



Just beautiful?! What determines butterfly species for nature conservation

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Abstract

Prioritization is crucial in nature conservation, as land and financial resources are limited. Selection procedures must follow objective criteria, and not primarily subjective aspects, such as charisma. In this study, we assessed the level of charisma for all European butterflies. Based on these data, we analysed the charisma values of the species listed on the annexes of the EU Habitats Directive and of the species being of conservation priority according to criteria derived by three objective criteria: Species ecological specialisation, distribution, and threat. The mean level of charisma was higher for species of the EU Habitats Directive than for species of conservation priority and for not-listed species. Five of the twenty most charismatic species were also listed on the EU Habitats Directive, but none occurred on the list of species being of conservation priority. A trait space analysis revealed remarkable differences between the different species assortments: The species listed on the EU Habitats Directive covered a large trait space and included many species with high charismatic value, but low ecological and biogeographical relevance, while species of high conservation priority covered a restricted trait space and did not overlap with charismatic species. According to our findings, the selection of species for nature conservation still follows a mix of being aesthetic combined with some ecological criteria.

Keywords Butterflies · Biodiversity conservation · Prioritizing · Charismatic species · Endangered species · Specialist species · EU Habitat Directive

Introduction

Prioritization is a main task in nature conservation, as land for conservation is scarce and financial resources are limited (Arponen 2012; Hill et al. 2016; Essens et al. 2017). Thus, prioritization includes all spatial scales: Ecotones across the globe (Myers et al. 2000), single ecosystems, communities, particular species and populations (Hill et al. 2016). Various tools have been developed to identify the most threatened and rarest ecosystems or

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which of them are characterized by extraordinarily high species richness or particularity in their species composition (Arponen 2012; Gauthier et al. 2013). Similarly, at the species level, many strategies focus on the conservation of the most endangered ones, species with geographically restricted distributions, and on species which are most sensitive to environmental changes (Simberloff 1998; Peterson et al. 2010). At the population level, conservation strategies frequently focus on the preservation of relict populations or on groups being characterized by unique genetic structures (Hampe and Petit 2005; Habel et al. 2011).

However, the applied selection procedures to identify the most appropriate ecosystems, species, or populations only rarely follow objective selection criteria (Cardoso 2012; Hochkirch et al. 2013a). Consequently, most organisms selected for the purpose of nature conservation are large and charismatic species, mostly vertebrates or vascular plants (Stork and Habel 2014, with references therein), but also incorporate beautiful invertebrates, such as colourful butterflies (Barua et al. 2012). Thus, the level of beauty of species strongly impacts the selection of taxa for nature conservation (Barua et al. 2012). However, charismatic species are of key relevance to sell nature conservation to politics and the public (Landová et al. 2018). Studies have shown that charismatic species positively influence attitudes towards nature conservation, increase awareness, and thus the acceptance of conservation action (Ducarme et al. 2013; Brambilla et al. 2013) and financial support (Bowen-Jones and Entwistle 2002; Home et al. 2009). Consequently, flagship, indicator and umbrella species are often taxa, which are extraordinary beautiful (Leader-Williams and Dublin 2000). This fact is also supported by the success story of the flag-ship-species-concept in nature conservation (Heywood 1995; Simberloff 1998; Barua et al. 2012). Without denying the importance of individual species as flagships in nature conservation, we are convinced that nature conservation should mainly follow ecological evidence (Pullin and Knight 2003; Harrison et al. 2008). However, it is still rarely studied, to which degree different approaches of selecting priority species in nature conservation are influenced by objective ecological criteria or by the level of beauty (Macdonald et al. 2017).

We assume that objective ecological criteria make nature conservation most efficient and transparent (see also Harrison et al. 2008). Therefore, in a previous study on the prioritization to conserve butterflies, Habel et al. (2019) presented a selection protocol based on three criteria: 1. Distribution of species (range restricted species, endemism), 2. Ecological specialisation (species demanding specific ecological requirements), and 3. Level of endangerment (according the IUCN Red List). This study showed that selection of species for nature conservation based on these three criteria do not agree with the species listed on the annexes of the EU Habitats Directive for the group of butterflies. In the study presented here, we therefore assessed the level of charisma for all 404 European butterfly species (except some species restricted to the Macaronesian islands, due to biogeographical reasons) based on wing characters. The most charismatic species (CS hereafter) identified according to our scoring were then compared with (1) the species listed on the annexes of the EU Habitat Directive (HD hereafter), (2) the species identified as species of conservation priority (SCP hereafter) according to the criteria defined in Habel et al. (2019), and (3) all remaining species not included in any of the three groups mentioned above (i.e. not considered, NC hereafter). We hypothesize that (1) species of all four groups (CS, HD, SCP, NC) differ in their trait space with species of HD having a higher and SCP a mostly similar charismatic value than not classified species, and that (2) HD species cover a larger trait space than SCP because HD species include charismatic species as well as species with high ecological relevance, but underrepresent species of high geographic relevance, as well as the truly threatened species. In addition, we asked citizens to rank the beauty of all CS, HD and SCP species to test whether our own scoring based on simple wing characters

reflects the perception of beauty by the society. We finally discuss how these results should influence future prioritization of species for nature conservation.

