ORIGINAL PAPER



Can protected areas and habitats preserve the vulnerable predatory bush cricket *Saga pedo*?

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Received: 20 February 2023 / Accepted: 26 May 2023 / Published online: 9 June 2023 © The Author(s) 2023

Abstract

Inconspicuous species challenge conservationists when it comes to delineate long-term conservation planning or assess their status, particularly when their actual distribution is poorly known. Invertebrates in particular feature among the less represented taxa in conservation assessments. Here we follow a multidisciplinary approach for assessing the conservation coverage and address future management of the threatened orthopteran *Saga pedo* across Europe, shedding light on its ecological preferences and associations with protected habitats at continental and regional scales. When assessing coverage by Natura2000 and Nationally Protected Areas, we found that ca. 30% of the known populations of the species are currently not protected across Europe. However, this value is likely to be an underestimate as our species distribution models showed that ca. 70% of the potential range is not protected. At regional scale, we disclose that the species is more likely to occur in legally protected dry grassland habitat types than in non-protected grassland, yet not all protected habitats seem to represent an effective tool for the species' conservation.

Implications for insect conservation Taken together, our results provide an effective framework for addressing knowledge gaps and evaluate the conservation coverage not only of our target species, but more in general of poorly investigated species, at the same time pointing at the urgent need of transnational, coordinated, and increased efforts in monitoring and conserving insects, particularly in the case of threatened species.

Keywords Gap analysis · Habitats directive · Insect conservation · Orthoptera · Saga pedo · Species distribution modeling

Introduction

Protected areas are a key instrument for conserving nature, and are in fact one of the main pillars of both global and continental-scale conservation tools (Watson et al. 2014). Europe stands out, in terms of wildlife conservation, by being the world area with the highest numbers of protected areas (Gaston et al. 2008), whose abundance strongly relies on the Natura 2000 network, one of the two main tools,

Leonardo Ancillotto leonardo.ancillotto@cnr.it together with species protection regime, implemented by EU countries in application of the Habitats Directive. The latter is also paired by the network of Nationally protected areas such as national parks, nature reserves and so on. Evaluating the success of protected areas in guaranteeing species' and habitats' long-term persistence is the main objective of the Habitats Directive reporting (art. 17), as well as of protected areas in general (Geldmann et al. 2013). The effectiveness of the network of protected areas in preserving nature worldwide has been widely assessed in terms of safeguarding (i) habitats' loss or degradation (Geldmann et al. 2013), (ii) present and future species distribution coverage (Watson et al. 2014), as well as (iii) evidence of concrete effects on demography, abundance, and extinction risk trends of wildlife (Gray et al. 2016), although with inconsistent results across taxa and geographical contexts (Rodrigues et al. 2004). Moreover, the efforts spent in evaluating the appropriateness of protected areas in conserving species have been taxonomically and geographically biased (Godet

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and Devictor 2018), and so far insufficient to evaluate the status of biodiversity as a whole. Namely, few studies to date explored the conservation status and representation of specific taxonomic groups, invertebrates above all, within European protected areas, if compared to the wide literature on birds and mammals (Samways 1993; Boitani et al. 2011; Hernàndez-Manrique et al. 2012; de Carvalho et al. 2017).

Insects represent a major part of animal biodiversity, and their role in ecosystem functioning has long been acknowledged (Yang and Gratton 2014). Insects in fact play key roles in all ecosystems by being a major component of the environmental biomass, and by occupying virtually all the possible ecological positions among consumers within trophic networks (Stork 2018; Wagner 2020; Kehoe et al. 2021). Nonetheless, and despite a wide consensus of an "insect conservation crisis" (Goulson 2019), insect conservation is still far from being an exhaustive and spread discipline, possibly due to the taxonomic instability and identification challenges that most groups pose to conservationists, besides their low appeal as perceived by the wider public (Hart and Sumner 2020).

Global reviews on the role of protected areas in fostering insect conservation indicate that despite sharp declines in insect abundance and diversity recorded e.g. in Europe and North America (Cardoso et al. 2020; Van Klink et al. 2020; Wagner et al. 2021; Warren et al. 2021), more than ³/₄ of insect species are not sufficiently covered by the current network of protected areas (Chowdhury et al. 2023). The actual effects of the conservation regime within protected areas have been rarely quantified on insects, and even though there is evidence that declines inside protected areas may be weaker than in non-protected areas (Van Klink et al. 2020), the overall picture of how protected areas foster insect conservation is still unclear (Chowdhury et al. 2022).

