

Research article

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The effects of short-term climate change on the range of species: the case of the expanding European dwarf mantis *Ameles spallanzania* in northern Italy (Mantodea: Amelidae)

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Abstract

Climate change is altering the distribution of many species, which shift their range chasing the suitable conditions to survive and reproduce. Within a few years, the European dwarf mantis (*Ameles spallanzania*) seems to have expanded its range towards northern Italy, settling in the Po Valley and reaching the Alps. Our goal was to investigate the relationship between the climate of the last four decades in Italy and the distribution of this species in the current period and in the past. The results indicate that, during the last decades, a rapid and remarkable increase in climatically suitable area for this species has occurred in northern Italy, while in the historical presence sites it has remained rather constant. The existence of corridors such as railways, embankments, and roadsides may have accelerated its dispersal. These results suggest that rapid climate change, in particular the rise in average annual temperature, may contribute significantly to the rapid expansion of a thermophilic species, with hitherto unknown consequences on the ecological communities it reaches.

Key words: *Ameles spallanzania*, maxent, range expansion, nonnative species, alien species.

Introduction

Climate change refers to a change in the state of the climate that can be identified by changes in the mean and/or the variability of its properties and that persists for an extended period, typically decades or longer (IPCC 2014). The human-induced warming on global scale is unequivocal and consisted of an increase of about 0.2 °C per decade from the pre-industrial period to 2017 (Allen et al. 2018). Central Europe, including Italy (Brunetti et al. 2006), is facing increasingly hot and dry summers (Seneviratne et al. 2006), and temperatures are expected to rise further during the twenty-first century (Tomozeiu et al. 2014; Bucchignani et al. 2016).

Range shift is one of the expected responses of species to climate change (Parmesan & Yohe 2003; Chen et al. 2011). As formerly unsuitable habitat becomes suitable, and vice versa, many species shift their ranges to follow changes in habitat and climate. Even among European insects, there are many examples where species have recently started both northward (Parmesan et al. 1999; Devictor

et al. 2012; Mason et al. 2015) and upward (Dieker et al. 2011; Menéndez et al. 2014; Rödder et al. 2021) distributive shifts. Local conditions and microclimates are altered by climate change, sometimes in different ways, evolving discontinuously and creating peculiar local climate patterns that affect local populations (Suggitt et al. 2011, 2018; Potter et al. 2013; Battiston & Biondi 2015).

In this study we analysed the Italian distribution of the European dwarf mantis *Ameles spallanzania* (Rossi, 1792) in the last decades, a period during which the species was observed more and more frequently in northern Italy (Battiston et al. 2020a). According to Battiston et al. (2020a) this species, not migrant, tendentially sedentary and linked to warm climate, could have recently expanded its range, thanks to the recent rising temperatures and the presence of man-made corridors and human transport. We have therefore investigated the relationship between the climate of the last four decades in Italy and the distribution of this species, as a case study to investigate the influence of climate on low-mobility species between natural and human-mediated habitats.

Material and methods

Study species

The European dwarf mantis *Ameles spallanzania* is a small-sized mantis, distributed in almost all the Mediterranean basin (Battiston 2020). Females are brachypterous and tendentially sedentary while males are macropterous and able to fly over short distances (Battiston et al. 2010). The general coloration, shape of the body, and movements mimic the vegetation where this species rests and hunts. Its natural habitats are maquis, garrigue, and mediterranean steppe but it can be found as well in many arid and thermophilous discontinuity of natural vegetation inside artificial environments (unmanaged gardens, deposits, roadside verges, etc.) (Battiston et al. 2020b; Cassar 2020). This species has been recorded standing on a variety of forbs and shrubs: *Artemisia campestris* L., *Centaurea paniculata* L., *Eryngium campestre* L., *Echinops sphaerocephalus* L., *Foeniculum vulgare* L., *Lavandula* spp., *Mentha* spp., *Odontites luteus* (L.), *Salvia rosmarinus* Spenn. (= *Rosmarinus officinalis* L.), *S. officinalis* L., *Satureja* spp. (Battiston et al. 2010; Leandri et al. 2013; Anselmo 2022; WDP pers. obs.). It is also found in abandoned orchards, with a layer of *Genista umbellata* (L'Her.) Poir. and/or *Ly-*

