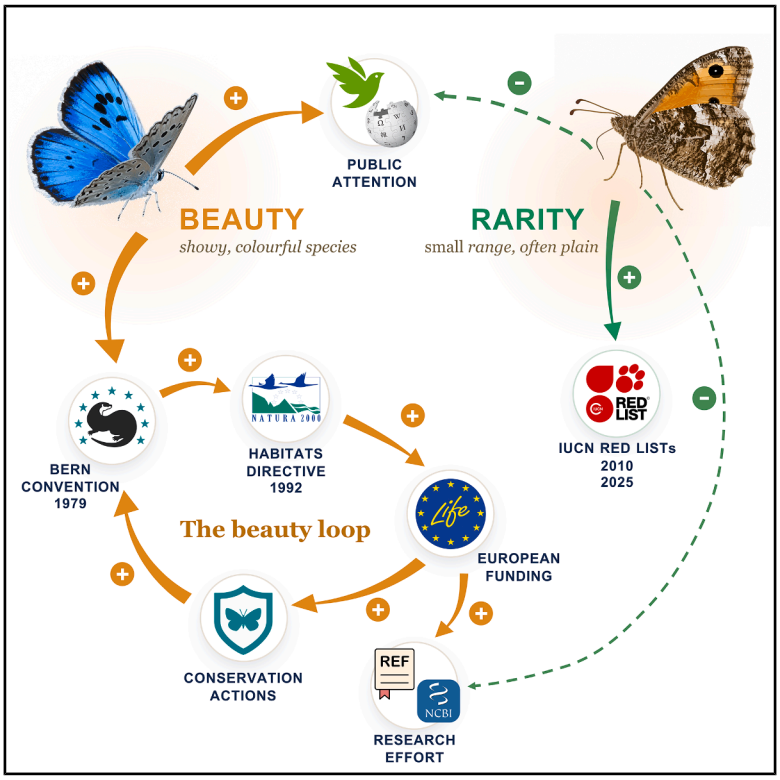
Report

Current Biology

Beauty bias in butterfly research and conservation

Graphical abstract



Highlights

- Butterfly beauty is associated with public attention, research, and conservation
- Beautiful species are overrepresented in the Bern Convention and Habitats Directive
- European IUCN Red Lists are not biased toward beautiful species
- Recognizing beauty bias can help align conservation with ecological urgency

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In brief

Dapporto et al. show that butterfly beauty is associated with public attention, research, and EU conservation policy. Beauty bias spans the conservation landscape, yet European IUCN Red Lists identify threatened species independently of beauty, revealing a mismatch between institutional conservation priorities and extinction risk.

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Beauty bias in butterfly research and conservation

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SUMMARY

Conservation biases have been documented since the first emergence of the concept of biodiversity in the 1980s,[1–3] showing a systematic disproportion in the allocation of research and conservation efforts among taxa.[4–11] One factor underlying this disproportion, gaining prominence in recent literature, is species' perceived beauty, shaped by human visual preferences.[12–17] Here, we integrate a large-scale survey of the perceived beauty of European butterflies yielding >21,000 survey completions from >100 countries into a time-explicit network linking species' beauty, public attention, research and conservation efforts, and the EU regulatory framework. We found that species beauty is consistently associated with public attention, research, and conservation efforts in a temporally structured pattern compatible with a cumulative beauty bias. Research effort and public attention concentrate on widespread and visually attractive species, whereas species included in the legal conservation framework, particularly the Convention on the Conservation of European Wildlife and Natural Habitats (hereafter, Bern Convention, BC, 1979)[18] and the EU Habitats Directive (hereafter, HD, 1992)[19] are disproportionately represented by visually appealing and historically protected taxa. Because these frameworks guide funding and management actions, early associations between species beauty and BC/HD inclusion have contributed to long-lasting institutional patterns in butterfly research and conservation. By contrast, European IUCN Red Lists[20,21] do not overrepresent beautiful species and identify more inconspicuous taxa as threatened. This mismatch reveals a tension between scientific assessments of extinction risk and historically embedded conservation priorities. Our findings suggest that recognizing beauty bias is vital for aligning conservation with actual ecological urgency.

RESULTS AND DISCUSSION

Morphological and colorimetric features explain the perceived beauty of European butterflies

A multilingual online survey yielded 21,131 survey completions (Figure S2). Respondents were presented with nine butterfly images and asked to score their perceived beauty on a 0–10 scale. This produced 171,348 beauty scores across 4,442 images belonging to 492 European butterfly species. Mean values for beauty scores were calculated for each visual pattern of each species, ranging from one to four (1 = no sexual dimorphism, one side observable in nature; 4 = sexual dimorphism, both sides observable). Scores were modeled using participants' personal information (Figure S2), with the returning residuals being

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weighted by respondents' country and by the number of scores obtained by each image and averaged among visual patterns, thus resulting in the Averaged Beauty Scores.

A boosted regression trees analysis showed that Averaged Beauty Scores were strongly explained by standardized morphological and colorimetric features extracted from a European butterfly guide[22] (64.8% explained variance, Figure S3). A clear preference emerged for colorful patterns (Figure 1A). Primary colors like blue or yellow were preferred over tertiary ones (Figure 1B) and elongated wings with tailed hindwings over more compact wings (Figures 1C and S4). Preferences also emerged for contrasting forewing-hindwing coloration (Figure 1D), aggregated (low complexity) instead of scattered (high complexity) patterns (Figure 1E), and for highly divergent colors (Figure 1F). These results align with some aspects of processing fluency theory,[23,24] which holds that stimuli that are easier to process (e.g., because of low complexity or high contrast) tend to be perceived as more pleasant.

The SBI

Averaged Beauty Scores for different visual patterns of each species were averaged to obtain the species beauty index (SBI). Based on a cumulative resampling in which randomly shuffled beauty scores were divided into equal-sized groups, the mean change in SBI showed a rapid decline with increasing sample size and approached an asymptote of about 0.02, corresponding to less than 0.5% of the variation shown by this index (Figure S6). This confirms that the number of participants was sufficient to produce a stable and robust SBI.

Throughout this study, SBI is interpreted as a measure of perceived aesthetic attractiveness due to formal features such as color pattern and shape. However, as aesthetic judgments of beauty likely emerge from the interaction of perceptual with affective, cognitive, and attentional processes,[25–27] the index may implicitly incorporate correlated dimensions, including charisma, familiarity, memorability, and recognizability or detectability (see below).

Species with a high SBI tend to display sexually selected, aposematic, or startling colorations such as highly contrasting patterns, metallic colors, and/or morphological camouflage like tails or leaf-like wing margins. Consequently, SBI was strongly clustered and conserved across evolutionary lineages, resulting in a strong phylogenetic signal (Pagel's $\lambda = 0.84$, $p < 0.001$) when

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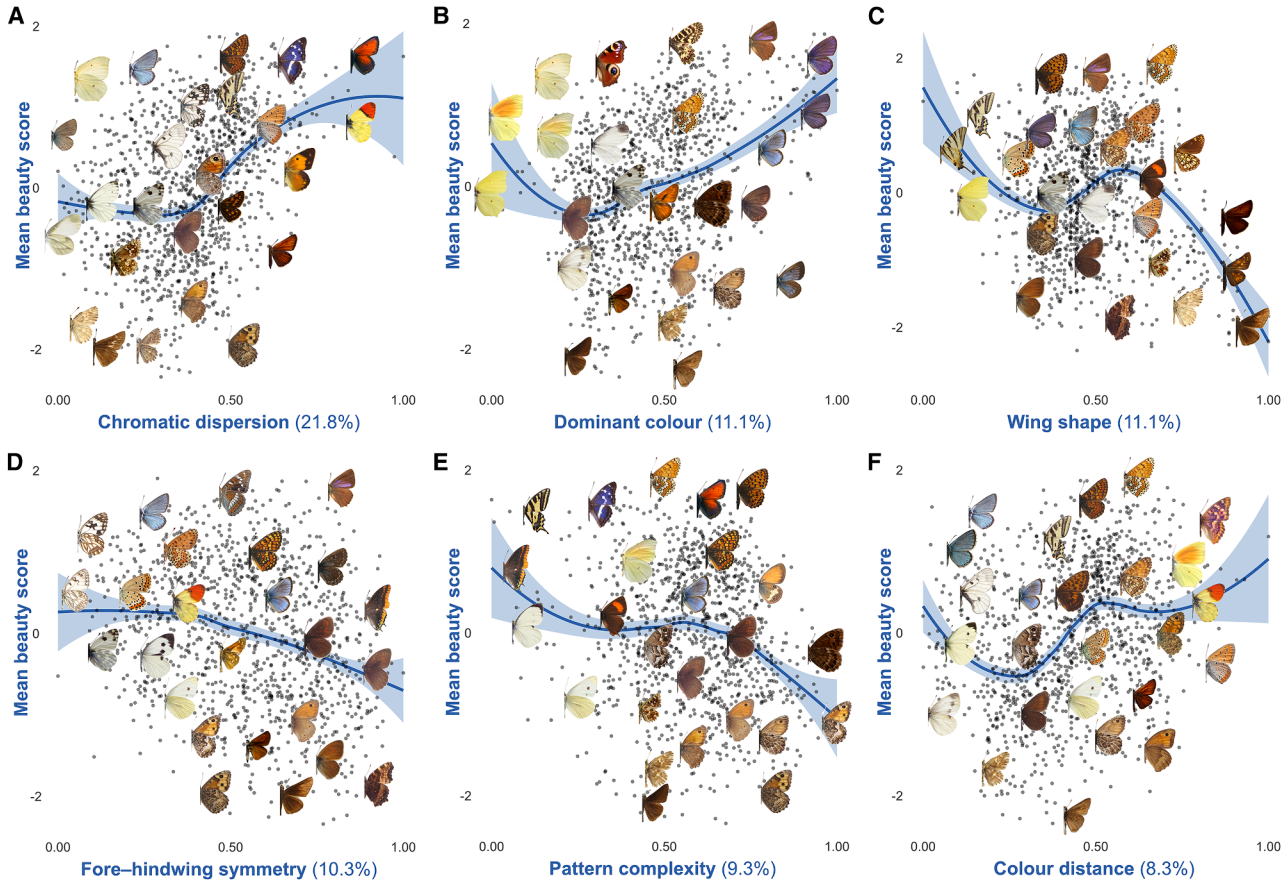

