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Past and current climate as a driver in shaping the distribution of the *Longitarsus candidulus* species group (Coleoptera: Chrysomelidae)

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Longitarsus candidulus (Foudras) is a thermophilic flea beetle species widely distributed in the Mediterranean Basin and associated with *Daphne gnidium* L. and *Thymelaea hirsuta* (L.). *Longitarsus laureolae* Biondi and *Longitarsus leonardii* Doguet, phylogenetically closely related to *L. candidulus*, show together a peculiar and rare disjunct distribution along the central-southern Apennines and the Cantabrian-Pyrenean mountain system, respectively. Both are associated with *Daphne laureola* L. in mesophilic habitats. We used "ecological niche modeling" to infer the Pleistocene dynamics in the distribution of the three flea beetle species and their host plants. We interpreted their current distributions, paying particular attention to the presumed time of species divergence as inferred from recent studies. The differentiation of *L. laureolae* and *L. leonardii* from *L. candidulus* likely represents a response to the marked climatic changes during the Late Pliocene. Such a split was likely associated with a trophic niche shift of the *laureolae*/*leonardii* ancestor towards the typically mesophilic host plant *D. laureola*. The subsequent split between *L. laureolae* and *L. leonardii*, possibly due at first to the niche competition, was then boosted by an allopatric divergence during the Middle Pleistocene, likely caused by a large area of low environmental suitability for both species, mainly located between the northern Apennines and the south-western Alps.

Key words: ecological modeling, Alticini, marine isotope stage 19, Thymelaeaceae

Introduction

Climate changes, past and ongoing, have important implications in the ecosystem dynamics, being intimately related to current biodiversity patterns (Walther et al. 2002, 2010, Parmesan 2006). As it is well known, present climate change is having a profound impact on many taxa, including insects. The effects on insects are complex, affecting their distribution, population dynamics, and ecology even in the more extreme environments (e.g., Contador et al. 2020, Wilson and Fox 2021), and can be responsible for forest tree decline (Pureswaran et al. 2018, Scheller et al. 2018), agricultural damages (Iannella et al. 2021a), spread of alien species (Iannella et al. 2019a, b, 2020, Liebhold et al. 2021), and general ecosystem services loss (De Simone et al. 2020, Iannella et al. 2021b).

Hundreds of studies have combined data on species occurrences with climate descriptions from interpolated weather stations to better understand the past and future distribution of animals and plants ecological. In this context, ecological niche modeling (ENM) is a quantitative tool that combines species occurrence data with environmental variables, to predict the potential distribution of species. Ecological niche models (ENMs) operate under the assumption that species distributions are in equilibrium with the environment and that species occurrences are limited by environmental factors. To run ENMs, data on species locations (presence-only or presence–absence) and a set of environmental covariates that describe these locations are needed. The models produce maps that represent the potential distribution of the environmental suitability for a given species based on the covariates considered. The growing use of these models is evident in numerous studies that investigate past and current ecological patterns and forecast potential changes in species distributions due to environmental alterations (e.g., Guisan et al. 2017, Brown et al. 2018, Araújo et al. 2019, Srivastava et al. 2019, Melo-Merino et al. 2020).

The application of ENM techniques on insects is particularly problematic, considering the great difficulty in the taxonomic recognition of the numerous species in this class and the lack of detailed knowledge of their geographical distribution (Wallacean shortfall). Nevertheless, ENMs can contribute to bridging this shortfall by predicting potential distributions based on known and reliable occurrence points and environmental variables. ENMs are mainly instrumental in hypothesizing plausible distributions for poorly documented species, also providing a foundational tool for biogeographic studies (e.g., Buckley et al. 2010, Biondi et al. 2023a, Mirzaee et al. 2023).

Leaf beetles (Coleoptera: Chrysomelidae), a family of phytophagous insects, can be exceptional model organisms to understand the complex relationships between ecological interactions and climate (Biondi et al. 2023b). In fact, many of the 40,000 species worldwide are associated with one or a few plant species, being monophagous or oligophagous (Jolivet and Hawkeswood 1995, Biondi 1996, Gikonyo et al. 2019, Salvi et al. 2019). This geographically constrains the insects to the distribution of specific plants, which, in turn, are directly influenced by climatic factors (among others, Facon et al. 2021, Bhagarathi and Maharaj 2023, Franić et al. 2023, Letsch and Beran 2023). Nevertheless, host plant shift is common in phytophagous insects and can trigger different phenomena ranging from the widening of the species trophic spectrum to sympatric and/or allopatric speciation events (among others, Berlocher and Feder 2002, Forbes et al. 2017, Jousselin and Elias 2019, Rodríguez et al. 2021, Jones et al. 2022, Ravigné et al. 2024). Therefore, climatic factors act as a limiting factor for the distribution of the plants and the associated insects in complex ways, shaping intricate and peculiar biodiversity patterns.

Longitarsus Latreille is a mega-diverse and the most speciose genus among flea beetles (Coleoptera: Chrysomelidae: Alticini) with more than 700 known species (Salvi et al. 2019). It is widespread through all zoogeographical regions, and ecologically diversified, with specialized feeders, monophagous or oligophagous on different angiosperm families (Schoonhoven et al. 2005).

The *Longitarsus candidulus* species group, including *L. candidulus* (Foudras) (Fig. 1A), *Longitarsus laureolae* Biondi (Fig. 1B), and *Longitarsus leonardii* Doguet (Fig. 1C) represents a clade whose definitive differentiation was estimated to have occurred during the Pleistocene (Berrilli et al. 2024). It constitutes a very homogeneous group of species sharing similar external, aedeagic, and spermathecal morphology, as well as being mainly associated with host plants of the family Thymelaeaceae (Biondi 1988, Bergeal and Doguet 1991). The primary association with the Thymelaeaceae plant family is peculiar, representing a unique case among western Palearctic *Longitarsus* (Salvi et al. 2019, Berrilli et al. 2024). *L. candidulus* shows a typical Holo-Mediterranean distribution, with a higher frequency of occurrences in the western sector. It is a thermophilic species mainly found in coastal and sub-coastal environments, which extends into inland continental areas only in the Iberian Peninsula and the Maghreb (Berrilli et al. 2024). *L. laureolae* and *L. leonardii* show more limited distributions and are associated with medium altitude environments; the former is occurring, mainly in the undergrowth of mesophilic woods, in the central-southern Apennines, including the Sicilian range, while *L. leonardii*, mainly associated with forest clearings, is distributed in the Cantabrian-Pyrenean mountain chain (Biondi 1988, 1996). Regarding host plants, *L. candidulus* is associated with *Daphne gnidium* L. and *Thymelaea hirsuta* (L.) Endl., while *L. laureolae* and *L. leonardii* are both associated with *Daphne laureola* L. (Biondi 1996).

Our study aimed to disentangle the unique and complex distribution patterns in the *L. candidulus* species group, which are marked by significant disjunctions. We seek to uncover the ecological and climatic factors driving these peculiar distributional patterns, offering insights into the historical biogeography and adaptive strategies of these closely related beetle species. Starting from the hypothesis proposed by Berrilli et al. (2024) that the separation of the *laureolae/leonardii* lineage from *candidulus* was likely due to a marked climatic change during the transition from the Pliocene to the Pleistocene (Piacenzian age), we used ENM techniques to test that hypothesis by identifying the possible specific factors that favored the diversification processes in these insects. Considering the strict association between the flea beetle species and distinct host plants, we paid particular attention to the historical availability of host plants during the Middle Pleistocene, the period during which the differentiation between *L. laureolae* and *L. leonardii* should be placed (Berrilli et al. 2024). Specifically, based on a set of bioclimatic variables, we reconstructed the possible dynamics in the distribution of the three *Longitarsus* species and their respective host plants and compared the models obtained in the current with those obtained for the late Middle Pleistocene. Our hypothesis posits that host plants played a key role in the diversification processes of these insects, driven by climatic factors. This hypothesis will be supported if habitat suitability for both insects and plants is linked to bioclimatic factors in both current and past scenarios, if distribution models show that the host plants of *candidulus* (*D. gnidium* and *T. hirsuta*) and *laureolae/leonardii* (*D. laureola*) had different habitat suitability distributions during the late Middle Pleistocene, and if correlations between habitat suitability for insects and their respective host plants are high while correlations between insects and non-host plants are low in both current and past scenarios.

