Title

The open bar is closed: restructuration of a native parasitoid community following successful control of an invasive pest.

Authors

David Muru[1], Nicolas Borowiec[1], Marcel Thaon[1], Nicolas Ris[1], Elodie Vercken[1].
Corresponding author: david.muru@inra.fr

Affiliations

[1] Institut Sophia Agrobiotech - INRAE, Université Côte d'Azur, CNRS, ISA, France.

Keywords

Dryocosmus kuriphilus, *Torymus sinensis*, community structure, biocontrol, co-occurrence, niche displacement, exploitative competition, native parasitoids.

Abstract

When an invasive species establishes in a new area and reaches high densities, antagonists may benefit from this bonanza situation. How such a newly formed community may then be challenged after the regulation of the invaders by external outputs – e.g. the deliberate introduction of specialized natural enemies – remains however poorly documented. To investigate this issue, we used the case study of the invasion of the Asian chestnut gall-wasp *Dryocosmus kuriphilus* Yasumatsu in France and its subsequent control by the exotic parasitoid *Torymus sinensis*. From the survey of 26 locations during 5 years after the *T. sinensis* introduction, we analyzed how the patterns of co-occurrence between the different native parasitoid species changed through time.

Our results demonstrate that native parasitoid communities experienced increased competition as the *D. kuriphilus* levels of infestation decreased. During the last year of the survey, two alternative patterns were observed: either native parasitoid communities were almost inexistent, or they were dominated by one main parasitoid: *Mesopolobus sericeus*. We observe that the two patterns correlate with the habitat and that they may be explained by environmental features such as differences in the natural reservoirs for native parasitoids. These results highlight how the "boom-and-bust" dynamics of an invasive pest followed by successful biological control can deeply alter the structure of native communities of natural enemies.

Introduction

Biological invasions are defined as the introduction, establishment and expansion of populations outside of their native area. Apart from their well-known effects on human health (like the transmission of diseases by insect vector) or agricultural production (see Mc Michael and Bouma 2000 for a review), biological invasions are also identified as major drivers of global changes in biodiversity worldwide. This is particularly true on islands or other geographically isolated environments in which an invasive species can drive local prey or host populations to extinction (Jehl and Everett 1985, Keitt et al 2002, Blackburn et al 2004, Cox and Lima 2006, Steadman 2006, Sax and Gaines 2008). More generally, invasions are known to have a diversity of direct and indirect negative effects on native ecosystems (see McGeoch et al 2015 for a review of environmental impacts caused by invasion). In particular, they can deeply alter predator-prey interactions and restructure native communities, often with negative consequences (Ricciardi and Isaac 2000, Ricciardi 2001, Carroll 2007). For instance, invasive predators, parasitoids or pathogens were proven to drastically reduce the size of resident prey or host populations (Daszak et al 2000) or to compete with other species from the same trophic level (Hamilton et al 1999, Grosholz 2002).

While much research has focused on invasive top-consumers (predators, parasitoids, etc), a smaller amount of literature examines the impact of invasive species as a new resource for the native community (Carlsson et al 2009). This phenomenon is referred to as a form of "facilitation" and the invasive species acts as a "trophic subsidy" (Rodriguez 2006). Examples of trophic subsidies include some invasive macroalgae (Olabarria et al 2009, Rossi et al 2010, Suarez-Jimenez et al 2017), some phytophagous insects as *Halyomorpha halys* (Jones et al 2014, Haye et al 2015, Herlihy et al 2016, Noyes 2017), *Drosophila suzukii* (Mazzetto et al 2016) or four invasive gall-wasp species (Schonrogge and Crawley 2000). Such host range expansions may change the established equilibrium between native parasitoids and their respective hosts and therefore may have significant impacts on the structure of native communities. Even when the invasion is only transient, its consequences on native communities can be lasting on the recipient community. Mallon et al (2017) have recently reported a permanent niche displacement of native species caused by a failed invasion by *Escherichia coli* in soil microcosms, and referred to it as a "legacy effect". Overall, empirical data on the response of native community dynamics to transient invasion remain scarce, as most of the attention is focused on well-established invasions that prove a lasting, unresolved environmental challenge.