Material and methods

Data set

We used 404 butterfly species, which are recorded from the 27 member states of the European Union (according to the 2010 revision of the Taxonomy Commission of Butterfly Conservation, Wiemers et al. 2018, modified). We excluded all species that in the EU are restricted to the Macaronesian Islands because they represent a separate entity most closely related to North Africa; Schmitt (2020), species that became extinct in Europe prior to World War II, as well as temporary vagrants, and those that are not constantly established. For controversially discussed species complexes and sister species, we only considered the oldest species name (Kudrna et al. 2015).

We classified all remaining European butterfly species into (1) Species that are listed in the annexes of the EU Habitat Directive (HD) (European Union 1992), (2) Species which are of conservation priority (SCP) based on criteria related to ecological specialization, distribution patterns, and the level of threat (see Habel et al. 2019), (3) Charismatic species (CS) (classification described below), and (4) All other species not selected by one of these approaches (NC). Species of conservation priority (SCP) were identified based on their geographical distribution, level of threat, and ecological specialization (the latter composed of assessing larval food plant specialisation, habitat specialisation of imagoes, dispersal behaviour of imagoes); thus, species with restricted distributions, high degree of ecological specialization, and/or high level of threat were ranked as SCP in an iterative process (cf. Habel et al. 2019). A list of all species with respective classification is given in electronic Appendix 1.

Classification of charismatic species (CS)

The term charisma first appeared in conservation literature as a specific trait in flagship species identification (Heywood 1995). Quantifications of the level of charisma have been performed already in previous studies. For example, Brichetti and Gariboldi (1997) created an “anthropogenic value index” (based on bibliographic references), and Macdonald and colleagues (2017) calculated appeal scores for mammals across the globe using morphological characteristics and rarity (see also Courchamp et al. 2006; Macdonald et al. 2015). For our study, we used four morphological wing characteristics, that are known to be of particular relevance when it comes to the general beauty of a butterfly, i.e. being big, colourful, shiny or with conspicuous wing shape features (see Farroni et al. 2005; Manesi et al. 2015; Lopez-Collado et al. 2016), and thus are assumed to foster environmental concern and environment-friendly attitudes (Root-Bernstein et al. 2013; Tam et al. 2013; Ahn et al. 2014): (A) average size of forewing (> 40 mm: 2 points; > 30 mm: 1 point; ≤ 30 mm: 0 points); (B) colour of upper wing side (three or more contrasting colours: 2 points; similar, but one of these colours not conspicuous or two contrasting colours: 1 point; all others: 0 points); (C) shiny upper wing side (conspicuously shiny: 2 points; shiny, but not conspicuous: 1 point; not shiny: 0 points), and (D) shape of wings (with long tails or conspicuously curved margin: 2 points; similar, but not conspicuous: 1 point; no specific appendices

or shape: 0 points). Previous studies showed that these selected factors particularly attract attention and can enhance prosocial behaviour among people (Manesi et al. 2015; Lopez-Collado et al. 2016). We summed the values of all four wing traits and defined species with three or more points as charismatic species. Note that we have not weighted the respective characteristics here as each applied weighting of the four characteristics also might be biased by personal preferences and opinions and thus might not be objectively justifiable, we argue that an equal contribution of all four characteristics might be the most appropriate way here. The obtained scoring of charisma of each butterfly species is given in electronic Appendix 2.

In order to validate our method of estimating the charisma of the European butterfly species based on the four wing characters by the perception of citizens, we conducted an additional enquiry containing all species belonging to CS, HD or SCP. We prepared insect boxes (40 cm × 30 cm), each of them containing 16 equally sized unit trays. Individuals of each of the 94 taxa were pinned in the middle of each unit tray. These butterflies were provided to 34 citizens (all non-lepidopterologists). Each participant completed one questionnaire to classify the level of charisma of each butterfly species with values ranging from 1 (not charismatic) to 4 (highly charismatic). For each butterfly species, we calculated the median charisma rank given by all citizens. These data were regressed against the charisma values obtained by wing characters. Obtained data are provided in electronic Appendix 2.

Statistics

To test for significant differences in median charismatic values (morphological characters) between the four classifications (CS, HD, SCP, NC), we used an Ordinal logistic regression, i.e. Cumulative Link Mixed Model fitted with the Laplace approximation (clmm and Anova function (type II), packages “ordinal” (Christensen 2019), “car” (Fox & Weisberg 2019), “RVAideMemoire” (Hervé 2021)) with the classification as predictor, the charismatic value as response and the species identity as random factor. For post-hoc comparisons between classifications we used Tukey-adjusted comparisons (lsmeans and cld function, packages “multcompView” (Graves et al. 2019), “emmeans” (Lenth 2021)). To test for significant differences in median charismatic values (questionnaire) between the three classifications (CS, HD, SCP), we used a linear mixed effects model fit by REML (lmer and anova function (type II) with Satterthwaite’s method, packages “lmerTest” (Kuznetsova et al. 2017)) with the classification as predictor, the charismatic value as response and the species identity as random factor. For post-hoc comparisons between classifications we used Tukey-contrasts (glht function, package “multcomp” (Hothorn et al. 2008)). We plotted the probabilities of charismatic values for each of the four classifications (CS, HD, SCP, NC) based on either the ordinal-response or the linear model using the emmeans function in the “lsmeans” package (Lenth 2016).

