RESEARCH ARTICLE

Global Change Biology **WILEY**

Combining environmental niche models, multi-grain analyses, and species traits identifies pervasive effects of land use on butterfly biodiversity across Italy

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Abstract

Understanding how species respond to human activities is paramount to ecology and conservation science, one outstanding question being how large-scale patterns in land use affect biodiversity. To facilitate answering this question, we propose a novel analytical framework that combines environmental niche models, multi-grain analyses, and species traits. We illustrate the framework capitalizing on the most extensive dataset compiled to date for the butterflies of Italy (106,514 observations for 288 species), assessing how agriculture and urbanization have affected biodiversity of these taxa from landscape to regional scales (3–48 km grains) across the country while accounting for its steep climatic gradients. Multiple lines of evidence suggest pervasive and scale-dependent effects of land use on butterflies in Italy. While land use explained patterns in species richness primarily at grains ≤12 km, idiosyncratic responses in species highlighted "winners" and "losers" across human-dominated regions. Detrimental effects of agriculture and urbanization emerged from landscape (3-km grain) to regional (48-km grain) scales, disproportionally affecting small butterflies and butterflies with a short flight curve. Human activities have therefore reorganized the biogeography of Italian butterflies, filtering out species with poor dispersal capacity and narrow niche breadth not only from local assemblages, but also from regional species pools. These results suggest that global conservation efforts neglecting large-scale patterns in land use risk falling short of their goals, even for taxa typically assumed to persist in small natural areas (e.g., invertebrates). Our study also confirms that consideration of spatial scales will be crucial to implementing effective conservation actions in the Post-2020 Global Biodiversity Framework. In this context, applications of the proposed analytical framework have broad potential to identify which mechanisms underlie biodiversity change at different spatial scales.

KEYWORDS
agriculture, biodiversity conservation, functional traits, grain, insect declines, resolution, scale, species distribution models, urbanization

1 | INTRODUCTION

Anthropogenic loss of native habitat is a primary threat to biodiversity worldwide (Davison et al., 2021; Warren et al., 2021). Understanding how species respond to widespread human activities such as agriculture, resource extraction, and urbanization has therefore become a central theme in ecology and conservation (Callaghan et al., 2021; Riva & Nielsen, 2021; Sirami et al., 2019). Yet, our understanding of these complex dynamics remains partial, one outstanding question being how land use affects the distribution of species across large spatial scales (Davison et al., 2021). Climates are typically thought to control the distribution of species at large spatial scales, whereas factors including habitat types, contingencies, and biotic interactions should determine local biodiversity patterns (McGill, 2010; Soberón, 2007), suggesting that land use should more strongly affect biodiversity at finer spatial scales (Vellend et al., 2017). Nevertheless, the spatial domains at which a transition occurs between these "bottom-up", local effects, and "top-down", climatic effects, remain surprisingly poorly understood (Belmaker & Jetz, 2011; McGill, 2010).

Like many patterns and processes in ecology (Levin, 1992; Wiens, 1989), responses in species and biodiversity to land use are scale-dependent (e.g., Chase et al., 2018; Riva & Fahrig, 2022). Therefore, concepts and approaches drawn from scaling theory are key to understanding the spatial domains of environmental impacts from human activities on biodiversity (Belmaker & Jetz, 2011; McGill, 2010). Specifically, there are two facets of spatial scales that determine our insight into relationships between species or biodiversity and the environment—grain, the minimum spatial unit in the data (e.g., plot size or raster resolution), and extent, the total area under consideration (Wiens, 1989; Figure 1). While both grain and extent provide important, complementary information (Rahbek, 2004), studies assessing how land use affects biodiversity are generally conducted at relatively small extents (i.e., mostly <10,000 km^2; Davison et al., 2021), such that responses typically cannot be assessed at coarse grains. In turn, because human activities interest millions of km^2 of land worldwide (Bowler et al., 2020; Riva et al., 2022), focusing on small grains risks missing patterns in responses to large-scale land use that might only be appreciated at larger spatial grains (Davison et al., 2021; Riva & Fahrig, 2022).

Exploring grain-dependent patterns is, nevertheless, pivotal to capturing the signature of different ecological processes affecting ecosystems in human-dominated regions. For instance, grain mediates our understanding of the drivers of biodiversity (Belmaker & Jetz, 2011; Keil & Chase, 2019; Rahbek, 2004) and of the occurrence of species (Connor et al., 2019; Hodgson et al., 2022; Mertes & Jetz, 2018). At finer grains, species responses to environmental factors might represent habitat preferences or the use of space, whereas at larger grains responses might represent metacommunity dynamics, or even biogeographical and energetic constraints (Belmaker & Jetz, 2011; Connor et al., 2019; Johnson, 1980; Mertes & Jetz, 2018). Ultimately, understanding at which grain different environmental factors affect the distribution of species can shed light on which processes determine biodiversity in different systems. Unraveling grain-dependencies is also crucial for conservation, because cross-scale extrapolations and mismatches between the assumed and actual scale at which an environmental gradient affects biodiversity or species can lead to improper conservation recommendations (Fahrig et al., 2022; Randin et al., 2009; Riva & Fahrig, 2022; Seo et al., 2009).

Here, we propose a novel analytical framework that integrates environmental niche models (ENMs), cross-grain analyses, and species traits to assess how biodiversity responds to land use across spatial scales (Figure 2). Fitting ENMs across multiple grains and for many species allows assessing how relationships between environmental gradients and the occurrence of each species vary across spatial scales, and whether species traits can predict different patterns in response to land use. Crucially, assessing coarse grains of analysis here is not a means to address positional errors for biodiversity data (Gábor et al., 2022), but rather a deliberate approach
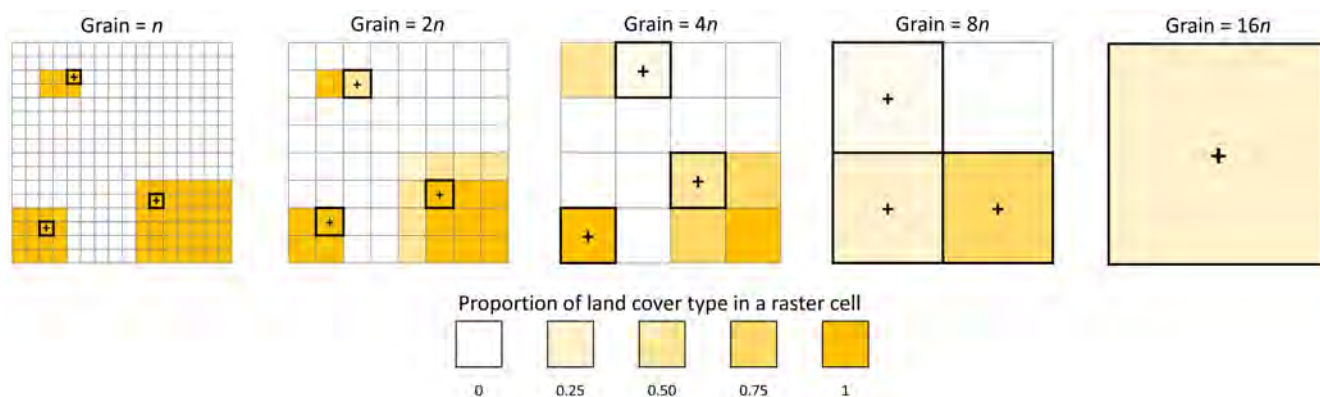

