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ORIGINAL PAPER

Beetlehangers.org: harmonizing host–parasite records of *Harmonia axyridis* and *Hesperomyces harmoniae*

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Abstract

Citizen science is an increasingly powerful tool to gather large quantities of biological data and to engage the public. The number of citizen science initiatives has rapidly increased in the last 15 years. Invasive alien species such as the harlequin ladybird, *Harmonia axyridis* (Coleoptera, Coccinellidae), provide a particularly good opportunity for broad-scale use of such initiatives. *Harmonia axyridis* is parasitized by a fungus, *Hesperomyces harmoniae* (Ascomycota, Laboulbeniales), that can be found throughout the range of its host. Here we present Beetlehangers.org, a website and data repository where we combine observations of *He. harmoniae* from literature, online databases, and citizen science initiatives, including new records of both *Ha. axyridis* and *He. harmoniae*. Whereas *Ha. axyridis* is now present in 86 countries across six continents (including seven new country records), the distribution of its parasite *He. harmoniae* comprises 33 countries in five continents (including two new country records since its description in 2022). We explore spatiotemporal trends of *He. harmoniae* in light of these records. Finally, we discuss challenges and new opportunities for citizen science in relation to species interactions such as these and provide future perspectives for the website as a home for future Laboulbeniales research and outreach.

Keywords Citizen science · Coccinellidae · Ectoparasitic fungi · iNaturalist · Invasive non-native species · Invasive range · Laboulbeniales · Species distribution

Introduction

Citizen science (CS) is defined as the involvement of non-professionals in voluntarily collecting scientific data (Pocock et al. 2017). Data collection by citizen scientists has become an established approach to engage people with biodiversity,

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including environmental issues, while generating new knowledge and encouraging public participation in conservation actions (Turrini et al. 2018). While CS is often less structured and contains more noise and bias than research projects with data gathered by professional researchers (Boakes et al. 2010; Probert et al. 2022), the sheer quantity of observations cannot be matched by traditional research approaches (Chandler et al. 2017; Klemann-Junior et al. 2017; Bradter et al. 2018). Large-scale, mass-participation CS projects have grown in number over the last decades and are increasingly being used in biodiversity monitoring to inform conservation, ecology, and management of natural resources (McKinley et al. 2017; Pocock et al. 2017). CS initiatives that span large scales are useful for mapping species distributions and, when covering long time periods, can contribute to studies on climate change and tracking changes in species distributions including those of alien species (Dickinson et al. 2010). Finally, CS projects not only serve to answer research questions, they also increase species literacy and engagement with the natural world among the public (Hooykaas et al. 2022). This, in turn, can build broad-based support for nature conservation and management (Home et al. 2009).

Management of invasive alien species (IAS) greatly benefits from CS projects, since they can cover a much larger geographical area, map ecological interactions of IAS, and identify possible biological control agents (Haelewaters et al. 2017; Encarnação et al. 2021; Groom et al. 2021; Pocock et al. 2024). The harlequin ladybird *Harmonia axyridis* (Coleoptera, Coccinellidae) is an IAS that was introduced from eastern Asia to North America and Europe as a biocontrol agent of aphids and scale insects and has since spread around the world (Lombaert et al. 2010; Roy et al. 2016; Soares et al. 2022). Due to its negative effects on native insect communities and food production (Koch et al. 2006; Roy et al. 2012; Brown and Roy 2018), it is considered one of the worst pests in Europe (Nentwig et al. 2018). *Harmonia axyridis* makes a good subject for CS efforts because it is a brightly colored, charismatic, and easily recognized species (Soares et al. 2022). As a result, there is increasing interest to use CS data to monitor it around the world (Stals and Prinsloo 2007; Brown et al. 2008; Steenberg and Harding 2009; Grez et al. 2016; Brown and Roy 2018; Hiller and Haelewaters 2019; Werenkraut et al. 2020; Weyman et al. 2022; Angelidou et al. 2023).

Harmonia axyridis is host to a multitude of natural enemies, including parasites, parasitoids, pathogens, and predators (Ceryngier et al. 2012, 2018; Haelewaters et al. 2017) of which several are poorly known (Roy et al. 2017). Among these, *Hesperomyces harmoniae* (Ascomycota, Laboulbeniales) is a specialized biotrophic microfungus that is uniquely associated with *Ha. axyridis* (Haelewaters et al. 2022b). It produces tiny three-dimensional structures, or thalli, that grow externally on the integument of the host. *Hesperomyces harmoniae* is the most recorded species in *Hesperomyces virescens* sensu lato, a complex of species that are segregated by host and geographic location (Haelewaters et al. 2018a; Van Caenegem et al. 2023). Although the first records of *He. harmoniae* within the native range of *Ha. axyridis* date from the 1930s (Haelewaters et al. 2014), these were previously referred to as *He. virescens*. Recent results from laboratory experiments point at the potential for the fungus as a biocontrol agent against its invasive host (Haelewaters et al. 2020; Knapp et al. 2022; de Groot and Haelewaters 2022). In different locations in the invasive range of *Ha. axyridis*, a time lag is observed between the establishment of the ladybird in the wild and the first observation of *He. harmoniae* (Haelewaters et al. 2017). However, data are limited and would benefit from CS initiatives to increase the number of records in space and time.

In this study, we collated records of *He. harmoniae* associated with *Ha. axyridis* from multiple independent sources. The aims were threefold: (1) present an online dataset of global records made available through a newly introduced website Beetlehangers.org, (2) improve our understanding of the spatiotemporal patterns of *He. harmoniae*, and (3) discuss ways to increase the number of records of *He. harmoniae* alongside those of *Ha. axyridis* with the help of citizen scientists.