To compare species specific trait spaces covered by the four groups of species defined above, we conducted an ordination analysis. First, we used the Gower dissimilarity coefficient (Gower 1971) with Podani’s (1999) extension to ordinal variables to create a distance matrix from our trait data (gowdis function in the FD package; Laliberté and Legendre 2010; Laliberté et al. 2014). We used: Proportion of total distribution within EU (binary: < 50%/≥ 50%), endemicity (binary: < 35,000 km²/≥ 35,000 km²), threat (ordinal: 0=LC (Least Concern), 1=NT (Near Threatened), 2=VU (Vulnerable), 3=EN (Endangered), 4=CR (Critically Endangered)), larval hostplant specialisation (ordinal: 0=polyphagous, 1=oligophagous, 2=monophagous), habitat specialisation (ordinal: 0=generalist, 1=intermediate;

2=specialist), dispersal behaviour (ordinal: 0=sedentary, 1=dispersive, 2=migratory), and the additive values of the four wing characteristics (continuous: size, ordinal: colour, shininess, shape). Second, we performed a non-metric multidimensional scaling (two axes) on the Gower distance matrix using the metaMDS function in the vegan package (Oksanen et al. 2016). We tested for differences between groups in trait space using PERMANOVA (adonis function, 1000 permutations). For illustration, traits were plotted post-hoc using the envfit function with 1000 permutations. All analyses were conducted in R 3.5.1 (R Core Team 2018). An overview of all parameters used and of all species-specific classifications is given in electronic Appendix 2.

Results

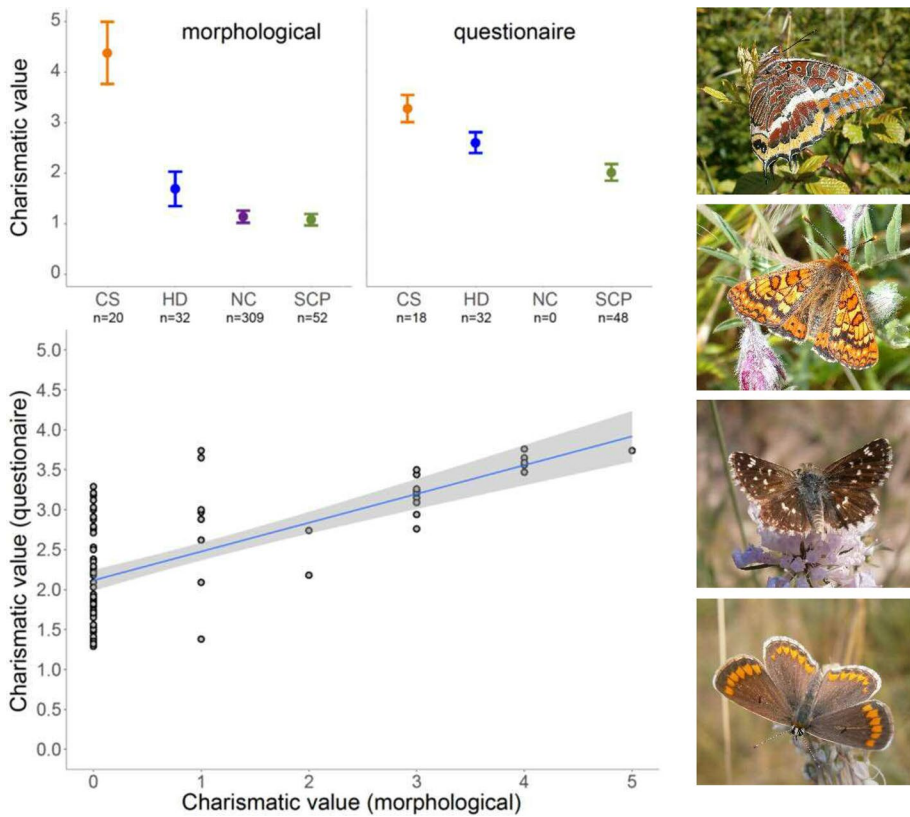
The charismatic value assessed by four wing characters for all 404 butterfly species differed significantly between the four classifications (Cumulative Link Mixed Model: $\chi^2 = -119.69$, $p < 0.001$). The charismatic value was higher for CS than for HD (z-ratio=7.094, $p < 0.0001$), NC (z-ratio=9.855, $p < 0.0001$) and SCP (z-ratio=8.747, $p < 0.0001$), higher for HD than for NC (z-ratio=3.435, $p < 0.01$) and SCP (z-ratio=3.182, $p < 0.01$), but did not differ between NC and SCP (z-ratio=1.143, $p < 0.6629$) (Tukey-adjusted comparisons) (Fig. 1).

