallows, both habitat types show remarkable colinearities in the ecological traits of the species being lost (Fig. 2). These colinearities are unlikely to be influenced by the differences in management and connectivity, but apparently are triggered by large-scale environmental factor complexes provoking destructive impacts on butterfly communities in general, independently from habitat type. As a result, these impacts cause a similar evolutionary trend towards species poor and generalist-dominated communities, and thus represent a more holistic problem for the conservation of biodiversity (e.g. McKinney and Lockwood 1999, Warren et al. 2001, Polus et al. 2007).

Interpreting the observed functional rearrangements of the community structures reflected by strong modifications in the proportional assignments to the different species traits analysed, two major fields of impacts might have predominant influence on the observed calcareous grasslands and vineyard fallows. Eutrophication and monotonisation of the landscape might mostly explain the strong decline of monophagous, sedentary and xerothermophilic species whereas climate change might mostly impact hygrophilic, mesophilic and continental species. However, the combined influence of both factors might enhance their single effects.

While it is obvious that rising global temperatures should harm hygrophilic, mesophilic and continental species not adapted to warmer environment, they also should, on the other hand, favour heat-loving species. However, eutrophication of habitats is strongly enhancing growth capacities of plants, hereby remarkably deteriorating the microclimatic conditions close to the ground. This microclimatic cooling still is not compensated by the global increase of temperatures and is particularly affecting the successful development of pre-imaginal stages of xerothermophilic species. These climatic changes are even aggravated by the missing connectivity of the landscape not allowing species to shift their habitats for compensating negative climatic effects (cf. Hof et al. 2011). All these aspects together foster communities dominated by common generalist species and the successive and unrecoverable loss of specialists (cf. Bourn and Thomas 2002; Wenzel et al. 2006). Therefore, island-like nature reserves have shown to be able to preserve habitat structures, but they have not been capable to conserve the functional characteristics of an interconnected system of habitats necessary to preserve their complex biological diversity. Without adjustments in nature conservation strategies and considerably enhanced efforts in enlarging and connecting high quality habitats, the future perspectives cannot be seen more optimistic.

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How fine is fine-scale? – Questioning the use of fine-scale bioclimatic data in species distribution models used for forecasting abundance patterns in butterflies

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Abstract. The use of species distribution models (SDMs) to predict the spatial occurrence and abundance of species in relation to environmental predictors has been debated in terms of species' ecology and biogeography. The predictive power of these models is well recognized for vertebrates, but has not yet been tested for invertebrates. In this study, we aim to assess the use of SDMs for predicting local abundances of invertebrates at a macroscale level. A maximum entropy algorithm was used to build SDMs based on occurrence records of 61 species of butterflies and bioclimatic information with a 30 arc second resolution. Predictions of habitat suitability were correlated with butterfly abundance data derived from independently conducted field surveys in order to check for a relationship between the predictions of the model and local abundances. Even though the model accurately described the current distributions of the species in the study area at a macroscale the observed occurrences of the species (i.e. presence/absence) recorded by the field surveys differed significantly from the model's predictions for the corresponding grid cells. Moreover, there was no correlation between observed abundance and the model's predictions for most species of butterflies. We conclude that the spatial abundance of butterflies cannot be predicted from environmental suitability modelled at a resolution as large as in this study. Using the finest scale bioclimatic information currently available (i.e. 30 arc seconds) it is not adequate to predict species abundances as structural and ecological factors as well as climatic patterns acting at a smaller scale are key determinants of the occurrence and abundance of invertebrates. Therefore, future studies have to account for the role of the resolution in environmental predictors when assessments of spatial abundances via SDMs will be conducted.

Key words. Invertebrates, spatial abundance, environmental suitability, environmental niche model, MAXENT

INTRODUCTION

Environmental conditions and population processes determine the spatial distribution of species and hence biodiversity patterns over geographic ranges (Gaston, 2003). In this context, species distribution models (SDMs) are commonly used to predict the potential distribution of species with regard to their ecological niches (e.g. Soberon & Nakamura, 2009; Franklin, 2009; Araújo & Peterson, 2012). Based on multiple climatic and environmental variables recorded over the known distribution, these models aim to predict spatial patterns of environmental suitability and are used to infer the likelihood of species' occurrence across a given geographic range. In recent times, SDMs have emerged as powerful tools for addressing important topics in ecology (Ficetola et al., 2007; Rödder et al., 2009), evolution (Habel et al., 2010; 2011) and conservation (Rodriguez et al., 2007; Araújo et al., 2011). Despite the well recognized relationship between environmental suitability and local abundance of species, only a few authors have tried to deduce spatial abundance patterns of species from SDMs (Pearce & Ferrier, 2001; Pearce & Boyce, 2006; Nielsen et al., 2005; VanDerWal et al., 2009). The basic idea behind this assumption is that environmental suitability predicted by a SDM for a given location can be used as an indicator of species' abundance as it indicates how well the physical and ecological constraints of species are met. If this is the case then the species will be abundant at locations with high environmental suitability and vice versa. Hence, models that predict environmental suitability based on occurrence data might also provide information on spatial variation in abundance.

It is much more difficult to obtain data on the abundance of species within their ranges than data on their occurrence. Species often vary greatly in abundance in time and in the different habitats within their ranges (Murphy et al., 2006). Even closely related species differ greatly in their mean population densities in the same range (Bink, 1992). Furthermore, the ease with which individuals can be detected strongly depends on season, time of day, weather conditions, habitat type, faunal activity and the skill of the observer. Therefore, detailed data on abundance are available for only a few species at a local scale and area-wide information is commonly lacking because collecting such data for a large number of species requires a lot labour and is consequently expensive. Assuming a positive correlation between habitat quality and species abundance within a region, such information can be used to target field surveys over large geographical areas. Moreover, modelling species abundances could provide information that could be used to develop regional conservation programs. However, their effective implementation at large scales require that there is a good correlation between "high-quality" habitats and species abundance. As relative abundance is likely to be a good indicator of population viability and reflect factors such as reproductive success, carrying capacity and susceptibility of populations to extinction (Keller et al., 1986; Hobbs & Hanley, 1990), deducing abundance from environmental suitability and extrapolating the results

across a region might be a useful tool. The use of SDMs to predict species specific abundance patterns might be a feasible way of determining spatially explicit assessments of species' abundances, which, in turn, could be used to optimise specific conservation efforts.

Since SDMs have been only used to predict spatial patterns in abundance of vertebrates (cf. VanDerWal et al., 2009; Brambilla & Ficetola, 2012), we aim to apply this approach to invertebrates for the first time, using central European species of butterflies as the model system. Occurrence records for 61 species were used to develop species distribution models using the maximum entropy algorithm MAXENT (Phillips et al., 2006). Predictions of environmental suitability were than correlated with abundance data obtained from standardized field surveys in order to investigate whether it is possible to predict variations in the spatial abundance of species of butterflies using SDMs.

The aim of this study was to determine the suitability of the data on bioclimatic information at the finest resolution (30 arc seconds) currently available in the Worldclim database (Hijmans et al., 2005; www.worldclim.org), which is the standard source of variables for modelling species distributions world-wide (i.e. Hijmans et al. (2005), as demonstrated by a citation index of 1,432 (ISI Web of Science query, 6-6-2012)). However, even if the resolution is quite fine on the macroscale (grid cell resolution equates approximately 1 km² along the equator), we hypothesize that it might be difficult or even impossible at this level of resolution to use SDMs to predict accurately abundance patterns. If so, then this study will demonstrate the limitations of the current method of assessing abundance data using the bioclimatic datasets currently available.

METHODS

Species abundance data were obtained from field surveys carried out at 14 locations in south-western Germany in 2010 and 2011 using a standardized transect method developed for the British Monitoring Scheme (Pollard & Yates, 1993). Butterflies were counted when walking along transects, which varied in length between 123 and 1430 m. Each butterfly seen within 5 m ahead and 2.5 m on each side of the observer was counted. Individuals were either identified and counted without capturing them or caught using a butterfly net for closer determination. All locations were surveyed several times each year (monthly between April and October) to avoid misinterpretation of extreme or zero abundances that can arise from single surveys and seasonal variations in the numbers of certain butterfly species. The means of the species counts for each month were transformed to numbers per 1000 m of transect and summed to give an annual value taking into account the differences in transect length. The transformed monthly counts of species were summed to give a single annual value for each transect.

Species distribution modelling (SDM) requires environmental and species occurrence data.

Occurrence of butterflies was obtained from intensive field surveys at 148 locations across the study area and from a GBIF query (http://www.gbif.org). We selected a region between 50.5° N and 48.9° N and 5.8° E and 8.2° E, which includes an area in south-western Germany and adjacent regions in Luxembourg and France (Fig. 1). The long history of human settlement and different land-uses in this region resulted in a complex landscape matrix, which ensured the survival of a diversity of species including a larger number of butterfly taxa. The landscape encompasses a mosaic consisting of residential areas, arable fields, vineyards, meadows, forests and semi-natural calcareous grassland. The latter especially is a favourable habitat for many butterfly species and rare and endangered taxa (Wenzel et al., 2006). Therefore, butterflies have been well studied in this area.

Information on the occurrence of a total of 61 butterfly species, for which there was information on their abundance available, was used. The mean number of occurrence records per species was 48, ranging from 5 to 126 records for a single species (Table 1). Even if modelling algorithms have a high potential error rate if the information on occurrence is limited to just a few locations (Hernandez et al., 2006; Wisz et al., 2008), all species were included, because the information on occurrence was mainly limited by the rarity of a given species. Since most of the rare butterflies in the study area are habitat specialists, we assumed they have a high preference for a specific niche. Thus, rare species with a very limited range of environmental tolerance can also result in accurate SDMs, even if information on their occurrence is scarce (*sensu* Hernandez et al., 2006; de Siqueira et al., 2009).

Bioclimatic information with a spatial resolution of 30 arc seconds was obtained from the Worldclim database (Version 1.4, http://www.worldclim.org; Hijmans et al., 2005). Nineteen Bioclim variables, all of which are assumed to strongly influence the occurrence and abundance of butterfly species, were checked for multi-colinearity by conducting pairwise Pearson correlations. High inter-correlations between predictor variables might inflate the performance of SDMs (Heikkinen et al., 2006), when redundant information was used for calculating the climatic niche of a species. If $r^2 > 0.75$, we therefore selected only one of these strongly inter-correlated variables. In these cases we preferred those with a higher relevance to butterfly biology (i.e. extremes rather than means) as extremes seem to limit butterfly distributions in a more direct way than means. The final data set included eight variables: 'isothermality' (bio3), 'temperature seasonality' (bio4), 'maximum temperature of warmest month' (bio5), 'minimum temperature of coldest month' (bio6), 'mean temperature of wettest quarter' (bio8), 'mean temperature of driest quarter' (bio9), 'precipitation of driest month' (bio14) and 'precipitation seasonality' (bio15).

We used MAXENT 3.3.3k (Phillips et al., 2006; Elith et al., 2011; available through: http://www.cs.princeton.edu/~shapire/maxent), a machine-learning algorithm following the principles of maximum entropy, for species distribution modelling. MAXENT models potential

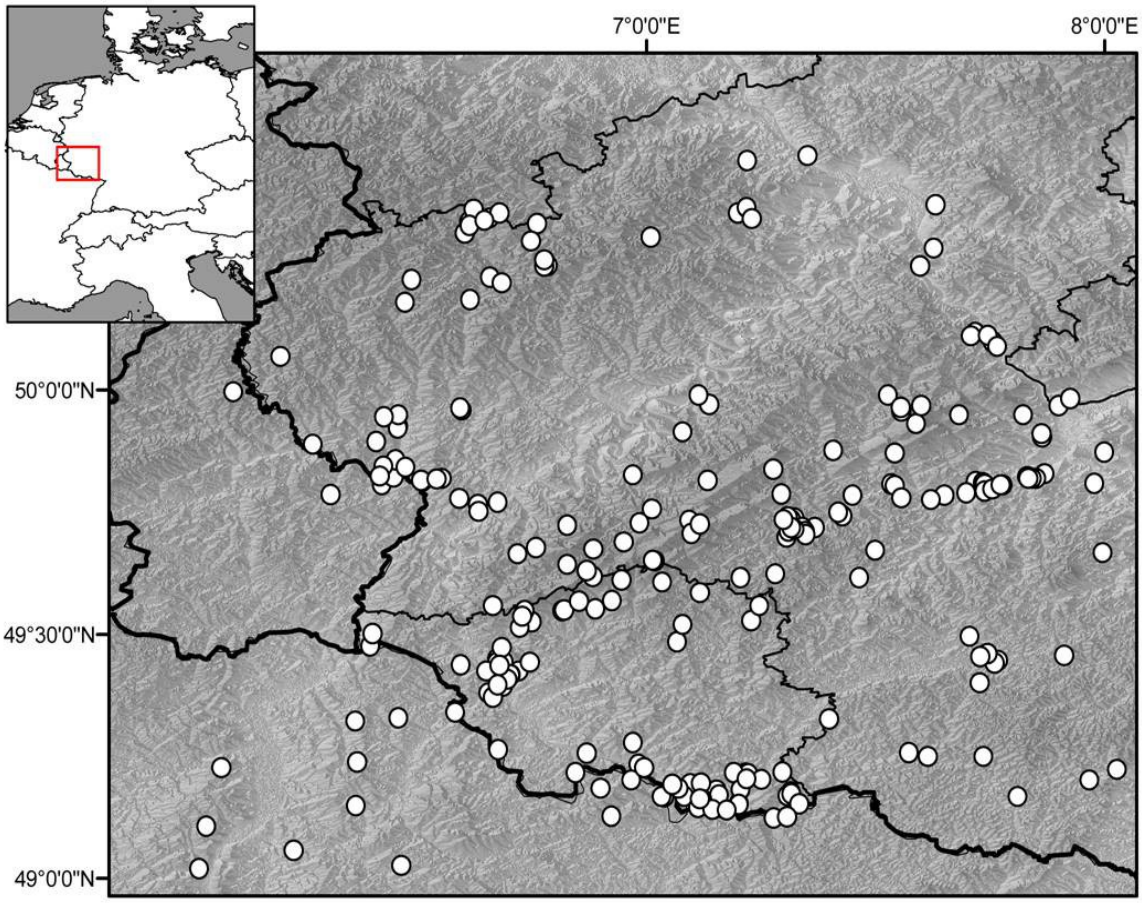

Fig. 1. Map showing the location of the study area in central Europe. Circles indicate the occurrence locations for which there was information on butterfly species available.

species distributions based on environmental predictors (i.e. the above mentioned eight bioclimatic variables in this case) and presence-only data (Elith et al., 2011). In doing so, this algorithm frequently outperforms other methods (e.g. Elith et al., 2006). In addition, and even more important in the context of this study, MAXENT is the best of the available algorithms when there are few species records (Hernandez et al., 2006; Pearson et al., 2007; Wisz et al., 2008). This is particularly important when modelling the distribution of the rare species of butterflies included in this survey.