Materials and methods

Data collection

We define a "record" of *He. harmoniae* as an observation of one host individual of *Ha. axyridis* that is infected with *He. harmoniae*, irrespective of the number of thalli. Records of *He. harmoniae* were collated from multiple sources. First, a total of 41 CS networks, national organizations, and entomological and mycological societies across Europe were contacted to share unpublished records of *He. harmoniae*—as part of M.C.'s short-term stay at Ghent University funded by the Alien-CSI European network. Records were retrieved from naturgucker.de (Germany), Projekt LIFE ARTEMIS (Slovenia), National Biodiversity Network (UK), Ukrainian Biodiversity Information Network (Ukraine), and Dutch National Database Flora and Fauna (NDFF, The Netherlands) (Supplementary file S1). Curated records from NDFF were not shown with their exact coordinates, following the conditions of use. They were provided as polygons, of which the centroids were calculated in QGIS 3.32 (QGIS Development Team 2023). The coordinates of the centroids were used in the final Beetlehangers dataset.

Second, records were extracted from published papers. Location descriptions were saved in text format (e.g., "Boston, MA") and transformed into geographic coordinates using a Python script that leveraged the *Geopandas* package (Jordahl 2014). The number of *He. harmoniae* records (infected host individuals) were manually counted per location, when this information was available.

Third, digital records were searched and pooled from three online platforms: iNaturalist (https://www.inaturalist.org/home), Waarnemingen.be (https://waarnemingen.be/), and Flickr (https://www.flickr.com/). Records from iNaturalist were downloaded using their in-house data portals on 11 July 2023. In addition to the collation of previous data from iNaturalist, a dedicated project was initiated, "Beetle Hangers" (https://www.inaturalist.org/projects/beetle-hangers), in tandem with a social media campaign in spring 2022 (Fig. 1; Supplementary file S2), to encourage users to submit observations of *He. harmoniae* in Europe through this project. A flyer was produced and shared through Facebook and X (then Twitter). To ensure correct identifications of *Hesperomyces* on iNaturalist given recent taxonomic changes (Haelewaters et al. 2022b), M.D.d.G. and D.H. searched for observations of "*Hesperomyces*", checked their suggested identifications, and suggested the appropriate ID towards reaching "Research-Grade" observation status (Iwane 2023). For the final Beetlehangers dataset, all iNaturalist records that were not identified as *He. harmoniae* were filtered out, even if they belonged in the *He. virescens* complex.

Records from Waarnemingen.be were searched on 2 October 2023 using "*Hesperomyces harmoniae*" as query. The three resulting photo records were manually checked; no validated records of *He. harmoniae* were retained. Data associated with relevant photo records on Flickr were extracted automatically on 23 September 2022 (i.e., before the formal description of *He. harmoniae*) following Wu (2019) and with the help of Python's *FlickrAPI* package (Ando and Pousson 2022). The search queries used were "*Hesperomyces*" and "*Hesperomyces virescens*". These records along with their geographic coordinates and other metadata were then combined into a single CSV file (Wu 2019) and later compiled within the final Beetlehangers dataset. Records were only pulled from Flickr when geographic coordinates were present, and thus records of *He. harmoniae* without coordinates are currently not in our dataset. Duplicate records were manually identified and removed in Excel 2210 (Microsoft Corporation, Redmont, Washington).

Data curation

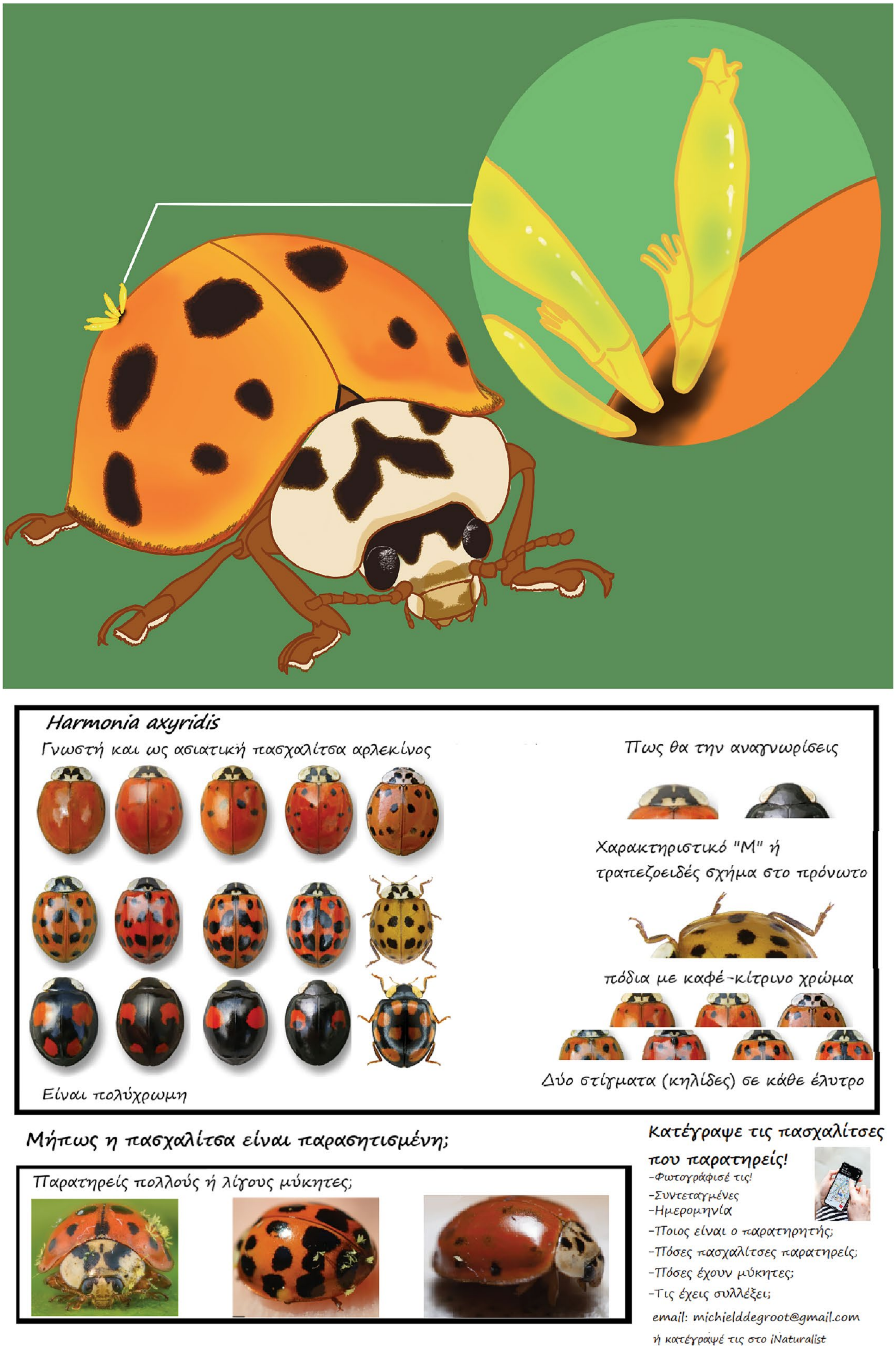
All photographic records received were manually checked for accuracy of species identification. Incorrectly identified records were not retained in the final Beetlehangers dataset. Geographic coordinates (lat, long) were used to assign locations, administrative divisions (states, regions, provinces), two-letter ISO 3166–1 alpha-2 country codes, country names, and continents to all records in the database with the help of the *Geopandas* and *Pycountry* packages (Jordahl 2014; Theune 2022). The naming conventions of several countries by *Geopandas* yielded names with special characters not recognized by Microsoft Excel. These country names were manually fixed. For some records, *Geopandas* failed to retrieve the necessary location information based on the provided coordinates. Those were manually corrected. Dates of observation were reported for all records (observed_on). However, dates pooled from different sources were not standardized with some following the "little endian" format as mm/dd/yyyy and others the "middle endian" format as dd/mm/yyyy. We employed the *datetime* package in Python to harmonize the date notations and accurately extract the year for each record. For other date formats, the *datetime* package was unable to interpret and generated the output "needs year". These records were manually checked and corrected.

