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OPINION

Ecological Entomology

Invasive intraguild predators: Evidence of their effects, not assumptions

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INTRODUCTION

The spatial range of many species is shifting dramatically over time in response to environmental change (MacLean & Beissinger, 2017). Climate change is an important driver of both expansions and contractions of the range extent for insects (Beckmann et al., 2015; Chen et al., 2011; Hickling et al., 2005; Parmesan & Yohe, 2003). The introduction of non-native species is another important factor determining the change in distribution of some species; indeed, the rate of translocation of species beyond their natural ranges is increasing rapidly over time and showing no sign of slowing (Seebens et al., 2017). In many cases, such introductions have negligible effects on biodiversity and ecosystems. Some non-native species may provide benefits to people and nature, but others have adverse, and sometimes unexpected, consequences (Vilà et al., 2011). Understanding the effects of non-native species, whether negative, positive or neutral, is important to underpin decision-making. However, it is widely acknowledged that evidence of the ways in which human activities are altering biodiversity and ecosystem functioning is lacking (Vilà et al., 2011). The global invasion of the harlequin ladybird, *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) (Roy et al., 2016) has provided opportunities for collaborations to explore the potential impacts of a non-native species originally introduced into many regions of the world as a beneficial insect for pest control (Koch, 2003). Much of the emphasis of the research on *H. axyridis* has focused on hypotheses in relation to the unintentional adverse impacts of the species. Some of these have been unfounded, but many have been supported (Roy & Brown, 2015). There are still many knowledge gaps and an urgent need for improved understanding of implications for ecosystem function and particularly in the context of the interactions amongst multiple drivers of environmental change (Bonebrake et al., 2019).

In a recently published Opinion Piece, Kindlmann et al. (2021) draw on some of our recent research on the effects on native ladybirds of *H. axyridis*. Kindlmann et al. (2021) state some widely held views on methodological procedures and appropriate statistical analyses, which scientists should take into account within their studies. The recommendations presented are not new, but many will no doubt already be in the minds of all scientists as they rigorously develop their scientific work. Unfortunately, Kindlmann et al. (2021) misrepresent the findings from our peer-reviewed studies, and as such, here we present a short rebuttal in response to some of the points made within their Opinion Piece.

DISCUSSION

Kindlmann et al. (2021) begin by criticising the use of percentages to represent changes in species communities, inappropriately citing examples of our work to support this point. We acknowledge the obvious shortcomings of using percentage data, but for reasons of clarity and communication, these are sometimes useful and used, with care, recognising the limitations and often in combination with actual counts (Brown & Roy, 2018; Grez et al., 2016). The study by Grez et al. (2016) appears to be criticised over this issue, yet their fig. 5 presents actual abundance of coccinellids (mean individuals/trap/field) rather than percentages. Brown and Roy (2018) present actual abundance data very clearly and transparently in their Results section, albeit in conjunction with percentages.

The length of time series over which effects of species interactions are considered is another criticism of our research by Kindlmann et al. (2021). A paper by Diepenbrock et al. (2016) using an impressively long 118-year time series is used as an example of best practice. However, some of our research (Brown & Roy, 2018) uses abundance data that have been very consistently collected using a standardised sampling protocol, whereas it is very unlikely that such an approach is achievable by studies spanning many decades. Diepenbrock et al. (2016) present an interesting analysis that we do not criticise, but the small sample sizes of ladybird data per year and the non-standard way that data were collected are severe limitations of that type of study, which does not seek to present abundance data as we do. The work of Honěk et al. (2016) is one of the best examples we know of a very long-term study with standardised counts of species within ladybird communities, spanning 40 years. Our studies are shorter, for example, 5 years (Grez et al., 2016) and 11 years (Brown & Roy, 2018), but we argue that if scientists were always to wait multiple decades before publishing their findings, little progress would ever be made. Also, such long timeframes are largely irrelevant for insect conservation action, which mostly find an evidence base in red listing, which, according to IUCN criteria, ideally consider 10 years (or three generations) for trend assessments (Adriaens et al., 2015). Moreover, regarding biological invasions and the associated risks, the precautionary principle should be adopted (e.g., in terms of potentially restricting further releases of a potentially high-risk biocontrol agent) and, consequently, potential harms should be communicated as soon as possible. On the other hand, we agree with both Diepenbrock et al. (2016) and Honěk et al. (2016) that factors including land use change and agricultural change are likely to have had an influence on ladybird assemblages over long time periods. Roy et al. (2012) describe the long-term trends of ladybird occurrences before and after the arrival of *H. axyridis* in Belgium and the United Kingdom, based on citizen science data. This study shows that for some species, such as *Adalia bipunctata* Linnaeus (Coleoptera: Coccinellidae), the trend may have been increasing (United Kingdom) or already decreasing (Belgium) before the arrival of *H. axyridis*, but that declines of *A. bipunctata* were more pronounced in both countries after the arrival of the invasive non-native species. This kind of before/after observational study (with a different date of arrival depending on the location) is probably one of the best designs to study causal relationships when large-scale experimentation is unfeasible. Citizen science data are prone to various potential biases, but there are many ways to address these to derive robust conclusions (Isaac & Pocock, 2015). Furthermore, there are advantages of using multiple approaches, for example, by combining citizen science data with standardised sampling designs but sometimes over shorter periods of time (as presented in Roy et al., 2012; Grez et al., 2016). Kindlmann et al. (2021) also criticised the work of Grez et al. (2016) for concluding from a short-time series an adverse impact of *H. axyridis* on the abundance of native species. On the contrary, these authors did not conclude this, and actually indicated that ‘there was no significant relationship ($R^2 = 0.524$, $p = 0.167$; fig. 5b)’ (Grez et al., 2016).