Materials and Methods

Study Area and Species Databases

The study area encompassed southern Europe and the regions and islands of the Mediterranean Basin where the three examined species are distributed; it also included areas where no biogeographical barriers occur, thus comprising in the modeling process the “accessible area” of the Biotic–Abiotic-Mobility (BAM) diagram *sensu* Peterson and Soberon (2012), to contemplate the suites of factors that determine geographic distributions of species.

The occurrences of flea beetles included 107 localities: 81 for *L. candidulus*; 19 for *L. laureolae*; 7 for *L. leonardii*. The three datasets were built using information from field data, critical screening of the entomological literature (Peyerimhoff 1911, Dodero 1925, Alfieri 1976, Biondi, 1988, Bergeal and Doguet 1991, Doguet 1994, Baselga and Novoa 2000, 2001, Baviera and Biondi 2015, Sakin and Özdikmen 2022, Berrilli et al. 2024), and identification of specimens preserved in the following public repositories and collections: BAQ: Italy, University of L’Aquila, Collection M. Biondi; BOS: Spain, University of Oviedo, Arthropod Collection; MCIZ: Italy, University of Messina, Museo Zoologico Cambria; MCZR: Italy, Rome, Museo Civico di Zoologia; MNCN: Spain, Madrid, Museo Nacional de Ciencias Naturales; MNHN: France, Paris, Musèum National d’Histoire Naturelle; MSNG: Italy, Genoa, Museo Civico di Storia Naturale “Giacomo Doria”; MSNM: Italy, Milan, Museo Civico di Storia Naturale; MZBS: Spain, Barcelona, Museo de Zoología; MZRO: Italy, Verona, Museo Civico di Storia Naturale “P. Zangheri”; MZUF: Italy, Florence, Museo di Storia Naturale “La Specola” (the abbreviations listed above follow the list on the website “The Insect and Spider Collections of the World”; Evenhuis 2021).

The occurrence localities of the host plants were downloaded from GBIF with the help of the “coordinate-cleaner” R package. The three databases comprised *D. gnidium*, 7,000 occurrences (https://doi.org/10.15468/dl.wwj2y4); *D. laureola*, 5,532 (https://doi.org/10.15468/dl.eas4kq); *T. hirsuta*, 7,000 (https://doi.org/10.15468/dl.ht8k6t). The geographic coordinates for each locality of presence

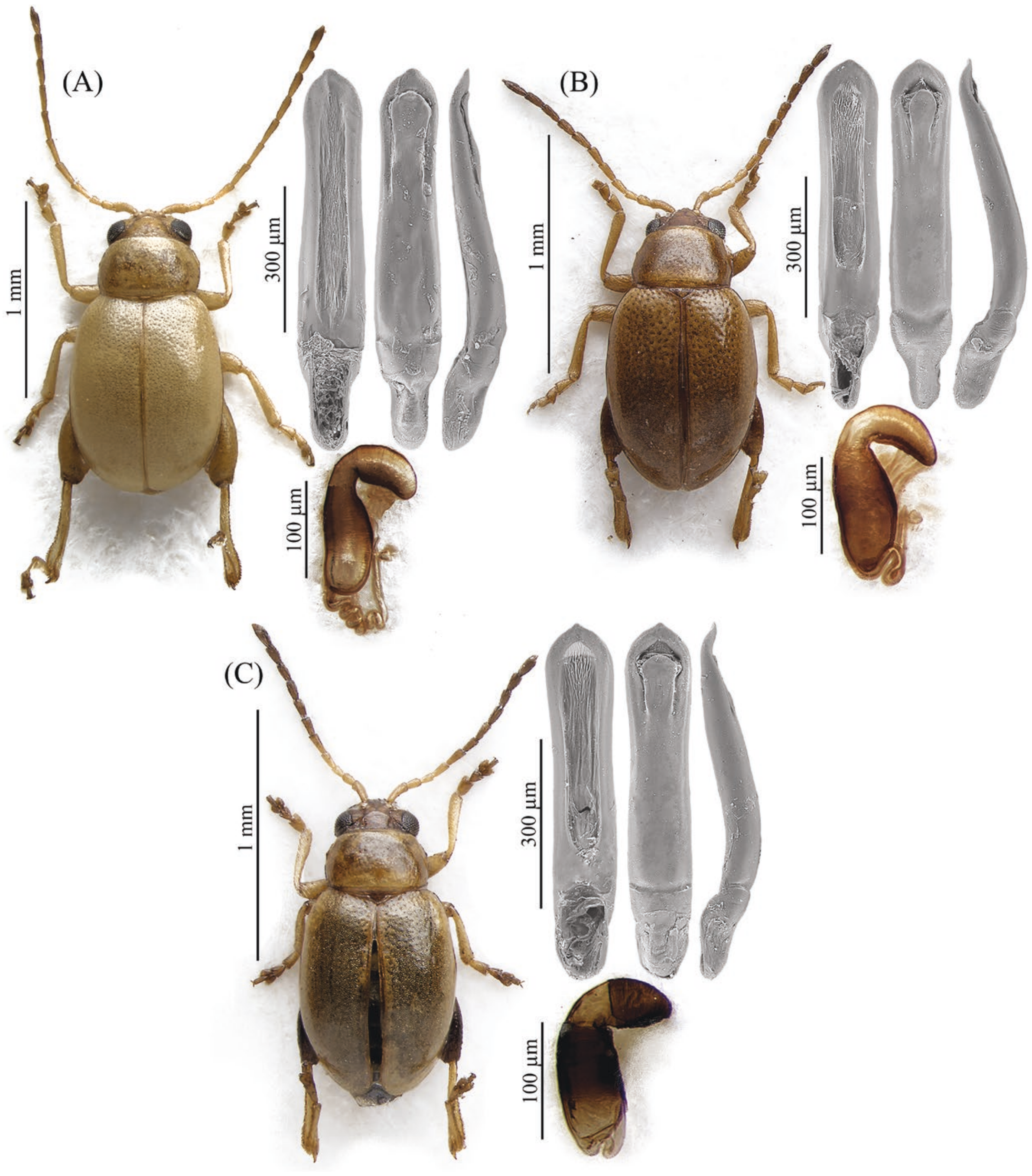

Fig. 1. Habitus, aedeagus, and spermatheca of the *Longitarsus candidulus* species group, modified from Berrilli et al. (2024). A) *Longitarsus candidulus* (Foudras). B) *Longitarsus laureolae* Biondi. C) *Longitarsus leonardii* Doguet. For each species, the habitus (left), the median lobe of the aedeagus (top right) in ventral, dorsal, and lateral view (from left to right), and the spermatheca (bottom right) are shown. Original figure used by permission of Current Zoology.

(WGS84 datum) for the insect species and their host plants are available from the authors upon request.

Model Building and Evaluation

For the implementation of the ENMs, we downloaded (i) CURRENT: the set of 19 bioclimatic variables available from the Worldclim.org repository, choosing the 'current' dataset (ver. 2.1, 2.5 arc-sec resolution), namely BIO1: annual mean temperature; BIO2: mean diurnal range (mean of monthly (max temp–min temp)); BIO3: isothermality (BIO2/BIO7) (×100); BIO4: temperature seasonality (standard deviation × 100); BIO5: max temperature of warmest month; BIO6: min temperature of coldest month; BIO7: temperature annual range (BIO5–BIO6); BIO8: mean temperature of wettest quarter; BIO9: mean temperature of driest quarter; BIO10: mean temperature of warmest quarter; BIO11: mean temperature of coldest quarter; BIO12: annual precipitation; BIO13: precipitation of wettest month; BIO14: precipitation of driest month; BIO15: precipitation seasonality (coefficient of variation); BIO16: precipitation of wettest quarter; BIO17: precipitation of driest quarter; BIO18: precipitation of warmest quarter; and BIO19: precipitation of coldest quarter. (ii) MIS19 (Marine Isotope Stage 19): the set of 14 bioclimatic variables from Paleoclim.org repository, choosing

'Pleistocene: MIS19 (ca. 787 Ka)' dataset (ver. 1.0, 2.5 arc-sec resolution), namely BIO1, BIO4, BIO8, BIO9, BIO10, BIO11, BIO12, BIO13, BIO14, BIO15, BIO16, BIO17, BIO18, and BIO19; they are the same bioclimatic variables of the Worldclim.org repository, thus permitting comparisons among them and concurrent use in modeling studies. MIS19 occurs at roughly 787 Kya before present (BP), in the Calabrian age (1.8–0.774 Mya) between Gelasian (2.58–1.8 Mya) and Chibanian (0.774–0.126 Mya) (Head 2021) and is the oldest Pleistocene interglacial covered by the latest EPICA Antarctic ice core (Lüthi et al. 2008). This allowed the use of well-constrained greenhouse gas concentrations of CO_2, CH_4, and N_2O and accurate orbital parameters, making the extrapolations of the climate variables reliable (Brown et al. 2018).