Visualizations

We constructed interactive coordinate maps for the USA and Europe with Google My Maps, showing all collated records of *He. harmoniae* with *Ha. axyridis*, each with geographic coordinates, collection date (dd/mm/yyyy), source, and link to original observation when applicable. In addition to these interactive maps, we created static choropleth maps for the world, the United States of America (USA), and Europe with CS records of *He. harmoniae*, using Google Sheet's Geochart functionality. We plotted the accumulated number of records of *He. harmoniae* over time using Excel 2210, including records from the literature (summarized in Haelewaters et al. 2022b) and CS-based observations.

To gain a better understanding of the habitats in which *He. harmoniae* has been reported thus far, we used the raster layer showing anthropogenic biomes at 5 arc-minute resolution, downloaded from NASA's Socioeconomic Data and Applications Center (Ellis and Ramankutty 2008a). These anthropogenic biomes are based on population density, land use, and vegetation cover and are organized into six broad groupings: dense settlements, villages, croplands, rangelands, forests, and wildlands (Ellis and Ramankutty 2008b). These data are commonly used for ecological applications and provide global land use information during a specific time frame, useful for studying human–environment interactions. We processed these maps in QGIS 3.32 to calculate the percentage *He. harmoniae* records in each biome.

Finally, to map the spread of *He. harmoniae* and *Ha. axyridis,* both distributions were overlaid using Python's *plotly geo* package (Sievert et al. 2021). The global distribution of *Ha. axyridis* was retrieved from Brown et al. (2011), Orlova-Bienkowskaja et al. (2015), Gorczak et al. (2016),


Harmonia axyridis
Γνωστή και ως ασιατική πασχαλίτσα αρλεκίνος
Είναι πολύχρωμη
Πως θα την αναγνωρίσεις
Χαρακτηριστικό "Μ" ή τραπεζοειδές σχήμα στο πρόνωτο
πόδια με καφέ-κίτρινο χρώμα
Δύο στίγματα (κηλίδες) σε κάθε έλυτρο
Μήπως η πασχαλίτσα είναι παρασητισμένη;
Παρατηρείς πολλούς ή λίγους μύκητες;
Κατέγραψε τις πασχαλίτσες που παρατηρείς!
-Φωτογράφισέ τις!
-Συντεταγμένες
-Ημερομηνία
-Ποιος είναι ο παρατηρητής;
-Πόσες πασχαλίτσες παρατηρείς;
-Πόσες έχουν μύκητες;
-Τις έχεις συλλέξει;
email: michielddegroot@gmail.com
ή κατέγραψέ τις στο iNaturalist

◂**Fig. 1** Representative images used in outreach. *Above*: illustration by Linshan Feng (Leiden University). *Below*: Greek version of the visual guide (dubbed "spotting chart") used for our 2022 social media campaign with an overview of *Harmonia axyridis* features, images of *Hesperomyces harmoniae*-infected specimens, and instructions on how to submit observations

Camacho-Cervantes et al. (2017), Ceryngier and Romanowski (2017), Biranvand et al. (2019), Hiller and Haelewaters (2019), and iNaturalist.

Results

Records of *Hesperomyces harmoniae*

A total of 4,053 photos were manually checked for accuracy of the identity of the fungus. A total of 3,286 records of *He. harmoniae* were collected from CS networks, organizations, societies, and online platforms: 2,987 records from iNaturalist, 198 from naturgucker.de, 88 from NDFF, 9 from Flickr, 2 from Ukrainian Biodiversity Information Network, and 1 from Projekt LIFE ARTEMIS and National Biodiversity Network each. In addition, 92 collections of *Ha. axyridis* infected with *He. harmoniae* were retrieved from the literature, excluding records covered in the sources above (Garcés and Williams 2004; Riddick and Schaefer 2005; Riddick 2006, 2010; Harwood et al. 2006a, b; Nalepa and Weir 2007; Riddick and Cottrell 2010; Steenberg and Harding 2010; De Kesel 2011; Haelewaters and De Kesel 2011; Cottrell and Riddick 2012; Herz and Kleespiel 2012; Haelewaters et al. 2012a, b; 2014, 2015, 2016, 2017, 2018a, b, 2019, 2022a, b; Ceryngier and Twardowska 2013; Ceryngier et al. 2013; Pfliegler 2014; Raak-van den Berg et al. 2014; Cornejo and González 2015; Gorczak et al. 2016; van Wielink 2017; López-Arroyo et al. 2018; Orlova-Bienkowskaja et al. 2018; Fiedler and Nedvěd 2019; Crous et al. 2021; Knapp et al. 2022). Those collections consisted of one to hundreds of infected ladybirds each, together accounting for 4,559 individual records. All curated records with metadata are available in GitHub: https://github.com/dannyhaelewaters/teamlaboul/tree/main/beetlehangers (in the Data directory).

