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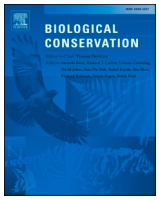

One in five butterfly species sold online across borders

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ABSTRACT

Humankind's appreciation for butterflies spans cultures and millennia, including the practice of assembling butterfly collections. We monitored the global e-commerce platform eBay.com for one year and obtained 50,555 time-stamped transactions of 3767 species (739 genera) of butterflies. This is nearly 20% of all butterfly species on Earth. A total of 552 sellers were based in 44 countries across five continents. At least 96% of the traded species required transportation of the specimen from its country of origin to its seller, usually from the Global South to the United States and Europe. To our knowledge, this is the most spatially and temporally detailed record of trans-boundary wildlife movement of any taxonomic group. We quantified the aesthetics of butterflies deemed desirable (*e.g.,* size, shape, and color) and showed that while endangered species command higher prices, a butterfly's aesthetic ranking, not its range, abundance, nor phylogenetic status, best predicts its trade volume. These results emphasize the complicated interplay between wildlife market economics and human aesthetic appreciation.

1. Introduction

Butterflies are universal cultural symbols, appearing from the Egyptian tomb of Nebamun to the Chinese tales of *Chuang-tzu's Dream* (Nazari and Evans, 2015; Möller, 1999). Charles Darwin, Alfred Russel Wallace, Winston Churchill, and Vladimir Nabokov are only a few of the many historical figures who were avid butterfly collectors. During the late 19th century, an era of global biological exploration, colonial surveyors employed legions of villagers to search for rare and beautiful butterflies. They shipped specimens from the tropics to Europe where private collectors and museum staff scientists vied for these biological curios (Wallace, 1886). Modern enthusiasm for butterflies has not waned, as evidenced by the prevalence of butterfly houses and shadowboxes in natural history museums and art galleries (Barkham, 2012; Boppré and Vane-Wright, 2012; Klein and Brosius, 2022). Since most butterflies have limited geographic distributions (Pinkert et al., 2022), assembling colorful, multi-species displays requires sourcing butterflies from across the globe.

Although they are aesthetic objects for collection and often heralded as flagships of invertebrate conservation (Preston et al., 2021), butterflies and other insects are seldom mentioned in the discourse on global wildlife trade (Fukushima et al., 2020; Scheffers et al., 2019). From 1998 to 2007, roughly equal numbers of CITES-regulated mammals (0.4 million) and butterflies (0.3 million) were traded in Southeast Asia, even though *ca.* 850 mammal species require CITES reporting compared to fewer than 70 butterfly species (Nijman, 2010). Unlike the high-profile media coverage of shark fin, tiger paw, and ivory, butterflies glide under the radar because (1) most sellers operate within a loosely regulated online ecosystem rather than physical markets, which make transactions difficult to monitor (Gippet et al., 2023; Marshall et al., 2022; Banerjee et al., 2023); and (2) dried butterfly specimens inside international parcels are difficult to detect and intercept by customs officials, in part because they don't show up on X-rays.

In this study we quantify the extent of the online butterfly trade and its pattern of global transactions from the global e-commerce platform eBay.com. Legal wildlife trade records (*i.e.*, those reported to CITES

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database) show extensive flow of natural resources from the Global South (previously called developing countries) to the developed countries (Liew et al., 2021). However, only by recording transaction price and volume could we contextualize the extent of economic impact of wildlife trade on local livelihood. We compiled daily wages for each country involved in the trade. Furthermore, we compiled a database of biological traits (including threat status) of traded butterflies to look at factors affecting individual species trade price and volume. We hypothesize that butterflies designated as "threatened" or "endangered" by the International Union for Conservation of Nature (IUCN) are sold at higher prices than common ones. Long distance needed to transport exotic specimens and the phylogenetic uniqueness of some species could also increase sale price and volume. These predictions are consistent with the "anthropogenic Allee effect" (Siriwat et al., 2019; Courchamp et al., 2006), which posits that rare (or unusual) species are disproportionately exploited in wildlife trafficking.