Classical biological control – i.e. the deliberate introduction of an exotic biological control agent to durably regulate a target (usually exotic) pest (Eilenberg et al. 2001) - can provide valuable empirical data on the dynamics of communities disturbed by two successive invaders, the pest and its introduced natural enemy. Long term direct and indirect impacts of either the pest or its natural enemy on the recipient community have been documented (see Louda et al 2003 for a review of 10 case studies with quantitative data). In some cases, the arrival of an abundant resource can stabilize otherwise fragile communities (Carlsson et al. 2011). Sometimes the native parasitoids are displaced from their native hosts to an invasive one. However, in the case of a biological control program the native community of parasitoids can be repelled from the exotic pest from the exotic

parasitoid (Naranjo 2017). In other words, the introduction of an exotic parasitoid to control an exotic pest often leads to a displacement of the native community of parasitoids that have become associated with the exotic pest (Bennett 1993, Lynch and Thomas 2000, van Lenteren et al. 2006). This happens logically when the introduced parasitoid is a superior competitor or more adapted to find and exploit the pest than its native counterparts (Naranjo 2017). The resulting displacement might only be a step backwards, bringing the system back to its previous equilibrium (before the pest invaded the area), or a novel equilibrium might emerge, depending on the resilience of the native community. However, the temporal dynamics and spatial variability of these processes remain poorly understood and empirical data are greatly lacking at this point with, to our knowledge, no reports of such non-intentional effect in the context of biological control. Therefore, here we use successful classical biological control of an invasive pest as a framework to properly investigate how these two subsequent invasions impact the structure of native communities.

The Asian chestnut gall-wasp *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera Cynipidae), native to China, was accidentally introduced in Italy in 2002 (Brussino et al 2002) and is now distributed throughout Italy and other European countries (EPPO, 2014). In absence of competitors (Bernardo et al., 2013) and specialized antagonists, D. *kuriphilus* was able to proliferate quickly and massively. Therefore, it became a trophic subsidy for several native parasitoids previously associated to gall-wasps from other plants/trees (Francati et al 2015, Noyes 2019). In response to damage observed on chestnut production and also apiculture, classical biological control programs were quickly implemented in newly infested countries. *Torymus sinensis* was chosen as a biological control agent due to its high specificity of parasitism (Quacchia et al 2008) and its previous effective control of the target pest outside Europe (Gyoutoku and Uemura 1985, Cooper and Rieske 2007, 2011). In France, *T. sinensis* has been proven established with fast and significant impacts on the targeted pest in the subsequent years (Borowiec et al 2018). This thus led to the quite unique opportunity to investigate how local communities evolve with regard to the deprivation of their trophic subsidy.

Methodology

Biological control introductions

In France, first isolated spots of *D. kuriphilus* were observed from 2005 close to the Italian border but its pervasive presence in South of France was only patent from 2010. *T. sinensis* was introduced in this area between 2011 and 2014, on a total of 48 sites (chestnut orchards) separated by at least 4 km. The introductions covered a wide geographical area (920 km from North to South, 1 030 km from East to West) in metropolitan France including Corsica. According to some predefined modalities, 100 to 1000 *T. sinensis* were released, *T. sinensis* establishing itself in all sites whatever the initial propagule size (see Borowiec et al. 2018 for more details). For this study we kept only the 26 sites for which at least a 5-years of post-release survey was available (Figure 1).

