SCIENTIFIC DATA

OPEN

DATA DESCRIPTOR

A new comprehensive trait database of European and Maghreb butterflies, Papilionoidea

Joseph Middleton-Welling[1], Leonardo Dapporto[2], Enrique García-Barros[3], Martin Wiemers[4,5], Piotr Nowicki[6], Elisa Plazio[6], Simona Bonelli[7], Michele Zaccagno[7], Martina Šašić[8], Jana Liparova[9], Oliver Schweiger[5], Alexander Harpke[5], Martin Musche[5], Josef Settele[5,10], Reto Schmucki[11] & Tim Shreeve[1] ✉

Trait-based analyses explaining the different responses of species and communities to environmental changes are increasing in frequency. European butterflies are an indicator group that responds rapidly to environmental changes with extensive citizen science contributions to documenting changes of abundance and distribution. Species traits have been used to explain long- and short-term responses to climate, land-use and vegetation changes. Studies are often characterised by limited trait sets being used, with risks that the relative roles of different traits are not fully explored. Butterfly trait information is dispersed amongst various sources and descriptions sometimes differ between sources. We have therefore drawn together multiple information sets to provide a comprehensive trait database covering 542 taxa and 25 traits described by 217 variables and sub-states of the butterflies of Europe and Maghreb (northwest Africa) which should serve for improved trait-based ecological, conservation-related, phylogeographic and evolutionary studies of this group of insects. We provide this data in two forms; the basic data and as processed continuous and multinomial data, to enhance its potential usage.

Background & Summary

The taxonomy, distribution, and biology of European butterflies has been studied since the 18th century. Due to the precise knowledge of changes in distribution and abundance, driven by extensive citizen science contributions, and their trophic specialisation and immediate responses to environmental changes[1] they are frequently used as indicators of environmental change[2]. Recently, a series of comprehensive resources have been published for European butterflies comprising a detailed taxonomic list[3], a dataset for 15,609 sequences for the COI mitochondrial markers for all Western-Central European species[4], a dated phylogenetic tree for all European species[5], atlases describing their detailed distributions[6], and climatic risk assessments[7]. In turn, species traits are fundamental descriptors of feeding ecology, life-history, morphology, resource use, behaviour and physiological constraints[8]. It has long been recognised[9] that the availability of such data is largely limited and incomplete. Only recently has a geographically extensive series of traits describing climatic preferences based on temperature and precipitation been produced[10] along with a series of six traits describing some features of feeding ecology,

[1]Centre for Ecology, Environment and Conservation, Faculty of Health and Life Sciences, Oxford Brookes University, Oxford, OX3 0BP, UK. [2]ZEN lab., Dipartimento di Biologia dell'Università di Firenze, Via Madonna del Piano 6, 50019 Comune di Sesto Fiorentino, Firenze, Italy. [3]Department of Biology, Universidad Autónoma de Madrid, Campus Cantoblanco, 28049, Madrid, Spain. [4]Senckenberg Deutsches Entomologisches Institut, Eberswalder Str. 90, 15374, Müncheberg, Germany. [5]Department of Community Ecology, Helmholtz Centre for Environmental Research - UFZ, Theodor-Lieser-Strasse 4, 06120, Halle, Germany. [6]Institute of Environmental Sciences, Jagiellonian University, Gronostajowa 7, 30-387, Kraków, Poland. [7]Department of Life Sciences and Systems Biology, Università degli Studi di Torino, Via Accademia Albertina 13, 10123, Torino, Italy. [8]Croatian Natural History Museum, Demetrova 1, 10 000, Zagreb, Croatia. [9]Institute of Entomology, Biology Centre CAS, Branisovska 31, Ceske Budejovice, Czech Republic. [10]iDiv, German Centre for Integrative Biodiversity Research, Halle-Jena-Leipzig, Deutscher Platz 5e, 04103, Leipzig, Germany. [11]UK Centre for Ecology and Hydrology, Maclean Building, Benson Lane, Crowmarsh Gifford, Wallingford, OX10 8BB, UK. ✉e-mail: tgshreeve@brookes.ac.uk

morphology, and life histories of butterflies from Western and Central Europe[4]. Species traits have been used to explain extinction risk and conservation status[11–13], colonisation and distribution changes[14,15], phenology and potential for range shifts in relation to climate change[16–18] and phylogeographic patterns[4] over large spatial scales. More detailed trait information at smaller spatial scales has been used to identify ecological groupings of species, for both butterflies in the British Isles[19] and macromoths of Central Europe[20]. However, most studies which have used trait information to identify ecological relationships, current extinction risks and distributions have tended to use either limited sources of information and/or limited numbers of butterfly species or have been concentrated at the regional scale[21,22].

Because single sources of trait information may be limited (e.g. in geographical scope) or conflict with each other[23], we present a new comprehensive open-access trait database[24,] with a maintained version (https://butterflytraits.github.io/European-Butterfly-Traits/index.html) of the European and Maghreb butterflies. We have aimed to pull together all the existing trait information available for each species. This has been done by synthesising the existing information from field guides, ecological atlases, reliable on-line sources, expert opinion and journal articles. Our database provides trait information for 542 taxa and covers 25 main traits (some subdivided - giving 217 trait states in total), including life history, resource use by all life-cycle stages, and behavioural information. Where specific traits are variable within species we also give data on this variability. We also process this data to provide multinomial and continuous variables and measures of their variability, resulting in a matrix of 542 species by 31 variables. We also list our information sources for the traits. Although some previous trait-based analyses have included vegetation associations, our trait database does not include these for two reasons. First, the habitat a species occurs in is determined by the occurrence and spatial distributions of species-specific resources[25,26]. Second, resource, life-history and behavioural traits can be used to predict the vegetation structures in which species occur[19].

Our database provides an outstanding resource for improving our understanding of fundamental mechanisms and processes such as how traits define species occurrence and co-occurrences, their responses to environmental change, their spatial dynamics, and their associations with vegetation structures. Since traits vary within different taxonomic groups, understanding their evolution and variability within different branches of the tree of life can also provide insights into phylogenetic constraints on species resource requirements and ultimately on their local abundance and large-scale occurrence and vulnerability to environmental change.

Methods

Taxon and geographic coverage. Our dataset (542 taxa) represents the complete butterfly fauna of mainland Europe including the western parts of Russia, the European islands, Macaronesia and the Maghreb (North Africa). This includes all of the 496 species occurring in Europe according to the latest checklist of European butterflies[3], but we have also included taxa (Table 1) that are confined the Maghreb or have very divergent traits from the nominate species according to some sources within our study area (Fig. 1). The nomenclature is consistent with that used in the checklist[3]. Trait information is recorded for all the families of butterflies included in the geographic area (Papilionidae, Hesperiidae, Pieridae, Riodinidae, Lycaenidae and Nymphalidae). For species that also occur beyond the study area, trait information was taken from the main study area, if possible. For example, for those species that have a pan-Palearctic distribution only information from the European range was included in our dataset.

Trait information was gathered from sources including field guides, books and atlases[27–62], scientific papers[63–166], and some selected online resources (https:/butterfliesoffrance.com, https://iucnredlist.org, https://lepidoptera.sk, http://luontoportti.com/suomi/en http://leps.it, http://eurobutterflies.com http://www.lepiforum.de, https://minambiente.it/home_natura https://micheltarrier.com/micheltarrier-com/rhopalocera, http://babochki-kavkaza.ru, http://pyrgus.de, http://butterflyeurope.co.uk, http://lepiforum.de) and direct observation in the field. Species-specific information sources are given in the database[24] and website (https://butterflytraits.github.io/European-Butterfly-Traits/index.html). In cases with multiple sources of trait information, data from peer reviewed papers were preferentially used; in practice this made up a small proportion of the total trait data. In cases where differences were identified in trait information between different sources, and could be identified as representing trait diversity, all sets of information were included in the trait database. Where sources clearly conflicted, we used the information that we deemed the most reliable. When published information was lacking, we inferred traits using photographs from two reliable sources (https://www.leps.it & http://pyrgus.de) if the traits could be unequivocally determined. This included hostplants and hostplant types, egg-laying location, larval location, adult feeding, adult basking type and basking sites. Trait information based on photographs was independently assessed by the authors in order to check the validity of the inferences. For some taxa certain trait information was not available in any source, and thus it is missing in the database.