Figure 1. Morphological and colorimetric features underlying perceived beauty in European butterflies

Relationships between the Averaged Beauty Scores and the six most important morpho-colorimetric features (variance importance by each variable is reported within parentheses) in a boosted regression trees analysis. Trend lines were obtained using Locally Estimated Scatterplot Smoothing (LOESS) regression.

(A) Chromatic dispersion, the total distance of pixels from the centroid in colorimetric space.

(B) Dominant pixel colors (from yellow, through orange and brown, to blue).

(C) Wing shape (the third component of a wing geometric morphometrics analysis), describing a gradient from elongated and tailed wings to compact shapes.

(D) Horizontal symmetry, from species with markedly different forewings and hindwings to those with similar wings.

(E) Pattern complexity, ranging from species with aggregated colors to scattered ones.

(F) Distance between the six main color clusters (STAR Methods).

See also Figures S3 and S4.

SBI is mapped onto the butterfly phylogeny[28] (Figures 2 and S5). Hesperiidae and Satyrinae subfamilies have low SBI with limited variability, Nymphalidae and Papilionidae have higher SBI, and Pieridae show intermediate values (Figures 2 and S5). Lycaenidae (often dimorphic both sexually and between wing surfaces) display the greatest divergence between maximum and minimum scores (Figure S5).

Butterfly beauty is consistently linked to public attention, research, and conservation efforts

The SBI relies on survey-based beauty scores ranging from 0 to 10 and captures low-stakes, rapid evaluations of perceptual features with minimal cognitive elaboration and emotional engagement. We investigated whether these low-stakes perceptual evaluations are associated with multiple dimensions of human engagement with butterflies, including high-stakes decisions by researchers, policymakers, and conservationists (Figure S1).

A principal component analysis (PCA; Figure 3A) was conducted on species-level attributes, including size, spatial range, temporal detectability of adults, public attention (Flickr, iNaturalist, and Wikipedia), extinction risk assessments (inclusion in the International Union for Conservation of Nature [IUCN] Red Lists of European butterflies, RLs[20,21]), and conservation interest and efforts (inclusion in LIFE projects, i.e. the EU's funding instrument for the environment and climate action, in the Bern Convention, BC,[18] and the Habitats Directive, HD,[19] listings and conservation actions), as well as research effort (number of NCBI genetic sequences and Web of Science and Scopus indexed studies). The first axis captured a gradient from spatio-temporal detectability to public attention and research effort, whereas the second axis was primarily associated with conservation effort. When the SBI was projected as a color gradient, visually attractive species clustered with higher public and research attention, whereas less conspicuous species were associated with a higher extinction risk in the 2025 RL.

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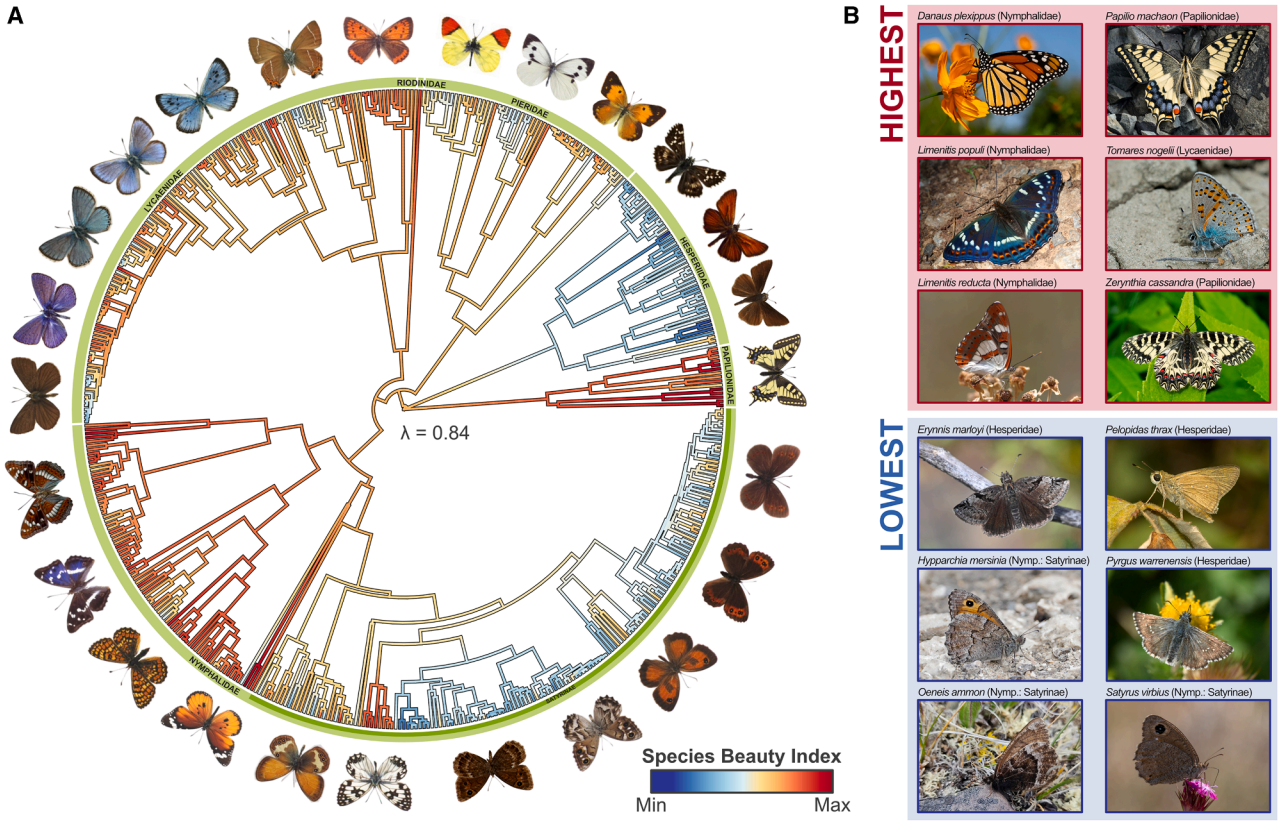

Figure 2. The SBI of European butterflies

(A) Projection of the SBI on the phylogenetic tree of European butterflies. Red colors indicate higher SBI values, and blue colors lower values. A subset of representative species illustrations is included to aid visual interpretation.

(B) Examples of species from different families among the ten showing the highest and lowest SBI.

See also Figure S5.