gos sphaerocarpa (L.) Heyw. interspersed with herbs and tall grasses (Payne 2017). Nymphs and mature females usually hide on low vegetation amongst leaves, buds or flower heads while adult males use to cling on higher stems, especially if they are following the female pheromones (Payne 2017). *A. spallanzania* is capable of adapting its lifecycle to latitude: in Mediterranean and warmer areas it can produce two generations per year, either with overwintering nymphs or with mixed populations of overwintering nymphs and oothecae; in northern and continental localities only one generation per year is produced and overwintering oothecae are able to tolerate sub-zero temperatures (Battiston & Galliani 2011).

Past and current occurrences

According to the historical checklist and distribution of the Italian fauna (Fontana et al. 2005), the past distribution of *A. spallanzania* was mainly concentrated near the West inland coastline and in the islands, referring to 99 generically indicated localities from 1878 to 2001 (grouped in 77 UTM square cells of 10 x 10 km). Among these data, those falling in northern Italy refer mainly to the western part, near the Ligurian coast and the nearby inland, while to the East only two occurrences were recorded in 1963 and

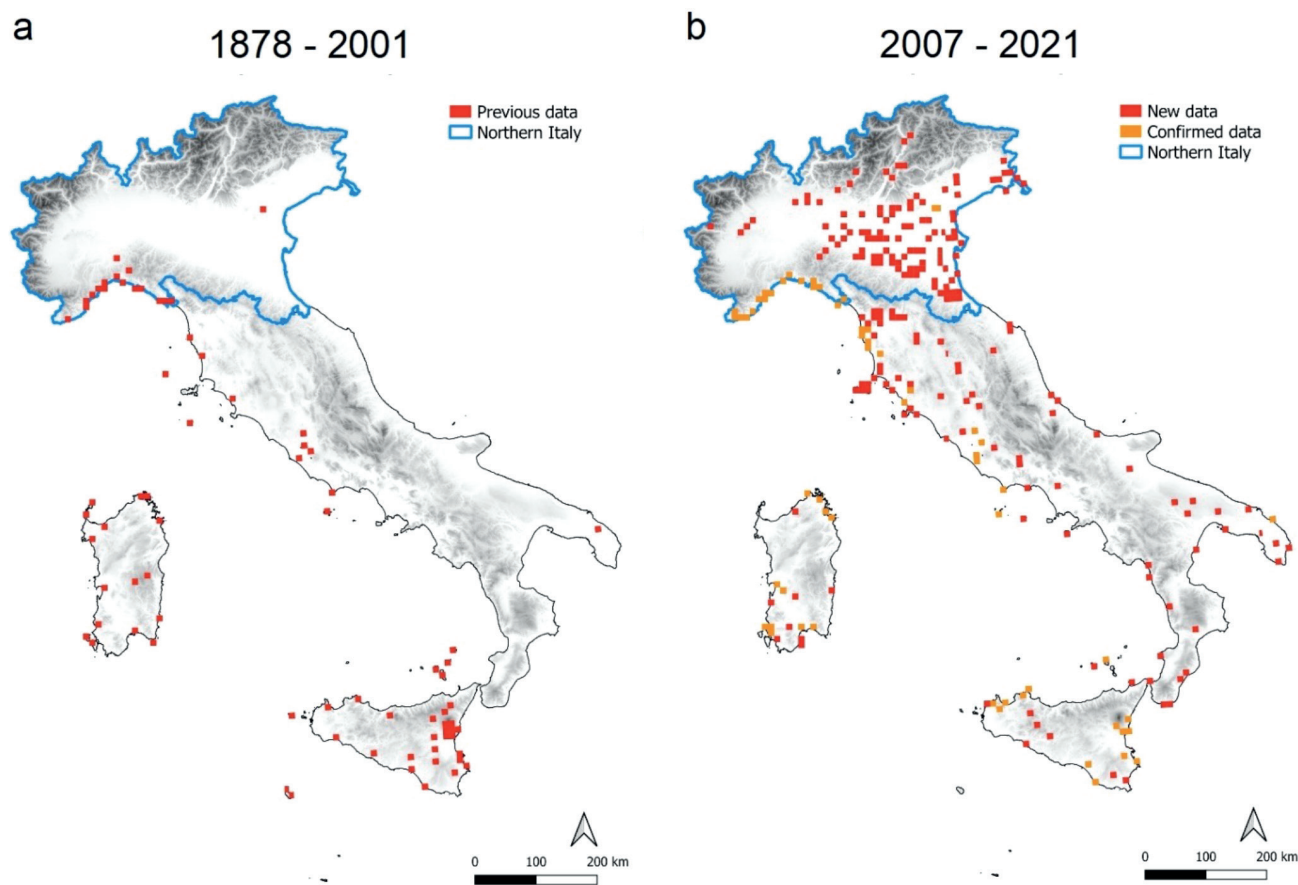


Fig. 1 – Distribution of *Ameles spallanzania* in Italy across **a**, past period and **b**, current period. Confirmed data refer to already known presence cells in the previous time interval.

1969 in the Province of Padova (Fig. 1a). Subsequently, the presence of this species was recorded more and more frequently in northern Italy (Cogo & Battiston 2007; Battiston & Buzzetti 2012; Uliana & Battiston 2012; Leandri et al. 2013; Buzzetti et al. 2018; Battiston et al. 2020a; Battiston 2021), even in the Alps (Ballini & Wilhelm 2014; Tabarelli de Fatis & Debiasi 2020; Anselmo 