The first version of the trait database[24] was finalised after three steps had been completed for all taxa. These were 1) mining all the standard references (e.g guides and atlases) for trait information, 2) filling gaps in trait information through a thorough literature search via Google Scholar and PubMed, and 3) emailing and asking experts on particular taxa for additional trait information.

Trait types. Our database covers the traits of all stages of the butterfly life cycle. Many trait types included in the database along with their subdivisions into individual states were derived from an earlier treatment of the butterflies of the British Isles[19] but the trait types have been extended for this database. Individual traits were defined prior to the beginning of data collation to allow for unambiguous coding. Comprehensive trait definitions are in the file traitdefinitions.pdf on the Dryad repository[24] and curated on-line version (https://butterflytraits.github.io/European-Butterfly-Traits/index.html). Most of the traits types in our raw data trait database (state table) are coded as binary, variables, but a minority are continuous (Online-only Table 1). Most traits included in this dataset are divided into multiple sub-traits. For example, the trait 'overwintering stage' comprises four binary

Species	Reason
Anthocharis belia	Non-European (Maghreb Endemic)
Argynnis auresiana	Non-European (Maghreb Endemic)
Berberia Abdelkader	Non-European (Maghreb Endemic)
Berberia lambessanus	Non-European (Maghreb Endemic)
Cigaritis allardi	Non-European (Maghreb Endemic)
Cigaritis siphax	Non-European (Maghreb Endemic)
Cigaritis zohra	Non-European (Maghreb Endemic)
Coenonympha arcanioides	Non-European (Maghreb Endemic)
Coenonympha corinna elbana	Sub-species
Coenonympha fettigii	Non-European (Maghreb Endemic)
Coenonympha gardetta darwiniana	Sub-species
Coenonympha vaucheri	Non-European (Maghreb Endemic)
Cupido minimus carswelli	Sub-species
Deudorix livia	Very small (possibly doubtful) European range
Euchloe falloui	Non-European (N Africa & SW Asia)
Hipparchia algirica	Non-European (Maghreb Endemic)
Hipparchia azorina occidentalis	Sub-species
Hipparchia caroli	Non-European (Maghreb Endemic)
Hipparchia ellena	Non-European (Maghreb Endemic)
Hipparchia genava	Disputed species
Hipparchia hansii	Non-European (Maghreb Endemic)
Hipparchia powelli	Non-European (Maghreb Endemic)
Hyponephele maroccana	Non-European (Maghreb Endemic)
Lasiommata meadewaldoi	Non-European (Maghreb Endemic)
Lycaena phoebus	Non-European (Maghreb Endemic)
Lysandra punctifera	Non-European (Maghreb Endemic)
Melanargia lucasi	Non-European (Maghreb Endemic)
Melitaea deserticola	Non-European (Maghreb Endemic)
Muschampia mohammed	Non-European (Maghreb Endemic)
Papilio saharae	Non-European (N Africa & SW Asia)
Pieris segonzaci	Non-European (Maghreb Endemic)
Plebejus allardii	Non-European (Maghreb Endemic)
Plebejus martini	Non-European (Maghreb Endemic)
Plebejus vogelii	Non-European (Maghreb Endemic)
Polyommatus atlanticus	Non-European (Maghreb Endemic)
Polyommatus dolus virgilius	Sub-species
Polyommatus icarus andronicus	Sub-species
Pontia glauconome	Non-European (N Africa & SW Asia)
Pseudochazara atlantis	Non-European (Maghreb Endemic)
Pseudochazara mamurra	Non-European in southern Balkans
Pseudochazara mniszechii	Non-European in southern Balkans
Pseudophilotes fatma	Non-European (Maghreb Endemic)
Pyronia janiroides	Non-European (Maghreb Endemic)
Tarucus rosaceus	Non-European (Maghreb Endemic)
Thymelicus hamza	Non-European (Maghreb Endemic)
Tomares mauretanicus	Non-European (Maghreb Endemic)

Table 1. Species not in the European checklist[3] but included in the trait database of European and Maghreb butterflies.

sub-traits each of which indicates one stage of a species' life cycle: egg, larva, pupa or adult. A species can have any combination of 0 and 1 for each of these sub-traits. This allows for the coding of trait plasticity across a species' range. Likewise, voltinism is coded as binary values for different states. This coding of the basic data (state table) has been transformed (traits table) into a series of multinomial traits, derived from binary states in the state table, and as continuous data, where the data in the state table is also continuous (Online-only Table 2). Additional variables are added in the traits table to describe variability within traits, resulting in a matrix of 542 species x 31 trait variables. Presenting the basic data within the database (state table) facilitates adding data in the future, which could include novel combinations of sub-trait states, whilst providing the processed data (traits table) and original raw data (state table) aids different analytical procedures.

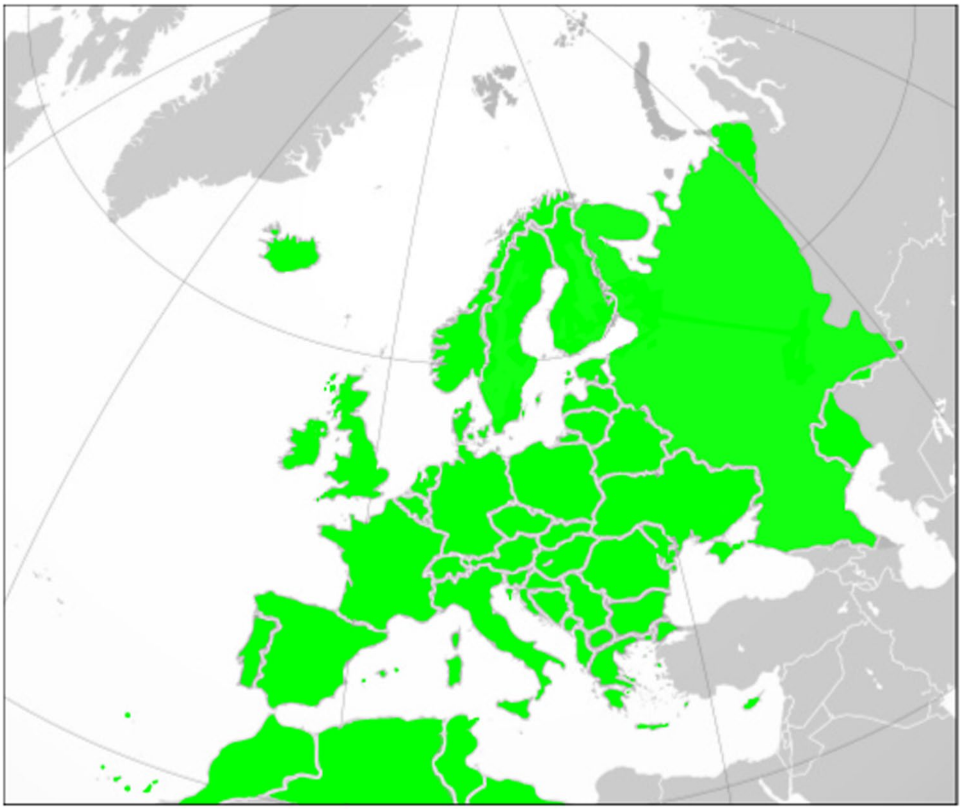

Fig. 1 The geographic area covered by the European and Maghreb butterfly database.

Traits are divided into four main types: 'life history', 'morphological', 'resource-based', and 'behavioural'. Life history traits describe a species' life cycle related to reproduction and also to growth and survival, including the number of generations per year (voltinism), egg laying strategy (egg laying type) and overwintering stage. We use wing size (both forewing length and precisely defined wingspan) as key morphological traits because they have been used in previous trait-based analyses, being correlated with mobility[167–169], development time[170], and reproductive output[171], as size correlates with many aspects of life history[172,173]. Wingspan is included as it also includes an approximate measure of thoracic size, and thus flight muscle mass which may influence flight capacity and dynamics. 'Resource-based traits' describe species' relationships with environmental resources. Resources include consumables that can be depleted over time when used or utilities that are not depleted. For example, 'adult feeding' describes the range of resources consumed by adults which may be temporarily or permanently depleted. Likewise, 'adult roosting' describes structures (utilities) used for roosting behaviour; these structures are resources, and although not directly consumed there may be a finite number of suitable features of this type within a location which may be limiting factors for local populations and may become the subject of both interspecific and intraspecific competition[25,26].