To avoid potential correlation among the 19 Worldclim bioclimatic variables, which leads to the lowering of the model performance, we measured both the variance inflation factor (VIF, calculated from $VIF = 1/(1 - R^2)$, where R^2 is obtained from regressing each variable against all others). For this purpose, we used the "vifstep" and "vifcor" functions of the "usdm" R package (Naimi et al. 2017) with a commonly accepted threshold = 10 (Guisan et al. 2017), and the Pearson's $|r| < 0.75$, following Dormann et al. (2007) and Elith et al. (2006). The variables obtained as the outcomes of the analyses were then selected as predictors to both calibrate and project the models to the CURRENT and to the MIS19.

To identify the climatic factors most likely influencing insect diversification, acting on insects and host plants, we selected variables based on two criteria: high model contribution and distinctive trends in response curves. A variable had to meet both criteria to be selected. Specifically, we focused on variables that significantly contributed to the models and exhibited distinctive ecological responses. Distinctive trends were classified by examining how the response curves differed for each species. For example, a distinctive trend could be identified if one response curve showed an increasing trend while another exhibited a decreasing trend for the same predictor variable. Another example is Gaussian trends with peaks at different positions, indicating different optimal conditions for each species. This approach allowed us to highlight the variables that not only significantly influenced the models but also provided insights into the different ecological responses of the species. Since host plants had a high number of occurrences, to avoid overfit of the models due to possible clustered localities, the initial datasets were rarefied through the "Spatial thinning" function in ArcGIS Pro 3.2.2, with a minimum locality distance set to the same spatial extent of the predictors (Sillero and Barbosa 2021). The final number of occurrences of *D. gnidium*, *D. laureola*, and *T. hirsuta* used for the models was 1,694, 1,885, and 589, respectively.

Spatial thinning did not apply to the *Longitarsus* species datasets because there were already few occurrences of *L. laureolae* and *L. leonardii* (Fig. 2A). We applied the Moran test from the "Spatial Autocorrelation (Global Moran's I)" toolbox in ArcGIS Pro 3.2.2. to further verify the absence of autocorrelation among the records. This test determines whether the localities exhibit regular occurrence, clustering, or spatial independence (ESRI 2023).

The ENM process was performed using the "Presence-only Prediction (Maxent)" tool in the ArcGIS Spatial Analyst. This tool permits to infer, based on a set of environmental predictors and occurrence localities (specifically, a presence-only dataset), the suitability of a certain taxon across an area, also giving marginal response curves of the predictors with respect to the predicted suitability. Maxent is a widely used algorithm for presence-only data, leveraging the principle of maximum entropy to predict the geographic distribution of species based on environmental constraints (Elith et al. 2006, Phillips et al. 2006). This method is particularly effective when only presence data are available, as it can generate robust predictions from incomplete information. Its main advantage in terms of discrimination capability of the models is the possibility to calibrate and evaluate performances through a spatial jackknifing procedure (ESRI 2023). Briefly, the study area was divided into n random groups ($n = 5$, in this case), based on the Voronoi tessellation procedure (Voronoï 1908, Watson 1981, ESRI 2023) applied to occurrence localities; $n - 1$ groups are used for calibration, while the remaining one is iteratively used for validation. This procedure enables the modeling process to manage different datasets, even the ones with few occurrence localities (ESRI 2023), as in our case. Also, the linear, product, and quadratic expansions were selected; all other parameters were left to default.

Each ENM performance was evaluated by assessing the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) (Phillips et al. 2006), automatically resulting from the ArcGIS tool, the True Skill Statistics (TSS) (Allouche et al. 2006) and the Continuous Boyce Index (CBI), particularly useful for presence-only models (Hirzel et al. 2006, Leroy et al. 2018), calculated through the "ecospat.boyce" function in the "ecospat" R package (Di Cola et al. 2017).

We discretized the modeling outcomes based on their four quantiles intervals (Li et al. 2015, Iannella et al. 2019) to compare the most suitable areas across the time frames considered and for each species. This approach is consistent with common practices in species distribution modeling (Cianfarani et al. 2011, Van Gils et al. 2014). We used the Maxent modeling approach with the "cloglog" output, which provides an estimate of the probability of species presence (Phillips et al. 2017). The cloglog transform, as a continuous index of habitat suitability, is particularly effective in estimating presence probability and ensuring good discrimination across the full range of values (0–1) (Renner et al. 2015). This method is scale-independent and produces reliable predictions across different species and spatial scales. Therefore, areas with higher suitability are emphasized, aligning with our interpretation that such areas are likely to be of greater importance for species presence (Fithian et al. 2015). Then, possible correlation (Pearson's r) among the ENMs obtained (as raster files) was calculated through the "Band Collection Statistics" tool in ArcGIS Pro 3.2.2. Benjamini–Hochberg P-value correction was calculated through the "testcor" R package. Raster correlation can be employed in comparing species distribution models to quantitatively assess the degree of similarity between the predicted spatial distributions of species across different models, even when depicting different spaces and times (e.g., Chefaui and Serrão 2017). This technique enables us to reveal how these species may respond to environmental variables, highlighting potential ecological interactions or shared habitat preferences.

Correlations between the suitability distributions of insects and host plants were calculated using the R package TestCor (Gannaz 2020). Comparing the suitability of each *Longitarsus* species with that of plants not known as its host can provide further confirmation that the insect and the plant do not show significant correlations in their distributions. This comparative analysis helps to validate the specificity of host–plant relationships by demonstrating a lack of significant overlap in suitable habitats for non-host plants.

Extension of the suitability areas for the three species of *Longitarsus* analyzed was calculated with ArcGis Pro 3.2.2. both at 51–75% and 76–100% predicted probability of presence, and compared with that of their host plants both in the MIS19 and CURRENT models. This allowed to evaluate whether extension varied accordingly between insects and their respective host plants, and highlighted possible significant deviations between suitability areas and actual occurrences in the current scenario.