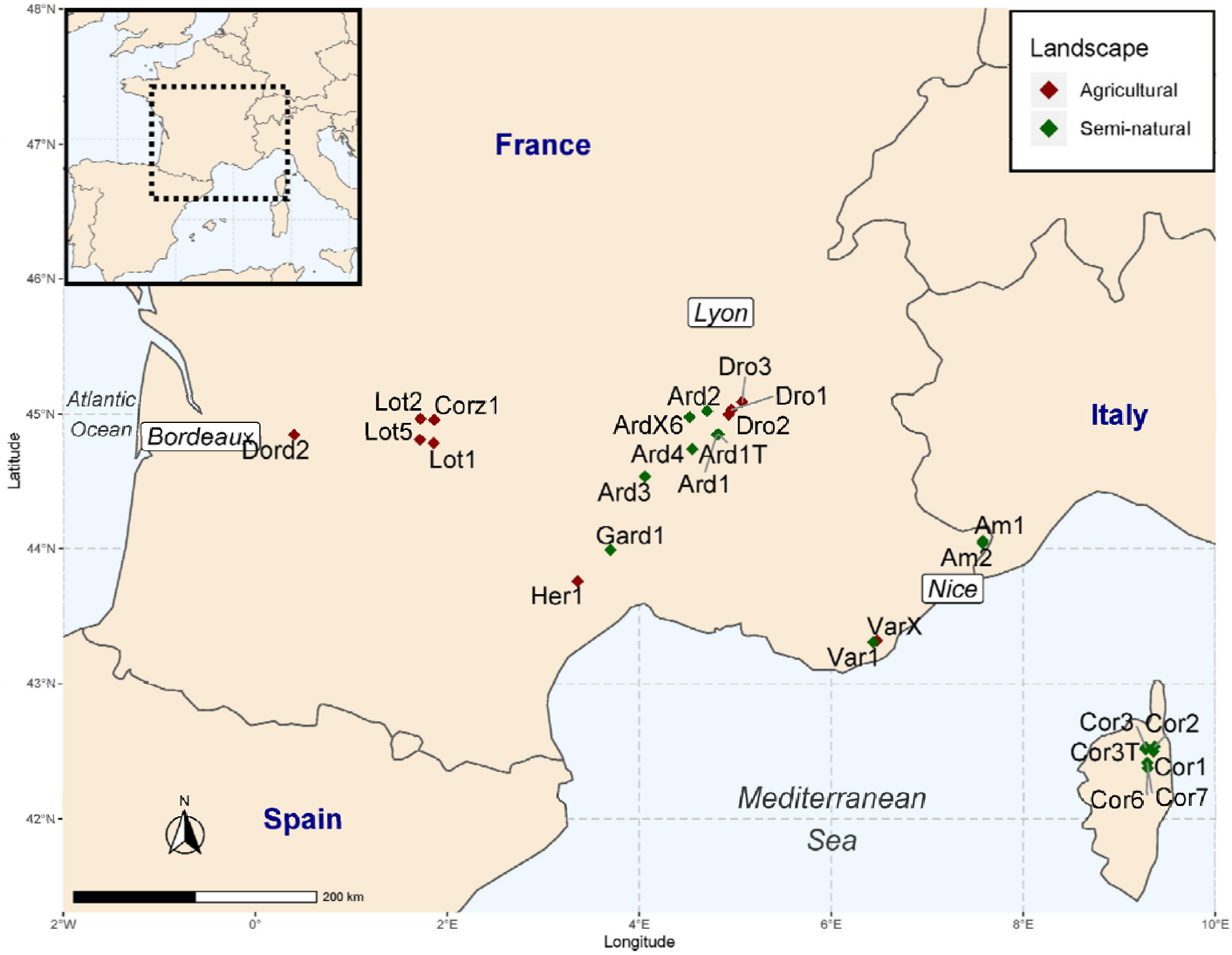

Figure 1 - Map of the survey. Red points correspond to Agricultural habitats whereas green points correspond to semi-natural habitat.

Sampling of insect communities associated with chestnut galls

- Estimation of *D. kuriphilus* levels of infestation

10 trees / site / year were sampled and, for each of them, 10 twigs were randomly selected and inspected. From these, the infestation levels of *D. kuriphilus* were estimated, by combining information on the mean percentage of buds with at least one gall and on the mean number of galls per bud as shown in Table 1.

Table 1 - Table showing how the classes of infestation by D. kuriphilus were determined

		Mean number of galls per bud		
		<1	[1-2[	2≤
Mean percentage of buds with at least one gall	[0-33%]	1	2	3
	[34-66%]	2	3	4
	[67-100%]	3	4	5

- Diversity and abundance of associated parasitoids

As detailed in Borowiec *et al.* 2018, both the exotic *Torymus sinensis* and the native parasitoids were counted from "winter dry galls". We collected 2000 to 5000 galls / site during the two first years and then only 500 to 2000 / site. Once collected, galls were put in hermetic boxes (500 galls of a single origin in one box) placed outdoors from January to October. All emerged insects were collected and then stored in alcohol 96°. Species identification was based on morphological characters and barcoding when necessary to confirm identification. *Eupelmus* species were identified using the latest descriptions of the *Eupelmus urozonus* complex (AlKhatib et al 2014 and 2016). Other species were identified by using an unpublished key to chalcidoid parasitoids in oak cynipid galls (Askew and Thuroczy). In addition to the exotic and ubiquitous *T. sinensis*, nine main native parasitoids were finally identified:

-*Aulogymnus* spp., specialized parasitoids of Cynipidae.
-*Eupelmus azureus*, a specialized parasitoid of Cynipidae.
-*Eupelmus kiefferi* and *Eupelmus urozonus*, two extremely polyphagous species targeting several orders of insects.
-*Eurytoma setigera* a poorly documented species but described by Murakami et al. (1994) as a primary parasitoid of cynipids.
-*Megastigmus dorsalis,* maybe a complex of cryptic parasitoid species but specialized on Cynipidae
-*Mesopolobus sericeus,* a parasitoid specialized on the Cynipini tribe within the Cynipidae family.
-*Torymus auratus*, a parasitoid specialized on Cynipidae.
-*Sycophila biguttata*, a parasitoid specialized on Cynipidae.

Statistical analysis

Co-occurrence null model analyses

To assess the patterns of co-occurrence between parasitoid species, and their evolution over time, we used the C-score (Stone and Roberts 1990) from each annual matrix of presence-absence of the nine native species. As *T. sinensis* was always present, it was excluded of the analysis.

The C-score measures the mean number of checkerboard units between all pairs of species in a data matrix. The number of checkerboard units for each pair of species is calculated as follows:

$$CU = \sum \frac{(S_i - Q)(S_k - Q)}{\frac{R(R-1)}{2}}$$

where Q is the number of shared sites, S_i and S_k are the number of sites in which $_i$ and $_k$ are respectively found and R is the number of rows (=species) in the matrix (Stone and Roberts 1990, Gotelli 2000). When compared to other co-occurrence indices such as CHECKER (Diamond 1975), V-ratio (Robson 1972, Schluter 1984) and COMBO (Pielou and Pielou 1968), C-score has the smallest probability of type I and II errors (Gotelli 2000).

A low value of C-score is indicative of an aggregative pattern, while a high value is indicative of an exclusion pattern. However, because the value of the C-score depends on the frequency of occurrence of the species, inter-annual comparisons cannot be performed directly. We thus used the co-occurrence null model from the EcoSimR package (Gotelli 2015) of R (R Development Core Team 2018) to create null assemblages based on our observed presence-absence species matrices. This was done by randomizing (by transposing sub-matrices) species occurrences but keeping row and columns totals fixed (Gotelli 2000). Thus, differences between sites are maintained, making this method appropriate to detect patterns of species interactions (Gotelli 2000). Each randomization produces one matrix in which a 'simulated' C-score is calculated. Such randomization is replicated ten thousand times. The significance of the observed C-scores was computed as the proportion of simulated values equal to or more extreme than the observed C-score value.

In order to graphically compare each year, all c-score values were normalized by using:

$$Adjusted\ C_{score} = \frac{x - \mu(Simulated\ Cscore)}{\sigma(Simulated\ C_score)}$$

where *x* takes the values of observed and simulated C-score.

Native parasitoids community structure

We described the community structure each year after the release of *T. sinensis* by using the R package 'pheatmap' (Raivo 2019). We created clustered heatmaps with the 'pheatmap' function to visualize how communities of native parasitoids are structured during the survey. Sites were clustered depending on their native parasitoid diversity and abundance using aggregative clustering according to the method *complete*. At the beginning of the process, each element is in a cluster of its own. The clusters are then sequentially combined into

larger clusters aggregating the clusters with most resemblance in terms of parasitoid abundance and diversity.

Spatial heterogeneity

In order to try to evaluate the potential role of ecological factors on the community structure during the last year of survey, we used a Principal Component Analysis (PCA) considering the abundances of each native species using the 'FactoMineR' package of R (Husson et al. 2019). We then plotted the two main categories of habitat: (i) orchards located within an agricultural landscape with a poor amount of semi-natural habitat; (ii) orchards located within semi-natural habitats (forest, hill, mountain, etc.).