Some traits in the database are primarily behavioural such as 'mate locating type', but these traits are also closely linked with traits that relate more directly to resource-usage (in this case with 'mate locating location'); thus, behavioural traits can also be linked to resources. Larval hostplants are examined in detail in several traits because of their importance for the life cycle and population structure of butterflies. Some authors of previous work using butterfly traits have included 'habitat breadth' as a trait[14,174], although the physical structures/vegetation types occupied by species are not traits themselves, but the result of species occurring in those locations where their essential resources co-occur in spatial patterns and densities that they can use and these can change substantially across the geographic area our database covers. Essentially, species habitats are defined by their resources[25,26] and the resource requirements that species have are fundamental traits. Biotope or habitat associations are therefore not included in this dataset as they can be derived from the traits described in our database[24]. Additionally, biotope traits have been shown to have poor reproducibility among different trait sources[23] and have been found to be less useful than other types of traits for understanding the responses of butterflies to environmental change over time at a large scale[19,23]. At a smaller scale, biotope associations may be useful characteristics for aiding in butterfly conservation and habitat classification, but any attempt to synthesise information at a large geographic scale describing habitat preferences from multiple sources would likely be both error-prone and probably too coarse for most analyses. We also did not include measures of climatic requirements and geographic ranges in our dataset since they are already publicly available in the CLIMBER dataset[10].

Trait	Percentage of species within families with missing trait data						All (n = 542)
	Papiionidae (n = 16)	Hesperiidae (n = 49)	Pieridae (n = 61)	Riodinidae (n = 1)	Lycaenidae (n = 146)	Nymphalidae (n = 269)	
Overwintering stage	0	16.3	4.9	0	17.8	15.6	14.6
Overwintering location	12.5	40.8	24.6	0	37.0	54.3	43.7
Pupal location	18.8	36.7	19.7	0	38.4	40.1	36.3
Voltinism minimum	0	0	0	0	0	0.4	0.2
Voltinism maximum	0	0	0	0	0	0.4	0.2
Ant association	0	0	0	0	39.4	1.5	11.3
Wing index	0	0	0	0	0	0	0
Wing index variation	0	0	0	0	0	0	0
Hostplant specificity	0	4.1	1.7	0	4.8	15.9	9.8
Hostplant trophic category	0	4.1	0	0	3.4	15.9	9.2
Hostplant specificity index	6.3	8.2	6.6	0	9.6	11.9	10.1
Hostplant type	6.3	10.2	9.8	0	17.1	38.3	25.8
Hostplant growth form	6.3	10.2	9.8	0	17.8	36.1	24.9
Hostplant part	25.0	36.7	21.3	0	32.9	52.0	41.1
Hostplant age	43.8	67.3	41.0	0	74.6	81.0	72.3
Larval environment	0	36.7	21.3	0	28.1	40.9	33.6
Hostplant patch size	93.8	79.6	91.8	0	85.6	86.6	86.3
Egg laying type	6.25	36.7	14.8	0	37.7	43.9	37.1
Egg laying location	12.5	34.7	14.8	0	22.6	37.2	29.7
Egg laying light environment	75	75.5	82	0	77.4	82.2	79.9
Flight months min., max., av.	0	0	0	0	0	0	0
First and last flight months	0	0	0	0	0	0	0
Adult feeding	0	16,3	14.8	0	21.2	25.7	21.6
Adult roosting	37.5	81.6	44.3	0	75.3	68.0	67.5
Mate locating type	18.8	63.3	27.9	0	65.1	66.1	59.8
Mate locating location	18.8	67.3	32.8	0	76.0	73.6	67.3
Basking type	0	44.9	27.8	0	53.4	42.4	42.6
Basking location	0	44.9	32.8	0	51.4	43.1	43.0

Table 2. The percentage of each family within the European and Maghreb butterflies trait database with incomplete trait data, described by 31 multinomial and continuous variables in the traits table.

Data Records

The database[24] deposited on the Dryad Digital Repository and the live version (https://butterflytraits.github.io/European-Butterfly-Traits/index.html) including species specific information sources and a PDF-file describing each of the variables in the raw state table and traits table (ButterflyTraitDefinitions.pdf). The live version includes a mechanism for feedback and adding new information. For some taxa there are missing data and some traits currently have more missing values than others. Life history and hostplant related traits are extensively covered with few missing values, but behavioural traits have the most missing values as they usually require direct observation in the field, thus the disparity. However, the types of traits with missing data (Table 2) indicate where targeted fieldwork is required. Likewise, species with poor overall data also warrant targeted future effort.

Technical Validation

The records included in the database are based on previously published information from field guides, ecological atlases and peer reviewed journal articles, supplemented with the authors' personal observations. We are therefore confident as to their accuracy. When sources highlighted that records for a particular trait were doubtful, this information was not included in the dataset. The author team comprises experts on butterfly ecology coming from seven countries across Europe thus ensuring the highest level of repeated quality control while providing best knowledge across the biomes in Europe. The authors have examined the dataset to check for errors and to assess the accuracy of the trait information included. All data included in the dataset is fully referenced which allows anyone to go back to the original records for any piece of trait information. The dataset currently contains some missing values, especially for highly localised species and we intend to keep the database 'live' and to manage updates with new information. Certain traits such as voltinism and phenology (flight months) are known to vary across the latitudinal gradient as these traits may in part be responses to accumulated growing degree days[175]. We are confident that we have captured variability of these traits for the majority of species by consulting trait sources that encompass both the full European range as well as smaller areas. We will accept data into our live version of the database from existing resources, unpublished information and new published information. Each species has its own reference list so existing data can be checked and new information correctly integrated into the database. Data submission methods are described in the live database.

Usage Notes

We have provided the first extensive database of butterfly traits in Europe and North Africa. Of particular value is the species and geographic coverage and the extensive sets of traits that we have included. This provides an outstanding resource for improving our understanding of fundamental processes such as how traits define species co-occurrences and their responses to environmental change, their spatial dynamics, and their associations with vegetation structures. Since traits vary within different taxonomic groups, understanding their evolution and variability among different branches of the tree of life can also provide insights into phylogenetic constraints on species resource requirements and ultimately on their local abundance and large-scale occurrence and vulnerability to environmental change. As our trait database includes a large component of resource requirements for all life-history stages it can also be used to aid conservation efforts by focusing on resources that may be limited for vulnerable species at small to large spatial scales. Additionally, the inclusion of behavioural traits within the database can contribute to increasing our understanding of the roles of behavioural characteristics in determining species occurrences and resource use.

We have minimised processing of the data within the state table of the database. Individual variables in this state table may have poor linear relationships or spurious negative correlations due to their statistical distributions and outlier effects which can constrain both phylogenetic and ecological analyses. Although fuzzy methods of multivariate analyses may accommodate these issues[176] the processed multinomial and continuous variables with measures of variability provided in the traits table facilitates more conventional approaches to multivariate analyses. For some species there is missing data and some traits currently have more missing values than others. Whilst updating the database will supply some missing data there are imputation methods[177,178] that can be used to predict these values and we are confident that in the absence of verified data, imputed data can be used to retain both species and traits with missing values within analyses.