The enquiry on being a charismatic butterfly species yielded median scorings of the subset of 94 species (i.e. all CS, HD and SCP taxa) of 2.5 (25%: 1.73/75%: 3.09), i.e. the majority of species were assessed as little to medium attractive. In line with the results presented above, the citizens in the enquiry (Linear mixed effects model: $F_{3,73.64} = 22.82$, $p < 0.001$) ranked CS (n=20) higher than HD (N=32) (z=4.269, $p < 0.001$) and SCP (n=48) (z=8.098, $p < 0.001$), and HD higher than SCP (z=4.670, $p < 0.001$) (Fig. 1). For the subset of species for which the questionnaire was conducted, the charismatic values of the two methods applied correlated strongly (Spearman's rank correlation: $\rho = 0.691$, $p < 0.001$) (Fig. 1).

The ordination analysis showed that species selected by the three approaches occupy different trait spaces (Fig. 2, ANOSIM $F_{3,409} = 56.238$, $R^2 = 0.29$, $p < 0.0001$; stress value: 0.13). The most important discriminating factor was endemism ($R^2 = 0.761$, $p < 0.001$), followed by dispersal ($R^2 = 0.629$, $p < 0.001$), habitat specialization ($R^2 = 0.613$, $p < 0.001$) and geographic distribution ($R^2 = 0.422$, $p < 0.001$). Hostplant specialization ($R^2 = 0.300$, $p < 0.001$), wing size ($R^2 = 0.231$, $p < 0.001$), wing shape ($R^2 = 0.215$, $p < 0.001$), threat ($R^2 = 0.196$, $p < 0.001$), colour ($R^2 = 0.190$, $p < 0.001$) and shininess ($R^2 = 0.027$, $p < 0.01$) explained much less. CS and SCP each occupied comparatively small areas in the trait space, which were largely located at different ends. CS were mainly characterised by wing traits and a high dispersal ability, SCP by a distribution mainly in the EU and by endemism. The HD species as well as the species not classified in any of the three groups were widely distributed over the whole trait space, but the distribution of the HD species was even wider than that of the not-classified species.

Discussion

Our results show that the mean level of charisma is higher for species of the EU Habitats Directive than for species of conservation priority and for not-listed species. Five of the twenty most charismatic species are also listed on the EU Habitats Directive, but none occurred on the list of species being of conservation priority. A trait space analysis show that species listed on the EU Habitats Directive cover a comparatively large trait space and



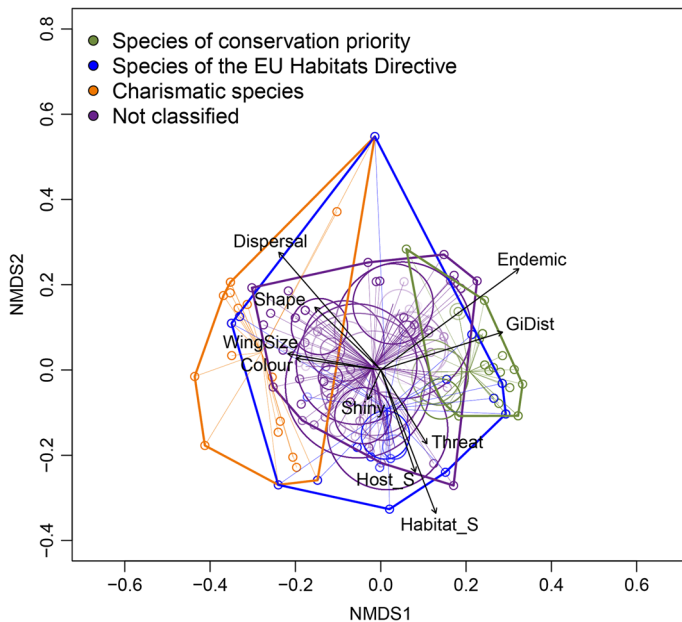


Fig. 2 Ordination plot (Non-metric Multidimensional Scaling, two axes, stress=0.13) of trait space occupied by species of conservation priority (SCP; green), species of the annexes of the EU Habitats Directive (HD; blue), charismatic species based on morphological traits (CS; orange) and not-classified species (NC; purple). Coloured spider graphs show centroids and hulls of each group. Each dot shows the position of one or more species, scaled by the number of species at each position (maximum 18). Black arrows show species traits including wing size (numeric), traits representing species distributional range (binary traits: endemism, range size 0 = $\geq 35,000$ km², 1 = $< 35,000$ km²; geographical distribution, distribution within Europe 0 = $> 50\%$, 1 = $\leq 50\%$) and traits related to dispersal propensity (0 = sedentary, 1 = dispersive, 2 = migratory), habitat specialization (0 = generalist, 1 = intermediate; 2 = specialist), larval hostplant specialization (0 = polyphagous, 1 = oligophagous, 2 = monophagous), and threat according to IUCN list (1 = Least concern LC, 2 = Vulnerable VU, 3 = Endangered EN, 4 = Critically Endangered CR)

or species existing in small and isolated relict populations in Europe, where they are at the margin of their distribution range (Hochkirch et al. 2013a).