MAXENT allows for the calculation of the 'area under the receiver operation characteristic curve' (AUC) in order to test the predictive outcome of SDMs (Phillips et al., 2006). AUC values range from 0.5 for models with no predictive ability to 1.0 for those giving perfect predictions (Swets, 1988) and can be used to assess the ability of the model to distinguish species records from background data (Phillips et al., 2006). Models were computed with 30% of the records randomly omitted as test points from the model during training in 100 iterations, in order to assess the internal consistency of the model (Phillips et al., 2006). Subsequently, the average of all 100 models automatically computed by MAXENT was used in further analyses. The logistic output of

MAXENT is a continuous map interpreted as the potential distribution of the species studied in the area of interest based on the predicted environmental suitability from 0 (unsuitable conditions) to 1 (optimal conditions). We used a non-fixed threshold as recommended by Liu et al. (2005) and set the minimum training presence prediction value as presence/absence threshold.

We compared the expected occurrence (represented by the presence/absence prediction in the corresponding grid cell as derived from the SDM) with the observed occurrence (i.e. species presence/absence along each transect) for each species and tested the general deviance across all species using the χ^2-test. In addition, spearman rank correlations between the abundance information for each species for each transect and the corresponding predictions derived from the SDMs for the respective grid cells (i.e. the predicted environmental suitability for the respective butterfly species ranging from 0 to 1) were obtained. Calculations were conducted in R 2.15 (R development core team, 2012).

Results

The distribution of butterfly species in the study area was patchy and the number of occurrence records varied considerably between species and habitats. A total of 65 species were recorded during transect walks. The highest number of species (n = 59) was recorded in calcareous grasslands, most of which were protected areas. Fifty three of the 65 species of butterfly were recorded in vineyard fallows in cultivated landscapes. The frequency of detection of a species mostly depended on its rarity in this region, i.e. the number of records was positively correlated with the mean number of individuals per transect along which the species in question was present (r^2 = 0.38). The most frequent species was the Meadow Brown (*Maniola jurtina, n* = 858 individuals). More than 100 individuals were recorded of 15 species, 51-100 of eight species, 11-50 of 21 species and ten or fewer individuals of 21 species. The abundance data for all species recorded along all transects is given in Table 1.

The AUC values of the model's performance averaged across the set of 61 butterfly species analyzed (i.e. 4 of the 65 species were not modelled, due to insufficient occurrence records) was 0.785 (sd: 0.057). Therefore, the model can be considered as 'useful' for predicting the local presence or absence of a species according to the classification scheme adapted from Swets (1988) and modified by Araújo et al. (2005). The lowest AUC value for a species was that for *T. betulae* (AUC = 0.56, n = 12), i.e. it is not possible to reliably predict the distribution of this species in the study area, and highest for *L. dispar* (AUC = 0.93, n = 6), i.e. the prediction of the distribution of this species in the study area is reliable. There is no linear relationship between the number of occurrences and the performance of the model (r^2 = 0.003, p = 0.67), thus the distribution of common and widespread butterfly species, on average, were not better predicted by the model than

Table 1. Summary table for 61 species of butterflies for which abundance data was collected in the field and SDMs conducted (n locations: number of occurrence records used in the development of the model; AUC: Area Under the receiver operation characteristic Curve; sum abundance: recorded abundances of species during field surveys; % congruence: percentage of congruence between expected and observed presence of species, r: spearman rank correlation coefficient; p: p-value of spearman rank correlation)

species	n locations	Test AUC	Sum abundance	% congruence	*r*	*p*
A. aglaja	32	0.72	59	78.6	0.27	0.354
A. cardamines	40	0.78	60	92.9	-0.12	0.674
A. crataegi	25	0.80	22	42.9	0.30	0.298
A. hyperanthus	63	0.78	326	100.0	0.45	0.104
A. ilia	5	0.78	1	85.7	0.10	0.726
A. iris	18	0.68	5	28.6	0.36	0.208
A. levana	53	0.80	25	78.6	-0.31	0.283
A. paphia	52	0.79	22	71.4	0.03	0.928
B. dia	46	0.81	29	28.6	-0.15	0.612
B. ino	17	0.66	2	14.3	-0.10	0.730
B. selene	26	0.86	2	57.1	0.42	0.133
C. alceae	21	0.82	3	50.0	0.46	0.097
C. alfacariensis	41	0.81	2	92.9	0.45	0.109
C. arcania	51	0.78	139	92.9	0.72	**0.003**
C. argiolus	30	0.84	17	71.4	0.19	0.517
C. hyale	64	0.79	45	71.4	-0.25	0.397
C. minimus	33	0.78	81	50.0	0.36	0.206
C. palaemon	32	0.82	1	7.1	-0.45	0.109
C. pamphilus	126	0.76	272	100.0	0.57	**0.033**
C. rubi	54	0.84	54	78.6	0.62	**0.018**
C. semiargus	57	0.76	61	85.7	-0.08	0.776
E. medusa	40	0.82	2	7.1	0.45	0.109
E. tages	56	0.80	7	14.3	-0.21	0.478
G. rhamni	73	0.80	35	85.7	0.68	**0.007**
I. lathonia	58	0.76	30	85.7	-0.63	**0.017**
L. camilla	16	0.84	6	78.6	0.53	**0.049**
L. dispar	6	0.93	2	64.3	-0.17	0.571
L. maera	7	0.63	1	92.9	0.45	0.109
L. megera	78	0.78	36	71.4	-0.60	**0.023**
L. phlaeas	42	0.79	17	71.4	0.04	0.897
L. sinapis	71	0.76	118	100.0	0.03	0.911
L. tityrus	54	0.79	10	42.9	0.30	0.303
M. athalia	23	0.78	48	64.3	0.25	0.392
M. aurelia	24	0.77	5	21.4	0.07	0.800
M. cinxia	15	0.82	13	57.1	-0.13	0.646
M. diamina	21	0.89	3	85.7	0.24	0.414
M. galathea	93	0.77	805	100.0	0.17	0.557
M. jurtina	123	0.78	857	100.0	-0.01	0.976
N. c-album	28	0.81	13	64.3	0.23	0.432
N. io	74	0.78	58	92.9	-0.01	0.976
N. polychloros	18	0.76	10	50.0	-0.25	0.380
N. quercus	13	0.90	2	85.7	0.25	0.382
N. urticae	88	0.78	79	100.0	0.17	0.568
O. sylvanus	43	0.77	120	78.6	-0.26	0.364
P. aegeria	44	0.80	17	57.1	0.26	0.376
P. bellargus	33	0.86	1	92.9	-0.24	0.407
P. brassicae	69	0.76	56	92.9	-0.21	0.467
P. coridon	68	0.79	335	28.6	0.05	0.856
P. icarus	119	0.78	226	100.0	-0.02	0.958
P. machaon	56	0.75	21	85.7	0.19	0.526
P. malvae	43	0.83	24	85.7	0.38	0.186
P. napi	98	0.77	103	100.0	-0.18	0.542
P. rapae	91	0.76	512	100.0	-0.34	0.233
S. pruni	23	0.76	16	78.6	0.13	0.664
S. sertorius	31	0.81	3	21.4	0.03	0.909
T. acteon	55	0.79	2	21.4	0.36	0.205
T. betulae	12	0.56	12	57.1	0.30	0.297
T. lineola	51	0.76	419	100.0	0.06	0.834
T. sylvestris	59	0.76	302	85.7	0.20	0.502
V. atalanta	46	0.76	16	78.6	-0.06	0.848
V. cardui	68	0.77	12	57.1	0.33	0.247

local and rare taxa. However, the variance of the predictive power was high for species for which there were few records of occurrence (Fig. 2), meaning that the degree of uncertainty of the model's predictions for a species increased as the numbers of records of occurrence of this species decreased.

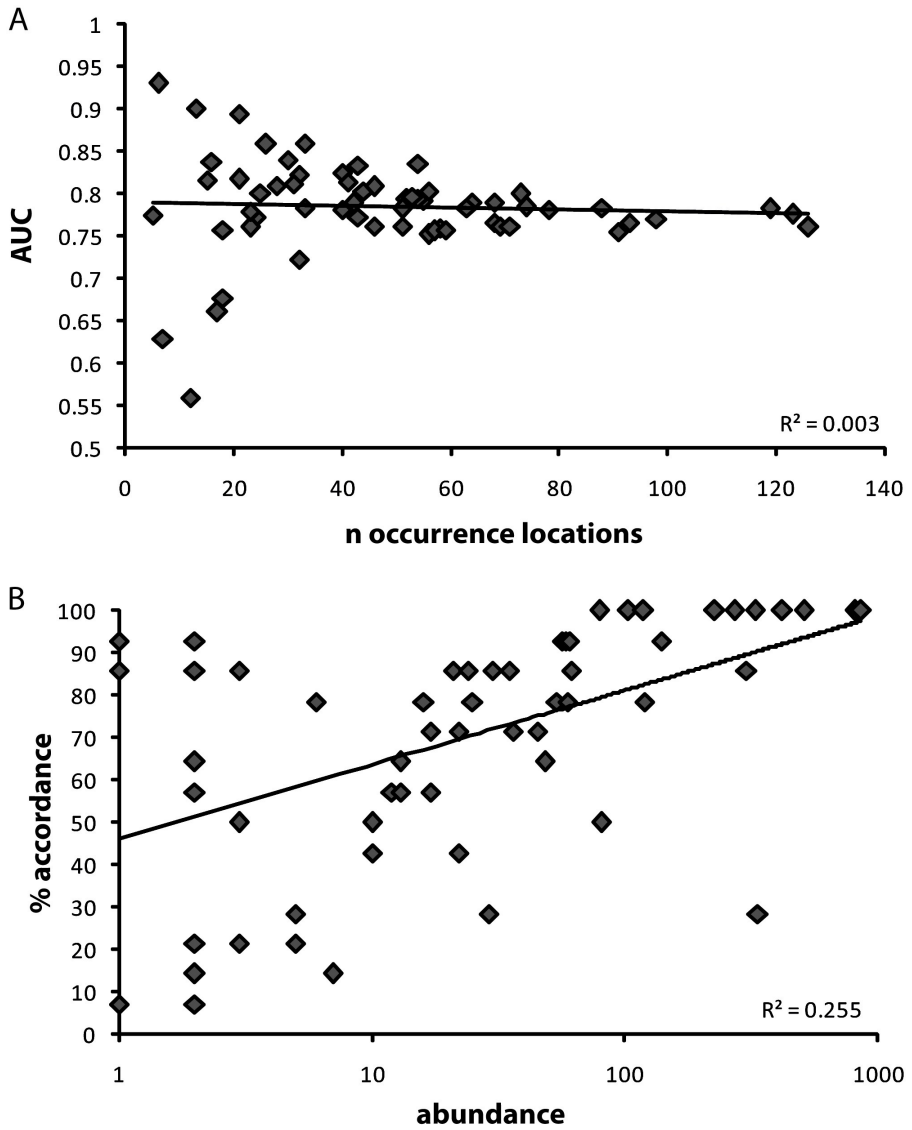

Fig. 2. The relationships between A) the AUC values (Area Under the receiver operation characteristic Curve, AUC) and number of occurrences and B) % accordance (expected / observed presence) and observed abundance.

The observed butterfly species occurrence (i.e. presence/absence) along the 14 transects differed significantly from the model's predictions for the corresponding grid cells ($\chi^2 = 47.08$, df = 1, $p < 0.0001$). Thus, the model was not able to predict the presence or absence of butterfly species along transects. The percentage of congruence between expected (i.e. modelled) and observed presence was highest for common species that were abundant in the area (e.g. *M. jurtina, P. rapae, P. icarus*

and *P. pamphilus*) and decreased from species that were abundant to those that were scarce (Fig 2b, $r^2 = 0.255$, $p = 0.002$). However, the occurrence of a few rather rare species (e.g. *H. comma, A. iris, M. diamina* and *M. aurelia*) was well predicted, as the model predicted mostly species absence. For most species there was no correlation between abundance and the model's prediction tested using spearman rank correlation. However, for five species (i.e. *C. arcania, C. pamphilus, C. rubi, G. rhamni* and *L. camilla*) there are significant correlations with the amount of explained variance ranging from 30 to 66% (Table 1). Thus, the model can be used to predict the local abundance of these species. On the other hand, the correlation was significantly negative for *I. lathonia* and *L. megera*, and therefore it is not possible to use this model for predicting the local abundance of these two species.