Interactive distribution maps of *He. harmoniae* in the USA and Europe are available at https://beetlehangers.org/ladybirdproject/ladybird-distributions/. Records are colored by source, and metadata of each record are available by clicking on the icon. Choropleth maps of records of *He. harmoniae* in the world, the USA and Europe are shown in Figs. 2 and 3. Slovenia and Ukraine represent new country records for *He. harmoniae* since its formal description by Haelewaters et al. (2022b). Within the USA, new state records are reported from California, Colorado, Delaware, Illinois, Indiana, Iowa, Kansas, Louisiana, Maine, Minnesota, Missouri, South Carolina, Texas, and Washington.

The accumulated number of records of *He. harmoniae* over time are shown in Fig. 4. When multi-year records in publications were presented in a way that made it impossible to count the number of specimens by year, the first year of observations was used in the plot. *Hesperomyces harmoniae* was first observed on museum specimens of *Ha. axyridis* collected in the 1930s in China (Haelewaters et al. 2014) but these records are not shown in the plot. The first field-observed record of *He. harmoniae* dates from May 2002 (Virginia, USA; Haelewaters et al. 2017). While the number of records retrieved from the literature is higher, the number of CS records is making a steep increase with two thirds of CS observations having been made in the last three years alone (Fig. 4). Using the anthropogenic biome dataset from Ellis and Ramankutty (2008a), we found that *He. harmoniae* was most recorded in the urban biome (43.2%), followed by the residential rainfed mosaic biome (19.4%), rainfed mosaic villages (13.7%), and dense settlements (10.7%) (Fig. 5). Records of *He. harmoniae* were very rare in other biomes, ranging from 4.6% in residential irrigated cropland to 0% in cropped & pastoral villages, remote croplands, populated rangelands, and wild forests.

Harmonia axyridis is currently present in 86 countries and 6 continents (Fig. 6; Supplementary file S3). Compared to previous literature, this study adds seven countries to the global distribution of *Ha. axyridis*: El Salvador (North America), Bolivia (South America), Estonia, Finland (Europe), Armenia (Eurasia), and Algeria and Botswana (Africa). *Hesperomyces harmoniae* is present in 33 countries and 5 continents (Fig. 6). Since its formal description (Haelewaters et al. 2022b), *He. harmoniae* has been reported from Slovenia and Ukraine. In Africa, *He. harmoniae* has only been observed in South Africa. It has not been observed in the Middle East, Central Asia, southeastern Asia, Antarctica, and Oceania. Compared with *Ha. axyridis*, the distribution of *He. harmoniae* encompasses fewer countries in South America, Europe, Africa, and Asia.

Records of *Hesperomyces* spp.

During curation of records, 133 records were separated; only those of *He. harmoniae* were retained in the final Beetlehangers dataset. Of the 133 separated records, eight represent new country and island records of *He. virescens* s.l. These are: Vanuatu on *Olla v-nigrum* (iNaturalist #113191012, #118881273); Martinique on *Cladis nitidula* (#148527333); Peru on *Cycloneda sanguinea* (#55402948) and *Psyllobora* sp. (#168800632); Haiti on *Cycloneda sanguinea* (#69453498); Puerto Rico on *Cycloneda sanguinea* (#179605779); Cuba on *Cycloneda sanguinea* (#17474775). Additionally, seven new country and island

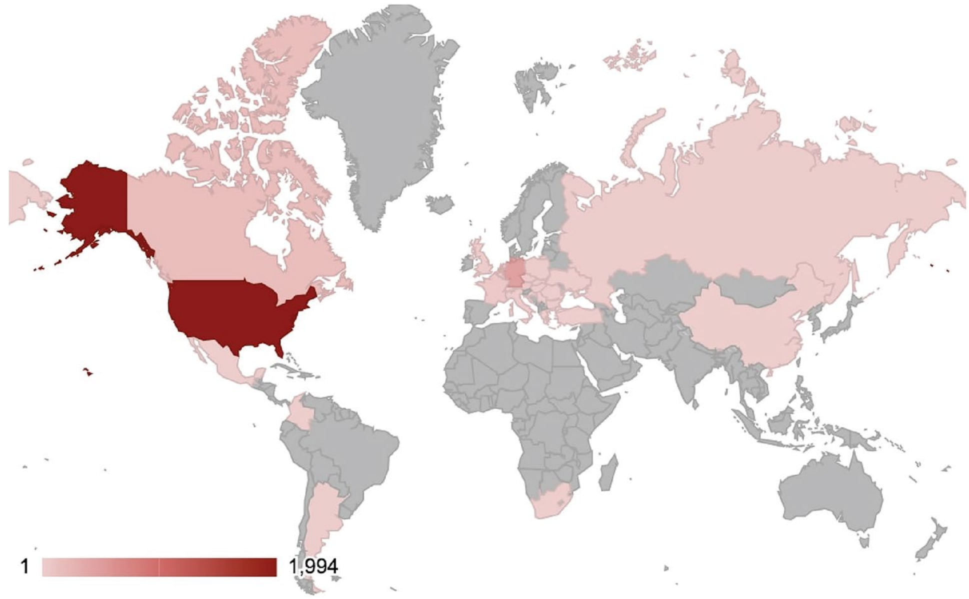


Fig. 2 A choropleth map showing the global distribution of citizen science records of *Hesperomyces harmoniae*

records of *Hesperomyces* spp. are reported from Australia on *Cryptolaemus montrouzieri* (iNaturalist #172129139) and *Rhyzobius lophanthae* (#2648522), Bermuda on *Scymnus loewii* (#115450130), and New Zealand on *Rhyzobius fagus* (#1050649, #170578845) and *R. forestieri* (#159954218, #170581377).