Results

Control of *Dryocosmus kuriphilus* by *Torymus sinensis*

As shown in Figure 2, a fast increase of the *Torymus sinensis*' density was observed during the 5 years of survey, 90% of galls being finally parasitized by *T. sinensis*. In parallel, the infestation levels of *D. kuriphilus* decreased markedly. The concomitance between these two patterns highly suggests that *T. sinensis* is able to control *D. kuriphilus* populations efficiently.

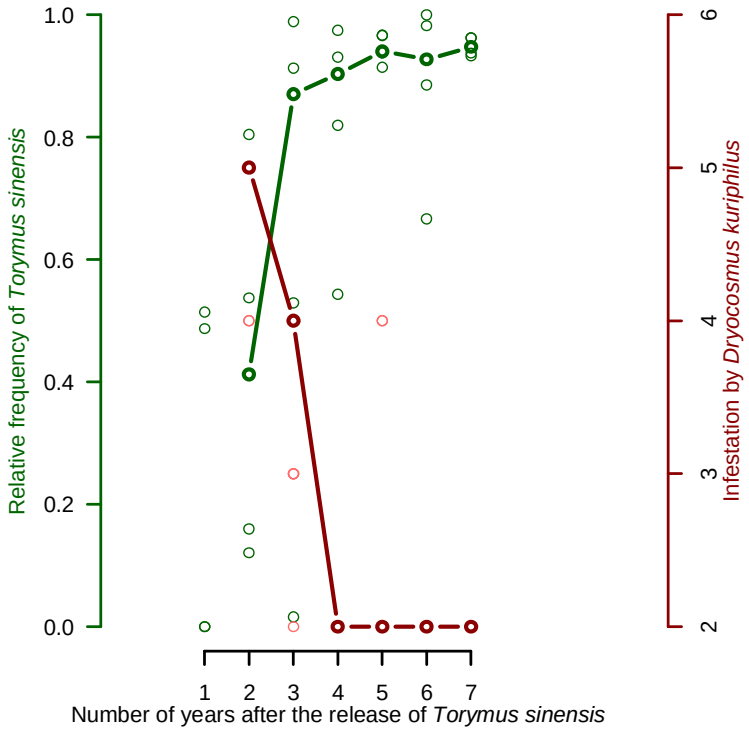

Figure 2 - Infestation levels of D. kuriphilus and Relative frequency of T. sinensis in galls each year of the survey.

Diversity and abundances of native species

Taken as a whole, 71494 specimens of *T. sinensis* and 12016 native parasitoids were obtained from 284425 galls in the 26 sites and during the 5 years of the survey.
In terms of abundance, the native species were ordered as follows: *Mesopolobus sericeus* (n=3792), *Eupelmus urozonus* (n=2069), *Megastigmus dorsalis* (n=1877), *Eupelmus azureus* (n=1752), *Eurytoma setigera* (n=586), *Eupelmus kiefferi* (n=491), *Aulogymnus* spp. (n=403), *Sycophyla biguttata* (n=116), *Torymus auratus* (n=19). 911 individuals remained undetermined and were thus discarded from the analysis.

In terms of occurrence, *Torymus sinensis* was observed in the 130 possible site-by-year combinations. In comparison, the results for native species were as follows: *Eupelmus urozonus* (n=111), *Eurytoma setigera* (n=86), *Eupelmus kiefferi* (n=74), *Megastigmus dorsalis* (n=59), *Mesopolobus sericeus* (n=50), *Eupelmus azureus* (n=49), *Aulogymnus* spp. (n=33) *Sycophyla biguttata* (n=26), *Torymus auratus* (n=7).

The mean abundances of all nine native parasitoids are given for each year in Figure S1 (*Supplemental Figure 1*). Taken as a whole, they peaked during the second and/or third years of the survey.