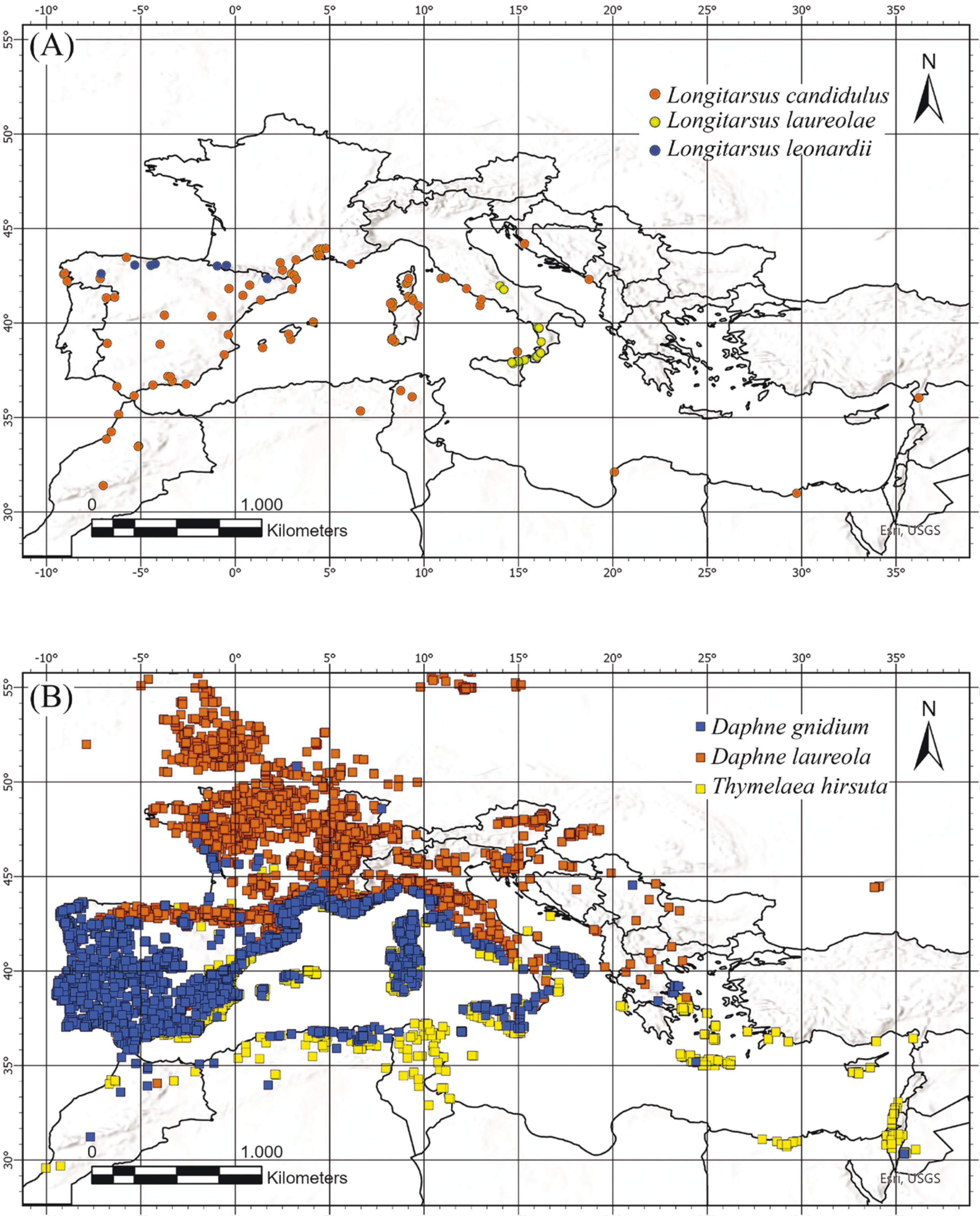

Fig. 2. Occurrence localities. A) *Longitarsus candidulus* species group. B) Host plants of the *Longitarsus candidulus* species group.

Results

The obtained distribution of the occurrence localities for the three *Longitarsus* species is reported in Fig. 2A, while Fig. 2B shows the distribution of the occurrence localities for the three host plants. *L. candidulus* distribution was much broader compared to *L. laureolae* and *L. leonardii*. Indeed, no species occurrence dataset reported spatial autocorrelation after the thinning process (I = – 0.0001719, expected I = –0.001923, Z = 0.37, and P = 0.71

for *T. hirsuta* [number of thinned occurrences = 589], $I = -0.000814$, expected $I = -0.000624$, $Z = 0.06$, and $P = 0.95$ for *D. gnidum* [number of thinned occurrences = 1,695], $I = -0.000149$, expected $I = -0.000084$, $Z = 0.09$, and $P = 0.74$ for *D. laureola* [number of thinned occurrences = 1,885], $I = -0.003344$, expected $I = -0.000006$, $Z = 0.08$, and $P = 0.54$ for *L. laureolae*, $I = 0.000147$, expected $I = -0.000006$, $Z = 0.39$, and $P = 0.70$ for *L. leonardi*, and $I = -0.022203$, expected $I = -0.021277$, $Z = -0.10$, and $P = 0.92$ for *L. candidulus*). After the VIF and Pearson's correlation analyses, we selected a set of five uncorrelated bioclimatic variables for the CURRENT (BIO8, BIO9, BIO14, BIO15, BIO19), which were used to calibrate the models and then to project to the past climatic Pleistocene conditions.

CURRENT and MIS19 Habitat Suitability for Insects and Host Plants

For the three *Longitarsus* species examined, the suitability models scored high AUC ($AUC_{leonardii} = 0.977$; $AUC_{laureolae} = 0.972$; $AUC_{candidulus} = 0.895$), TSS ($TSS_{l33eonardii} = 0.789$; $TSS_{laureolae} = 0.871$; $TSS_{candidulus} = 0.725$), and CBI values ($B_{leonardii} = 0.857$; $B_{laureolae} = 0.916$; $B_{candidulus} = 0.829$). Figures 3 and 4 report the patterns of predicted habitat suitability, also referred to as the probability of presence, obtained, respectively, for the CURRENT and MIS19. We identified four classes of probability: very low (0–25%), low (26–50%), medium (51–75%), and high (76–100%). The medium and high suitability areas for *L. candidulus* in the CURRENT closely matched the known distribution range of the species, in the western Mediterranean region (Fig. 3A); in the eastern Mediterranean some highly suitable areas also occurred, mainly in Greece and in northeastern Turkey (Fig. 3A). Considering the models obtained for the two host plants (*D. gnidium* and *T. hirsuta*) (Fig. 3B), a highly significant overlap in the distribution of suitability areas with those of *L. candidulus* were reported ($r = 0.823$, $P < 0.001$) (Table 1, Fig. 3F). The CURRENT model for *L. laureolae* (Fig. 3C) showed high suitability in the areas where the species is actually present, with other possible limited suitable areas scattered throughout the northern and central Apennines. The high suitability area for *L. leonardii* in the CURRENT model (Fig. 3E)

