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Conservation Biology

REVIEW

A roadmap for ladybird conservation and recovery

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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,

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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

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 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).

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

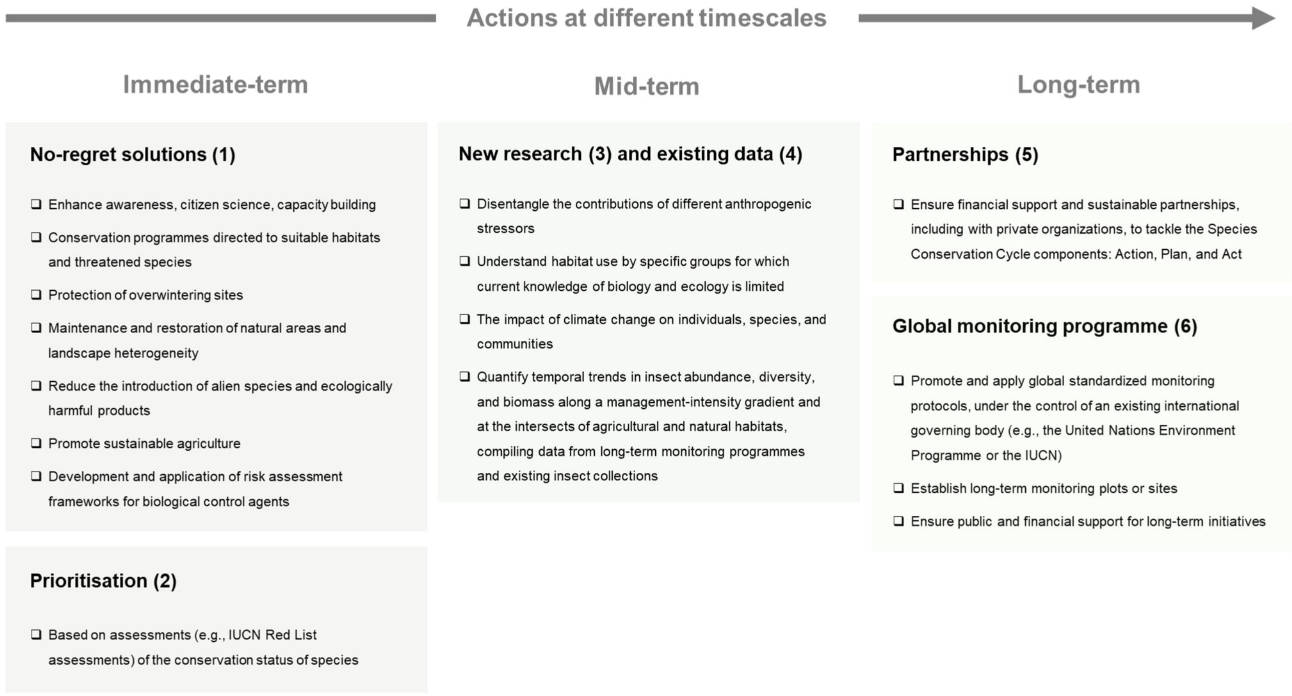

FIGURE 1 Schematic representation of the proposed roadmap to ladybird conservation and recovery (based on the framework of Harvey et al. [2020]). Actions are on different timescales.

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 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 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 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.

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SUPPORTING INFORMATION

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

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