These patterns were tested using a Bayesian multivariate model evaluating whether aesthetic preferences can propagate through a temporally structured sequence of public, scientific, and institutional processes. Specifically, we hypothesized that beauty bias initiates a self-reinforcing dynamic, akin to the Matthew effect,[29] whereby aesthetically appealing species are more intensively studied, more likely to be included in conservation lists, attract greater funding, and consequently receive further attention.[12–14]

To strengthen our potentially causal interpretation while acknowledging the observational nature of the data,[30] we specified an a priori causal structure in which public attention, research effort, institutional protection, and conservation action variables form a temporally ordered and interconnected system. Conservation and research efforts targeting individual species were partitioned into time windows spanning the late 20th and early 21st centuries, aligned with four major milestones: the BC (1979[18]), the HD (1992[19]), and the 2010 and 2025 RLs.[20,21] This temporal stratification constrains the direction of potential effects by allowing earlier processes to influence later outcomes while largely excluding reverse causation. It also allows historically distinct stages of the same process (e.g., research effort or conservation actions before and after major conservation milestones) to be modeled separately into temporally ordered sequences. In addition, species size, spatial range, and temporal detectability, showing low pairwise correlations to each other (Table S2), were incorporated into the model, thus reducing the likelihood that observed relationships are driven by confounding effects.

The resulting model revealed several significant and potentially causal links among variables (Table S1). Both the species' temporal and spatial detectability and the SBI showed positive effects on most measures of public attention, research effort, and the EU bodies of legislation, whereas wing size had a weaker effect (Table S1; Figure 3B). Despite differences in user motivations, Wikipedia, iNaturalist, and Flickr metrics were all consistently associated with the SBI, alongside the expected positive association with species detectability. Similarly, the number of available sequences and papers published was positively correlated with both the SBI and detectability but also positively explained by inclusion in LIFE projects. Inclusion in the BC was positively explained by the SBI, by short adult phenologies, and by pre-1979 conservation actions, the latter also explained by the SBI. The HD largely adopted the BC list, retaining 21 of its 32 protected butterfly species.[20,31] Accordingly, BC was the only significant predictor of HD inclusion in the multivariate

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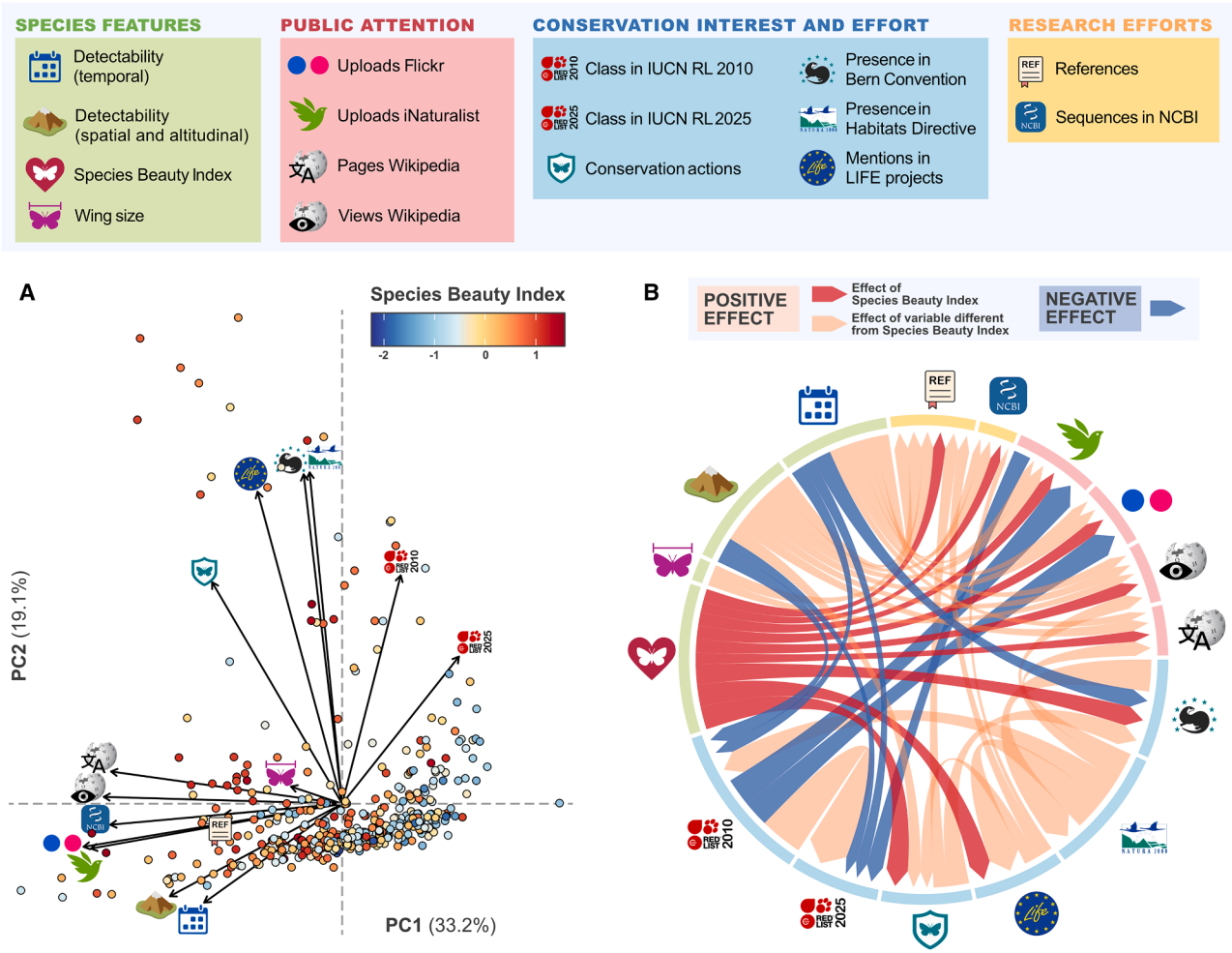

Figure 3. Multivariate structure of species attributes, public attention, conservation, and research effort

(A) A PCA showing the correlation structure among variables describing species features, public attention, conservation, and research efforts. The SBI was excluded from the PCA to avoid shaping the ordination pattern but is displayed as a color scale for species (dots).

(B) Significant relationships (red, positive; blue, negative) identified in a Bayesian multivariate model. The model incorporates a temporally stratified network of hypothesized causal pathways, allowing earlier processes to influence later outcomes while limiting reverse causation. Results for different temporal partitions of variables are available in Table S1. Link width reflects effect strength. The effects of SBI are highlighted in red for clarity.

See also Figure S1 and Tables S1 and S2.

model, and the extensive species overlap resulted in the HD retaining much of the BC beauty bias (see univariate analyses below). As the main EU legal framework guiding conservation funding and management actions, the HD subsequently propagated this bias to later conservation instruments, notably LIFE projects, which predominantly target HD species.[32] Inclusion in the 2010 and 2025 RLs showed significant associations with smaller geographic range size (consistent with IUCN criterion B) not observed in the BC and HD, and shorter adult flight period as found for BC. Inclusion in the 2025 RL was negatively explained by the number of iNaturalist occurrences. Notably, inclusion in the 2010 RL had no significant effect on subsequent research, conservation efforts, or genetic sequencing (Figure 3B).

As multivariate models capture interdependent relationships, the effects of individual predictors can be obscured by stronger pathways, complicating direct inference. We adopted a complementary univariate approach to test beauty bias directly as the overrepresentation of aesthetically appealing species within conservation and risk lists. We compared the observed mean SBI of listed species with a null distribution generated from 10,000 randomizations of equally sized samples drawn from non-listed species (Figure 4). This framework was applied to the BC, the HD, and Threatened and Near Threatened (NT) categories of RLs. Consistent with the multivariate analyses, the BC shows a strong beauty bias, with protected species having higher SBI than expected under random selection (Figure 4A). The HD shows a similar overrepresentation. No such pattern is observed for species listed as Critically Endangered (CR), Endangered (EN), or Vulnerable (VU) in the European 2010 RL nor for NT species, whereas the 2025 RL shows an anti-beauty bias among Threatened species (i.e., species with substantially lower SBI than expected under random selection; Figure 4A). This likely reflects ecological reality rather than