Intriguingly, unlike vertebrates, public awareness of insects does not focus on the rare and exotic (Wang et al., 2021). Historically, butterflies were portrayed and acquired as *objet d'art*; it is possible that people buy butterflies online because they are beautiful. Aesthetic experiences inspired by nature profoundly affect our emotion and conservation decision-making (Jarić et al., 2020; Stokes, 2007; Martín-López et al., 2007). How nature's "cultural ecosystem services" influence human behavior are only starting to be unraveled in the discipline of "aesthetic science" (Shimamura and Palmer, 2012; Langlois et al., 2021; Scholte et al., 2015). To evaluate whether human aesthetic appreciation of butterflies corresponds with their trade volume, we invited human judges to rank curated images of traded butterflies and analyzed the relationships among human rankings, trade volume, and price.

2. Methods

See Supplementary Material for detailed methods description.

2.1. Trade data collection

We compiled a list of accepted names and historical synonyms of all butterflies (Barve, 2021; Lamas, 2015). To quantify the extent of the global butterfly trade, we scraped the global e-commerce platform eBay.com over the course of one year by generating targeted URLs that matched search terms (*i.e.,* butterfly names, Python package Request 2.18.4, Reitz, 2022) and parsing information contained in each URL (Python package BeautifulSoup4 v4.9.3, Richardson, 2022). Repeated purchases of the same listed item generated separate URL records. The number of butterflies sold in each URL was counted to tally total sale volume. Specifically, we logged every confirmed sale that included a butterfly binomial and recorded the price, time, and seller's location. When required, a third-party service was used to solve CAPTCHAs (Proxycrawl, 2022). We annotated sale details such as transaction amount (multiple *vs.* single individuals) and specimen status (framed, sex, abnormality) from the item description and images. We trained machine learning models to automate quality control for data annotation (Vertex AI, 2022; Erickson et al., 2020).

2.2. Species trait data

For each traded species, we compiled a database of its country-level distribution range (Pinkert et al., 2022), abundance (approximated by number of museum occurrence records and research-grade citizen science sightings, GBIF.org, 2022; iNaturalist Contributors, 2022), protection status (IUCN, 2022; CITES, 2022), wingspan (measured from Gall, 2022; MCZ Harvard University, 2022; D'Abrera, 1995 and verified with Middleton-Welling et al., 2020; Shirey et al., 2022), and phylogenetic distinctiveness (from tribal level phylogeny of Espeland et al., 2018; evolutionary distinctiveness calculated using the evol.distinct function in R package PICANTE, Kembel et al., 2010). Since IUCN Red List and CITES Appendices are similar indicators of threat level (CITES, by definition, should regulate trade of endangered species), we categorized species that either had an IUCN status of "Vulnerable", "Endangered" or "Critically Endangered," or a CITES Appendix listing of I or II as "endangered". For each transaction, we conservatively concluded that a transboundary transaction had occurred only when the seller was located in a country outside of the butterfly's distribution range. To estimate the transportation distance of each transboundary specimen, we calculated the distance between the seller's city and the nearest border of a country where the butterfly occurs.

2.3. Aesthetic appreciation

For each traded species we acquired at least one image of a pinned and spread male specimen for aesthetic analysis (Gall, 2022; GBIF.org, 2022; MCZ Harvard University, 2022; Warren et al., 2016). To understand the aesthetic appreciation by consumers for different butterflies, we quantified the wingspan, wing shape, and color palette of all traded species using a high-throughput image processing pipeline (Chan et al., 2022). Wing shapes were quantified with geometric morphometrics and summarized as principal components (Bonhomme et al., 2014; Owens et al., 2020; Fig. S3F). Butterfly color was analyzed in both RGB (red, green, and blue) and HSV (hue, saturation, and value) color space.