FIGURE 1 The scale of analysis, described by extent and grain, mediates our understanding of the relationship between species occurrence and land use. In this example, the extent is kept constant, while grain increases geometrically with a common ratio of 2. When manipulating grain, the prevalence of a species (squares occupied, highlighted with thick edges) increases from ~1% to 100% of a study area, and a strong local relationship with a land cover type (in gold) fades. Analyses that focus on different grains, therefore, capture the signal of different ecological processes.
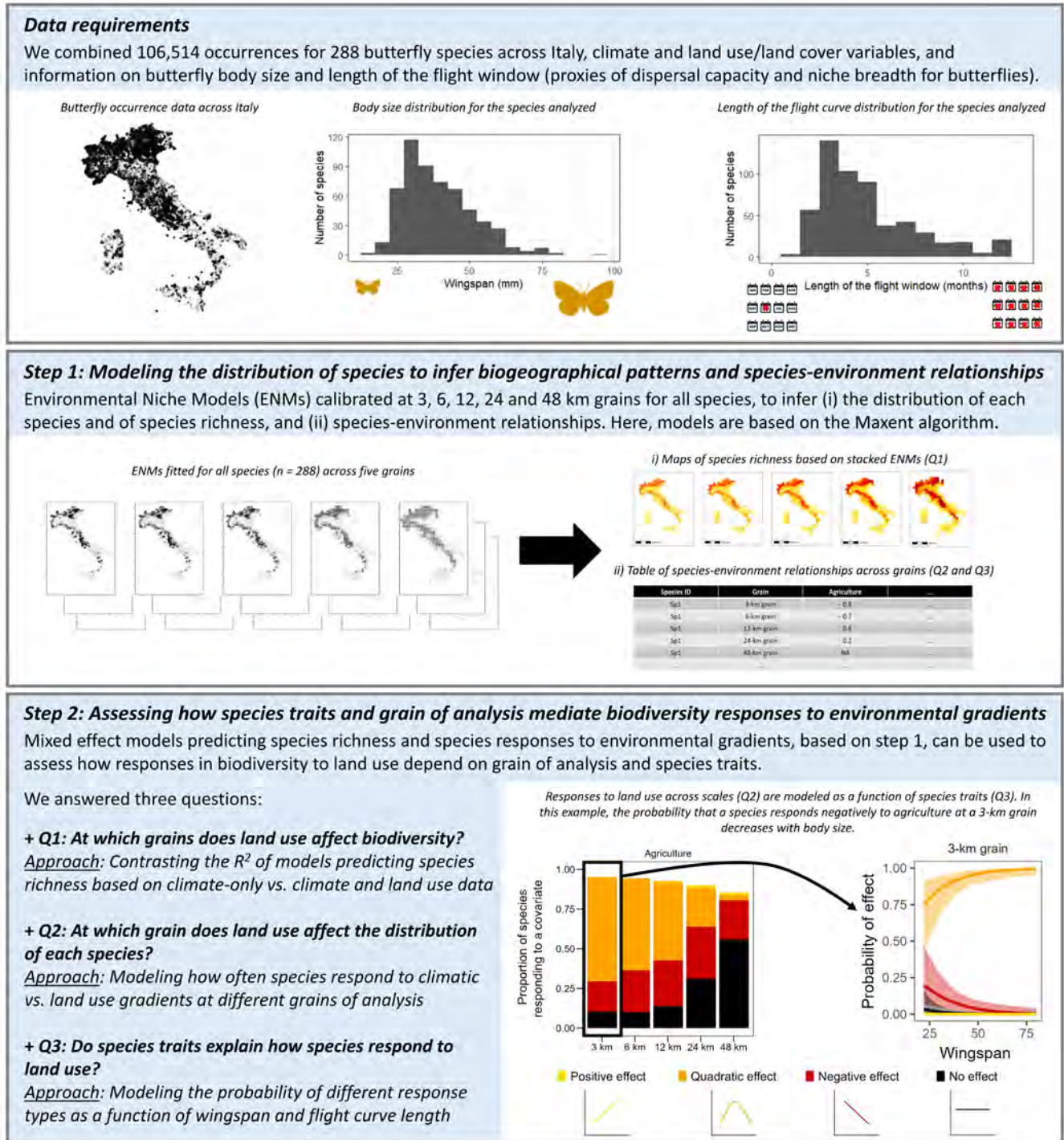
FIGURE 2 Summary of the analytical framework proposed in this study.

to assess large-scale patterns in response to land use (Belmaker & Jetz, 2011; Keil & Chase, 2019). We implemented the framework using the largest dataset of species occurrences compiled to date for the butterflies of Italy (Lepidoptera: Papilionoidea; 106,514 observations for 288 species), focusing on responses in biodiversity to urbanization and agriculture, the two main drivers of habitat loss in Italy (Bonelli et al., 2011; Falcucci et al., 2007), while accounting for

climatic gradients. Specifically, we designed a case study addressing three questions for the butterflies of Italy (Figure 2):

(i) At which grains does biodiversity (species richness) respond to land use?

(ii) At which grains do individual species respond to land use?

(iii) Do species traits explain responses in species to land use?

Butterflies are among the most studied organisms globally, and how these taxa respond to land use has been studied extensively. For instance, mounting evidence suggests that climate change will interact with land use in determining population demography and biodiversity (Forister et al., 2010, 2021; Oliver et al., 2015; Titeux et al., 2009), that landscape-level land use patterns moderate local community composition (Oliver et al., 2017; Pellissier et al., 2020), and that land use can influence the capacity of species to track suitable climatic conditions (Hodgson et al., 2022). Our analysis provides complementary, novel information to these studies because we focus on much coarser grains of analysis, assessing the presence of species and biodiversity in spatial units more akin to landscapes (3–6 km grains) and regions (48-km grain; Riva et al., 2020; Settele et al., 2008), whereas these analyses are based on biodiversity data collected at local sampling sites (e.g., along monitoring transects).

Because previous studies suggested that butterflies can persist in very small patches of early seral habitat (i.e., <1 km^2; Hendriks et al., 2009; Riva et al., 2020; Warren et al., 2021), we predicted that the effects of land use on the distribution of butterflies in Italy should be rare at coarse grains (e.g., >100 km^2, or 10-km grain). At these large scales, little bits of native habitat are present even in the most disturbed regions of Italy (Figures S3 and S4). In turn, land use should explain patterns in butterfly species richness primarily at fine grains, and ENMs should capture more often an effect of land use and land cover (LULC) at fine grains. Last, because dispersal and niche breadth mediate responses in species to land use (Callaghan et al., 2021; Ritchie, 2009; Riva et al., 2020), we predicted that small butterflies and butterflies with a short flight curve should be more likely to respond negatively to agriculture and urbanization.

