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Author for correspondence:
Morelia Camacho-Cervantes
e-mail: mcc@cmarl.unam.mx

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Could non-native species boost their chances of invasion success by socializing with natives?

Morelia Camacho-Cervantes[1,2], Reuben P. Keller[3] and Montserrat Vilà[4,5]

[1]Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México, Ciudad Universitaria, 04510 Mexico City, Mexico
[2]School of Biological Sciences, Monash University, Melbourne, 3800 Victoria, Australia
[3]School of Environmental Sustainability, Loyola University Chicago, 1032 W. Sheridan Rd, Chicago, IL 60660, USA
[4]Estación Biológica de Doñana-Consejo Superior de Investigaciones Científicas (EBD-CSIC), Avda. Américo Vespucio 26, 41005 Sevilla, Spain
[5]Department of Plant Biology and Ecology, University of Sevilla, 41004 Sevilla, Spain

MC-C, 0000-0002-7123-7924

Most invasions start with the introduction of a few individuals and the majority fail to establish and become invasive populations. A possible explanation for this is that some species are subject to Allee effects—disadvantages of low densities—and fail to perform vital activities due to the low availability of conspecifics. We propose that 'facilitation' from native individuals to non-natives through heterospecific sociability could enhance chances of the latter establishing in novel environments by helping them avoid Allee effects and even reducing the minimum number of non-native individuals necessary to achieve the density for a viable population (the Allee effect threshold). There is evidence from experiments carried out with freshwater fish, snails, lizards, mussels and bird that supports the idea of heterospecific sociability between native and non-native species as a process to promote invasion success. We propose that to understand invasion success in social non-native species we need to investigate how they integrate into the recipient community. Furthermore, to manage them, it may be necessary to reduce population density not just below the Allee effect threshold but also to understand how natives could help them shift the conspecific Allee effect threshold to their benefit.

This article is part of the theme issue 'Mixed-species groups and aggregations: shaping ecological and behavioural patterns and processes'.

1. Introduction

Invasive species are recognized as one of the main drivers of biodiversity change, often leading to biotic homogenization [1–3]. There are four main stages of the invasion process: transport, introduction, establishment and spread [4]. Survival and reproduction are the two main barriers that must be overcome if a species is to succeed at the establishment stage; these barriers could be particularly difficult to surpass due to the disadvantages of being part of a small introduced population. Most non-native species introductions fail to establish, possibly due to the shortage of conspecific individuals to perform vital tasks that require a group, such as avoiding predators or finding mates [5,6]. Then, the number of individuals introduced into novel environments is an important predictor for invasion success [7].

It is well known that increasing propagule pressure by the introduction of more individuals makes it more likely that a population will become established and there is a well-described positive relationship between establishment probability and founding population size [8,9]. This positive effect of non-native population size on fitness and thus on the survival of the population is known as the Allee effect. In this article, we explore the circumstances in which native species might offset the small population size of non-natives in early stages of