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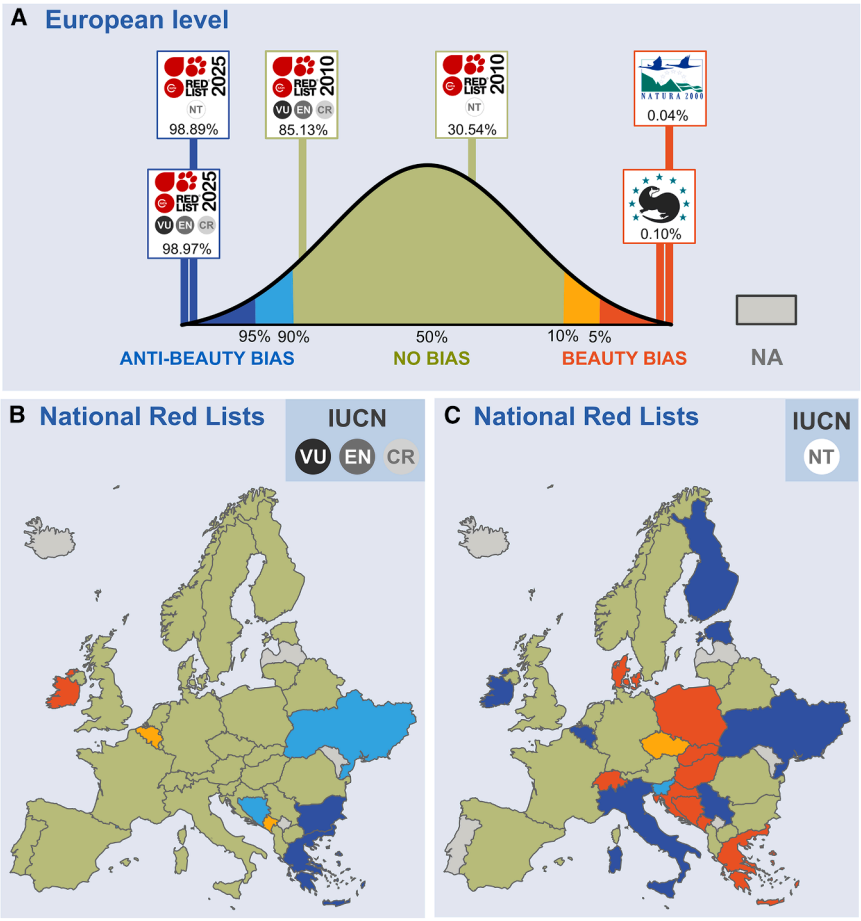

Figure 4. Geographic patterns of beauty bias in butterfly conservation at national and European scales

Colors indicate the strength and direction of the bias, i.e., the percentage of 10,000 resampling iterations (exemplified in the Gaussian distribution in A) in which the mean SBI of randomly selected species was lower than that of species listed in IUCN threatened categories, the BC, and the HD. Blue colors denote anti-beauty bias (selected species showing lower SBI than average random sampling), red denotes beauty bias (higher SBI than random), green indicates no bias, and gray indicates not available data (NA).

(A) European-level bias calculated for species listed in the Vulnerable (VU), Endangered (EN), and Critically Endangered (CR) categories of the IUCN[20,21] Red Lists compared with an equal-size random subset of Least Concern (LC) species for species in the NT list versus LC ones and for species in the priority lists of the BC and the HD versus non-listed species. Please refer to Figure 3 for icons legend.

(B) National-level bias calculated for species occurring within each country in VU+EN+CR categories versus LC ones.

(C) Same analysis as in (B), but restricted to species listed as NT versus LC ones.

deliberate bias correction and aligns with evidence that duller, darker insect species are often more environmentally vulnerable.[33] Indeed, many 2025 threatened species belong to Satyrinae mountain specialists characterized by dark, tertiary colors, e.g., *Erebia*, deeply affected by climate change, and *Hipparchia* and *Pseudochazara*, which often have small, isolated populations.

The analysis of mean SBI of species included in national RLs[34] revealed an anti-beauty bias in Ukraine and some Balkan countries, in line with the 2025 IUCN RL (Figure 4B). A clear positive beauty bias only occurred in Ireland, while Montenegro and Belgium showed a weak tendency in this direction (Figure 4B). Beauty bias appeared more widespread for NT species (10 countries; Figure 4C), whereas eight countries showed an anti-beauty bias.

The IUCN RLs' reliance on structured expert data and collaborative peer-review processes might have reduced the influence of visual appeal on extinction risk in 2010 and 2025 RLs. A tendency for beauty bias found in NT species in several RLs suggests that this category, characterized by greater interpretative flexibility, may be more susceptible to aesthetic bias.

Taken together, these findings highlight the combined influence of epistemic and non-epistemic (aesthetic) factors on butterfly research, conservation, and public engagement. While the association of beauty with public attention, measured as the decision to upload images on iNaturalist or Flickr or to read and produce Wikipedia pages, was expected, its correlation with research and conservation actions deserves particular attention. Indeed, opportunistic citizen-science datasets currently represent about 80% of the Global Biodiversity Information Facility (GBIF) data since 2010.[35] Better-documented species are more likely to provide sufficient evidence for decline, strengthening their case for conservation listing. Alternatively, because the 2025 RL explicitly uses GBIF butterfly records data to establish distribution metrics[20] underpinning Criterion B, species with fewer records may appear more range-restricted. In our model, species with fewer iNaturalist records are more often classified as threatened in the 2025 RL. Although genuine rarity likely explains much of this pattern, beauty-driven observation patterns may also contribute to inferred rarity. As citizen-science data become standard in conservation evaluations, low-stakes, beauty-driven observations may influence high-stakes, institutional decisions. This calls for critical evaluation of opportunistic data and targeted documentation of less attractive species.

Our results showed that aesthetically appealing species were more likely to be included in the BC and then in the HD, indicating a non-random overrepresentation of visually attractive species. The analyses, however, were not designed to reconstruct the historical, political, and institutional decision-making processes that gave rise to these patterns. The BC marked a major advance in invertebrate protection, yet it primarily regulates direct human persecution (e.g., capture, killing, collection, and trade) and explicitly acknowledges aesthetic values in its *Preamble*, thus suggesting that visually appealing species, which may be disproportionately targeted for collection or trade, are also

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more likely to be listed. Contrary to expectations, species' inclusion in the BC and HD was unrelated to range distribution and prior scientific publication volume, implying that policy decisions relied on sources beyond extent and area of occupancy or established knowledge, possibly including gray literature (non-indexed studies, technical reports, and expert data). Disentangling these issues lies beyond the scope of our study.

Overall, our findings suggest that the BC-based HD may warrant re-evaluation for two main reasons. First, taxonomic obsolescence. Frameworks anchored in 1979–1992 taxonomy overlooked cryptic and geographically restricted taxa. Of the six species classified as CR in the 2025 RL, only *Pseudochazara cingovskii* was recognized as a distinct species in the 1975 checklist.[36,37] Butterfly taxonomy has since advanced rapidly, with the description of new species that often have narrower ranges and smaller populations,[38–40] increasing their likelihood of falling into high-threat categories.[38]

The second reason is changes in biodiversity threats. In the 2010 RL, 12 of 37 threatened species were HD-listed. In the 2025 RL, only 7 of 65, indicating increasing misalignment. A major current threat to many butterfly species is climate change,[41] particularly for those confined to southern diversity hotspots, mountain ranges, or islands. Evidence of widespread climate change impacts on butterfly populations was limited in 1979 and 1992[42] and only began to emerge in 1999.[43,44] In the 2025 RL, 52% of threatened species are reported as affected by climate change, a proportion likely to increase.

Beauty bias may also extend beyond species protection to the ecosystem level. Because HD implementation and LIFE funding are often triggered by the presence of priority species, habitat conservation efforts tend to concentrate on areas hosting historically listed taxa.[45,46] Importantly, HD-listed butterfly species fail to capture the functional diversity of European butterflies, leaving substantial portions of the multidimensional functional trait space underprotected.[47,48]

Our study has several limitations that highlight opportunities for future research. First, we relied on a screen-based survey, thereby operating within the "extinction of experience" framework,[49] where nature is primarily encountered digitally—which is a known barrier to conservation. However, SBI was also consistently associated with the choices of iNaturalist users and researchers, groups that likely experience direct interactions with nature. Second, we adopted a minimal, stimulus-driven, visually centered definition of beauty, disregarding other sensory modalities and slower, knowledge-mediated forms of appreciation.[16,50,51] However, operationalizing aesthetic appreciation as an evaluation of low-stakes visual stimuli allowed us to test its association with broader forms of human engagement with biodiversity. Future work should disentangle the relative contributions of the multiple dimensions likely embedded within human aesthetic experience, including charisma, memorability, affective responses associated with rarity or vulnerability, and other distinctive ecological or evolutionary characteristics. An additional limitation concerns the WEIRD (Western, educated, industrialized, rich, and democratic) nature of our participants[52] (Figure S2). Nevertheless, since WEIRD actors dominate global policy, our findings are a wake-up call toward decolonized, transdisciplinary, community-based conservation.[53,54] Expanding beauty assessments beyond WEIRD populations would help better understand how culture shapes preferences.