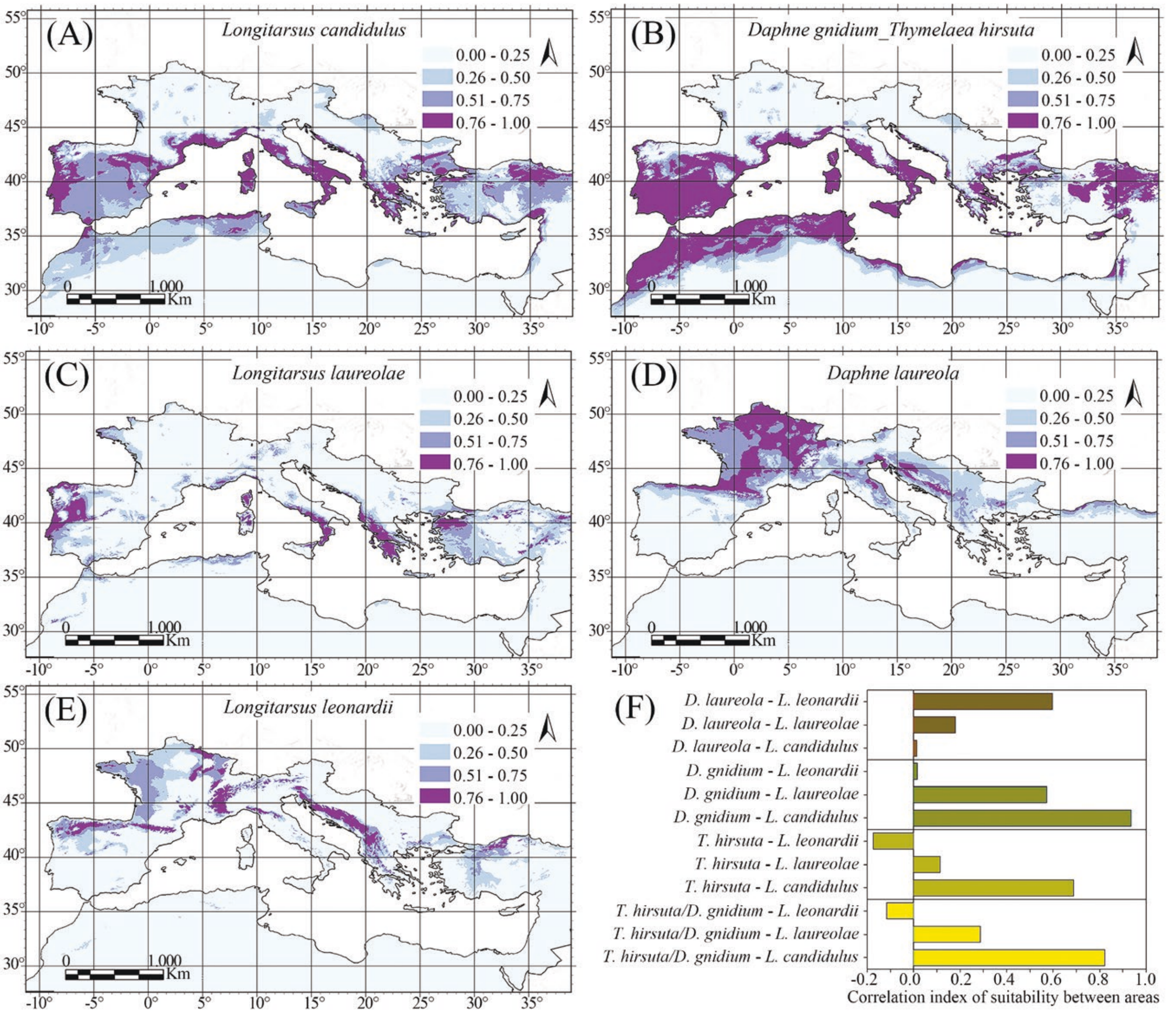

Fig. 3. Distribution models in the CURRENT climatic conditions. A) *Longitarsus candidulus*. B) *Daphne gnidium* and *Thymelaea hirsuta*. C) *Longitarsus laureolae*. D) *Daphne laureola*. E) *Longitarsus leonardii*. F) Histogram of the insect-insect and insect-host plant correlations. (A)–(E): different colors refer to different probabilities of presence, as in the legends.

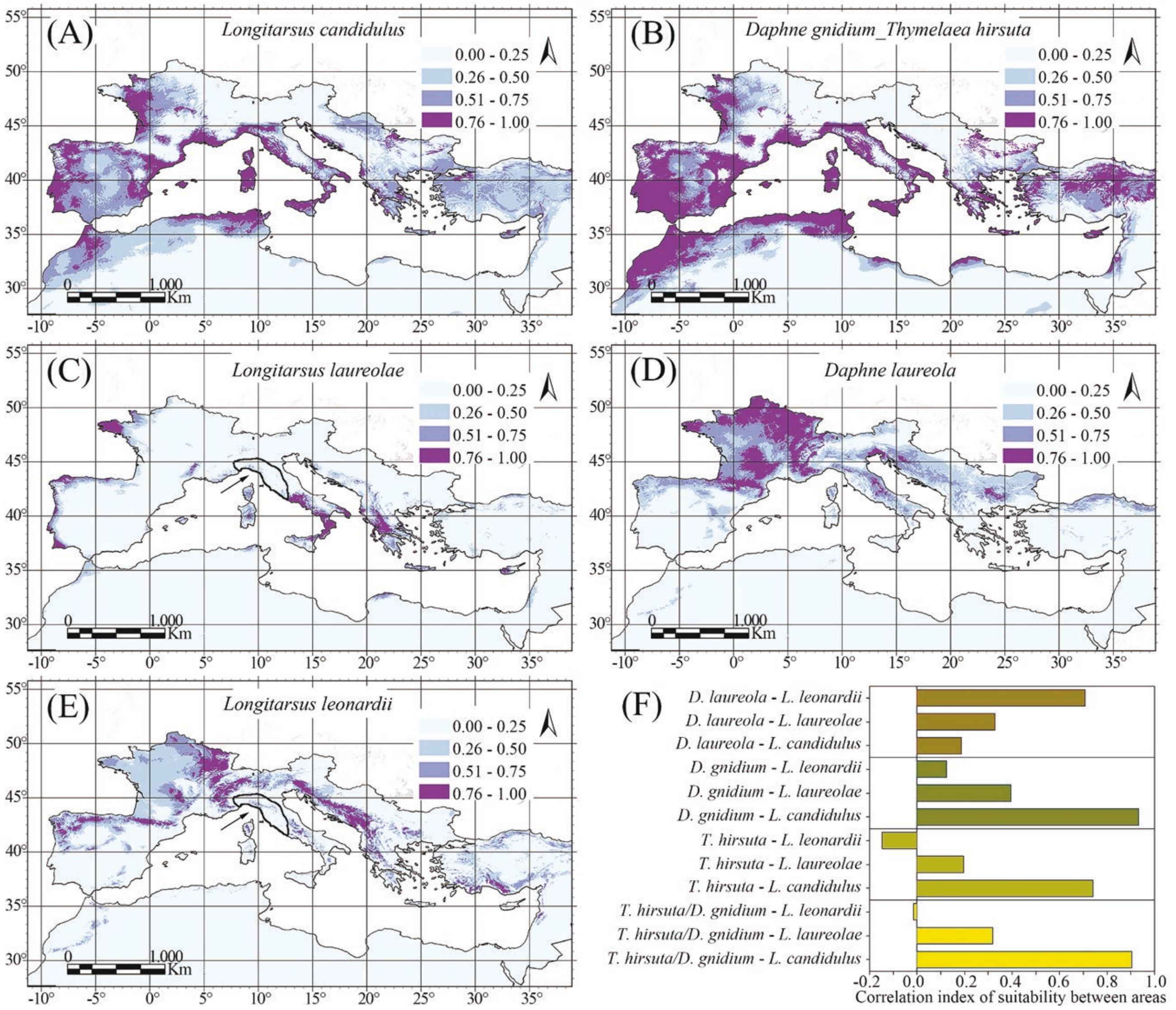

Fig. 4. Distribution models in the MIS19 climatic conditions. A) *Longitarsus candidulus*. B) *Daphne gnidium* and *Thymelaea hirsuta*. C) *Longitarsus laureolae*. D) *Daphne laureola*. E) *Longitarsus leonardii*. F) Histogram of the insect–insect and insect–host plant correlations. (A)–(E): different colors refer to different probabilities of presence, as in the legends. (C, E): the black line pointed by the arrow delimits the area at low suitability hypothesized for *L. laureolae* and *L. leonardii*.

significantly exceeded the current known range of the species, since it also included some mountain systems of southern Europe, such as the Western Alps and the Balkan area. From the MIS19 to the CURRENT, *L. candidulus* showed a clear shift of its suitability areas in the S and E direction, with a decrease of −7.3% of the suitable areas with probability of presence higher than 50% (Figs. 3A and 4A). Its two host plants, *D. gnidium* and *T. hirsuta* (model discrimination in terms of $AUC_{gnidium} = 0.942$ and $AUC_{hirsuta} = 0.941$), showed a very similar trend (Figs. 3B and 4B). *L. laureolae* too (Figs. 3C and 4C) showed a significant shift of the suitability areas to S and E directions, but with an increase of +84.3% of the suitability areas with a probability of presence higher than 50%. *L. leonardii* (Figs. 3E and 4E) had a similar distribution of the highest suitability areas in both MIS19 and CURRENT, with a decrease of −6.4% of the suitable areas with probability of presence higher than 50%.