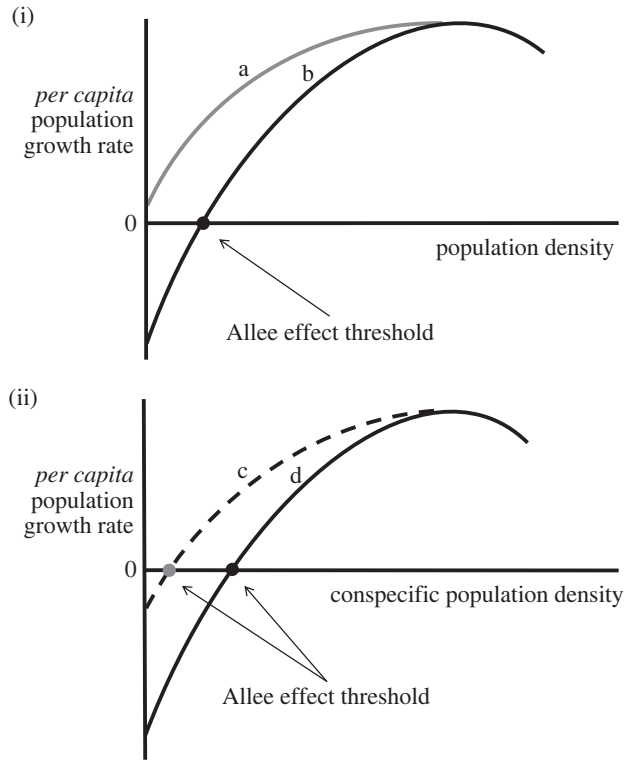

Figure 1. (i) a A weak Allee effect indicates a slow but not negative *per capita* population growth rate at small population densities that increases with population density. (i) b A strong Allee effect occurs when the *per capita* growth rate is negative at low population density until reaching the Allee threshold, which is the minimum population size to ensure population growth. (ii) The Allee threshold for non-native species might shift to a lower conspecific population density if non-natives socialize with natives to perform at least some of their vital group activities and thus enhance their chances of invasion success. (ii) c *Per capita* population growth rate of non-native individuals that socialize with natives. (ii) d *Per capita* population growth rate of non-native individuals that only socialize with conspecifics. (Modified from Tobin *et al.* [6].)

invasion. We first searched for and analysed evidence of beneficial interactions between natives and non-natives, and we then propose further questions that could improve our understanding of this phenomenon.

2. Allee effects during the first stages of the invasion process

The disadvantages of being part of a small population are often referred to as Allee effects. They are called 'component Allee effects' when particular components of individual fitness decrease due to low conspecific density, or 'demographic' if the overall population fitness decreases. When component Allee effects are strong enough, they can lead to demographic effects [10,11]. For example, the mate-finding component Allee effect could lead to a demographic Allee effect as the time individuals must invest in mate searching increases and thus available time for feeding or avoiding predators decreases [12,13]. The most general consequence of Allee effects is a critical population density or Allee effect threshold below which a negative *per capita* growth rate is likely to occur [14]. This threshold is defined as the minimum number of individuals required in a population to ensure its viability (figure 1*a*).

To our knowledge there are no studies—either for non-native species or for other species—that have found the Allee effect threshold. Still, for some extinct species, it is believed their populations disappeared after they fell below such a threshold. For example, the extinct passenger pigeon (*Ectopistes migratorious*), which was native to North America, was heavily hunted in the nineteenth century and their populations became extinct after their numbers fell below the minimum required individuals for efficient foraging [11,15]. Since biological invasions typically begin with small propagule sizes, the first stages of invasion could act as a real-time experiment that can reveal important information to understand and possibly quantify the Allee effect threshold.

Theoretical studies indicate that Allee effects affect the population dynamics of non-native species, especially during the establishment stage for species introduced at low densities [6,14]. If Allee effects are sufficiently strong they result in a minimum population size threshold below which the population of introduced species would decline to zero [8,14]. We propose that non-native species subject to Allee effects could shift their critical conspecific population size threshold and effectively increase their group numbers through interactions with native species in recipient communities (figure 1*b*).

3. Beneficial interactions between natives and non-natives

Interactions between non-native species and their biotic and abiotic environments occur across multiple trophic and functional groups, and some of these interactions could be beneficial for non-natives without a direct disadvantage for natives [16]. For example, recruitment of the invasive barnacle (*Chthamalus proteus*) was found to be positively correlated with the density of the native limpet (*Siphonaria normalis*) [17], although the mechanisms driving this association are not well known. There are many examples of mutualistic interactions involving native/non-native species of plants (e.g. pollination, seed dispersal, etc; see Traveset & Richardson, [18]), but fewer for animals. In this paper we focus on animals' native/non-native facilitative interactions (i.e. those that result in a fitness increase of species involved in the interaction) because it is an open question as to how these might benefit non-natives. In particular, we focus on social interactions between species that are at the same trophic level.

Sociability usually happens among conspecifics and occurs when individuals share time and space. Heterospecific sociability (also called interspecific, polyspecific or mixed species groups) is known for many taxa [19]. Heterospecific sociability relies on the benefits of grouping out-weighing any disadvantages such as sharing resources or parasite transmission [19,20]. These associations could be between species from different orders but are most common between taxonomically closely related species [21]. An example of a pair of native species benefiting from heterospecific sociability is the interaction between lesser kestrels (*Falco naumanni*) and jackdaws (*Corvus monedula*), in which each benefits from sharing nesting colonies by reducing the costs associated with predator vigilance [22]. Similarly, zebras (*Equus quagga*) herding in mixed groups that include giraffes (*Giraffa*