Discussion

The use of bioclimatic data for modelling the distributions of species has recently become more common in ecological research (e.g. Franklin, 2009). Some studies even link predictions derived from SDMs with other ecological patterns like productivity (Brambilla & Ficetola, 2012) or species abundance (Pearce & Ferrier, 2001; VanDerWal, 2009; Huntley et al., 2012). However, there are no such studies on invertebrates or on the use of state-of-the-art variable sets for such analyses. Therefore, this study aimed to determine whether species distribution models (SDMs) based on fine-scale bioclimatic variables can be used to forecast species specific abundance patterns for butterflies in a heterogeneous landscape.

In general, both the simple presence/absence predictions and observations for specific sites and more specifically the forecast of species abundance and that of the prediction for the corresponding grid cells where transects were located differed greatly. Consequently, our data support, with a few exceptions, the contention that species abundance of butterflies cannot be predicted using models based on bioclimatic variables recorded at this scale in central Europe. Even a reliable prediction of presence or absence of a species was impossible. Thus, it is likely that fine-scale bioclimatic data with a resolution of 30 arc seconds is too coarse, in terms of representing landscape features that might be responsible for species occurrence (Brambilla et al. 2009, Cord & Rödder 2011). Moreover, depending on the geographical extent of the study, the use of variables at this resolution might blur model predictions. Thus, local factors might have masked the effects of the climatic variables used.

It is evident, however, that the AUC values, which are measures of model quality, indicated a good fit in most cases (Table 1, Fig 2a). The use of this statistic for discriminating between models has been often criticized in the past (e.g. Lobo et al. 2008, Jiminez-Valverde 2011), but because of the lack of an alternative measure (Baldwin 2009, but see Hijmans 2012) it is still widely used in niche

modelling studies. In this study, the AUC values did not reflect the presence/absence situation of butterfly species at the study sites investigated, because the factors included in the model do not reflect the finer scale variation (see below) that is important in determining the distribution of the butterflies. Therefore, we recommend careful and critical use of AUC values when they alone are used to determine the goodness of fit of a model's predictions with reality.

Although mesoclimatic conditions strongly influence regional distribution patterns, their importance at finer (i.e. local) scales is considerably reduced as other factors become the key determinants of the occurrence and abundance of species. Structural and ecological parameters are especially important at the micro-scale, as butterflies often need highly complex habitat conditions for oviposition, larval development, growth of larval food-plants and imagos' nectar-plants (e.g. Settele et al. 1999, Asher et al. 2001). These conditions are often strongly influenced by the nature of the soil and the use of the land by humans (Schmitt & Rákosy, 2007; Dover & Settele, 2009). It is not possible to include these parameters in SDMs as such fine scale data is not available for large areas (but see Cord & Rödder, 2011; Brambilla & Ficetola, 2012; Pfeifer et al., 2012). In this context, it is also necessary to emphasize the importance of the microclimatic conditions that are markedly influenced by human activities, such as the construction of traditional stone walls, ecologically rich waysides and slopes, hedgerows and small eroded patches. All of these provide suitable conditions for butterflies at places not predicted by the SDMs because they considerably increase temperature and modulate humidity at a very local scale of some few square metres. This is far below the spatial resolution of the climatic data currently used in model construction so that it is necessary to determine the abundance of butterflies and other invertebrates with complex habitat requirements by means of time- and labour-intensive field work, and this likely to continue to be the case for the foreseeable future.

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Biodiversität und Klimawandel – Auswirkungen auf geschützte und schutzwürdige Arten (Amphibien und Reptilien)

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Beschreibung der Artengruppe

Amphibien und Reptilien zählen zu den wechselwarmen Wirbeltieren; ihre Aktivität und physiologische Leistungsfähigkeit hängen somit stark von der Umgebungstemperatur ab. Temperaturextreme wirken sich negativ auf die Fitness der Tiere aus, daher fehlen sie in den Kaltklimaten der Erde. Temporäre Kältephasen, ebenso wie Hitzeperioden, können Amphibien und Reptilien durch Überwintern bzw. Übersommern überdauern (Huey 1983, Duellman & Trueb 1986). Amphibien sind – im Gegensatz zu Reptilien – wegen ihrer zumeist aquatischen Eier und Larven bzw. ihrer durchlässigen Haut außerdem stark von der Verfügbarkeit von Süßwasser abhängig.

Bei beiden Gruppen hat vor allem die Temperatur Einfluss auf die Dauer der Embryogenese bzw. Larvalentwicklung sowie das Größenwachstum und die Reproduktionsfähigkeit. Temperatur und/ oder Niederschlag sind oftmals auch Auslöser für die Fortpflanzung. Darüber hinaus wird bei einigen Reptilien das Geschlecht der Nachkommen durch die Umgebungstemperatur während der Embryonalphase bestimmt.

Das Klima hat folglich für die Verbreitung, Fitness und Phänologie von Amphibien und Reptilien eine große Bedeutung. Einhergehend mit dem eher geringen Ausbreitungspotenzial dieser Tiere ist zu vermuten, dass sich rasche Klimaveränderungen negativ auf sie auswirken können (vgl. Henle et al. 2010, Rödder & Schulte 2010, Sinervo et al. 2010). Bei der Bewertung von beobachteten Veränderungen an Populationen sollten jedoch auch andere Faktoren, wie z. B. die Landnutzung, einbezogen werden. Beide Artengruppen zeigen für eine Vielzahl von Umweltveränderungen eine hohe Anfälligkeit. Dies macht sie zu viel genutzten Indikatororganismen für die Bewertung von Lebensräumen und zu wichtigen Gruppen für den Arten- und Biotopschutz. In Europa spielen sie beispielsweise für die Denition von Schutzgebieten nach der Fauna- Flora-Habitat- (FFH) Richtlinie eine besondere Rolle. Dennoch stellt sich die Frage, ob sich Amphibien und Reptilien auch als Indikatororganismen für die Auswirkungen von Klimaveränderungen eignen.

Datenverfügbarkeit

Es gibt derzeit kein flächendeckendes Monitoringprogramm, das die Bestände von Amphibien und Reptilien bundesweit erfasst. Die meisten Informationen über den Zustand der Arten stammen aus regionalen Tierartenerfassungsprogrammen (TEAP, bspw. Niedersachsen). Auf nationaler und europäischer Ebene werden zudem Bestandsdaten aus den Berichten über den Zustand von Arten und Lebensräumen nach der EU-Naturschutzrichtlinie (FFH-Richtlinie) zu einem aktuellen Verbreitungsbild von Amphibien und Reptilien zusammengefügt.

Für Deutschland existieren daneben auch die Daten der Roten Listen der Amphibien und Reptilien (s.u.), die durch verschiedene Monitoringprogramme gespeist werden. Informationen über Verbreitung und Schutzstatus gefährdeter Arten lassen sich im Weltmaßstab auch über die IUCN Red List of reatened Species (www.iucnredlist.org) einholen. Weitere Datenquellen sind Forschungsvorhaben, die beispielsweise Auswirkungen invasiver Arten oder des Amphibien-Chytridpilzes untersuchen, wie das EU-Projekt RACE (Risk Assessment of Chytridiomycosis to European Amphibian Biodiversity; http://www.bd-maps.eu/). Naturschutzorganisationen wie der NABU dokumentieren bundesweit Amphibienwanderungen und führen interaktive Schutzzaun-Datenbanken im Internet, die neben Monitoringprogrammen die regionale Verbreitung und Häugkeit der Arten zeigen.

Ein Verbreitungsatlas der Amphibien und Reptilien Deutschlands (Günther 1996), der umfangreiche Artmonographien von 21 Amphibien- und 14 Reptilienarten umfasst, erschien 1996 und wurde im vergangenen Jahr neu aufgelegt. Zusätzlich bestehen für eine Reihe von Amphibien und Reptilien Artmonographien, die den aktuellen Kenntnisstand zusammenfassen (z. B. Schulte 2008, Thiesmeier et al. 2009, Blanke 2010) sowie regionale Werke zur Verbreitung von Amphibien und Reptilien in Deutschland (z. B. Laufer et al. 2007, Zöphel & Steens 2002), die in unregelmäßigen Abständen aktualisiert werden. Eine verstärkte Datensammlung über das GBIF-(Global Biodiversity Information Facility; www.gbif.org) Portal wird angestrebt. Auch andere internetbasierte Plattformen sammeln meist zufällig aufgenommene Daten zu Verbreitung und Häufigkeit von Amphibien und Reptilien und könnten in Zukunft verstärkt für Auswertungen genutzt werden.

Naturschutzfachliche Bedeutung der Artengruppe

Alle 22 vorkommenden Amphibien- und alle 13 Reptilienarten sind in der Bundesartenschutzverordnung (BArtSchV) enthalten und stehen nach §7 und § 39 des Bundesnaturschutzgesetzes unter besonderem Schutz. Die BArtSchV (§1 Abs. 1) stuft alle einheimischen Amphibien- und Reptilienarten als „besonders geschützt“ ein; zusätzlich gelten zwei als „streng geschützt“.

Eine wichtige Grundlage für den Artenschutz ist die Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands (Kühnel et al. 2009a,b). Diese stuft bei den Amphibien sieben Arten als „gefährdet“ bis „vom Aussterben bedroht“ ein (Kategorien 1 – 3); eine weitere wird in der Kategorie „Gefährdung unbekannten Ausmaßes“ geführt. Bei den Reptilien stehen acht Arten in den Kategorien 1 – 3 (Kühnel et al. 2009a,b). Grundlage dieser Einstufungen sind die Parameter Arealverlust, Habitatrückgang, Populationsanzahl und -größe. Sie sind ausreichend, auch mögliche Auswirkungen von Klimaveränderungen auf Amphibien und Reptilien zu erfassen, da diese

Einfluss auf die erwähnten Parameter ausüben könnten. Festzuhalten ist aber, dass der Klimawandel potenziell nicht nur die derzeit gefährdeten, sondern alle einheimischen Amphibien und Reptilien betrifft, so dass bald Bedarf für eine Überarbeitung der Roten Liste bestehen könnte. In diesem Zusammenhang sind die Arten hervorzuheben, für die Deutschland eine besondere Verantwortung besitzt. Hierzu zählen solche, deren Gesamtareal oder Arealzentrum zu großen Teilen auf Deutschland entfällt sowie solche, die Relikt-/ Vorpostenvorkommen hierzulande aufweisen (Steinicke et al. 2002).

Über die nationale Gesetzgebung hinaus stehen von den in Deutschland vorkommenden Amphibien- und Reptilienarten 16 bzw. 8 in den Anhängen II, IV und V der FFH-Richtlinie. Anhang II erfordert die Ausweisung von Schutzgebieten (NATURA 2000), während sich die Anhänge IV und V direkt auf den Schutz von Arten beziehen. Diese beiden Anhänge können daher anhand der Reaktionen von Arten auf den Klimawandel ausgelegt werden. Das NATURA 2000-Netzwerk ist hingegen nicht auf den Klimawandel ausgerichtet (Ssymanck et al. 1998).

Veränderungen: Beobachtete Veränderungen anhand von wissenschaftlichen Untersuchungen oder Monitoring

Arten- und Populationsrückgänge

Seit mehreren Jahrzehnten wird weltweit ein eklatanter Rückgang an Amphibien beobachtet (Stuart et al. 2008). Spärliche Angaben zu den Reptilien zeigen regional und lokal ähnliche Trends (z. B. Gibbons et al. 2000). Hierfür wird u.a. der Klimawandel verantwortlich gemacht, allerdings v.a. in tropischen Regionen (z. B. Whiteld et al. 2007).

In Bezug auf Amphibien sehen einige Autoren klimatische Veränderungen im Zusammenspiel mit anderen Ursachen als bedeutend für Artensterben bzw. Populationseinbrüche an. Collins & Storfer (2003) stellen den Klimawandel zu den „neuen“ Bedrohungen. Sie diskutieren Wechselwirkungen zwischen „neuen“ und „alten“ Bedrohungen und halten einen Zusammenhang für möglich zwischen dem Klimawandel und:

(1) der Fragmentierung und Homogenisierung der Landschaft einschließlich der verminderten Erreichbarkeit und der Zerstörung von Lebensräumen (vgl. z. B. Becker et al. 2007, 2009a)
(2) Interaktionen mit gebietsfremden etablierten Arten, wie das Beispiel sich ausbreitender nordamerikanischer Wasserschildkröten in Europa zeigt (Cadi & Joly 2003). Collins & Storfer (2003) gehen auch von Wechselwirkungen aus zwischen Klimawandel und:
(3) dem Einsatz von Pestiziden in der Landwirtschaft. Chen & McCarl (2001) prognostizieren, dass der Klimawandel in vielen landwirtschaftlichen Kulturen zu verstärktem Pestizideinsatz führen kann. Es ist eine Reihe von negativen Effekten von Agrochemikalien auf Amphibienlarven bekannt (vgl. Mann et al. 2009).

(4) dem Einfluss sich ausbreitender Infektionskrankheiten. Hier ist v.a. die Chytridiomykose zu nennen, eine o tödliche Hautpilzerkrankung, die durch den Amphibien-Chytridpilz (*Batrachochytrium dendrobatidis*) verursacht wird. Bosch et al. (2007) vermuten, dass Amphibien- Massensterben in Spanien mit ungewöhnlichen Klimaereignissen und Chytridiomykose im Zusammenhang stehen.