Discussion

Beetlehangers.org, a new resource for Laboulbeniales research

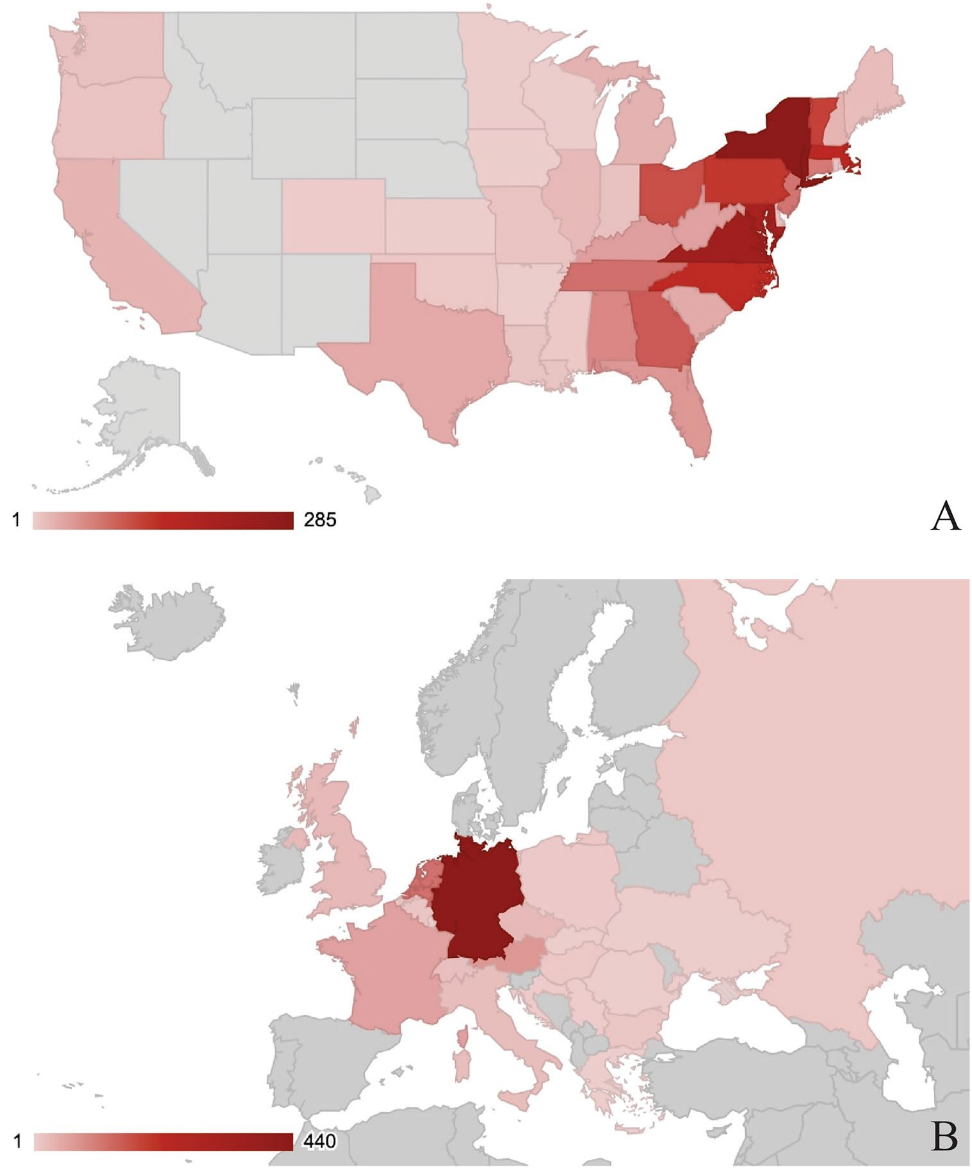
Already in the nineteenth century, Laboulbeniales microfungi were colloquially referred to as "beetle hangers" (Cooke 1892). This is where the name stems from for our website and data archive with records of *He. harmoniae* from published literature, online databases, and citizen science initiatives: Beetlehangers.org. The online interactive distribution maps of *He. harmoniae* will be updated when new records are contributed and corrected when an error in data entry is reported to the corresponding author. New records will be quality-screened based on the criteria presented above before being added to the Beetlehangers dataset. With Beetlehangers.org, we hope to (1) promote research on this common ectoparasite of *Ha. axyridis* (Haelewaters et al. 2018a, 2022b), (2) increase public knowledge and interest in the utility of CS records of parasitic fungi, and (3) continue to increase records including in poorly sampled regions with the help of targeted social media campaigns, such as the one we did in Europe in collaboration with local researchers.

While Beetlehangers.org was initially established in 2018 as a small-scale project for *He. harmoniae* records, we now intend the website to become a resource of Laboulbeniales knowledge for the general audience as well as an open-access data repository. For instance, in the past few years, Laboulbeniales on bat flies (Diptera, Nycteribiidae and Streblidae) have garnered some attention (e.g., Dogonniuck et al. 2019; Szentiványi et al. 2019; Liu et al. 2020) and a dataset of bat–bat fly–Laboulbeniales interactions is under construction (de Groot et al. 2020). Additionally, a database of all known species of Laboulbeniomycetes along with their holotype location and other geographic records was created (Haelewaters et al. 2024) and will continue to be updated on Beetlehangers.org. Since Laboulbeniales infect a swathe of different arthropod hosts, there are many opportunities for projects focusing on different host groups. We envision Beetlehangers.org to become a home to provide public outreach and share research results of different projects related to Laboulbeniales microfungi.

Records of *Hesperomyces harmoniae* over time and space

This study aimed at investigating observations of *He. harmoniae* on a spatiotemporal scale. The usefulness of CS platforms to track species over time and space may be limited due to geospatial biases inherent to CS-based projects (see below). However, they do hold a lot of power for analytical work given the high number of records that cannot be achieved by traditional research (Chandler et al. 2017; Adler et al. 2020). For example, data from CS projects have previously been used for questions related to geographic distributions (van Strien et al. 2013), population trends (Horns et al.

Fig. 3 Choropleth maps showing the distribution of citizen science records of *Hesperomyces harmoniae* in (**A**) the United States of America (at state level) and (**B**) across European countries



2018), and the spread of invasive species (Brown et al. 2001; Howard et al. 2022). To our knowledge, our Beetlehangers dataset is the first to track an organism alongside its invasive host.