Finally, our observational design does not allow causal inference. However, temporal stratification, explicit hypotheses about directional relationships among variables, and controls for major alternative explanations strengthen the interpretation of the observed associations. The consistency of beauty-related associations across multiple conservation outcomes, generated by different actors, further reduces the likelihood that they are explained by unmeasured confounder(s). Future studies should more directly identify the mechanisms underlying the beauty bias.

In conclusion, understanding the factors driving human preferences for certain species is crucial to clarify how biodiversity is perceived and prioritized in conservation.[55] Historically, aesthetic values have mobilized public engagement and helped bring biodiversity into political agendas. Yet our results on European butterflies suggest that today beauty is associated with systematic biases in attention, conservation, and research priorities, and that these patterns persist through institutional frameworks, with long-lasting consequences for conservation governance. Acknowledging the beauty bias is a first step toward more transparent, balanced decision-making. As Douglas[56] notes, the choice is not whether values and interests exist in science but whether we manage them or let them operate unchecked. Pragmatically, counteracting beauty bias in butterfly research requires large-scale projects focusing on obtaining data from complete taxa at a continental scale without any arbitrary selection (e.g., DNA barcoding library,[57] Psyche project for genomes,[58] and comprehensive efforts to establish trends like eBMS projects, which follow the European Butterfly Monitoring Scheme, created by Butterfly Conservation Europe[59]), evidence-based policy revision, and cooperative transdisciplinary networks. Only by confronting the pervasive influence of beauty bias can conservation governance more effectively align with the urgency of the biodiversity crisis.

RESOURCE AVAILABILITY

Lead contact

Requests for further information and resources should be directed to, and will be fulfilled by, the lead contact, Mariagrazia Portera (mariagrazia.portera@unifi.it).

Materials availability

This study did not generate any new materials.

Data and code availability

- The data supporting the findings of this study have been deposited at Zenodo: 10.5281/zenodo.20638260, and are publicly available as of the date of publication.
- Original code has been deposited at Zenodo and is publicly available as of the date of publication. DOIs are listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

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AUTHOR CONTRIBUTIONS

Conceptualization, L.D., N.M., A.C., and M.P.; data collection, all authors; data curation, L.D., A.B., M.G., and V.Z.; formal analysis, L.D. and N.M.; funding acquisition, L.D. and M.P.; investigation, L.D., N.M., A.B., A.C., C.B., M.G., V.Z., and M.P.; methodology, L.D., N.M., A.C., and M.P.; software, L.D. and N.M.; supervision, L.D., A.C., and M.P.; visualization, L.D., A.C., and M.M.; writing – original draft, all authors; writing – review and editing, all authors.

DECLARATION OF INTERESTS

The authors declare no competing interests.

DECLARATION OF GENERATIVE AI AND AI-ASSISTED TECHNOLOGIES IN THE WRITING PROCESS

During the preparation of this work, the authors used ChatGPT and Gemini for minimal language editing. After using these tools, the authors reviewed the content as needed and take full responsibility for the content of the publication.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
All data used for the analyses	This paper, available at Zenodo	10.5281/zenodo.20638260
All R codes used for the analyses	This paper, available at Zenodo	10.5281/zenodo.20638260
Online survey structure	This paper and van Tongeren et al.[17]	10.1371/journal.pone.0283360
Software and algorithms		
tpsdig v. 2.31	Rohlf[60]	N/A
R software v 4.4.1	R Core Team	https://www.r-project.org/
R package: glmmTMB v.1.1.11	Brooks et al.[61]	10.32614/CRAN.package.glmmTMB
R package: geomorph v.4.0.10	Baken et al.[62]	10.32614/CRAN.package.geomorph
R package: colorspace v.2.1.1	Zeileis et al.[63]	10.32614/CRAN.package.colorspace
R package: imagefluency v.0.2.5	Mayer[64]	10.32614/CRAN.package.imagefluency
R package: colordistance v.1.1.2	Weller and Westeneat[65]	10.32614/CRAN.package.colordistance
R package: ade4 v.1.7-23	Dray and Dufour[66]	10.32614/CRAN.package.ade4
R package: rentrez v 1.2.4.	Winter[67]	10.32614/CRAN.package.rentrez
R package: *gbm v.2.2.2*	Edwards et al.[68]	10.32614/CRAN.package.gbm
R package: phytools v 2.5–2	Revell[69]	10.32614/CRAN.package.phytools
R package: BRMS v.2.23.0	Bürkner[70]	10.32614/CRAN.package.brms

EXPERIMENTAL MODEL AND STUDY PARTICIPANT DETAILS

The online survey

The evaluation of species attractiveness was obtained through an online survey active from July 4th, 2022 to January 20th, 2026, yielding 21,131 survey completions from 103 countries; only countries with >=10 surveys and from participants aged 14 and older were considered for data analysis (see Figure S2). The survey[17] was divided into five sections, i.e. socio-demographic data collection, evaluation of aesthetic preferences of butterfly digital images, assessment of the influence of morphological features on aesthetic preferences, emotional engagement and a final set of questions about respondents' interests and dispositional variables. For this study, we used data from the first section (socio-demographic data) and the second section (scoring) of the survey. The first section collected general participant information anonymously: gender (male, female, other), age, nationality, education level (4 levels), employment sector (7 categories), and a color blindness test (negative-positive). In the second scoring section, participants were presented with a panel of nine butterfly images. By clicking on each picture, users could assign a beauty score on a 0-10 scale in response to the question: *"How beautiful do they look to you?"* (beauty scores). Images were randomly selected from a database representing all European butterfly species, with selection probabilities adjusted throughout the survey to ensure balanced sampling across images. Selected images were then randomly assigned to positions within the nine-image panel to minimize presentation-order effects. Consequently, participants were generally exposed to different image combinations, reducing systematic comparison effects and the possibility that scoring patterns were driven by a fixed sequence of stimuli. The survey was available in seven languages (Dutch, English, French, German, Italian, Polish, Spanish) and was disseminated via multiple media channels (print and online press, radio, and television interviews), through dedicated social media posts (Facebook, Instagram, X, and BlueSky) and through international mailing lists, including scientific societies, research networks, universities. It was further promoted at conferences and public engagement events. Additionally, outreach involved social media influencers active in broad scientific communication on the web.

Species list and image collection

We used 492 of the 496 butterfly species reported from Europe, adopting as a taxonomic reference the recent checklist of the European fauna.[39] A phylogeny associated with the checklist is also available.[28]

Butterfly wing patterns differ between the dorsal and the ventral side of wings in most species and in several instances also between males and females, thus producing four potentially distinct visual patterns per species. Additionally, human perception of beauty can be swayed by the specific background or context in which the butterfly is shown. Accordingly, for each species, we

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collected citizen science pictures of living individuals taken in their natural environment (available in supplemental information), representing combinations of: i) male or female, ii) dorsal or ventral view, and iii) the presence or absence of a flower in the background. To further reduce potential biases related to image quality,[71] two independent datasets of pictures were collected for the same set of species and used at different times during the survey. This resulted in a theoretical maximum of 16 images per species (2 genders × 2 wing aspects × 2 background types × 2 datasets). In practice, the number of available images per species was often lower (mean=9.03 sd=3.68) due to: A) monomorphic species showing no visible sexual dimorphism; B) species that rarely visit flowers, preventing flower-background shots; C) species that typically rest with closed wings, making dorsal-view images unavailable; and D) rare species that were not photographed under all desired conditions.

A total of 4,442 images were collected. Most pictures were obtained from the iNaturalist citizen science platform, selecting only images with a Creative Commons (CC) license. Contributor photo credits were available for download on the survey website throughout its duration. Other images were sourced from websites specifically asking for permits (see Acknowledgments).

To ensure a balanced number of scores per image, the selection procedure favored images that had been presented less frequently in previous surveys. This was achieved by assigning each image a selection score obtained by summing (i) a random value between 0 and 1 and (ii) the standardized frequency with which the image had already been selected (number chosen / maximum number chosen). Images that had been presented more frequently therefore tended to receive higher scores, whereas the random component maintained stochasticity in the selection process. For each survey, the nine images with the lowest selection scores were presented to the participant and subsequently scored. We only included participants who scored at least 6 of the 9 presented pictures, as some surveys were terminated before completion.

