Ecological determinants of butterfly vulnerability across the European continent

Tijl Essens1, Chris A.M Van Swaay1, Rutger A. Vos2 and Michiel F. Wallis de Vries1, 3\*\*

1De Vlinderstichting / Dutch Butterfly Conservation, P.O. Box 506, 6700 AM Wageningen, The Netherlands

2Naturalis Biodiversity Center, P.O. Box 9517, 2300 RA Leiden, The Netherlands

3Wageningen University, Laboratory of Entomology, P.O. Box 16, 6700 AA Wageningen, The Netherlands

\*Corresponding author [michiel.wallisdevries@vlinderstichting.nl](mailto:michiel.wallisdevries@vlinderstichting.nl)

# Abstract

In drawing up Red Lists, extinction risks of butterflies and other insects are currently assessed by information on status and trends in distribution and abundance. Incorporating information on species traits may increase our ability to predict species responses under environmental change and, hence, their vulnerability. We derived ecologically relevant biological and climatic trait dimensions, and used these to explain the variation in vulnerability indicators for 397 European butterfly species, out of 482 species present in Europe. For all but one vulnerability indicator, climatic traits predicted more variation than biological traits. The biological trait component reflecting mobility, development rate and overwintering stage, proved the major biological determinant of species vulnerability. We propose that this trait component offers a preferable alternative to the frequently used, but ecologically misleading generalist-specialist continuum. Size was a phylogenetically based trait component, and not relevant to explain species vulnerability. Our analysis contributes to the development of trait-based approaches to prioritizing vulnerable species for conservation at a European scale. Further regional scale analyses are recommended as a next step to improving our understanding of the biological basis of species vulnerability.

*Keywords: Life-history traits, Vulnerability, Conservation, Red Lists, Butterflies*

*Acknowledgements:* The authors wish to thank Albert Vliegenthart of the Dutch Butterfly Conservation, who kindly provided his expert knowledge on butterfly mobility.

# Introduction

The worldwide decline of biodiversity leads to losses of a broad array of ecosystem services, such as pollination in agricultural landscapes and recreational and cultural benefits (Nelson et al. 2009, Cardinale et al. 2012, Garibaldi et al. 2013). The European strategy and the Convention on Biological Diversity (CBD) aim to halt biodiversity loss by 2010-2020 (Balmford et al. 2005, European Commission 2011). Accomplishing this objective requires both continuous assessments of biodiversity status and ecological understanding of species vulnerability in relation to their environmental drivers. The threat status is currently assessed by the IUCN Red List methodology with increasingly reliable data from national to continental scales (IUCN 2005, Rodrigues et al. 2006, Keith et al. 2013). Data on insects are still limited however, despite signals that insects are particularly sensitive to environmental change (Thomas et al. 2004, Settele et al. 2008, Rasmont et al. 2015). Butterflies form the exception as their biology is comparatively well studied over a wide range of species and their conservation status is primarily based on population trends and distribution changes derived from decades of systematic monitoring (Van Swaay et al. 2008, 2010, 2011). At present, 37 butterfly species are listed as threatened on the Red List in Europe (9%), but national trends in abundance indicate alarming declines in many species; e.g., 48% in the Netherlands since 1992 and 76% in UK since 1976 (Fox et al. 2015, Van Swaay et al. 2016). Moreover, predictive scenarios of increased economic development and climate change suggest that as much as 78% of European butterfly species may lose >50% of the climatic niche area by 2080 (Settele et al. 2008). However, the ecological understanding of species vulnerability in relation to environmental change remains far from adequate. The growing recognition that the persistence of butterfly populations strongly depends on species’ intrinsic life-history characteristics to cope with environmental change, provides the opportunity to derive a mechanistic understanding of the observed population and distribution trends (e.g., Roy et al. 2001, Matilla et al. 2008, Diamond et al. 2011, Newbold et al. 2012, Nieto‐Sánchez et al. 2015, De Palma et al. 2015, Eskildsen et al. 2015).

Morpho-physio-phenological and behavioural traits impact fitness via their effects on growth, reproduction and survival (Violle et al. 2007). A set of life-history traits within a species is therefore most likely to be the outcome of long-term environmental selection of fitness and performance qualities for a population to persist (limited by the available phylogenetic space of individual species). Consequently, environmental gradients are often indicative for the composition of life-history traits (Carnicer et al. 2013, Leingärtner et al. 2014). Trait-continua in many taxa range from specialized to more generalist species and/or from slow to fast life-styles, and are often the result of growth vs. survival trade-offs that impact performance (Blackburn 1991, Wright et al. 2004, DeVictor et al. 2007, Bielby et al. 2007, Sæther et al. 2011, Janz and Nylin 2008). Previous studies suggest that environmental changes are likely to filter out Lepidoptera species that display a narrow niche breadth (food and habitat), slow development and sedentary behaviour (e.g., Matilla et al. 2006, 2011, Warren et al. 2001, Bartonova et al. 2014, WallisDeVries 2014). Conversely, butterfly species equipped with a set of adaptive traits, including high dispersal capacity, multiple generations per year, broad trophic as well as thermal niches, have the potential to expand their range and initiate adaptive radiations (e.g., Börschig et al. 2013, Ohlemüller et al. 2008).

