ORIGINAL RESEARCH

Hidden in plain sight: unveiling the distributions of green-winged grasshoppers (*Aiolopus* spp.) with citizen-science data

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Abstract

Understanding the geographical distribution of phenotypically highly similar species (i.e. cryptic species) represents a challenge to biogeographers, due to the obvious difficulties in identifying such taxa without specific expertise. Besides, citizen science is increasingly emerging as a key approach for supporting biodiversity data collection, but remains hard to apply in the case of cryptic species. Here we aim to test the combination of community records and photography-based quantitative methods, for assessing the distribution of cryptic taxa, by using two grasshopper species of the genus *Aiolopus* as models. To achieve these objectives, we first assess the reliability of photography-based diagnostic criteria to differentiate between *A. thalassinus* and *A. puissanti* without ambiguity from correctly identified records, and then apply such criteria to geographical regions of potential range overlap between the two species, in order to clarify their respective distributions. By applying a multivariate classification approach based on ratio measurements taken from photographs, we provide a quantitative tool to successfully identify the two species, and disclose that *A. puissanti* widely occurs outside of its currently known range, and outline potential research avenues on the biogeography of these poorly studied species. Our results also point at how some types of cryptic species may be effectively identified by adopting a quantitative photography-based approach, with applicability for clarifying species' distributions at wide scales by exploiting publicly available citizen-science records. Our study thus, besides shedding light onto the biogeography and distributions of *Aiolopus* grasshoppers across the Mediterranean, represents an effective and repeatable framework to disentangle the distributions of poorly studied cryptic species.

Introduction

Cryptic species are distinct biological entities that largely overlap in their external characters such as morphology and coloration, consequently posing a challenge to scientists, since their identification usually relies on the collection or measurement of very specific traits, or biological tissues for genetic sampling, that cannot be retrieved by non-trained operators (Struck et al., 2018). Ignoring cryptic species though hampers our understanding of biodiversity patterns, for example, by underestimating richness within a taxon or geographical area, and

undermines conservation of species that, going unnoticed, may be excluded from conservation actions and/or remain undescribed (Chenuil et al., 2019; Korshunova et al., 2019). Due to the obvious difficulties in recognizing cryptic species, particularly in the case of speciose taxonomic groups, their estimated distributions are often likely to provide an inaccurate picture of their actual geographical ranges, so that effective alternative identification methods are required. Citizen – or community – science is increasingly emerging as a key approach for biodiversity data collection, fostering the study of wildlife worldwide, and namely addressing the urge of clarifying and

understanding species' distributions for ecological studies and conservation (Campanaro et al., 2017). The reliability of citizen-science derived data is often questioned, yet numerous studies indicate that citizen science can provide high-quality data, comparable to those collected by trained scientists (Aceves-Bueno et al., 2017), even though their applicability to the study of cryptic species remains limited (Gorleri et al., 2022).

Insects, thanks to their approachability by people and frequent visual identifiability, are recurrent targets of citizen-science campaigns, particularly in the case of attractive taxa appreciated by a wide public, for example, butterflies and bees (Koffler et al., 2021; Wang Wei et al., 2016), while other less-charismatic groups, such as Orthoptera (crickets, grasshoppers and katydids), have so far received much less attention, despite being also threatened by global changes (Hochkirch et al., 2016). Within European orthopterans, species from the genus *Aiolopus* Fieber, 1853 have received rather low interest from entomologists compared to other taxa, despite the occurrence of four species from this genus across Mediterranean Europe, namely *A. strepens* (Latreille, 1804), *A. simulatrix* (Walker, 1870), *A. thalassinus* (Fabricius, 1781), and *A. puissanti* Defaut, 2005. Among these, *A. strepens* is the best known species, and poses few problems in its identification, while *A. simulatrix* is mainly found in the African continent, being only marginally present in Europe (on the island of Sardinia; Ingrisch, 1983). *Aiolopus thalassinus* is also supposed to be largely spread across the Palearctic, African and Australasian regions (Hollis, 1968). The latest described taxon within the genus, *A. puissanti*, has only been reported from the Western Mediterranean basin (Morocco, Iberian peninsula, France) and, more recently, from Qatar (Defaut, 2021), yet further work is still needed to clarify the taxonomic status of these Eastern populations (e.g., relative to *A. oxianus* Uvarov, 1926). Several factors though converge in suggesting that the range of *A. puissanti* has been largely underestimated in the Eastern part of the Mediterranean basin, such as (i) the close morphological resemblance with *A. thalassinus*, paired to a very high intraspecific variation in color traits for both species, which make it hard to distinguish these two taxa even by experts, (ii) the need of exact measurements as key traits for unmistakably identify *A. puissanti*, and (iii) the limited span of the relatively recent description of this species (Defaut, 2005), which might have hindered the search for this species across its potential range.