Examples of species that were included in the Habitats Directive annexes based on a mixture of beauty and ecological speciality are the three “Large Blues” of the genus *Phengaris* (formerly *Maculinea*). These species show highly peculiar parasitic interactions with ants (e.g. Witek et al. 2013; Filz and Schmitt 2015), but also their beauty was scored well above average in our enquiry. Due to their specific and highly sensitive life cycles, these species are vanishing across Europe, and consequently they are red-listed (Van Swaay et al. 2010). Thus, these species are of high relevance for regional nature conservation (Munguira and Martín 1999), but do not meet the requirements to be of high conservation priority (SCP), as most of their distribution ranges is located outside of the EU, where most of the populations are non-threatened in the centres of their distributions further east (Tshikolovets 2011). Similarly, the Festoon *Zerynthia polyxena* and the Large Copper *Lycaena dispar* also have comparatively high beauty scorings according our enquiry (> 3) due to their colourful wings with a filigree patterning of the former and the shiny red wing colour of the latter. In addition, both have a relatively large size. However, both species are considered as least concern in the red list of Europe (Van Swaay et al. 2010). Here, the main

distribution areas again are beyond the EU (Tshikolovets 2011), and their conservation will also not preserve a specific habitat of particular threat. Consequently, such species can generate public awareness for nature conservation, but their specific protection is unlikely to achieve the objective of the most efficient and targeted conservation.

Our second hypothesis states that HD species cover a larger trait space than SCP because HD species include charismatic species as well as species of high ecological relevance, but underrepresent species of high geographic relevance as well as the truly threatened species. Since the selection of the butterfly species of the Habitats Directive annexes covers aesthetic, ecological, biogeographical and conservation aspects as a whole, it is not surprising that they occupy the largest trait space in our analyses. This is even larger than for the species selected for their charismatic wing features and the not listed species, both representing groups with high ecological and biogeographical diversity. SCPs occupy the by far smallest trait space as they only include specialists who usually have low dispersal capabilities, a limited number of larval food plants and often inhabit small ranges (Habel et al. 2019). These findings support our second hypothesis. Since similar phenomena are also obvious in other taxonomic groups, it is not surprising that the composition of the Habitats Directive annexes is often criticised (e.g. Cardoso 2012; Hochkirch 2013a, b; Habel et al. 2019). However, there are also opinions that on the one hand accept these criticisms, but fear that an intensive discussion of the annex species could weaken nature conservation in Europe. Such voices advise that it is better to have an effective nature conservation tool with known deficiencies than to jeopardise it by attempting to optimise it (e.g. Maes et al. 2013).

Therefore, we have to scrutinise the value of charismatic species in nature conservation. In general, the use of such species is also known as flag-ship species concept (Heywood 1995), which also can be successfully applied to invertebrates (Barua et al. 2012). Rodrigues and Brooks (2007) showed that such flag-ships, in addition to being charismatic and thus attractive to people, can represent suitable surrogates to conserve entire species communities and ecosystems under threat. However, surrogates have their strong limitations. Thus, Rodrigues and Brooks (2007) clearly underlined that surrogates have a particularly high probability of being effective if they are part of the target group. Nevertheless, even in this case, careful verification is necessary. For example, it has been shown that the large mammalian species in Africa are a good surrogate for all mammals, but not the famous "Big Five" (Williams et al. 2000). Surrogates across major taxonomic units performed substantially less well (Rodrigues and Brooks 2007), suggesting that the focus on vertebrates in European nature conservation could be one reason for the on-going decline of terrestrial invertebrates (e.g. Habel et al. 2016; Hallmann et al. 2017; Seibold et al. 2019; Van Klink et al. 2020). The selection of accurate invertebrate surrogates is therefore elementary for an optimised nature conservation addressing biodiversity as a whole.

The political and societal acceptance of charismatic flag-ship species is high and thus a prerequisite to implement nature conservation in real-life action (Barua et al. 2012). The willingness to protect species is increasing with their beauty (Landová et al. 2018). However, these species frequently miss conservation targets because of rather limited ecological significance for the conservation goal (Rodrigues and Brooks 2007). Therefore, the use of charismatic flagship species has already been severely criticised (Lorimer 2007; Brichetti and Gariboldi 1997; Ballourad et al. 2011; Brambilla et al. 2013). Previous studies also underlined that focusing on a few charismatic species not only neglect other (relevant) species (Pillon and Chase 2007; Amori et al. 2008), but may have even negative effects towards "non-charismatic species" (i.e. "background species") due to specifically adapted management regimes (Simberloff 1998; Andelman and Fagan 2000).

