Received: 24 November 2021 | Revised: 25 May 2022 | Accepted: 30 May 2022

DOI: 10.1111/cobi.13965

Conservation Biology

REVIEW

A roadmap for ladybird conservation and recovery

António O. Soares[1,2] | Danny Haelewaters[2,3,4,5] | Olga M. C. C. Ameixa[6] | Isabel Borges[1] | Peter M. J. Brown[7] | Pedro Cardoso[8] | Michiel D. de Groot[3,9] | Edward W. Evans[10] | Audrey A. Grez[11] | Axel Hochkirch[12,13] | Milada Holecová[14] | Alois Honěk[15] | Ján Kulfan[16] | Ana I. Lillebø[6] | Zdenka Martinková[15] | J. P. Michaud[17] | Oldřich Nedvěd[4,5] | Omkar[18] | Helen E. Roy[19] | Swati Saxena[18] | Apoorva Shandilya[18] | Arnaud Sentis[20] | Jiri Skuhrovec[15] | Sandra Viglášová[16] | Peter Zach[16] | Tania Zaviezo[21] | John E. Losey[2,22]

[1]Center for Ecology, Evolution and Environmental Changes / Azorean Biodiversity Group (cE3c–ABG) / CHANGE – Global Change and Sustainability Institute, Faculty of Science and Technology, University of the Azores, Ponta Delgada, São Miguel Island (Azores), Portugal

[2]IUCN SSC, Ladybird Specialist Group

[3]Department of Biology, Faculty of Sciences, Ghent University, Ghent, Belgium

[4]Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic

[5]Biology Centre of the Czech Academy of Sciences, Institute of Entomology, České Budějovice, Czech Republic

[6]Centre for Environmental and Marine Studies (CESAM) & Department of Biology, University of Aveiro, Aveiro, Portugal

[7]Applied Ecology Research Group, School of Life Sciences, Anglia Ruskin University, Cambridge, UK

[8]Laboratory for Integrative Biodiversity Research, Finnish Museum of Natural History LUOMUS, University of Helsinki, Helsinki, Finland

[9]Research Institute for Nature and Forest (INBO), Geraardsbergen, Belgium

[10]Department of Biology, Utah State University, Logan, Utah, USA

[11]Facultad de Ciencias Veterinarias y Pecuarias, Universidad de Chile, Santiago, Chile

[12]Department of Biogeography, Trier University, Trier, Germany

[13]IUCN SSC Invertebrate Conservation Committee, Trier, Germany

[14]Department of Zoology, Faculty of Natural Sciences, Comenius University, Bratislava, Slovak Republic

[15]Crop Research Institute, Prague, Czech Republic

[16]Institute of Forest Ecology, Slovak Academy of Sciences, Zvolen, Slovak Republic

[17]Agricultural Research Center – Hays (ARCH), Department of Entomology, Kansas State University, Hays, Kansas, USA

[18]Ladybird Research Laboratory, Department of Zoology, University of Lucknow, Lucknow, India

[19]UK Centre for Ecology & Hydrology, Wallingford, UK

[20]UMR RECOVER, National Research Institute for Agriculture, Food and the Environment (INRAE) & Aix-Marseille University, Aix-en-Provence, France

[21]Facultad de Agronomía e Ingeniería Forestal, Pontificia Universidad Católica de Chile, Santiago, Chile

[22]Department of Entomology, Cornell University, Ithaca, New York, USA

Correspondence
António O. Soares, Center for Ecology, Evolution and Environmental Changes/Azorean Biodiversity

Abstract

Ladybirds (Coleoptera: Coccinellidae) provide services that are critical to food production, and they fulfill an ecological role as a food source for predators. The richness,

António O. Soares and Danny Haelewaters contributed equally to this work.

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.
© 2022 The Authors. *Conservation Biology* published by Wiley Periodicals LLC on behalf of Society for Conservation Biology.

15231739, 2023, 1, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/cobi.13965 by Universidade Dos Acores, Wiley Online Library on [06/02/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Group (cE3c–ABG)/CHANGE – Global Change and Sustainability Institute, Faculty of Science and Technology, University of the Azores, Rua da Mãe de Deus, 13-A, 9500-321 Ponta Delgada, São Miguel Island (Azores), Portugal.
Email: antonio.oc.soares@uac.pt
Danny Haelewaters, Department of Biology, Faculty of Sciences, Ghent University, K.L. Ledeganckstraat 35, 9000 Ghent, Belgium.
Email: danny.haelewaters@gmail.com

Article impact statement: In light of major ecological threats, mitigating actions at different timescales are crucial for ladybird conservation and recovery.

Funding information
VES19 INTER-COST, Grant/Award Number: MSMT-15739/2019-6; Scientific Grant Agency of the Ministry of Education, Science, Research and Sport of the Slovak Republic, Grant/Award Number: VEGA2/0032/19; National Fund for Scientific and Technological Development of the Government of Chile, Grant/Award Number: 1180533; Czech Ministry of Agriculture, Grant/Award Number: RO0418; FEDER, Grant/Award Numbers: ACORES-01-0145-FEDER-000072, ACORES-01-0145-FEDER-000081; National Agency for Agricultural Research, Grant/Award Number: QK 1910281; FCT/MCTES, Grant/Award Numbers: UIDP/50017/2020, UIDB/50017/2020; Research Foundation – Flanders: Fundamental Research Fellowship, Grant/Award Number: 1142722N; Agence Nationale de la Recherche, Grant/Award Number: ANR-19-CE02-0001-01; Research Foundation – Flanders: Junior Postdoctoral Fellowship, Grant/Award Number: 1206620N; Natural Environment Research Council, Grant/Award Number: NE/R016429/1

abundance, and distribution of ladybirds, however, are compromised by many anthropogenic threats. Meanwhile, a lack of knowledge of the conservation status of most species and the factors driving their population dynamics hinders the development and implementation of conservation strategies for ladybirds. We conducted a review of the literature on the ecology, diversity, and conservation of ladybirds to identify their key ecological threats. Ladybird populations are most affected by climate factors, landscape composition, and biological invasions. We suggest mitigating actions for ladybird conservation and recovery. Short-term actions include citizen science programs and education, protective measures for habitat recovery and threatened species, prevention of the introduction of non-native species, and the maintenance and restoration of natural areas and landscape heterogeneity. Mid-term actions involve the analysis of data from monitoring programs and insect collections to disentangle the effect of different threats to ladybird populations, understand habitat use by taxa on which there is limited knowledge, and quantify temporal trends of abundance, diversity, and biomass along a management-intensity gradient. Long-term actions include the development of a worldwide monitoring program based on standardized sampling to fill data gaps, increase explanatory power, streamline analyses, and facilitate global collaborations.

KEYWORDS
Coccinellidae, ecological threats, ecosystem services, roadmap to conservation, short-, mid-, and long-term timescale actions, temporal and spatial trends

Resumen
Las catarinas (Coleoptera: Coccinellidae) proporcionan servicios que son críticos para la producción de alimento, y juegan un papel ecológico como fuente de alimento para depredadores. Sin embargo, la riqueza, abundancia y distribución de catarinas están en peligro debido a muchas amenazas antropogénicas. La carencia de conocimiento sobre el estatus de conservación de la mayoría de las especies y los factores que inciden en su dinámica poblacional dificulta el desarrollo e implementación de estrategias de conservación para las catarinas. Realizamos una revisión de la literatura sobre la ecología, diversidad y conservación de catarinas para identificar sus amenazas ecológicas clave. Las poblaciones de catarinas fueron afectadas mayormente por factores climáticos, composición del paisaje e invasiones biológicas. Proponemos acciones de mitigación para la conservación y recuperación de catarinas. Acciones a corto plazo incluyen programas de ciencia y educación ciudadana, medidas de protección para la recuperación de hábitat y de especies amenazadas, prevención de la introducción de especies no nativas y el mantenimiento y restauración de áreas naturales y la heterogeneidad del paisaje. Acciones a mediano plazo implican el análisis de datos obtenidos de programas de monitoreo y colecciones de insectos para desenmarañar el efecto de las diferentes amenazas a las poblaciones de catarinas, comprender el uso del hábitat por taxa de los que se tiene conocimiento limitado y cuantifica las tendencias temporales de la abundancia, diversidad y biomasa a lo largo de un gradiente de intensidad de manejo. Acciones a largo plazo incluyen el desarrollo de un programa de monitoreo a nivel mundial basado en muestreos estandarizados para subsanar la falta de datos, incrementar el poder explicativo, optimizar los análisis y facilitar colaboraciones globales.

PALABRAS CLAVE
acciones en escala de tiempo a corto, amenazas, mediano y largo plazo, guia para la conservación, servicios ecosistémicos, tendencias temporales y espaciales

【摘要】
随着世界范围内人类与野生动物的冲突不断升级, 对野生动物的宽容和接纳等概念变得越来越重要。然而, 当代保护研究表明, 人们对人类与野生动物积极互作的认识有限, 导致可能难以准确描述人类与动物的相遇。如果不解决这些

15231739, 2023, 1, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/cobi.13965 by Universidade Dos Acores, Wiley Online Library on [06/02/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

局限性,就会导致野生动物和景观管理计划的设计和实施存在不足,以及对本土生态知识的否定。我们利用印度喀拉拉邦瓦亚纳德野生动物保护区森林中的阿迪瓦西族Kattunayakans部落的民族志证据,来研究印度原住民对于人类与野生动物共存的观点。通过定性的实地研究(包括访谈和在森林样带调查),我们发现Kattunayakans部落表现出对野生动物的宽容和接纳,其特点是深入的共存,包括三个中心思想:野生动物是有理性的交流者;野生动物是神、老师和平等的族群;野生动物是实行 “*dharmam*”的具有共同起源的亲戚。我们认为,充分理解以上几点有助于将Kattunayakan部落的观点引入印度的森林管理,并更广泛地解决人类与野生动物的冲突。

关键词: 瓢虫科, 生态系统服务, 生态威胁, 时空趋势, 保护路线图, 短期、中期和长期时间尺度的行动

INTRODUCTION

Global growth of the human population and per capita consumption—particularly since the 1970s—have increased demand for natural resources and often led to their unsustainable use (Dasgupta, 2021). This has damaged trophic networks and ecosystem integrity and decreased species richness and abundance (Eggleton, 2020). Insect biomass is declining, and some species are at risk of extinction due to habitat loss and fragmentation, introduction of non-native species, pollution by agrochemicals, climate change, and overharvesting (e.g., Harvey et al., 2020; van Klink et al., 2020; Wagner et al., 2021). However, the evidence is not equivocal and the insect decline debate is complex (Saunders et al., 2020). Insects are among the least represented taxa in global biodiversity data sets, extinction risk assessments, and conservation projects (Mammola et al., 2020). Information is lacking on insect population sizes, temporal trends, distributions, and ecological threats, leaving the conservation status of most insect species unknown and unassessed in the context of red listing—limiting the implementation of conservation actions (Cardoso et al., 2011). Finally, international conservation targets are not being met (Hochkirch et al., 2020).