METHOD DETAILS

Obtaining Averaged Beauty Scores

Because each image received a different number of beauty scores, from different positions within the 3×3 grid (positions 1-9, left-to-right, top-to-bottom) and provided by participants with varying demographics, we first modelled the raw individual beauty scores (n = 171,348 from 21,131 participants) as done by Haukka[71] as:

$$\begin{aligned}\text{model} <\text{-}\ \text{glmm}\,(\text{Score} \sim\ &\text{GridPosition}\,(1\text{–}9) + \text{Gender}\,(\text{male}, \text{female}, \text{non-binary}) + \text{Age}\,(14\text{–}98)\\ &+ \text{ColourBlindness}\,(\text{positive}/\text{negative}) + \text{education level}\,(4\ \text{levels}), \text{employment sector}\,(7\ \text{categories})\\ &+ \text{day}(\text{days passed since the survey started}) + (1|\text{Test\_ID}))\end{aligned}$$

where 1|Test_ID represents a random factor accounting for different absolute scales of scoring among participants. Residuals were extracted from the model as adjusted beauty scores and were subsequently averaged for each image[71] using two weighting factors. We used the glmmTMB function of the glmmTMB R package (v. 1.1.11).[61]

First, since participants were unevenly distributed among countries (with ~72% from Italy), we weighted each residual of beauty score by:

$$Wc = 1/\sqrt{(Nc)},$$

where (Nc) is the number of participants from each country.

Second, to correct for unequal sampling among images, we averaged the residual beauty scores of the different images belonging to the same visual pattern of the same species (4 potential ones: male-female and ventral-dorsal) using the inverse square root of the number of times each image was presented. This procedure allowed us to compute Averaged Beauty Scores for each visual aspect of species

Species Beauty Index (SBI)

Averaged Beauty Scores for each visual aspect of species were aggregated by their means to obtain a Species Beauty Score (SBI). In some cases, a butterfly may attract attention primarily through its most striking feature - for example, the European peacock (*Aglais io*) is widely recognized for its multicoloured dorsal wings bearing four prominent eyespots, while its ventral side displays a far less conspicuous, dark pattern. To account for this, we replicated the computation of SBI using only the visual patterns showing maximum and minimum Averaged Beauty Scores. This resulted in three Species Beauty Indexes per species: a) mean SBI (SBI hereafter), i.e. the averaged scores of all the visual patterns of a species; b) max SBI, and c) min SBI, representing the averaged scores of the visual patterns receiving the highest and the lowest scores, respectively. A distribution of max and min SBI is provided in Figure S4. Averaged scores among visual patterns without any correction were also included in the final table.[71]

The stability of the SBI with increasing survey numbers, was assessed using a resampling approach. The 171,348 beauty scores were randomly shuffled and divided into 34 groups of equal size, counting about 5000 beauty scores (on average 10 per species; see Figure S6). The SBI for each species was then calculated incrementally: starting with the first group, successive groups were cumulatively added, and the index was recalculated at each step. For each species, the absolute difference in index values after adding each new group was computed. The mean and standard deviation of these differences across species were plotted to evaluate whether an asymptotic trend close to zero was reached, indicating stability of the index (Figure S5).

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Morphometric and colorimetric data

We assumed that butterflies' features in the survey's digital images - sourced from the iNaturalist citizen science platform and originating from field observations - aligned with those depicted in the Tolman and Levington butterfly guide,[22] which serve as professional references for species identification. While we consider this a sound assumption regarding wing morphology and pattern complexity, color perception and thus human perceived attractiveness may be slightly more problematic. In general, differences between iNaturalist and Tolman images likely persist, especially regarding perceived color, due to intraspecific variation, individual condition (e.g., wing wear), ambient lighting, and other contextual factors inherent to field photography. We expect, however, that these differences remain minimal in comparison to interspecific variation. Tolman and Levington images of butterflies were scanned in high resolution (300 dpi), then cropped and resized to the same size (500x500 pixels). For the dorsal view, we retained only the right wings and the body. For the ventral sides, where only the left wings and bodies were available, we rotated the pictures, so they matched the orientation of the dorsal ones.

Morphology

For morphometric analyses, we digitized a series of 48 landmarks composed of 7 fixed landmarks and 41 sliding semilandmarks (Figure S4) per each species' dorsal image using tpsdig 2.31.[60] Generalized Procrustes Analysis (GPA) was applied -using the *geomorph* R package[62]- and a Principal Component on the resulting landmark coordinates applied using the dedicated gm.prcomp function of *geomorph*. Inspection of deformation patterns indicated that PCs beyond PC3 captured only minor, local shape variation; thus, only PC1, PC2 and PC3 (see Figure S4 for interpretation) were used in the analyses.

Colorimetric features

Colorimetric features[50] were obtained in the CIELAB color space, which expresses colors with three values: L^* for lightness, a^* and b^* for the four unique colors of human vision: red, green, blue, and yellow. Chromatic dispersion was quantified in CIELAB space, measured as the centroid size of pixel colors. For each image, pixel-level L*, a*, and b* values were standardized using global z-scores, and chromatic dispersion was calculated as the mean squared distance of all pixels from the color centroid, analogous to geometric morphometric centroid size. The higher these values, the more heterogeneous and distant the colors of an image and thus the higher is the chromatic dispersion.

A second variable was the heterogeneity in the four colors. We first obtained a *K*-means clustering algorithm to separate pixels from standard images in six clusters based on their location on the a^* and b^* axes using a fixed number of 6 clusters after preliminary analyses performed on the studied images. Based on these clusters, we calculated the mean distance between all cluster centers in the a^*b^* color metrics: color distance.

Lightness and saturation

Lightness and saturation were computed using the HSV (Hue, Saturation, Value) color space as implemented in the *colorspace* R package (v.2.1.1).[63] In this representation, hue (H) corresponds to the azimuth, with each angle representing a distinct color segment; value (V), hereafter called lightness, corresponds to the height along the central axis, ranging from 0 (black) at the bottom to 1 (white) at the top; and saturation (S) corresponds to the radial distance from the axis. Also ranging from 0 at the center to 1 at the edge, S represents the intensity of the color compared to the maximum possible intensity. S and V were measured for each pixel of the image (after removing the white background) and for both, we computed the mean and the standard deviation.

Symmetry and self-similarity

Horizontal symmetry (forewing vs hindwing) and self-similarity were computed using the img_symmetry function of the *imagefluency* v.0.2.5 R package.[64] The horizontal symmetry value (thereafter variable fore-hindwing symmetry) mirrors the symmetry of an image (i.e. the degree to which the pattern and shape of forewings reflect that of hindwings). As the perceptual mirror axis is not necessarily exactly in the middle of a picture, the function estimates in a first step several symmetry values with different positions for the mirror axis. Then, the overall symmetry score is computed as the maximum of the symmetry scores given the different mirror axes.[72] Self-similarity estimates whether the wing pattern shows a consistent, repeated structure across multiple spatial scales. Image self-similarity was quantified from the slope of the log–log power spectrum.[72] Natural images typically exhibit a slope close to –2, indicating a fractal-like structure. We report the transformed index (abs(slope + 2) $\times$ –1), where values near 0 denote high self-similarity and increasingly negative values indicate lower self-similarity.

Main wing coloration

Main wing coloration was quantified using the *colordistance v.1.1.2* R package.[65] For each standardized book image, 10,000 pixels in the CIELAB color space were divided into two main groups of pixels, creating two bins of pixels after removing the white background. Pairwise color distances between images were computed among these bins to obtain a color-distance matrix. A PCA was then performed on this matrix (dudi.pca function of the *ade4 v.1.7-23* R package[66]) to extract the main axes of chromatic variation. The first four principal components were retained and used as color descriptors (dominant color 1-4).

Species traits, conservation interest and efforts, research efforts and public attention

We integrated the SBI with multiple datasets on species traits and on various measures of human interest (including research effort public attention, and conservation efforts), along with data on species size (''wing size'', i.e. wing index[73]) and estimated species detectability, assuming that more detectable (common) species might receive greater public attention and research interest.

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Detectability

Detectability was quantified using a principal component analysis (PCA, *prcomp* function of the stat R package) on five standardized variables: (i) area of occupancy in Europe,[20] (ii–iii) maximum flight altitude and altitudinal range[20,74] and (iv-v) number of flight months per year and first month of flight.[73]

Two components were retained according to the Kaiser criterion (eigenvalues > 1) and subsequently subjected to an orthogonal varimax rotation to improve interpretability. The rotated components explained 41.1% (RC1) and 37.8% (RC2) of the total variance, respectively. RC1 primarily captured a spatial detectability gradient, associated with geographic range size and altitudinal distribution (DetectabilitySpatialAltitudinal), whereas RC2 represented a temporal detectability gradient, related to flight phenology (DectactabilityTemporal). Rotated component scores (Figure S7) were used as predictors in all subsequent analyses.