Here we aim to test the combination of citizen-science records and photography-based quantitative methods for assessing the distribution of phenotypically highly similar taxa, by using green-winged grasshoppers as models, specifically testing the hypothesis that *A. puissanti* currently known distribution represents an underestimation. To achieve these objectives, we first (i) assess the reliability of photography-based diagnostic criteria to differentiate between *A. thalassinus* and *A. puissanti* without ambiguity within their known range of co-occurrence, and then (ii) apply such criteria to other geographical regions, in order to clarify the respective species' ranges.

Materials and methods

Assessing reliability of photographic identification

We measured traits from photos posted and identified to research grade on iNaturalist.org platform, retrieved by searching for both species' names. To build a valid reference database of morphological traits (ratio values, see further), we first limited our search to the spatial extent where the distinction between *A. puissanti* and *A. thalassinus* has already been conducted for several years (France, Spain, and Portugal; pers. obs.); moreover, we only used records with a 'Research Grade' quality rate on iNaturalist, that is, for which consensus among experts was reached on the given identifications, that were also confirmed by some of the authors (MP and BN), and thus considered as reliable. Each observation was considered as an independent record. If any doubt about the possible multiplicity of specimens for the same observation or the identification were sensed, or the photo quality was too poor (e.g., individual not fully pictured, not a good profile, blurred photo), the photo was discarded from further analyses. Only photos of adults for which the sex of the specimen could be determined were retained (based on the shape of the tip of the abdomen). Since reference scales are virtually absent on citizen-science derived photos, we focused on length ratios as potential discriminant criteria. Thus, only lengths measured on the same photos (expressed as ratios between numbers of pixels) were used for a given ratio. According to published keys (Defaut, 2012, 2021), the following ratios, besides direct measurements (Defaut & Jaulin, 2008) differ between *A. thalassinus* and *A. puissanti* and may thus be used as discriminant traits: (1) Eye length/Subocular groove length, (2) Eye length/Interocular distance, (3) Pronotum length (Pr)/Tegmina length (T), (4) Tegmina length/Femur length (F), (5) Tegmina extension (Text; i.e., the portion of tegmina extending beyond the distal end of femur)/Tegmina length, and (6) Tegmina extension/Femur length. Nonetheless, traits 1–2 are hard to measure from photos due to the difficulties in locating reliable body landmarks and/or to the need of more than one photo of the same individual (i.e., from different angles), so we only focused on traits 3–6, which only need a good profile picture and, in the case of trait #3, should also be robust enough to the "parallax effect" due to variability in the angle of photographs, since both lengths are oriented along the same direction (Figure S1). The photos were downloaded from iNaturalist and traits were measured with ImageJ using standard body landmarks for orthopterans (Fig. 1), for calculating the above mentioned ratio values. We also preliminarily assessed the reliability of the selected ratios by evaluating errors derived from measurements taken by three operators upon the same sub-sample of pictures ($n = 14$); since median error on ratio values was on average <3% (Figure S2), and in order to reduce error due to inter-operator variability, all final measurements were taken by the same operator. For assessing the efficacy of the selected values in discriminating *A. thalassinus*

from *A. puissanti*, we ran a quadratic discriminant function analysis (qDFA) with cross validation on the calculated ratios, using all retrieved records. We built several qDFA models by testing all combinations among the four ratio values, in order to identify the best performing model(s). The discriminant functions were run by following a re-substitution approach that is, dividing records into two random sub-samples for training and validating the models (70 and 30% of records, respectively). Correct and erroneous classification rates were then calculated by the confusion matrix. Models were run and evaluated by using the *MASS* package (Ripley et al., 2013) for R 4.2.1 (R Core Team, 2013).