We implemented the Elo rating system (Elo, 1967) to evaluate human aesthetic preferences for butterfly images. The Elo system generates highly dispersed ranking of a large number of objects through pairwise comparisons (Goodspeed, 2017). It is used in determining worldwide player ratings in chess, competitive sports, and online gaming. Pairwise contest results change the Elo score of each contestant; the magnitude of change is proportional to differences in current contestant scores. We designed an assessment platform that treated each butterfly image as a contestant and invited human judges to evaluate pairs of butterfly images and "Pick the one you like better" (Supplementary Material and Code Availability). These aesthetic judges were recruited in groups of 20 through Amazon Mechanical Turk (MTurk, Crowston, 2012). MTurk is a crowdsourcing tool routinely used in sociology surveys for quickly fulfilling data collection needs (Shank, 2016); in our case it was used to direct potential participants to a customized platform to serve as aesthetic judges. MTurk participants in this study were restricted to the United States, with no other demographic specifications. We could not assess age, gender, or other demographic aspects of participants. Each aesthetic judge selected their favorite butterfly image from each of 100 pairs (*i.e.*, 100 "iterations"). Ethics (Institutional Review Board) approval for this study was waived because we did not (and could not) record any personal information or participant choices (see Code Availability for our platform design); only the collective aesthetic ranking was used in our analysis. We monitored the stability in ranking of each butterfly image by calculating the variance of its ranking history in the past 5000 iterations. We defined aesthetic rankings as "stable" when mean variance of each decile stopped decreasing. We iterated our recruitment of aesthetic judges until aesthetic ranking stabilized (Fig. S2A—D).

2.4. Analysis

We used butterfly traits as predictors to build linear regression models of species price, log-transformed price, sales volume, and log-transformed volume (Table S1C, S1D). We removed sales of framed samples, "freak" samples (*e.g.,* hybrids and gynandromorphs), and multi-species sales (*e.g.,* wholesale of a lot of different species) in our analysis. For the subset of traded species that had images with aesthetic rankings, we used these rankings as a predictor of price and volume (Table S1E). We then calculated the relative importance of each variable in our models (Lindeman et al., 1980; Grömping, 2006). We built generalized linear models of the above-mentioned predictor-variable sets and applied random forest models to account for non-linear effects

and interactions among predictors (Breiman, 2001; Liaw and Wiener, 2002). We calculated the increase in mean square error and node purity when each variable was excluded from the model as an indicator for variable importance.

3. Results

After filtering 63,000 potential transactions, we verified a total of 50,555 butterfly specimen transactions from Sep 2020 to Sep 2021. While the International Union for Conservation of Nature (IUCN) lists 214 butterfly species as "traded" (IUCN, 2022), we recorded 3767 species from 739 genera—this is seventeen times more traded species than listed by IUCN and more than 19% of all described butterfly species on Earth (Lamas, 2015).

A total of 552 sellers were based in 44 countries across five continents (Fig. 1A, orange circles). At least 96% of the traded species required transportation of the specimen from its country of origin to the eBay seller, usually from the Global South to the United States and Europe (mean transport distance = 4814 km, s.d. = 3609 km). While large, colorful butterflies such as the swallowtails (family Papilionidae) were especially popular (see exemplars from Fig. 1B), almost every tribe of butterfly was on sale (Fig. 1C). The median price of an unframed butterfly was $6.75 (mean = 16.61, s.d = 55.91; the average framed specimen cost $35.90). This amounts to *ca.* one-third of the average daily wage in the specimens' countries of origin (World Bank, 2022; Fig. 1D).

While endangered species command higher prices, a butterfly's aesthetic appeal best predicts its trade volume (Fig. 2). Except for outliers such as hybrids and gynandromorphs (2.14% of all specimens; hybrids increased prices by $47 per specimen, and gynandromorphs by $270), the best linear predictor for the sale price per species was its perceived rarity status—that is, being listed as "vulnerable" or "endangered" on the IUCN Red List or being regulated by CITES (Fig. 2A, Table S1). As of 2021, the IUCN Red List includes 207 "vulnerable" or "endangered" butterflies; 51 of these were sold on eBay in the past year. While only 2% of the traded butterflies are considered "endangered", these accounted for 4 of the top 10 (and 18 of the 100) most expensive species. A male and female pair of *Bhutanitis ludlowi* originating in India and sold in Russia fetched $8998. This species is renowned for its rediscovery in a single habitat in Bhutan 76 years after being presumed extinct (Harada et al., 2012).