The transboundary nature of butterfly distributions, environmental change and butterfly conservation efforts across the European continent, justifies up-scaling of trait-based studies. Here, we establish the relationships between trait components and species vulnerability indicators (RL status, endemicity, range size, habitat specialization, natural vs. anthropogenic habitat). We tested if, on a continental scale, (i) species can be ordered along ecologically relevant life-history traits (e.g., specialized to more generalist species, slow to fast life-styles, low to high mobility, narrow to broad climatic requirements), and (ii) that these main will explain a major part of the variation in butterfly vulnerability.

# Methodology

## Phylogenetic inference

When comparing traits across species the possibility must be taken into account that the observed distribution of trait values is not shaped by selection, but by auto-correlation caused by shared ancestry: some species might resemble one another merely because they are closely related rather than because of a common selective regime. Hence, the pattern of relatedness must be corrected for in any comparative analysis (Harvey & Pagel, 1991). To obtain an estimate of phylogeny for this purpose, we re-used the results of a recent survey of gene genealogies of the cytochrome oxidase I (COI) barcode marker in European Lepidoptera (Mutanen et al., 2016). Because the authors relied on computationally intensive methods of phylogenetic inference and incorporated numerous haplotypes per species, scalability constraints required their analyses to be partitioned into a number of monophyletic higher taxa. However, in our comparative analysis, we require a single, composite estimate. We synthesized this following a two-step approach similar to Antonelli et al. (2016) by first inferring a backbone tree and then grafting the trees for the monophyletic higher taxon partitions from Mutanen et al. (2016) onto it. To obtain input data for backbone tree inference we subsampled exemplar taxa from each of the higher taxon partitions and aligned their COI sequences using muscle (Edgar 2004), under default settings. COI generally aligns without problems, and this was the case here as well, as visually inspection demonstrated. From this alignment, we constructed a starting tree that we optimized with the “best” hill-climbing algorithm of PhyML (which picks the optimal topology recovered from either NNI or SPR branch swapping, Guindon et al., 2010) under a GTR+γ substitution model (Tavaré 1986). This starting tree we then provided as input for RAxML (Stamatakis 2014), which further improved the topology (under the same substitution model). On our backbone topology we then grafted the gene tree estimates from Mutanen et al. (2016). Since these gene trees include multiple haplotypes per species we first collapsed these to species level, under a conservative approach where every case where haplotypes from different species were entangled (i.e. cases of polyphyly or paraphyly), these were collapsed to a multifurcation that included all entangled species. When reconciling the taxa in this grafted tree with those for which trait data (described below) were available, we needed to prune numerous taxa from the tree lowering the number of tips from 4970 to 238, out of which three were taxonomically synonymized, to wit, *Cupido decolorata* (also in usage is the specific epithet *C. decoloratus*), *Erebia aethiopellus* (alternatively, *E. aethiopella*), and *Agriades aquilo* (alternatively, *Plebejus aquilo*).

## Species traits

For 397 European butterfly species, we incorporated five traits associated with species’ climatic preferences (i.e., climate optima and breadth of organisms) and six traits associated with species’ biology (i.e., morphological, physiological, phenological and behavioural adaptations innate to an organism) (**Table 1, Suppl. Mat. Table 1**). Climatic traits were adopted from Schweiger et al. (2014) and included species-specific niche optima and breadth of temperature, precipitation and soil water moisture content of the distribution area. For temperature and precipitation, we selected the annual mean and sum respectively, as well as the mean annual range, in order to capture main climatic variation along gradients of latitude, elevation and continentality (Schweiger et al. 2014).

Biological traits included average male/female forewing length and egg-volume. Wing size may play a role in dispersal capacity and survival ability (REF?), while egg size can act as a phylogenetic corrective for wing-size, given the allometric slopes between wing-size and egg-size for many butterfly subtaxa (García-Barros 2002). Larval diet breadth is an important limiting factor in butterfly vulnerability, in terms of range size, dispersal capacity and landscape use (e.g., García-Barros & Romo Benito 2010). Species phenology is associated with colonization ability, ranging from restricted climatic environments to wide distributions across a variety of climatic environments. Phenological traits included voltinism (i.e., the average number of generations per year), and overwintering stage (i.e., indicating how early species can reproduce in the season). Vagrancy reflects dispersal capacity and landscape use, and was based on a slightly adapted version of the classification by Dennis et al. (2004), complemented by expert knowledge for a total of 220 species. We used a linear regression model with voltinism, wingspan and range size to explain vagrancy with available data, and made predictions for the remaining 177 species (R2 = 0.505, df1,219, SE = 1.128), using the following equation:

Vagrancy = -0.472 + 0.482\*(Voltinism) + 0.44\*(Wingspan) + 0.001(Range Size)

## Species vulnerability

Vulnerability indicators included the *Red List status*, *Endemicity*, *Range size*, species *Affinity for natural habitats* and *Habitat specificity* (**Table 1**). The *Red List status* and *Endemicity* and *Range size* were adopted from Van Swaay et al. (2010); in further analyses *Red List status* and *Endemicity* were treated as binary values (Red List status: 1 if ‘Near Threatened’ or higher threat category, *Endemicity*: 1 for European endemics), because of small sample size of individual categories. Butterfly *Affinity for natural habitats* was derived from Van Swaay et al. (2006) as recorded occurrence in CORINE biotopes (Moss & Wyatt 1994). Species were categorized into users of (1) natural landscapes and (2) agricultural land and artificial landscapes (see details in **Suppl. Mat. Table 2**). *Habitat specificity* was assessed on the basis of the above-mentioned habitat use data by Van Swaay et al. (2006), using the species specialization index (SSI) (Julliard et al. 2006); the SSI takes into account variation in density among occupied habitats, assuming equal densities in occupied habitat and null densities in others. Values for wing size, egg size, range size and SSI were log10-transformed prior to analysis.