2 | METHODS

2.1 | Overview

The analytical framework we propose requires fitting environmental niche models (ENMs), also called species distribution models (SDMs), at different spatial grains and for multiple species (Figure 2). Based on the results of these ENMs, that is, species-environment relationships and range maps, one can then ask questions on how environmental gradients relate to biodiversity across grains of analysis, and on how species traits mediate these relationships. We illustrate the framework by conducting a case study using data for 288 butterfly species occurring in Italy and Maxent models fitted at five different spatial grains (3, 6, 12, 24, and 48 km; geometric growth in grain following standards in scaling theory; Ritchie, 2009). We chose wingspan and length of the flight window as candidate traits to explain responses in butterfly species to land use because these traits approximate processes deemed important for environmental filtering in butterflies—dispersal and niche breadth (Callaghan et al., 2021; Riva et al., 2020).

Italy provides an ideal system to investigate biodiversity change across scales in human-dominated landscapes. Italy covers ~300,000 km^2, an area larger in extent than over 90% of the studies on the effects of land use on biodiversity (Davison et al., 2021), and is characterized by complex biogeography and steep environmental gradients. The Italian peninsula extends into the Mediterranean sea with diverse environmental gradients, including two major mountain ranges, the Alps and the Apennines, a latitudinal gradient, and a peninsular effect (Bonelli et al., 2018). Located at the center of the Mediterranean basin biodiversity hotspot (Myers et al., 2000), ~290 butterfly species or ~37% of the Euro-Mediterranean butterfly fauna have been documented in this country (Balletto et al., 2007, 2014). Many unique Italian species of flora and fauna are the result of Last Glacial Maximum refugia and of insular endemism (Balletto et al., 2007; Bonelli et al., 2018). Finally, land use is widespread in Italy due to a history of agriculture and high population density (Falcucci et al., 2007), with the country falling in the 90th percentile in terms of prevalence of anthropogenic land cover worldwide (Riva et al., 2022).

2.2 | Data characteristics

Our ENMs are based on distributional data for butterflies, the responses in our models, and on data on LULC and climate, the covariates in our models (Figure 2). These datasets are spatially explicit (projection: UTM zone 32N, datum WGS84). We selected our data matching the 1990–2019 period to maximize the number of unique observations available, minimize the effects of land cover change on our inference, and match climatic averages. Species ranges likely responded in the last 30 years to climatic change (Hällfors et al., 2021; Hodgson et al., 2022), and land cover changes also occurred—although these have been much slower after 1990 (Falcucci et al., 2007). Given our large sample size and relatively coarse grains of analyses, we assume that these changes have minimal effects on our inference on scaling patterns in species-environment relationships.

2.2.1 | Butterfly occurrence data

We assembled the most extensive dataset of current (1990–2019) species occurrences for the butterflies of Italy. A large portion of the dataset was created by georeferencing the CkMap dataset (Balletto et al., 2007), an earlier effort to digitize data on the Italian fauna from various literature sources and museum collections. In addition to CkMap, we included all suitable data available in the global biodiversity information facility ("GBIF"; https://www.gbif.org/).

The published version of CkMap counted 248,898 butterfly occurrence data recorded at a grain of ~10 km (i.e., coordinates associated with the centroid of UTM polygons approximating 100-km^2 squares). Samples in CkMap were recorded with a locality toponym (i.e., Municipality, Province, and Region, and often an address), and we used the Google Maps Geocoding application programming

interface to leverage this spatially-implicit information and assign more accurate geographic coordinates to each record. We validated the spatial coordinates obtained using Google Maps Geocoding by removing all the points being distant more than 7.1 km (i.e., the distance between the center of a 100-km^2 square and its corners) from the centroid of the UTM square associated to the original CkMap (188,851 observations retained), assuming an accuracy of 3-km grain. From these observations, we removed duplicates and retained only one observation per species from those recorded between 1990–2019. We then performed manual databasing and georeferencing for species with fewer records (i.e., <15), adding more information per work effort (Ballesteros-Mejia et al., 2017). Compared to the CkMap dataset published in 2007, our dataset also includes new validated records based on recent yearly updates, totaling 62,340 observations. We then downloaded all data for the butterfly species recorded in Italy from GBIF, matching the accuracy and temporal resolution of the CkMap data, finding 44,174 additional unique occurrences.

The final dataset included 106,514 unique species-by-cell (3-km grain) observations from 288 species. This is one of the most comprehensive biodiversity datasets ever assessed at similar extents and grains, and it is available at a comparatively high spatial resolution (Santini et al., 2021). Repeating the analysis using only observations from CkMap, and integrating both CkMap and GBIF data, finds analogous results. We present in the manuscript only results based on analysis of the full dataset.

2.2.2 | Environmental covariates

We selected LULC and climatic covariates relevant to the biology of butterflies (Riva & Nielsen, 2020, 2021; Supporting Information). To describe LULC, we used the Corine Land Cover database. We aggregated the original data to six LULC classes (Agriculture, Forest, Urban, Herbaceous [e.g., meadows and grasslands], Bare soil, Water), and calculated the proportion of each LULC category within 3-km raster cells. This transformed the initial categorical LULC dataset into six continuous rasters representing the proportion of each category. We subtracted "Water" from 1 to obtain the proportion of terrestrial land cover in each cell, which allowed us to control for land area in our models. To describe bioclimatic gradients, we evaluated 19 variables from WorldClim and 18 from ENVIREM. Both datasets were available at a resolution of 30 arc-seconds (~1 km) and were resampled at 3-km resolutions using a mean function. We conducted a covariate selection according to Pearson correlation coefficients <.7 to avoid collinearity (Dormann et al., 2013). When two or more covariates were highly correlated, we selected one variable that we estimated to be the most relevant (Merow et al., 2014). We retained five climatic covariates (Annual Mean Temperature, Mean Monthly Potential Evapotranspiration [PET] of Wettest Quarter, Annual Precipitation, Precipitation of Coldest Quarter, and Seasonality).

2.3 | Analysis

2.3.1 | Step 1: Fitting ENMs

The first step of our analytical framework consists in fitting ENMs for each species available in the biodiversity dataset, at multiple grains. ENMs are one of the most widely used approaches to understanding species responses to environmental change (Santini et al., 2021; Valavi et al., 2022), increasingly so also for insects (Mammola et al., 2021). In a nutshell, ENMs leverage information from locations where species have been observed to infer species-environment relationships, a proxy of their niche (Soberón, 2007), and to generate predictive maps of the distribution of species (Guisan et al., 2013).

To fit ENMs, we used Maxent (Phillips et al., 2017) via the ENMeval 2.0 package (Kass et al., 2021) in software R (R Core Team, 2021). We contrasted the environmental conditions observed at occurrence locations with the conditions extracted at locations where the presence of that species is unknown, that is, background locations, to infer the conditions at which a species is more likely to be observed. We used the "maxnet" implementation of Maxent because we fitted thousands of models, and this implementation is faster than the traditional implementation in Java. The two approaches are very similar, although maxnet does not calculate a metric of variable importance. To address this shortcoming, we re-run a subset of the analyzed models with the R package dismo (Hijmans et al., 2022), and extracted variable importance for all species at all scales (see Figure S9). More details on the modeling pipeline are provided below and in Supporting Information (see also, e.g., Guisan et al., 2013; Merow et al., 2013, 2014; Santini et al., 2021).