While perceived rarity was correlated with higher prices, it had no significant effect on sales volume (Fig. 2C, Table S1). We hypothesized that the sale volume of a species might reflect aesthetic appreciation rather than a collector's zeal for rarity. Relative aesthetic ranking among butterfly images stabilized after 20,000 iterations of the Elo tournament (*i.e.,* a total recruitment of 200 aesthetic judges, Fig. S2E, S2F). As much as 49.30% of the variance in aesthetic ranking could be explained by butterfly wingspan, shape, and color (Fig. S3, Table S1FG). Aesthetic appeal quantified using subjective rankings correlates significantly with a species' sales volume (Fig. 2B, Table S1DE). The butterflies ranked as most appealing were often large with brilliant structural colors, such as *Morpho menelaus* and *Papilio ulysses* (Fig. 2D).

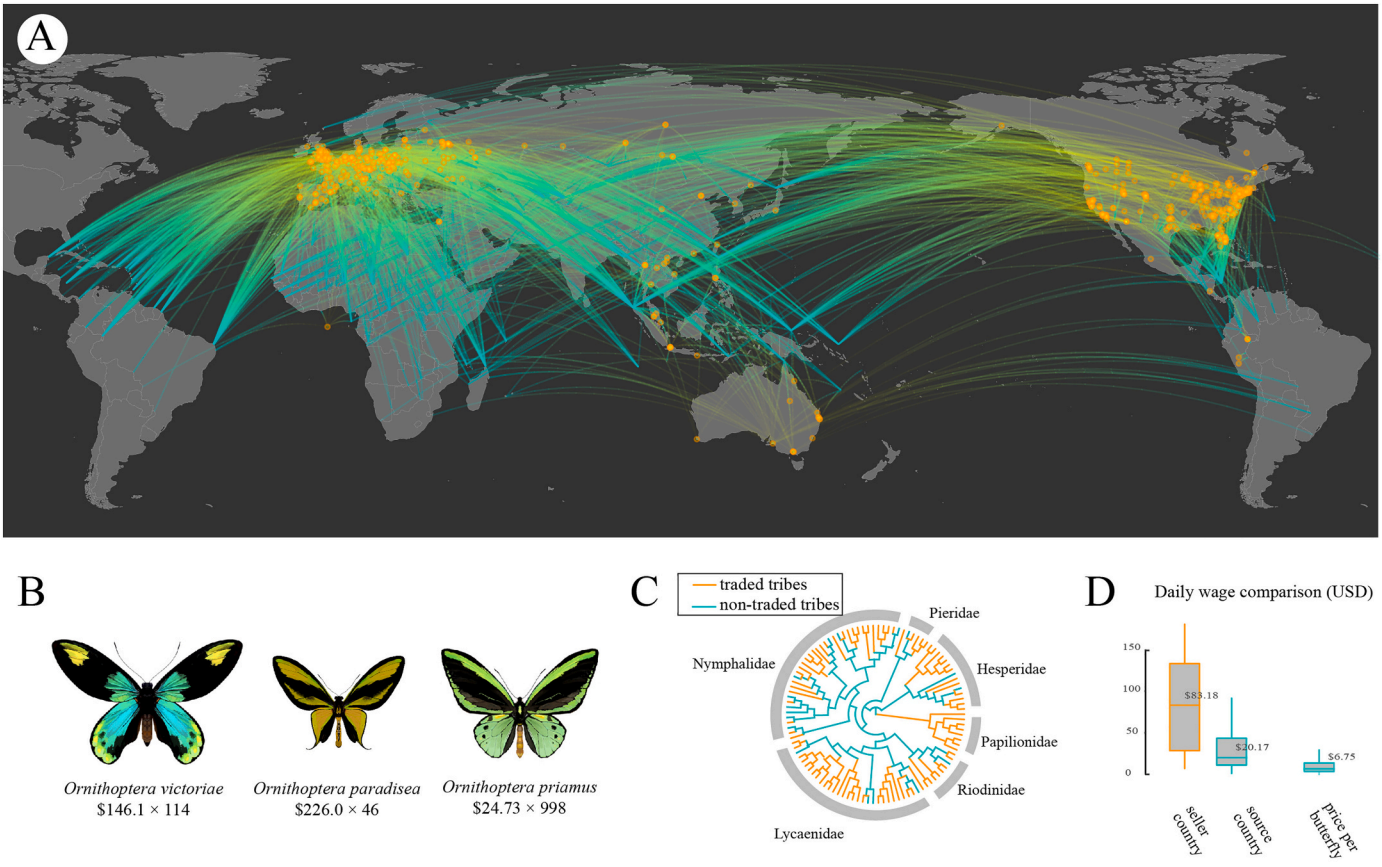

Fig. 1. Fine-scale records of butterfly trade across borders. (A) Online transactions of 3767 species: each line connects the seller (orange dot) to the closest point in the species' endemic range. (B) Exemplars of birdwing butterfly mean sales prices and annual sale volumes. All species in the genus *Ornithoptera* and *Troides* have been listed under CITES Appendix II; these large and visually appealing butterflies are coveted by collectors. (C) Extent of butterfly trade mapped onto a tribal-level phylogeny. Each tip indicates a butterfly tribe; orange tips indicate tribes that are traded online. Family names are labeled. (D) Comparisons of average daily wages in butterfly source countries, seller countries, and the median butterfly sales price.