2022). We then gathering overall 401 georeferenced data from 2007 to 2021 (Fig. 1b) available from the aforementioned literature, GBIF (<https://doi.org/10.15468/dl.ggb4u5>), iNaturalist (<https://www.inaturalist.org>), data collected by the authors also through the “Segnala una mantide” (= “Report a mantis!”) of Mantidi Lovers Italia citizen science project (<https://www.facebook.com/MantidiLoversItalia>). We only selected data and with a precision lower than 300 m.

Climatic variables

For the purposes of our study, high resolution layers of monthly precipitation amount, maximum and minimum temperature from 1980 and 2019 were obtained from the CHELSA V2.1 database (Karger et al. 2017, 2021), with original resolution on Italy of about 655 m. These data were averaged over 10-year subsets and used to produce 19 bioclimatic variables for each, with the package *dismo* v. 1.3-9 (Hijmans et al. 2022) in the software R v. 3.6.3 (R Core Team 2020). A selection of climatic variables from the decade 2010-2019 was carried out (Merow et al. 2013; Fourcade et al. 2018), identifying the groups of variables most correlated (Spearman correlation > 0.7) with the package *ENMTools* v. 1.0.6 (Warren et al. 2021) and choosing the supposed most ecologically important variable for each group (Forcaude et al. 2018). The resulting set of variables from this procedure were bio1 (mean annual temperature), bio8 (mean diurnal temperature range), bio2 (mean daily temperatures of the wettest quarter), bio15 (precipitation seasonality) and bio19 (mean monthly precipitation amount of the coldest quarter). No land cover variables were used, as this species is capable of settling in marginal small microhabitats (e.g. roadsides) possibly present within almost any land cover and above. Furthermore, these microhabitats are not identifiable at the same resolution of the climatic variables.