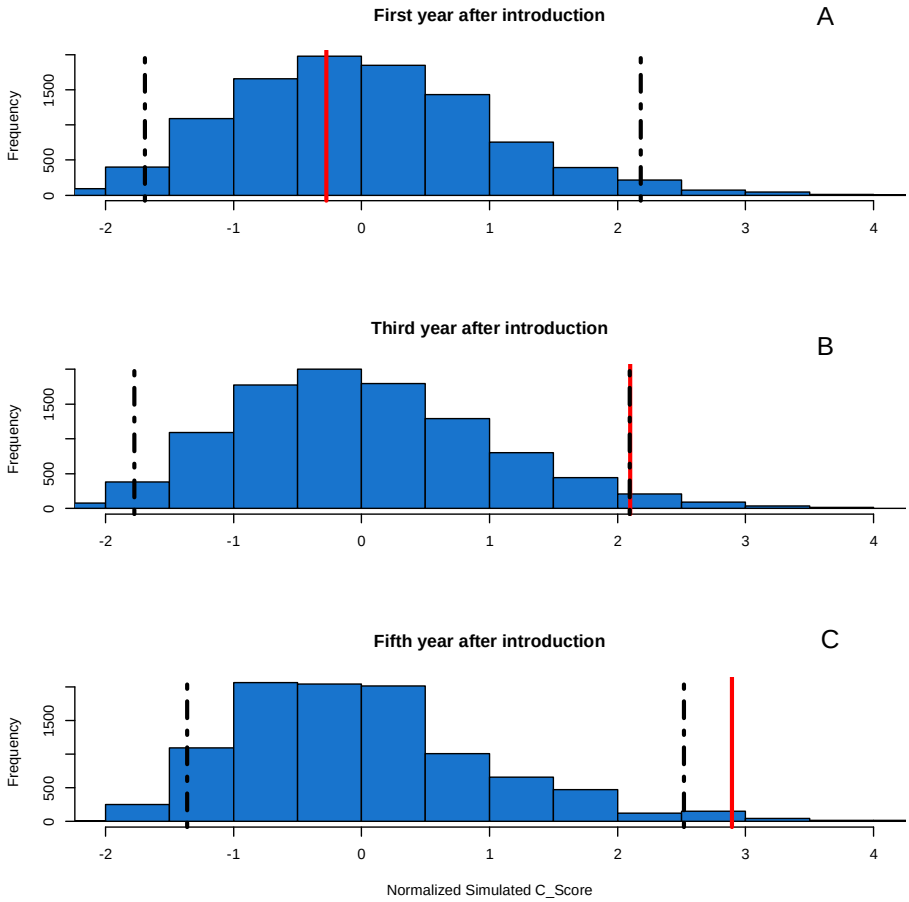

Figure 3 - C-score values for the native community of parasitoids for the first (A), third (B) and fifth year (C) after the release of T. sinensis. Blue histogram represents the simulated values, the red bar represents the observed C-score and the dotted lines represent the 95% confidence interval.

Co-occurrence null model analyses

Figure 3 shows the temporal evolution of the observed C-score (red bar) with regard to the related distribution of simulated C-score values (histograms in blue, 95% confidence interval in-between the dotted black bars). The higher the observed value compared to the simulated values, the more the community is structured by exclusion patterns. Conversely, the lower the observed value, the more the community structure relies on association patterns. Here, a clear trend is observed towards an overall exclusion which seems to appear around the third year of the survey.

Inter-site variability

The overall tendency to species exclusion seems to result from two alternative patterns (Figure 4): (i) in 19 sites, cluster community is poor or even sometimes non-existent during the 5th year of survey (Figure 4, top); (ii) in the remaining 7 sites, the community is dominated by *Mesopolobus sericeus* (Figure 4, bottom).