Insects are an important component of biodiversity in most ecosystems. They provide numerous services critical to food production, including pollination, nutrient cycling, and pest control (Ameixa et al., 2018), in addition to their critical role as a food source for vertebrates. Disruption of insect populations and their habitats could irreversibly harm the stability and abundance of biotic communities, leading to the simplification of food webs and subsequent loss of ecosystem services (Derocles et al., 2018; Samways et al., 2020). Beetles (Coleoptera) of the family Coccinellidae, referred to as ladybirds (also ladybugs or ladybird beetles), form a group that plays diverse and important roles in ecosystems. Therefore, a global synthesis of ladybird studies is needed to identify knowledge gaps and propose actions for ladybird conservation.

Through a literature review, we sought to update the major ecological threats to ladybirds. We also identified projects and actions that could contribute to the protection of ladybird populations and identified knowledge gaps that hamper conservation efforts. Finally, we devised conservation actions for ladybirds under the framework of Harvey et al. (2020).

COCCINELLIDAE

General characteristics

The family Coccinellidae contains 6000–7000 described species, but precise evolutionary relationships of tribes and even some genera are unclear (Tomaszewska et al., 2021). Not all species have been studied equally because most studies focus on large, conspicuous generalists, invasive species, and those important for biological control (Sloggett, 2005). Although many well-known species are widely distributed (Gordon, 1985; Kovář, 2007), many newly described species may be threatened under the International Union for Conservation of Nature (IUCN) Red List criteria, based on limited geographic distribution, declining populations, or extreme population fluctuations. Ladybirds are cosmopolitan, but there is a distributional unevenness in their study; the African continent and parts of Asia are among the least studied areas (Appendix S1).

Ecosystem services

A framework of ecosystem service indicators is available in the Common International Classification of Ecosystem Services (CICES) (https://cices.eu/). Ameixa et al. (2018) developed a rule-based approach to assess the ecological and cultural services delivered by insects, and we applied this framework to identify ecosystem services provided by ladybirds (Appendix S2). Ladybirds contribute to provisioning, regulation, maintenance, and cultural services. Provisioning services include their biological activities (e.g., multiple functions of ladybird alkaloids), whereas regulation and maintenance services include pest control and pollination (Ameixa et al., 2018). Cultural services range from carriers of good luck (CICES elements of living systems that have sacred or religious meaning), to subjects of children's nursery rhymes (CICES elements of living systems used for entertainment or representation), to country-specific symbols of cultural (CICES characteristics or features of living systems that have an existence value) or religious significance (CICES elements of living systems that have sacred or religious

15231739, 2023, 1, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/cobi.13965 by Universidade Dos Acores, Wiley Online Library on [06/02/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

meaning), all of which ensure their popularity, even among people who do not normally like insects. The cultural significance of ladybirds underscores their suitability as flagship species for the conservation of other insect taxa.

MAJOR ECOLOGICAL THREATS

Accumulating data from different geographic areas have revealed long-term changes in ladybird populations (Appendix S3). However, how ecological factors affect the abundance and diversity of ladybirds remains understudied. We summarized how climate factors, landscape composition, and biological invasions affect ladybird populations based on the available evidence.

Climate change

Temperature governs the pace of life for ladybirds (Dixon et al., 2005). Metabolic, developmental, and feeding rates have hump-shaped temperature dependences; optimum, upper, and lower thresholds vary among species (Dixon et al., 2009). By increasing average temperature and the amplitude of thermal fluctuations, climate change will alter the demography of ladybird populations (Skirvin et al., 1997). Many effects of constant temperatures on ladybird physiology are well documented, but the impacts of temperature fluctuations and extreme events—heat waves, droughts—remain largely unexplored. Recent studies suggest that increased temperature variations may pose a greater risk to survival than gradually increasing mean temperatures (Harvey et al., 2020; Ma et al., 2021; Vasseur et al., 2014). Increasing the frequency and amplitude of heat waves can decrease larval body mass and affect predator–prey interactions (Sentis et al., 2013). Ladybird populations should be monitored alongside bioclimatic variables to better understand how rapid environmental change may influence their abundance, survival, reproduction, distribution, and, ultimately, their ecosystem services.

Temperature also affects interspecific interactions, such that co-occurring ladybird species with different thermal sensitivities can affect the fate of others in the food web (Gutierrez et al., 2008; Skirvin et al., 1997). Intraguild predation among aphidophagous predators may increase as warming increases (Sentis et al., 2014; Soares et al., 2003), which can drive local extinctions of intraguild prey. In general, warming increases the ladybird feeding rate up to a thermal maximum, above which feeding rate decreases (Sentis et al., 2012). Thus, warming could increase predation pressure on prey in the short term, but long-term impacts will hinge on ladybird demography and the temperature-dependent responses of their prey and host plants. To persist and grow under warming, ladybird populations need to assimilate more energy to cover higher metabolic demands, which means they will require increased prey abundance. Aphids are also sensitive to temperature (Hullé et al., 2010) and do not thrive in hot weather. Warming can also influence ladybird sensitivity to chemical cues (Boullis et al., 2016; Sentis, Ramon-Portugal, et al., 2015), microhabitat selection (Schmitz & Barton, 2014), and seasonal phenology (Dixon et al., 2005). These factors, in turn, can affect trophic interactions and ecosystem services. Thus, interactions among species should be monitored to better understand the consequences of rapid environmental change.

Aphid symbionts can affect the survival of their hosts and ladybird predators in various ecological contexts (Costopoulos et al., 2014), and the evolutionary responses of prey to extreme temperatures can cascade upward to affect ladybird populations. For example, evolution of heat-shock tolerance can happen rapidly in aphid strains with stably inherited bacterial endosymbionts (Harmon et al., 2009). The evolutionary responses of ladybirds to climate change could, in turn, cascade downward to affect prey populations. For example, darker melanic morphs should be selected against in warmer environments (Michie et al., 2011) because they have a lower thermal optimum for activity than paler morphs (Soares et al., 2003). Counter selection of dark morphs may lead to reduced predation on aphid populations at low temperatures (de Jong & Brakefield, 1998). Finally, plastic phenotypic responses to warming could affect predator–prey interactions (Donelson et al., 2018; Sentis, Morisson, et al., 2015). Incorporating plastic responses in species distribution models might reduce the projected vulnerability of ladybirds to climate change (Bush et al., 2016).

In plans to mitigate the impacts of climate change on ladybirds and the ecosystem services they provide, the ecology and evolution of interacting species needs to be considered (Trumble & Butler, 2009). Also needed is improved understanding of the impacts of temperature fluctuations and extremes on ladybird survival and trophic ecology to assess the consequences of biological control in a warmer and more thermally unpredictable world (Bruno & Cardinale, 2008). Moisture and humidity regimes may also influence ladybird distribution and abundance (Sloggett & Zeilstra, 2020) and will be labile to climate change.

Agricultural intensification, landscape simplification, and urbanization

Agricultural intensification, landscape simplification, and urbanization affect assemblages of ladybirds, especially those restricted to native habitats (Egerer et al., 2018; Gardiner et al., 2021; Grez et al., 2013, 2021; Honek et al., 2017). Natural habitats, such as wetlands and heathlands, are rapidly disappearing. This damages ladybird communities because these habitats often support specialist ladybird species with restricted ranges that are thus rare and endangered (Adriaens et al., 2015). Such natural and seminatural habitats may play an important role in conserving ladybirds. In central Chile, for example, the abundance and richness of native ladybirds are higher in less disturbed habitats, whereas non-native species are more abundant in agricultural crops (Grez et al., 2013). Furthermore, these less disturbed habitats provide important refugia for crop-inhabiting ladybirds when prey become scarce in agricultural habitats (Gardiner et al., 2009; Grez et al., 2013; Woltz & Landis, 2014).

15231739, 2023, 1, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/cobi.13965 by Universidade Dos Acores, Wiley Online Library on [06/02/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Landscape heterogeneity has both compositional (i.e., proportional area in different vegetation types) and configurational (i.e., spatial arrangements of cover types) components that affect arthropod biodiversity in agricultural landscapes (Fahrig et al., 2011). However, agricultural intensification has resulted in landscape simplification and a decline in faunal biodiversity (Lichtenberg et al., 2017). Ladybirds in crops are influenced by surrounding landscape characteristics (Caballero-López et al., 2012; Gardiner et al., 2009; Woltz & Landis, 2014). In Chile, native ladybirds are more abundant and diverse in alfalfa fields when surrounded by more heterogeneous landscapes with woodlands and hedgerows, and the loss of these nonproductive habitats could threaten ladybirds, especially native species (Grez et al., 2021). Similar results have been found for ladybirds in soybean fields across a gradient of agricultural intensification in southern Michigan (Woltz & Landis, 2014). In contrast, Gardiner et al. (2009) found that native ladybirds in soybean fields were more abundant in low-diversity landscapes, where native grasslands dominated. The replacement of crops with others less favorable for ladybirds may eliminate key resources, such as overwintering sites, alternative prey, or plant-derived foods. This is illustrated by the disappearance of *Coccinella septempunctata* from the Azores after wheat production was abandoned (Soares et al., 2018).