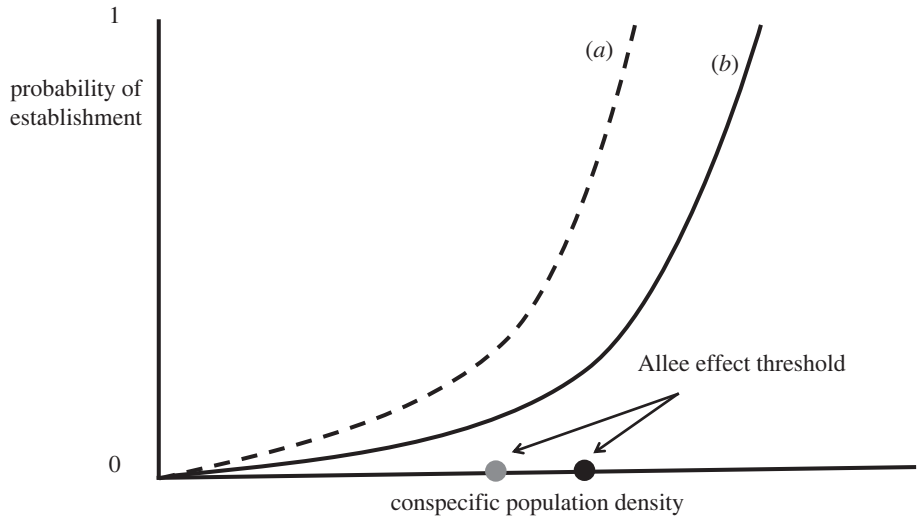

Figure 2. The probability of establishment for non-native species subject to Allee effects increases as the conspecific population density increases. The inflection point could be at lower conspecific population density for species that are able to socialize with natives and avoid some Allee effects by doing so. (*a*) Probability of establishment of non-native individuals that socialize with natives. (Allee effect threshold shown by the grey dot.) (*b*) Probability of establishment of non-native individuals that only socialize with conspecifics. (Allee effect threshold shown by the black dot.)

camelopardalis) reduce their vigilance behaviour as giraffes deliver them information on predation risk [23].

Access to resources and information is influenced by social networks [24]. In biological invasions by animals, through positive or neutral behavioural interactions, non-native species might benefit by joining other species to functionally increase the size of their social group. For non-native individuals, acquiring information via trial-and-error strategies from a novel environment can be costly and even fatal [25]. Heterospecific interactions can allow individuals to acquire important information about their surroundings more quickly and safely [26]. This could be especially relevant for non-native species when they encounter natives with whom they share ecological requirements and/or predators, as these heterospecific interactions could provide non-natives with information to improve their chances of survival and establishment. For example, in the context of migration, Mönkkönen & Forsman [27] found that arriving birds prefer to associate with residents to acquire information on food availability and potential breeding grounds. Keeping track of the foraging choices of other species with the same food requirements can lead individuals to information as valuable as that gathered from individuals of the same species [28]. Whether this occurs between native and non-native species and its consequences for invasion success have been less explored.

Positive heterospecific interactions among non-native or invasive species have been recognized as facilitating invasion success; these interactions are often referred to in the literature as 'invasional meltdown' [29–31]. However, very little is known about how heterospecific interactions with native species could promote invasion success. Many non-native species can be novel competitors or predators for native species, but they can also be allies to help protect them from other competitors or predators, and thus promote better decisions on where to shelter and/or forage [32]. This benefit of non-natives to natives can also act the other way around. In this paper, we review the scientific evidence supporting the possibility that 'facilitation' from native individuals to non-natives through heterospecific sociability could enhance the chances of the latter establishing in the novel environments where they arrive and become invasive (figure 2).

4. Evidence of benefits for non-natives and further questions

We performed a systematic literature review for published scientific studies that investigated how invasion success was affected by positive heterospecific interactions between native and non-native animal species. Our search focused on interactions between natives and non-native species and used the WebofScience search engine to find articles published before 22 September 2022 that contained 'facilitation', 'cooperation' or 'sociability' with a combination of the following keywords: interspecific, heterospecific, polyspecific, mixed species, invasion, invader, invasive, alien, exotic, Allee effects and Allee threshold. This search yielded 1441 publications (544 from the search using keywords, and 897 from references and citations of the first selected publications; please refer to the Flowchart in the Electronic Supplementary Material for further details on the systematic review and our publication selection process). Based on their titles and abstracts we selected 19 publications to read in full, and from these 19 we selected those that tested and found benefits from native to non-native animals experimentally or observationally in the field; modelling studies were excluded. Although the highly restrictive selective criteria might have resulted in few articles, we think that the information from abstracts and titles makes it unlikely that a significant number of relevant papers were missed.