Correlations between Suitability Distributions of Insects and Host Plants

The models returned a wide overlap of *L. candidulus* in the CURRENT, both with *D. gnidium* ($r = 0.936$, $P < 0.001$), and with *T. hirsuta* ($r = 0.688$, $P = 0.019$); correlation with *D. gnidium* slightly increased compared to that of the MIS19 ($r = 0.934$, $P = 0.029$); correlation with *T. hirsuta* slightly lowered than in the MIS19 ($r = 0.741$, $P < 0.001$) (Table 1, Figs. 3F and 4F). There was a significant (positive) correlation between the suitability distribution of *L. leonardii* and that of *D. laureola* (model discrimination $AUC_{laureola} = 0.943$), especially in the MIS19 model ($r = 0.706$, $P < 0.001$) and, to a lesser extent, the CURRENT ($r = 0.596$, $P < 0.001$). On the other hand, the suitability of *L. leonardii* was totally independent, both from that of *D. gnidium* ($r = 0.016$, $P < 0.001$ in the CURRENT; $r = -0.123$, $P < 0.001$ in the MIS19) and from that of *T. hirsuta* ($r = -0.173$, $P = 0.020$ in the CURRENT; $r = -0.148$, $P < 0.001$ in the MIS19) (Table 1, Figs. 3F and 4F). *L. laureolae* had a relatively low correlation with respect to all three plants: *D. laureola* ($r = 0.180$, $P < 0.001$ in the CURRENT; $r = 0.327$, $P < 0.001$ in the MIS19), *D. gnidium* ($r = 0.573$, $P < 0.001$ in the CURRENT; $r = 0.395$, $P = 0.004$ in the MIS19), and *T. hirsuta* ($r = 0.115$, $P = 0.019$ in the CURRENT; $r = 0.196$, $P < 0.001$ in the MIS19) (Table 1, Figs. 3F and 4F). Since *D. gnidium* and *T. hirsuta* are both host plants of *L. candidulus*, we also calculated the correlation between the combined distribution

Table 1. Pearson's *r* correlation indices, *t*-values, *P*-values, and Benjamini–Hochberg correction (B–H corr), between suitability layers in different combinations of the *Longitarsus candidulus* species group and their host plants in CURRENT and MIS19 ecological niche models.

Suitability correlations	Pearson's (*r*)	*t*	*P*	B–H correction
L_candidulus (CURRENT-MIS19)	0.765	695.51	<0.001	<0.001
L_laureolae (CURRENT-MIS19)	0.593	411.57	<0.001	<0.001
L_leonardii (CURRENT-MIS19)	0.754	620.27	<0.001	<0.001
D_gnidium–L_candidulus (CURRENT)	0.846	77.33	<0.001	<0.001
D_gnidium–L_laureolae (CURRENT)	0.489	24.14	<0.001	<0.001
D_gnidium–L_leonardii (CURRENT)	0.013	16.40	<0.001	<0.001
D_gnidium–L_candidulus (MIS19)	0.934	2.18	0.029	0.030
D_gnidium–L_laureolae (MIS19)	0.395	2.90	0.004	0.005
D_gnidium–L_leonardii (MIS19)	0.123	6.15	<0.001	<0.001
D_laureola–L_candidulus (CURRENT)	0.014	81.02	<0.001	<0.001
D_laureola–L_laureolae (CURRENT)	0.181	11.92	<0.001	<0.001
D_laureola–L_leonardii (CURRENT)	0.596	55.32	<0.001	<0.001
D_laureola–L_candidulus (MIS19)	0.186	2.44	0.015	<0.001
D_laureola–L_laureolae (MIS19)	0.327	59.68	<0.001	<0.001
D_laureola–L_leonardii (MIS19)	0.706	70.99	<0.001	<0.001
T_hirsuta–L_candidulus (CURRENT)	0.659	2.33	0.020	0.022
T_hirsuta–L_laureolae (CURRENT)	0.082	1.56	0.119	0.119
T_hirsuta–L_leonardii (CURRENT)	−0.192	2.32	0.020	0.022
T_hirsuta–L_candidulus (MIS19)	0.741	19.41	<0.001	<0.001
T_hirsuta–L_laureolae (MIS19)	0.196	49.02	<0.001	<0.001
T_hirsuta–L_leonardii (MIS19)	−0.148	47.59	<0.001	<0.001
D_gnidium/T_hirsuta–L_candidulus (CURRENT)	0.823	996.14	<0.001	0.005
D_gnidium/T_hirsuta–L_laureolae (CURRENT)	0.287	208.87	<0.001	0.018
D_gnidium/T_hirsuta–L_leonardii (CURRENT)	−0.117	81.94	<0.001	0.022
D_gnidium/T_hirsuta–L_candidulus (MIS19)	0.905	233.99	<0.001	0.022
D_gnidium/T_hirsuta–L_laureolae (MIS19)	0.319	1479.43	<0.001	0.030
D_gnidium/T_hirsuta–L_leonardii (MIS19)	−0.015	10.28	<0.001	<0.001

of *D. gnidium/T. hirsuta* and those of the three target species of *Longitarsus* (Table 1, Figs. 3F and 4F). The results highlighted, also in this case: (i) the high correlation with *L. candidulus* ($r = 0.823$, $P < 0.001$ in the CURRENT; $r = 0.905$, $P < 0.001$ in the MIS19); (ii) the complete independence from *L. leonardii* ($r = -0.117$, $P < 0.001$ in the CURRENT; $r = -0.015$, $P < 0.001$ in the MIS19); (iii) the non-significant positive correlation with *L. laureolae* ($r = 0.287$, $P < 0.001$ in the CURRENT; $r = 0.319$, $P < 0.001$ in the MIS19).

Bioclimatic Variables Relevance

As regards the CURRENT (Fig. 5A–D), BIO8 (mean temperature of wettest quarter) was particularly significant as responsible for the different species ecological response, with higher values for *L. candidulus* (mainly > 10 °C; variable contribution (VC) = 12.5%) compared to *L. leonardii* (about between −5 and 5 °C; VC = 32.6%) and *L. laureolae* (about between 5 and 17 °C; VC = 4.7%) (Fig. 5A). BIO8 was also the most significant variable for the host plants (Fig. 5B and D): 8–15 °C for *D. laureola*; >8 °C (VC = 27.8%) and >11 °C for *D. gnidium* (VC = 18.9%), and *T. hirsuta* (VC = 23.2%), respectively. As regards the models projected at the MIS19 (Fig. 6), the precipitation-related variables BIO14 and BIO19 considerably contributed to the separation between the suitability areas of *L. leonardii* and those of *L. candidulus* (BIO14: 0–40 mm for *L. leonardii* [VC = 53.6%], <10 mm for *L. candidulus* [VC = 8.6%]; BIO19: >400 mm for *L. leonardii* [VC = 12.8%], 200–500 mm for *L. candidulus* [VC = 57.1%]) (Fig. 6C and D). BIO14 also contributed to the differences in suitability areas between *L. laureolae* and *L. candidulus* (>20 mm for *L. laureolae* [VC = 36.9%] and <10 mm for *L. candidulus* [VC = 8.6]) (Fig. 6C). The temperature-related variables BIO8 and BIO9 (Fig. 6A and B) contributed to the separation of *L. leonardii* (BIO8 < 5 °C; BIO9 < 12 °C) from *L. candidulus* and, to a lesser extent, from *L. laureolae*; their values for *L. laureolae* were instead partially overlapping with *L. candidulus* even though, on average, lower (Fig. 6A and B).

Extension of the Suitability Areas

From the MIS19 to the CURRENT a slight decrease in the suitability areas was predicted for *L. candidulus* (−9.5% for probability of presence 51–75%; −6.7% for probability of presence 76–100%) (Figs. 3A, 4A, and 7). About its host plants, *D. gnidium* and *T. hirsuta*, they showed a significant decrease in the areas with medium probability (−64.9%) and a slight increase in the areas with high probability (+6.7%) (Figs. 3B, 4B, and 6). A slight decrease in the suitability areas was also predicted for *L. leonardii* (−11.9% for probability of presence 51–75%; −3.7% for probability of presence 76–100%) (Figs. 3E, 4E, and 7), while *L. laureolae* showed a considerable increase in the extension in both the medium (+50.7%) and high suitability areas (+70.3%) (Figs. 3C, 4C, and 7). Their shared host plant, *D. laureola*, was predicted to have a small increase in both medium (+3.6%) and high (+3.1%) suitability intervals considered (Figs. 3D, 4D, and 7).