Received: 14 May 2020; Accepted: 14 September 2020;
Published online: 15 October 2020

References

1. Devictor, V. *et al*. Differences in the climatic debts of birds and butterflies at a continental scale. *Nat. Clim. Change* **2**, 121–124 (2012).
2. Thomas, J. A. Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philos. T. Roy. Soc B* **360**, 339–357 (2005).
3. Wiemers, M. *et al*. An updated checklist of the European Butterflies (Lepidoptera, Papilionoidea). *ZooKeys* **811**, 9–45 (2018).
4. Dapporto, L. *et al*. Integrating three comprehensive data sets shows that mitochondrial DNA variation is linked to species traits and paleogeographic events in European butterflies. *Mol. Ecol. Resour.* **19**, 1623–1636 (2019).
5. Wiemers, M., Chazot, N., Wheat, C., Schweiger, O. & Wahlberg, N. A complete time-calibrated multi-gene phylogeny of the European butterflies. *ZooKeys* **938**, 897–124 (2020).
6. Kudrna, O. *et al. Distribution Atlas of Butterflies In Europe* (Gesellschaft für Schmetterlingsschutz e.V., 2011).
7. Settele J. *et al. Climatic Risk Atlas Of European Butterflies. BioRisk 1* (Pensoft Publishers, 2008).
8. Moretti, M. *et al*. Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Funct. Ecol.* **31**, 558–567 (2017).
9. Balletto, E. & Kudrna, O. Some aspects of the conservation of butterflies in Italy, with recommendations for a future strategy (Lepidoptera, Hesperiidae and Papilionoidea). *Boll. Soc. Entomol. Ital.* **117**, 39–59 (1985).
10. Schweiger, O., Harpke, A., Wiemers, M. & Settele, J. CLIMBER: Climatic niche characteristics of the butterflies in Europe. *ZooKeys* **367**, 65–84 (2014).
11. Kotiaho, J. S., Kaitala, V., Komonen, A. & Päivinen, J. Predicting the risk of extinction from shared ecological characteristics. *P. Natl. Acad. Sci. USA* **102**, 1963–1967 (2005).
12. Bubova, T., Kulma, M., Vrabec, V. & Nowicki, P. Adult longevity and its relationship with conservation status in European butterflies. *J. Insect Conserv.* **20**, 1021–1032 (2016).
13. Essens, T., van Langevelde, F., Vos, R. A., Van Swaay, C. A. & WallisDeVries, M. F. Ecological determinants of butterfly vulnerability across the European continent. *J. Insect Conserv.* **21**, 439–450 (2017).
14. Pöyry, J., Luoto, M., Heikkinen, R. K., Kuussaari, M. & Saarinen, K. Species traits explain recent range shifts of Finnish butterflies. *Glob. Change Biol.* **15**, 732–743 (2009).
15. Woodcock, B. A. *et al*. Identifying time lags in the restoration of grassland butterfly communities: A multi-site assessment. *Biol. Conserv.* **155**, 50–58 (2012).
16. Diamond, S. E., Frame, A. M., Martin, R. A. & Buckley, L. B. Species' traits predict phenological responses to climate change in butterflies. *Ecology* **92**, 1005–1012 (2011).
17. Schweiger, O. *et al*. Increasing range mismatching of interacting species under global change is related to their ecological characteristics. *Glob. Ecol. Biogeogr.* **21**, 88–99 (2012).
18. Fric, Z. F., Rindoš, M. & Konvička, M. Phenology responses of temperate butterflies to latitude depend on ecological traits. *Ecol. Lets.* **23**, 172–180 (2020).
19. Shreeve, T. G., Dennis, R. L. H., Roy, D. B. & Moss, D. An ecological classification of British butterflies: ecological attributes and biotope occupancy. *J. Insect Conserv* **5**, 145–161 (2001).
20. Pavlikova, A. & Konvička, M. An ecological classification of Central European macromoths: habitat associations and conservation status returned from life history attributes. *J. Insect Conserv.* **16**, 187–206 (2012).
21. Eskildsen, A. *et al*. Ecological specialization matters: long-term trends in butterfly species richness and assemblage composition depend on multiple functional traits. *Divers. Distrib.* **21**, 792–802 (2015).
22. Bonelli, S., Cerrato, C., Loglisci, N. & Balletto, E. Population extinctions in the Italian diurnal Lepidoptera: an analysis of possible causes. *J. Insect Conserv.* **15**, 879–890 (2011).
23. Middleton-Welling, J., Wade, R. A., Dennis, R. L. H., Dapporto, L. & Shreeve, T. G. Optimising trait and source selection for explaining occurrence and abundance changes: A case study using British butterflies. *Funct. Ecol.* **32**, 1609–1619 (2018).
24. Middleton-Welling, J. *et al*. Trait data of European and Maghreb butterflies. *Dryad Digital Repository* https://doi.org/10.5061/dryad.6m905qfx6 (2020).
25. Dennis, R. L. H., Shreeve, T. G. & Van Dyck, H. Habitats and resources: the need for a resource-based definition to conserve butterflies. *Biodivers. Conserv.* **15**, 1943–1966 (2006).
26. Dennis, R. L. H. *A Resource-Based Habitat View For Conservation: Butterflies In The British Landscape* (John Wiley & Sons, 2010).