If one compares the HD and the SCP species, the iterative selection process of the latter ensures that they are good surrogates for the general conservation of butterflies in Europe and might also represent other groups of invertebrates. Thus, they might be a suitable group for the general conservation of invertebrates. However, the large majority of these butterfly species have rather limited public awareness, because most of them are neither big, colourful or otherwise particularly charismatic. This lack of appealing characteristics might be detrimental for the political formulation of conservation laws and their local and regional implementation (cf. Landová et al. 2018). Although the existing list of butterfly species in the Habitats Directive annexes does not have the problem of lack of acceptance, as several of them belong to the exceptionally beautiful species (see above), their suitability as surrogates must be questioned, partly because of their lack of ecological significance and partly because of their highly specialised and rare niches. If we focus exclusively on species of the Habitat Directive, we would likely miss the conservation of many ecologically relevant species and species communities. It is therefore important to establish a link between species appeal and their suitability to act as flagship and umbrella for as many diverse species communities as possible (see Lorimer 2007; Caro 2010; Macdonald et al. 2015; Verissimo and McKinley 2016).

In conclusion, we suggest that prioritisation is first made on the basis of objective (i.e. science-based) ecological criteria, such as for the SCPs, in order to identify the most relevant species for the conservation of their respective communities. In a second step, these communities can then be further supplemented by some charismatic flagships, which will achieve highest possible acceptance in politics and the society. With respect to our study, several aspects should be considered when interpreting the results: 1. Local perceptions of beauty by people and the relation of local people to nature may strongly vary and might play a stronger role in conservation acceptance than the charisma of single species (Kellert 1996a, b; Czech et al. 1998; Brackney and McAndrew 2001; Knight 2008; Tam et al. 2013; Ahn et al. 2014). For example, Macdonald et al. (2017) indicated cultural differences in stakeholder attitudes (see also Bowen-Jones and Entwistle 2002) and thus underlined that beauty is a very subjective value, which may strongly vary among ethnic groups. 2. In our study, we exclusively considered butterflies, because of the broad ecological knowledge available for this group. By selecting this generally rather charismatic group within the order Lepidoptera we included a bias associated with beauty in our study. However, our result show clear biases associated with beauty even within this group and we expect this to be even much clearer when including moths or other less charismatic groups. 3. We have to critically request the robustness of our scoring of charisma. The different factors were not weighted, which may lead to a bias in subjective perception, but also every applied weighting might be subjective as clear and universal measures of what makes an animal beautiful do not exist. 4. Lastly, butterflies, the selected group in this study, already underline this dilemma, since they represent a small group of all lepidoptera with the moths being much more species-rich and even of greater ecological relevance. However, moths neither scientifically nor socially enjoys the same attention as do butterflies. Thus, the selection of butterflies for this study also is largely a consequence of charisma consideration.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10531-021-02204-9>.

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Author contributions All authors developed the idea. JCH and TS compiled the data. MMG did the statistics. TS performed the enquiry with citizens. All authors contributed with writing and the interpretation of data.

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References

- Ahn H-K, Kim HJ, Aggarwal P (2014) Helping fellow beings: anthropomorphized social causes and the role of anticipatory guilt. *Psychol Sci* 25:224–229
- Amori G, Gippoliti S, Helgen KM (2008) Diversity, distribution, and conservation of endemic island rodents. *Quatern Int* 182:6–15
- Andelman SJ, Fagan WF (2000) Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? *Proc Natl Acad Sci* 97:5954–5959
- Arponen A (2012) Prioritizing species for conservation planning. *Biodivers Conserv* 21:875–893
- Ballouard J-M, Brischoux F, Bonnet X (2011) Children prioritize virtual exotic biodiversity over local biodiversity. *PLoS ONE* 6:e23152
- Barua M, Gurdak DJ, Ahmed RA, Tamuly J (2012) Selecting flagships for invertebrate conservation. *Biodivers Conserv* 21:1457–1476
- Bowen-Jones E, Entwistle A (2002) Identifying appropriate flagship species: the importance of culture and local contexts. *Oryx* 36:189–195
- Brackney M, McAndrew FT (2001) Ecological worldviews and receptivity to different types of arguments for preserving endangered species. *J Environ Educ* 33:17–20
- Brambilla M, Gustin M, Celada C (2013) Species appeal predicts conservation status. *Biol Conserv* 160:209–213
- Bricchetti P, Gariboldi A (1997) *Manuale pratico di ornitologia*. Edagricole, Bologna
- Cardoso P (2012) Habitats Directive species lists: Urgent need of revision. *Insect Conserv Divers* 5:169–174
- Caro TM (2010) *Conservation by proxy: indicator, umbrella, keystone, flagship, and other surrogate species*. Island Press, Washington, DC
- Christensen RHB (2019) Ordinal-regression models for ordinal data. R package version 2019.12-10. <https://CRAN.R-project.org/package=ordinal>
- European Union (1992) Council directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. Official J., (July), 7–50
- Courchamp F, Angulo E, Rivalan P, Hall RJ, Signoret L, Bull L, Meinard Y (2006) Rarity value and species extinction: The anthropogenic allee effect. *PLoS Biol* 4:e415
- Czech B, Krausman PR, Borkhataria R (1998) Social construction, political power, and the allocation of benefits to endangered species. *Conserv Biol* 12:1103–1112
- Ducarme F, Luque G, Courchamp F (2013) What are ‘charismatic species’ for conservation biologists? *BioSci Master Rev* 1:1–8
- Essens T, van Langevelde F, Vos RA, Van Swaay CAM, WallisDeVries MF (2017) Ecological determinants of butterfly vulnerability across the European continent. *J Insect Conserv* 21:439–450
- Farroni T, Johnson MH, Menon E, Zulian L, Faraguna D, Csibra G (2005) Newborns’ preference for face-relevant stimuli: effects of contrast polarity. *Proc Natl Acad Sci* 102(47):17245–17250
- Filz KJ, Schmitt T (2015) Niche overlap and host specificity in parasitic *Maculinea* butterflies (Lepidoptera: Lycaenidae) as a measure for potential extinction risks under climate change. *Org Divers Evol* 15:555–565
- Fox J, Weisberg S (2019) *An {R} companion to applied regression*, third edition. Thousand Oaks CA: Sage. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>