Even within the relatively few works dealing with insect conservation assessments, taxonomic biases are clearly evident, with a strong prevalence of studies focusing on more charismatic and aesthetically appreciated groups such as diurnal Lepidoptera (Burton 2001; Chowdhury et al. 2022; Piccini et al. 2022), or on speciose taxa with a long history of studies dealing with their taxonomy, ecology and distributions, such as Coleoptera (e.g., saproxylic beetles: (D'Amen et al. 2013; Bosso et al. 2018). Orthoptera, i.e. crickets, grasshoppers and katydids, are a very diverse and yet understudied and underrepresented insect group, with about 1,082 species of orthopterans occurring in Europe (Hochkirch et al. 2016), but only 11 species listed on the Habitats Directive, and none being considered as a conservation priority. Among European orthopterans, the genus Saga includes 17 species of large-sized carnivorous bush crickets that inhabit grasslands and semi-open habitats. One of these, S. pedo-also known as the Predatory bush cricket or Spiked magician-is listed on the Annex IV of the Habitats

Directive, where identified threats are habitat encroachment by afforestation and pasture abandonment, the use of pesticides, and overgrazing (Lemonnier-Darcemont et al. 2009). The species is in fact considered as associated with natural and semi-natural grasslands, yet its actual ecological requirements are poorly known, as very common for insects, probably due to the species' low detectability, semi-nocturnal habits, and short life-span, that make it hard to conduct exhaustive field studies (Holuša et al. 2013). Consequently, the actual area of occupancy of the species has been probably underestimated so far, and new observations keep on being recorded at novel locations (Nerozzi, et al. 2022). As such, assessing its potential distribution by species distribution models (SDMs) instead of record-based evaluations may prove more efficient in targeting its conservation at wide geographical scales (Herkt et al. 2017), an approach though never attempted to date.

An alternative for guaranteeing the conservation of poorly detectable species in absence of detailed field data may also be the use of surrogate taxa or entities (e.g., habitats) that are presumably easier to locate and thus conserve, and to which the target species may be associated (Mumby et al. 2008). Such a strategy may include the granting of protection to habitats representing highly suitable areas to the species, as implemented for some saproxylic beetles whose conservation is guaranteed by conserving old-growth forests with specific characteristics (Parisi et al. 2019). Even though S. pedo is considered as associated with specific grassland types (e.g., dry grasslands on calcareous substrates; Kaltenbach 1990), no quantitative assessment of presumed association with legally protected grassland habitats, i.e. Habitats Directive habitats, has ever been tested on the species to date.

Here we aim at unveiling the macroecological ecological factors that favor the occurrence of the threatened *S. pedo* and assess its conservation coverage in Europe. We tackle these objectives by developing SDMs of *S. pedo* across Europe in order to (i) map the species' potential distribution and determine the main ecological factors that drive its occurrence at range-wide scale, and (ii) quantify the species' representation within the network of protected areas across Europe by following two alternative approaches. Moreover, we conducted a detailed regional-scale analysis focusing on a testing area in order to (iii) assess whether the legally protected grassland habitats listed in the Annex I of the Habitats Directive may actually sustain *S. pedo* populations by featuring higher suitability in comparison to non-protected habitats.

Materials and methods

Study area and record collection

We defined the study area as the one encompassing all European countries where *S. pedo* is known to occur with > 1 location. This resulted in the inclusion of the area ranging from Portugal to western Siberia to the east, and from Sicily to Czech Republic and Slovakia to the north (Fig. 1).

Occurrence records were retrieved and cleaned from different sources, including gbif database (via the *rgbif* package: Chamberlain et al. 2017), authors' own data from field surveys, and published references (see reference list in Supplementary materials). Additional records were also collected from iNaturalist (www.inaturalist.org). We then removed duplicated records as well as those lacking coordinates or with an accuracy < 1 km, and used the *spThin* package (Aiello-Lammens et al. 2015) to thin data at 5 km distance, i.e. reducing multiple records within such distance to a single one, in order to avoid spatial autocorrelation and overestimating the importance of environmental variables' from over-sampled geographical areas. Such a procedure led to the inclusion of 3,278 independent records.