27. Balletto, E., Barbero, F., Bonelli, S., Casacci, L. P., & Dapporto, L. *Butterflies (Lepidoptera: Papilionoidea)* Vol. I (Calderini, Verona, In Press).
28. Beneš, J. *et al. Butterflies Of The Czech Republic: Distribution and Conservation I & II* (SOM, 2002).
29. Bink, F. A. *Ecologische Atlas Van De Dagvlinders An Noordwest-Europa* (Schuyt & Co., 1992).
30. Dapporto, L. & Casnati, O. *Le Farfalle dell'Arcipelago Toscano* (Parco Nazionale Arcipelago Toscano, 2008).
31. Dennis, R. L. H. *A Resource-based Habitat View For Conservation: Butterflies In The British Landscape* (John Wiley & Sons, 2010).
32. Fernández-Rubio, F. *Guía De Mariposas Diurnas De La Península Ibérica, Baleares, Canarias, Azores y Madeira* (Pirámide, 1991).
33. García-Barros, E., Munguira, M. L., Stefanescu, C. & Vives, A. *Fauna Iberica, Lepidoptera: Papilionoidea*. Vol. 37 (Museo Nacional de Ciencias Naturales, CSIC, 2013).
34. Henriksen, H. J. & Kreutzer, I. B. *The Butterflies Of Scandinavia In Nature* (Skandinavisk Bogforlag, 1982).
35. Hesselbarth, G., Van Oorschot, H. & Wagener, S. Die Tagfalter Der Türkei: Unter Berücksichtigung Der Angrenzenden Länder. *Bd. 2. Spezieller Teil: Nymphalidae. Fundortverzeichnis, Sammlerverzeichnis, Literaturverzeichnis, Indices* (Wagener, 1995).
36. Higgins, L. G. & Riley, N. D. *A Field Guide To The Butterflies Of Britain And Europe* 3rd Edn (Collins, 1980)
37. Kudrna, O. *A Revision Of The Genus Hipparchia* (Classey, 1977).
38. Lafranchis T. *Butterflies Of Europe: New Field Guide And Key* (Diatheo, 2004).
39. Lafranchis, T. & Geniez, P. *Les Papillons De Jour De France, Belgique Et Luxembourg Et Leurs Chenilles* (Biotope Editions, 2000)
40. Layberry, R. A., Hall, P. W. & Lafontaine, J. D. *The Butterflies Of Canada* (University of Toronto Press, 1998).
41. LSPN. *Les Papillons De Jour Et Leurs Biotopes* (Pro Natura, 1987).
42. Luquet, G. C. & Demerges, D. *Papilions De L'annexe IV De La Directive 92/43/CEE. Papilio hospiton* (Ministère de L'écologie Du Développement Et De L'Aménagement Durables, 2007).
43. Maravalhas, E. *As Borboletas De Portugal / The Butterflies of Portugal*. (Apollo Books, 2003).
44. Munguira, M. L., Barea-Azcón, J. M., Castro, S., Olivares, J. & Miteva, S. *Species Recovery Plan For The Zullichi's Blue (Agriades zullichi)* (Butterfly Conservation Europe, 2015).
45. Munguira, M. L., Castro, S, Barea-Azcón, J. M., Olivares, J. & Miteva, S. *Species Recovery Plan For The Sierra Nevada Blue Polyommatus (Plebicula) golgus* (Butterfly Conservation Europe, 2015).
46. Munguira, M. L., Barea-Azcón, J. M, Castro,S., Olivares, J. & Miteva, S. *Species Recovery Plan For the Andalusian Anomalous Blue (Polyommatus violetae)* (Butterfly Conservation Europe, 2015).
47. Munguira, M. L., Olivares, J,, Castro, S., Barea-Azcón, J. M., Romo, H. & Miteva, S. *Species Recovery Plan For The Spanish Greenish Black-tip (Euchloe bazae)* (Butterfly Conservation Europe, 2015).
48. Muñoz Sariot, M. G., *Biología Y Ecología De Los Licénidos eEspañoles*. (Muñoz Sariot, 2011).
49. Newland, D., Still, R., Swash, A. & Tomlinson, D. *Britain's Butterflies: A Field Guide To The Butterflies Of Britain And Ireland - Fuly Revised And Updated 3rd Edn* (Princeton University Press, 2015).
50. Pamperis, L. N. *The Butterflies Of Greece* (Bastas-Plessas Graphic Arts, 1997).
51. Paolucci, P. *Butterflies And Burnets Of The Alps And Their Larvae, Pupae and Cocoons* (WBA-Books, 2013).
52. Settele, J. *et al. Climatic Risk Atlas Of European Butterflies* (Pensoft, 2008).
53. Settele, J., Steiner, R., Reinhardt, R., Feldmann, R. & Hermann, G. *Schmetterlinge: Die Tagfalter Deutschlands* (Ulmer, 2015)
54. Thompson, R. & Nelson, B. *The Butterflies And Moths Of Northern Ireland* (Blackstaff Press, 2006).
55. Tolman, T. & Lewington, R. *Collins Butterfly Guide: The Most Complete Guide To The Butterflies Of Britain and Europe* (Collins, 2008).
56. Tshikolovets, V. V. *Butterflies of Europe & The Mediterranean Area*. (Tshikolovets Publications, 2011).
57. Tutin, T. *et al. Flora Europaea*; Vol. 1–5 (Cambridge University Press, 1964-1980).
58. Gilbert, F. & Zalat, S. *Butterflies Of Egypt: Atlas, Red Data Listing And Conservation* (BioMAP, 2007).
59. Korshunov, Y. & Gorbunov, P. *Dnevnye Bbabochki Aziatskoi Chasti Rossii. Spravochnik. [Butterflies of the Asian part of Russia. A handbook* in Russian] (Ural University Press, 1995).
60. F. *Die Tagfalter Mitteleuropas - Östlicher Teil, Bestimmung - Biotope Und Bionomie - Verbreitung - Gefährdung* (Self-published, 2004).
61. Nekrutenko, Y. P. The Butterflies Of The Caucasus. Keys To Their Identification. *Papilionidae, Pieridae, Satyridae, Danaidae* (Dumka, 1990).
62. Baytas A. *A Field Guide To The Butterflies Of Turkey*. (NTV, 2007).
63. Aguiar, A. M. F., Wakeham-Dawson, A. & Jesus, J. G. F. The life cycle of the little known and endangered endemic Madeiran Brimstone Butterfly *Gonepteryx maderensis* Felder, 1862 (Pieridae). *Nota Lep.* **32**, 145–157 (2009).
64. Aussem, B. & Hesselbarth, G. Die Praeimaginalstadien von *Pseudochazara cingovskii* (Gross, 1973) (Satyridae). *Nota Lep.* **3**, 17–23 (1980).
65. Back, W. Die Praimaginalstadien von *Euchloe charlonia* (Donzel, 1842) im Vergleich tu *Euchioe penia* (FREYER, 1852) und *Euchloe transcaspica* ssp. *amseli* (Gross & Ebert, 1975). *Atalanta* **22**, 357–363 (1991).
66. Bartonova, A., Benes, J. & Konvička, M. 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 (2014).
67. Bitzer, R. J. & Shaw, K. C. Territorial behavior of *Nymphalis antiopa* and *Polygonia comma* (Nymphalidae). *J. Lepid. Soc.* **37**, 1–13 (1983).
68. Bonelli, S., Barbero, F., Casacci, L. P. & Balletto, E. Habitat preferences *of Papilio alexanor* Esper [1800]: implications for habitat management in the Italian Maritime Alps. *Zoosystema* **37**, 169–177 (2015).
69. Camerini, G., Groppali, R. & Minerbi, T. Observations on the ecology of the endangered butterfly *Zerynthia cassandra* in a protected area of Northern Italy. *J. Insect Conser.* **22**, 41–49 (2018).
70. Celik, T. Adult demography, spatial distribution and movements of *Zerynthia polyxena* (Lepidoptera: Papilionidae) in a dense network of permanent habitats. *Eur. J. Entomol.* **109**, 217–227 (2013).
71. Cho, Y., Choi, D. S., Han, Y. G. & Nam, S. H. Conservation of *Hipparchia autonoe* (Esper) (Lepidoptera: Nymphalidae), Natural Monument in South Korea. *Entomol. Res.* **41**, 269–274 (2011).
72. Corbera, G., Escrivà, À. & Corbera, J. Hilltopping de les Papallones diürnes al turó d'Onofre Arnau (Mataró, Maresme). *L'Atzavarza* **20**, 59–68 (2011).
73. Courtney, S. Notes on the biology of *Zegris eupheme* (Pieridae). *J. Lepid. Soc.* **36**, 132–135 (1982).
74. Dennis, R. L. H. & Shreeve, T. G. Does the Marbled White butterfly *Melanargia galathea* (L.) (Papilionoidea: Satyrinae) behave like a white'? *Antenna* **28**, 139–194 (2004).
75. Dincă, V., Cuvelier, S., Zakharov, E. V., Hebert, P. D. & Vila, R. Biogeography, ecology and conservation of *Erebia oeme* (Hübner) in the Carpathians (Lepidoptera: Nymphalidae: Satyrinae). *Ann. Soc. Entomol. Fr.* **46**, 486–498 (2010).
76. Dincă, V., Kolev, Z. & Verovnik, R. The distribution, ecology and conservation status of the Spinose Skipper *Muschampia cribrellum* (Eversmann, 1841) at the western limit of its range in Europe (Hesperiidae). *Nota Lep.* **33**, 39–57 (2010).
77. Diringer, Y. Chronique d'élevage 3: L'élevage des coridon espagnols: *Polyommatus* (*Lysandra*) *albicans* (HERRICH-SCHÄFFER, 1852) et *Polyommatus* (*Lysandra*) *caelestissima* (VERITY, 1921) (Lepidoptera: Lycanidae). *Lépidoptères* **19**, 50–59 (2010).
78. Eichel, S. & Fartmann, T. Management of calcareous grasslands for Nickerl's fritillary (*Melitaea aurelia*) has to consider habitat requirements of the immature stages, isolation, and patch area. *J. Insect Conserv.* **12**, 677–688 (2008).
79. Fiedler, K. European and North West African Lycaenidae (Lepidoptera) and their associations with ants. *J. Res. Lepid.* **28**, 239–257 (1991).