Species distribution modelling

The modelling was performed with the package *Biomod2* v. 3.5.1 (Thuiller et al. 2021) in R. Individual models were built with the MaxEnt algorithm (Phillips et al. 2006), a machine learning method that applies the principle of maximum entropy to predict the potential distribution of species from presence-only data (Elith et al. 2011; Phillips & Dudík 2008). Compared to other methods, this algorithm is more efficient and reliable (Elith et al. 2006; Guisan et al. 2007; Peterson et al. 2007), providing useful results even with small samples (Pearson et al. 2006; Wisz et al. 2008) and is less influenced by unequal sampling levels

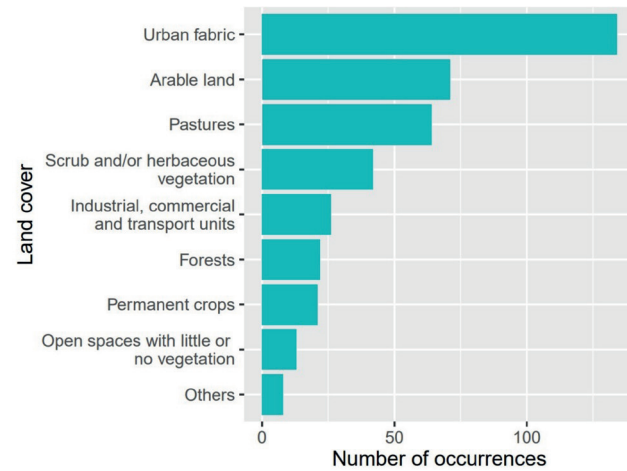


Fig. 2 – Land use in the occurrences of the current period.

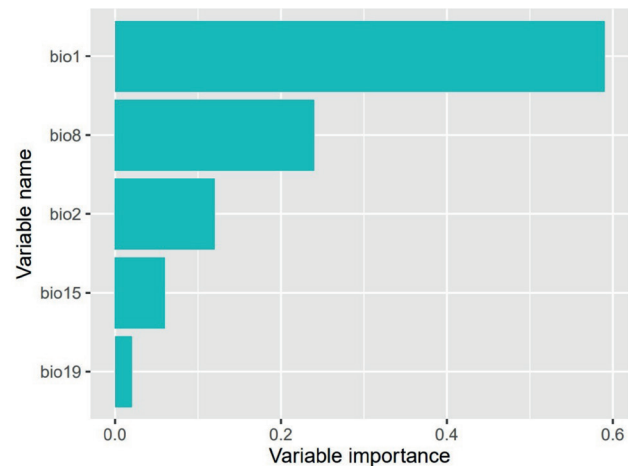


Fig. 3 – Importance of climatic variables used to model the distribution of *Ameles spallanzania*.

(Tsoar et al. 2007). The models were built using one occurrence per pixel referred to the current period (2007-2021) resulting in 325 points, and the climatic variables referred to the current period (2010-2019) prepared as described in the previous steps. In the modelling procedure a random sample of 10'000 pseudo-absences were generated across the study area. To evaluate model performance, the algorithm was calibrated with 80% of the data and tested with the remaining 20%. The procedure was replicated 10 times and each model was evaluated by the Area Under the Curve (AUC) and the True Skill Statistic (TSS): Models with AUC below 0.6 are not considered reliable, 0.6-0.7 are considered poor, 0.7-0.8 right, 0.8-0.9 good and higher than 0.9 excellent (Arújo et al. 2005). Models with TSS measures below 0.4 are considered poor, 0.4-0.8 useful, and higher than 0.8 good-excellent (Allouche et al. 2006). An ensemble model was created by averaging the individual models, trained on the 10 sampling replicates, and then projected in the current period and in each past decade in order to obtain suitability maps through time (with suit-