Our dataset shows a steep increase in the number of CS records since 2019 (Fig. 4). First, CS apps and online platforms are becoming more user-friendly and accessible to non-professionals, leading to more records being amassed through them (Boakes et al. 2016; Petersen et al. 2021; Price-Jones et al. 2022). Second, Laboulbeniales research – and *Hesperomyces* research in particular – has seen a recent surge by D.H. and collaborators, associated with active efforts to perform public outreach efforts and to adopt open science practices. Third, many CS initiatives have involved the public in the recording of ladybirds, and in particular *Ha. axyridis* since its arrival as an IAS around the world (Grez et al. 2010; Gardiner et al. 2012; Brown and Roy 2018; Werenkraut et al. 2020; Skuhrovec et al. 2021). The combination of these three factors may have resulted in a domino effect, whereby increasingly more people become aware of both the ladybird and its associated fungus and start recording their observations.

We used the complete Beetlehangers dataset to create visualizations of the geospatial distribution of records of *He. harmoniae* in relation to its host (Fig. 6). As *He. harmoniae* is an obligate parasite – i.e., it cannot survive without its host – its distribution is expected to fall completely within the distribution of *Ha. axyridis.* However, *He. Harmoniae*'s range reaches neither the highest nor the lowest latitudes of the range of *Ha. axyridis.* These results indicate that the habitable climatic range of the ladybird may be wider than that of the fungus. A recent field-based study showed that

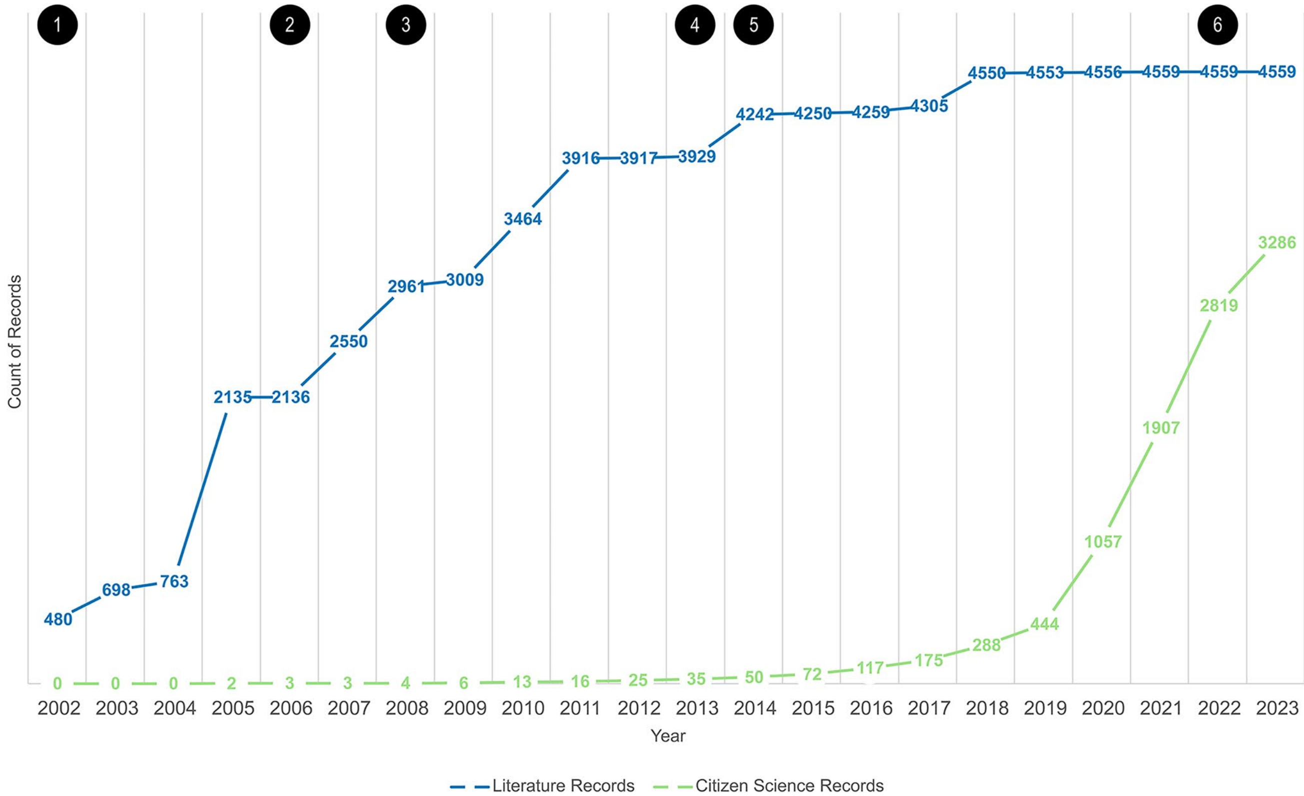


Fig. 4 Total cumulative observations of curated *Hesperomyces harmoniae* records over time, with differentiation between citizen science records (in green) and literature records (in blue). Relevant events are indicated: **1**, first record of *He. harmoniae* in the USA (Virginia); **2**, first record of *He. harmoniae* in Europe (Belgium); **3**, launch of iNaturalist; **4**, first record of *He. harmoniae* in Africa (South Africa); **5**, first record of *He. harmoniae* in South America (Ecuador); **6**, formal description of *He. harmoniae*. Color scheme from https://colorbrewer2.org by C.A. Brewer, Department of Geography, Pennsylvania State University