- Gauthier P, Foulon Y, Jupille O, Thompson JD (2013) Quantifying habitat vulnerability to assess species priorities for conservation management. *Biol Conserv* 158:321–325
- Gower JC (1971) A general coefficient of similarity and some of its properties. *Biometrics* 27:857
- Graves S, Piepho H-P, Selzer L, with help from Dorai-Raj S (2019) MultcompView: Visualizations of paired comparisons. R package version 0.1-8. <https://CRAN.R-project.org/package=multcompView>
- Habel JC, Rödder D, Schmitt T, Nève G (2011) Global warming will affect the genetic diversity and uniqueness of *Lycaena helle* populations. *Glob Change Biol* 17:194–205
- Habel JC, Segerer A, Ulrich W, Torchyk O, Weisser WW, Schmitt T (2016) Butterfly community shifts over two centuries: shifts in butterfly communities. *Conserv Biol* 30:754–762
- Habel JC, Gossner MM, Schmitt T (2019) What makes a species a priority for nature conservation? *Anim Conserv* 23:28–35
- Hallmann CA, Sorg M, Jongejans E, Siepel H, Hofland N, Schwan H et al (2017) More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS ONE* 12:e0185809
- Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecol Lett* 8:461–467
- Harrison S, Viers JH, Thorne JH, Grace JB (2008) Favourable environments and the persistence of naturally rare species. *Conserv Lett* 1:65–74
- Hervé M (2021) RVAideMemoire: testing and plotting procedures for biostatistics. R package version 0.9-79. <https://CRAN.R-project.org/package=RVAideMemoire>
- Heywood VH (ed) (1995) Global biodiversity assessment. Cambridge University Press, Cambridge
- Hill SLL, Harfoot M, Purvis A, Purves DW, Collen B, Newbold T, Burgess ND, Mace GM (2016) Reconciling biodiversity indicators to guide understanding and action. *Conserv Lett: J Soc Conserv Biol* 9(6):405–412
- Hochkirch A, Schmitt T, Beninde J, Hiery M, Kinitz T, Kirschey J, Proelss A (2013a) Europe needs a new vision for a Natura 2020 network. *Conserv Lett* 6:462–467
- Hochkirch A, Schmitt T, Beninde J, Hiery M, Kinitz T, Kirschey J et al (2013b) How much biodiversity does Natura 2000 cover? *Conserv Lett* 6:470–471
- Home R, Keller C, Nagel P, Bauer N, Hunziker M (2009) Selection criteria for flagship species by conservation organizations. *Environ Conserv* 36:139–148
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biom J* 50:346–363
- Kellert SR (1996a) The value of life: biological diversity and human society. Island Press [for] Shearwater Books, Washington, DC
- Kellert SR (1996b) The value of life: biological diversity and human society. Island Press [for] Shearwater Books, Washington, DC
- Kudrna O, Pennerstorfer J, Lux K (2015) Distribution atlas of European butterflies and skippers. Wissenschaftlicher Verlag Peks, Schweinfurt
- Kuznetsova A, Brockhoff PB, Christensen RHB (2017) lmerTest package: Tests in linear mixed effects models. *J Stat Softw* 82:1–26
- Laliberté E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299–305
- Laliberte E, Zemunik G, Turner BL (2014) Environmental filtering explains variation in plant diversity along resource gradients. *Science* 345:1602–1605
- Landová E, Poláková P, Rádlová S, Janovcová M, Bobek M, Frynta D (2018) Beauty ranking of mammalian species kept in the Prague Zoo: does beauty of animals increase the respondents' willingness to protect them? *Sci Nat* 105:69
- Leader-Williams N, Dublin HT (2000) Charismatic megafauna as flagship species. In: Entwistle A, Dunstone N (eds) Priorities for the conservation of mammalian diversity: has the panda had its day? Cambridge University Press, Cambridge, pp 53–81
- Lenth RV (2016) Least-Squares Means: The R package lsmeans. *J Stat Softw* 69:1–33
- Lenth RV (2021) Emmeans: estimated marginal means, aka least-squares means. R package version 1.5.5-1. <https://CRAN.R-project.org/package=emmeans>
- Lopez-Collado J, Cruz-Salas LL, García-Albarado JC, Platas-Rosado DE, Calyecac-Cortero HG (2016) Size doesn't matter but color does: preference of neotropical butterfly species to make souvenirs. *J Entomol Zool Stud* 4:159–165
- Lorimer J (2007) Nonhuman charisma: Which species trigger our emotions and why? *Environ Plann D* 25:911–932
- Macdonald DW, Loveridge AJ, Dickman A, Johnson PJ, Jacobsen KS, Preez BD (2017) Lions, trophy hunting and beyond: knowledge gaps and why they matter. *Mamm Rev* 47(4):247–253