Clarifying species' ranges

Values of correct classification rates >0.7 are indicative of a good model for classification for DFA (Eiras et al., 2021). As such, we selected DF models reaching high efficiency (>0.7) to classify iNaturalist photographic records from outside of the known range of co-occurrence of our target species, selecting geographical areas where records of *A. thalassinus* are present and *A. puissanti* is likely to occur. Namely, we screened for suitability, and subsequently tested, records from Italy, Croatia, Albania, Greece, Crete, Turkey, Cyprus and Israel. Data selection and measurements from photographic records followed the very same procedure specified for method calibration. Records reaching excellent assignment probabilities (>90%) were considered as reliable, and identified as the species assigned by the qDFA. For two sites from Italy, we also confirmed species identification by directly measuring collected individuals (with a digital caliper, to the nearest 0.01 mm) and following the available keys (Defaut, 2021). As a final step, we re-evaluated and mapped both species' records as classified by the qDFA, and estimated their respective geographic ranges across Mediterranean Europe.
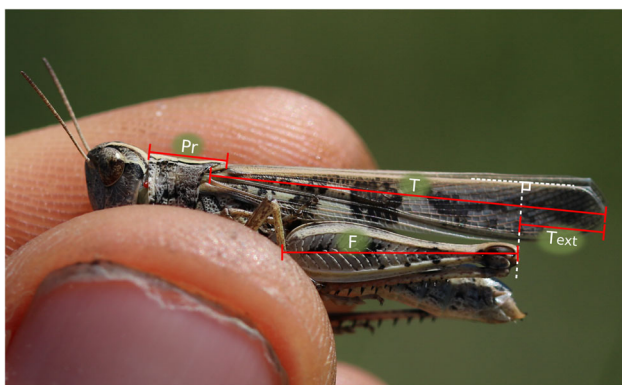
Figure 1 Example of body measurements taken from photos (F = femur length, T = tegmina length, Pr = pronotum length, Text = tegmina extension) for the calculation of ratios used for species discrimination, here on a female *Aiolopus thalassinus* from southern France. Photo by M. Pélissié.

Results

Assessing reliability of photographic identification

We obtained a total of 100 photographic records of *Aiolopus* grasshoppers from the known co-occurrence range of *A. thalassinus* (*n* = 37) and *A. puissanti* (*n* = 63) fulfilling our inclusion criteria. The four ratio values considered varied between the two species with different degrees (Fig. 2a–h), with the most discriminating trait, in terms of factor loadings, being the ratio between tegmina extension (Text) and total tegmina length (T). The qDFA obtained a satisfactory proportion of correct classification rates, with the best result being that including all four of our selected ratio values (86.5% of correct classifications); most influencing predictors for correct classification were the two ratios including the values of the tegmina extension (Text/F and Text/T, respectively showing loading correlation values of 19.34 and 6.17). Namely, only eight out of 63 *A. puissanti* and six out of 37 *A. thalassinus* were misclassified by the best model (see Fig. 2i).

Clarifying species' ranges

We retrieved a total of 69 independent records of *Aiolopus* spp. from the iNaturalist platform that fulfilled our inclusion criteria, covering most part of the genus' range in the Mediterranean basin, and namely coming from Italy (*n* = 32), Greece (*n* = 11), Croatia (*n* = 7), Turkey (*n* = 5), Albania (*n* = 3), Bulgaria (*n* = 3), Macedonia (*n* = 2), Austria, Montenegro, Slovenia, Cyprus and Israel (1 from each country). Of these records, only four fell within the overlap area between *A. thalassinus* and *A. puissanti*, within the multidimensional space defined by the qDFA (two records from Italy, two from Greece). Thus, they were excluded from further considerations and not assigned to either species. Of the remaining 65 records, 34 were confidently assigned to *A. thalassinus* (15 from Italy, six from Greece, three from Albania, two from Bulgaria, two from Croatia, two from Macedonia, one from Slovenia, one from Austria, and one from Turkey), and 31 to *A. puissanti* (15 from Italy, five from Croatia, three from Greece, four from Turkey, one from Montenegro, one from Bulgaria, one from Cyprus and one from Israel; Fig. 3). Besides, among 13 specimens collected in central Italy, seven were unequivocally confirmed as *A. puissanti* (two from Bolsena Lake, five from Rome), based on diagnostic body measurements (tegmina extension >5.3 mm in males, and >6.3 in females), while the remaining six individuals fell within the known size range of *A. thalassinus*.