80. Fric, Z. Adult population structure and behaviour of two seasonal generations of the European Map Butterfly, *Araschnia levana*, species with seasonal polyphenism (Nymphalidae). *Nota Lep.* **23**, 2–25 (2000).
81. Friedrich, E. Zur Biologie von *Limenitis populi* L. (Lep., Nymphalidae). *Entomol. Z.* **81**, 266–269 (1971).
82. García-Barros, E. Comparative data on the adult biology, ecology and behaviour of species belonging to the genera *Hipparchia*, *Chazara* and *Kanetisa* in central Spain (Nymphalidae: Satyrinae). *Nota Lep.* **23**, 119–140 (2000).
83. García-Villanueva, V., Moreno Tamaurejo, J. A., Vazquez Prado, F. M., Nieto Manzano, M. A. & Novoa Pérez, J. M. *Melitaea aetherie* (Hübner [6]) en la provincia de Badajoz: nuevos datos sobre su biología y distribución (Lepidoptera: Nymphalidae). *Bol. Soc. Entomol. Aragonesa* **42**, 279–288 (2008).
84. Gascoigne-Pees, M., Trew, D., Pateman, J. & Verovnik, R. The distribution, life cycle, ecology and present status of *Leptidea morsei* (Fenton 1882) in Slovenia with additional observations from Romania (Lepidoptera: Pieridae). *Nachr. Entomol. Ver. Apollo N. F.* **29**, 113–121 (2008).
85. Gascoigne-Pees, M., Verovnik, R., Wiskin, C. & Luckens, C. & Đurić, M. Notes on the lifecycle of *Melitaea arduinna* (Esper, 1783) ("Freyer's Fritillary") (Lepidoptera: Nymphalidae) with further records from SE Serbia. *Nachr. Entomol. Ver. Apollo, N. F.* **33**, 9–14 (2012).
86. Gascoigne-Pees, M., Verovnik, R., Franeta, F. & Popović, M. The lifecycle and ecology of *Pseudochazara amymone* (Brown, 1976), (Lepidoptera: Nymphalidae, Satyrinae). *Nachr. Entomol. Ver. Apollo, N. F.* **35**, 129–138 (2014).
87. Gascoigne-Pees, M., Wiskin, C., Đurić, M. & Trew, D. The lifecycle of *Nymphalis vaualbum* ([Denis & Schiffermüller], 1775) in Serbia including new records and a review of its present status in Europe (Lepidoptera: Nymphalidae. *Nachr. Entomol. Ver. Apollo, N. F.* **35**, 77–96 (2014).
88. Grill, A., Schtickzelle, N., Cleary, D. F., Neve, G. & Menken, S. B. Ecological differentiation between the Sardinian endemic *Maniola nurag* and the pan-European *M. jurtina. Biol. J. Linn. Soc.* **89**, 561–574 (2006).
89. Hernández-Roldán, J. L., Vicente, J. C., Vila, R. & Munguira, M. L. Natural history and immature stage morphology of *Spialia* Swinhoe, 1912 in the Iberian Peninsula (Lepidoptera, Hesperiidae). *Nota Lep.* **41**, 1–22 (2018).
90. Hernández-Roldán, J. L., Munguira, M. L. & Martin, J. Ecology of a relict population of the vulnerable butterfly *Pyrgus sidae* on the Iberian Peninsula (Lepidoptera: Hesperiidae). *Eur. J. Entomol.* **106**, 611–618 (2009).
91. John, E. & Parker, R. Dispersal of *Hipparchia cypriensis* (Holik, 1949) (Lep.: Satyridae) in Cyprus, with notes on its ecology and life-history. *Ent. Gaz.* **53**, 3–18 (2002).
92. John, E., Gascoigne-Pees, M. & Larsen, T. B. *Ypthima asterope* (Klug, 1832) (Lepidoptera: Nymphalidae, Satyrinae): its biogeography, lifecycle, ecology and present status in Cyprus, with additional notes from Rhodes and the eastern Mediterranean. *Ent. Gaz.* **61**, 1–22 (2010).
93. Jutzeler, D. Okologie und erste Stände des italienischen Schachbrettes *Melanargia arge* (Sulzer, 1776) (Lepidoptera: Satyridae). *Nota Lep.* **16**, 213–232 (1994).
94. Jutzeler, D. & Grillo, N. Une visite a l'ile de Vulcano (dans les iles Eoliennes, Sicile) pour *Hipparchia leighebi* (Kudrna, 1976) (Lepidoptera: Nymphalidae, Satyrinae). *Linn. Belg.* **15**, 119–126 (1995).
95. Jutzeler, D. & De Bros, E. Observations dans la nature et élevage de *Pseudochazara hippolyte williamsi* (Romei, 1927) et *Erebia hiapania* (Butler, 1868) de la Sierra Nevada (Andalousie, Espagne méridionale) (Lepidoptera: Nymphalidae, Satyrinae). *Linn. Belg.* **15**, 173–181 (1995).
96. Jutzeler, D., Biermann, H. & De Bros, E. Élevage de *Coenonympha corinna elbana* (Staudinger, 1901) du Monte Argentario (Toscane, Italie) avec explication géologique de l'aire de répartition du complexe corinna (Lepidoptera: Nymphalidae, Satyrinae). *Linn. Belg.* **15**, 332–347 (1996).
97. Jutzeler, D. & de Bros, E. D. Écologie, élevage et statut taxinomique de *Coenonympha corinna trettaui* (GROSS, 1970) de l'Isola di Capraia (Toscane, Italie) (Lepidoptera: Nymphalidae, Satyrinae). *Linn. Belg.* **16**, 70–78 (1997).
98. Jutzeler, D. *et al*. Study on the biology, morphology and etiology of *Hipparchia sbordonii* Kudrna, 1984 from Isola di Ponza (Latium, Italy) and *Hipparchia neapolitana* (Stauder, 1921) from the Monte Faito (Campanie, Italy) and data on the biology of *Hipparchia leighebi* (Kudrna, 1976) (Lepidoptera: Nymphalidae, Satyrinae). *Linn. Belg.* **16**, 105–132 (1997).
99. Jutzeler, D., Biermann, H., Grillo, N. & Volpe, G. On the taxonomical status of *Hipparchia blachieri* (Fruhstorfer, 1908) from Sicilia (Lepidoptera: Nymphalidae, Satyrinae). *Linn. Belg.* **17**, 69–83 (1999).
100. Jutzeler, D., Embacher, G., Hesselbarth, G., Malicky, M., Stangelmaier, G. & Cameron-Curry, V. Breeding experiments with *Erebia claudina* (Borkhausen, 1779) from the Radstaedter Tauern (Salzburg, Austria) (Lepidoptera: Nymphalidae, Satyrinae. *Linn. Belg.* **17**, 11–21 (1999).
101. Jutzeler, D., Russel, P. & Volpe, G. Nouveaux points de vue sur la position taxonomique des cinq populations insulaires du complexe d' *Hipparchia wyssii* Christ (1889) se basant sur la connaissance de leurs états pré-imaginaux (Lepidoptera: Nymphalidae, Satyrinae). *Linn. Belg.* **20**, 9–44 (2007).
102. Kleckova, I., Konvička, M. & Klecka, J. Thermoregulation and microhabitat use in mountain butterflies of the genus *Erebia*: importance of fine-scale habitat heterogeneity. *J. Therm. Biol.* **41**, 50–58 (2014).
103. Koestler, W. The preimaginal stages of *Hipparchia mersina* Staudinger, 1871 - biology, ecology, phenology and breeding Lepidoptera Nymphalidae. *Entomol. Z.* **1152**, 85–90 (2005).
104. Kolev, Z. New data on the taxonomic status and distribution *of Polyommatus andronicus* Coutsis & Ghavalas, 1995 (Lycaenidae). *Nota Lep.* **28**, 35–48 (2005).
105. Konvička, M., Nedved, O. & Fric, Z. Early-spring floods decrease the survival of hibernating larvae of a wetland-inhabiting population of *Neptis rivularis* (Lepidoptera: Nymphalidae). *Acta Zool. Acad. Sci. Hungar.* **48**, 79–88 (2002).
106. Kuras, T., Beneš, J. & Konvička, M. Behaviour and within-habitat distribution of adult *Erebia sudetica sudetica*, endemic of the Hrubý Jeseník Mts., Czech Republic (Nymphalidae, Satyrinae). *Nota Lep.* **24**, 69–83 (2001).
107. Lafranchis, T. Biologie, écologie et répartition de *Carcharodus orientalis* (Reverdin, 1913) en Grèce. Comparaison avec *Carcharodus flocciferus* (Zeller, 1847) (Lepidoptera, Hesperiidae). *Linn. Belg.* **19**, 140-146 (2003).
108. Leigheb, G., Jutzeler, D. & Cameron Curry, V. The breeding of *Pseudophilotes barbagiae* De Prins & Van Der Poorten, 1970, an endemic species of the *Gennargentu massif*, Sardinia, Italy (Lepidoptera: Lycaenidae). *Linn. Belg.* **17**, 239–246 (2000).
109. Lopez-Villalta, J. S. Ecological trends in endemic Mediterranean butterflies. *Bull. Insectol.* **63**, 161–170 (2010).
110. Leigheb, G. & Cameron-Curry, V. Observations on the biology and distribution of *Pseudophilotes barbagiae* (Lycaenidae, Polyommatini). *Nota Lep.* **21**, 66–73 (1998).
111. Leigheb, G., Jutzeler, D. & Cameron Curry, V. The breeding *of Pseudophilotes barbagiae* De Prins & Van Der Poorten, 1970, an endemic species of the Gennargentu massif, Sardinia, Italy (Lepidoptera: Lycaenidae). *Linn. Belg.* **17**, 239–246 (2000).
112. Manino, Z., Leigheb, G., Cameron-Curry, P. & Cameron-Curry, V. Descrizione degli stadi preimarginali di *Agrodiaetus humedasae* Toso & Balletto, 1976 (Lepidoptera, Lycaenidae). *Boll. Mus. Reg. Sci. Nat. Torino* **5**, 97–101 (1987).
113. Möllenbeck, V., Hermann, G. & Fartmann, T. Does prescribed burning mean a threat to the rare satyrine butterfly *Hipparchia fagi*? Larval-habitat preferences give the answer. *J. Insect Conser.* **13**, 77–87 (2009).
114. Nardelli, U., Olivares, J. & Jutzeler, D. Etudes sur l'ecologie et le developpement de *Melanargia ines* (Hoffmannsegg, 1804) en Andalousie et comparaison avec les especes les plus proches (Lepidoptera: Nymphalidae, Satyrinae). *Linn. Belg.* **16**, 183–191 (1998).
115. Ômura, H. & Honda, K. Feeding responses of adult butterflies, *Nymphalis xanthomelas*, *Kaniska canace* and *Vanessa indica*, to components in tree sap and rotting fruits: synergistic effects of ethanol and acetic acid on sugar responsiveness. *J. Insect Physiol.* **49**, 1031–1038 (2003).