Urbanization often drives declines in the abundance and richness of native species. Non-native vegetation can deter native ladybirds and favor invasive species. Both *Harmonia axyridis* in Europe (Roy et al., 2016) and *Adalia bipunctata* in Japan (Sakuratani et al., 2000) commonly use urban areas. In cities, untended vacant spaces and urban gardens can harbor a rich assemblage of ladybirds (Gardiner et al., 2013). But just as in agricultural areas, native ladybirds in urban landscapes depend on locally available natural habitats (Gardiner et al., 2021). In Santiago de Chile, green spaces support a rich community of native and non-native ladybirds, although they are negatively affected by urbanization, especially natives (Grez et al., 2019). Some species may benefit when urban settings support abundant prey (Honek et al., 2017), but these benefits are typically transitory (Sloggett, 2017).

Landscape variables may also affect ladybird-associated natural enemies, which may be important for integrated pest management. For example, recent work has investigated the influence of habitat composition on the infection probability of *Hesperomyces virescens*, an ectoparasitic fungus that causes increased mortality of *H. axyridis* (Haelewaters et al., 2020, 2022). Knowing the environmental conditions—habitat composition, temperature, humidity—the ectoparasite thrives in may prove crucial for potential management programs targetingr invasive populations of *H. axyridis*.

Biological invasions

The negative impacts of invasive ladybirds are best illustrated by *C. septempunctata* in the Nearctic region and *H. axyridis* worldwide. In Europe, 12 non-native ladybird species were intentionally released as biocontrol agents, although *H. axyridis* is the only one regarded as invasive (Soares et al., 2018). Interspecific competition and intraguild predation arising from ladybird invasions may cause declines of native species and structural changes in local assemblages. A complete picture of the impacts of invasive ladybirds remains to be assessed (Kindlmann et al., 2011) and would benefit from an enhanced understanding of their ecology in their native ranges and their interactions with co-evolved species (Li et al., 2021).

The invasion of Florida citrus ecosystems by *H. axyridis* revealed its various competitive advantages over most native species in terms of diet breadth and intraguild interactions (Michaud, 2000, 2002). The abundance and diversity of native species in alfalfa in Chile declined after the arrival of *H. axyridis* in 2008, with species richness declining from 11 to 4 species (Grez et al., 2016). Nevertheless, several long-term data sets suggest overall levels of pest control in particular crops may remain unchanged following the invasion of *H. axyridis*, despite significant declines in the diversity and abundance of native species (Alyohkin & Sewell, 2004). The dominance of invasive ladybirds in agricultural habitats appears mediated by competitive exclusion, likely reinforced by intraguild predation, and may drive the retreat of native species to uncultivated habitats (Bahlai et al., 2013).

An often-unappreciated consequence of biological invasions is their impact on natural enemies. Natural enemies may be introduced together with an invasive host (co-introduction), they may follow their host into a new geographic range after a time lag (host pursuit), or host shifts may occur between ecologically similar hosts (Pfliegler et al., 2018). *Hesperomyces virescens* associated with *H. axyridis* may have spread around the world with its host—with a time lag between establishment of *H. axyridis* and acquisition of the parasite (Haelewaters et al., 2017).

APPROACHES TO LADYBIRD CONSERVATION AND RECOVERY

Harvey et al. (2020) formulated actions across different timescales toward insect conservation. Using their work as a blueprint, we present a roadmap to the conservation and recovery of ladybirds (Figure 1). The immediate implementation of certain measures is usually required to arrest insect declines and define at-risk and priority species for conservation. Midterm actions aim to address new research objectives in consideration of existing data. Finally, longer term actions aim to implement permanent conservation strategies for vulnerable or endangered species.

Short-term actions

Organisms targeted for conservation often evoke emotions in participants (Groom et al., 2021), either positive (Sequeira et al., 2014) or negative (Palmer et al., 2017; Porter et al., 2019). Ladybirds are charismatic insects that are widely recognized as beneficial for the role they play in controlling pests (Hodek et al., 2012; Honek et al., 2017). Most ladybirds are relatively

15231739, 2023, 1, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/cobi.13965 by Universidade Dos Acores, Wiley Online Library on [06/02/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Conservation Biology

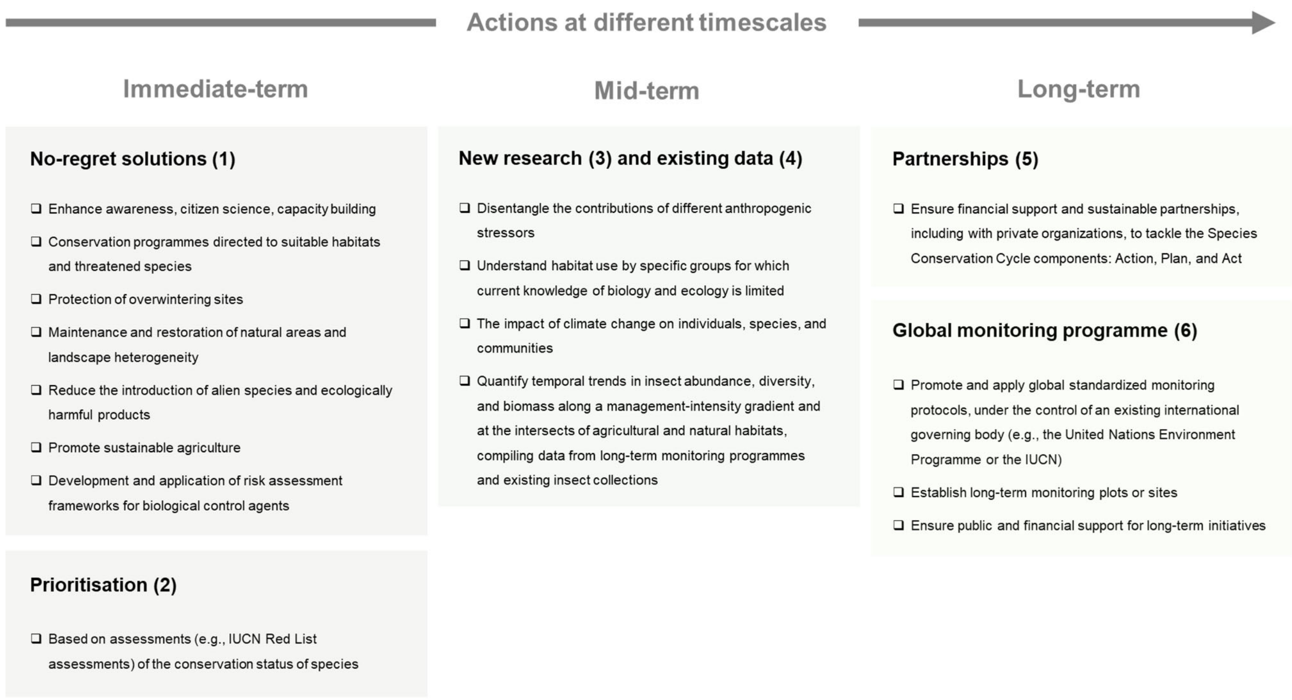

FIGURE 1 Schematic representation of the proposed roadmap to ladybird conservation and recovery (based on the framework of Harvey et al. [2020]). Actions are on different timescales.

easy to identify from photos (Jouveau et al., 2018), rendering them an excellent subject for citizen science projects (Gardiner et al., 2012). Population changes occur across vast geographic areas over many years, posing a challenge for conventional surveys conducted by specialists (Losey et al., 2012). Programs that incorporate nonscientists can generate observations over broader scales (Appendix S4). Partly based on these observations, threats to native ladybird species have been recognized in several subnational units (e.g., Connecticut and New York in the United States), at the national level (e.g., COSEWIC in Canada), and internationally (e.g., NatureServe). Citizen scientists have monitored the invasion of *H. axyridis* (Grez et al., 2016; Hiller & Haelewaters, 2019; Roy et al., 2020). Inspired by the success of such programs, a smartphone application for recording and identifying European ladybirds was developed to encourage people to share their sightings, improve their understanding of ladybird ecology, and increase public appreciation of these insects. Additionally, it provides a mechanism for early detection of new invasive species (Skuhrovec et al., 2021).

In temperate regions with high population density and intensive agriculture, direct measures to protect particular ladybird species may be necessary. During the growing season, protective measures can be directed at woodlots and urban green spaces, where ladybird abundance is usually high and application of pesticides is restricted (Honek et al., 2017). Additional strategies include adding native and noncrop vegetation around agricultural crops to enhance alternative resources and shelter for ladybirds (Muñoz et al., 2021). Furthermore, ladybird populations may be protected on crops for which yield losses are tolerable or refundable from the state agricultural.

Protection of overwintering sites can be critical to the survival of ladybirds in temperate agroecosystems. Some populations of *A. bipunctata* and *Ceratomegilla undecimnotata* shelter from freezing temperatures by overwintering in caves and buildings. Many species native to the Nearctic region, such as *Coleomegilla maculata* and *Hippodamia convergens*, are cold tolerant and overwinter in natural areas, often forming aggregations in sheltered sites. Overwintering sites outside agricultural areas may be subject to anthropic factors that negatively affect ladybirds, such as prescribed burning, recreational activities, and changes in land use. Reconciling the needs of agriculture and the protection of ladybirds can be difficult due to conflicting interests. One serious concern is the widespread adoption of neonicotinoid seed treatments by industrial-scale agriculture in North America, driven largely by corporations that offer farmers no alternative to treated seed for crops, such as corn, sorghum, and soybeans. These systemic insecticides have lethal and sublethal effects on ladybirds (Bredeson & Lundgren, 2019; Moscardini et al., 2015) and create agricultural deserts in which insects are absent from the crop for 6–8 weeks after germination, leading to prey deprivation and exclusion of predatory arthropods (Michaud, 2018).