## Statistical analysis

We applied principal component analysis (PCA) to assess the scores of individual species along the main orthogonal axes of adaptive species traits. We separated biological and climatic traits in order to assess their relative contributions. We repeated PCA trait-based analyses at the level of butterfly families, to assess family-related differences. We chose not to apply further post-correction for phylogeny. Multiple linear least square regressions were used to identify the relative contribution of the species-specific PC values (predictive variables) to vulnerability indices (response variables). Analyses were executed in JMP software (Sall et al. 2005).

The trend data underlying the European Red List still rely to a substantial degree on expert opinion due to a lack of systematic monitoring data. Therefore, we checked if the obtained results of the multiple regression of vulnerability indicators against trait components at a European scale were consistent with two more quantitatively based vulnerability indicators at the national scale in the Netherlands: Red List category (on a scale from 1-6; Bos et al. 2006) and abundance trend slopes for the period 1992-2015 from the Dutch Butterfly Monitoring Scheme (Van Swaay et al. 2016).

# Results

## Phylogenetic inference

Our estimate of phylogeny is substantially based on the results of Mutanen et al. (2016), at least for the relationships between closely related taxa. As noted in the Methodology section, these results are haplotype trees, which we collapsed to species level, forming multifurcations anywhere where haplotypes from different species are topologically entangled. Nevertheless, following this strategy the tree still has a resolution (i.e. the number of nodes in the focal tree divided by the number for a fully resolved tree) of approximately 0.93. We reconstructed the deeper relationships across the monophyletic higher taxa of Mutanen et al. (2016) using the COI barcode marker. Our results for this backbone generally reflect our understanding of the systematics of the taxa in our sample.

## Trait components on Principal Component Axes

For biological traits, three components explained 78% of trait variation between species (**Table 2**). The first axis was strongly positively correlated to *Vagrancy*, *Voltinism* and *Overwintering stage*. The second axis was correlated to *Size* (wing and egg), whilst the third and least important axis was highly correlated to the degree of larval *Food plant specialization*.

For the climatic traits, we found two equally important axes, explaining 88% of variation (**Table 2**). The first rotated axis was best represented by a negative relationship between *Temperature range* on the one hand, and on the other hand, *Precipitation range* and *Species temperature index*. The 2nd axis was also correlated to the *Species temperature index* and in addition to water availability through *Annual precipitation* and *Soil moisture content*. Thus, *Species temperature index* played contributed to both axes.

The correlation between biological and climatic trait components was significant in four out of six cases P<0.01 for r>0.13), but its magnitude was low. The strongest correlation, r=-0.33 between PC-B1 and PC-C2, suggests an association of species from cool, moist climates with biological traits reflecting sedentary behaviour, producing a single generation per year and overwintering in early developmental stages; such trait combinations are typically found in artic-alpine species.

The PC values did vary significantly between butterfly families, but failed to produce significant family contrasts with the exception of one biological trait component (**Table 3**). Only the size–determined trait component PC-B2 showed substantial phylogenetic differences between families, with smallest values for Lycaenidae and largest in Papilionidae.

## Relationship between traits and vulnerability indicators

All five vulnerability indicators were strongly correlated or associated with each other (P<0.0001; generally positively, with the evident exception for *Range size* which showed negative correlations and associations); only *Endemicity* and *Habitat specificity* (SSI) were not significantly correlated with Red List status. The species-specific scores for biological and climatic trait components (**Suppl. Mat. Table 1**), were used to explain the variation in five vulnerability indicators. All five indicators were significantly related to a combination of several biological and climatic trait components. In general, relative contributions from climatic traits were more important to explain species vulnerability than biological traits, with the exception of the vulnerability indicator *Affinity for natural habitats*.

The explained variation in vulnerability indicators was highest for species *Range size* (**Table 4**). The phylogenetically determined component PC-B2 (wing and egg size) was the only one not significantly correlated with any of the vulnerability indicators. The contribution of trait components to the proportion of explained variation was mostly higher for climatic variables than for biological traits, except for the affinity of species for natural habitats, which was mainly determined by biological traits (**Fig. 1**). For the latter, the developmental traits were dominant, whilst *Food specialism* was least important for *Affinity for natural habitats*.

*RL status* was least explained by the trait components, but the predicted occurrence of species on the *Red List* still was adequately explained (83.4% correctly classified; kappa 0.16±0.06 P=0.0002). Species were more likely to be on the Red List in cool and moist climates with high annual ranges in temperature and precipitation. All vulnerability indicators, with the exception of the *Red List status*, were higher for species with strong host plant specialization. In contrast, vulnerability was lower for vagrant species, for species with large *Range size* as well as for multivoltine species overwintering at advanced developmental stages.

The response of vulnerability indicators to PC-C1 (annual temperature and precipitation range) was variable; it was positive for *RL status,* negative for species’ *Endemicity* and *Affinity for natural habitats* and curvilinear for the other two vulnerability indicators. The results for *Range size* and *Habitat specificity* indicate that higher species vulnerability occurs at either low or high values of species-specific *Temperature* and *Precipitation ranges*. PC-C2 (moisture) also pointed to higher vulnerability at climatic extremes (dry / wet climates) for *Red List status*, *Range size* and *Habitat specificity,* whereas *Endemicity* was typically higher in wetter climates.