We found 13 articles that provided evidence of non-native animal species deriving benefits from heterospecific sociability with natives (table 1). These are the types of benefits that may allow non-native species to overcome Allee effects during the first stages of invasion. The articles were published between 2010 and 2021. Most studies involved freshwater fish, but others dealt with snails, birds, mussels and lizards (table 1). The types of interactions and benefits studied are (a) sociability (individuals sharing space and time), (b) growth, (c) transmission of information on food

Table 1. Summary of published studies on heterospecific sociability between non-native and native species as a potential facilitation mechanism for invasion success.

interactions & benefits	species (observational or experimental)	findings	references
sociability	freshwater fish – *Leucaspius delineatus, Poecilia reticulata & Salvelinus fontinalis* (experimental)	non-native fish associate with heterospecific natives, possibly to gain the benefits of being in larger groups	Beyer *et al*. [33]; Camacho-Cervantes *et al*. [34]; Camacho-Cervantes, Ojanguren *et al*. [35]; Wallerius *et al*. [36].
growth	freshwater fish – *Hypophthalmichthys nobilis* (experimental)	non-native juvenile fish increased their size when with native fish at low densities.	Nelson *et al*. [37]
	snails – *Potamopyrgus antipodarum* (experimental)	non-native snails gained the benefit of an increase in size when foraging in the company of native snails	Sardiña *et al*. [38]
transmission of information on food availability and foraging behaviour	freshwater fish – *Poecilia reticulata* (experimental)	non-native fish copy food searching behaviour of natives that have information on food availability when they do not	Camacho-Cervantes *et al*. [39]
	lizards – *Podarcis sicula* (experimental)	non-native lizards are able to better solve a foraging task using social information from natives	Damas-Moreira *et al*. [40]
	freshwater fish – *Poecilia reticulata* (experimental)	non-native fish are more efficient when foraging in bigger groups, even if the group size increases with heterospecific natives	Camacho-Cervantes *et al*. [41]
predator avoidance	birds – *Myiopsitta monachus* (observational)	non-native parakeets associated for nesting with native species to reduce predation risk	Hernández-Brito [42]; Hernández-Brito *et al*. [43]
	mussels – *Xenostrobus secures* (experimental)	survivorship of non-native mussels was enhanced when with native mussels	Gestoso *et al*. [44]
boldness	freshwater fish – *Poecilia reticulata* (experimental)	non-native fish are equally bold in exploring a novel environment when accompanied by a conspecific or a native heterospecific	Camacho-Cervantes *et al*. [39]; Santiago-Arellano *et al*. [45]

availability and foraging behaviour, (d) predator avoidance and (e) boldness (table 1). In the following sections we discuss each of these interactions separately.

(a) Sociability

Sociability between non-native and native species occurs and can be beneficial for non-natives, at least during some stages of their lives. Non-natives could associate with heterospecifics to gain the advantages of being part of a larger population when availability of conspecifics is low. We found evidence of these associations from experiments carried out using freshwater fish as models [33,34,36]. The outcomes of these interactions could be either positive or negative, but the fact that non-native individuals actively join heterospecific shoals suggests that benefits outweigh the disadvantages. For example, non-natives could benefit from the encounter-dilution effect while associating with natives and avoid parasites that seek their hosts and are directly transmitted [46,47], an idea that has not been tested in the invasion context.

In some cases, the aggregation process is reinforcing, meaning large groups attract more individuals. We expect this to occur in situations where non-native individuals increase the group size with natives, and by doing this they could encounter more conspecifics if these are joining the group. This could be tested by observing the tendency of males and females to associate with bigger heterospecific groups compared to smaller conspecific groups, and we hypothesise that in most cases individuals will prefer a

bigger group. Authors of all the reviewed studies on sociability describe how the association between their focal non-native species and natives could lead the former to advantages such as predator avoidance and improved foraging efficiency, but more studies should explore cases where these associations might benefit invaders in their reproduction. To test this, individual reproduction success (e.g. copulations, number of offspring, etc.) could be compared between small conspecific groups and larger heterospecific groups.