Introductions of non-native species are increasing globally (Seebens et al., 2017). After the successful introduction of *Rodolia cardinalis* from Australia to California (U.S.A.) in the late 1800s to control populations of the coccid *Icerya purchasi* infesting citrus orchards, several other ladybird species were introduced to new regions for classical biological control (Roy & Migeon, 2010; Soares et al., 2018). A prime example is the introduction—intentionally and inadvertently—of *H. axyridis* to

15231739, 2023, 1, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/cobi.13965 by Universidade Dos Acores, Wiley Online Library on [06/02/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

many countries (e.g., Camacho-Cervantes et al., 2017; Hiller & Haelewaters, 2019; Roy et al., 2016). Because the management of established invasive species may be difficult to achieve (Booy et al., 2017), prevention is always preferable (Pyšek et al., 2020). Horizon-scanning tools can be used to identify invasive species that pose the greatest threat (Roy et al., 2020), prioritize species for risk assessment (Roy et al., 2018), and guide policy development (Vanderhoeven et al., 2017), such as prevention campaigns that raise awareness among stakeholders.

Ladybirds represent an ideal system for generating potential synergies between disciplines. Biocontrol practitioners have developed risk assessment frameworks for biocontrol agents that evaluate their potential to establish, disperse, expand their host range, or affect nontarget species (van Lenteren et al., 2003). Invasion biologists have also developed a plethora of other risk assessment tools, in part to meet the needs of the EU Regulation on Invasive Alien Species 1143/2014 and, specifically, to inform the list of invasive non-native species of European Union concern (Roy et al., 2018). Recently, the IUCN launched a global standard for classifying the severity and type of impacts caused by non-native species, the Environmental Impact Classification for Alien Taxa (Hawkins et al., 2015). Surprisingly, the fields of biological control and invasion biology rarely intersect, despite a need for collaborative approaches and best practices.

Despite a tendency to compartmentalize the various drivers of environmental change with mitigation approaches targeted at single drivers, conservation strategies must respond to drivers acting at varying temporal and spatial scales (Bonebrake et al., 2019; Diaz et al., 2019). Declines in ladybird populations and distributions have largely been attributed to invasive species and land-use changes, often operating in tandem. An increased understanding of direct and indirect interactions among drivers of change is required, particularly where synergistic interactions accelerate detrimental changes to ladybird communities. The promotion of more heterogeneous agricultural landscapes could address multiple threats simultaneously for multiple species (Michaud, 2018). More heterogeneous landscapes provide better availability of prey, overwintering habitats, and supplemental resources. The availability of stable microclimates and physical shelters from agricultural disturbance will complement these benefits and further improve spatiotemporal continuity of resources for natural enemies (Iuliano & Gratton, 2020; Landis et al., 2000). Unmanaged natural and seminatural areas provide many of these resources and contribute to resource continuity for natural enemies (Holland et al., 2020; Landis et al., 2000). Crop diversification can also contribute to regional resource continuity for natural enemies when crops differ in prey availability and seasonal phenology (Gontijo, 2019; Iuliano & Gratton, 2020). Improved continuity of resource availability in agricultural landscapes can promote the persistence of natural enemies at the landscape scale, even though they may experience periodic extirpations, enhancing ladybird conservation and biological control services (Iuliano & Gratton, 2020; Michaud, 2018; Zaviezo et al., 2021).

Mid-term actions

Local differences in species abundance and community composition could provide clues to the causes of temporal changes and address gaps in knowledge of ladybird spatial distributions. Honek (2012) compiled data from 125 articles on ladybird communities prior to 2012. Most studies investigated field crops (78 papers), mainly fodder plants (23), cereals (18), and maize (1). Orchards were surveyed in 38 studies, but fewer examined broadleaf plants (5) and coniferous forests (3); only 1 examined medicinal plants. The studies emanated largely from Europe and the Mediterranean (58) and North America (56); 11 were from other parts of the world. Even in well-studied areas, knowledge of ladybirds in certain habitats is lacking (e.g., ladybirds inhabiting the upper strata of tree canopies). Often, data are restricted to observations of adults; data on larval populations are scarce (Radwan & Lövei, 1983; Takahashi & Naito, 1984), even though these are specifically associated with breeding habitats. The locations of hibernation sites and their patterns of use by different species remain insufficiently studied (Susset et al., 2017). Ladybird abundance data can be challenging to obtain. Many ladybirds move among habitats to forage, reproduce, and hibernate, and more efforts are needed to understand sequential patterns of habitat utilization (Sloggett & Majerus, 2000). Midterm actions should include studies of habitat use by taxa for which knowledge of biology and ecology is limited (e.g., *Scymnus* spp.).

Other mid-term actions should actively protect ladybird populations by promoting reproduction and reducing mortality of susceptible life stages, which can be challenging in an intensively managed landscape. Compromises will be required between the protection of crops from pests and the protection of ladybirds from the side effects of protective measures. In industrial agriculture, pesticides are often applied in response to initial pest detections, rather than economic thresholds, or even prophylactically, in the case of neonicotinoid seed treatments. When all phytophagous arthropods are killed, ladybirds and other natural enemies suffer prey deprivation and leave agricultural crops. Interventions can be directed toward preserving uncultivated habitats as prey-bearing refuges and overwintering sites. Most ladybird species overwinter on nonagricultural land (debris fields, rock formations, steppes, forest edges). Informing owners of the importance of these habitats, with the focus on disturbance prevention, could be crucial for the protection of ladybirds.

Implementation of recommendations for ladybird protection will require legislation and education programs to raise awareness. Legislative measures should target reductions in pesticide applications and justification of their use in particular contexts, perhaps including an environmental tax. Other measures could promote the preservation and expansion of habitat heterogeneity in uncultivated areas because landscape mosaics promote diverse ladybird communities and support rare species that migrate seasonally among habitats (Evans, 2017). Increased support of organic farming would foster increased tolerance of

15231739, 2023, 1, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/cobi.13965 by Universidade Dos Acores, Wiley Online Library on [06/02/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

pests in agricultural crops, yielding positive effects for ladybird populations, and promoting greener cities would help conserve ladybirds in urban areas (Grez et al., 2019).

Long-term actions

Systematic long-term monitoring of insect abundance and diversity is fundamental to understanding of insect declines (Borges et al., 2018; Gardiner & Roy, 2022). Most insect taxa, including ladybirds, lack monitoring programs that extend over large spatial or temporal scales. Ladybirds can be used as a "pilot group" to develop and test such long-term monitoring schemes because they are easy to spot in transect sampling and they are readily identified (also by smartphone applications [Skuhrovec et al., 2021]), whereas their diversity is relatively low. Detailed research on long-term variations in ladybird abundance began only recently (Honek et al., 2017), and a paucity of reliable information impedes conservation efforts and recovery programs. Most efforts to record ladybirds are done at the national level. As a result, existing data on relative abundance are often not directly comparable, limiting understanding of patterns and drivers of diversity loss. A worldwide monitoring system with a standardized sampling protocol would help fill data gaps, increase explanatory power, streamline analyses, and facilitate the development of a global monitoring network (Montgomery et al., 2021). This need not require abandoning successful monitoring networks, even if they differ in methodology, but rather a pragmatic realignment of existing monitoring efforts focusing on standardization (Montgomery et al., 2021). Standardizing sampling efforts by habitat, region, and season would seem a relatively simple task. Computational optimization tools exist for both the sampling protocols, and their adoption would enable monitoring beyond what is possible with ad hoc sampling.

Finally, monitoring methods based on machine learning should be rapidly adopted (Høye et al., 2021). Cameras coupled with deep learning models can be used to identify insects to some taxonomic level and eventually automate count and biomass data collection. It might be possible to automatically identify most adult ladybirds to species level, track their abundances in space and time, and relate these to alert systems that pinpoint when and where species are declining or altering their range (Venegas et al., 2021).

ASSESSING, PLANNING, AND ACTING

The IUCN Species Survival Commission (SSC) recently adopted a strategic approach to species conservation, the Species Conservation Cycle (https://www.iucn.org/commissions/species-survival-commission/our-work). At its core are 3 components: assess (red-list assessments, identification of key biodiversity areas, etc.), plan (strategic conservation planning), and act (implementation of actions and policies). To date, no ladybird species have been assessed for the IUCN Red List, but the recent establishment of an IUCN SSC Ladybird Specialist Group raises hope in this regard. Although red-list assessments do not necessarily prevent extinctions, they may instigate conservation actions, as they have for other invertebrates (e.g., Bröder et al., 2020). The IUCN Red List is a leading indicator of global biodiversity trends (Stuart et al., 2010), and representation of ladybirds on it will be crucial to placing this group on international agendas. In addition to species-specific conservation plans, mitigation of pesticide impacts on ladybirds should be a global priority. Ladybird experts need to engage and collaborate with nongovernmental organizations, conservation authorities, protected area managers, and other actors to achieve these ends. Citizen science and public engagement projects could also play an important role. Targeted species conservation projects at the local level may serve as lighthouse projects to instigate similar projects elsewhere. Monitoring will be an important tool to evaluate the success of such projects, but rare and threatened species will require a more targeted approach because these are not recorded frequently enough to infer population trends (Potts et al., 2020). Such data, however, are crucial to monitoring conservation success and enabling red-list and green-status assessments (Akçakaya et al., 2018) as well as key biodiversity area assessments (International UniCN, 2016).