## Application to trends in the Netherlands

The Red List status of 73 species native to the Netherlands was explained significantly by the European traits (R2=0.377) with 80% of the explained variation accounted for by the negative relation with the biological traits in PC-B1 (F=27.23, P<0.0001). The climatic component PC-C1 was the only other factor contributing significantly (F=5.34, P=0.024).

Abundance trend slopes of 40 species from the Dutch Butterfly Monitoring Scheme over the period 1992-2015 were explained to a lesser extent by the five trait components (R2=0.260), with only PC-B1 contributing significantly (F=7.19, P=0.011).

# Discussion

## Climatic dimensions of butterfly vulnerability

We detected ecologically meaningful trait dimensions, and used these to predict variation in vulnerability indicators for 397 European butterfly species, equivalent to 82% of the 482 species currently recognized for Europe. The dimensions found reflect climatic conditions, mobility, development rate and larval food specialization. Size was a major, phylogenetically-based trait component, but was least relevant to explain species vulnerability. Climatic traits predicted more variation in vulnerability indicators, except for species *Affinity for natural habitats*, which was mostly influenced by biological traits. The low degree of variation at family-level in the trait components affecting species vulnerability, suggested that phylogeny is a minor factor in determining the vulnerability of butterfly species.

We found that species restricted to the extremes of climatic gradients across the European continent are particularly vulnerable. In support of this result, the climatic rarity syndrome hypotheses (Willis and Whittaker 2000, amended by Ohlemüller et al. 2008), postulate that centres of high species rarity coincide with unusual climate conditions that differ greatly from the surrounding areas. Various centres of high species rarity are higher and colder and harbour numerous isolated relics that presumably resulted from climatic warming since the last ice age. The organisms in these vulnerable areas will be affected disproportionally by environmental change.

For butterflies, areas of special conservation concern can be found in the Alps, Pyrenees and the Carpathians that face increasing temperatures, shorter snow seasons, longer growing seasons (Ceppi et al. 2012, Brocard et al. 2013, Lindner et al. 2008, Gilbert & Vincent 2013, Beniston 2012). Consequently, species shift to higher elevations (Badeck et al. 2001, Wilson et al. 2005, Lenoir et al. 2010, Karolewski et al. 2007, Vanhanen et al. 2007), or northward in the case of boreal regions (EEA 2009). In addition, climatic variability may strongly impact insect development, predictability of food availability and phenological synchronicity between interdependent taxa (Walther et al. 2005, Vasseur et al. 2014). For the Alps, wetter winter/spring conditions in combination with drier summers are expected (Nemec et al. 2013, EEA 2009). Prolonged droughts are of particular concern for the Mediterranean, Central Europe and the Black Sea region, potentially leading to decreased growth rates, reduced fecundity and survival in insects (Cannon 1998, Ayres and Lombardero, 2000, Bale et al. 2002, Parmesan 2006, Rouault et al. 2006). These aforementioned areas concur largely with three priority areas for conservation conveyed by traditional biogeography (Glacial Mediterranean refugia, Glacial refugia in the eastern Palearctic and arctic and/or alpine refugia to the North and/or into the high mountain systems), although more potentially important areas have been distinguished since (e.g., Schmitt and Varga 2012).

## Biological dimensions of butterfly vulnerability

We found that the “biological trait complex” of voltinism, overwintering stage & mobility explains a large share of variation in species vulnerability. In explaining, well-established population trends and Red List status of butterfly species in the Netherlands, this even proved the major contributing trait component. To a lesser extent, the degree of larval food specialization also constitutes a significant factor determining species vulnerability. These results are in agreement with the regional-scale analysis for North-western Europe (WalisDeVries 2014; see **Suppl. Mat. Table 3** for correlations between trait components from that study with the present one), indicating that slow-growing sedentary species are most at risk for the European continent. Similarly, Matilla et al. (2006, 2008, 2011) demonstrated that diet and habitat specificity, overwintering in larval and pupal stages and short flight period and body size predispose Lepidoptera in Finland to distribution decline. Other studies highlighted the role of host plant growth form and life strategies in relation to butterfly development, voltinism and larval specificity (Dennis et al. 2004, Cizek et al. 2006, 2012, Bartonova et al. 2014). We propose that the abovementioned “biological trait complex” offers a suitable substitute to the widely used, but misleading specialist-generalist continuum (e.g. Dapporto & Dennis 2013). We find the term misleading because the inferred specialization does not have a biological basis, but is rather determined by the modern context of anthropogenic influence instead of the ecological conditions under which species evolved (see WallisDeVries 2014). Indeed, we showed that species affinity with natural habitats was mainly determined by this trait component.

The low but significant correlation between climate and biological traits in this study may reflect the influence of climatic gradients on the coincidence of plant-host relationships and butterfly phenology. In agreement, butterflies from the Iberian Peninsula and the Alps, exhibit a trait continuum with altitude, ranging from multivoltine trophic generalists with high dispersal capacity and broad climatic niches, to univoltine, trophic specialist species with restricted dispersal and narrow climatic niches (Carnicer et al. 2013, Leingärtner et al. 2014).