Discussion

Unveiling the geographical distribution of cryptic species represents a challenge to biologists and biogeographers, particularly in the case of relatively poorly studied species (Chenuil et al., 2019), such as the orthopterans we focused on in this work. Our results point at how two closely resembling species
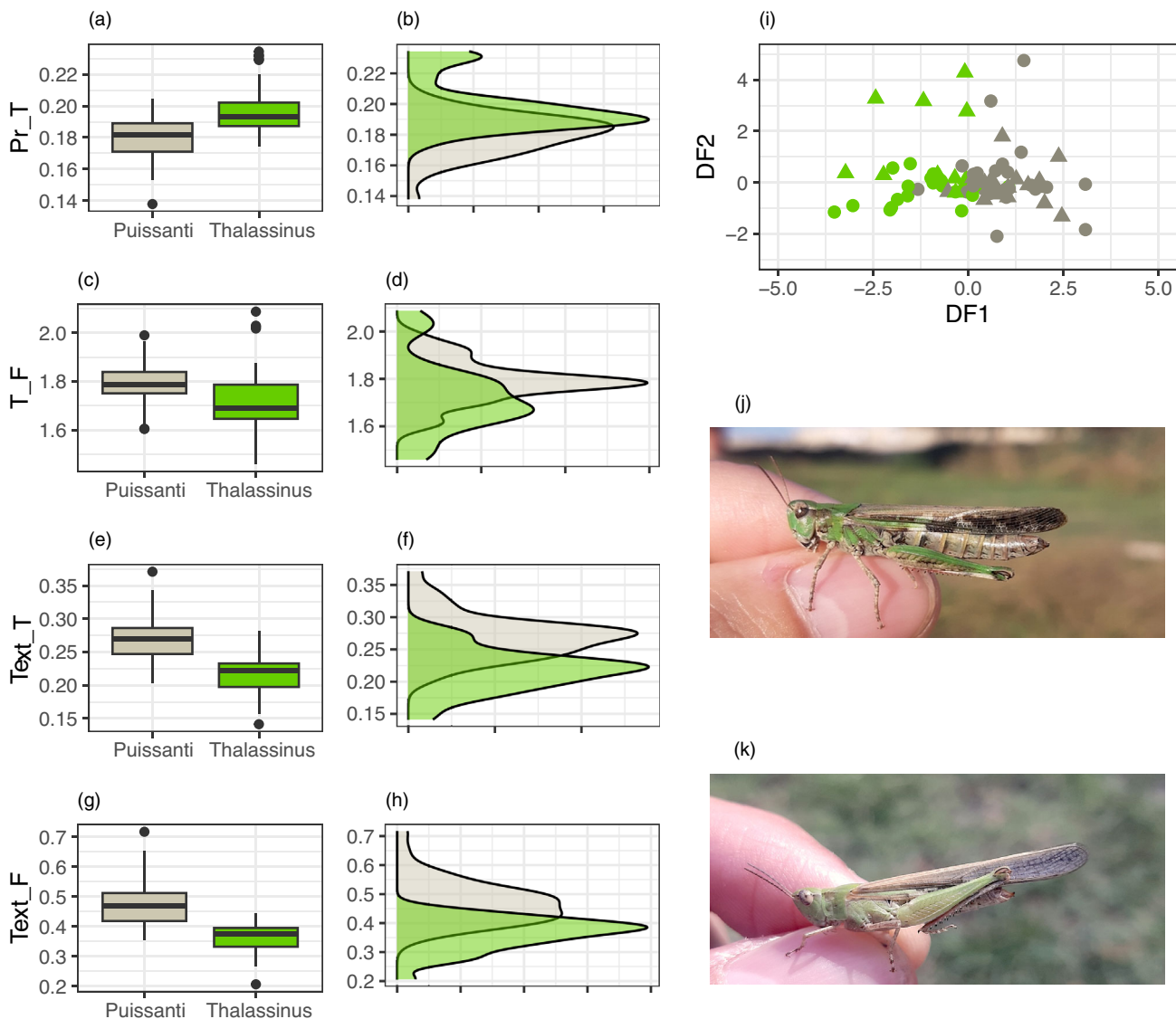
Figure 2 Morphological trait variation between two species of green-winged grasshoppers from the genus *Aiolopus* (*A. thalassinus*, $n = 37$; *A. puissanti*, $n = 63$). Traits are ratios calculated from photographs: Pr_T = Pronotum length/Tegmina length, T_F = Tegmina length/Femur length, Text_T = Tegmina extension/Tegmina length, Text_F = Tegmina extension/Femur length. a–c–e–g: boxplots showing trait variation between *A. thalassinus* (in green) and *A. puissanti* (in gray); b–d–f–h: density distribution of traits values between the two species; i: scatterplot showing the distribution of sampled individuals in the multivariate space defined by quadratic discriminant functions (DF1, DF2); green symbols = *A. thalassinus*; gray symbols = *A. puissanti*; triangles = males, circles = females; j and k: adult *A. thalassinus* (j) and *A. puissanti* (k). Photos by L. Ancillotto.