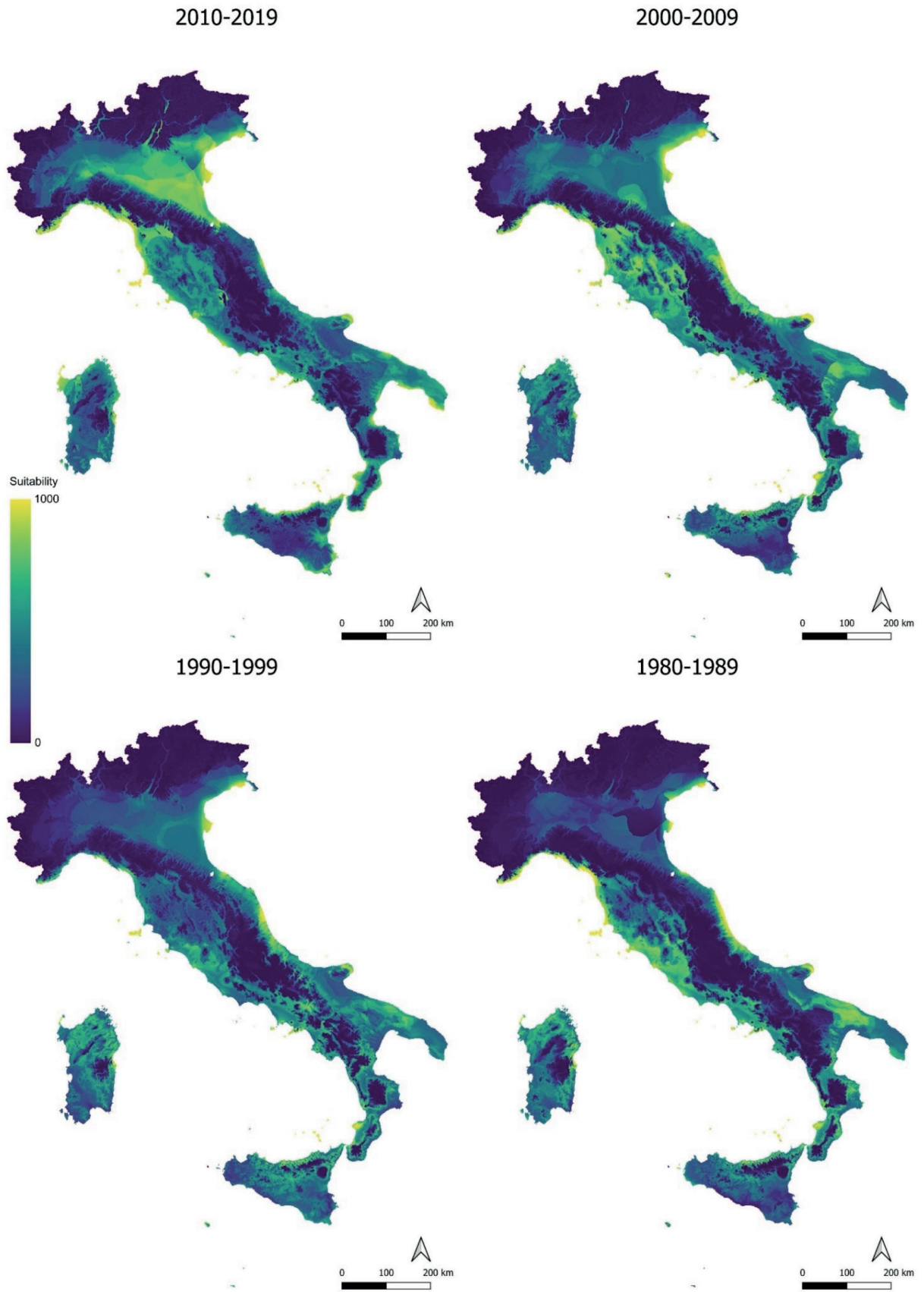


Fig. 4 – Suitability maps of *Ameles spallanzania* referred to each decade.

ability values from 0 to 1000), also building binary projections of presence-absence (1 for presence and 0 for absence) using the threshold that maximizes the TSS scores, with the Biomod2 package (Thuiller et al. 2021).