In Deutschland unterliegen kurz- und langfristig ca. 60% der Amphibienarten einem mäßigen bis sehr starken Rückgang. Bei den Reptilienarten zeigen kurzfristig sogar nahezu 70% und langfristig alle Arten Rückgänge (Kühnel et al. 2009a, b). Innerhalb der Amphibien sind bei 90% und innerhalb der Reptilien bei 77% der lokal beobachteten Rückgänge die wirkenden Risikofaktoren nicht feststellbar (Kühnel et al. 2009a, b), was auf mögliche Wechselwirkungen, wie unter (1) bis (4) angesprochen, schließen lassen könnte. Die Rolle von Klimaveränderungen bleibt zum jetzigen Zeitpunkt reine Spekulation. Festzuhalten ist jedoch Folgendes:

Zu (1) Klimaveränderungen können zum lokalen Erlöschen von Populationen führen. Angesichts der projizierten Geschwindigkeit des Klimawandels ist zu befürchten, dass die Migrationsfähigkeit vieler Arten nicht ausreicht, um in einer fragmentierten Landschaft neue, klimatisch günstige Habitate zu besiedeln. Das kann zu genetischer Erosion führen, wie Fallstudien am Laubfrosch (*Hyla arborea*) und der Wiesenotter (*Vipera ursinii*) aufzeigen (Ferchaud et al. 2011, Luquet et al. 2011).

Zu (2) Als invasive Arten in Deutschland gelten der Amerikanische Ochsenfrosch (*Lithobates catesbeianus*), die Mauereidechse (*Podarcis muralis*), die Europäische Sumpfschildkröte (*Emys orbicularis*) sowie neuweltliche Schmuckschildkröten der Gattung *Trachemys*. Alle genannten Arten gelten aus verschiedensten Gründen als Gefahr für die einheimische Fauna (z. B. Ficetola et al. 2010, Schulte et al. 2011). Unter Konkurrenzbedingungen im Labor konnte beispielsweise ein negativer Effekt von Schmuckschildkröten auf die Körpermassen und Mortalitätsraten heimischer Sumpfschildkröten nachgewiesen werden (Cadi & Joly 2004).

In Deutschland existieren mindestens 83 eingeschleppte Mauereidechsen-Vorkommen unterschiedlichster Herkunft (Schulte et al. 2011). Bei gebietsfremden Populationen konnte ein bis zu vier Wochen früherer Schlupf der Jungtiere im Vergleich zu heimischen Populationen beobachtet werden (U. Schulte, G. Deichsel, unpubl.). Innerhalb von Kontaktzonen in Baden-Württemberg konnte eine weiträumige Hybridisierung zwischen heimischen Mauereidechsen und zahlreichen italienischen Linien nachgewiesen werden (Schulte et al. unpubl.). Das Resultat ist eine schnelle genetische Assimilation der heimischen Population.

Zu (3) Intensiv landwirtschaftlich genutzte Flächen stellen in Deutschland kein bedeutendes Habitat für Amphibien oder Reptilien dar. Jedoch werden extensiv genutzte Saumbiotope, Gewässer

oder zeitweise überflutete Felder durchaus angenommen (z. B. Flottmann & Laufer 2004, Sowig 2007). Da etwa die Hälft der Fläche Deutschlands landwirtschaftlich genutzt wird, kann von einem signifikanten Einfluss von Pestiziden auf deutsche Amphibien- und Reptilienpopulationen ausgegangen werden.

Zu (4) Der Amphibien-Chytridpilz kommt nahezu flächendeckend in Deutschland bei fast allen Arten vor (Ohst et al. 2011); einzige Ausnahme ist der Alpensalamander (*Salamandra atra;* unpubl. Ergebnisse der Autoren). Massensterben, wie etwa in Spanien sind bisher nicht aufgetreten. Es ist jedoch nicht auszuschließen, dass Populationsrückgänge, wie bei der Geburtshelferkröte (*Alytes obstetricans*) im Zusammenhang mit der Chytridiomykose stehen (unpubl. Ergebnisse der Autoren).

Arealveränderungen

Arealverschiebungen in Richtung der Pole oder in größere Höhenlagen, die auf den Klimawandel zurückzuführen sind, wurden weltweit bereits für viele Arten propagiert (z. B. Araújo et al. 2006, Hodkinson et al. 2011). Dies steht im Zusammenhang mit der fundamentalen Klimanische einer jeden Art, die hier limitierend wirkt. Dies kann z. B. Die Maximaltemperatur des wärmsten Quartals oder Monats sein, die die Entwicklung von Reptilieneiern bestimmt (z. B. Rödder et al. 2009b). Auch plötzliche Kälteeinbrüche während der Kaulquappenentwicklung bei früh laichenden Amphibien können limitierend wirken. Bei den meisten Amphibien und Reptilien ist jedoch wenig über die limitierenden Klimaparameter bekannt. Aufgrund der relativ großen Gesamtareale der einheimischen Arten kann jedoch angenommen werden, dass sie generell eine große Nischenbreite aufweisen.

In Deutschland erreichen neun Amphibien und sechs Reptilienarten ihre Arealgrenzen (Kühnel et al. 2009a, b): Alpensalamander (*Salamandra atra*), Bergmolch (*Ichthyosaura alpestris*), Fadenmolch (*Lissotriton helveticus*), Feuersalamander (*Salamandra salamandra*), Geburtshelferkröte (*Alytes obstetricans*), Gelbbauchunke (*Bombina variegata*), Springfrosch (*Rana dalmatina*), Rotbauchunke (*Bombina bombina*), Wechselkröte (*Pseudepidalea viridis*); Äskulapnatter (*Zamenis longissimus*), Aspisviper (*Vipera aspis*), Mauereidechse (*Podarcis muralis*), Östliche Smaragdeidechse (*Lacerta viridis*), Westliche Smaragdeidechse (*Lacerta bilineata*) und Würfelnatter (*Natrix tessellata*). Folgende Arten besitzen in Deutschland Relikt-/Vorpostenvorkommen, was eine besondere nationale Verantwortung bedeutet (Steinicke et al. 2002, Kühnel et al. 2009a, b): Moorfrosch (*Rana arvalis*), Springfrosch (*Rana dalmatina*); Äskulapnatter (*Zamenis longissimus*), Europäische Sumpfschildkröte (*Emys orbicularis*), Östliche Smaragdeidechse (*Lacerta viridis*), Westliche Smaragdeidechse (*Lacerta bilineata*) und Würfelnatter (*Natrix tessellata*). Bei keiner dieser, noch bei einer anderen Amphibien- oder

Reptilienart Deutschlands liegen bislang Hinweise über erfolgte oder sich vollziehende klimabedingte Arealveränderungen vor (Henle et al. 2010, Rödder & Schulte 2010). Es handelt sich jedoch um die Amphibien- und Reptilienarten, bei denen sich am ehesten Auswirkungen einer Arealverschiebung in Deutschland nachweisen ließen. Bis auf dem aktuell ungefährdeten Springfrosch, der aufgrund dieser Tatsache als schutzwürdige Art bezeichnet werden kann, sind alle diese Arten geschützt. Ihre Bestände sollten in Zukunft verstärkt überwacht werden. Gleiches gilt für Arten, deren Areal schwerpunktmäßig in Deutschland liegt, womit sich ebenfalls eine besondere nationale Verantwortlichkeit ergibt: Bergmolch (*Ichthyosaura alpestris*), Feuersalamander (*Salamandra salamandra*), Gelbbauchunke (*Bombina variegata*), Kreuzkröte (*Epidalea calamicalamita),* Nördlicher Kammmolch (*Triturus cristatus*) und Teichfrosch (*Pelophylax* kl. *esculentus*). Die als ungefährdet geltenden Arten Bergmolch, Feuersalamander und Teichfrosch qualifiziert das als schutzwürdige Arten, sofern man von einer Beeinträchtigung durch den Klimawandel ausgehen kann.

Phänologie, Demographie und Fitness

Wie eingangs erwähnt, sind bei Amphibien und Reptilien die Dauer von Winter- bzw. Sommerruhe sowie bei Amphibien die Laichzeiten eng an klimatische „trigger“ geknüpft. Gerade bei Letzteren konnte in den gemäßigten Breiten verschiedentlich ein Trend zu verfrühten Laichaktivitäten als offensichtliche Folge einer Temperaturerhöhung in Winter und Frühjahr beobachtet werden. Überdurchschnittlich warme Temperaturen während der Larvalphase können auch zu einem früheren Eintritt der Metamorphose, einhergehend mit einer reduzierten individuellen körperlichen Fitness, Überlebensfähigkeit und einem geringeren Reproduktionserfolg führen (z. B. Jakob et al. 2002). Jedoch sind die Beobachtungen und Trends abhängig von der Art und der Region (vgl. Beebee 1995) und daher keinesfalls zu pauschalisieren. Ein genereller Temperaturanstieg kann möglicherweise sogar positive Auswirkungen auf die Embryonalentwicklung bei Arten in kälteren Regionen haben (vgl. Arribas & Galán 2005).

Auch bei europäischen Reptilien konnte gezeigt werden, dass sie die Eiablage in Jahren mit warmen Frühjahrsmonaten früher vollzogen als in Jahren mit kaltem Frühjahr (z. B. Olsson & Shine 1997). Die Erhöhung der Temperatur kann zudem zu einer früheren und längeren Aktivität im Jahr führen (Moreno-Rueda et al. 2009).

Zu den Amphibien Deutschlands liegen regional ebenfalls Beobachtungen bezüglich einer im Schnitt etwa um drei Wochen früheren Fortpflanzung vor (Münch 1999). Hierzu zählen Erdkröte (*Bufo bufo*) und Grasfrosch (*Rana temporaria*), aber auch Schwanzlurche, wie Teichmolch (*Lissotriton vulgaris*) und Bergmolch (*Ichthyosaura alpestris*). Der Nördliche Kammmolch (*Triturus cristatus*), für den Deutschland „in hohem Maße verantwortlich“ ist, weil 10 – 30 % seines

Areals, zugleich Teil seines Arealzentrums, auf Deutschland entfallen (Kühnel et al. 2009b), wanderte 2001 im Mittel 25 Tage eher an als 21 Jahre zuvor (Münch 2001).

Ein Einfluss des Klimawandels auf die Fitness adulter Amphibien und Reptilien wird ebenfalls diskutiert. Die Umgebungstemperatur beeinflusst maßgeblich die Leistungsfähigkeit und Aktivitätsmuster dieser wechselwarmen Tiere. Klimaerwärmung in den Aktivitäts- und Ruhephasen kann zu einer Beeinflussung des Stoffwechsels führen. Wärmere Winter führen bei den Amphibien und Reptilien zu erhöhtem Energieverbrauch und folglich zu reduzierter Fitness. Dies kann wiederum mit einem geringeren Reproduktionserfolg gekoppelt sein (Reading 2007).

So besteht während des Winters für Amphibien und Reptilien durch Kälteeinbrüche ein verstärktes Risiko, vor allem in sonst eher milden Wintern. Die Tiere sind aufgrund warmer Witterung dann teilweise schon aus ihren tiefen Winterquartieren gekommen, so dass Massensterben die Folge sein kann (Henle 1998, Anholt et al. 2003). Bei der Kreuzotter (*Vipera berus*) wurden in der Vergangenheit bundesweite Bestandseinbrüche unter anderem in Verbindung mit ungewöhnlich warmen Tagen und frostigen Nächten im Februar/März 2003 diskutiert (Podloucky et al. 2005).

Im Zusammenhang mit dem Klimawandel muss vertieft werden, dass bei einigen Reptilien das Geschlecht über die Temperatur während der Embryonalentwicklung bestimmt wird. Ein ausgeglichenes Geschlechterverhältnis ist für die Aufrechterhaltung einer vitalen Population essenziell und wird in einem bestimmten Temperaturbereich erreicht. Je schmaler dieser angelegt ist, umso anfälliger ist eine Art für klimatische Veränderungen (Hulin et al. 2009, Mitchell & Janzen 2010). Die Gefahr für eine durch den Klimawandel bedingte Verschiebung des Geschlechterverhältnisses innerhalb einer Population ist jedoch bisher nicht belegt, da auch natürliche Temperaturschwankungen sehr unterschiedliche Auswirkungen auf die Geschlechterentwicklung bei Reptilien zeigen (Janzen 1994). Die einzige heimische Reptilienart, für die eine temperaturabhängige Geschlechtsdetermination nachgewiesen werden konnte, ist die Europäische Sumpfschildkröte (*Emys orbicularis*). In einer Population in Deutschland wurde über Jahre hinweg ein erhöhter Anteil weiblicher Individuen beobachtet. Neben geschlechtsspezifisch unterschiedlicher Mortalität und Emigration könnte diese Beobachtung durch den Klimawandel erklärt werden (Schneeweiß et al. 1998).

Vorhergesagte Veränderungen anhand von Modellierungen und Experimenten

Projektionen zur zukünftigen Verbreitung existieren bereits für eine Reihe von europäischen Amphibien und Reptilien (z. B. Araújo et al. 2006). Hierbei lassen die Modelle meist starke Einbußen im Mittelmeerraum befürchten sowie ein Zurückziehen kälteliebender Arten in höhere Lagen, wobei sich die potenziellen Areale vieler Arten auch nach Norden ausweiten könnten. Neben

Veränderungen in den Temperaturen scheinen für Amphibien veränderte Niederschlagsregime und Extremwetterereignisse die stärksten Auswirkungen zu haben.

Aufgrund von Modellprojektionen zählen in Deutschland bei den Amphibien z. B. der Europäische Laubfrosch (*Hyla arborea*), der Springfrosch (*Rana dalmatina*) und die Geburtshelferkröte (*Alytes obstetricans*) zu den potenziellen Gewinnern des Klimawandels. Dagegen projizieren Modelle größere mögliche Arealverluste in Deutschland z. B. bei der Rotbauchunke (*Bombina bombina*), dem Moorfrosch (*Rana arvalis*) und dem Kleinem Wasserfrosch (*Pelophylax lessonae*). Bei den in Deutschland vorkommenden Reptilien zeigt sich ein ähnliches Bild. Hier wären z. B. die Westliche Smaragdeidechse (*Lacerta bilineata*) und die Mauereidechse (*Podarcis muralis*) als potenzielle Gewinner zu nennen. Potenzieller Arealverlust unter Klimawandels zeigt sich in den Modellprojektionen z. B. der Schlingnatter (*Coronella austriaca*) (A. Jaeschke, unpubl.). Ebenso sind kälteadaptierte Arten wie die Kreuzotter (*Vipera berus*) vermutlich negativ vom Klimawandel betroffen.