For assessing the species' association to legally protected grassland habitats as listed in the Habitats Directive, we focused on Apulia–southern Italy (Fig. 1b) – a region where the species is relatively common and frequently recorded (33.3% of Italian records) and for which detailed and exhaustive mapping of listed grassland habitats is available i.e., also including areas outside of the Natura2000 network.

Species distribution models

We downloaded 19 bioclimatic variables as descriptors of climatic conditions from Worldclim2 (Fick and Hijmans 2017), with a 10 km² resolution. We controlled

for multicollinearity among variables by running a Variance Inflation Factor (vif) analysis, retaining only variables with vif values < 10 (Curto and Pinto 2011). This procedure led us to maintain six independent bioclimatic variables (bio2, bio6, bio8, bio15, bio18, and bio19). We also included, as predictor variable, the most recent layer of grassland cover at European scale available (https:// land.copernicus.eu/pan-european/high-resolution-layers/ grassland/status-maps/grassland-2018), which features a 10 m resolution raster mapping of natural and semi-natural grasslands (e.g., including heathlands, sparsely vegetated grasslands, semi-arid steppes, and meadows), all known to potentially host *S. pedo*.

We built our SDMs based on a bioclimatic envelope concept (Pearson and Dawson 2005), and by adopting an ensemble forecasting approach as implemented in the sdm R package (Naimi and Araùjo 2016), a well-established procedure that reduces uncertainty of predictions by single model algorithms (Watling et al. 2015). We considered three modelling techniques: Generalized Linear Models (GLMs), Random Forests (RFs), and Maximum Entropy Models (Maxent), performing 10 runs for each technique; for RFs and GLMs, we generated pseudo-absences (background data, n = 10,000) by adopting a randomization approach (Barve et al. 2011). The combination of these algorithms is considered among the best performing ones, providing robust and reliable prediction when used in an ensemble (Kaky et al. 2020). For model training, we randomly selected 70% of occurrence data, using the remaining 30% for model performance testing. Model performance was assessed by inspecting the values of the area under the receiver operating characteristic curve (AUC) and the True Skill Statistics (TSS), two validation methods widely used in sdms (Araùjo and New 2007) and that evaluate model discrimination abilities (AUC) and the ratio of correct predictions and randomly corrected ones,



Fig. 1 Distribution of occurrence records of *Saga pedo* (before thinning) across its entire European range (A) and in Apulia (southern Italy–B). Inset shows the location of the regional focus within Italy

a recommended approach when assessing the performance of predictive models (Allouche et al. 2008).

The effect of each environmental predictor on the probability of occurrence of *S. pedo* was assessed by inspecting the response curves, while each variable's relative importance was calculated by the specifically devoted function in the *sdm* package (*getVarImp*), which determines the change in AUC values due to the inclusion of each target variable. As a final step, we also binarized the model by using a threshold maximizing sensitivity (the percentage of correctly predicted presence) and specificity (the percentage of correctly predicted absence) (Fielding and Bell 1997).

Conservation gap analysis

We assessed the degree of protection granted to S. pedo by PAs in Europe by carrying out a conservation spatial gap analysis, based on both the full occurrences dataset and the binarized potential distribution map. We overlayed each dataset with the shapefiles defining boundaries of both Natura2000 and Nationally protected areas for Europe, as downloaded from the websites of the European Environmental Agency (https://www.eea.europa.eu/data-and-maps/data/ natura-8) and UNEP's World Conservation Monitoring Centre (www.protectedplanet.net), respectively, processing both layers in order to remove marine reserves. We conducted this analysis both at the entire range and single-country scales. We excluded from this analysis those countries with n records < 5, those not within the EU area, and those which did not feature suitable habitat as predicted by our SDM. We thus calculated the percent of records and of suitable area to S. pedo overlapping with either Natura2000, Nationally protected areas, and their combination. To assess whether the two types of protected areas differed in their efficacy in preserving the species, we ran a repeated measure two-way ANOVA test upon the percent coverage values of each class of protected areas and for type of data (records vs suitable range), using Tukey's post hoc tests for assessing significance in coverage between each compared pair of values.