Model tuning
Feature types and regularization multipliers determine model tuning with Maxent. Feature types represent the shape of the relationships assessed between covariates and the occurrence of a species. We explored only linear and linear plus quadratic relationships in our models because (i) simple models yield response curves that can be linked directly to niche theory; (ii) when comparing fine and coarse grains, sample size necessarily decreases (Figure 1), in which case simpler models are preferable; (iii) limiting the potential parameter space is typically recommended for hypothesis testing (Merow et al., 2014; Soberón, 2007).

Regularization multipliers determine a penalty associated with including covariates or their transformations in the model. From the environmental covariates available, Maxent selects those that best predict the distribution of a species based on a combination of model likelihood and a complexity penalty (Phillips et al., 2017). This favors model fit while penalizing model complexity, similarly to information-theoretic approaches (Burnham & Anderson, 2002; Merow et al., 2013). Higher regularization multiplier values penalize more complex models. We evaluated five regularization multipliers—1 to 5—following Radosavljevic and Anderson (2014).

Regularization automatically accounts for differences in sample size across species and scales, such that fewer covariates and simpler feature types are typically retained for rarer species and at coarser grains. We, therefore, chose to include in the analyses all species for which we could successfully fit the Maxent algorithm, instead of, e.g., imposing a minimum sample size for our models. Because between 91% and 86% of the species analyzed at each grain counted at least 10 observations, depending on the grain of analysis (Figure S6), our inference is robust to potential issues due to limited sample sizes in some models.

Model extent

Model extent determines the distribution of background locations and the area where the occurrence of a species is predicted (Merow et al., 2013). An extent too small risks sampling a range of environmental covariates that is insufficient in capturing the environmental space to which a species is exposed, whereas an extent too large risks including areas that were not accessible to the species due to, e.g., biogeographical processes (Connor et al., 2019; Santini et al., 2021). To avoid calibrating the models in areas that do not support populations of a species, we reduced the extent of our model to a subset of Italy for every species, in two steps. First, we generated four broad biogeographical regions (Figure S2). The extent of model fitting for a species was limited to the biogeographical region(s) where at least one individual of that species was observed. Then, we impose a second filter, limiting the extent to an area of 300 km around the minimum and maximum latitudes and longitudes observed for a species. This ensured that all species were modeled in an area reasonably likely to support them. Note that the issue of niche truncation (Chevalier et al., 2022) does not affect our inference because we do not use correlation structures between environmental covariates and the occurrence of species to infer distributional changes with, for example, climate change or land use. Instead, we accounted for climatic preferences while assessing the grain at which land use affects the distribution of butterflies in Italy.

Background locations

Number and distribution of background locations affect the estimated species-environment relationships, for example, due to sampling bias (Merow et al., 2013). Some areas across Italy were sampled more intensely (Figure S5), and we generated background locations following the same pattern. This reduced potential bias in the data because areas more heavily sampled are also more heavily represented in the background locations (Merow et al., 2013). We generated a number of background locations proportional to the number of raster cells present in the model extent of each species (Supporting Information).

Model selection and performance

The combination of two feature types per five regularization multipliers gives 10 Maxent models per 288 species per five grains (14,400 potential Maxent models). For each species and grain, we selected the best among these 10 models using the Akaike Information Criterion

adjusted for small sample sizes (Burnham & Anderson, 2002; Kass et al., 2021), and used this ~1400 most-supported models to infer a species-environment associations matrix. Species-environment associations were retained for each butterfly species for which the number of occurrences was sufficient to fit a Maxent model (i.e., minimum 3 observations, but >10 observations for 91%–86% of models depending on grain; Supporting Information). We evaluated model performance by assessing the area under the receiver operating characteristic curve (AUC); a value larger than .7 generally suggests good predictive performance (Settele et al., 2008; Thuiller et al., 2009). We also use null models to test whether the observed AUCs were significantly higher than expected by chance, that is, we compared the AUC value of the models fitted using the true biodiversity data with an empirical distribution of AUC values for 50 randomly generated models.

2.3.2 | Step 2: Analyzing the results of multi-species, cross-grain ENMs

The second step of the framework consists in analyzing how biodiversity and species responded to land use based on the spatial predictions and estimated species-environment relationships (i.e., model coefficients) from the ENMs generated in Step 1. This requires fitting additional models, which we did by using the package brms (Bürkner, 2017). We followed a Bayesian framework and used uninformative priors. Details including posterior parameter estimates, R^2, and sample size are provided in Supporting Information for all models discussed in the manuscript. We described below how we answered three research questions (see Section 1; Figure 2).

(Q1) What is the importance of land use in determining biodiversity patterns across spatial scales?

We generated maps of species richness by stacking ENMs predictions reclassified from continuous to binary maps using an equal sensitivity and specificity rule (Liu et al., 2005; Figure 2). For the species for which we could not fit Maxent models (i.e., always species with <10 occurrences, representing 5%–15% of our sample depending on grain), we created binary maps conservatively assuming such species to be present only in cells containing records. Note that these species are typically not data-deficient, but rather localized populations and/or endemic species for which only a few occupied sites are known in Italy (see, e.g., Bonelli et al., 2018). We then fit linear models assuming a Gaussian distribution to predict species richness as a function of (i) a climate-only model, including the effect of annual mean temperature, annual precipitation, and their interaction, and (ii) a climate and land use model, including the effect of annual mean temperature, annual precipitation, their interaction, plus the amount of Urban and of Agriculture land cover. Assessing spatial autocorrelation using Moran's *I* and correlograms confirmed that a spatially-implicit model was appropriate for the data (Diniz-Filho et al., 2003). Temperature and precipitation are well-known drivers of butterfly species richness (Comay et al., 2021; Kerr et al., 2001), and we used

these climatic gradients as an ecological null model to assess the importance of land use in determining biodiversity patterns after controlling for climate. To this end, we compared model goodness-of-fit, measured as R^2, when including land use to the climatic model (Figures 2 and 3). Smaller increases in R^2 when including LULC to climatic variables at coarser grains would support the hypothesis that land use determines biodiversity primarily at fine grains.

(Q2) What is the importance of land use in determining the distribution of species across spatial scales?

Next, we assessed patterns in species responses to environmental gradients. Our most-supported 1318 ENMs gave, for every species modeled, each covariate, and each grain, four categories of response—"no effect", "positive effect", "negative effect", and "unimodal effect" (Figures 2 and 4). We, therefore, evaluated how often species responded to both climatic and LULC covariates, and how this changed with the grain of analysis. As grain coarsens, sample size decreases (Figure 1), and thus, we expect fewer covariates to be retained in the Maxent models, because regularization penalizes overfitting. We used climatic covariates as a reference and tested whether the proportion of "no effect" was more common in LULC than in climatic covariates at coarse scales. We fitted a mixed-effect model assuming a Gaussian distribution where the proportion of "no effect" responses was modeled as a function of two categorical factors, "climatic covariates" or "LULC covariates", in interaction with a continuous "grain" parameter, specifying a random effect to account for different covariates within the two fixed factors. A higher proportion of "no effects" at coarse scales for LULC covariates would support the hypothesis that LULC determines biodiversity primarily at fine grains.