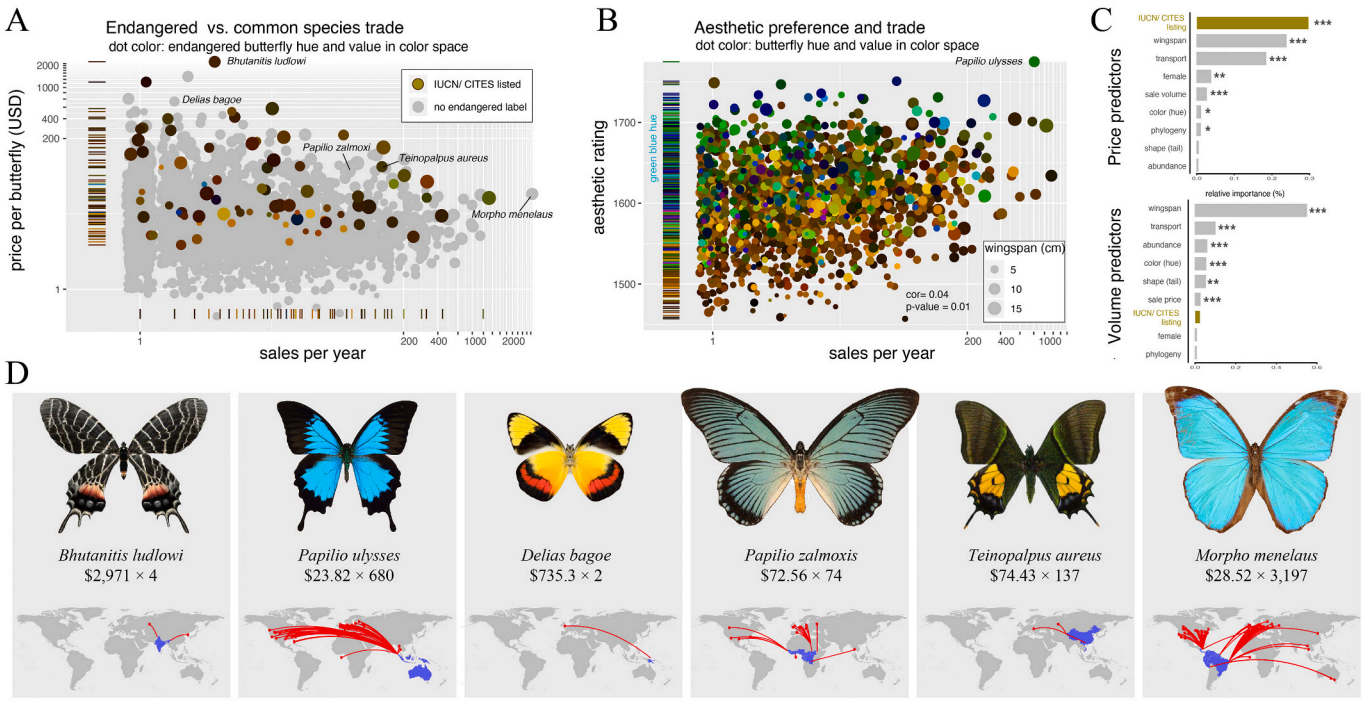

Fig. 2. Endangered species command higher prices, while a butterfly's aesthetic appeal best predicts its trade volume. (A) Range of average sale price and volume of sales for 3767 species: each species is represented as a point; species with endangered status (criteria defined in text; $n = 82$) are colored according to their respective hue (H) and value (V) in hue, saturation and value (HSV) color space. Point size is proportional to a species' wingspan. (B) Species with aesthetic rankings ($n = 1659$) are represented as points colored with their respective HSV and sized proportionally to their wingspan. Higher aesthetic rating on the y-axis indicates human preference, which significantly correlates with higher hue value (green and blue) and higher sale volumes. (C) Factors affecting sales price and volume. In linear regression models, endangered status is the most important predictor of high sale price (top, olive-colored bar), while it is not a predictor of sale volume, which is significantly correlated with aesthetic variables such as wingspan and color. (D) Exemplars of traded species mean price and sales volume per year. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

4. Discussion

4.1. Interplay of economics and aesthetics

To our knowledge, this is the most spatially and temporally detailed record of trans-boundary wildlife movement of an entire taxonomic group. Our methodology underestimates the total volume and distance of specimen transport (see Supplementary Methods). We found no mention of governmental import/export documentation on any seller's webpage, and we suspect that most of these butterflies are wild caught, not captive bred. Butterfly breeding is costly because it requires a constant supply of fresh hostplant foliage specific to each butterfly species. Several additional lines of evidence suggest that most are taken from the wild: (1) one of the largest butterfly pupae importers in the world (LPS, 2022) lists fewer than 100 captive bred species in their regular inventory and 300 species in their entire catalog from providers around the world. If this approximates the current number of captive bred species, it is an order of magnitude less than the 3767 species sold as dry specimens on eBay. (2) Less than half of all butterfly hostplants are known (Robinson et al., 2020). Even with species that are frequently reared, captive breeding requires avoidance of pathogens and knowledge of each species' mating requirements and hostplant choice, all of which are often poorly understood. (3) Many eBay sellers explicitly list the specimen collecting location in the item description.