Neben den reinen Arealveränderungen könnten aber einige andere Faktoren indirekt auf Amphibien wirken. So könnte der durch Klimawandel evtl. begünstigte Einsatz von Organophosphat-Pestiziden, die immunsuppressiv auf Wirbeltiere wirken, diese nach Galloway & Handy (2003) für Parasiten und Krankheiten anfälliger machen. In Zukunft ist zudem die Anpflanzung herbizidresistenter GVP absehbar, so dass nicht-selektive Herbizide gegen Ackerunkräuter gespritzt werden können (Duke & Powles 2008). Langfristig könnten sich allerdings bei nicht nachhaltigem Anbau Resistenzen ausbilden (Powles & Wilcut 2008), welche zusätzlich mit selektiven Herbiziden bekämpft werden müssten und somit eventuell sogar zu einer Mehrbelastung von Amphibien und Reptilien in Deutschland mit Pestiziden führen könnten. Zudem scheinen bestimmte Totalherbizide selbst bei umweltrelevanten Konzentrationen zu den auf Amphibien am schädlichsten wirkenden Pestiziden zu gehören (z. B.Williams & Semlitsch 2010).
Auch die negativen Auswirkungen durch invasive Arten (z. B. Amerikanischer Ochsenfrosch *Lithobates catesbeianus*, gebietsfremde Mauereidechsen (*Podarcis muralis*) und neuweltliche Schmuckschildkröten der Gattung *Trachemys*) könnten sich verstärken, da diese unter dem Klimawandel eine günstige Prognose haben (z. B. Ficetola et al. 2010, Schulte et al. 2011). Im Falle invasiver Schmuckschildkröten könnte ein Temperaturanstieg zur Ausbreitung in bisher klimatisch ungünstige Regionen Deutschlands führen (Rödder et al. 2009a) und den Druck auf indigene Arten verstärken.

Der Klimawandel könnte aber auch Auswirkungen auf die Phänologie von Amphibien und Reptilien haben, so z. B. bei der Europäischen Sumpfschildkröte, für die ein Temperaturanstieg im späten Frühjahr eine Verschiebung des Geschlechterverhältnisses auf Kosten der Männchen zur Folge haben könnte (Schneeweiß et al. 1998). Wärmere Winter können bei den Amphibien und

Reptilien außerdem zu erhöhtem Energieverbrauch und folglich zu reduzierter Fitness führen. Dies kann wiederum mit einem geringeren Reproduktionserfolg gekoppelt sein.
Andere Forschungsarbeiten zeigen aber, dass der Klimawandel auch positive Auswirkungen zeigen könnte. So könnte ein Anstieg der Temperaturen im Frühsommer bei allen oviparen heimischen Reptilienarten (wie bereits innerhalb eingeschleppter Mauereidechsen-Populationen belegt, s.o.) einen früheren Schlupf der Jungtiere zur Folge haben, der generell die Chancen der Jungtiere für eine erfolgreiche Überwinterung steigert. Ähnlich kann ein Temperaturanstieg im Frühsommer auch bei heimischen ovoviviparen (eierlebendgebärenden) Reptilienarten, so eventuell bei der Kreuzotter (*Vipera berus*), der Schlingnatter (*Coronella austriaca*) oder der Waldeidechse (*Zootoca vivipara*), eine Beschleunigung der Embryonalentwicklung und damit einhergehend einen früheren Schlupf der Jungtiere zur Folge haben. Auch könnte z. B. eine verringerte klimatische Eignung für den Amphibien-Chytridpilz zu einer geringeren Belastung der einheimischen Amphibien führen (Rödder et al. 2010).

Diskussion: Wissenslücken und Forschungsbedarf sowie Ideen zur Verbesserung der Datenbasis als Entscheidungshilfe für Stakeholder

Obwohl international bereits viele Studien zu den Auswirkungen des Klimawandels auf Amphibien und Reptilien vorliegen, sind diese für Deutschland deutlich unterrepräsentiert. Wie die heimische Amphibien- und Reptilienfauna auf sich verändernde Temperaturen und Niederschlagsereignisse reagieren wird, ist noch weitestgehend ungeklärt. Erste mögliche Veränderungen wurden, wie oben beschrieben, bereits beobachtet, doch sind weitere Studien erforderlich, um diese mit dem Klimawandel in Verbindung bringen zu können. Zudem ist es notwendig, die einzelnen Wirkfaktoren artbezogen zu untersuchen. Hier gewinnen in Deutschland besonders Projekte an Bedeutung, die neben Verbreitungsdaten auch Daten zu phänologischen, demographischen und genetischen Anpassungen sowie zu sich ausbreitenden Pathogenen (z. B. der Amphibien-Chytridpilz) bei Amphibien und Reptilien hinzuziehen. Eine Ermittlung der artspezischen Klimasensitivität für die einheimische Fauna, etwa wie bei Foden et al. (2008) durchgeführt, scheint darüber hinaus als Basis für zukünftige Schutzbemühungen sinnvoll.

Daten zu Bestandsveränderungen und Arealverschiebungen sind für die Errichtung und Validierung von Schutzgebieten besonders wichtig. Verbreitungsmodelle bieten dabei nur bedingt verlässliche Prognosen, da sie zwar unter bestimmten Klimaszenarien potenzielle Areale für Arten vorhersagen, jedoch weitere Einflussfaktoren (vor allem biotische Interaktion) außer Acht lassen. Von großer Bedeutung ist, dass bei der Ausweisung von Schutzgebieten und deren Verknüpfung durch Korridore (etwa zwischen FFH-Gebieten) neben klimatischen Veränderungen sowohl die Ausbreitungsfähigkeit von Arten, als auch mögliche Veränderungen der Landnutzung berücksichtigt

werden.

Zwei Aspekte, die in Zukunft verstärkt Beachtung finden werden, sind Veränderungen in der Landwirtschaft durch den Einsatz gentechnisch veränderter Pflanzen (GVP) und Neozoen. Insbesondere der tatsächliche, langfristige Herbizideinsatz beim Anbau von GVP wird derzeit kontrovers diskutiert (Benbrook 2009). Inwieweit jedoch ein verstärkter Einfluss von GVP auf die Krankheitsanfälligkeit der Tiere besteht, bedarf der Klärung. Gebietsfremde Arten, besonders aus dem mediterranen Raum, die Modellvorhersagen zufolge dort zunehmend Arealverluste verzeichnen, könnten in Zentraleuropa zukünftig zu den „Gewinnern“ des Klimawandels zählen. Es besteht somit das Risiko, dass konkurrenzfähigere Arten einheimische Arten dabei zunehmend verdrängen. Um Auswirkungen von Neozoen auf die hiesigen Amphibien und Reptilien abzuschätzen, sind entsprechende Studien unumgänglich (z. B. Arealmodellierungen).

Weiterhin ist der Einfluss sich ausbreitender Infektionskrankheiten eine kontinuierliche Bedrohung, besonders für Amphibien. Massensterben bei Amphibien in Spanien wurden bereits in Zusammenhang mit ungewöhnlichen Klimaereignissen und Infektionen mit dem Amphibien-Chytridpilz gesetzt (z. B. Bosch et al. 2007). Ob eine Ausbreitung von Erregern durch den Klimawandel jedoch gefördert wird, ist Gegenstand der Forschung.

Festzuhalten ist, dass Veränderungen in Fitness, Phänologie und Verbreitung der Arten wahrscheinlich nicht auf Klimaveränderungen allein, sondern auf eine Kombination sich wandelnder Klima- und Umweltfaktoren zurückzuführen sein werden. Voraussetzung für zusätzliche Untersuchungen zu aktuellen Klimaeinflüssen auf Amphibien und Reptilien sowie Projektionen über potenzielle zukünftige Auswirkungen des Klimawandels auf beide Gruppen ist eine valide Datenbasis. Es besteht Potenzial zur Verbesserung der Datenlage für Untersuchungen zu Klimawandelauswirkungen auf Reptilien und Amphibien in Deutschland. Für ein Monitoring von Amphibien und Reptilien wurde bereits eine Richtlinie des Verbandes der Deutschen Ingenieure (VDI, Richtlinie 4333) verfasst, die genutzt werden könnte, um ein entsprechendes Monitoringprogramm, nicht nur vor dem Hintergrund der Bedrohungen durch invasive Arten oder Chytridiomykose, sondern auch durch Umweltveränderungen, zu initiieren. Darauf aufbauend könnten Veränderungen, nicht nur für einzelne Arten oder regional begrenzt, abgeschätzt werden, sondern bundesweit für alle Arten.

Indikatoren

Keine Amphibien- oder Reptilienart gilt derzeit als Indikator für Klimaveränderungen. Bedingt durch ihre Physiologie und Ökologie sind beide Artengruppen jedoch stark von den habitatbestimmenden Klimaparametern abhängig und es ist zu erwarten, dass sie zeitnah auf Klimaveränderungen reagieren. Veränderungen in der Umgebungstemperatur oder im

Wasserhaushalt können potenziell zu Anpassungsreaktionen bei den Tieren oder lokalen Aussterbeereignissen führen. Gemeinsam mit ihrem geringen Ausbreitungspotenzial begründen diese Eigenschaften die Eignung beider Tiergruppen als mögliche Klimaindikatoren. Jedoch gilt möglicherweise, dass weder für Amphibien noch für Reptilien der Klimawandel als alleiniger Faktor für Populationsveränderungen gelten wird. Beide Artengruppen zeigen für eine Vielzahl von Umweltveränderungen eine hohe Anfälligkeit, die viel eher als der Klimawandel oder in Verbindung mit ihm zum Tragen kommen, so dass Faktoren wie die Landnutzung bei der Bewertung einbezogen werden müssen.

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SUMMARY

Global change, i.e. climate and land use changes, severely impact natural ecosystems at different scales. Poikilothermic animals as butterflies, amphibians and reptiles have proven to be useful indicators for global change impacts as their phenology, spatial distribution, individual fitness and survival strongly depend on external environmental factors. In this aspect, phenological changes in terms of advanced flight or breeding periods, immigrations of foreign species, range shifts concomitant with temperature increases and even local population declines have been observed in both species groups. However, to date much attention has been paid to global change impacts on the species or population level and analyses concerning entire ecosystems are scarce. Applying a novel statistical modelling algorithm we assessed future changes in the extent and composition of terrestrial ecoregions as classified by the World Wide Fund for Nature (WWF). They are defined as coarse-scale conservation units containing exceptional assemblages of species and ecological dynamics. Our results demonstrate dramatic geographical changes in the extent and location of these ecoregions across all continents and even imply a repriorisation of conservation efforts to cope with future climate change impacts on biodiversity.

On the local scale, climate change impacts become unequivocal. Comparing historical to contemporary butterfly assemblages on vineyard fallows of the Trier Region, a significant decline in butterfly richness, but also a severe depletion in trait diversity was observed. Comparisons of community temperature indices reveal a striking shift in community composition leading to a replacement of sedentary and monophagous habitat specialists by ubiquitous species. Similar changes have been observed in nature reserves in the Saar-Mosel-area. Monitoring data reveal strong losses of species diversity and remarkable shifts of community compositions at the expense of habitat specialists. Besides climatic variability, these findings are largely attributed to changes in habitat structures, mostly due to eutrophication and monotonisation. Management activities are unlikely to counterbalance these effects, thus severely questioning current conservation strategies.

Most dramatic global change impacts are suspected on closely associated species and disruptions of biotic interactions are often hold responsible for species declines. A strong host-parasite association has developed in *Myrmica* ants and *Maculinea* butterflies, the later crucially depending on specific host ants for their larval survival. Applying environmental niche models we determined considerable niche dynamics in the observed parasite-host relation with a pronounced niche plasticity in the butterfly species adapting to previous evasive niche shifts in their host ants.

Moreover, the new emergence of species continuously expanding their northernmost range

borders concomitant with global warming like the Short-tailed blue (*Cupido argiades*) is attributed to climate change. However, species distribution models predict a severe habitat loss and shifts of potentially suitable habitats of this species towards north-eastern Europe and higher altitudes under several IPCC scenarios making the presence of this species in the Trier region a contemporary phenomenon.

Species distribution models have emerged as powerful tools to predict species distributions over spatial and temporal scales. However, not only the presence of a species, but also its abundance have significant implications for species conservation. The ability to deduce spatial abundance patterns from environmental suitability might more efficiently guide field surveys or monitoring programs over large geographical areas saving time and money. Although the application of species distribution models to deduce vertebrate abundances is well recognized, our results indicate that this method is not an adequate approach to predict invertebrate abundances. Structural and ecological factors as well as climatic patterns acting at the microscale are key drivers of invertebrate occurrence and abundances limiting conclusions drawn from modeling approaches.

Population declines should be interpreted with care as in butterflies and amphibians various reasons are debated. Both species groups are acknowledged to be highly susceptible to land use changes and variations in landscape structure. Moreover, climate and land use are not independently operating factors. The combined impact of both is demonstrated in our study linking climate-driven changes in amphibian phenologies to temporal advanced applications of pesticides and fertilizers. Both environmental factors already represent severe threats to amphibians when standing alone, but linking their combined impacts may result in an potentiated risk for amphibian populations. As all amphibians and numerous butterfly species are legally protected under the Federal Nature Conservation Act, intensifications of agricultural land use in large parts of Germany as well as new agrarian practices (including genetically manipulated plants accompanied by new herbicide technologies) might severely challenge regional conservation activities in the future.