(Q3) Do species traits predict patterns in species responses to land use across spatial scales?

To investigate candidate mechanisms underlying how species respond to land use, we modeled, assuming a multinomial distribution, the probability of observing the four response categories to urban and agriculture LULC classes, across grains, and as a function of two traits: (i) wingspan, a proxy of mobility (Burke et al., 2011), because species with lower mobility should suffer from increased mortality in anthropogenic matrices, and thus could respond negatively to land use (Fahrig et al., 2022); and (ii) length of flight curve, that is, the number of months a species is present as adult butterflies throughout the year, because species with longer flight curves face more diverse climatic conditions, and thus should be less specialized (Callaghan et al., 2021), thereby more easily persisting in anthropogenic landscapes. These two traits were extracted from Middleton-Welling et al. (2020), were not correlated (Supporting Information), and were selected a priori to avoid spurious inferences (Palacio et al., 2022). We selected these traits because they are proxies of movement and niche breadth, two phenomena that could provide essential insights into how species interface with their habitat across spatial scales (Johnson, 1980; Ritchie, 2009). Grain-dependent responses to land use were tested by fitting an interaction between

species traits and grain size (Figure 5), accounting for phylogenetic relationships among species by incorporating a "species within Family" nested random effect.

The R script and data necessary to replicate the results presented in this manuscript have been uploaded and are openly available in a repository on Dryad (Riva et al., 2023).

3 | RESULTS

We fit 13,080 ENMs, of which the most supported 1308 were used to generate maps and to identify species-environment relationships. These models represent most of the butterflies of Italy (i.e., from 95% to 86% of our species) across five grains of analysis (3–48 km, Figure 1; Supporting Information). Model performance was good, with the average AUC decreasing from .85 to .73 as grain coarsened (Figure S7). Null model analysis found that the AUCs of our ENMs were significantly better than expected by chance for 94%, 94%, 92%, 87% and 61% of species, as grain coarsened from 3 to 48 km (Figure S8). Stacked ENMs performed well, generating biodiversity patterns congruent with those reported in the European Red List of Butterflies and in the Distribution Atlas of Butterflies in Europe (Settele et al., 2008; van Swaay et al., 2011; Figure 3a).

3.1 | Q1: At which grains does land use affect butterfly biodiversity patterns in Italy?

Including the effect of urban and agricultural land cover to climate increased the R^2 of models predicting species richness primarily at grains ≤12 km (Figure 3b). For models including only climatic covariates versus climatic and land use covariates, R^2 increased from .54 to .67, from .58 to .71, from .64 to .73, from .66 to .69, and from .64 to .67 as the grain increased from 3 to 48 km (Figure 3b).

3.2 | Q2: At which grains does land use affect the distribution of Italian butterflies?

When assessing patterns in species responses to climate and LULC, we found that all covariates—both climatic and land use covariates—explain the distribution of some species at fine and coarse grains (Figure 4). Temperature, seasonality, and PET were the most retained climatic covariates in our models, whereas proportions of agricultural, urban, and forest land cover were the most retained LULC covariates. Based on variable importance analysis, temperature and proportion of agricultural land cover were the most important environmental factors to predict the distribution of butterflies across Italy, although all covariates resulted important for some species (Figure S9). Species showed typical unimodal responses particularly at finer grains and not only to climatic gradients, but also for LULC covariates. As expected, the number of covariates retained after regularization and model selection decreased with grain size, but we
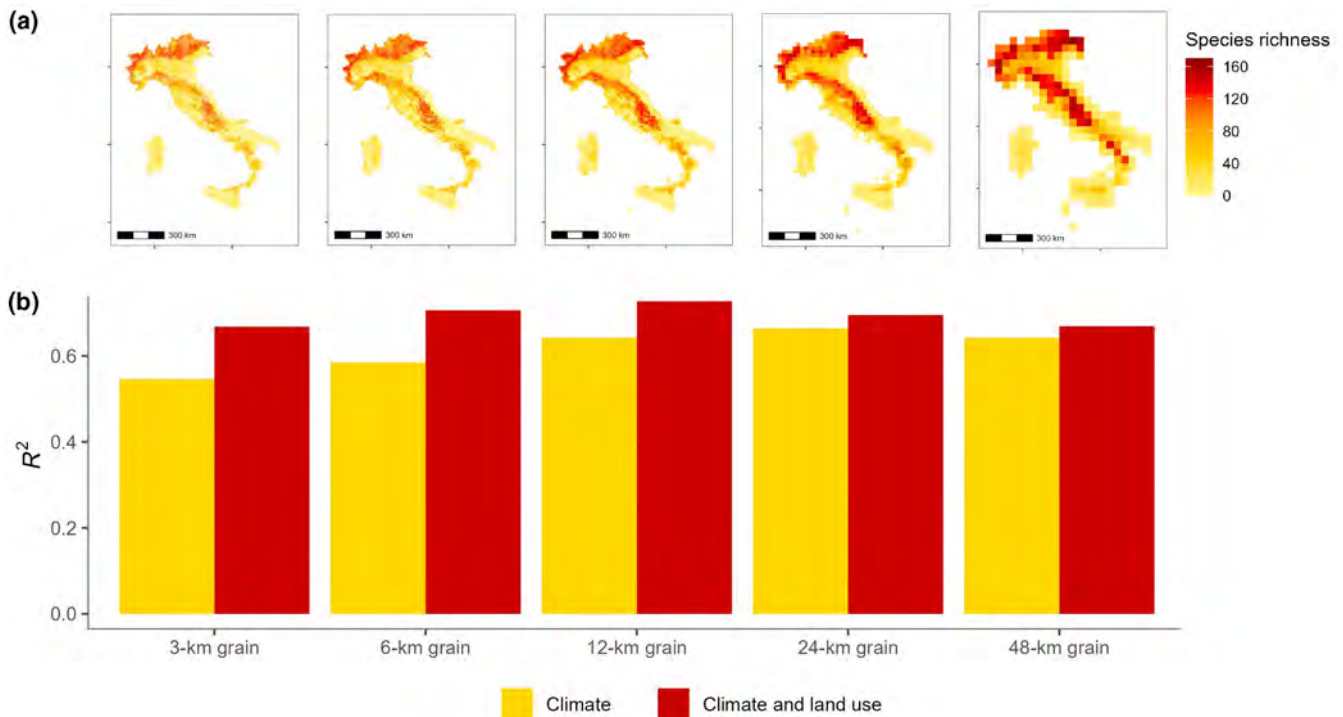
FIGURE 3 (a) Patterns in species richness for the butterflies of Italy, based on stacks of environmental niche models calibrated at five grains—3, 6, 12, 24, and 48 km grains; (b) Variation in species richness of the butterflies of Italy explained by climatic covariates (temperature, precipitation, and their interaction; gold bars) versus climatic and land use covariates (temperature, precipitation, and their interaction plus urban and agricultural land cover; red bars). Including land use in our model substantially increased model goodness-of-fit, measured with R^2, at grains of 3, 6, and 12 km ($\Delta R^2 > .09$), whereas model improvements were marginal at grains of 24 and 48 km ($\Delta R^2 = .03$).

found little evidence that LULC becomes less important in determining the distribution of species at coarse grain (Figure 4). A model predicting the proportion of "no effect" for LULC versus climatic covariates found no support for different scaling patterns in different covariate categories ($\beta = .07$, CI $= -.09–.22$).