Distribution analysis

We evaluated the change of distribution of *A. spallanzania* in the last four decades, in terms of predicted suitability and predicted presence area with the package raster v. 3.5-15 (Hijmans 2022) in R. The areas on which the comparison was carried out corresponds to northern Italy (i.e. the merging of the administrative regions Valle d'Aosta, Piedmont, Lombardy, Trentino-Alto Adige, Veneto, Friuli-Venezia Giulia, Liguria and Emilia-Romagna) and to the historical range, i.e. the 10 x 10 km presence cells provided 10 x 10 km cells provided in the checklist and distribution of the Italian fauna (Fontana et al. 2005).

For descriptive purposes, the land cover in the occurrences related to the current period was reported, based on CORINE Land Cover 2018 (CLC) produced by the Copernicus Land Monitoring Service (Büttner et al. 2021).

Results

The performance of the models was deemed sufficient to consider reliable the predictions and carry out the distribution analyses, as they showed AUC greater than 0.7 (mean = 0.79, SD = 0.02) and TSS greater than 0.4 (mean = 0.46, SD = 0.05). The most important variables driving the distribution of *A. spallanzania* were the temperature variables, in particular the mean annual temperature (bio1) showed the greatest influence (Fig. 3). In contrast, the precipitation-derived variables (bio15 and bio19) were not of great importance. The suitability of northern Italy for this species has gradually increased over the decades (Figs 4-5), from the mean value of 111.3 (SD = 158.7) referred to the decade 1980-1989 to 295.4 (SD = 300.8) of the last decade. In this geographical context, the presence area indicated by the binomial transformation of the suitability map has also greatly increased over time, from 3553.3 km² to 30385.4 km² between the first and last decade considered (Fig. 6). In comparison, the suitability within the historical distribution cells has only slightly increased over time (Fig. 5), showing a mean value of 370.2 (SD = 272.3) in the first decade and of 494.75 (SD = 271.61) in the last decade, and so has the predicted presence area, from 1589.4 km² to 2082.1 km² (Fig. 6).

Based on the CLC, the occurrences in the current period fell mostly on the urban fabric (N = 134), followed by other more natural land covers (Fig. 2).

Discussion

The efficiency of the models built only with climatic variables demonstrates that these were of great importance in the distribution of *Ameles spallanzania*. The average annual temperature plays a fundamental role in predicting the distribution of this species and its recent rise (WMO 2022) may explain the increase of its observations in northern Italy. The low importance of the variables related to rainfall instead suggests that this species can survive even in places with a not distinctly Mediterranean climate and therefore, *A. spallanzania* should be considered a thermophilic species rather than a xero-thermophilic species. According to the models, while habitat suitability has remained quite similar over time within areas of historical presence, it has much increased in northern Italy (+62.3% since the 1980s; average inter-decade increase of 27.9%, SD = 1.7%). The area of potential presence has also increased considerably in northern Italy (+88.3% since the 1980s; average inter-decade increase of 43.4%, SD = 38.3%). These results suggest a rapid expansion of this species due to the progressive gain in the climatically suitable area, especially

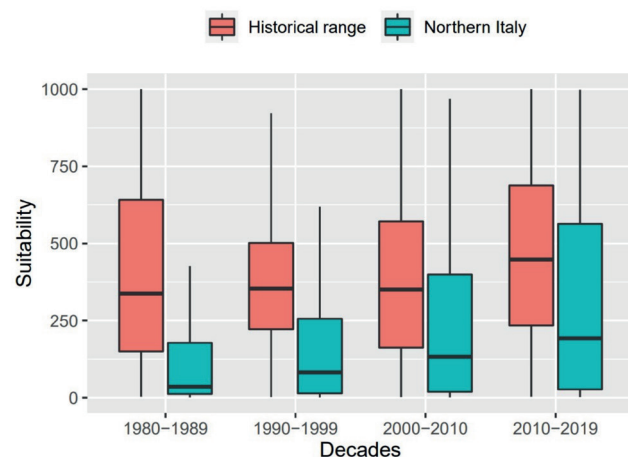


Fig. 5 – Boxplots of suitability per decade referred to the historical range and northern Italy.