(b) Growth

There is evidence for an increase in the body size of individuals grouping with heterospecifics in freshwater snails and fish [37,38]. Increases in size in snails associating with heterospecifics were evident in adults but not in juveniles, while for fish it was the other way around. Because sociability is a spectrum that varies among species, and that for some species changes through their lives, it would be important to study the tendencies of non-natives to associate with natives at different life stages.

These differences in when species benefit from heterospecific sociability highlight the variation that occurs in sociability both within the life-history stages of individual species and across species. Future research needs to examine not only how sociability functionally affects growth, but how this varies across different species with varying degrees of con- and heterospecific social tolerance as well as across different life stages. An increase in size could mean reaching sexual maturity faster or being able to breed and/or better protect more offspring, which may enable non-natives to overcome Allee effects and establish populations more rapidly. To test this, we propose to compare growth rates from juvenile to adult stages between individuals that are alone or in small conspecific groups with individuals in larger heterospecific groups that include natives. We hypothesise that when in larger groups, regardless of the species composition, individuals will reach maturity faster.

(c) Transmission of information and foraging behaviour

The increase in body size when in heterospecific contexts could be due to an increase in information about the location and/or quality of food resources. Indeed, non-native fish and lizards were able to acquire information on food availability and were more efficient when foraging with natives than when alone or in smaller conspecific groups [39–41]. This information acquisition could lead to fewer losses associated with trial and error in a novel habitat [48]. Moreover, being more efficient at foraging and in turn being able to grow faster could reduce the time during which individuals are vulnerable to predators.

For non-native individuals that recently arrived in a novel environment food sources may be cryptic; by associating with natives they could copy their behaviour and avoid or diminish risks associated with food search. Foraging efficiency of non-native individuals that are naive to food sources when alone or with other non-native naive individuals could be tested against when socializing with native individuals that are knowledgeable. If species have similar foraging habits, we hypothesize that the foraging efficiency of non-natives will increase when with knowledgeable non-native individuals. This transmission of information could also be tested for other traits, such as recognizing threats or finding refuge.

(d) Predator avoidance

Predator avoidance is another key behavioural trait enhancing survival, and grouping is recognized as a mechanism that contributes to the dilution effect when facing a predator [49]. In changing or novel environments this behaviour could help non-natives to find safety in numbers by joining native heterospecific groups. Non-native mussels and parakeets reduce predation risk by associating with native species [42–44]. Since being in groups reduces the time that each individual needs to devote to vigilance, grouping with natives could allow non-native individuals to benefit from allocating more time to foraging or reproductive activities, which would provide a different perspective on the benefits of grouping with heterospecifics. Since direct predator avoidance could be complex to test experimentally owing to ethical guidelines, observational studies in the wild could provide valuable indirect information of the benefits non-natives may be deriving from socializing with natives, as in the studies we found.

(e) Boldness

Another behavioural characteristic known to enhance invasion success is boldness. As with social learning, this too can be enhanced for non-natives when socializing with natives [45]. Boldness and exploratory behaviour have been researched only for fish [39,45] but they are likely important characteristics for other non-native species as they could promote establishment success and/or range expansion. When non-native individuals are in low numbers, grouping with other species allows them to gain the safety of being in a larger group while conspecific individuals are scarce or absent. Being bold could lead to exploratory behaviour, which is key for the dispersal of populations. Specific traits that could be tested for non-natives when with natives include the discovery and use of shelter, nesting or resting sites, and/or novel food sources.

5. Future directions

Our systematic review found only 13 studies from eight species that have considered heterospecific sociability between non-natives and natives as a mechanism that might contribute to establishment success of non-native species. The idea that recipient communities have 'biotic resistance' to non-natives is widespread in the literature [50–52]. However, the notion that social interactions between native and non-native animals may facilitate invasions has been seldom explored. We found evidence that non-native species can derive benefits from social interactions with native species. We note that there has been very little published research on this type of interaction, and we believe it is highly likely that additional non-native taxa may also benefit from heterospecific interactions with natives. Mammals may be of particular interest because they tend to be highly social and they represent an important proportion of the most damaging terrestrial invasive vertebrates [53]. In figure 3 we propose variables and taxa that could be studied to better understand how natives might facilitate non-natives' invasion process.