3.3 | Q3: Do species traits explain how species respond to land use?

Inspecting relationships between species traits and patterns in species responses, we found that both wingspan and length of the flight curve predict responses in butterflies to land use (Figure 5). Negative responses to urban and agricultural land covers (Figure 5, red lines) were more common in small species and in species with a shorter flight curve, with effects consistent across land use types and grains, but peaking at intermediate grains (i.e., 12-km or 24-km grains). Conversely, large species and species with a longer flight curve typically display unimodal responses to land use (Figure 5, orange lines). This result suggests common positive responses in these species to environmental heterogeneity, particularly at fine grains (i.e., ≤12-km grains). Positive effects (Figure 5, gold lines) were virtually absent for agricultural land cover but present for urban land cover, being disproportionately common for large species and for species with a long flight curve. When assessing responses at coarse grains (24- and

48-km grains), the proportion of species that do not respond to agriculture and urbanization increased (Figure 5, black lines), but negative responses to land use persisted (Figure 5, red lines).

4 | DISCUSSION

Implementing a novel analytical framework that capitalizes on big data, ENMs, multi-grain analyses, and species traits (Figure 2) delivered multiple lines of evidence that demonstrate pervasive effects of human activities on butterfly biodiversity across Italy (Figures 3–5). Our case study provides a rare example of cross-grain, large-scale assessments of responses in biodiversity to land use (Davison et al., 2021), and identifies unexpected effects persisting up to regional species pools (Figures 4 and 5). Signatures of land use on the biodiversity and distributions of Italian butterflies emerged across a 16-fold increase in grain, confirming that the effects of human activities on biodiversity in Italy are pervasive not only for vertebrates (Falcucci et al., 2007) but also for insects. These findings complement extensive work documenting effects of land use and climate on butterfly biodiversity, but with a focus on local monitoring sites (e.g., Forister et al., 2010, 2021; Oliver et al., 2015, 2017; Pellissier et al., 2020). We elaborate on the relevance of our work to global biodiversity conservation before reflecting on the potential applications of the analytical framework we proposed in this manuscript.
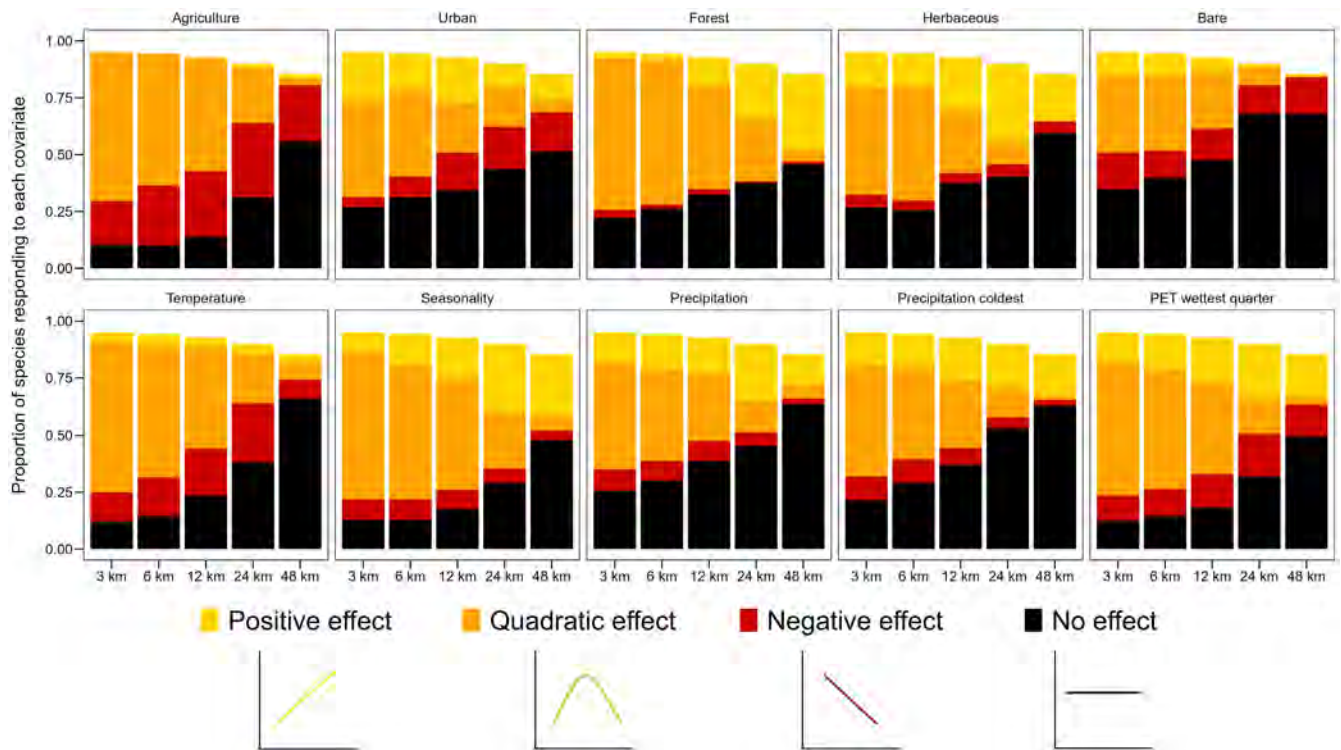
FIGURE 4 Effect of each covariate tested in our models to predict the occurrence of 288 butterfly species (*y* axis) across five grains (*x* axis). Insets in the top row show land use and land cover covariates, whereas insets in the bottom row show climatic covariates. Colors illustrate the proportion of the 288 species that responded to each covariate with four types of response. Because we could not model a few rare species (between 5% and 15% of our sample, depending on grain), bars never reach 1.00 on the *y* axis. Black areas ("no effect") represent cases where a covariate was not retained in the most supported Maxent models. Gold areas ("positive effect") illustrate species that were more likely to be observed as a covariate increased, red areas ("negative effect") species that were more likely to be observed as a covariate decreased, and orange areas ("quadratic effect") species that were more likely to be observed at intermediate levels for that covariate.