116. Özden, Ö. & Hodgson, D. J. Butterflies (Lepidoptera) highlight the ecological value of shrubland and grassland mosaics in Cypriot garrigue ecosystems. *Eur. J. Entomol.* **108**, 43–437 (2011).
117. Page, R. J. C. Perching and patrolling continuum at favoured hilltop sites on a ridge: A mate location strategy by the Purple Emperor butterfly *Apatura iris*. *Entomol. Rec. J. Var.* **22**, 61–70 (2010).
118. Pennekamp, F., Monteiro, E. & Schmitt, T. The larval ecology of the butterfly *Euphydryas desfontainii* (Lepidoptera: Nymphalidae) in SW-Portugal: food plant quantity and quality as main predictors of habitat quality. *J. Insect Conserv.* **17**, 195–206 (2013).
119. Pinzari, M. A comparative analysis of mating recognition signals in graylings: *Hipparchia statilinus* vs. *H. semele* (Lepidoptera: Nymphalidae, Satyrinae). *J. Insect Behav.* **22**, 227–244 (2009).
120. Pinzari, M. & Sbordoni, V. Species and mate recognition in two sympatric Grayling butterflies: *Hipparchia fagi* and *H. hermione genava* (Lepidoptera). *Ethol. Ecol. Evol.* **25**, 28–51 (2013).
121. Pittaway, A. R. *et al. Papilio saharae* Oberthür, 1879, specifically distinct from *Papilio machaon* Linnaeus, 1758 (Lepidoptera: Papilionidae). *Ent. Gaz.* **45**, 223–249 (1994).
122. Polcyn, D. M. & Chappell, M. A. Analysis of heat transfer in Vanessa butterflies: effects of wing position and orientation to wind and light. *Physiol. Zool.* **59**, 706–716 (1986).
123. Radchuk, V., Turlure, C. & Schtickzelle, N. Each life stage matters: the importance of assessing the response to climate change over the complete life cycle in butterflies. *J Anim. Ecol.* **82**, 275–285 (2013).
124. Rutowski, R. L. Variation of eye size in butterflies: inter-and intraspecific patterns. *J. Zool.* **252**, 187–195 (2000).
125. Sariot, M. M. Ciclo biológico, morfología de los estadios preimaginales y nuevos datos sobre la distribución de *Borbo borbonica zelleri* (Lederer, 1855) (Lepidoptera: Hesperiidae) en la provincia de Cádiz, Españ. *Rev. Gaditana Entomol.* **4**, 137–158 (2013).
126. Scott, J. A. Population biology and adult behavior of the circumpolar butterfly, *Parnassius phoebus* F. (Papilionidae). *Insect Syst. Evol.* **4**, iii–168 (1974).
127. Schurian, K. Beobachtungen zur Biologie und Ökologie von *Azanus ubaldus* (Cramer, 1782) auf den Kanarischen Inseln (Lepidoptera: Lycaenidae). *Nachr. Entomol. Ver. Apollo, N.F.* **37**, 41–46 (2016).
128. Slamova, I., Klecka, J. & Konvička, M. Diurnal behavior and habitat preferences of *Erebia aethiops*, an aberrant lowland species of a mountain butterfly clade. *J. Insect Behav.* **24**, 230–246 (2011).
129. Slancarova, J., Garcia-Pereira, P., Fric, Z. F., Romo, H. & Garcia-Barros, E. Butterflies in Portuguese 'montados': relationships between climate, land use and life-history traits. *J. Insect Conserv.* **19**, 823–836 (2015).
130. Slancarova, J. *et al.* Co-occurrence of three Aristolochia-feeding Papilionids (*Archon apollinus, Zerynthia polyxena* and *Zerynthia cerisyi*) in Greek Thrace. *J. Nat. Hist.* **49**, 1825–1848 (2015).
131. Stefanescu, C., Pintureau, B., Tschorsnig, H. P. & Pujade-Villar, J. The parasitoid complex of the butterfly *Iphiclides podalirius feisthamelii* (Lepidoptera: Papilionidae) in north-east Spain. *J. Nat. Hist.* **7**, 379–396 (2003).
132. Stuhldreher, G. & Fartmann, T. Oviposition-site preferences of a declining butterfly *Erebia medusa* (Lepidoptera: Satyrinae) in nutrient-poor grasslands. *Eur. J. Entomol.* **112**, 493–499 (2015).
133. Szentirmai, I. *et al.* Habitat use and population biology of the Danube Clouded Yellow butterfly *Colias myrmidone* (Lepidoptera: Pieridae) in Romania. *J. Insect Conserv.* **18**, 417–425 (2014).
134. Templado, J. Datos biológicos sobre *Melitaea deione* (Geyer) (Lep., Nymphalidae). *Bol. Estac. Cent.l Ecol.* **5**, 97–102 (1976).
135. Toso, G. G. & Balletto, E. Una nuova specie del genere *Agrodiaetus* Hübn. (Lepidoptera, Lycaenidae). *Annali Mus. Civico Storia Nat. G. Doria* **81**, 124–130 (1977).
136. Tóth, J. P. & Varga, Z. Morphometric study on the genitalia of sibling species *Melitaea phoebe* and *M. telona* (Lepidoptera: Nymphalidae). *Acta Zool. Hung.* **56**, 273–282 (2010).
137. Tvrtkovic, N., Mihoci, I. & Sasic, M. *Colias caucasica balcanica* Rebel, 1901 (Pieridae) in Croatia-the most western distribution point. *Natura Croatica* **20**, 375–385 (2011).
138. Väisänen, R., Kuussaari, M., Nieminen, M. & Somerma, P. Biology and conservation of *Pseudophilotes baton* in Finland (Lepidoptera, Lycaenidae). *Ann. Zool. Fenn.* **31**, 145–156 (1994).
139. Verovnik, R. *et al.* Conserving Europe's Most Endangered Butterfly: the Macedonian Grayling (*Pseudochazara cingovskii*). *J. Insect Conserv.* **17**, 941–947 (2013).
140. Verovnik, R., Franeta, F., Popović, M. & Gascoigne-Pees, M. The discovery of *Polyommatus aroaniensis* (Brown, 1976) in Bosnia and Herzegovina (Lepidoptera: Lycaenidae). *Nachr. Entomol. Ver. Apollo, N.F.* **36**, 177–180 (2015).
141. Vieira, V. Lepidopteran fauna from the Sal Island, Cape Verde (Insecta: Lepidoptera). *SHILAP-Rev. Lepidopt.* **6**, 243–252 (2008).
142. Vila, R. Comparative analysis and taxonomic use of the morphology of imma-ture stages and natural history traits in European species of *Pyrgus* Hübner (Lepidoptera: Hesperiidae, Pyrginae). *Zootaxa* **347**, 1–71 (2012).
143. Vovlas, A., Balletto, E., Altini, E., Clemente, D. & Bonelli, S. Mobility and oviposition site-selection in *Zerynthia cassandra* (Lepidoptera, Papilionidae): implications for its conservation. *J. Insect Conserv.* **18**, 87–597 (2014).
144. Wahlberg, N. The life history and ecology of *Melitaea diamina* (Nymphalidae) in Finland. *Nota Lep.* **20**, 70–81 (1997).
145. Wahlberg, N. Comparative descriptions of the immature stages and ecology of five Finnish Melitaeine butterfly species (Lepidoptera: Nymphalidae). *Entomol. Fennica* **11**, 167–174 (2000).
146. Wahlberg, N. On the status of the scarce fritillary *Euphydryas maturna* (Lepidoptera: Nymphalidae) in Finland. *Entomol. Fennica* **12**, 244–250 (2001).
147. Wiemers, M. The butterflies of the Canary Islands. A survey on their distribution, biology and ecology (Lepidoptera: Papilionoidea and Hesperioidea). *Linn. Belg.* **15**, 63–84 (1995).
148. Franeta, F., Kogovšek, N. & Verovnik, R. On the presence of *Pontia chloridice* (Lepidoptera: Pieridae) in the Republic of Macedonia. *Phegea* **40**, 17–20 (2012).
149. Franeta, F. & Đurić, M. On the distribution of *Colias caucasica balcanica* Rebel, 1901, with two new records for Serbia (Lepidoptera: Pieridae. *Nachr. Entomol. Ver. Apollo, N.F.* **32**, 31–37 (2011).
150. Coutsis, J. Revision of the *Turanana endymion* species-group (Lycaenidae). *Nota Lep.* **27**, 251–272 (2005).
151. Acosta Fernández, B. Una nueva subespecie de *Euchloe belemia* (Esper, [1800]) de la isla de Gran Canaria, Islas Canarias, España (Lepidoptera: Pieridae). *SHILAP-Rev. Lepidopt.* **36**, 173–182 (2008).
152. Brown, J. & Coutsis, J. G. Two newly discovered Lycaenid butterflies (Lepidoptera: Lycaenidae) from Greece, with notes on allied species. *Entomol. Gaz.* **29**, 201–213 (1978).
153. Brown, J. On the status of a little known Satyrid butterfly from Greece. *Entomol. Rec. J. Var.* **92**, 280–281 (1980).
154. De Prins, W. & Van der Poorten, D. Een nieuwe *Pseudochazara*-soort voor de wetenschap uit Noordoost-Griekenland (Lepidoptera, Satyridae). *Phegea* **10**, 7–21 (1981).
155. De Prins, W. & Van der Poorten, D. Overzicht van het genus *Pseudophilotes* in Europa en Noord-Afrika, met beschrijving van een soort uit Sardinie, nieuw voor de wetenschap (Lepidoptera, Lycaenidae). *Phegea* **10**, 61–76 (1982).
156. Higgins, L. G. *Hipparchia (Pseudotergumia) wyssii* Christoph, with descriptions of two new subspecies. *Entomol.* **100**, 169–171 (1967).
157. Kolev, Z. *Polyommatus dantchenkoi* (Lukhtanov & Wiemers, 2003) tentatively identified as new to Europe, with a description of a new taxon from the Balkan Peninsula (Lycaenidae). *Nota Lep.* **28**, 25–34 (2005).
158. Manil, L. Découverte de *Hipparchia (Pseudotergumia) wyssii* Christ dans l'île de La Palma (Canaries) et description d'une nouvelle sous-espèce: *Hipparchia wyssii tilosi* nova spp. (Lepidoptera Satyridae). *Linn. Belg.* **9**, 359–366 (1984).
159. Olivier, A. & Coutsis, J. G. A revision of the superspecies *Hipparchia azorina* and of the *Hipparchia aristaeus* group (Nymphalidae: Satyrinae). *Nota Lep.* **20**, 150–292 (1997).