of grasshoppers may be effectively identified by adopting a quantitative photography-based approach, with applicability for clarifying species' distributions at wide scales by exploiting publicly available citizen-science records (Aceves-Bueno et al., 2017; Gallozzi et al., 2022).

Specifically, and in agreement with our hypothesis – also previously advanced by Defaut (2005) – we found that *A. puissanti* actually occurs outside of its currently known range, namely in the Italian Peninsula, possibly in sympatry with *A. thalassinus* throughout the Tyrrhenian coasts (as also

confirmed by collected specimens), as well as in Sardinia, a result partly expected due to the close proximity to the known distribution of the species in southern France and Corsica (Defaut, 2021). Besides, we also highlight the occurrence of only *A. thalassinus* along the Adriatic coasts of southern Italy, an area from which this taxon was formerly not recorded (Iorio et al., 2019). Since we only retrieved one or few testable records from other locations, and in absence of any measured specimen from these sites, we hold back from assuming that *A. puissanti* is certainly present in other parts of the study
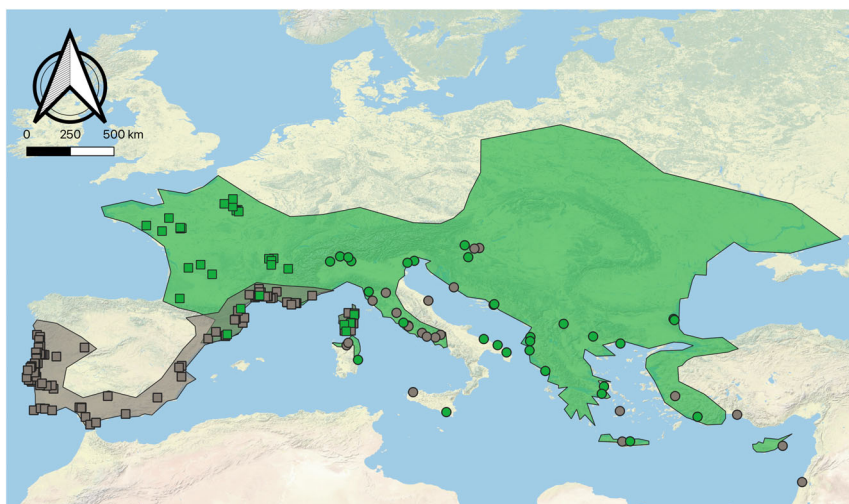
Figure 3 Distribution map of *Aiolopus thalassinus* (in green) and *A. puissanti* (in gray) across Western Europe and Eastern Mediterranean regions, depicted as colored polygons (adapted from the Global Biodiversity Information Facility). Squares: calibration records; filled circles: occurrences identified through quantitative photography-based classification of citizen science records (from the iNaturalist.org platform). Circles falling outside of the respective polygons indicate potential new locations.