- Macdonald EA, Burnham D, Hinks AE, Dickman AJ, Malhi Y, Macdonald DW (2015) Conservation inequality and the charismatic cat: *Felis felix*. *Global Ecol Conserv* 3:851–866
- Maes D, Collins S, Munguira ML, Šašić M, Settele J, van Swaay C et al (2013) Not the right time to amend the annexes of the European Habitats Directive: Annexes of the European Habitats Directive. *Conserv Lett* 6:468–469
- Manesi Z, Van Lange PAM, Pollet TV (2015) Butterfly eyespots: their potential influence on aesthetic preferences and conservation attitudes. *Plos One*. <https://doi.org/10.1371/journal.pone.0141433>
- Munguira ML, Martín J (1999) Action plan for *Maculinea* butterflies in Europe. Council of Europe. Nature and Environment, Strasbourg
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, et al (2016) *Vegan: Community Ecology Package*. Vienna
- Peterson AT, Navarro-Sigüenza AG, Li X (2010) Joint effects of marine intrusion and climate change on the Mexican avifauna. *Ann Assoc Am Geogr* 100:908–916
- Pillon Y, Chase MW (2007) Taxonomic exaggeration and its effects on orchid conservation. *Conserv Biol* 21:263–265
- Podani J (1999) Extending Gower's general coefficient of similarity to ordinal characters. *Taxon* 48:331–340
- Pullin AS, Knight TM (2003) Support for decision making in conservation practice: an evidence-based approach. *J Nat Conserv* 11:83–90
- R Core Team (2018) *A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna
- Rodrigues ASL, Brooks TM (2007) Shortcuts for biodiversity conservation planning: the effectiveness of surrogates. *Annu Rev Ecol Evol Syst* 38:713–737
- Root-Bernstein M, Douglas L, Smith A, Veríssimo D (2013) Anthropomorphized species as tools for conservation: utility beyond prosocial, intelligent and suffering species. *Biodivers Conserv* 22:1577–1589
- Schmitt T (2020) *Molekulare Biogeographie: Gene in Raum und Zeit*, 1st edn. Haupt Verlag, Bern
- Seibold S, Gossner MM, Simons NK, Blüthgen N, Müller J, Ambarlı D et al (2019) Arthropod decline in grasslands and forests is associated with landscape-level drivers. *Nature* 574:671–674
- Simberloff D (1998) Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biol Conserv* 83:247–257
- Stork NE, Habel JC (2014) Can biodiversity hotspots protect more than tropical forest plants and vertebrates? *J Biogeogr* 41:421–428
- Tam K-P, Lee S-L, Chao MM (2013) Saving Mr. Nature: anthropomorphism enhances connectedness to and protectiveness toward nature. *J Exp Soc Psychol* 49:514–521
- Tshikolovets VV (2011) *Butterflies of Europe & the Mediterranean area*. Tshikolovets Publications, Pardubice
- van Klink R, Bowler DE, Gongalsky KB, Swengel AB, Gentile A, Chase JM (2020) Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science* 368:417–420
- van Swaay C, Cuttelod A, Collins S, Maes D, López Munguira M, Šašić M et al (eds) (2010) *European red list of butterflies*. Publications Office of the European Union, Luxembourg
- Veríssimo D, McKinley E (2016) Introducing conservation marketing: why should the devil have all the best tunes? *Oryx* 50:14–14
- Wiemers M, Balletto E, Dincă V, Fric ZF, Lamas G, Lukhtanov V, Verovnik R (2018) An updated checklist of the European Butterflies (Lepidoptera, Papilionoidea). *ZooKeys* 811:9–45
- Williams PH, Burgess ND, Rahbek C (2000) Flagship species, ecological complementarity and conserving the diversity of mammals and birds in sub-Saharan Africa. *Anim Conserv* 3:249–260
- Witek M, Casacci LP, Barbero F, Patricelli D, Sala M, Bossi S et al (2013) Interspecific relationships in co-occurring populations of social parasites and their host ants. *Biol J Lin Soc* 109:699–709

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