## Challenges and opportunities in conservation

Trait-based approaches to species vulnerability pose certain limitations. Shifts in response to climate warming vary greatly among species, suggesting that range shifts depend on multiple species traits and external drivers of change (e.g. Chen et al. 2011), while potentially important traits may not be included for all species, due to gaps in knowledge of species ecology. Detailed trait information, such as was available for species from North-Western Europe (WallisDeVries 2014), remains to be collected for many other European species. We did initially consider a number of additional traits (host plant growth form, aestivation, altitudinal limits, as well as other climatic variables, such as standard deviation of temperature and precipitation), but we decided to exclude them from the analysis due to methodological issues of trait variation and correlations between climatic variability and range size. Also we chose not to do detailed phylogenetic corrections, since taxonomic data are still incomplete (e.g., taxonomical changes for cryptic species). Moreover, there is considerable debate about the added value phylogenetic correction in trait-based studies, and in fact, numerous studies showed that correlative patterns among life-history traits remain largely undistorted even after a correction for phylogeny (Matilla et al. 2006, 2008, 2011, Päivinen et al. 2005, Wilson et al. 2004, Pavoine et al. 2012, Bartonova et al. 2014, Leingärtner et al. 2014). However, increasingly detailed trait data might also reveal regional differences for traits of the same species. Traits are, after all, primarily the result of environmental adaptation and filtering. Also evolutionary plasticity of traits likely varies between species and between populations of the same species. Depending on the genetic variation and environmental pressure, traits continue to change. A final point of attention, is that endemicity was typically higher in wetter climates, but as Europe constitutes the North-Western Edge of the Palaearctic region, as good as all species preferring dry or steppic conditions are not endemic (most of them also occur in Asia or Africa), making endemicity a biased variable.

In spite of the limitations, this study clearly shows a weak response of the Red List status in relation to species traits, which begs the question if the Red List status should be more strongly rooted in a biological basis. An important candidate for improving underlying biological arguments, could be the trait complex of voltinism, overwintering stage and mobility. Here, we propose a tentative list of 56 candidate Red List species with below-median values for PC-B1 and for range size (**Suppl. Mat. Table 4;** a further18 species meeting these criteria are already on the Red List). Similar attempts to predict extinction risk using multiple ecological traits, Kotiaho et al. (2005) for instance, revealed that threatened butterflies are characterized by narrow niche breadth, restricted resource distribution, poor dispersal ability, and short flight period. Based on this study, they were able identify seven vulnerable species for which the conservation status should be reconsidered in Finland.

Complementary regional analyses, for which specific biological trait information is more complete and climatic variation is less pronounced are still necessary to deepen our mechanistic understanding of species vulnerability. For the present study, the variation in climatic conditions across broad spatial scales is large, e.g., variation in continentality / oceanity with longitude or daily as well as seasonal variation in temperature and precipitation regimes with latitude and altitude (Settele et al. 2013, Schweiger et al. 2014). Again here, it seems advisable to distinguish regions on ecologically relevant grounds. Thermoclimatic conditions relevant to butterflies may, for instance, be incorporated as variables to select geographical areas for further disentanglement of biological traits in spatially explicit studies.

In conclusion, this analysis provides a basis to identify ecologically relevant species groups and prioritizes vulnerable species for conservation at European level. Although trait information is still limited at the European scale, our study indicates its potential to assess species vulnerability. Species vulnerability indicators were significantly determined by species-specific traits, primarily climate requirements. Furthermore, the biological trait complex reflecting mobility, development rate and overwintering stage proved another consistent determinant of species vulnerability that may be used to replace the anthropogenically determined specialist-generalist continuum. Further systematic regional scale analyses are recommended as a next step to improve the biological basis for species vulnerability.

# References

Antonelli, A, Hettling, H, Condamine, FL, Vos, K, Nilsson, RH, Sanderson, MJ, Sauquet, H, Scharn, R, Silvestro, D, Töpel, M, Bacon, CD, Oxelman, B, Vos RA (2016) Towards a Self-Updating Platform for Estimating Rates of Speciation and Migration, Ages, and Relationships of Taxa (SUPERSMART). Syst Biol doi:10.1093/sysbio/syw066

Ayres MP, Lombardero MJ (2000) Assessing the consequences of global change for forest disturbance from herbivores and pathogens. Sci Tot Environ 262:263–286

Badeck FW, Lischke H, Bugmann H, Hickler T, Höniger K, Lasch P, Lexer MJ, Mouillot F, Schaber J, Smith B (2001) Tree species composition in European pristine forests: Comparison of stand data to model predictions. Clim Chang 51:307–347

Bale JS, Masters GJ, Hodkinson ID, Awmack C, Bezemer TM, Brown VK, Butterfield J, Buse A, Coulson JC, Farrar J, Good JEG, Harrington R, Hartley S, Jones HT, Lindroth RL, Press MC, Symrnioudis I, Watt AD, Whittaker JB (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Glob Change Biol 8:1–16

Balmford A, Bennun L, Brink BT, Cooper D, Cote IM, Crane P et al (2005) The convention on biological diversity’s 2010 target. Science 307:212–213

Bartonova A, Benes J & Konvicka M (2014) Generalist-specialist continuum and life history traits of Central European butterflies (Lepidoptera) – are we missing a part of the picture? Eur J Entomol 111:543-553

Beniston M (2012) Is snow in the Alps receding or disappearing? WIRES Clim Chang 3:349–358