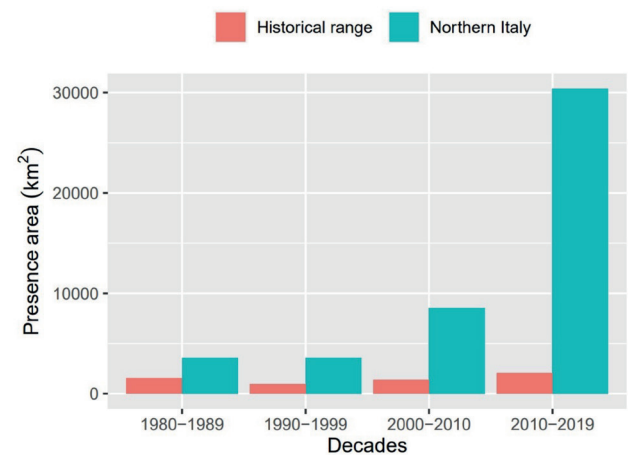


Fig. 6 – Extent of predicted presence areas derived from binary maps.

occurred in the last decade 2010-2019. The rapidity with which this low-mobility species has expanded (considering females are unable to fly), could be linked to the use of roadsides or railway embankments as corridors for active dispersal; additionally, the use of wagons or ornamental plants for laying oothecae has also been hypothesized (Battiston & Buzzetti 2012; Battiston et al. 2020a). However, it should be emphasized that these surrogate habitats that may have been most involved in the dispersal of *A. spallanzania* (i.e. the railways embankments) have existed with the same arrangement for a long time (Battiston et al. 2020a). Therefore, assuming a higher survival of the species due to the increased climatic suitability in new areas, the presence of these pre-existing corridors may have only facilitated its expansion. Furthermore, by preferring habitats with scarce and sometimes degraded vegetation (Battiston et al. 2020b; Cassar 2020; Anselmo 2022), *A. spallanzania* could perhaps have easily found suitable environments in the urbanized areas, e.g. along the communication routes. In this sense the land cover of the urban fabric, coinciding with the 33.5% of the occurrences recorded from 2007 to 2021, seems to confirm this ability.

Based on the results obtained from this study, a further northward and upward expansion of *A. spallanzania* and the formation of stable populations could be foreseen in northern Italy and perhaps in the rest of Europe, where the temperatures are rapidly rising almost everywhere (WMO 2022). The recent finding of this species in other localities further north of the range known seems confirm this trend, i.e. in Germany (Schwarz & Ehrmann 2018), France and Switzerland (Borer et al. 2023).

Our results suggest that a short-term climate change occurred within a few decades may contribute significantly to the expansion of a thermophilic species, with unknown consequences on the ecological communities reached by it. Climate change is already altering the distribution of many species (Lenoir & Svenning 2015) and will continue in the near future, increasingly blurring the distinction between those species traditionally considered native and non-native (Thomas & Ohlemüller 2010, Essl et al. 2019). How much human-induced climate change compares to unintentional or deliberate human introduction in favouring the expansion of species? A critical analysis of the concepts that distinguish alien species from native species (Richardson et al. 2000, 2011; Battiston et al. 2017; Essl et al. 2018) and the extent of their threat to biodiversity (Pyšek et al. 2020) may be increasingly necessary. In the case of *A. spallanzania*, anthropogenic climate change could reduce or eliminate the biogeographic barriers which have so far precluded survival and reproduction in areas geographically contiguous to its native range. This same mechanism will be essential to the survival of many imperilled species, which will be able to survive climate change only by expanding outside their historical ranges (Thomas & Ohlemüller 2010). From this perspective, the

northward expansion of *A. spallanzania* in response to anthropogenic climate changes and human mediated actions, would correspond at least in part to the definition proposed by Essel et al. (2019, 2021) of “neonative” species, i.e. range-expanding species that track environmental changes without human assistance. Only through further research will it be possible to determine the extent to which this species may affect the new recipient ecosystems.

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