Another facet of the criticism of Kindlmann et al. (2021) involves the existence and effects of intraguild predation (IGP). In their section ‘Intraguild predation as a causative factor’ Kindlmann et al. (2021) start from the premise that IGP intensity is difficult to determine and is rare in ladybird guilds (Kindlmann & Houdková, 2006). We concede that rigorous assessments of IGP intensity are not easy, but there is evidence from a range of studies that IGP takes place in field and laboratory situations and may be common. These studies include chemical identification of alkaloids in field samples of agricultural (Hautier et al., 2008) as well as urban (Hautier et al., 2011) ecosystems, molecular techniques to analyse field samples (Thomas et al., 2013), laboratory tests in small arenas (Katsanis et al., 2013; Ware & Majerus, 2008) and finally, direct evidence from film recordings (Meyhöfer, 2001). At least two studies reveal the occurrence of IGP (albeit reduced) even in the presence of extraguild prey (Ingels & de Clercq, 2011; Nóia et al., 2008). Lucas et al. (2007) refer to 24 studies on the impact of *H. axyridis* on competitors, 15 of which demonstrated a negative impact by exploitative competition or IGP. The question is, what effects does IGP have on the population dynamics of the protagonists? This is a very interesting question but a very challenging one to answer, and indeed it has not been fully addressed by population ecologists, with no studies to our knowledge in which mortality rates are included in population models. As such, this should be a priority for research. In the meantime, should evidence of asymmetric IGP by *H. axyridis* be ignored? We suggest not. Furthermore, research should be extended to consider the effect of IGP on ecosystem function.

Regarding Kindlmann et al.’s (2021) section on ‘Spatial reshuffling’, it is of course true that if a species is seen to decline at a site (or in a region), this could be because of negative effects on it (e.g., IGP or habitat change) or, alternatively, because the species moved elsewhere to escape such effects (Evans, 2004). With site-specific monitoring, such as reported by Brown and Roy (2018), Masetti et al. (2018) or Kenis et al. (2020), it is not possible to address this point. However, the data from Roy et al. (2012) go some way in answering the criticism in that these analyses use data from multiple sampling techniques and from all habitat types with ladybird records. Available evidence from large-scale ladybird surveys as well as detailed monitoring across different regions in Europe suggest the decline in *A. bipunctata* was exacerbated by the arrival of *H. axyridis*. This decline is apparent in habitats where *A. bipunctata* was formerly a very common species and where the niche overlap with *H. axyridis* is highest (Adriaens et al., 2008; Kenis et al., 2017). Monitoring studies in Switzerland confirm this decline of *A. bipunctata* in broadleaved trees and hedges, where *H. axyridis* became the dominant species and *A. bipunctata* disappeared altogether. The latter was also no longer found in meadows, pine and spruce stands in the last decade of the monitoring (Kenis et al., 2020). We struggle to think of appropriate alternative habitats for *A. bipunctata* that are not included in these studies.

In the context of the arrival of *H. axyridis* lowering the biological control potential of the ladybird guild, some of the citations to our work by Kindlmann et al. (2021) are erroneous. For example, Kindlmann et al. (2021) cite three papers about this issue in their ‘Introduction’ section—Soares et al. (2008), Brown et al. (2011) and Roy et al. (2012). However, two of these papers do not state that *H. axyridis* lowers biological control potential of the ladybird guild. Indeed, the paper by Brown et al. (2011) makes very limited reference to biological control, whilst Soares et al. (2008) do not once claim that *H. axyridis*, or other non-native ladybird species, lower the biological control potential of the ladybird guild. On the contrary, we tend to agree with the general point made by Kindlmann et al. (2021) that *H. axyridis* may increase biological control function in some ecosystems, at least in the short term. At the end of their paper, in the section ‘Predatory effectiveness in regulating the abundance of their prey’, Kindlmann et al. (2021) indicate that there is increasing evidence that predators may not strongly regulate pests in nature. In this regard, we suggest looking at a recent review about the role of non-native ladybirds introduced for biological control, including *H. axyridis* (Rondoni et al., 2021). Additionally, the role in biological control of *H. axyridis* is not necessarily in conflict with the concept that it may also have adverse non-target effects within the native ladybird guild, as we and other researchers have reported from different countries (Brown & Roy, 2018; Kenis et al., 2020; Masetti et al., 2018).

In summary, several of our papers present evidence that *H. axyridis* is adversely affecting some native ladybirds, whilst recognising that other factors are also important. We maintain that there is evidence from a range of studies that, combined, strongly suggest a negative influence of *H. axyridis* on native ladybird communities. When studies from research groups working in different parts of the world broadly align, we feel this strengthens the case, rather than being ‘a snowball effect of unsupported expectations’. Alongside the continuation of long-term insect monitoring schemes, we feel further community and ecological interaction research are needed to assess the resilience of ladybird assemblages to environmental change, including the invasion by species such as *H. axyridis*. Finally, networking and collaboration are critical if we are to address the unprecedented rate of global environmental change, and the consequences for nature and people; we are fortunate to be part of a global community that aspires to such rigour as called upon by Kindlmann et al. (2021).

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CONFLICT OF INTEREST

PMJB is a Fellow of the Royal Entomological Society and HER is President of the Royal Entomological Society.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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