Bielby J, Mace GM, Bininda-Emonds OP, Cardillo M, Gittleman JL, Jones KE, Orme CDL,Purvis A (2007) The fast–slow continuum in mammalian life-history: an empirical reevaluation. Amer Nat 169:748–757

Blackburn TM (1991) Evidence for a fast slow continuum of life-history traits among parasitoid hymenoptera. Funct Ecol 5:65–74

Börschig C, Klein AM, von Wehrden H, Krauss J (2013) Traits of butterfly communities change from specialist to generalist characteristics with increasing land-use intensity. Basic Appl Ecol 14:547–554

Bos FG, Bosveld MA, Groenendijk DG, Van Swaay CAM, Wynhoff I. & De Vlinderstichting (2006). De Dagvlinders van Nederland: Verspreiding en Bescherming. Leiden: Nederlandse Fauna 7. Nationaal Natuurhistorisch Museum Naturalis (in Dutch), KNNV Uitgeverij and EIS-NL

Brocard E, Philipona R, Jeannet P, Begert M, Romanens G, Levrat G, Scherrer SC (2013) Upper air temperature trends above Switzerland 1959–2011. J. Geophys Res Atmos 118: 4303–4317

Cannon RJC (1998) The implications of predicted climate change in the UK, with emphasis on non-indigenous species. Glob Change Biol 4:785–796

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, Kinzig AP, Daily GC, Loreau M, Grace JB,Larigauderie A, Srivastava DS, Naeem S. (2012) Biodiversity loss and its impact on humanity. Nature 486:59–67

Carnicer J, Stefanescu C, Vila R, Dinca V, Font X, Peñuelas J (2013) A unified framework for diversity gradients: the adaptive trait continuum. Glob Ecol Biogeogr 22:6–18

Ceppi P, Scherrer SC, Fischer AM, Appenzeller C (2012) Revisiting Swiss temperature trends 1959–2008. Int J Climat 32:203–213

Cizek L, Fric Z, Konvicka M (2006) Host plant defences and voltinism in European butterflies. Ecol Entomol 31:337–344

Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Science 333:1024–1026

Dapporto L, Dennis RLH (2013) The generalist–specialist continuum: Testing predictions for distribution and trends in British butterflies. Biol Conserv 157:229–236

De Palma A, Kuhlmann M, Roberts SP, Potts SG, Börger L, Hudson LN, Lysenko I, Newbold T, Purvis A (2015) Ecological traits affect the sensitivity of bees to land‐use pressures in European agricultural landscapes. J Appl Ecol 52:1567-1577

Dennis RLH, Hodgson JG, Grenyer R, Shreeve TG, Roy DB (2004) Host plants and butterfly biology. Do host-plant strategies drive butterfly status? Ecol Entomol 29:12–26

Devictor V, Julliard R, Jiguet F (2008) Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos 117(4):507–514

Diamond S, Frame A, Martin R, Buckley L (2011) Species’ traits predict phenological responses to climate change in butterflies. Ecology 92:1005–1012

Edgar, RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. Nucleic Acids Res. 32(5):1792-1797

EEA (2009) Regional climate change and adaptation. The Alps facing the challenge of changing water resources. Copenhagen, Denmark, 143 p. http://www.riob.org/IMG/pdf/EEA\_Report\_8-2009\_Alps.pdf. Accessed 20 May 2016

Eskildsen A, Carvalheiro LG, Kissling WD, Biesmeijer JC, Schweiger O, Høye TT (2015) Ecological specialization matters: longterm trends in butterfly species richness and assemblage composition depend on multiple functional traits. Divers Distrib 21:792–802

European Commission (2011) Our life insurance, our natural capital: an EU biodiversity strategy to 2020. COM (2011) 244. Brussels.

Fox R, Brereton TM, Asher J, August TA, Botham MS, Bourn NAD, Cruickshanks KL, Bulman CR, Ellis S, Harrower CA, Middlebrook I, Noble DG, Powney GD, Randle Z, Warren MS, Roy DB (2015). The State of the UK’s Butterflies 2015. Butterfly Conservation and the Centre for Ecology & Hydrology, Wareham, Dorset.

Garcia-Barros E (2002) Taxonomic patterns in the egg to body size allometry of butterflies and skippers (Papilionoidea & Hesperiidae). Nota lepidopterologica 25:161–176

Garcia‐Barros E, Romo Benito H (2010) The relationship between geographic range size and life history traits: is biogeographic history uncovered? A test using the Iberian butterflies. Ecography 33:392–401

Garibaldi LA, Steffan-Dewenter I, Winfree R, Aizen MA, Bommarco R, et al. (2013) Wild pollinators enhance fruit set of crops regardless of honey bee abundance. Science 339:1608–1611

Gilbert A, Vincent C (2013) Atmospheric temperature changes over the 20th century at very high elevations in the European Alps from englacial temperatures. Geophys Res Lett 40:2102–2108

Guindon S., Dufayard J.F., Lefort V., Anisimova M., Hordijk W., Gascuel O. (2010) New Algorithms and Methods to Estimate Maximum-Likelihood Phylogenies: Assessing the Performance of PhyML 3.0. Systematic Biology, 59(3):307-21

Harvey, PH, Pagel, MD (1991). The comparative method in evolutionary biology (Vol. 239). Oxford: Oxford university press.