CHALLENGES AND OPPORTUNITIES

Even though ladybirds are subject to many anthropogenic threats and may serve as flagship species for insect preservation for aforementioned reasons, few ongoing projects directly address their conservation and recovery. A number of dilemmas and shortfalls prevent effective conservation strategies (Cardoso et al., 2011). Ladybirds, especially their ecological services, are in part unknown to the general public (public dilemma), policy makers and stakeholders are mostly unaware of ladybird conservation issues (political dilemma), basic research on their biology and ecology is scarce and underfunded (scientific dilemma), a considerable part of their estimated species diversity is still undescribed (Linnean shortfall), the distribution of described species remains largely unknown (Wallacean shortfall), the abundance of species and their changes in space and time are unknown (Prestonian shortfall), and the functional role of ladybirds and their sensitivities to habitat change are largely unknown (Hutchinsonian shortfall).

Active collaborations among professionals and citizen scientists, conservation practitioners, and policy makers are essential for sharing information, coordinating data collection, prioritizing research objectives, and disseminating results. Efforts will be spearheaded by the IUCN SSC Ladybird Specialist Group to address the gaps of assessment and prioritization, in light of the adoption of strategic plans for species conservation. The scarcity of information outlined above restricts assessments, prioritization, and implementation of conservation programs for ladybirds. We highlighted the increasing importance of maintaining natural areas and landscape heterogeneity in urban and agricultural contexts and reducing the application of pesticides. Management of invasive species is a priority, but the prevention

15231739, 2023, 1, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/cobi.13965 by Universidade Dos Acores, Wiley Online Library on [06/02/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

of introductions is preferable. Many questions remain regarding potential responses of ladybirds to climate change and habitat destruction, and these provide new research opportunities. Recommendations for ladybird protection should inform legislative actions and be supplemented with education and public awareness programs. Long-term public–private partnerships, supported by sustainable financing, should aim to restore and protect vital insect habitats while managing key threats.

ACKNOWLEDGMENTS

We dedicate this paper to the memory of Dr. Ivo Hodek (1931–2021) who was and remains an inspiration to us all. Ivo was a pioneer in ladybird conservation research, leader of the international community of researchers of aphidophagous insects, and author of fundamental books on the biology and ecology of ladybirds. A.O.S. and I.B. were financed 85% by FEDER and 15% by Azorean Public funds through Operational Program Azores 2020 under the following projects: AZORESBIOPORTAL – PORBIOTA (ACORES-01-0145-FEDER-000072) and ECO^2 – TUTA (ACORES-01-0145-FEDER-000081). The work of D.H. and M.D.d.G. is supported by the Research Foundation – Flanders (Junior Postdoctoral Fellowship 1206620N to D.H., Fundamental Research Fellowship 1142722N to M.D.d.G.). O.M.C.C.A. and A.I.L. thank CESAM and FCT/MCTES for the financial support through national funds (UIDP/50017/2020, UIDB/50017/2020, LA/P/0094/2020). O.M.C.C.A. is funded by national funds (OE), through FCT, in the scope of the framework contract foreseen in the numbers 4, 5, and 6 of article 23 of the Decree-Law 57/2016 of 29 August, changed by Law 57/2017 of 19 July. A.A.G. and T.Z. are supported by the National Fund for Scientific and Technological Development of the Government of Chile (FONDECYT 1180533). A.H., Z.M., and J.S. were supported by VES19 INTER-COST MSMT-15739/2019-6, and grants from the National Agency for Agricultural Research (QK 1910281) and the Ministry of Agriculture of the Czech Republic (RO0418). M.H., J.K., and P.Z. were supported by the grant VEGA 2/0032/19 of the Scientific Grant Agency of the Ministry of Education, Science, Research and Sport of the Slovak Republic. H.E.R. is supported by the Natural Environment Research Council, award number NE/R016429/1, as part of the UK-SCAPE program delivering National Capability. A.S. was supported by the EcoTeBo project (ANR-19-CE02-0001-01) from the French National Research Agency (ANR).

ORCID

António O. Soares https://orcid.org/0000-0001-7922-6296
Danny Haelewaters https://orcid.org/0000-0002-6424-0834
Olga M. C. C. Ameixa https://orcid.org/0000-0002-5422-1090
Peter M. J. Brown https://orcid.org/0000-0002-6163-4504
Pedro Cardoso https://orcid.org/0000-0001-8119-9960
Michiel D. de Groot https://orcid.org/0000-0002-0406-1076
Edward W. Evans https://orcid.org/0000-0002-7273-7744
Audrey A. Grez https://orcid.org/0000-0002-6907-1283
Axel Hochkirch https://orcid.org/0000-0002-4475-0394
Alois Honěk https://orcid.org/0000-0002-0460-4798
Ana I. Lillebo https://orcid.org/0000-0002-5228-0329
Zdenka Martinková https://orcid.org/0000-0003-3402-9242
Oldřich Nedvěd https://orcid.org/0000-0001-9932-3456
Omkar https://orcid.org/0000-0002-0218-3184
Helen E. Roy https://orcid.org/0000-0001-6050-679X
Swati Saxena https://orcid.org/0000-0003-2970-0265
Apoorva Shandilya https://orcid.org/0000-0002-8647-3110
Arnaud Sentis https://orcid.org/0000-0003-4617-3620
Jiri Skuhrovec https://orcid.org/0000-0002-7691-5990
Tania Zaviezo https://orcid.org/0000-0002-4993-0386

REFERENCES

Adriaens, T., San Martin y Gomez, G., Bogeart, J., Crevecoeur, L., Beuckx, J.-P., & Maes, D. (2015). Testing the applicability of regional ICUN Red List Criteria on ladybirds (Coeloptera, Coccinellidae) in Flanders (north Belgium): Opportunities for conservation. *Insect Conservation and Diversity*, *8*, 404–417.

Akçakaya, H. R., Bennett, E. L., Brooks, T. M., Grace, M. K., Heath, A., Hedges, S., Hilton-Taylor, C., Hoffmann, M., Keith, D. A., Long, B., Mallon, D. P., Meijaard, E., Milner-Gulland, E. J., Rodrigues, A. S. L., Rodriguez, J. P., Stephenson, P. J., Stuart, S. N., & Young, R. P. (2018). Quantifying species recovery and conservation success to develop, an IUCN Green List of Species. *Conservation Biology*, *32*, 1128–1138.

Alyokhin, A., & Sewell, G. (2004). Changes in a lady beetle community following the establishment of three alien species. *Biological Invasions*, *6*, 463–471.

Ameixa, O. M. C. C., Soares, A. O., Soares, A. M. V. M., & Lillebø, A. I. (2018). Ecosystem services provided by the little things that run the world. In B. Şen & O. Grillo (Eds.), *Selected studies in biodiversity* (pp. 267–302). IntechOpen Limited.

Bahlai, C. A., Colunga-Garcia, M., Gage, S. H., & Landis, D. A. (2013). Long-term functional dynamics of an aphidophagous coccinellid community remain unchanged despite repeated invasions. *PLoS ONE*, *8*, e83407.

Bonebrake, T. C., Guo, F., Dingle, C., Baker, D. M., Kitching, R. L., & Ashton, L. A. (2019). Integrating proximal and horizon threats to biodiversity for conservation. *Trends in Ecology & Evolution*, *34*, 781–788.

Booy, O., Mill, A. C., Roy, H. E., Hiley, A., Moore, N., Robertson, P., Baker, S., Brazier, M., Bue, M., Bullock, R., Campbell, S., Eyre, D., Foster, J., Hatton-Ellis, M., Long, J., Macadam, C., Morrison-Bell, C., Mumford, J., Newman, J., … Wyn, G. (2017). Risk management to prioritise the eradication of new and emerging invasive non-native species. *Biological Invasions*, *19*, 2401–2417.

Borges, P. A. V., Cardoso, P., Kreft, H., Whittaker, R. J., Fattorini, S., Emerson, B. C., Gil, A., Gillespie, R. G., Matthews, T. J., Santos, A. M. C., Steinbauer, M. J., Thébaud, C., Ah-Peng, A., Amorim, I. R., Aranda, S. C., Arroz, A. M., Azevedo, J. M. N., Boieiro, M., Borda-de-Água, L., & Gabriel, R. (2018). Global Island Monitoring Scheme (GIMS): A proposal for the long-term coordinated survey and monitoring of native island forest biota. *Biodiversity and Conservation*, *27*, 2567–2586.

Boullis, A., Detrain, C., Francis, F., & Verheggen, F. J. (2016). Will climate change affect insect pheromonal communication? *Current Opinion in Insect Science*, *17*, 87–91.

Bredeson, M. M., & Lundgren, J. G. (2019). Thiamethoxam seed treatments reduce foliar predator and pollinator populations in sunflowers (*Helianthus annuus*), and extra-floral nectaries as a route of exposure for seed treatments to affect the predator, *Coleomegilla maculata* (Coleoptera: Coccinellidae). *Crop Protection*, *106*, 86–92.

Bröder, L., Tatin, L., Hochkirch, A., Schuld, A., Pabst, L., & Besnard, A. (2020). Optimization of capture–recapture monitoring of elusive species illustrated with a threatened grasshopper. *Conservation Biology*, *34*, 743–753.

Brown, P. M. J., & Roy, H. E. (2018). Decline in native ladybird species caused by the invasive harlequin ladybird *Harmonia axyridis*: Evidence from a long-term field study. *Insect Conservation & Diversity*, *11*, 230–239.

Bruno, J. F., & Cardinale, B. J. (2008). Cascading effects of predator richness. *Frontiers in Ecology and the Environment*, *6*, 539–546.

15231739, 2023, 1, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/cobi.13965 by Universidade Dos Acores, Wiley Online Library on [06/02/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Bush, A., Mokany, K., Catullo, R., Hoffmann, A., Kellermann, V., Sgrò, C., McEvey, S., & Ferrier, S. (2016). Incorporating evolutionary adaptation in species distribution modelling reduces projected vulnerability to climate change. *Ecology Letters*, *19*, 1468–1478.