We found that CITES-regulated species are not associated with reduced trade volume, although they fetched higher sale prices (Fig. 2A). Demand for endangered butterflies could drive sale price high enough to induce illegal poaching, or it is possible that some CITES-listed species are no more difficult to capture (or no less abundant in nature) than unlisted ones. In support of the latter explanation, recent studies of several CITES-listed, illegally-traded butterflies show that they are habitat-specific but locally abundant (Wang et al., 2018; Wang et al., 2022). Anthropogenic habitat threat should be the main consideration when deciding to list an insect as endangered or threatened (Wagner et al., 2021); as a result, "threat status" might not reflect population abundance in the right habitat. When a locally abundant species was listed, legal consequences for collectors could be severe. In 2002, collectors were sentenced to up to 13 years of jail in China for netting *Teinopalpus aureus*, a CITES-listed butterfly (Li et al., 2013). Despite such punishment, our data show that twenty years later, six eBay dealers sold this species in 134 transactions (Fig. 2D). It is undoubtedly important to regulate wildlife trade through coordinated international agreements such as CITES, but conservation practitioners would also benefit from more fine-scaled assessments of the biological reality (*e.g.*, species abundance) and economic incentives (*e.g.*, market demand) behind high-volume trades of endangered butterflies.

While trade volume could not be satisfactorily explained by perceived butterfly rarity, the connection between volume and aesthetic rankings suggests that consumers are buying butterflies in bulk because they are beautiful. Aesthetic taste varies with age, culture, and gender (*e.g.*, Sorokowski et al., 2014; Bao et al., 2016; Pugach et al., 2017), but when it comes to butterflies, our 200 judges agreed on their favorites. These judges are from the United States, the country with the most butterfly sellers on eBay. The variance of collective aesthetic ranking decreased and stabilized but did not reduce to zero, suggesting nuanced variation in taste across different demographics, as we might expect for artistic preferences.