area. Yet, our results strongly suggest a wider occurrence of this taxon throughout the eastern Mediterranean, that is, Sicily, Greece, Israel, Turkey, and Cyprus, also with a possibly isolated record from the Balkans; moreover, the species' range may well extend beyond the boundaries of our study area, as also suggested by specimens from Qatar (Defaut, 2021). As such, we urge increased research efforts in these areas of potential occurrence, in order to confirm, for example, by direct measurements and/or molecular approaches, the specific identity of green-winged grasshoppers of the genus *Aiolopus* occurring therein. Nonetheless, we also disclose that our approach does not rule out the potential occurrence of other – currently undescribed – taxa within this species complex that may have been erroneously identified as either *A. puissanti* or *A. thalassinus* by our exercise, again highlighting the importance of further investigation on this genus. All four ratios considered for the method involve the tegmina length or extension, and are therefore sensitive to rare cases of macropterism (Steenman et al., 2015) that may affect species classification. As an example of the potential limits of our approach, the isolated Croatian records our functions assigned to *A. puissanti* actually feature wing patterns more consistent with potentially macropterous *A. thalassinus*, a possibility that our method cannot rule out. We refrained to adopt wing color pattern as a potentially discriminating factor between *A. thalassinus* and *A. puissanti* since this is a far more qualitative trait prone to subjective appraisal, whose analysis would have required a different approach and photographic records collected under standardized conditions, thus hampering the use of citizen science data.

The discovery of *A. puissanti* in Italy – not mentioned by a very recent review on Italian Orthoptera (Iorio et al., 2019) – opens novel and promising research avenues on the ecology of this genus of orthopterans and more in general on insect

biogeography across the Mediterranean. As an example, exact location of records and field evidence both suggest that *A. thalassinus* is more dependent upon water bodies and wet grasslands than *A. puissanti*, which is found in a wider variety of habitat types, including drier grasslands (pers. obs.). Consequently, environmental niche segregation may have played an active role in the evolutionary radiation within the genus *Aiolopus*, at the same time representing a key driver of their current distributions and potential responses to climate change, as evidenced for other taxa (Vaissi, 2022), including orthopterans (*Oecanthus* tree crickets: Labadessa & Ancillotto, 2022). The apparent tolerance to drier conditions suggested by the distribution of *A. puissanti* may in fact promote its poleward range expansion (Mammola & Isaia, 2017), a prediction also supported by the morphological dissimilarities between the two species, suggesting higher dispersal abilities by *A. puissanti* (Steenman et al., 2015). *Aiolopus* grasshoppers are being increasingly recorded as range-expanding in central Europe (Fischer, 2018; Mückstein & Vlk, 2015), yet our results suggest caution and urge to verify whether such expansion is occurring in *A. thalassinus* and/or *A. puissanti*. As such, *Aiolopus* grasshoppers may represent an excellent study system to test ecological hypotheses and unveil subtle biogeographical patterns by being targeted by more in-depth investigations.

The use of measurements taken from photographs allowed us to provide a robust approach in species' assignment, as already common for individual-based recognition methods (De Lutio et al., 2021; Ferreira et al., 2020), a factor that is key to the use of citizen-science records, particularly in the case of cryptic species (Gorleri et al., 2022). We acknowledge that our approach is only applicable to cryptic species with identifiable morphological differentiation that correspond to levels 2 and 3 of the classification proposed by Chenuil et al., 2019. The same authors suggest that such cases of cryptic species *sensu*

lato where our approach is suitable often stem from taxonomic causes rather than truly evolutionary processes, and yet might represent a significant part of the so-called cryptic species cases among arthropods (Chenuil et al., 2019). Yet, molecular analyses are still crucial to clarify the level of genetic differentiation, which are currently lacking for our focal species pair. Our approach may also represent a first step in the development or improvement of automatic species recognition systems, by following an artificial intelligence approach (Schermer & Hogeweg, 2018), possibly including more or all species within this genus. However, artificial intelligence still largely lacks the possibility to inform the operator about the diagnostic traits to differentiate between species (Wäldchen & Mäder, 2018), and thus can have limited relevance for more traditional taxonomic studies relying on sets of explicit diagnostic characters. Our results also add to the increasing evidence highlighting the invaluable role of data collected by citizen scientists in contributing to understand species' distributions and ecology, as well as for fostering species' conservation at different spatial scales (Allen-Ankins & Schwarzkopf, 2022; Wang Wei et al., 2016). To our best knowledge, this is the first case study to apply a quantitative photography-based identification method for discriminating phenotypically highly similar species from citizen-science records, thus representing an effective and repeatable framework to disentangle the distributions of poorly studied species.