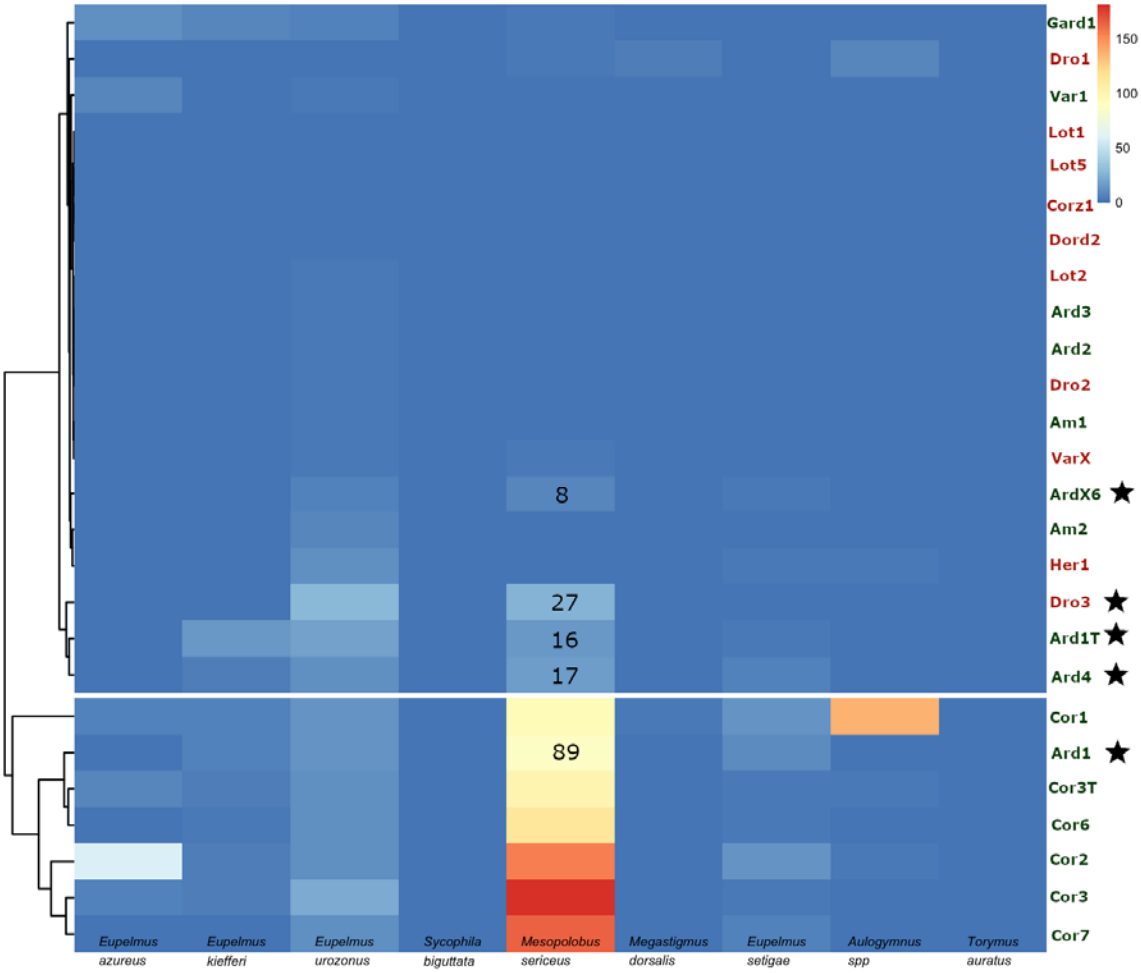

Figure 4 - Heatmap representing the abundances of all native parasitoid species during the fifth year after the release of T. sinensis. The colour of location' names refer to the type of habitat (red: agricultural habitat – green: semi-natural habitat). Stars refer to the continental sites containing M. sericeus and that are discussed in the discussion section.