ZUSAMMENFASSUNG

Der globale Wandel, d.h. Klima- und Landnutzungswandel, beeinflussen Tiere und Pflanzen auf unterschiedlichen Ebenen. Wechselwarme Tiere, wie Tagfalter, Amphibien und Reptilien, eignen sich besonders gut als Indikatoren solcher Veränderungen, da ihre Verbreitung, Phänologie, Fitness und Überlebensraten wesentlich von äußeren Umweltfaktoren abhängen. Schon heute oft beobachtete Reaktionen dieser Tiergruppen beinhalten phänologische Veränderungen der Flug- und Laichzeiten, die Einwanderung neuer Arten, Verschiebungen der Arealgrenzen analog der Temperaturerhöhung nach Norden und in höhere Lagen bis hin zu rückläufigen Populationstrends. Die meisten bisherigen Untersuchungen beziehen sich jedoch auf die Art- oder Populationsebene. Vorhersagen gesamte Ökosysteme betreffend sind selten. In einer neuartigen Modellierungsstudie haben wir in dieser Arbeit die Auswirkungen des Klimawandels auf Ökosysteme am Beispiel der Ecoregion-Klassifizierung des World Wide Fund for Nature (WWF) vorhergesagt. Diese sind als groß-skalige Biodiversitätseinheiten mit hoher Schutzpriorität definiert. Unsere Ergebnisse sagen nicht nur dramatische, klimabedingte Verschiebungen und Veränderungen innerhalb der Ökoregionen voraus, sondern implizieren darüber hinaus für die Zukunft eine Repriorisierung der globalen Naturschutzziele.

Auch auf regionaler Ebene sind bereits ökologische Veränderungen durch Klima- und Landnutzungswandel spürbar. Über die vergangenen 40 Jahre konnten wir nicht nur einen signifikanten Rückgang des Tagfalterreichtums auf den Weinbergsbrachen des Trierer Raums beobachten, sondern vielmehr eine dramatische Verarmung der Tagfaltergemeinschaften in Bezug auf Habitatspezialisten. Wie Vergleiche der Zönosen und Berechnungen der Community Temperature Indices zeigen, setzen sich die Tagfaltergemeinschaften vermehrt auf Kosten von standorttreuen, monophagen und kälteangepassten Arten aus Wärme liebenden Habitatgeneralisten zusammen. Ähnliche Veränderungen sind über den gleichen Zeitraum auch in den Naturschutzgebieten des Saar-Mosel-Gaus zu beobachten gewesen. Auch hier zeigen Kartierungen der Tagfalterzönosen dramatische Populationsrückgänge und Verschiebungen in der Artenzusammensetzung zu Gunsten von Habitatgeneralisten. Neben klimatischen Veränderungen scheinen besonders Veränderungen der Habitatstruktur, vor allem bedingt durch Stickstoffeinträge, für die Diversitätsrückgänge verantwortlich zu sein. Diese scheinen auch durch Pflegemaßnahmen in den Naturschutzgebieten nicht gebremst zu werden und langfristig die derzeitigen Schutzbemühungen in Frage zu stellen.

Besonders drastisch scheinen sich diese Veränderungen auf Arten auszuwirken, die auf enge

biotische Interaktionen angewiesen sind, wie die Ameisenbläulinge der Gattung *Maculinea*, deren Larven einen Sozialparasitismus mit Ameisen der Gattung *Myrmica* ausgebildet haben. Am Beispiel dieser Tagfaltergattung haben wir die Nischendynamik in Wirts-Parasit-Beziehungen untersucht. Unsere Ergebnisse weisen auf eine erhebliche Nischenplastizität und Adaptionsfähigkeit der Tagfalter hin, um evolutionäre Nischenverschiebungen ihrer Wirte auszugleichen.

Auch das Auftreten neuer Arten wie des Kurzschwänzigen Bläulings (*Cupido argiades*), der sein Areal seit einigen Jahren systematisch nach Norden erweitert und in unserer Region als Klimawandelgewinner gilt, wird der globalen Erwärmung zugeschrieben. Verbreitungsmodelle zeigen jedoch, dass das Auftreten dieser Art in Süddeutschland eher ein Gastspiel sein wird und sie sich unter Klimawandelbedingungen langfristig in die kühl-gemäßigten Lagen Nordost-Europas und des alpinen Raums zurückziehen wird. Artverbreitungsmodelle haben sich in den vergangen zehn Jahren als zuverlässige Methode entwickelt, um die Verbreitung von Arten über Zeit und Raum vorherzusagen. Für den Artenschutz ist jedoch nicht nur das Vorkommen einer Art, sondern auch deren Häufigkeit, respektive Seltenheit, relevant. Die mathematische Vorhersage der Häufigkeit einer Art auf Basis der prognostizierten Habitateignung innerhalb einer Region, könnte langfristig zeitaufwendige Monitoringprogramme ersetzen. Allerdings ist unseren Studien zur Folge diese Möglichkeit derzeit auf Säugetiere und Vögel beschränkt. Mikrohabitatstrukturen, wie sie oft Vorkommen und Häufigkeit von Invertebraten wie Tagfaltern bestimmen, werden von den heutigen Klima- und Verbreitungsmodellen nur unzureichend erfasst, um zuverlässige Aussagen über die Häufigkeit dieser Arten zu treffen.

Jedoch ist zu sagen, dass weder für Tagfalter, noch für Amphibien und Reptilien, Klimaveränderungen als alleiniger Grund für Populationsrückgänge gelten. Beide Artengruppen zeigen auch eine hohe Anfälligkeit für Landschafts- und Landnutzungsveränderungen. Das Klima- und Landnutzungswandel nicht unabhängig von einander wirken zeigt unsere Studie, die das verfrühte Laichverhalten von Amphibien mit der zeitlichen Verschiebung des Pestizideinsatzes in der Landwirtschaft verbindet. Haben schon Pestizide als auch klimabedingte, phänologische Veränderungen im Laichverhalten allein ein hohes Schadpotenzial für Amphibienarten auf landwirtschaftlich genutzten Flächen, potenziert die Kombination beider Wirkfaktoren das Risiko langfristiger Populationsschäden. Da alle in Deutschland vorkommenden Amphibienarten nach §7 des Bundesnaturschutzgesetzes unter besonderem Schutz stehen, stellt die landwirtschaftliche Nutzung großer Teile Deutschlands sowie die potenzielle Einführung neuer Agrarmethoden im Rahmen effizienter Biotechnologien eine besondere Herausforderung für den Naturschutz dar.

APPENDIX

Appendix 1 Butterfly abundances recorded on vineyard fallows in the Trier Region in 1973. Butterfly surveys were conducted from March till October every ten days (if weather permitted) by Matthias Weitzel.

	Tiergarten 1	Tiergarten 2	Tiergarten 3	Hill	Kernscheid	Brettenbach 1	Brettenbach 2	Avelertal 3
Hesperidae								
Erynnis tages (L., 1758)	4	7	2	2	3	1		9
Carcharodus alceae (Esp., 1780)	2	4	4	3	3	2		7
Spialia sertorius (Hoff., 1804)	1	7	2	1	1			2
Pyrgus malvae (L., 1758)	21	9	27	14	18	19	3	76
Carterocephalus palaemon (Pal., 1771)		1	1					1
Thymelicus lineola (O., 1808)	14	49	17	14	11	17	14	28
Thymelicus sylvestris (Poda, 1761)			14	7	6	3		71
Ochlodes sylvanus (Esp., 1778)	14	17	14	18	14	9	2	23
Papilionidae								
Papilio machaon L., 1758	2	4	5	3	4	3	1	14
Pieridae								
Leptidea sinapis (L., 1758)/ *reali* Reiss, 1989	4	2	11	14	5	5	2	11
Anthocharis cardamines (L., 1758)	12	8	7	14	5	23	21	47
Aporia crataegi (L., 1758)	1		3	3	1	1		2
Pieris brassicae (L., 1758)	21	24	29	31	4	11	14	55
Pieris rapae (L., 1758)	111	116	92	119	78	112	117	179
Pieris napi (L., 1758)	71	112	114	101	104	107	146	152
Colias croceus (Fourc, 1785)			1					1
Colias hyale (L., 1758)	4	7	2	7	4	3	1	21
Gonepteryx rhamni (L., 1758)	21	24	26	49	18	21	20	28
Lycaenidae								
Hamearis lucina (L., 1758)		2		7	1	1		5
Lycaena phlaeas (L., 1761)	22	28	21	14	28	13	10	42
Lycaena tityrus (Poda, 1761)	11	14	21	4	7	22	12	31
Lycaena hippothoe (L., 1761)		1						
Thecla betulae (L., 1758)	3	1	1	14	3	3	4	14
Neozephyrus quercus (L., 1758)				1		1		2
Callophrys rubi (L., 1758)	7	9	9	17	4	11	6	28
Satyrium w-album (Knoch, 1782)		1	1					2
Satyrium pruni (L., 1758)	4	7	5	11	2	2	11	17
Cupido minimus (Fues., 1775)	2	3	1					2

Celastrina argiolus (L., 1758)	7	9	8	14	11	11	3	32
Polyommatus semiargus (Rott., 1775)	4	7	7	2	1	3		11
Polyommatus icarus (Rott., 1775)	28	31	28	19	36	34	14	114
Polyommatus coridon (Poda, 1761)		2	2					1
Nymphalidae								
Argynnis paphia (L., 1758)	11	11	17	18	14	11	4	11
Argynnis aglaja (L., 1758)	1	1	7	8	2	2		8
Issoria lathonia (L., 1758)		1			1	2		3
Brentis ino (Rott., 1775)		1		1				
Boloria selene ([Den. & Schiff.], 1775)	2	11	7	8	1	9	11	3
Vanessa atalanta (L., 1758)	4	2	2	5	3	7	1	3
Vanessa cardui (L., 1758)	7	2	11	4	6	7	4	7
Inachis io (L., 1758)	22	24	27	28	26	24	28	74
Aglais urticae (L., 1758)	112	114	76	104	78	42	76	104
Polygonia c-album (L., 1758)	3	7	6	14	11	12	3	11
Araschnia levana (L., 1758)	7	11	4	14	3	3	11	22
Nymphalis polychloros (L., 1758)			1	1				1
Melitaea cinxia (L., 1758)			1		1			4
Melitaea diamina (Lang, 1789)		2	4	7	2	2		14
Melitaea athalia (Rott., 1775)	2	4	1	1	4	1		19
Limentis populi (L., 1758)				1	1			
Limentis camilla (L., 1764)		2	11	14	17	4		3
Apatura iris (L., 1764)			1	3	1	1		
Pararge aegeria (L., 1758)	2	1	2	22	3	14	8	6
Lasiommata megera (L., 1767)	11	17	29	12	19	3		11
Coenonympha arcania (L., 1761)	4	19	8	7	2	11	3	5
Coenonympha pamphilus (L., 1758)	128	147	131	178	211	178	56	201
Pyronia tithonus (L., 1771)	78	136	156	101	114	48	29	816
Aphantopus hyperantus (L., 1758)	54	38	69	54	38	58	23	212
Maniola jurtina (L., 1758)	121	139	147	143	104	96	78	427
Erebia medusa ([Den. & Schiff.], 1775)	3	7	7	11	1	3		3
Melanargia galathea (L., 1758)	8	11	17	19	14	23	4	114

Appendix 2 Butterfly abundances recorded on vineyard fallows in the Trier Region in 1986. Butterfly surveys were conducted from March till October every ten days (if weather permitted) by Matthias Weitzel.

	Tiergarten 2	Hill	Avelertal
Hesperidae			
Erynnis tages (L., 1758)	5	6	2
Carcharodus alceae (Esp., 1780)	14		5
Spialia sertorius (Hoff., 1804)			
Pyrgus malvae (L., 1758)	9	4	5
Carterocephalus palaemon (Pal., 1771)			
Thymelicus lineola (O., 1808)	33	19	19
Thymelicus sylvestris (Poda, 1761)	15	30	13
Ochlodes sylvanus (Esp., 1778)	47	9	36
Papilionidae			
Papilio machaon L., 1758	19	5	20
Pieridae			
Leptidea sinapis (L., 1758)/ *reali* Reiss, 1989	31	23	39
Anthocharis cardamines (L., 1758)	31	37	33
Aporia crataegi (L., 1758)	4		
Pieris brassicae (L., 1758)	18	25	55
Pieris rapae (L., 1758)	133	82	157
Pieris napi (L., 1758)	80	92	97
Colias croceus (Fourc, 1785)	2	1	
Colias hyale (L., 1758)	36	3	40
Gonepteryx rhamni (L., 1758)	29	32	23
Lycaenidae			
Hamearis lucina (L., 1758)			2
Lycaena phlaeas (L., 1761)	25	13	11
Lycaena tityrus (Poda, 1761)	1		1
Lycaena hippothoe (L., 1761)			
Thecla betulae (L., 1758)			2
Neozephyrus quercus (L., 1758)			1
Callophrys rubi (L., 1758)	17	25	16
Satyrium w-album (Knoch, 1782)			
Satyrium pruni (L., 1758)	8	19	7
Cupido minimus (Fues., 1775)	1		
Celastrina argiolus (L., 1758)	19	5	16
Aricia agestis ([Den. & Schiff.], 1775)	13		8
Polyommatus semiargus (Rott., 1775)	7		18
Polyommatus icarus (Rott., 1775)	76	18	245
Polyommatus coridon (Poda, 1761)			
Nymphalidae			
Argynnis paphia (L., 1758)			21
Argynnis aglaja (L., 1758)			1
Argynnis adippe ([Den. & Schiff.], 1775)			1
Issoria lathonia (L., 1758)			4
Brentis ino (Rott., 1775)			
Boloria selene ([Den. & Schiff.], 1775)			1
Boloria dia (L., 1767)			3

Vanessa atalanta (L., 1758)			38
Vanessa cardui (L., 1758)			20
Inachis io (L., 1758)			17
Aglais urticae (L., 1758)			46
Polygonia c-album (L., 1758)			22
Araschnia levana (L., 1758)			22
Nymphalis polychloros (L., 1758)			1
Melitaea cinxia (L., 1758)			
Melitaea diamina (Lang, 1789)			4
Melitaea athalia (Rott., 1775)			16
Limentis populi (L., 1758)			
Limentis camilla (L., 1764)			2
Apatura iris (L., 1764)			
Pararge aegeria (L., 1758)	46	29	19
Lasiommata megera (L., 1767)	37	6	23
Coenonympha arcania (L., 1761)	10	23	5
Coenonympha pamphilus (L., 1758)	70	46	145
Pyronia tithonus (L., 1771)	176	249	383
Aphantopus hyperantus (L., 1758)	150	156	148
Maniola jurtina (L., 1758)	297	187	481
Erebia medusa ([Den. & Schiff.], 1775)			
Melanargia galathea (L., 1758)	41		129

Appendix 3 Butterfly abundances recorded on vineyard fallows in the Trier Region in 2010. Butterfly surveys were conducted from March till October every ten days (if weather permitted) by Katharina Filz.