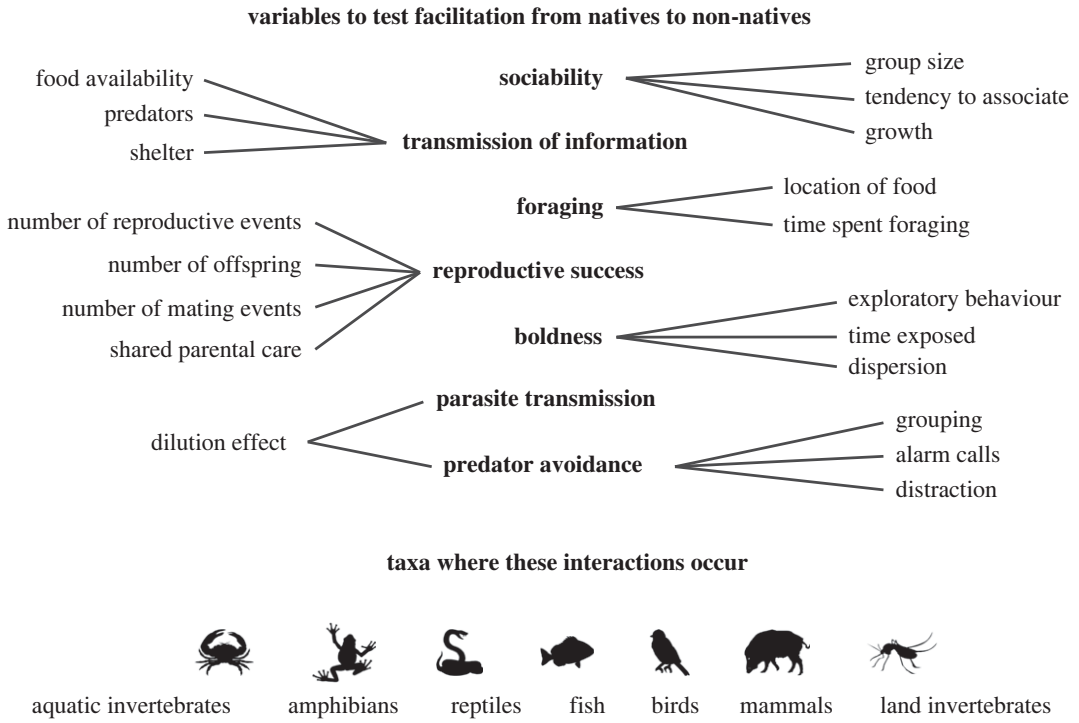

Figure 3. Variables and taxa where facilitation from natives to non-natives could occur.

We have focused on how heterospecific sociability with natives may be key during the first stages of invasion. However, for non-natives to become successful invaders, population size is of importance at all invasion stages. The role of heterospecific sociability could be exploited for management of invasive species [9]. For a species subject to Allee effects it is possible to eliminate a population by reducing its population below the Allee effect threshold [5]. Acknowledging that natives could help invaders shift the conspecific Allee effect threshold becomes important to fully understand biological invasions and should be considered a factor when managing and eradicating invasive species.

6. Conclusion

In introduced animals, it is known that behaviour is one of the first features that must be adjusted when an individual encounters new conditions or novel environments. Studying a broad range of behavioural traits and how these are affected by interactions with natives could help to better understand how some species become successful invaders while others do not. In this study, we focused on finding evidence for heterospecific interactions between natives and non-natives that are beneficial for the latter, but it is also important to evaluate the outcome for native species. The interactions discussed in this study could be either negative or positive for native species, and we note that whereas biological invasions researchers tend to focus more on negative outcomes, there is evidence that non-native species can have positive effects for natives [54]. If, for example, native species derived benefits from socializing with non-natives, the early stages of the invasion could be unnoticed as the negative effects would only become evident much latter. We conclude that much more research should be conducted on the facilitation that natives provide to non-natives. Positive heterospecific interactions between natives and non-natives have a strong potential to yield novel and relevant insights into the mechanisms underlying biological invasions.

Data accessibility. Further details about the methods are provided in electronic supplementary material [55].

Authors' contributions. M.C.-C.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, writing—original draft, writing—review and editing; R.P.K.: conceptualization, investigation, methodology, supervision, writing—review and editing; M.V.: conceptualization, investigation, methodology, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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