4.2. Scope and limitations

All transaction data and trait predictors are available for further analysis by interested researchers (for example, we might find

phylogenetic signal in trade price when a species-level butterfly phylogeny becomes available in the future). There are several caveats to our dataset. First, the high concentration of sellers in the United States and Europe might reflect a biased geographical distribution of eBay users rather than heightened regional interest in butterflies. Well-known butterfly transaction events in Asia, such as the Tokyo Insect Fair, or specialized online collector forums in non-English languages, still largely evade scrutiny. This dataset only brings to light the abundance of butterfly trading on a single e-commerce platform. It may also be susceptible to pitfalls of web-scraped trade analysis, such as potential "fake transactions" used by sellers to boost sale records, although we have detected consistent transaction patterns across the year and prominent weekend shopping peaks that are indicative of normal consumer behavior (Fig. S4).

Secondly, while we have strong evidence that specimens are transported across borders, this study does not capture the economic dynamics of "transboundary sales". The routes of transactions shown in Fig. 1A are shortest distances between known butterfly distributions and their sellers. We did not know (1) how much the sellers paid local collectors (which, combined with confirmed sales price in this dataset, would have given us an estimate of their profit margin); nor did we know (2) the distance of transport between sellers and online buyers. If we assume a peak eBay traffic time of evening to midnight (MarkSight, 2022), the timestamp of purchases suggest that buyers are in the same region as their sellers (Fig. S1)—but these inferences are tenuous. It is possible that the postage fee of the transaction, which is web-scrapable, could offer more information on buyer information, but we did not collect this information.

Finally, in our calculation of minimum transport distance from a butterfly's endemic range to seller location, we assumed that butterflies are not bred in captivity outside their endemic country. Outside tightly regulated entomological research laboratories, we are not aware of any instances of *ex situ* butterfly breeding across borders. Such husbandry is theoretically feasible for well-equipped individual sellers, provided they could clear the necessary permitting requirements, but is not a prevalent practice. For this reason, we inferred the occurrence of cross-border specimen transfer.

5. Conservation implications

Since the Victorian era, people across the globe acquired butterflies as *objet d'art*. This basic human instinct for the appreciation of nature could be leveraged to provide sustainable income for rural inhabitants of the Global South while incentivizing habitat conservation. E-commerce has proven important in revitalizing local craft industries in developing countries (Droege, 2022; Martins et al., 2020; Bellver et al., 2023), suggesting that local collectors could sell butterflies directly to consumers on eBay or other online platforms. Our analyses suggest that if direct trade from collectors to buyers were established, rural collectors could potentially earn an average local wage by selling around three specimens per day (Fig. 1D). Currently, such transactions rely on online sellers as mediators.

The prodigious reproductive capacity of r-selected insects means that collecting or ranching butterflies from the wild is sustainable if natural habitats are preserved (Bayliss-Smith, 2006; Matiku et al., 2013; Gordon and Ayiemba, 2003; Slone et al., 1997). Sustainable economic profitability might be the most parsimonious explanation for why most traded butterflies are wild-caught. However, this should be examined with an ecosystem service cost-effectiveness analysis. Selling wildlife to preserve wildlife might seem counter-intuitive, but careful analyses that consider local stakeholders in conservation strategies have arrived at similar conclusions involving vertebrates (Di Minin et al., 2016). Unlike their 19th century counterparts, modern collectors for the butterfly trade are stakeholders who depend on pristine habitats for their livelihood, and therefore have a vested interest in habitat conservation. We suggest that the scale and extent of global butterfly trade is best seen as a practice of sustainable, targeted resource extraction that has considerable potential in promoting the conservation of insect habitats.

Code availability

A guide to our web scraping pipeline is deposited on GitHub: https://github.com/Weilin37/ButterflyTradeEbay

Implementation of Elo-based aesthetic ranking is deposited on GitHub (front end: https://github.com/jzengg/butterfly-ui; back end: https://github.com/jzengg/butterfly).

CRediT authorship contribution statement

Zhengyang Wang: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Wei-Ping Chan:** Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Nhat Tan Pham:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – review & editing. **Jimmy Zeng:** Formal analysis, Investigation, Methodology, Visualization, Writing – review & editing. **Naomi E. Pierce:** Writing – review & editing. **David J. Lohman:** Conceptualization, Supervision, Resources, Writing – review & editing. **Weilin Meng:** Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare no competing interests.

Data availability

(1) All annotated butterfly transaction data; (2) species-level trait data used for price and volume predictions and (3) representative image clusters are deposited on Zenodo: https://zenodo.org/record/7825674#.ZDf_R-zMKWh

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110092.

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