4.1 | Land use shapes the biodiversity of Italian butterflies from local to regional scales

Consistently with previous studies, we found that the distribution of butterflies responds to both climatic and LULC covariates (Figures 3 and 4; Forister et al., 2010, Habel et al., 2021; Hodgson et al., 2022; Kerr et al., 2001; Titeux et al., 2009). Adding land use to a model predicting species richness based solely on climatic variables substantially increased the proportion of variation explained at our finer grains (i.e., increases in R^2 ~.1 at grains ≤12 km) but such increases became marginal at coarser grains (i.e., increases in $R^2 = .03$ at grains ≥24 km; Figure 3b). This pattern supports the general expectation that land use should affect biodiversity at finer scales, whereas climate should be the main determinant of broader biogeographical patterns (McGill, 2010; Soberón, 2007). Nevertheless, assessing responses in individual species revealed more nuanced patterns and widespread responses to land use even at regional scales (i.e., 48-km grain; Figures 4 and 5).

Species responded to climatic and LULC covariates heterogeneously, with positive, negative, and quadratic effects of all covariates, including agriculture and urbanization (Figure 4). A similar likelihood of retaining climatic and LULC covariates in the most-supported Maxent models across grains of analysis suggests that,

in Italy, land use can be an essential driver of the distribution of many species even across large spatial scales. This was also confirmed by variable importance estimates suggesting agriculture as the most important predictor of occurrence among LULC covariates, second overall only to temperature (Figure S9). Indeed, different species can respond to human activities idiosyncratically, suffering or benefitting from anthropogenic changes in habitat (Dornelas et al., 2019; Riva et al., 2020; Vellend et al., 2017), and some butterflies are well-adapted to persist in cities (Callaghan et al., 2021) and in agricultural landscapes (Bonelli et al., 2018)—at least in Italy, where agriculture is often not as intensive as in other countries (Wagner et al., 2021; Warren et al., 2021). Additionally, environmental heterogeneity often begets butterfly diversity (Riva et al., 2020; Sirami et al., 2019), a phenomenon that likely explains the high prevalence of quadratic effects of LULC on the distribution of butterflies in Italy (Figures 4 and 5). While these effects fade at our coarser grains of analysis, negative effects of land use persist at regional scales (Figures 4 and 5), demonstrating unexpected and pervasive negative effects of land use on the biogeography of butterfly biodiversity in Italy.

The fact that land use explained additional variation in species richness primarily at fine grains (Figure 3), but predicted the distribution of
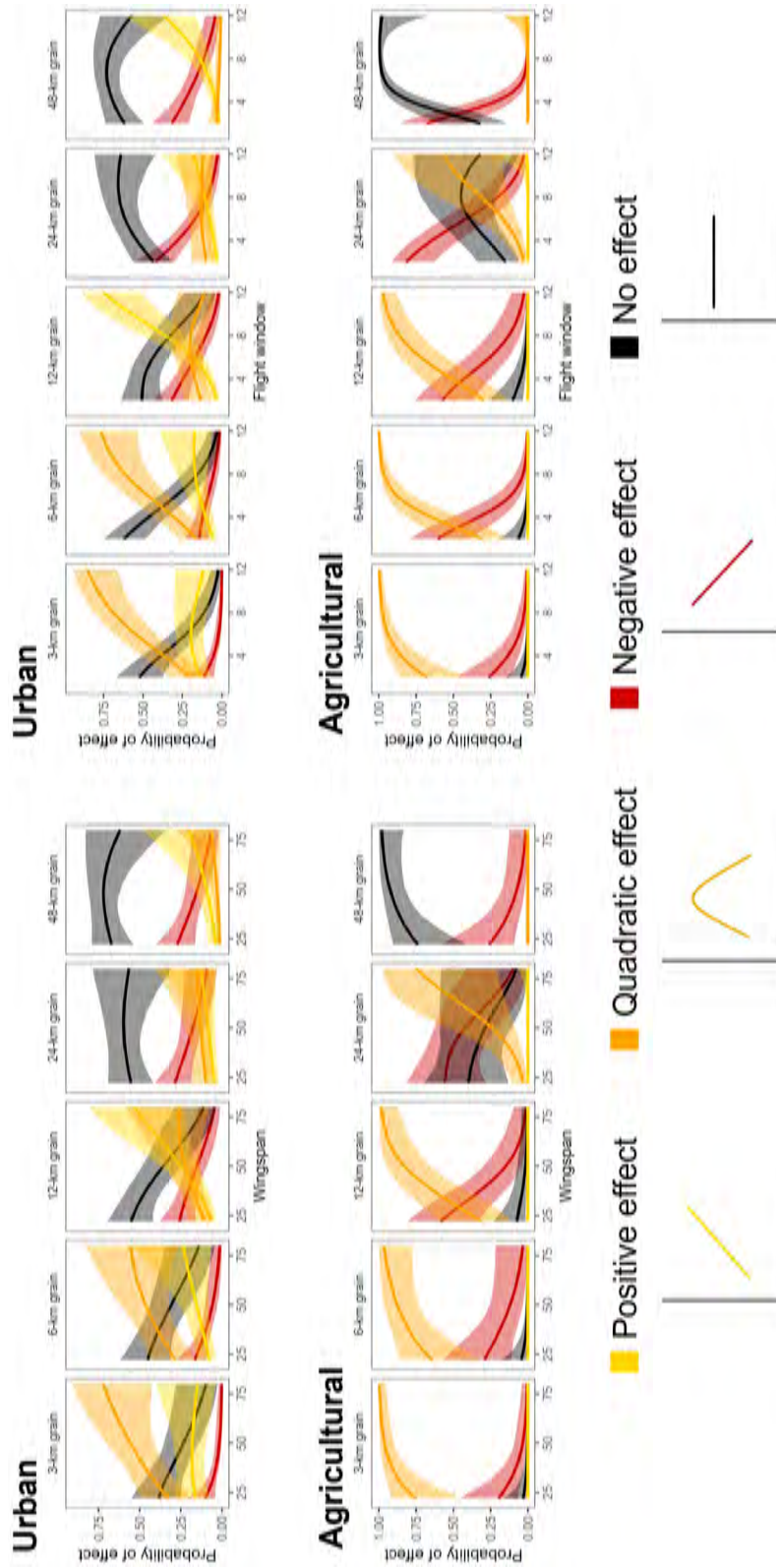
FIGURE 5 Grain and species' traits mediate responses to land use. Columns represent species' traits, that is, wingspan (mm), left column, and length of the flight curve (number of months a butterfly species can be observed as adult), right column, whereas rows represent land cover types, that is, urban land cover, top row, and agricultural land cover, bottom row. Negative effects of land use (red lines) are more likely for small species and for species with a short flight curve across all grains. Positive effects of urban land cover (gold lines) are more common for large butterflies and for butterflies with a long flight curve, but fade at coarse (>12-km) grains. Positive effects of agriculture are very rare at all grains. Quadratic effects (orange lines) representing optimal intermediate amounts of land use for different species are common at fine grains for large butterflies and for butterflies with a long flight curve, but always disappear at the coarsest (48-km) grain.

species also at coarse grains (Figures 4 and 5), suggests species turnover in areas affected by extensive land use. Indeed, we found that small butterflies and butterflies with a short flight curve were disproportionately likely to respond negatively to both urbanization and agriculture (Figure 5). These results support the predictions that species with lower mobility could suffer from widespread land use due to increased mortality in anthropogenic matrices surrounding patches of habitat (Fahrig et al., 2022), and that species with narrower niches should be those most likely to negatively respond to land use (Callaghan et al., 2021), hinting at the relevance of these two mechanisms in understanding declines in insect populations (Davison et al., 2021; Thomas et al., 2019; Wagner et al., 2021). The absence of horizontal trends when evaluating species' responses to land use in relation to their traits (Figure 5) demonstrates strong, deterministic, and scale-dependent environmental filters associated with human activities on the butterflies of Italy.