160. Olivier, A. Taxonomy and geographical variation of *Satyrium ledereri* (Boisduval, 1848) with the description of a new subspecies from the Greek island of Sámos. *Phegea* **17**, 1–25 (1989).
161. Smith, D. A. S. & Owen, D. F. Inter-island variation in the butterfly *Hipparchia (Pseudotergumia) wyssii* (Christ, 1889) (Lepidoptera, Satyrinae) in the Canary Islands. *Nota Lep.* **17**, 175–200 (1995).
162. Thomson, G. *Maniola chia* - a new Satyrid from the Greek island of Chios (Lepidoptera: Nymphalidae: Satyrinae). *Phegea* **15**, 13–22 (1987).
163. Thomson, G. *Maniola halicarnassus* - a new Satyrid from south-western Turkey (Lepidoptera: Nymphalidae: Satyrinae). *Phegea* **18**, 149–155 (1990).
164. Scalercio, S. *et al*. How long is 3km for a butterfly? Ecological constraints and functional traits explain high mitochondrial genetic diversity between Sicily and the Italian Peninsula. *J. Anim. Ecol.*, https://doi.org/10.1111/1365-2656.13196 (2020).
165. Cini, A. *et al*. Host plant selection and differential survival on two Aristolochia L. species in an insular population of *Zerynthia cassandra*. *J Insect Conserv* **23**, 239–246 (2019).
166. Hernández-Roldán, J. L. *et al*. Integrative analyses unveil speciation linked to host plant shift in Spialia butterflies. *Mol Ecol.* **25**, 4267–4284 (2016).
167. Dennis, R. L. H., Hardy, P. B. & Dapporto, L. Nestedness in island faunas: novel insights into island biogeography through butterfly community profiles of colonization ability and migration capacity. *J Biogeogr* **39**, 1412–1426 (2012).
168. Sekar, S. A meta analysis of the traits affecting dispersal ability in butterflies: can wingspan be used as a proxy? *J. Anim. Ecol.* **81**, 174–184 (2012).
169. Kuussaari, M., Saarinen, M., Korpela, E. L., Pöyry, J. & Hyvönen, T. Higher mobility of butterflies than moths connected to habitat suitability and body size in a release experiment. *Ecol. Evol.* **4**, 3800–381 (2014).
170. García-Barros, E. Body size, egg size, and their interspecific relationships with ecological and life history traits in butterflies (Lepidoptera: Papilionoidea, Hesperioidea). *Biol. J. Linn. Soc.* **70**, 251–284 (2000).
171. Wiklund, C. & Kaitala, A. Sexual selection for large male size in a polyandrous butterfly: the effect of body size on male versus female reproductive success in *Pieris napi*. *Behav. Ecol.* **6**, 6–13 (1995).
172. Peters, R. H. *The Ecological Implications Of Body Size*. (Cambridge University Press, 1983).
173. Chown, S. L. *et al*. Scaling of insect metabolic rate is inconsistent with the nutrient supply network model. *Funct. Ecol.* **21**, 282–290 (2007).
174. Betzholtz, P. E., Pettersson, L. B., Ryrholm, N. & Franzén, M. With that diet, you will go far: trait-based analysis reveals a link between rapid range expansion and a nitrogen-favoured diet. *Proc. Roy. Soc. B* **280**, 20122305 (2013).
175. Cayton, H. L., Haddad, N. M., Gross, K., Diamond, S. E. & Ries, L. Do growing degree days predict phenology across butterfly species? *Ecology* **96**, 1473–147 (2015).
176. Chevenne, F., Doleadec, S. & Chessel, D. A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biol.* **31**, 295–309 (1994).
177. Penone, C. *et al*. Imputation of missing data in life-history trait datasets: which approach performs the best? *Methods Ecol. Evol.* **5**, 961–970 (2014).
178. Stekhoven, D. J. & Bühlmann, P. Missforest – non-parametric missing value imputation for mixed-type data. *Bioinformatics* **28**, 112–118 (2012).

Acknowledgements
We thank András Ambrus, Ivan Bolotov, Andrea Grill, Frank Pennekamp, and János Pál Tóth who kindly provided unpublished observational data on species of interest. This paper is an output from two sECURE workshops kindly supported by sDiv, the Synthesis Centre of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig (DFG FZT 118; WG 4.28 sECURE).

Author contributions
J.M.W. and T.S. conceptualised an initial version of the database. M.W., O.S., E.G.B., L.D. and S.B. suggested expansions and assisted in conceptualizing the full version of the database. J.M.W., L.D., P.N., E.P., T.S. and E.G.B. extracted trait information from sources. J.M.W., L.D., S.B., M.Z., T.S. and E.G.B. contributed trait information. M.W., L.D. and T.S. assisted with standardising the nomenclature of the species names included in the database. J.M.W. and T.S. wrote the first draft of the manuscript. All authors contributed to the writing, editing and proofing of the manuscript and all approved the final version submitted.

Competing interests
The authors declare no competing interests.

Additional information
Correspondence and requests for materials should be addressed to T.S.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.