	Tiergarten 1	Tiergarten 2	Tiergarten 3	Hill	Kernscheid	Brettenbach 1	Brettenbach 2	Avelertal 2	Avelertal 3
Hesperidae									
Pyrgus malvae (L., 1758)	2	1	1			7		2	3
Thymelicus lineola (O., 1808)	9		1		1	10	60		59
Thymelicus sylvestris (Poda, 1761)	35	6	5			39	104	3	114
Ochlodes sylvanus (Esp., 1778)				3		5	6		16
Papilionidae									
Papilio machaon L., 1758	1	1	2		1	2		4	1
Pieridae									
Leptidea sinapis (L., 1758)/*reali* Reiss, 1989	9	4	3	6	2	23	21	5	19
Anthocharis cardamines (L., 1758)	8	8	14	7	1	1	2	6	5
Aporia crataegi (L., 1758)	1				2	1	2	1	5
Pieris brassicae (L., 1758)	1			2				4	1
Pieris rapae (L., 1758)	29	30	23	17	16	31	18	32	48
Pieris napi (L., 1758)	2	1		15	7	5		5	10
Colias hyale (L., 1758)	6	5	1		8	3			6
Gonepteryx rhamni (L., 1758)		2	1	2	1	2	1	2	3
Lycaenidae									
Lycaena phlaeas (L., 1761)	1	6	2	1	1		1		
Lycaena dispar (Haw., 1803)		1							
Lycaena tityrus (Poda, 1761)		1			1				3
Thecla betulae (L., 1758)					2				
Callophrys rubi (L., 1758)		2	1		1		3		4
Cupido argiades (Pallas, 1771)					1	1		1	
Celastrina argiolus (L., 1758)									2
Aricia agestis ([Den. & Schiff.], 1775)	11	26	13		2	7	12	2	30
Polyommatus semiargus (Rott., 1775)	1	2	1		1	7	8		15

Polyommatus icarus (Rott., 1775)	15	18	11		2	21	30	3	44
Nymphalidae									
Argynnis paphia (L., 1758)				1					
Argynnis aglaja (L., 1758)		1				1		1	1
Issoria lathonia (L., 1758)	3	4	6		3	1		1	5
Vanessa atalanta (L., 1758)	1	1		1	1			5	1
Vanessa cardui (L., 1758)								1	
Inachis io (L., 1758)	10	12	13	2	4	4	2	6	3
Aglais urticae (L., 1758)	5	10	9	1	9		3	2	4
Polygonia c-album (L., 1758)	3			2		1		1	1
Araschnia levana (L., 1758)	1		2	4	2			2	4
Melitaea cinxia (L., 1758)								1	4
Melitaea athalia (Rott., 1775)		2							1
Apatura iris (L., 1764)								1	
Pararge aegeria (L., 1758)				6					
Lasiommata megera (L., 1767)	2	5			1				
Coenonympha arcania (L., 1761)	1			3		2	4		2
Coenonympha pamphilus (L., 1758)	6	5	3		5	18	23	11	45
Pyronia tithonus (L., 1771)	6	4	5	8	9	6	58	6	32
Aphantopus hyperantus (L., 1758)	14		5	8	20	36	33	22	119
Maniola jurtina (L., 1758)	35	23	7	10	27	66	78	16	104
Melanargia galathea (L., 1758)	31	18	17	1	16	68	78	4	91

Appendix 4 Butterfly abundances recorded on vineyard fallows in the Trier Region in 2012. Butterfly surveys were conducted from March till October every ten days (if weather permitted) by Anne Herrig.

	Tiergarten 1	Tiergarten 2	Tiergarten 3	Hill	Kernscheid	Brettenbach 1	Brettenbach 2	Avelertal 2	Avelertal 3
Hesperidae									
Carcharodus alceae (Esp., 1780)	4								
Pyrgus malvae (L., 1758)	4	2			1	2		2	4
Thymelicus lineola (O., 1808)	13	5	3		1	2	14	1	47
Thymelicus sylvestris (Poda, 1761)	13	4	2		3	12	44	5	60
Ochlodes sylvanus (Esp., 1778)								2	
Papilionidae									
Papilio machaon L., 1758		1			1				3
Pieridae									
Leptidea sinapis (L., 1758)/*reali* Reiss, 1989		1		2		1	2	1	
Anthocharis cardamines (L., 1758)	1			3					
Pieris brassicae (L., 1758)	1	1		1	1				
Pieris rapae (L., 1758)	42	30	30	11	18	16	15	32	22
Pieris napi (L., 1758)	7	3	1	7	5	3	2	3	4
Colias hyale (L., 1758)	6	6	4		2	1	7		7
Gonepteryx rhamni (L., 1758)			1		2		1		
Lycaenidae									
Lycaena phlaeas (L., 1761)	2	3				2			2
Lycaena dispar (Haw., 1803)					1				
Lycaena tityrus (Poda, 1761)						1	1		2
Thecla betulae (L., 1758)			1						
Callophrys rubi (L., 1758)						1			
Cupido argiades (Pallas, 1771)	3	8	3		1		8	7	28
Celastrina argiolus (L., 1758)		1							1
Aricia agestis ([Den. & Schiff.], 1775)	3	16	6				2		8
Polyommatus semiargus (Rott., 1775)		4	1					1	5
Polyommatus	10	16				3	4	2	9

icarus (Rott., 1775)									
Nymphalidae									
Issoria lathonia (L., 1758)	1	10	2				2		1
Brenthis daphne (Berg., 1780)				1					1
Boloria dia (L., 1767)	1	6							
Vanessa atalanta (L., 1758)	1		1	1	1	2	1	2	1
Vanessa cardui (L., 1758)		1	3						
Inachis io (L., 1758)		1	1		1				
Aglais urticae (L., 1758)	1	1	2		3				1
Polygonia c-album (L., 1758)	1	2		9			1	1	
Araschnia levana (L., 1758)			1	3				1	1
Melitaea cinxia (L., 1758)									2
Coenonympha pamphilus (L., 1758)	9	10			4	16	16	7	23
Pyronia tithonus (L., 1771)	16	1		2	11	14	6	9	33
Aphantopus hyperantus (L., 1758)	4	1			10	1	9	8	29
Maniola jurtina (L., 1758)	16	2	3	1	6	6	21	6	23
Melanargia galathea (L., 1758)	14	1	1		8	6	32	5	62

Appendix 5 CTI-values calculated from butterfly species numbers and numbers of individuals recorded on vineyard fallows in the Trier region in the study year mentioned below.

CTI (Species)	1973	1986	2010	2011	2012
Avelertal 1				9.038	
Avelertal 2			9.030		9.004
Avelertal 3	8.972	8.998	8.928	9.073	9.151
Brettenbach 1	8.912		8.979	8.809	9.090
Brettenbach 2	8.868		9.054	9.028	9.208
Hill	8.880	9.054	9.015	8.973	9.284
Kernscheid	8.916		9.047	9.060	9.052
Tiergarten 1	8.933		9.049	9.060	9.169
Tiergarten 2	8.789	9.188	9.037	9.057	9.065
Tiergarten 3	8.945		9.001	9.013	9

CTI (Individuals)	1973	1986	2010	2011	2012
Avelertal 1				9.489	
Avelertal 2			9.108		9.387
Avelertal 3	9.481	9.409	9.229	9.689	9.401
Brettenbach 1	9.001		9.308	9.062	9.556
Brettenbach2	8.885		9.505	9.218	9.453
Hill	9.053	9.375	9.097	9.161	9.030
Kernscheid	9.127		9.136	9.266	9.312
Tiergarten 1	9.047		9.330	9.274	9.475
Tiergarten 2	9.116	9.387	9.382	9.164	9.282
Tiergarten 3	9.178		9.228	9.260	9.366

Appendix 5a Standard deviation of the respective CTI-values calculated from butterfly species numbers and numbers of individuals recorded on vineyard fallows in the Trier region in the study year mentioned below.

CTI (Species)	1973	1986	2010	2011	2012	all
Avelertal 1				0.783		0.783
Avelertal 2			0.736		0.789	0.732
Avelertal 3	0.856	0.833	0.721	0.764	0.817	0.865
Brettenbach 1	0.787		0.759	0.817	0.766	0.793
Brettenbach 2	0.71		0.773	0.833	0.719	0.728
Hill	0.872	0.725	0.723	0.718	0.881	0.896
Kernscheid	0.828		0.739	0.715	0.776	0.824
Tiergarten 1	0.824		0.77	0.696	0.875	0.8
Tiergarten 2	0.94	0.833	0.812	0.827	0.739	0.942
Tiergarten 3	0.869		0.782	0.725	0.684	0.859
all	0.952	0.833	0.707	0.759	0.781	0.957

CTI (Individuals)	1973	1986	2010	2011	2012	all
Avelertal 1				0.713		0.713
Avelertal 2			0.782		0.777	0.79
Avelertal 3	1.04	0.887	0.813	0.734	0.782	0.939
Brettenbach 1	0.777		0.713	0.748	0.751	0.776
Brettenbach 2	0.816		0.766	0.855	0.627	0.835
Hill	0.857	1.005	0.84	0.811	0.748	0.908
Kernscheid	0.88		0.883	0.78	0.937	0.867
Tiergarten 1	0.879		0.723	0.764	0.774	0.836
Tiergarten 2	0.932	0.886	0.709	0.832	0.597	0.887
Tiergarten 3	0.954		0.755	0.722	0.589	0.889
all	0.882	0.938	0.77	0.779	0.726	0.86

Appendix 6 Presence (+) of butterfly species on calcareous grasslands in the Saar-Moselle-Region in 1972. Butterfly surveys were conducted from March till October every ten days (if weather permitted) by Matthias Weitzel.

	Echternacherbrück	Freudenburg	Igel	Kelsen	Nittel	Wasserliesch
Hesperidae						
Erynnis tages (L., 1758)	+	+	+	+	+	+
Carcharodus alceae (Esp., 1780)					+	
Spialia sertorius (Hoff., 1804)	+	+	+	+	+	+
Pyrgus malvae (L., 1758)	+	+	+	+	+	+
Pyrgus serratulae (Ram., 1839)	+					
Carterocephalus palaemon (Pal., 1771)	+	+			+	+
Thymelicus lineola (O., 1808)	+	+	+	+	+	+
Thymelicus sylvestris (Poda, 1761)	+	+	+	+	+	+
Thymelicus acteon (Rott., 1775)	+				+	+
Hesperia comma (L., 1758)		+				
Ochlodes sylvanus (Esp., 1778)	+	+	+	+	+	+
Papilionidae						
Papilio machaon L., 1758	+	+	+	+	+	+
Pieridae						
Leptidea sinapis (L., 1758)/*reali* Reiss, 1989	+	+	+	+	+	+
Anthocharis cardamines (L., 1758)	+	+	+	+	+	+
Aporia crataegi (L., 1758)	+	+	+		+	+
Pieris brassicae (L., 1758)	+	+	+	+	+	+
Pieris rapae (L., 1758)	+	+	+	+	+	+
Pieris napi (L., 1758)	+	+	+	+	+	+
Pontia daplidice (L., 1758)					+	
Colias croceus (Fourc, 1785)	+	+			+	
Colias hyale (L., 1758)	+	+	+	+	+	+
Colias alfacariensis (Rib., 1905)	+	+	+		+	+
Gonepteryx rhamni (L., 1758)	+	+	+	+	+	+
Lycaenidae						
Hamearis lucina (L., 1758)	+	+	+		+	+
Lycaena phlaeas (L., 1761)	+	+	+	+	+	+
Lycaena tityrus (Poda, 1761)	+	+	+	+	+	+
Thecla betulae (L., 1758)	+	+	+	+	+	+
Neozephyrus quercus (L., 1758)	+	+			+	+
Satyrium ilicis (Esp., 1779)	+		+		+	+
Callophrys rubi (L., 1758)	+	+	+	+	+	+
Satyrium pruni (L., 1758)	+	+	+	+	+	+
Satyrium acaciae (Fab., 1787)	+		+		+	
Cupido minimus (Fues., 1775)	+	+	+	+	+	+
Celastrina argiolus (L., 1758)	+	+	+	+	+	+
Maculinea arion (L., 1758)	+		+		+	
Aricia agestis ([Den. & Schiff.], 1775)	+	+	+	+	+	+
Polyommatus semiargus (Rott., 1775)	+	+	+	+	+	+
Polyommatus icarus (Rott., 1775)	+	+	+	+	+	+
Polyommatus coridon (Poda, 1761)	+	+	+	+	+	+
Polyommatus bellargus (Rott., 1775)					+	
Nymphalidae						
Argynnis paphia (L., 1758)	+	+	+	+	+	+

Argynnis aglaja (L., 1758)	+	+	+	+	+	+
Issoria lathonia (L., 1758)	+	+	+	+	+	+
Boloria selene ([Den. & Schiff.], 1775)	+	+	+	+	+	+
Boloria euphrosyne (L., 1758)	+	+			+	+
Vanessa atalanta (L., 1758)	+	+	+	+	+	+
Vanessa cardui (L., 1758)	+	+	+	+	+	+
Inachis io (L., 1758)	+	+	+	+	+	+
Aglais urticae (L., 1758)	+	+	+	+	+	+
Polygonia c-album (L., 1758)	+	+	+	+	+	+
Araschnia levana (L., 1758)	+	+	+	+	+	+
Nymphalis polychloros (L., 1758)	+	+			+	+
Melitaea cinxia (L., 1758)	+	+	+	+	+	+
Melitaea diamina (Lang, 1789)		+				+
Melitaea athalia (Rott., 1775)	+	+	+	+	+	+
Melitaea aurelia (Nick., 1850)	+				+	
Limentis populi (L., 1758)	+					
Limentis camilla (L., 1764)	+	+	+		+	+
Apatura iris (L., 1764)	+	+	+		+	+
Pararge aegeria (L., 1758)	+	+	+	+	+	+
Lasiommata megera (L., 1767)	+	+	+	+	+	+
Lasiommata maera (L., 1758)			+			
Coenonympha arcania (L., 1761)	+	+			+	+
Coenonympha pamphilus (L., 1758)	+	+	+	+	+	+
Pyronia tithonus (L., 1771)	+	+	+	+	+	+
Aphantopus hyperantus (L., 1758)	+	+	+	+	+	+
Maniola jurtina (L., 1758)	+	+	+	+	+	+
Erebia medusa ([Den. & Schiff.], 1775)	+	+			+	+
Hipparchia semele (L., 1758)	+	+				
Melanargia galathea (L., 1758)	+	+	+	+	+	+

Appendix 7 Butterfly abundances on calcareous grasslands in the Saar-Moselle-Region in 2001. Butterfly surveys were conducted from March till October every ten days (if weather permitted) by Miriam Frede.