Conservation interest and effort

High-stakes conservation interest and effort were assessed as i) funding allocation, measuring the number of LIFE projects that mentioned the species in their title or abstract while recording the projects' start year (variable "Mentions in LIFE projects"), ii) resource-intensive interventions to prevent imminent ecological loss were quantified by recording translocation (sensu lato) and site-management actions (variable "Conservation actions"). We collected the number of interventions per species by searching in Web Of Science (hereafter, WOS) the number of published scientific papers containing the terms *TS=((reintroduction* OR *relocation* OR *translocation)* AND *(butterf* OR lepidoptera))* (338 documents examined) and *TS=((management* OR *restoration)* AND *(butterf* OR lepidoptera))* (13,750 documents examined). We examined the title and abstract of each paper, and when specific names of European butterflies were explicitly reported in the title, keywords, or abstract, we inspected the full text to identify the European location and the year in which the conservation action was initiated. Because many conservation actions are not necessarily documented in peer-reviewed scientific articles, or are reported only incidentally within broader studies, these data were complemented with dated translocation records from a recent synthesis[75] and with information obtained from conservation-agency websites for translocation and management actions. This strategy was designed to capture the best available evidence on the occurrence of high-stake conservation actions, acknowledging heterogeneity in reporting formats and sources. The number of actions per species was used as a variable.

Finally, we cross-referenced each species' conservation status by iii) checking their inclusion in the Bern Convention (1979) iv) in the EU Habitats Directive annexes (1992) and in species IUCN status using the v) 2010 and vi) 2025 European butterflies lists and the National IUCN red list (available in Maes[76] and from other sources included in the dataset. All data were collected in December 2025.

Research effort

Research effort was quantified using two complementary indicators. First, the number of DNA sequence vouchers available in GenBank (hereafter variable "Sequences in NCBI") was retrieved through automated queries to the NCBI nucleotide database using the *rentrez* R package,[67] searching each accepted species name together with all recognized synonyms (>100, available in supplementary data) and aggregating sequence counts across synonyms. Second, the number of published papers with automated bibliographic searches performed via the Web of Science Starter API (Clarivate) and the Scopus Search API (Elsevier) (hereafter variable "References"). For each accepted species name and its recognized synonyms, we queried title/abstract/keyword fields (Scopus: TITLE-ABS-KEY; WoS: TS) within the selected time windows (see subsection "Temporal dimension" below) and extracted the total number of matching records. To obtain a single bibliographic indicator per species, we averaged record counts returned by Scopus and Web of Science. All data were collected in December 2025.

Public attention

Public attention was evaluated as: i) the number of uploaded images on Flickr (Uploads Flickr) and iNaturalist (Uploads iNaturalist); ii) the number of Wikipedia pages available for each species (across all languages, Pages Wikipedia), iii) the total number of page views obtained from these Wikipedia pages since 2015 (Views Wikipedia), see Mouquet et al.[55] for detailed description of these metrics). All data were collected in December 2025.

QUANTIFICATION AND STATISTICAL ANALYSES

General

All analyses, unless if clearly specified, were performed in the R environment (*v. 4.4.1*)

Morphological/colorimetric traits and beauty scores

To investigate the relationship between butterfly morphological/colorimetric traits of each visual pattern and its Averaged Beauty Score, we used Boosted Regression Trees (BRT) using the *gbm v.2.2.2* R package[68] which can handle non-linear relationships, complex interactions, and diverse variable types without requiring prior data transformation or assuming specific distributions. All predictor variables described above were normalized to a 0-1 range to ensure comparability. To optimize the trade-off between model fit and generalization (avoiding overfitting), the following hyperparameters were defined: Learning Rate (shrinkage) was set to 0.01, allowing for a slow and precise convergence. Interaction Depth was set to 4, enabling the model to capture up to four-way interactions between features. Total Iterations were set to allow a maximum of 5,000 trees, with the Out-of-Bag (OOB) method used to determine the "best iteration" (optimal number of trees) to minimize predictive error. Model performance was evaluated by calculating the coefficient of determination (R2) between observed scores and those predicted by the model. The contribution of each butterfly trait to the SBI was quantified through Relative Influence (RI), which measures the frequency with which a variable is selected for splitting,

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weighted by the improvement to the model. To visualize the specific effect of the most influential traits, we generated Partial Dependence Plots (PDP). These plots illustrate the marginal effect of a single predictor on the response variable while holding all other predictors constant.

Phylogenetic analysis

The SBI was mapped on the phylogenetic tree of European butterflies[28] and the phylogenetic signal was computed using Pagel's λ[77] using the *phylosig* function of the *phytools* package v.0.2.2[69] using 1000 simulations in a randomization test.

Multivariate Analyses

Principal Component Analysis

To explore the multivariate relationships among variables describing public attention, research and conservation efforts, as well as species detectability, we performed a Principal Component Analysis (PCA). The categorical variable representing inclusion in the EU Habitats Directive (HD) was 0-1 coded, the IUCN[20,21] categories independently were coded as numeric variables 0-5 (least concern, near threatened, vulnerable, endangered, critically endangered). The PCA was computed in R using the *prcomp* native function. The first two principal components were retained for interpretation, as they captured the main structure of covariation among public attention, and research and conservation indicators. The SBI was excluded from the PCA but projected as a color gradient onto the species points in the ordination space, allowing the inspection of how aesthetic appeal covaries with the emerging multivariate structure.

Bayesian multivariate model

To jointly analyze the relationships among species traits, research effort, public attention interest, and conservation actions, we fitted a Bayesian multivariate model using the *brms* v.2.23.0 package[70] in R. The model was specified as a system of interconnected regression equations, each representing one component of the research-society-conservation dataset. The overall causal structure of the model, including the direction of effects and the temporal ordering of variables, is summarized below.

For each response variable, we specified an appropriate likelihood family. Gaussian models were used for approximately continuous variables after transformation (square-root transformed occurrences of iNaturalist records, DNA sequences, Flickr uploads, Wikipedia page views, and number of Wikipedia languages). Negative binomial models were used for count data that did not reach approximate normality after transformation (references, conservation actions and LIFE projects). Bernoulli models with a logit link were used for binary variables (inclusion in the Bern Convention and the EU Habitats Directive). Ordered categorical variables (IUCN threat categories in 2010 and 2025) were modelled using cumulative logit regressions.

All equations included species traits as predictors, namely the SBI, detectability proxies related to species range size and altitudinal breadth, and wing size. We assumed that these traits, including SBI, act as explanatory variables of different forms of human interest, rather than being shaped by them. Potential feedback effects, whereby public exposure through conservation campaigns or research attention might influence species detectability or perceived beauty, were beyond the scope of this study and warrant future investigation. In addition, several response variables were included as predictors in other equations, reflecting the hypothesis that public attention and research and conservation efforts form a sequentially connected system rather than independent outcomes. All equations were fitted jointly within a multivariate framework, with residual correlations among responses set to zero so that dependencies among processes were represented explicitly through directed predictors rather than through unexplained covariance.

Weakly informative priors were assigned to all parameters (normal priors for regression coefficients and intercepts, exponential priors for Gaussian residual variances, and Student-t priors for cumulative thresholds). Posterior distributions were estimated using four MCMC chains of 4,000 iterations each (2,000 warm-up), using the No-U-Turn Sampler and an adapt_delta of 0.95 to ensure convergence.

Temporal dimension

To reinforce causal plausibility, the model explicitly incorporated temporal stratification of several variables. Research effort and conservation actions were partitioned into time windows corresponding to four major conservation milestones: 1979 (BC),[18] 1992 (HD),[19] 2010 (IUCN Red List),[21] 2025 (IUCN Red List).[20] These milestones were selected because they mark key shifts in European conservation policy and assessment practices and are separated by broadly comparable time intervals (approximately 15 years), allowing sufficient time for earlier processes to plausibly influence subsequent outcomes but not vice versa. For example, research output prior to 1992 could contribute to the probability of inclusion in the HD, whereas post-1992 information was excluded. The full logic underlying the treatment, removal, and aggregation of temporally nested effects is detailed below. By jointly constraining both temporal precedence and directionality of trait effects, this framework strengthens causal interpretation while explicitly acknowledging the observational nature of the data and the possibility of residual feedback that cannot be fully resolved.

Model formula

Several predictors in the model describe temporally nested processes, such as scientific references (Ref) or conservation actions (Act) accumulated up to different dates (e.g. pre-1979, pre-1992, pre-2010), which can be considered potential determinants of subsequent processes that are modelled here as response variables (e.g. Bern Convention (Bern) , Habitats Directive (HD)). Conversely, variables accumulated after these milestones (e.g. post-1979, post-1992, post-2010) can be considered potential responses to these institutional frameworks and assessments. This temporal stratification does not model cyclic dependencies among the same variables. Instead, it separates historically distinct stages of the same process (e.g. research effort or conservation actions before

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and after major conservation milestones), allowing potential long-term feedback to be represented as temporally ordered sequences among different variables.