Association to habitats

We assessed whether protected habitats as listed in Annex I of the Habitats Directive provide an effective surrogate of *S. pedo*'s ecological needs for conservation, by focusing on a local (regional) scale. The grassland layer used for the models, and the habitat suitability raster were first clipped to the regional boundaries' geographical extent. We then selected three grassland habitats listed in Annex I of the Habitats Directive and occurring widely across the region and namely (i) semi-natural dry grasslands on calcareous substrates (Directive code: 6210), (ii) pseudo-steppe with

grasses and annuals of the Thero-Brachypodietea (6220), and (iii) Eastern sub-Mediterranean dry grasslands (62A0). These grassland types encompass most of the protected dry grassland habitats occurring in low- to mid-altitudes across Southern Europe, and are considered as priority habitats to conservation due to the high-diversity of both plants and invertebrates they host (Valkó et al. 2016). Habitat layers, that have been mapped within the entire regional territory by 2018, were provided by the regional authority as vector polygons (https://pugliacon.regione.puglia.it/). In order to separately consider grassland surfaces as listed and nonlisted habitats, we first excluded all portions of the grassland layer overlapping with any habitat polygons, i.e. leaving only grassland areas listed as "Non-habitat grassland". To assess the importance of different kinds of grasslands in fostering the occurrence of S. pedo by boosting habitat suitability, we calculated the percent amounts of all habitat and non-habitat extents within each suitable grid cell across the region. Subsequently, we quantified the relationship between suitability values and grassland composition by running a Generalized Linear Model (GLM), using suitability values as response variable, and the percent amounts of all habitats and nonhabitat grasslands as predictors, considering significant those effects with p<0.05 and whose confidence intervals did not encompass 0.

All analyses were run with R 4.2.1 (R Core Team 2022).

Results

Species distribution models

Our model reached a satisfactory level of predictive performance at both present and future time, as evaluated by AUC and TSS values (>0.90 and >0.85, respectively). Saga pedo potential distribution is apparently spread across the known range of the species, with large portions of Mediterranean and continental Europe being classified as potentially suitable, particularly in the eastern Iberian Peninsula, southern France, and peninsular Italy, as well as the Balkan and Carpathian regions (Fig. 2). The main drivers of S. pedo suitability in our models were the mean temperature of the coldest month (bio6; 18.5% of explained variance), and precipitation seasonality (bio15; 14.5%), followed by the presence of grasslands (11.9%), and precipitation of the warmest quarter (bio18; 10.4%). Overall, the species seems associated with grassland areas characterized by mild winter and dry summer, with predictable rainfall patterns throughout the year (i.e., low precipitation seasonality). Minor but significant role in influencing the probability of occurrence of the species in our models was also covered by precipitation of coldest quarter (bio19; 6.0%), suggesting that S. pedo also favors relatively wet winter months.



Fig. 2 Map of potential suitable range to Saga pedo in Europe, according to ensemble Species Distribution Models



Fig.3 Conservation coverage for *Saga pedo* by the networks of protected areas in Europe, expressed as percent per Country/area, based on predicted suitable range ("Suitable range") and exact records ("Occurrences"). *N2K* Natura2000 network, *NPA* Nationally pro-

tected areas, *Pas* N2K+NPA. Suitable range was mapped through species distribution models (SDMs) binarized maps. Numbers in brackets indicate numbers of records per Country/Area

Conservation gap analysis

The overall network of protected areas provides protection to ca. 1/3 (31%) of the potential distribution of *S. pedo* across the EU in which the species occurs. The

 Table 1 Effects of grassland habitats on the environmental suitability to Saga pedo obtained species distribution models, estimated by generalized linear models

Predictors	Suitability			
	Estimates	std. error	95% CI	р
Non-habitat grass- land	- 0.004	0.001	- 0.006-0.002	< 0.001
Habitat 6210	- 0.003	0.002	-0.008-0.001	0.119
Habitat 62A0	0.001	0.000	0.001-0.002	0.009
Habitat 6220	0.001	0.001	- 0.001-0.004	0.297
Observations	348			
R ²	0.442			

Habitat 6210, Habitat 6220 and Habitat 62A0 correspond to protected grasslands listed within the Annex I of the EU Habitats Directive). Predictors are quantified as percent amount of habitat within 10-km grid cells

Significant results are highlighted in italics

Fig. 4 Habitat suitability to Saga pedo in Apulia (Southern Italy) in relation to the percent amounts of different grassland habitats within suitable grid cells (n = 348) identified by ensemble species distribution modeling. Habitats are classified as either protected habitats listed within Annex I of the EU Habitats Directive (Eastern sub Mediterranean dry grasslands (a), pseudo-steppe with grasses and annuals of the Thero-Brachypodietea (b), semi-natural dry grasslands on calcareous substrates (c)) or as non-protected grasslands (d); *p<0.05; ***p<0.001