	Echternacherbrück	Freudenburg	Igel	Kelsen	Nittel	Wasserliesch
Hesperidae						
Erynnis tages (L., 1758)		2			1	7
Spialia sertorius (Hoff., 1804)		1				3
Pyrgus malvae (L., 1758)			2		2	3
Carterocephalus palaemon (Pal., 1771)	1					
Thymelicus acteon (Rott., 1775)	1					3
Thymelicus lineola (O., 1808)			2			2
Thymelicus sylvestris (Poda, 1761)	1	1	7	2	2	3
Ochlodes sylvanus (Esp., 1778)	2	5	1			4
Papilionidae						
Papilio machaon L., 1758	7	4	1			3
Pieridae						
Leptidea sinapis (L., 1758)/*reali* Reiss, 1989	1	21		1	2	11
Anthocharis cardamines (L., 1758)					1	1
Aporia crataegi (L., 1758)	1	4	3		3	5
Pieris brassicae (L., 1758)	3	21	5	2	5	2
Pieris rapae (L., 1758)	7	28	5	44	4	2
*Pieris napi (*L., 1758)			1	3	1	
Colias hyale (L., 1758)		2				
Gonepteryx rhamni (L., 1758)		6				
Lycaenidae						
Lycaena dispar (Haw., 1803)			1			
Thecla betulae (L., 1758)			1			
Callophrys rubi (L., 1758)	1					
Satyrium pruni (L., 1758)		1				
Cupido minimus (Fues., 1775)		15	3		3	6
Celastrina argiolus (L., 1758)			1			
Polyommatus semiargus (Rott., 1775)			2		1	1
Polyommatus icarus (Rott., 1775)	33	55	10	6	12	18
Polyommatus coridon (Poda, 1761)	21	48	14		34	43
Polyommatus bellargus (Rott., 1775)						1
Nymphalidae						
Argynnis aglaja (L., 1758)		1				
Issoria lathonia (L., 1758)		1				
Boloria dia (L., 1767)					1	11
Vanessa atalanta (L., 1758)		1			1	
Vanessa cardui (L., 1758)	1	2	1	4		
Inachis io (L., 1758)		2	2	1	1	1
Aglais urticae (L., 1758)	1	1	4	6		3
Araschnia levana (L., 1758)	1		4			
Melitaea cinxia (L., 1758)	2					
Melitaea diamina (Lang, 1789)		1				
Melitaea aurelia (Nick., 1850)		5				1
Pararge aegeria (L., 1758)		1				
Lasiommata megera (L., 1767)	3	7	5	6	9	
Coenonympha arcania (L., 1761)	5	48	10		18	49

Coenonympha pamphilus (L., 1758)	21	14	9	10	12	6
Pyronia tithonus (L., 1771)	39	44	61	25	8	158
Aphantopus hyperantus (L., 1758)	8	24	14	0	2	28
Maniola jurtina (L., 1758)	102	217	47	23	3	123
Erebia medusa ([Den. & Schiff.], 1775)		7				
Melanargia galathea (L., 1758)	88	148	33	7	50	83

Appendix 8 Butterfly abundances on calcareous grasslands in the Saar-Moselle-Region in 2001. Butterfly surveys were conducted from March till October every ten days (if weather permitted) by Katharina Filz.

	Echternacherbrück	Freudenburg	Igel	Kelsen	Nittel	Wasserliesch
Hesperidae						
Erynnis tages (L., 1758)		5		1	2	1
Spialia sertorius (Hoff., 1804)		1	1			1
Pyrgus malvae (L., 1758)	2	7	2		2	3
Thymelicus lineola (O., 1808)	18	4	3	1	4	41
Thymelicus sylvestris (Poda, 1761)	37	8	12	1	3	25
Hesperia comma (L., 1758)					2	
Ochlodes sylvanus (Esp., 1778)	1				3	2
Papilionidae						
Papilio machaon L., 1758	3	6	3		1	1
Pieridae						
Leptidea sinapis (L., 1758)/*reali* Reiss, 1989	5	29	7	9	10	13
Anthocharis cardamines (L., 1758)	2	12	1		2	2
Aporia crataegi (L., 1758)	2	1				3
Pieris brassicae (L., 1758)	3	13	5	15	6	4
Pieris rapae (L., 1758)	42	125	35	142	34	24
Pieris napi (L., 1758)	5	29	6	26	7	6
Colias hyale (L., 1758)	10	3	3	1		
Colias alfacariensis (Rib., 1905)	2					
Gonepteryx rhamni (L., 1758)	5	10	5	2	4	10
Lycaenidae						
Lycaena phlaeas (L., 1761)		1	2	1	1	
Lycaena tityrus (Poda, 1761)	3					1
Thecla betulae (L., 1758)		1	2			
Callophrys rubi (L., 1758)	1	32	1	1	13	21
Satyrium pruni (L., 1758)	2		5			1
Cupido minimus (Fues., 1775)	1	95	1	22	14	82
Celastrina argiolus (L., 1758)		2			1	1
Aricia agestis ([Den. & Schiff.], 1775)	10	7	7	11	4	7
Polyommatus semiargus (Rott., 1775)	2	14	4	7	8	6
Polyommatus icarus (Rott., 1775)	25	15	9	27	4	10
Polyommatus coridon (Poda, 1761)		278	27	3	137	231
Polyommatus bellargus (Rott., 1775)						
Nymphalidae						
Argynnis paphia (L., 1758)		2	3		3	4
Argynnis aglaja (L., 1758)	1	51	11		11	42
Issoria lathonia (L., 1758)	1	7	1	1	2	
Boloria selene ([Den. & Schiff.], 1775)		2				
Boloria dia (L., 1767)	2	24			16	15
Vanessa atalanta (L., 1758)		3			1	2
Vanessa cardui (L., 1758)			1			
Inachis io (L., 1758)		4	1	1	1	
Aglais urticae (L., 1758)	7	40	7	11	1	2
Polygonia c-album (L., 1758)		3	1			1

Araschnia levana (L., 1758)		4	2		1	
Euphydryas aurinia (Rott., 1775)					1	
Melitaea athalia (Rott., 1775)		124			5	26
Melitaea aurelia (Nick., 1850)	2					
Apatura iris (L., 1764)					1	
Pararge aegeria (L., 1758)		6	2		2	3
Lasiommata megera (L., 1767)	2	15	7	4	4	
Lasiommata maera (L., 1758)	1					
Coenonympha arcania (L., 1761)	6	80	27	8	9	169
Coenonympha pamphilus (L., 1758)	58	46	29	24	21	81
Pyronia tithonus (L., 1771)	14	42	113	44	10	103
Aphantopus hyperantus (L., 1758)	2	48	21	5	29	59
Maniola jurtina (L., 1758)	100	441	159	65	69	182
Melanargia galathea (L., 1758)	57	349	184	17	75	388

Appendix 9 Butterfly abundances on calcareous grasslands in the Saar-Moselle-Region in 2012. Butterfly surveys were conducted from March till October every ten days (if weather permitted) by David Jänicke.

	Freudenburg	Igel	Kelsen	Nittel	Wasserliesch
Hesperidae					
Pyrgus malvae (L., 1758)	4	4			4
Thymelicus sylvestris (Poda, 1761)		2		11	
Pieridae					
Leptidea sinapis (L., 1758)/*reali* Reiss, 1989	24	11	14	18	9
Anthocharis cardamines (L., 1758)		23	18		2
Pieris brassicae (L., 1758)	19	8	19	25	18
Pieris rapae (L., 1758)					3
Pieris napi (L., 1758)			5		1
Gonepteryx rhamni (L., 1758)	10	5	2	6	6
Lycaenidae					
Callophrys rubi (L., 1758)	16			19	4
Cupido minimus (Fues., 1775)	5	8	23	23	12
Celastrina argiolus (L., 1758)	1				
Aricia agestis ([Den. & Schiff.], 1775)		6			
Polyommatus icarus (Rott., 1775)	3	11	11	22	14
Polyommatus coridon (Poda, 1761)	101	45	19	53	155
Nymphalidae					
Argynnis paphia (L., 1758)	18			5	21
Boloria dia (L., 1767)	30	1	2	24	29
Vanessa atalanta (L., 1758)	8	7	5	4	1
Inachis io (L., 1758)		12	25	2	
Aglais urticae (L., 1758)	16	15	29	16	3
Polygonia c-album (L., 1758)			19		
Nymphalis polychloros (L., 1758)			24		
Melitaea aurelia (Nick., 1850)	108	16	26	28	79
Pararge aegeria (L., 1758)	3				
Lasiommata megera (L., 1767)	16				3
Coenonympha arcania (L., 1761)	76	43			79
Coenonympha pamphilus (L., 1758)	26	7	16	56	72
Pyronia tithonus (L., 1771)	29	36	11	19	63
Aphantopus hyperantus (L., 1758)	8	12	3	3	15
Maniola jurtina (L., 1758)	83	67	25	41	42
Melanargia galathea (L., 1758)	85	173	48	73	92

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Curriculum vitae

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Date of Birth, Birthplace	12 October 1984 in Darmstadt
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Education and Practical Experience

09/2013 – present	Scientific volunteer at the Museum of Natural History Dortmund
03/2010 – 10/2013	Doctoral Thesis (Trier University, Department of Biogeography) 'Global change impacts on biodiversity and their implications for species conservation'
11/2009	Graduation, Diplomathesis at the Alfred Wegener Institute of Polar and Marine Research, Bremerhaven 'Variation in growth of *Serripes groenlandicus* as an evidence for local climate changing in Kongsfjorden, Svalbard'
10/2004-11/2009	Trier University (Department of Biogeography) biogeography, botany, soil science, physical geography
04/2009-06/2009	Student research fellow at the Alfred Wegener Institute for Polar and Marine Research maintenance of captive cockle communities
12/2005-12/2008	Member of student councils at Trier University
03/2008-04/2008	Student research fellow at the Department of Geobotany, Trier University leaf analyses
09/2007-10/2007	Internship at the Seal Rehabilitation and Research Center Pieterburen, The Netherlands medical care, monitoring
03/2007-04/2007	Voluntary service at the Iguana Research and Breeding Station Utila, Honduras monitoring, environmental education, guided tours (German, English), captive breeding

04/2005	Internship at the Senckenbergische Naturforschende Gesellschaft, Department of Herpetology taxonomy
06/2004	School leaving examination (Abitur)
1995-2004	Viktoriaschule, Darmstadt
1991-1995	Käthe-Kollwitz-Schule, Darmstadt

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Grants and Funding

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04/2013	Travel Grant (Societas Europaea Herpetologica)
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03/2010-03/2013	Postgraduate Grant (Friedrich-Ebert-Foundation)
05/2010	Fund 'Arten- und Biotopschutz' (Ministry for Environment, Agriculture, Viticulture, Food and Forests Rhineland-Palatinate)
03/2007-11/2009	Undergraduate Grant (Friedrich-Ebert-Foundation)

Memberships in scientific organisations

since 2012	Ecological Society of Germany, Austria and Switzerland (GfÖ) including the working groups Macroecology and Young Modellers in Ecology
since 2012	International Biogeography Society (IBS)
since 2009	German Herpetological Society (DGHT)

Scientific meetings co-organized

05/2013	Exhibition 'Natura 2000'at Trier University, in cooperation with the Museum of Natural History Mainz
09/2011	16. European Herpetological Congress, Societas Europaea Herpetologica, Luxemburg and Trier
09/2011	Annual Scientific meeting of the German Herpetological Society, Trier
05/2010	Annual congress of the biogeography special interest group, Association of German University Geographers (VGDH), Trier

Skills

Languages	German (native speaker) English (fluent) Spanish (Unicert B1) French (basic knowledge)
IT	MS Office, Maxent, ArcGIS, Diva-GIS, Circuitscape, LaTex, R
Driving licence	