Because these variables represent partial sums of the same underlying processes, in some cases (e.g. post-1979, post-1992, post-2010) their effects are statistically non-independent and redundant by construction. Nevertheless, they are required to control for shared temporal structure and to isolate the effects of interest on downstream variables.

Taken together, the equations reported below constitute an explicit causal specification of the hypothesized system. The full network of relationships is too complex to be represented as a single readable directed acyclic graph (DAG), owing to the large number of temporally stratified variables and nested historical processes. Instead, causal assumptions are made explicit through the temporal ordering of predictors and responses, and through the distinction between variables used as controls, variables representing intermediate institutional states, and variables whose effects are interpreted. In this sense, the model formulae below serve the same purpose as a DAG while retaining the temporal detail required for implementation.

In the equations reported below, predictors included solely for control purposes are shown in italics. These variables are retained in the statistical models but are not interpreted in the results, nor reported in summary tables or figures, because their effects are subsumed by the corresponding cumulative variables. Variables shown in bold represent key intermediate states of the system (e.g. Bern Convention, Habitats Directive, IUCN assessments, cumulative research effort, LIFE projects), whose effects are interpreted only on outcomes occurring after their implementation. Accordingly, institutional frameworks, conservation assessments, research effort, conservation actions and LIFE projects are interpreted only for cumulative responses measured after the corresponding historical milestone (e.g. HD effects on conservation actions occurring after 1992).

Finally, because the Habitats Directive implements the Bern Convention, protecting 32 butterfly species, 21 of which were already included in the Bern Convention with the removal of only two species, the effects of the two frameworks are highly correlated and cannot be modelled simultaneously as predictors of the same response variable. In these cases, the larger and subsequent framework (HD) is used instead of the combination of the two.

Institutional conservation frameworks

Bern Convention

This model evaluates whether inclusion in the Bern Convention was associated with species traits and with pre-existing research effort and conservation actions. Time restricted predictors are included to verify the effects of historical availability of information prior to 1979.

Bern ~ 1 + **RefPre1979 + ActPre1979 +** SBI + DetectabilitySpatialAltitudinal+ DetectabilityTemporal + Wing_index

Habitats Directive

Inclusion in the Habitats Directive is modelled as a function of prior institutional protection, species traits, and pre-1992 research effort and conservation actions. Time stratified predictors are included to detect the effects of information available before adoption of the Directive.

HD ~ 1 + **Bern +** SBI **+ RefPre1992 + ActPre1992 +** DetectabilitySpatialAltitudinal+ DetectabilityTemporal + Wing_index

Conservation attention

Conservation lists and actions (high-stakes conservation efforts, LIFE projects, IUCN Red Lists)

These equations model conservation efforts across different temporal windows. Temporally stratified research variables are included to control for prior scientific attention and to prevent spurious attribution of effects to institutional frameworks or species traits (in italics). The cumulative number of conservation actions is interpreted in relation to species traits and institutional protection.

ActPre1979 ~ 1 + SBI + **RefPre1979** + DetectabilitySpatialAltitudinal+ DetectabilityTemporal + Wing_index

ActPre1992 ~ 1 + **Bern** + SBI + **RefPre1992** + DetectabilitySpatialAltitudinal+ DetectabilityTemporal + Wing_index

ActPre2010 ~ 1 + **Bern** + SBI + **RefPre1992** + DetectabilitySpatialAltitudinal + DetectabilityTemporal + Wing_index+**LIFEpre2010**

ActPost1979 ~ 1 + **Bern** + *poly(IUCN2010num,3)* + *AllRef* + *SBI* + *DetectabilitySpatialAltitudinal*+ *DetectabilityTemporal* + *Wing_index+LIFEtotal*

ActPost1992 ~ 1 + **HD** + *poly(IUCN2010num,3)* + *AllRef* + *SBI* + *DetectabilitySpatialAltitudinal*+ *DetectabilityTemporal* + *Wing_index* + **LIFEtotal**

ActPost2010 ~ 1 + *HD* + **poly(IUCN2010num,3)** + *AllRef* + *SBI* + *DetectabilitySpatialAltitudinal*+ *DetectabilityTemporal* + *Wing_index* + *LIFEtotal*

ActTotal ~ 1 + *HD* + *poly(IUCN2010num,3)* + **AllRef +** SBI + DetectabilitySpatialAltitudinal + DetectabilityTemporal + Wing_index + *LIFEtotal*

Mentions in LIFE projects. Similarly, mentions in LIFE projects, all successive to HD, are modelled as functions of inclusion in HD list, species traits, and number of studies. The inclusion in the IUCN[21] Red List is tested only on LIFE projects that have been accepted since 2010.

LIFEpre2010 ~ 1 + **HD +** SBI + RefPre2010 + DetectabilitySpatialAltitudinal + DetectabilityTemporal + Wing_index

LIFEpost2010 ~ 1 + *HD* + **poly(IUCN2010num,3)** + *SBI* + *AllRef* + *DetectabilitySpatialAltitudinal*+ *DetectabilityTemporal* + *Wing_index*

LIFEtotal ~ 1 + **HD** + *poly(IUCN2010num,3)* + **AllRef +** SBI + DetectabilitySpatialAltitudinal + DetectabilityTemporal + Wing_index

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Research effort

References

The effects on References are organized as for the high-stake conservation actions

RefPre1979 ~ 1 + SBI + DetectabilitySpatialAltitudinal+ DetectabiltyTemporal + Wing_index
RefPre1992 ~ 1 + **Bern+**SBI + DetectabilitySpatialAltitudinal + DetectabiltyTemporal + Wing_index
RefPre2010~ 1 + **HD+**SBI + DetectabilitySpatialAltitudinal + DetectabiltyTemporal + Wing_index
RefPost1979~ 1 + **Bern** + *poly(IUCN2010num, 3)* + *SBI* + *DetectabilitySpatialAltitudinal* + *DetectabilityTemporal* + *Wing_index*
RefPost1992~ 1 + **HD**+*poly(IUCN2010num, 3)*+*SBI* +*DetectabilitySpatialAltitudinal* + *DetectabilityTemporal* + *Wing_index*
RefPost2010~ 1 + *HD* + **poly(IUCN2010num, 3)** + *SBI* + *DetectabilitySpatialAltitudinal* + *DetectabilityTemporal* + *Wing_index*
AllRef ~ 1 + *HDpred* + *poly(IUCN2010num, 3)* + SBI + DetectabilitySpatialAltitudinal + DetectabilityTemporal + Wing_index

Sequences in NCBI

Number of available sequences are modelled as functions of species traits and institutional protection, no time stratification is applied since most data belong to years successive to 2010, no correlation with references is applied because most sequencing effort is published but such trivial correlation has no causal structure to define a response and a dependent variable.

Sequences ~ 1 + **HDIUCN2010num, 3) +** SBI + DetectabilitySpatialAltitudinal + DetectabilityTemporal + Wing_index

Public attention

Public attention indicators are modelled as functions of species traits and institutional protection; no time stratification is applied since most data belong to years successive to 2010.

(uploads iNaturalist, uploads Flickr, views Wikipedia, pages Wikipedia) ~ 1 + **HDIUCN2010num, 3) +** SBI + DetectabilitySpatialAltitudinal + DetectabilityTemporal + Wing_index

Beauty bias in National and European lists

Since the beauty bias identified by multivariate models stems from interconnected effects of multiple variables, it is difficult to reproduce directly. We simplified the assessment of this bias in risk or protection lists by calculating the mean value of the SBI included in each list. To see whether this mean value was unusually high or low, we simulated what would happen if species were chosen randomly for the risk or protection lists: we randomly selected the same number of species 10,000 times from the pool of available species and assessed the fraction of iterations showing a mean SBI lower than the observed one. Low fractions (<0.05) indicate a strong signal for the beauty bias showing that species were not selected randomly with respect to the SBI (meaning: species on the list are more attractive than random), values between 0.05 and 0.10 indicate a signal for a weak beauty bias, whereas high values (>0.95) indicate that the selected species were drawn from among the least attractive ones (meaning: species on the list are less attractive than random).

We applied this framework to the Bern Convention and the Habitats Directive, both key international legal tools for the protection of European species and habitats. For the Red Lists, two groups were analyzed separately: in the first one we included Vulnerable, Endangered, and Critically Endangered species, and in the second one Near Threatened species. This distinction was made because inclusion in the former group requires strict quantitative thresholds for population size and trends, whereas listing a species as Near Threatened is expected to follow more flexible and non strictly quantitative criteria.