Natura2000 network currently protects 18% of the species' potential range, a value comparable to that offered by Nationally protected areas (25%; p>0.05). When considering countries separately (Fig. 3), the highest percent of overall protected range is located in Hungary (38%) and Croatia (25%), while all other countries ranged between 13 and 22%. When running the same analysis on exact occurrence records, values were, on average, significantly higher (ANOVA $F_{1,23}$ = 109.9, p < 0.001), ranging from 24 to 99%, with 79% of overall observations falling within the overall network of protected areas across EU. There was no significant difference between the coverage provided by Natura2000 and Nationally protected areas, nor any interaction between the type of network and the type of data used (all p > 0.05).

Association to habitats

A total of 348 10 km² grid cells are environmentally suitable to *S. pedo* in Apulia according to our model, mostly falling within the Murgia plateau and its immediate surroundings, besides some suitable spots located on the grassy slopes of the Gargano massif. Probability of



occurrence of *S. pedo* within cells predicted to be suitable significantly varied according to grassland composition, with a positive effect of the amounts of 62A0 (Eastern sub-Mediterranean dry grasslands) only, and a negative effect of non-habitat grasslands (Table 1; Fig. 4).

Discussion

We provide the first assessment of the bioclimatic niche and conservation coverage of the vulnerable Predatory bush cricket *S. pedo*, by predicting its potential distribution across the European continent, and highlighting the species' relationship with both climate and land cover at two spatial scales. *Saga pedo* seems to be associated with grassland areas characterized by mild colder seasons, and relatively low but highly predictable precipitation in summer. Such preferences are also reflected by the abundance of the species in southern European regions with typically Mediterranean climate such as southern France and Apulia (Labadessa 2014; Labadessa et al. 2015), and by the isolated populations found in the Alpine and continental regions, usually restricted to relict xerothermic grasslands (Anselmo 2019; Maioglio & Repetto 2022).

Being a widely distributed species across Europe (Kaltenbach 1990), the conservation of S. pedo strongly relies on transnational efforts and coordinated conservation planning that require a large-scale assessment as the one we conducted. Its current conservation status within the EU (according to the Habitats Directive Report 2018) is rather inconsistent among countries, with only 10% of the available national reports classifying the species as in a "good" conservation status, all from the Pannonian biogeographical region (https://eunis.eea.europa.eu/speci es/317). Such uncertainty may surely be due to the lack of specific monitoring campaigns and difficulties in detecting the species in the field (Campanaro et al. 2017), yet is also likely paired to a currently insufficient coverage within European protected areas. Even though Nationally protected areas and Natura2000 both provide comparable protection to S. pedo in our analysis, only one third of the species' suitable range is currently protected. These findings suggest that the available network of protected areas may need to be expanded in order to secure its conservation, similar to other insect taxa (Bosso et al. 2018), particularly in the case of countries with large amounts of suitable habitats paired to low degree of protection and an increase in the numbers of known localities (e.g., Italy). Conversely, our analysis highlights that different proxies of species' distribution, namely occurrences vs potential range, provide very different pictures of S. pedo conservation coverage. When using presence records we obtained, as predicted, significantly better coverage values for S.

pedo, with several countries covering > 90% of the records with the overall network of protected areas, i.e. a keystone result for a legally protected species. The two approaches we followed in assessing the species' coverage by protected areas, i.e. exact records and SDM-based distribution, are both subjected to potential biases and limitations. Specifically, the use of occurrences in calculating conservation coverage may lead to an overestimation, since species' records are frequently spatially-biased e.g., due to unbalanced survey efforts in and out of protected areas and to observers' association to infrastructures (such as roads and trails), as highlighted for other similarly rare species (Jeliazkov et al. 2022). Conversely, SDMs are well-known to overpredict species' distributions-and in turn underestimate conservation coverage-due to a number of issues such as the difficulties in capturing biotic interactions and including dispersal abilities in the modeling procedure (Briscoe et al. 2019). As an example, these issues may often result in suitable areas located in actually unsuitable locations due to a lack of habitat or at sites impossible for the species to colonize (Velazco et al. 2020). By running the spatial conservation gap analysis selectively in countries where the species actually occurs, i.e. delimiting the area considered for model projection as we did, we may have only partially counteracted the underestimation of conservation coverage by SDMs, nonetheless providing more robust results and considerations (Cooper and Soberón 2018). As such, we suggest caution when assessing the conservation coverage by protected areas if only using either occurrences or SDMs, particularly in the case of species whose occurrence may easily pass unnoticed, as in the case of our study species (Herkt et al. 2017). The combined results by both approaches may instead provide a more realistic and comparable picture of the conservation coverage for poorly known species, with the 'actual' value possibly lying in-between the extremes provided by each method.