ACKNOWLEDGMENTS

References

Aceves-Bueno, E., Adeleye, A. S., Feraud, M., Huang, Y., Tao, M., Yang, Y., & Anderson, S. E. (2017). The accuracy of citizen science data: A quantitative review. *Bulletin of the Ecological Society of America*, **98**, 278–290.

Allen-Ankins, S., & Schwarzkopf, L. (2022). Using citizen science to test for acoustic niche partitioning in frogs. *Scientific Reports*, **12**, 1–7.

Campanaro, A., Hardersen, S., De Zan, L. R., Antonini, G., Bardiani, M., Maura, M., Maurizi, E., Mosconi, F., Zauli, A.,

& Bologna, M. A. (2017). Analyses of occurrence data of protected insect species collected by citizens in Italy. *Nature Conservation*, **20**, 265–297.

Chenuil, A., Cahill, A. E., Délémontey, N., Salliant du Luc, E. D., & Fanton, H. (2019). Problems and questions posed by cryptic species. A framework to guide future studies. In *From assessing to conserving biodiversity* (pp. 77–106). Springer, Cham.

De Lutio, R., She, Y., D'Aronco, S., Russo, S., Brun, P., Wegner, J. D., & Schindler, K. (2021). Digital taxonomist: Identifying plant species in community scientists' photographs. *ISPRS Journal of Photogrammetry and Remote Sensing*, **182**, 112–121.

Defaut, B. (2005). *Aiolopus puissanti*, espèce nouvelle proche d'*Aiolopus thalassinus* (Fabricius) (Acrididae, Oedipodinae). *Matériaux Orthoptériques & Entomocénotiques*, **10**, 103–113.

Defaut, B. (2012). Biométrie des types des caelifères de France (Orthoptera). 1. Définition des paramètres mesurés. 2. Mensurations chez les Tridactylidae, Tetrigidae, Pyrgomorphidae, Pamphagidae et Acrididae Calliptaminae. *Matériaux Orthoptériques & Entomocénotiques*, **17**, 21–56.

Defaut, B. (2021). Révision biométrique des taxons du genre *Aiolopus* en France et Algérie (Orthoptera, Acrididae). *Matériaux Orthoptériques & Entomocénotiques*, **26**, 31–56.

Defaut, B., & Jaulin, S. (2008). Nouvelles données taxonomiques et chorologiques sur *Aiolopus puissanti* Defaut et *A. thalassinus* (F.) (Orthoptera, Acrididae). *Matériaux Orthoptériques & Entomocénotiques*, **13**, 5–23.

Eiras, C. G. S., de Souza, J. R. G., de Freitas, R. D. A., Barella, C. F., & Pereira, T. M. (2021). Discriminant analysis as an efficient method for landslide susceptibility assessment in cities with the scarcity of predisposition data. *Natural Hazards*, **107**, 1427–1442.

Ferreira, A. C., Silva, L. R., Renna, F., Brandl, H. B., Renoult, J. P., Farine, D. R., Covas, R., & Doutrelant, C. (2020). Deep learning-based methods for individual recognition in small birds. *Methods in Ecology and Evolution*, **11**, 1072–1085.

Fischer, O. (2018). A record of *Aiolopus thalassinus* (Orthoptera: Acrididae) from Brno (Czech Republic). *Acta Musei Moraviae. Scientiae Biologicae*, **103**, 123–126.

Gallozzi, F., Colangelo, P., Senczuk, G., & Castiglia, R. (2022). Phylogeographic and bioclimatic determinants of the dorsal pattern polymorphism in the Italian Wall lizard, *Podarcis siculus*. *Diversity*, **14**, 519. https://doi.org/10.3390/d14070519

Gorleri, F. C., Jordan, E. A., Roesler, I., Monteleone, D., & Areta, J. I. (2022). Using photographic records to quantify accuracy of bird identifications in citizen science data. *Ibis (Lond. 1859)*, **165**, 458–471.

Hochkirch, A., Nieto, A., García Criado, M., Cálix, M., Braud, Y., Buzzetti, F. M., Chobanov, D., Odé, B., Presa Asensio, J. J., & Willemse, L. (2016). *European red list of grasshoppers, crickets and bush-crickets*. Publication Office of the EU.