4.2 | Implications for global biodiversity conservation

Insect populations are typically assumed to require much smaller patches of habitat than vertebrate populations to persist (e.g., >.1 km^2; Hendriks et al., 2009). Because habitat remnants of these sizes are widespread across Italy (Figures S3 and S4), but negative effects of land use persisted even at a 48-km grain (Figures 4 and 5), our analysis suggests that human activities resulted in extinctions of butterfly populations even across regions where habitat patches are still present. We interpret this pattern as evidence that changes in metacommunity dynamics (Chase et al., 2020) due to widespread agriculture and urbanization affected the biogeography of the most sensitive butterfly species in our sample, causing regional extinctions for small butterflies and/or butterflies with a short flight window (Figure 5).

One implication of this result is that protecting populations of conservation interest without considering patterns in land use around focal habitats will underestimate extinction risk. Specifically, insect conservation has often targeted populations of rare species inhabiting small patches of habitat, but protecting such populations without considering changes in land use surrounding them is likely to be ineffective (Warren et al., 2021). Indeed, the characteristics of landscapes surrounding sampling sites often moderate local trends in populations and biodiversity (Pellissier et al., 2020; Rada et al., 2019), a phenomenon that might explain why some protected areas fail to halt declines in butterflies (Rada et al., 2019; Warren et al., 2021). The regional extinctions we documented also suggest that species will fail to track suitable climates in areas with widespread human activity, as has already been recently observed in Lepidoptera (Hällfors et al., 2021; Hodgson et al., 2022; Maes & Van Dyck, 2022), a result that highlights the potential for complex interactions between land use and climate change (Riva et al., 2020).

Results also suggest that the scale at which the negative effects of land use on butterflies are most prominent in Italy is between 12 and 24-km grains. This provides a means to understand which anthropogenic footprints are likely threatening insect biodiversity in areas where biodiversity data as extensive as those analyzed here are not available. For instance, very few species respond negatively to urbanization at a 3-km grain, suggesting that the many villages scattered in the Italian backcountry still harbor relatively pristine butterfly assemblages despite their typically dense, but localized, footprint. Conversely, when urbanization is high at grains of 12-km, as in the case of large urban centers in Italy, the proportion of species responding negatively substantially increased (Figure 5). Similar patterns were observed for responses to agricultural land use, suggesting that human activities that condition habitat at these scales can push populations of sensitive butterfly species towards local extinctions. A slight decrease in the prevalence of negative effects of land use at a coarser grain of analysis likely occurs because large grains typically capture a mix of suitable and unsuitable areas due to spatial patterns in land use across Italy (Figures S3 and S4). This result confirms the importance of accounting for grain-dependent effects in analyses of biodiversity responses to land use.

While concerns around insect declines are growing globally (Thomas et al., 2019; Wagner et al., 2021; Warren et al., 2021), these taxa continue to be understudied and neglected in conservation (Chowdhury et al., 2022; Mammola et al., 2020). The post-2020 Global Biodiversity Framework will provide opportunities for addressing such gaps, e.g., the European Union Biodiversity Strategy requires the State Members to protect 30% of their land and sea area as natural areas by 2030. In Italy, approximately 21% of land is protected by a network of reserves that provides appropriate coverage for vertebrates (Maiorano et al., 2015), but it remains unknown whether arthropods are also covered. Yet, Italy is at the core of the Mediterranean biodiversity hotspot (Myers et al., 2000) and hosts ~37% of the European fauna of butterflies (Bonelli et al., 2018), making conservation actions in this country disproportionately important for butterfly and insect conservation at the continental and global levels. Readily incorporating insects in the decision-making for the creation of new nature reserves will therefore be crucial in this country. Our hope is that the results presented here will aid in informing this process.

5 | CONCLUDING REMARKS

Grain-dependent approaches are fundamental in ecology and conservation because they allow quantitatively assessing how different candidate processes structure biodiversity across spatial scales (Belmaker & Jetz, 2011; Keil & Chase, 2019; Mertes & Jetz, 2018). As the footprint of human activities continues to grow worldwide (Riva et al., 2022), assessing large grains will allow exploring phenomena that remain comparatively understudied in the literature that evaluates responses in biodiversity to land use (Davison et al., 2021). Understanding changes to landscape and regional species pools, or identifying the grain at which conservation and restoration actions should be designed to optimize investments, are themes that cannot be directly assessed based on studies measuring biodiversity at monitoring sites, because the processes determining biodiversity often change across

grain of analysis (Chase et al., 2018; Keil & Chase, 2019; Riva & Fahrig, 2022). Therefore, predictions of large-scale biodiversity patterns based on extrapolation of local relationships between biodiversity and land use should be tested with data collected and analyzed at proper grains (Fahrig et al., 2022; Riva & Fahrig, 2022). The analytical framework we propose has broad potential to facilitate this sort of test given its flexibility, as it can be implemented with other modeling approaches, at different grains and extents, and expanded to account for aspects including phylogenetic relationships across species or landscape moderation of biodiversity.

Ultimately, a transition from scale-implicit to scale-explicit ecology has been long in the making (Levin, 1992; McGill, 2010; Rahbek, 2004; Wiens, 1989), and the time is ripe to acknowledge the importance of these developments. Recent technological progress in remote sensing and biodiversity databases makes cross-grain analyses more feasible, with increasing availability of high-resolution, global datasets on environmental conditions and the occurrence of species (Jetz et al., 2019; Soroye et al., 2018). These datasets offer unprecedented opportunities to study biodiversity change across scales, leveraging either our framework or alternative grain-dependent approaches (Chase et al., 2018; Keil & Chase, 2019; Mertes & Jetz, 2018). Probing scale dependencies is an exciting frontier that will allow not only a better understanding of the processes determining biodiversity in space, but also designing effective conservation actions amidst a global biodiversity crisis that appears likely to hit insects particularly hard.

AUTHOR CONTRIBUTIONS

Francesca Barbero, Emilio Balletto, and Simona Bonelli contributed and curated the data. Federico Riva designed the analysis and led manuscript writing. All authors participated with intellectual contributions and revised the manuscript.

CONFLICT OF INTEREST STATEMENT

We have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data and script necessary to replicate the findings of this manuscript are openly available on Dryad at https://doi.org/10.5061/dryad.0cfxpnw6m (Riva et al., 2023). The models discussed in the manuscript can be re-run using the files contained in the repository, and parameter estimates of models discussed in the manuscript are presented in Supporting Information for convenience.

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SUPPORTING INFORMATION

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