Caballero-López, B., Bommarco, R., Blanco-Moreno, J. M., Sans, F. X., Pujade-Villar, J., Rundlöf, M., & Smith, H. G. (2012). Aphids and their natural enemies are differently affected by habitat features at local and landscape scales. *Biological Control*, *63*, 222–229.

Camacho-Cervantes, M., Ortega-Iturriaga, A., & Del-Val, E. (2017). From effective biocontrol agent to successful invader: the harlequin ladybird (*Harmonia axyridis*) as an example of good ideas that could go wrong. *PeerJ*, *16*, e3296.

Cardoso, P., Borges, P. A. V., Triantis, K. A., Ferrández, M. A., & Martín, J. L. (2011). Adapting the IUCN Red List criteria for invertebrates. *Biological Conservation*, *144*, 2432–2440.

Cardoso, P., Erwin, T. L., Borges, P. A. V., & New, T. R. (2011). The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation*, *144*, 2647–265.

Costopoulos, K., Kovacs, J. L., Kamins, A., & Gerardo, N. M. (2014). Aphid facultative symbionts reduce survival of the predatory lady beetle *Hippodamia convergens*. *BMC Ecology*, *14*, 5.

Dasgupta, P. (2021). *The economics of biodiversity: The Dasgupta review*. HM Treasury.

Day, W. H., & Tatman, K. M. (2006). Changes in abundance of native and adventive Coccinellidae (Coleoptera) in alfalfa fields, in northern New Jersey (1993-2004) and Delaware (1999-2004), U.S.A. *Entomological News*, *117*, 491–502.

de Jong, P. W., & Brakefield, P. M. (1998). Climate and change in clines for melanism in the two-spot ladybird, *Adalia bipunctata* (Coleoptera: Coccinellidae). *Proceedings of the Royal Society of London, Series B, Biological Sciences*, *265*, 39–43.

Derocles, S. A. P., Lunt, D. H., Berthe, S. C. F., Nichols, P. C., Moss, E. D., & Evans, D. M. (2018). Climate warming alters the structure of farmland tritrophic ecological networks and reduces crop yield. *Molecular Ecology*, *27*, 4931–4946.

Díaz, S., Settele, J., Brondízio, E. S., Ngo, H. T., Agard, J., Arneth, A., Balvanera, P., Brauman, K. A., Butchart, S. H. M., Chan, K. M. A., Garibaldi, L. A., Ichii, K., Liu, J., Subramanian, S. M., Midgley, G. F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., & Zayas, C. N. (2019). Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science*, *366*, eaax3100.

Dixon, A. F., Honek, A., Keil, P., Kotela, M. A. A., Šizling, A. L., & Jarošík, V. (2009). Relationship between the minimum and maximum temperature thresholds for development in insects. *Functional Ecology*, *23*, 257–264.

Dixon, A. F. G., Jarošik, V., & Honek, A. (2005). Thermal requirements for development and resource partitioning in aphidophagous guilds. *European Journal of Entomology*, *102*, 407–411.

Donelson, J. M., Salinas, S., Munday, P. L., & Shama, L. N. S. (2018). Transgenerational plasticity and climate change experiments: Where do we go from here? *Global Change Biology*, *4*, 13–34.

Eggleton, P. (2020). The state of the world's insects. *Annual Review of Environment and Resources*, *45*, 61–82.

Egerer, M., Li, K., & Ong, T. W. Y. (2018). Context matters: Contrasting ladybird beetle responses to urban environments across two US regions. *Sustainability*, *10*, 1829.

Evans, E. W. (2017). Fates of rare species under siege from invasion: Persistence of *Coccinella novemnotata* Herbst in western North America alongside an invasive congener. *Frontiers in Ecology and Evolution*, *5*, 152.

Fahrig, L., Baudry, J., Brotons, L., Burel, F. G., Crist, T. O., Fuller, R. J., Sirami, C., Siriwardena, G. V., & Martin, J. L. (2011). Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. *Ecology Letters*, *14*, 101–112.

Gardiner, M. M., Landis, D. A., Gratton, C., Schmidt, N., O'Neal, M., Mueller, E., Chacon, J., Heimpel, G. E., & DiFonzo, C. D. (2009). Landscape composition influences patterns of native and exotic lady beetle abundance. *Diversity and Distribution*, *15*, 554–564.

Gardiner, M. M., Allee, L. L., Brown, P. M. J., Losey, J. E., Roy, H. E., & Smyth, R. R. (2012). Lessons from lady beetles: Accuracy of monitoring data from US and UK citizen-science programs. *Frontiers in Ecology and the Environment*, *10*, 471–476.

Gardiner, M. M., Prajzner, S. P., Burkman, C. E., Sandra, A., & Grewal, P. S. (2013). Vacant land conversion to community gardens: Influences on generalist arthropod predators and biocontrol services in urban greenspaces. *Urban Ecosystems*, *17*, 101–122.

Gardiner, M. M., Perry, K. I., Riley, C. B., Turo, K. J., Delgado de la flor, Y. A., & Sivakoff, F. S. (2021). Community science data suggests that urbanization and forest habitat loss threaten aphidophagous native lady beetles. *Ecology and Evolution*, *11*, 2761–2774.

Gardiner, M. M., & Roy, H. E. (2022). The role of community science in entomology. *Annual Review of Entomology*, *67*, 437–456.

Gontijo, L. M. (2019). Engineering natural enemy shelters to enhance conservation biological control in field crops. *Biological Control*, *130*, 155–163.

Gordon, R. D. (1985). The Coccinellidae (Coleoptera) of America North of Mexico. *Journal of the New York Entomological Society*, *93*, 1–912.

Grez, A. A., Rand, T. A., Zaviezo, T., & Castillo-Serey, F. (2013). Land use intensification differentially benefits alien over native predators in agricultural landscape mosaics. *Diversity and Distributions*, *19*, 749–759.

Grez, A. A., Zaviezo, T., Casanoves, F., Oberti, R., & Pliscoff, P. (2021). The positive association between natural vegetation, native coccinellids and functional diversity of aphidophagous coccinellid communities in alfalfa. *Insect Conservation and Diversity*, *14*, 464–475.

Grez, A. A., Zaviezo, T., Gardiner, M. M., & Alaniz, A. J. (2019). Urbanization filters coccinellids composition and functional trait distributions in greenspaces across greater Santiago, Chile. *Urban Forestry & Urban Greening*, *38*, 337–345.

Grez, A. A., Zaviezo, T., Roy, H. E., Brown, P. M. J., & Bizama, G. (2016). Rapid spread of *Harmonia axyridis* in Chile and its effects on local coccinellid biodiversity. *Diversity and Distributions*, *22*, 982–994.

Groom, Q., Pernat, N., Adriaens, T., de Groot, M., Jelaska, S. D., Marčiulynienė, D., Martinou, A. F., Skuhrovec, J., Tricarico, E., Wit, E. T., & Roy, H. E. (2021). Species interactions: Next level citizen science. *Ecography*, *44*, 1781–1789.

Gutierrez, A. P., Ponti, L., d'Oultremont, T., & Ellis, C. K. (2008). Climate change effects on poikilotherm tritrophic interactions. *Climatic Change*, *87*, 167–192.

Haelewaters, D., Hiller, T., Ceryngier, P., Eschen, R., Gorczak, M., Houston, M. L., Kisło, K., Knapp, M., Landeka, N., Pfliegler, W. P., Zach, P., Aime, M. C., & Nedvěd, O. (2022). Do biotic and abiotic factors influence the prevalence of a common parasite of the invasive alien ladybird *Harmonia axyridis*? *Frontiers in Ecology and Evolution*, *10*, 773423.

Haelewaters, D., Hiller, T., Kemp, E. A., van Wielink, P. S., Shapiro-Ilan, D. I., Aime, M. C., Nedvěd, O., Pfister, D. H., & Cottrell, T. E. (2020). Mortality of native and invasive ladybirds co-infected by ectoparasitic and entomopathogenic fungi. *PeerJ*, *8*, e10110.

Haelewaters, D., Zhao, S. Y., Clusella-Trullas, S., Cottrell, T. E., De Kesel, A., Fiedler, L., Herz, A., Hesketh, H., Hui, C., Kleespies, R. G., Losey, J. E., Minnaar, I. A., Murray, K. M., Nedvěd, O., Pfliegler, W. P., Raak-van den Berg, C. L., Riddick, E. W., Shapiro-Ilan, D. I., Smyth, R. R., … Roy, H. E. (2017). Parasites of *Harmonia axyridis*: Current research and perspectives. *BioControl*, *62*, 355–371.

Harmon, J. P., Moran, N. A., & Ives, A. R. (2009). Species response to environmental change: Impacts of food web interactions and evolution. *Science*, *323*, 1347–1350.

Harvey, J. A., Heinen, R., Klein, A.-M., Armbrecht, I., Basset, Y., Baxter-Gilbert, J. H., Bezemer, M., Böhm, M., Bommarco, R., Borges, P. A. V., Cardoso, P., Clausnitzer, V., Cornelisse, T., Crone, E. E., Goulson, D., Dicke, M., Dijkstra, K.-D. B., Dyer, L., Ellers, J., … de Kroon, H. (2020). International scientists formulate a roadmap for insect conservation and recovery. *Nature Ecology & Evolution*, *4*, 174–176.

Harvey, J. A., Heinen, R., Gols, R., & Thakur, M. P. (2020). Climate change-mediated temperature extremes and insects: From outbreaks to breakdowns. *Global Change Biology*, *26*, 6685–6701.