Hollis, D. (1968). A revision of the genus *Aiolopus* Fieber (Orthoptera: Acridoidea). *Bulletin of the British Museum of Natural History*, **22**, 307–356.

Ingrisch, S. (1983). Neue Arten und faunistisch bemerkenswerte Nachweise von Orthopteren auf Sardinien. *Nachrichtenblatt der Bayerischen Entomologen*, **32**, 88–94.

Iorio, C., Roberto, S., Fontana, P., Buzzetti, F. M., Kleukers, R., Odé, B., & Massa, B. (2019). *Grasshoppers and crickets of Italy: A photographic field guide to all the species*. WBA Project Srl.

Koffler, S., Barbiéri, C., Ghilardi-Lopes, N. P., Leocadio, J. N., Albertini, B., Francoy, T. M., & Saraiva, A. M. (2021). A buzz for sustainability and conservation: The growing potential of citizen science studies on bees. *Sustainability*, **13**, 959.

Korshunova, T., Picton, B., Furfaro, G., Mariottini, P., Pontes, M., Prkić, J., Fletcher, K., Malmberg, K., Lundin, K., & Martynov, A. (2019). Multilevel fine-scale diversity challenges the 'cryptic species' concept. *Scientific Reports*, **9**, 1–23.

Labadessa, R., & Ancillotto, L. (2022). A tale of two crickets: Global climate and local competition shape the distribution of European Oecanthus species (Orthoptera, Gryllidae). *Frontiers of Biogeography*, **14**(4), e57538. https://doi.org/10.21425/F5FBG57538 Retrieved from: https://escholarship.org/uc/item/8jg834c6

Mammola, S., & Isaia, M. (2017). Rapid poleward distributional shifts in the European cave-dwelling *meta* spiders under the influence of competition dynamics. *Journal of Biogeography*, **44**, 2789–2797.

Mückstein, P., & Vlk, R. (2015). Record of *Aiolopus thalassinus* (Orthoptera: Acrididae) in the Žd'árské vrchy protected landscape area (bohemian-Moravian highlands, Czech Republic). *Acta Rerum Naturalium*, **18**, 1–2.

R Core Team. (2013). R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. http//www.R-project.org/

Ripley, B., Venables, B., Bates, D. M., Hornik, K., Gebhardt, A., Firth, D., & Ripley, M. B. (2013). Package 'mass.'. *Cran R*, **538**, 113–120.

Schermer, M., & Hogeweg, L. (2018). Supporting citizen scientists with automatic species identification using deep learning image recognition models. *Biodiversity Information Science and Standards*, **2**, e25268. https://doi.org/10.3897/biss.2.25268

Steenman, A., Lehmann, A. W., & Lehmann, G. U. C. (2015). Life-history trade-off between macroptery and reproduction in the wing-dimorphic pygmy grasshopper *Tetrix subulata* (Orthoptera Tetrigidae). *Ethology Ecology and Evolution*, **27**, 93–100.

Struck, T. H., Feder, J. L., Bendiksby, M., Birkeland, S., Cerca, J., Gusarov, V. I., Kistenich, S., Larsson, K.-H., Liow, L. H., & Nowak, M. D. (2018). Finding evolutionary processes hidden in cryptic species. *Trends in Ecology & Evolution*, **33**, 153–163.

Vaissi, S. (2022). The role of climatic niche divergence in the speciation of the genus *Neurergus*: An inter-and intraspecific survey. *Evolutionary Ecology*, **36**, 389–407.

Wäldchen, J., & Mäder, P. (2018). Machine learning for image based species identification. *Methods in Ecology and Evolution*, **9**, 2216–2225.

Wang Wei, J., Lee, B. P. Y. H., & Bing Wen, L. (2016). Citizen science and the urban ecology of birds and butterflies—A systematic review. *PLoS One*, **11**, e0156425.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Example of tegmina extension (Text) measurements taken when the femur is not parallel to the tegmina (F = femur, T = Tegmina, A = distance between the start of the tegmina and the start of the femur).

Figure S2. Relationship between the measurements made by Mathieu Pélissié and two authors on 14 testing specimens.