Insects may benefit from conservation actions and protection regimes that target other species or habitats, that may indirectly foster their conservation (Samways 1993; Chowdhury et al. 2022, 2023). Despite the currently limited evidence of positive effects of protected areas on insect conservation, e.g. by lower rates of decline in comparison to non-protected areas, it is likely that preservation measures may have long-term effects on insect demography and-in turn-conservation (Silva et al. 2019; Chowdhury et al. 2022, 2023). Yet, evidence suggests that only species with clear and strong ecological relationships with habitats and/or other species-or endemic to small well-targeted areas-may benefit from such indirect conservation efforts (Samways 2007). Such an approach has in fact raised concerns among conservationists, since even syntopic species may actually diverge in their small-scale ecological needs,

so that actions tackling one may prove useless to the others (Andelman and Fagan 2000; Labadessa and Ancillotto 2022). Our results when testing the regional-level relationships between S. pedo habitat suitability and the occurrence of protected habitats also confirm that non-specialist taxa, as S. pedo, do not necessarily benefit from conservation of other biological entities such as species or habitats (sensu Habitats Directive). Nonetheless, one of the legally protected grassland habitats of EU interest resulted as significant in increasing habitat suitability to S. pedo in southern Italy, while non-protected grasslands resulted as poorly profitable to the species. Such result highlights that at least some habitats of conservation concern such as the high diversity grasslands we focused on may provide particularly favorable conditions to non-target taxa e.g., by preserving well-structured plant assemblages that in turn foster richer orthopteran communities (Labadessa et al. 2015), a key food resource to the Predatory bush cricket. Interestingly, the only habitat whose extent favored S. pedo -Eastern sub-Mediterranean dry grasslands-is characterized by higher cover of perennial herbaceous species and a well-structured vegetation that may need longer times to recover after impacts such as wildfire, overgrazing and agricultural reclamation (Forte et al. 2005; Perrino and Wagensommer 2013).

Conclusions

By assessing the degree of protection provided to S. pedo's occurrences and suitable range we provide clear indications for its long-term conservation, and possibly monitoring, across Europe. Namely, we shed light on the species' needs in terms of ecological requirements, identifying important conservation areas that may significantly benefit from an increase in extent of protected areas. Moreover, our results highlight that habitat protection, exemplified by habitats listed within the Habitats Directive do not represent an efficient surrogate to preserve the Predatory bush cricket per se. Nonetheless, legally protected habitats may actually increase local suitability of grasslands to S. pedo, and may thus be important to preserve, even as small patches, in modified landscapes. Our work on S. pedo also represents a potential framework to be applied to other poorly-known species that share a similar conservation status, besides several orthopterans in urgent need of conservation assessment across Europe. The last Red List assessment of European Orthopterans highlights a very bleak scenario for this group of insects, indicating that most species currently lack sufficient information for properly assessing their status, beside one third of the species being currently listed as threatened and/ or demographically declining (Hochkirch et al. 2016). As such, SDM-based assessments may represent a timely and cost-efficient first step for preliminary evaluations of species hard to detect, also addressing future research and field monitoring efforts, and fostering the identification of key conservation areas for insects and, more in general, poorly known species.

Acknowledgements We thank two anonymous reviewers for their valuable comments and suggestion, which significantly improved a first version of this manuscript. Used data and scripts are available from the corresponding author, upon reasonable request. Leonardo Ancillottowas funded by the National Recovery and Resilience Plan (NRRP), Mission 4,Component 2, Investment 1.4, Decree n.3175 of the Italian Ministry of University and Research, funded by the European Union – NextGenerationEU;Award Number CN_00000033, CUP B83C22002930006, "National Biodiversity Future Center - NBFC".

Author contributions Both authors contributed to the study conception and design, and to data collection and curation. The first draft of the manuscript was written by LA, and both authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding Open access funding provided by Consiglio Nazionale Delle Ricerche (CNR) within the CRUI-CARE Agreement.

Declarations

Competing interests The authors declare they have no competing interest

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