Discussion

The results supported the initial hypothesis of Berrilli et al. (2024) that the differentiation of the *laureolae/leonardii* lineage from *candidulus* was likely due to the consequences of a marked climatic change between Late Pliocene and Early Pleistocene. In fact, the models obtained for the MIS19 clearly confirmed the conditions of thermophilic species for *L. candidulus* and mesophilic species for *L. laureolae* and *L. leonardii*. High values of the temperature-related variable BIO8 (mean temperature of wettest quarter) clearly

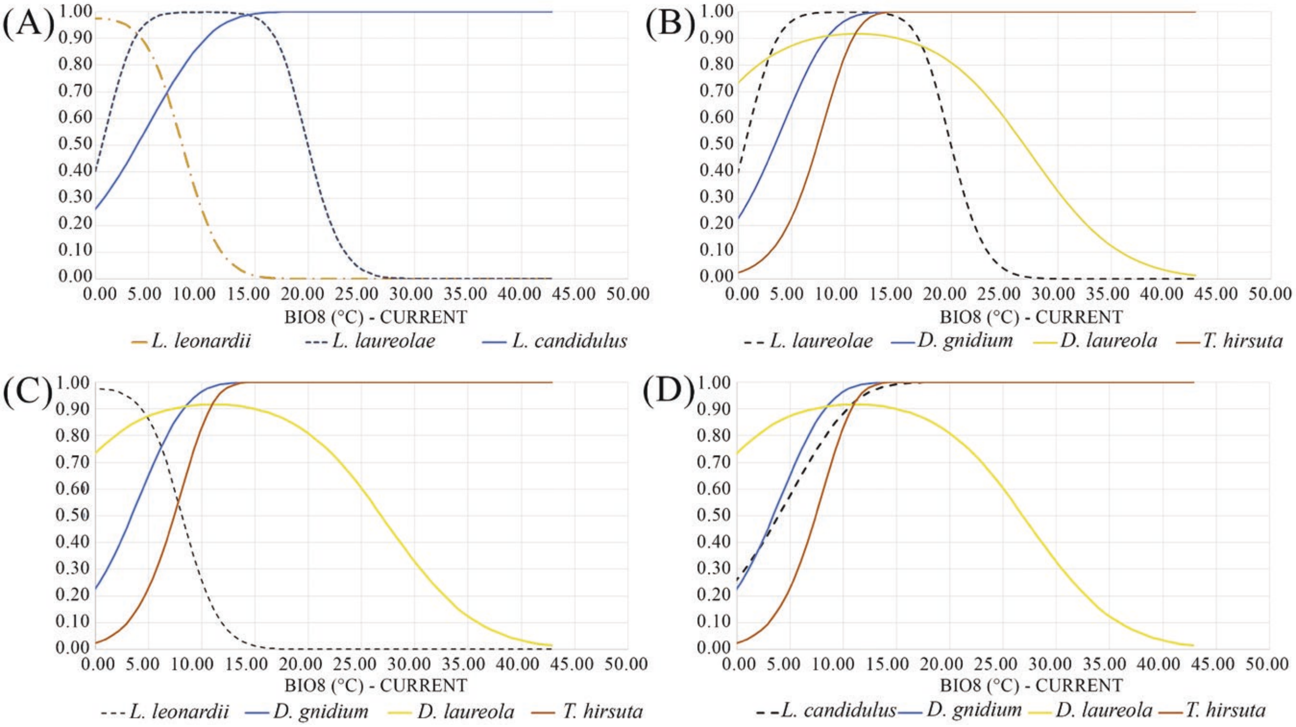

Fig. 5. Values of the variable BIO8 (mean temperature of wettest quarter) of the *Longitarsus candidulus* species group and their host plants in the CURRENT model. A) Comparison between flea beetle species. B–D) Comparison between each flea beetle species and host plants.

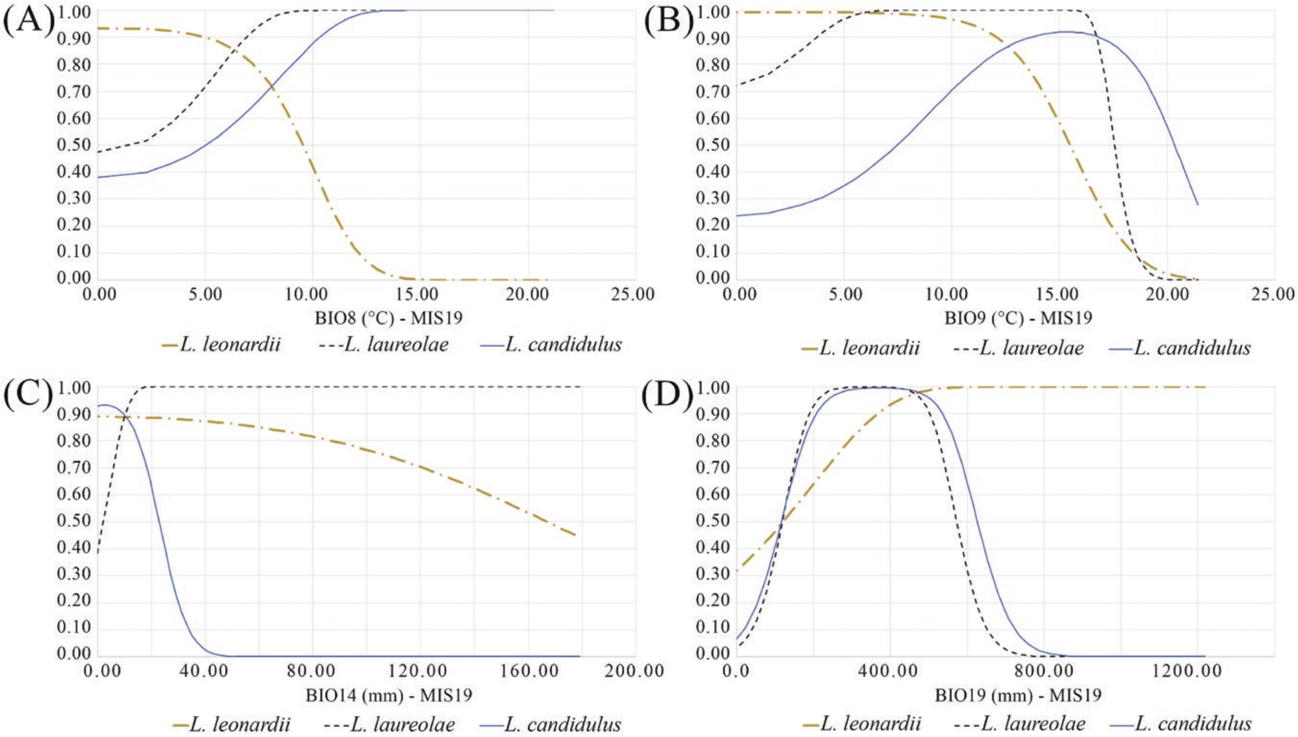

Fig. 6. Values of the variables that most contributed to the separation between the suitability areas of *Longitarsus candidulus*, *L. laureolae*, and *L. leonardii* in the MIS19 model. A) BIO8 (mean temperature of wettest quarter). B) BIO9 (mean temperature of driest quarter). C) BIO14 (precipitation of driest period). D) BIO19 (precipitation of coldest quarter).

distinguished the current areas of high suitability for *L. candidulus*, while lower values characterized suitability areas for *L. laureolae* and *L. leonardii* (Fig. 5A). In addition, the models linked the higher values of predicted probability of presence of *L. laureolae* and *L. leonardii* in the Middle Pleistocene to lower values, on average, of the temperature-related variables BIO8 and BIO9 (mean temperature