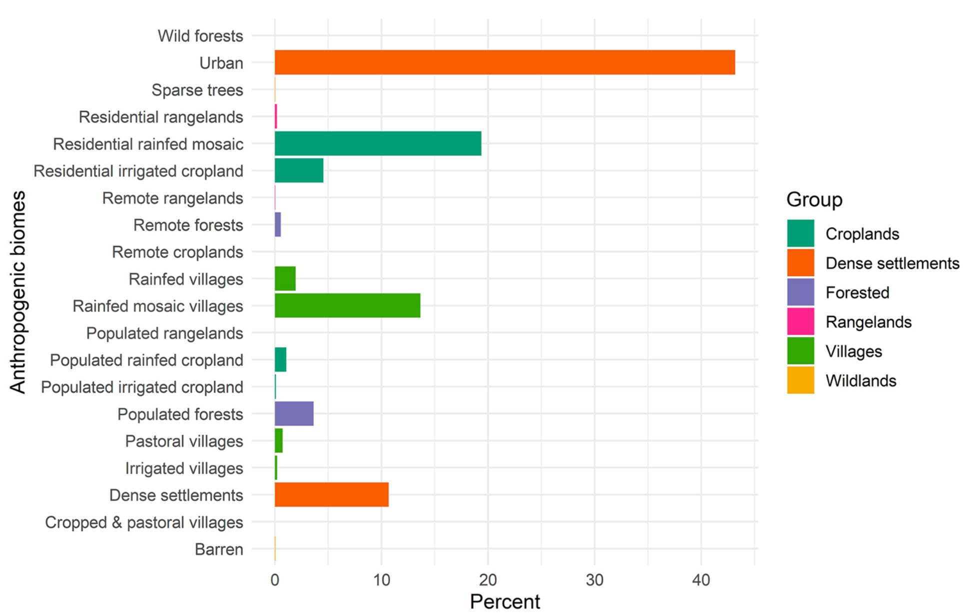


Fig. 5 Records of *Hesperomyces harmoniae* across anthropogenic biomes, colored by group (Ellis and Ramankutty 2008b). Shown is the percentage of records per each biome

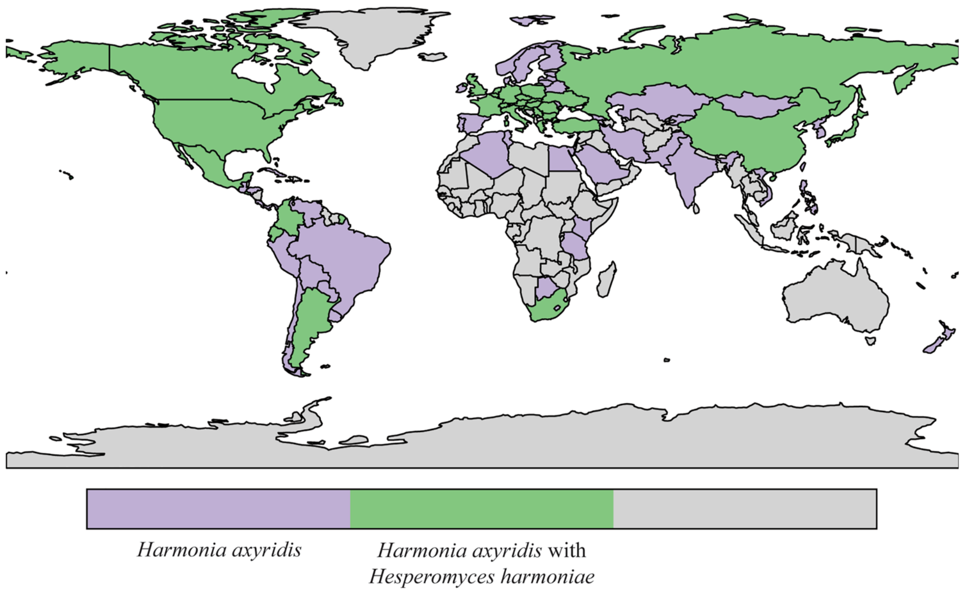


Fig. 6 The distributions of both *Harmonia axyridis* and *Hesperomyces harmoniae*, by country. Countries in purple have confirmed records of *Ha. axyridis*. Countries in green have confirmed records of *He. harmoniae*-infected *Ha. axyridis*. Countries in grey have no confirmed records of either *He. harmoniae* or *Ha. axyridis*. Note that Python's *plotly geo* package uses ISO 3166–1 alpha-3 country codes and thus while *He. harmoniae* is only known from England, the whole United Kingdom (also including North Ireland, Scotland, and Wales) is shown in green. Color scheme from https://colorbrewer2.org by C.A. Brewer, Department of Geography, Pennsylvania State University

climate factors did not have an effect on parasitism of *Ha. axyridis* by *He. harmoniae* but this study was limited to data from Central Europe (Haelewaters et al. 2022a). Laboratory experiments did show that there may be an optimal range of humidity and temperature for the fungus to grow (M.D. de Groot and B. Santamaria unpubl. data).

Challenges related to citizen science projects

Hundreds of biodiversity-related CS projects have been initiated during just the last decade (Theobald et al. 2015), many of which focus on IAS (Silvertown 2009; Adriaens et al. 2015; Brown and Roy 2018; Roy et al. 2018; Howard et al. 2022; Price-Jones et al. 2022). Among the general challenges in designing and running CS projects are the management of data quality (data curation), the recruitment and retaining of participants, and taxonomic and geospatial biases. We will discuss some of these biases in light of our work with Laboulbeniales microfungi and *He. harmoniae* more specifically.

Taxonomic biases

How to overcome taxonomic biases is an important challenge that becomes even more strenuous when dealing with ectoparasitic microfungi (e.g., Gonçalves et al. 2021; Lofgren and Stajich 2021). Public records are heavily skewed by organismal preference, as larger, more charismatic, and more easily identified species represent the majority of observed species in CS platforms (Kosmala et al. 2016; Járic et al. 2020). Our interactions with the 41 CS networks, national organizations, and societies that we had contacted for records of *He. harmoniae* underlined this taxonomic bias. We only received records from five of these sources (one additional source referred to Angelidou et al. 2023), and the number of records was relatively low: 290 combined records, contributed mostly by naturgucker.de and NDFF, versus 2,987 records from iNaturalist. Future CS projects focusing on Laboulbeniales may benefit from a combination of infographics, a dedicated project website, active social media outreach, instructional videos, and sharing of intermediate and final research results with the participants. Such a broad communication strategy along with an active training component can help to engage and motivate participants (Jordan et al. 2012; Maund et al. 2020). In general, microfungal ectobionts in the order Laboulbeniales represent a group of organisms that need advanced training and equipment for accurate species identification, which makes them harder to use in CS projects. Laboulbeniales can also "fall between two stools", where entomologists do not record the presence of fungal thalli, and mycologists do not routinely collect Laboulbeniales hosts. For this reason, targeted initiatives such as Beetlehangers.org can increase awareness and appreciation of this understudied fungal group.