IUCN (2005) Guidelines for Using the IUCN Red List Categories and Criteria, IUCN-SSC http://www.iucn.org/webfiles/doc/ SSC/RedList/RedListGuidelines.pdf. Accessed December 2015

Janz N, Nylin S (2008) The oscillation hypothesis of host plant range and speciation. Specialization, speciation, and radiation: the evolutionary biology of herbivorous insects (ed. by K.J. Tilmon), University of California Press, Berkeley, CA, pp. 203–215

Julliard R, Clavel J, Devictor V, Jiguet F, Couvet D (2006) Spatial segregation of specialists and generalists in bird communities. Ecol lett 9:1237–44

Karolewski P, Grzebyta J, Oleksyn J, Giertych MJ (2007) Effects of temperature on larval survival rate and duration of development of *Lymantria monacha* (L.) on needles of *Pinus silvestris* (L.) and of L. dispar (L.) on leaves of *Quercus robur* (L.). Pol J Ecol 55:595–600

Keith DA, Rodríguez JP , Brooks TM, Burgman MA, Barrow EG, Bland L, Comer PJ, Franklin J, Link J, McCarthy MA, Miller RM, Murray NJ, Nel J, Nicholson E, Oliveira-Miranda MA, Regan TJ, Rodríguez-Clark KM, Rouget, M, Spalding MD ( 2015) The IUCN red list of ecosystems: motivations, challenges, and applications*.* Cons letters 8: 214-226

Kotiaho JS, Kaitala V, Komonen A, Päivinen J (2005) Predicting the risk of extinction from shared ecological characteristics. PNAS 8:1963–1967

Leingärtner A, Krauss J, Steffan‑Dewenter I (2014) Species richness and trait composition of butterfly assemblages change along an altitudinal gradient. Oecologia 175:613–623

Lenoir J, Gégout JC, Guisan A, Vittoz P, Wohlgemuth T, Zimmermann NE, Dullinger S, Pauli H, Willner W, Grytnes JA, Virtanen R, Svenning JC (2010) Cross-scale analysis of the region effect on vascular plant species diversity in southern and northern European mountain ranges. PLoS ONE 5:1–13

Lindner M, Garcia-Gonzalo J, Kolström M, Green T, Reguera R, Maroschek M, Seidl R, Lexer MJ, Netherer S, Schopf A, Kremer A, Delzon S, Barbati A, Marchetti M, Corona P (2008) Impacts of climate change on European forests and options for adaptation. Report to the European Commission Directorate General for Agriculture and Rural Development 173 p. http://ec.europa.eu/agriculture/analysis/external/euro\_forests/full\_report\_en.pdf. Accessed 22 May 2016

Mattila M, Kotiaho JS, Kaitala V, Komonen A (2008) The use of ecological traits in extinction risk assessments: A case study on geometrid moths. Biol Conserv 141:2322–2328

Mattila N, Kaitala V, Komonen A, Kotiaho JS,Paivinen J (2006) Ecological determinants of distribution decline and risk of extinction in moths. Conserv Biol 20:1161–1168

Mattila N, Kaitala V, Komonen A, Paivinen J, Kotiaho JS (2011) Ecological correlates of distribution change and range shift in butterflies. Insect Conserv Diver 4:239–246

Moss D, Wyatt BK (1994) The CORINE biotopes project: a database for conservation of nature and wildlife in the European community. Appl Geogr 14(4):327–349

Mutanen, M, Kivelä, SM, Vos, RA, Doorenweerd, C, Ratnasingham, S, Hausmann, A, Huemer, P, Dincă, V, Van Nieukerken, EJ, Lopez-Vaamonde, C, Vila, R, Aarvik, L, Decaëns, T, Efetov, KA, Hebert, PDN, Johnsen, A, Karsholt, O, Pentinsaari, M, Rougerie, R, Segerer, A, Tarmann, G, Zahiri, R, Godfray, HCJ (2016) Species-Level Para- and Polyphyly in DNA Barcode Gene Trees: Strong Operational Bias in European Lepidoptera. Syst Biol 65 (6): 1024-1040

Nelson E, Mendoza G, Regetz J, Polasky S, Tallis J, Cameron DR, Chan KMA, Daily GC, Goldstein J, Kareiva PM, Londsdorf E, Naidoo R, Ricketts TH, Shaw MR (2009) Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. Front Ecol Environ 7:4–11

Nemec J, Grube C, Chimani B, Auer I (2013) Trends in extreme temperature indices in Austria based on a new homogenised dataset. Int J Climatol 33:1538–1550

Newbold T, Butchart SHM, Sekercioglu CHS, Purves DW, Scharlemann JPW (2012) Mapping functional Traits: comparing abundance and presence-absence estimates at large spatial scales. PLoS ONE 7(8):e44019

Nieto‐Sánchez S, Gutiérrez D, Wilson RJ (2015) Long‐term change and spatial variation in butterfly communities over an elevational gradient: driven by climate, buffered by habitat. Divers Distrib 21:950–961

Ohlemüller R, Anderson BJ, Araujo MB, Butchart SHM, Kudrna O, Ridgely RS, Thomas C (2008). The coincidence of climatic and species rarity: high risk to small-range species from climate change. Biol Lett 4:568–572

Päivinen J, Grapputo A, Kaitala V, Komonen A, Kotiaho JS, Saarinen K, Wahlberg N (2005) Negative density distribution relationship in butterflies. BMC Biology 3:5

Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annu Rev Ecol Evol S 37:637–669

Pavoine S, Baguette M, Stevens VM, Leibold MA, Turlure C, Bonsall MB (2014) Life history traits, but not phylogeny, drive compositional patterns in a butterfly metacommunity. Ecology 95:3304–3313

Rasmont P, Franzén M, Lecocq T, Harpke A, Roberts S, Biesmeijer J, Castro L, Cederberg B, Dvorak L, Fitzpatrick Ú, Gonseth Y, Haubruge E, Mahé G, Manino A, Michez D, Neumayer J, Ødegaard F, Paukkunen J, Pawlikowski T, Potts S, Reemer M, Settele J, Straka J, Schweiger O (2015) Climatic Risk and Distribution Atlas of European Bumblebees. BioRisk 10:1–236

Rodrigues ASL, Pilgrim JD, Lamoreux JF, Hoffman M, Brooks TM (2006) The value of the IUCN Red List for conservation. Trends Ecol Evol 21:71–7

Rouault G, Candau JN, Lieutier F, Nageleisen LM, Martin JC, Warzée N (2006) Effects of drought and heat on forest insect populations in relation to the 2003 drought in Western Europe. Annals of Forest Science 63:613–624

Roy DB, Rothery P, Moss D, Pollard E, Thomas JA (2001) Butterfly numbers and weather: predicting historical trends in abundance and the future effects of climate change. J Anim Ecol 70:201–217

Sæther BE, Grøtan V, Engen S, Noble DG, Freckleton RP (2011) Rarity, life history and scaling of the dynamics in time and space of British birds. J Anim Ecol 80:215–224

Sall J, Creighton L, Lehman A (2005) JMP Start Statistics: a guide to statistics and data analysis using JMP and JMP IN software. Brooks/Cole-Thomson Learning, Belmont.

Schmitt T, Varga Z (2012) Extra-Mediterranean refugia: The rule and not the exception? Front Zool 9:22

Schweiger O, Harpke A, Wiemers M, Settele J (2014) CLIMBER: Climatic niche characteristics of the butterflies in Europe. ZooKeys 367:65–84

Settele J, Kudrna O, Harpke A, Kühn I, Van Swaay C et al (2008) Climatic Risk Atlas of European Butterflies. Moscow: Pensoft

Stamatakis, A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30(9):1312-1313

Tavaré S (1986). Some Probabilistic and Statistical Problems in the Analysis of DNA Sequences. Lectures on Mathematics in the Life Sciences. American Mathematical Society. 17: 57–86.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont LJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger A, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, OrtegaHuerta MA, Peterson AT, Phillips OL, Williams SE (2004) Extinction risk from climate change. Nature 427:145–148

Van Swaay C, Cuttelod A, Collins S, Maes D, López Munguira M, Šašić M, Settele J, Verovnik R, Verstrael T, Warren M, Wiemers M, Wynhof I (2010) European Red List of Butterflies. http://ec.europa.eu/environment/nature/conservation/species/redlist/downloads/European\_butterflies.pdf. Accessed December 2015

Van Swaay C, Maes D, Collins S, Munguira ML, Sasic M, Settele J, Verovnik R, Warren M, Wiemers M, Wynhoff I, Cuttelod A (2011) Applying IUCN criteria to invertebrates: how red is the Red List of European butterflies? Biol Conserv 144:470–478

Van Swaay C, Piotr N, Settele J, van Strien J (2008) Butterfly monitoring in Europe: methods, applications and perspectives Biodivers Conserv 17:3455–3469

Van Swaay CAM, Termaat T, Kok J, Huskens K, Poot M (2016) Vlinders en libellen geteld. Jaarverslag 2015 (in Dutch). Report VS2016.001, De Vlinderstichting, Wageningen

Van Swaay C, Warren M, Loïs G (2006) Biotope use and trends of European butterflies. J Insect Conserv 10:189–209

Vanhanen H, Veteli TO, Pailvinen S, Kellomaki S, Niemala P (2007) Climate change and range shifts in two insect defoliators: gypsy moth and nun moth – a model study. Silva Fennica 41:621–638

Vasseur DA, DeLong JP, Gilbert B, Greig HS, Harley CDG, McCann KS, Savage V, Tunney TD, O’Connor MI (2014) Increased temperature variation poses a greater risk to species than climate warming. Proc R Soc B 281:20132612

Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional! Oikos 116:882–892

WallisDeVries MF 2014. Linking species assemblages to environmental change: Moving beyond the specialist-generalist dichotomy. Basic Appl Ecol 15:279–287

Walther GR, Beißner S, Burga C (2005) Trends in the upward shift of alpine plants. J Veg Sci 16:541–548

Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D, Thomas CD (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414:65–69

Willis KJ, Whittaker RJ (2000) Paleoecology—the refugial debate. Science 287:1406–1407

Wilson RJ, Gutiérrez D, Gutiérrez J, Martínez D, Agudo R, Monserrat VJ (2005) Changes to the elevational limits and extent of species ranges associated with climate change. Ecol Lett 8:1138–1146

Wilson RJ, Thomas CD, Fox R, Roy DB, Kunin WE (2004) Spatial patterns in species distributions reveal biodiversity change. Nature 432:393–396

Wright IJ, Reich PB, Westoby M et al (2004) The worldwide leaf economics spectrum. Nature 428:821–827