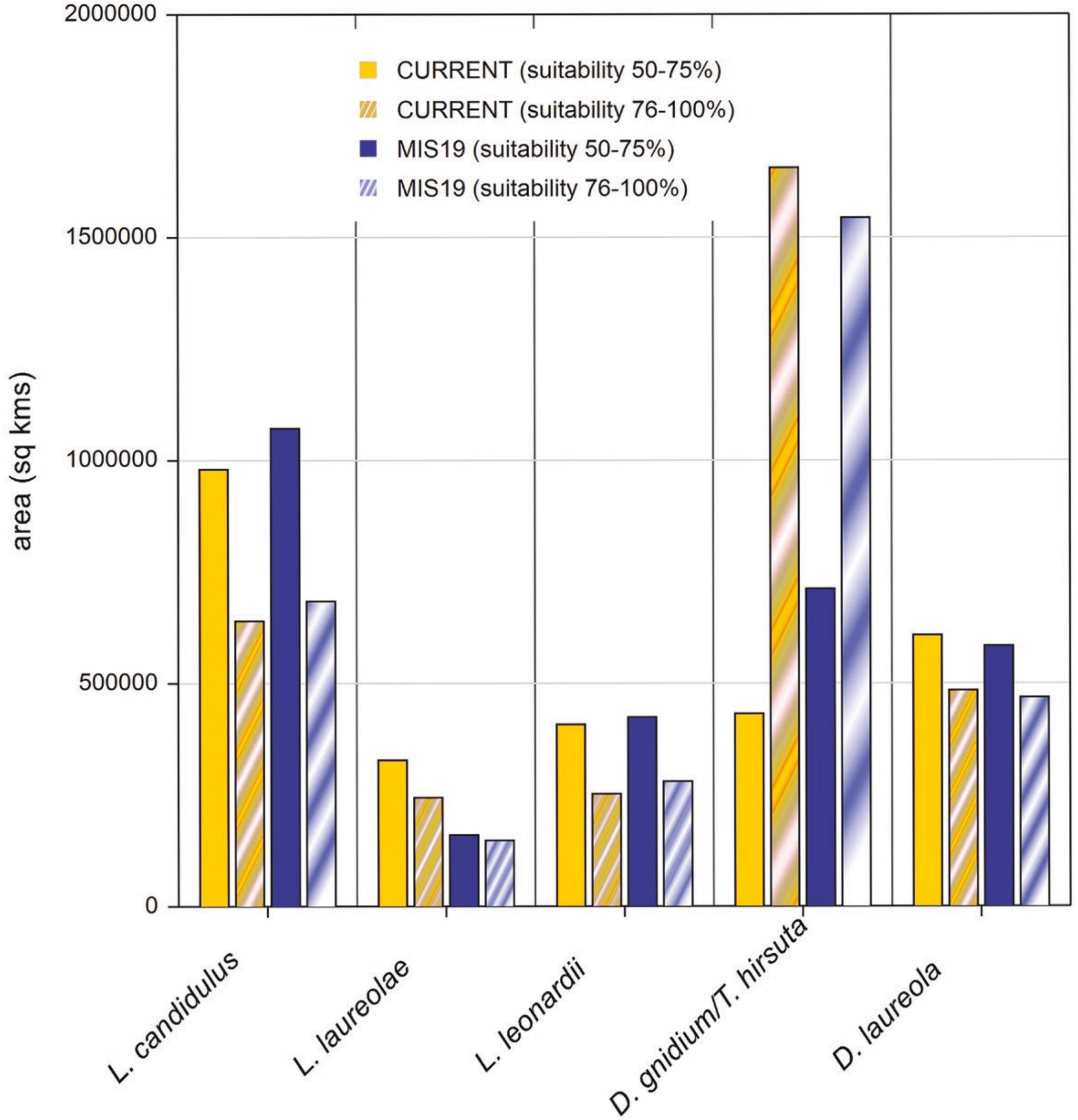

Fig. 7. Cumulative areas in the CURRENT and MIS19 models, at 51–75% and 76–100% of suitability, for the *Longitarsus candidulus* species group and their host plants.

of driest quarter), compared to *L. candidulus* (Fig. 6A and B), and higher levels of precipitation-related variables BIO19 (precipitation of coldest quarter), and especially BIO14 (precipitation of driest month) (Fig. 6C and D). The initial split of the *laureolae/leonardii* clade from *L. candidulus* has likely been boosted by the shift of the trophic niche toward a different, typically mesophilic host plant as *D. laureola*, growing in more stable climates with more abundant rainfall (Fig. 5B–D).

Intraspecific niche competition phenomena in some populations of the common ancestor might have triggered the differentiation process of *L. laureolae* and *L. leonardii* leading to their segregation in different areas. The models returned a large area of low environmental suitability for both species since the MIS19, which extended from the south-western Alps to the central-northern Apennines (Fig. 4C and E). This area could have acted as a barrier for the two species, favoring their segregation and determining their current distributions along the central-southern Apennines and Cantabrian-Pyrenean mountain system, respectively. These results again fit the scenario proposed by Berrilli et al. (2024), who hypothesized an allopatric divergence during the late Middle Pleistocene.

The high correlation between the distribution of *L. candidulus* and the distribution of its two host plants, *D. gnidium* and *T. hirsuta*, both in the MIS19 and CURRENT (Figs. 3F and 4F), suggested that the close insect–plants association could have driven the distributional dynamics of this flea beetle. Interestingly, the genera *Thymelaea* and *Daphne* are closely related and belong to a strongly supported clade within the subfamily Thymelaoideae (Van der Bank et al. 2002).

On the other hand, the distribution of *D. laureola* might have had a minor role in driving the distributional dynamics of the couple *L. laureolae*–*L. leonardii*, as indicated by the relatively low correlation both in the CURRENT and MIS19 (Table 1, Figs. 3F and 4F). Regarding the association *L. laureolae*–*D. laureola*, the environmental suitability maps, both in the MIS19 and especially in the CURRENT, indicate that the southern Apennines, where most of the occurrence localities of the flea beetle are known, represents a peripheral area of low suitability for its host plant (Figs. 3D and 4D). This finding could explain the low correlations in the predicted suitability distributions observed between *L. laureolae* and *D. laureola* (Table 1, Figs. 3F and 4F). In fact, the flea beetle appears to be associated with *D. laureola* mainly in conditions poorly favorable to the optimal growth of the plant, which in the southern Apennines is mostly occurring in hard habitats such as the undergrowth of beech forests at medium and high altitudes (Raimondo 2004).

The models suggested that increased presence of *L. candidulus* may also occur in the eastern sector of the Mediterranean Basin, which includes undersampled areas, as evidenced by the few contributions to the knowledge of the flea beetle fauna of this region (Biondi, unpublished data).

Similarly, the high suitability area for *L. laureolae* and *L. leonardii* significantly exceeds the species current known range since it also includes some mountain systems in southern Europe. The main limitation of the performed analyses is the few occurrence points used for *L. laureolae* and, especially, for *L. leonardii*, both characterized by a very limited geographic distribution, even though all localities known to date were considered in the construction of the models. Nevertheless, we are confident that possible future records will not significantly change the boundaries of the current range and the ecological profile of these two species. Despite that, other factors, such as geographic and ecological barriers, interspecific competition, and unavailability of host plants, have most likely limited the expansion of the two species to other ecologically suitable areas. This pattern of mixed constraints affecting distribution is not unique; a similar combination of factors has also been observed in other Chrysomelidae, such as *Cryptocephalus barii* (Brunetti et al. 2019) and the genus *Timarcha* (Gómez-Zurita et al. 2000, Gómez-Zurita and Vogler 2003).

A reliable interpretation of the results of ecological modeling must be founded on a deep taxonomic knowledge of the taxa, a necessary condition to avoid misinterpretation in ecological and distributional data. Taxonomic knowledge is the basis for correct phylogenetic analyses, but conversely, it is also the result of phylogenetic analyses, especially for problematic taxa (see Salvi et al. 2020, Berrilli et al. 2023). The careful and precise geographical localization of the occurrence data used in the modeling is also essential. The case study presented here on the *L. candidulus* species group and their host plants, being built on the previously inferred phylogenetic history of these flea beetles, allowed us to reconstruct a plausible scenario of how climatic pressures may have determined the current biogeographic pattern of these species.

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Maurizio Biondi (Conceptualization [equal], Formal analysis [equal], Writing—original draft [equal], Writing—review & editing [equal]), Paola D'Alessandro (Data curation [equal], Funding acquisition [Lead], Writing—original draft [equal], Writing—review & editing [equal]), Daniele Salvi (Data curation [equal], Writing—original draft [equal], Writing—review & editing [equal]), Emanuele Berrilli (Data curation [equal], Writing—original draft [equal], Writing—review & editing [equal]), and Mattia Iannella (Formal analysis [equal], Writing—original draft [equal], Writing—review & editing [equal])

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