Hawkins, C. L., Bacher, S., Essl, F., Hulme, P. E., Jeschke, J. M., Kuehn, I., Kumschick, S., Nentwig, W., Pergl, J., Pysek, P., Rabitsch, W., Richardson, D. M., Vila, M., Wilson, J. R. U., Genovesi, P., & Blackburn, T. M. (2015). Framework and guidelines for implementing the proposed IUCN Environmental

15231739, 2023, 1, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/cobi.13965 by Universidade Dos Acores, Wiley Online Library on [06/02/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Impact Classification for Alien Taxa (EICAT). *Diversity and Distributions*, *21*, 1360–1363.

Hiller, T., & Haelewaters, D. (2019). A case of silent invasion: Citizen science confirms the presence of *Harmonia axyridis* (Coleoptera, Coccinellidae) in Central America. *PLoS ONE*, *14*, e0220082.

Hochkirch, A., Samways, M., Gerlach, J., Bohm, M., Williams, P., Cardoso, P., Cumberlidge, N., Stephenson, P. J., Seddon, M., Clausnitzer, V., Borges, P. A. V., Mueller, G., Pearce-Kelly, P., Raimondo, D. C., Danielczak, A., & Dijkstra, K.-D. (2020). A strategy for the next decade to address data deficiency in neglected biodiversity. *Conservation Biology*, *35*, 502–509.

Hodek, I., van Emden, H. F., & Honek, A. (2012). *Ecology and behaviour of the ladybird beetles (Coccinellidae)*. Wiley–Blackwell.

Holland, J. M., Jeanneret, P., Moonen, A. C., van der Werf, W., Rossing, W. A., Antichi, D., Entling, M. H., Giffard, B., Helsen, H., Szalai, M., & Rega, C. (2020). Approaches to identify the value of seminatural habitats for conservation biological control. *Insects*, *11*, 195.

Honek, A. (2012). Distribution and habitats. In I. Hodek, H. F. van Emden, & A. Honek (Eds.), *Ecology and behaviour of the ladybird beetles (Coccinellidae)* (pp. 110–139). Wiley-Blackwell.

Honek, A., Dixon, A. F. G., Soares, A. O., Skuhrovec, J., & Martinkova, Z. (2017). Spatial and temporal changes in the abundance and composition of ladybird (Coleoptera: Coccinellidae) communities. *Current Opinion in Insect Science*, *20*, 61–67.

Høye, T. T., Ärje, J., Bjerge, K., Hansen, O. L. P., Iosifidis, A., Leese, F., Mann, H. M. R., Meissner, K., Melvad, C., & Raitoharju, J. (2021). Deep learning and computer vision will transform entomology. *Proceedings of the National Academy of Sciences of the United States of America*, *118*, e2002545117.

Hullé, M., d'Acier, A. C., Bankhead-Dronnet, S., & Harrington, R. (2010). Aphids in the face of global changes. *Comptes Rendus Biologies*, *333*, 497–503.

International Union for Conservation of Nature. (2016). *A Global Standard for the Identification of Key Biodiversity Areas*, Version 1.0. International Union for Conservation of Nature and Natural Resources. https://portals.iucn.org/union/sites/union/files/doc/a_global_standard_for_the_identification_of_key_biodiversity_areas_final_web.pdf

Jouveau, S., Delaunay, M., Vignes-Lebbe, R., & Nattier, R. (2018). A multi-access identification key based on colour patterns in ladybirds (Coleoptera, Coccinellidae). *ZooKeys*, *758*, 55–73.

Iuliano, B., & Gratton, C. (2020). Temporal resource (dis)continuity for conservation biological control: From field to landscape scales. *Frontiers in Sustainable Food Systems*, *4*, 127.

Kindlmann, P., Ameixa, O. M. C. C., & Dixon, A. F. G. (2011). Ecological effects of invasive alien species on native communities, with particular emphasis on the interactions between aphids and ladybirds. *BioControl*, *56*, 469–476.

Kovář, I. (2007). Coccinellidae. In I. Löbl & A. Smetana (Eds.), *Catalogue of Palaearctic Coleoptera. Volume 4. Elateroidea, Derodontoidea, Bostrichoidea, Lymexyloidea, Cleroidea, and Cucujoidea* (pp. 568–632). Apollo Books.

Landis, D. A., Wratten, S. D., & Gurr, G. M. (2000). Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology*, *45*, 175–201.

Li, H., Li, B., Lovei, G. L., Kring, T. J., & Obrycki, J. J. (2021). Interactions among native and non-native predatory Coccinellidae influence biological control and biodiversity. *Annals of the Entomological Society of America*, *114*, 119–136.

Lichtenberg, E. M., Kennedy, C. M., Kremen, C., Batáry, P., Berendse, F., Bommarco, R., Bosque-Pérez, N. A., Carvalheiro, L. G., Snyder, W. E., Williams, N. M., Winfree, R., Klatt, B. K., Åström, S., Benjamin, F., Brittain, C., Chaplin-Kramer, R., Clough, Y., Danforth, B., Diekötter, T., … Crowder, D. M. (2017). A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. *Global Change Biology*, *23*, 4946–4957.

Losey, J. E., Allee, L., & Smyth, R. (2012). The Lost Ladybug Project: Citizen spotting surpasses scientist's surveys. *American Entomologist*, *58*, 22–24.

Mammola, S., Riccardi, N., Prié, V., Correia, R., Cardoso, P., Lopes-Lima, M., & Sousa, R. (2020). Towards a taxonomically unbiased European Union biodiversity strategy for 2030. *Proceedings of the Royal Society B: Biological Sciences*, *287*, 20202166.

Michaud, J. P. (2000). Development and reproduction of lady beetles (Coleoptera: Coccinellidae) on the citrus aphids *Aphis spiraecola* Patch and *Toxoptera citricida* (Kirkaldy) (Homoptera: Aphididae). *Biological Control*, *18*, 287–297.

Michaud, J. P. (2002). Invasion of the Florida citrus ecosystem by *Harmonia axyridis* (Coleoptera: Coccinellidae) and asymmetric competition with a native species, *Cycloneda sanguinea*. *Environmental Entomology*, *31*, 827–835.

Michaud, J. P. (2018). Challenges to the conservation biological control of agricultural pests on the High Plains: One hundred years of evolutionary rescue. *Biological Control*, *125*, 65–73.

Michie, L. J., Masson, A., Ware, R. L., & Jiggins, F. M. (2011). Seasonal phenotypic plasticity: Wild ladybirds are darker at cold temperatures. *Evolutionary Ecology*, *25*, 1259–1268.

Montgomery, G. A., Belitz, M. W., Guralnick, R. P., & Tingley, M. W. (2021). Standards and best practices for monitoring and benchmarking insects. *Frontiers in Ecology and Evolution*, *8*, 579193.

Moscardini, V. F., Gontijo, P. C., Michaud, J. P., & Carvalho, G. A. (2015). Sublethal effects of two sunflower seed treatments on two nearctic lady beetles. *Ecotoxicology*, *24*, 1152–1161.

Muñoz, A. E., Amouroux, P., & Zaviezo, T. (2021). Native flowering shrubs promote beneficial insects in avocado orchards. *Agricultural and Forest Entomology*, *23*, 463–472.

Ma, C. S., Ma, G., & Pincebourde, S. (2021). Survive a warming climate: Insect responses to extreme high temperatures. *Annual Review of Entomology*, *66*, 163–184.

Palmer, J. R. B., Oltra, A., Collantes, F., Delgado, J. A., Lucientes, J., Delacour, S., Bengoa, M., Eritja, R., & Bartumeus, F. (2017). Citizen science provides a reliable and scalable tool to track disease-carrying mosquitoes. *Nature Communications*, *8*, 916.

Pfliegler, W. P., Báthori, F., Wang, T. W., Tartally, A., & Haelewaters, D. (2018). *Herpomyces* ectoparasitic fungi (Ascomycota, Laboulbeniales) are globally distributed by their invasive cockroach hosts and through the pet trade industry. *Mycologia*, *110*, 39–46.

Porter, W. T., Motyka, P. J., Wachara, J., Barrand, Z. A., Hmood, Z., McLaughlin, M., Pemberton, K., & Nieto, N. C. (2019). Citizen science informs human-tick exposure in the Northeastern United States. *International Journal of Health Geographics*, *18*, 9.

Potts, S., Dauber, J., Hochkirch, A., Oteman, B., Roy, D., Ahnre, K., Biesmeijer, K., Breeze, T., Carvell, C., Ferreira, C., Fitzpatrick, Ú., Isaac, N., Kuussaari, M., Ljubomirov, T., Maes, J., Ngo, H., Pardo, A., Polce, C., Quaranta, M., … Vujic, A. (2020). *Proposal for an EU pollinator monitoring scheme* (EUR 30416 EN). Publications Office of the European Union. https://doi.org/10.2760/881843

Pyšek, P., Hulme, P. E., Simberloff, D., Bacher, S., Blackburn, T. M., Carlton, J. T., Dawson, W., Essl, F., Foxcroft, L. C., Genovesi, P., Jeschke, J. M., Kühn, I., Liebhold, A. M., Mandrak, N. E., Meyerson, L. A., Pauchard, A., Pergl, J., Roy, H. E., Seebens, H., … Richardson, D. M. (2020). Scientists' warning on invasive alien species. *Biological Review*, *95*, 1511–1534.

Radwan, Z., & Lövei, G. L. (1983). Structure and seasonal dynamics of larval, pupal, and adult coccinellid (Col., Coccinellidae) assemblages in two types of maize fields in Hungary. *Zeitschrift für Angewandte Entomologie*, *95*, 396–408.

Roy, H. E., Brown, P. M. J., Adriaens, T., Berkvens, N., Borges, I., Clusella-Trullas, S., Comont, R. F., de Clercq, P., Eschen, P., Estoup, A., Evans, E. W., Facon, B., Gardiner, M. M., Gil, A., Grez, A. A., Guillemaud, T., Haelewaters, D., Herz, A., Honek, A., … Zhao, Z. (2016). The harlequin ladybird, *Harmonia axyridis*: Global perspectives on invasion history and ecology. *Biological Invasions*, *18*, 997–1044.