In the past, projects like the Big Seaweed Search (Brodie et al. 2023) and the FunDiS Northeast Rare Fungi Challenge (Fungal Diversity Survey 2022) have shone a light on neglected taxa with the help of citizen scientists.

Geospatial biases

Observations from citizen scientists are distributionally skewed towards temperate countries and easily accessible localities (Tiago et al. 2017), thereby mirroring the biases from traditional research projects (Rodrigues et al. 2010; Hortal et al. 2015; Meyer et al. 2015; Quandt and Haelewaters 2021). For Laboulbeniales, several species have extremely disjunct distribution patterns that are attributed to a lack of study across large geographical areas (Haelewaters et al. 2024). This Wallacean shortfall (sensu Lomolino 2004) helps to explain the uneven and patchy distribution of *He. harmoniae* as seen in Fig. 6. Our analysis of *He. harmoniae* records across anthropogenic biomes suggests that *He. harmoniae* is mostly present in areas with substantial human populations (Fig. 5). Both these observations are more likely to reflect the distribution of citizen scientists and active researchers rather than the actual species distribution. However, there may also be biological factors involved. Welch et al. (2001) reported that the parasite prevalence of *Hesperomyces* on *Adalia bipunctata* was highest in the city center of London and decreased rapidly towards the outskirts. The authors attributed this to the "urban island heat effect", which shortens winters and may promote aphid growth – increasing survival of ladybirds and thereby providing more opportunities for transmission of ascospores. An alternative explanation may come from the increased number of artificial shelters (attics, basements, windowsills, etc.) in city centers (Adriaens et al. 2008; Roy and Brown 2015) that results in more opportunities for spore transfer among ladybirds as they form dense aggregations in winter (Riddick and Shaefer 2005; Nalepa and Weir 2007).

Interesting records of *Hesperomyces virescens* sensu lato and *Hesperomyces* spp.

The genus *Hesperomyces* has recently received considerable attention. The main contributing reason for this is *He. harmoniae* being commonly observed as an ectoparasite of the globally invasive *Ha. axyridis*, and potential biocontrol applications for this fungus (Roy et al. 2011; Haelewaters et al. 2020, 2022a; de Groot and Haelewaters 2022). *Hesperomyces harmoniae*, however, was only formally described as a species in late 2022 (Haelewaters et al. 2022b). Previously, *He. harmoniae was* hidden under the name *Hesperomyces virescens* (Haelewaters et al. 2018a). As the "Beetle Hangers" project in iNaturalist was conceived before this taxonomic decision, the initial focus was *He. virescens* which, as mentioned above, is a complex of multiple species each with different hosts. As a consequence, various records of *He. virescens* sensu lato (s.l.), i.e., observations of the fungus of which the host was not *Ha. axyridis*, were recorded alongside *He. harmoniae*. Some turned out to be new records for the country or island in which they were found. Even though they do not represent species records in the narrow sense, these mark the first time that a member of *Hesperomyces* was reported in these localities, including Cuba, Haiti, Martinique, Puerto Rico (North America), Peru (South America), and Vanuatu (Oceania).

Hesperomyces on *Clavis nitidula* from Martinique in the Caribbean Sea represents the first record of *Hesperomyces* with this host genus. *Clavis* is part of the Chilocorini tribe, as are the genera *Chilocorus* (*Ch. stigma* is the host of *He. virescens* sensu stricto; Thaxter 1891) and *Parexochomus* (host to *He. parexochomi*; Crous et al. 2021). A few contributed records of *Hesperomyces* were associated with hosts in the tribes Coccidulini (*Cryptolaemus montrouzieri*) and Scymnini (*Rhyzobius* spp.). The only Coccidulini representative found with *Hesperomyces* thus far is *Azya orbigera* from Panama, host to an undescribed species of *Hesperomyces*. Thus, the records of *Hesperomyces* sp. on *Rhyzobius fagus* and *R. forestieri* from New Zealand and *R. lophanthae* from Australia are the first ones of *Hesperomyces* associated with this host genus. To date, Scymnini hosts have been found to be associated with *He. coccinelloides* and *He. papuanus*. *Hesperomyces papuanus* was described on a *Cryptolaemus affinis* from Papua New Guinea (Majewski and Sugiyama 1985). An integrative taxonomy approach is needed to confirm whether this is an actual species. Since photographic records cannot be identified with confidence to species level, the above records remain unidentified until more material is observed and collected for taxonomic investigation.

Towards increased engagement of citizen scientists for parasitology research

We extracted records of *He. harmoniae* from online databases, among other sources, and used these to identify anthropogenic biomes of high *He. harmoniae* abundance; our study is an example of how the public can contribute to parasitology research. Likewise, Doherty et al. (2021) pointed out that internet data from non-professionals were reliable to chart the spatial occurrence, temporal trends, and host usage patterns of an easily observed parasite. To date, most CS projects have focused on single-species observations – participants are asked to make observations of a single organism and upload photographs to an app or online platform. However, to gain a more complete picture of species interactions and ecological networks, projects should shift towards multi-species observations. Groom et al. (2021) refer to projects collecting data on species interactions through the public as "next-level" CS and point out that their success depends on eliciting an emotional connection in people, not overcomplicating project aims, sharing results, and designing research questions that are relevant to the participants' daily lives. To increase the resolution of our Beetlehangers dataset, we propose to incorporate observations of *Hesperomyces* into existing CS apps and programs for ladybirds, such as the UK Ladybird Survey (Brown and Roy 2018) and the European Ladybirds smartphone app (Skuhrovec et al. 2021).

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Data availability The data that support the findings of this study are available in the Supplementary Information section of this article. All curated records of *He. harmoniae* with metadata are available in GitHub (https://github.com/dannyhaelewaters/teamlaboul/tree/main/beetlehangers/Data).

Declarations

Competing interests The authors have no competing interests to declare that are relevant to the content of this article.

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