Roy, H., & Migeon, A. (2010). Ladybeetles (Coccinellidae). *BioRisk*, *4*, 293–313.

Roy, H. E., Rabitsch, W., Scalera, R., Stewart, A., Gallardo, B., Genovesi, P., Essl, F., Adriaens, T., Bacher, S., Booy, O., Branquart, E., Brunel, S., Copp, G. H., Dean, H., D'hondt, B., Josefsson, M., Kenis, M., Kettunen, M., & Zenetos, A. (2018). Developing a framework of minimum standards for the risk assessment of alien species. *Journal of Applied Ecology*, *55*, 526–538.

Roy, H. E., Peyton, J. M., & Booy, O. (2020). Guiding principles for utilizing social influence within expert-elicitation to inform conservation decision-making. *Global Change Biology*, *26*, 3181–3184.

15231739, 2023, 1, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/cobi.13965 by Universidade Dos Acores, Wiley Online Library on [06/02/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Sakuratani, Y., Marsumoto, Y., Oka, M., Kubo, T., Fuji, A., Uotani, M., & Teraguchi, T. (2000). Life history of *Adalia bipunctata* (Coleoptera: Coccinellidae) in Japan. *European Journal of Entomology*, *97*, 555–558.

Saunders, M. E., Janes, J. K., & O'Hanlon, J. C. (2020). Semantics of the insect decline narrative: Recommendations for communicating insect conservation to peer and public audiences. *Insect Conservation and Diversity*, *13*, 211–213.

Samways, M. J., Barton, P. S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C. S., Gaigher, R., Habel, J. C., Hallmann, C. A., Hill, M. J., Hochkirch, A., Kaila, L., Kwak, M. L., Maes, D., Mammola, S., Noriega, J. A., Orfinger, A. B., Pedraza, F., … Cardoso, P. (2020). Solutions for humanity on how to conserve insects. *Biological Conservation*, *242*, 108427.

Schmitz, O. J., & Barton, B. T. (2014). Climate change effects on behavioral and physiological ecology of predator–prey interactions: Implications for conservation biological control. *Biological Control*, *75*, 87–96.

Seebens, H., Blackburn, T., Dyer, E., Genovesi, P., Hulme, P. E., Jeschke, J. M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G., Capinha, C., Celesti-Grapow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H., … Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, *8*, 14435.

Sentis, A., Hemptinne, J. L., & Brodeur, J. (2012). Using functional response modelling to investigate the effect of temperature on predator feeding rate and energetic efficiency. *Oecologia*, *169*, 1117–1125.

Sentis, A., Hemptinne, J. L., & Brodeur, J. (2013). Effects of simulated heat waves on an experimental plant–herbivore–predator food chain. *Global Change Biology*, *19*, 833–842.

Sentis, A., Hemptinne, J. L., & Brodeur, J. (2014). Towards a mechanistic understanding of temperature and enrichment effects on species interaction strength, omnivory and food-web structure. *Ecology Letters*, *17*, 785–793.

Sentis, A., Morisson, J., & Boukal, D. S. (2015). Thermal acclimation modulates the impacts of temperature and enrichment on trophic interaction strengths and population dynamics. *Global Change Biology*, *21*, 3290–3298.

Sentis, A., Ramon-Portugal, F., Brodeur, J., & Hemptinne, J. L. (2015). The smell of change: Warming affects species interactions mediated by chemical information. *Global Change Biology*, *21*, 3586–3594.

Sequeira, A. M., Roetman, P. E., Daniels, C. B., Baker, A. K., & Bradshaw, C. J. (2014). Distribution models for koalas in South Australia using citizen science-collected data. *Ecology and Evolution*, *4*, 2103–2114.

Skirvin, D. J., Perry, J. N., & Harrington, R. (1997). The effect of climate change on an aphid–coccinellid interaction. *Global Change Biology*, *3*, 1–11.

Skuhrovec, J., Roy, H. E., Brown, P. M. J., Kazlauskis, K., Inghilesi, A. F., Soares, A. O., Adriaens, T., Roy, D. B., Nedvěd, O., Zach, P., Vigláśová, S., Kulfan, J. A., Honek, A., & Martinkova, Z. (2021). Development of the European ladybirds smartphone application: A tool for citizen science. *Frontiers in Ecology and Evolution*, *9*, 741854.

Sloggett, J. J. (2005). Are we studying too few taxa? Insights from aphidophagous ladybird beetles (Coleoptera: Coccinellidae). *European Journal of Entomology*, *102*, 391–398.

Sloggett, J. J. (2017). *Harmonia axyridis* (Coleoptera: Coccinellidae) smelling the rat in native ladybird declines. *European Journal of Entomology*, *114*, 455–461.

Sloggett, J. J., & Majerus, M. E. N. (2000). Habitat preferences and diet in the predatory Coccinellidae (Coleoptera): An evolutionary perspective. *Biological Journal of the Linnean Society*, *70*, 63–88.

Sloggett, J. J., & Zeilstra, I. (2020). Geographic variation in the habitat preference of a scarce predatory insect: Evolutionary and conservation perspectives. *Ecological Entomology*, *45*, 386–395.

Soares, A. O., Coderre, D., & Schanderl, H. (2003). Effect of temperature and intraspecific allometry on predation by two phenotypes of *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae). *Environmental Entomology*, *32*, 939–944.

Soares, A. O., Honek, A., Martinkova, Z., Brown, P. M. J., & Borges, I. (2018). Can native geographical range, dispersal ability and development rates predict the successful establishment of alien ladybird (Coleoptera: Coccinellidae) species in Europe? *Frontiers in Ecology and Evolution*, *6*, 57.

Stuart, S. N., Wilson, E. O., McNeely, J. A., Mittermeier, R. A., & Rodríguez, J. P. (2010). The barometer of life. *Science*, *328*, 177.

Susset, E. C., Magro, A., & Hemptinne, J. L. (2017). Using species distribution models to locate animal aggregations: A case study with *Hippodamia undecimnotata* (Schneider) overwintering aggregation sites. *Ecological Entomology*, *42*, 345–354.

Takahashi, K., & Naito, A. (1984). Seasonal occurrence of aphids and their predators (Col., Coccinellidae) in alfalfa fields. *Bulletin of the National Grassland Research Institute*, *29*, 62–66.

Tomaszewska, W., Escalona, H. E., Hartley, D., Li, J. H., Wang, X. M., Li, H. S., Pang, H., Slipinski, A., & Zwick, A. (2021). Phylogeny of true ladybird beetles (Coccinellidae: Coccinellini) reveals pervasive convergent evolution and a rapid Cenozoic radiation. *Systematic Entomology*, *46*, 611–631.

Trumble, J., & Butler, C. (2009). Climate change will exacerbate California's insect pest problems. *California Agriculture*, *63*, 73–78.

van Klink, R., Bowler, D. E., Gongalsky, K. B., Swengel, A. B., Gentile, A., & Chase, J. M. (2020). Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science*, *368*, 417–420.

van Lenteren, J. C., Babendreier, D., Bigler, F., Burgio, G., Hokkanen, H. M. T., Kuske, S., Loomans, A. J. M., Menzler-Hokkanen, I., van Rijn, P. C. J., Thomas, M. B., Tommasini, M. G., & Zeng, Q.-Q. (2003). Environmental risk assessment of exotic natural enemies used in inundative biological control. *BioControl*, *48*, 3–38.

Vanderhoeven, S., Branquart, E., Casaer, J., D'hondt, B., Hulme, P. E., Shwartz, A., Strubbe, D., Turbé, A., Verreycken, H., & Adriaens, T. (2017). Beyond protocols: Improving the reliability of expert-based risk analysis underpinning invasive species policies. *Biological Invasions*, *19*, 2507–2517.

Vasseur, D. A., DeLong, J. P., Gilbert, B., Greig, H. S., Harley, C. D. G., McCann, K. S., Savage, V., Tunney, T. D., & O'Connor, M. I. (2014). Increased temperature variation poses a greater risk to species than climate warming. *Proceedings of the Royal Society B: Biological Sciences*, *281*, 20132612.

Venegas, P., Calderon, F., Riofrío, D., Benítez, D., Ramón, G., Cisneros-Heredia, D., Coimbra, M., Rojo-Álvarez, J. L., & Pérez, N. (2021). Automatic ladybird beetle detection using deep-learning models. *PLoS ONE*, *16*, e0253027.

Wagner, D. L., Grames, E. M., Forister, M. L., Berenbaum, M. R., & Stopak, D. (2021). Insect decline in the Anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of Sciences of the United States of America*, *118*, e2023989118.

Woltz, J. M., & Landis, D. A. (2014). Coccinellid response to landscape composition and configuration. *Agricultural and Forest Entomology*, *16*, 341–349.

Zaviezo, T., Grez, A. A., Miall, J. H., & Mason, P. G. (2021). Conservation biological control. In P. G. Mason (Ed.), *Biological control: Global impacts, challenges and future directions of pest management* (pp. 37–66). CSIRO Publishing.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Soares, A. O., Haelewaters, D., Ameixa, O. M. C. C., Borges, I., Brown, P. M. J., Cardoso, P., de Groot, M. D., Evans, E. W., Grez, A. A., Hochkirch, A., Holecová, M., Honěk, A., Kulfan, J., Lillebø, A. I., Martinková, Z., Michaud, J. P., Nedvěd, O., Omkar, Roy, H. E., … Losey, J. E. (2023). A roadmap for ladybird conservation and recovery. *Conservation Biology*, *37,* e13965. https://doi.org/10.1111/cobi.13965

15231739, 2023, 1, Downloaded from https://conbio.onlinelibrary.wiley.com/doi/10.1111/cobi.13965 by Universidade Dos Acores, Wiley Online Library on [06/02/2023]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License