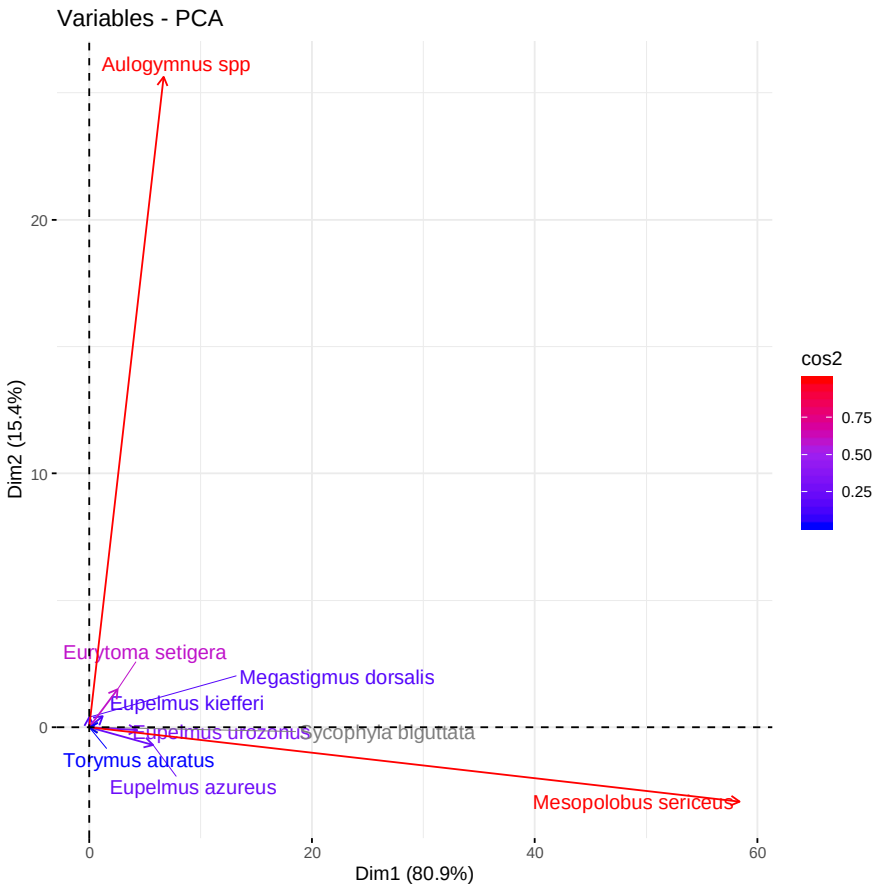

Figure 5 - Variables correlation plot of the PCA built from the abundance of native parasitoids.

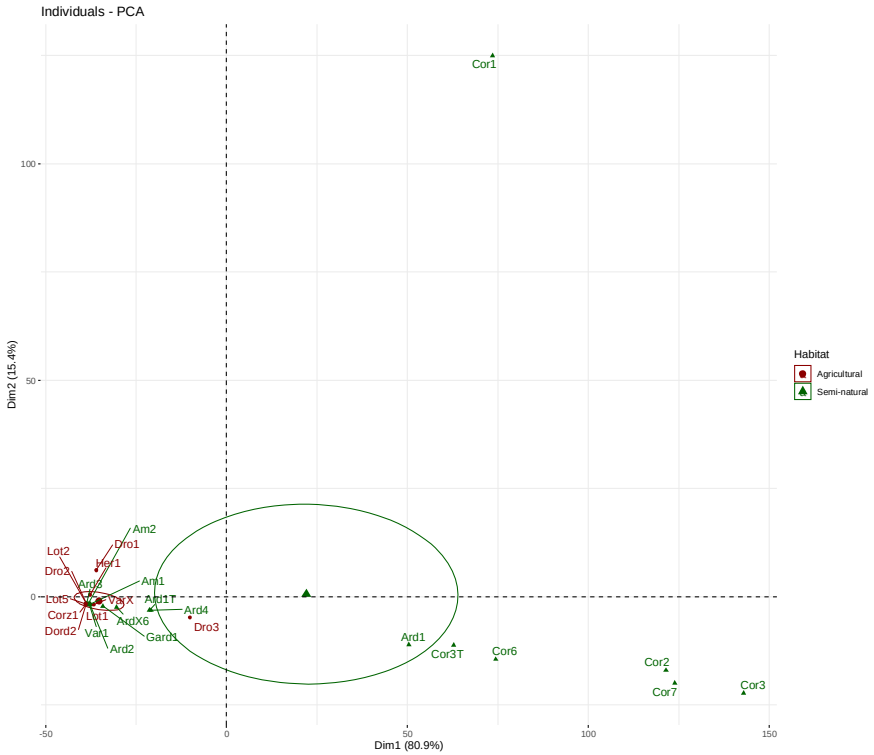

Figure 6 - Individual plot of the PCA. Th colors discriminate the two main habitat: Agricultural (red) and Semi-natural (green).

Role of the environment

The Principal Component Analysis on native parasitoid abundances confirms that, five years after the release of *T. sinensis*, communities are mostly structured by the local presence of *M. sericeus* (Figure 5). The analysis of the projection of the different sites highlights that the abundance of *M. sericeus* is correlated with the type of habitat, semi-natural orchards being more likely to host this particular species (Figure 6).

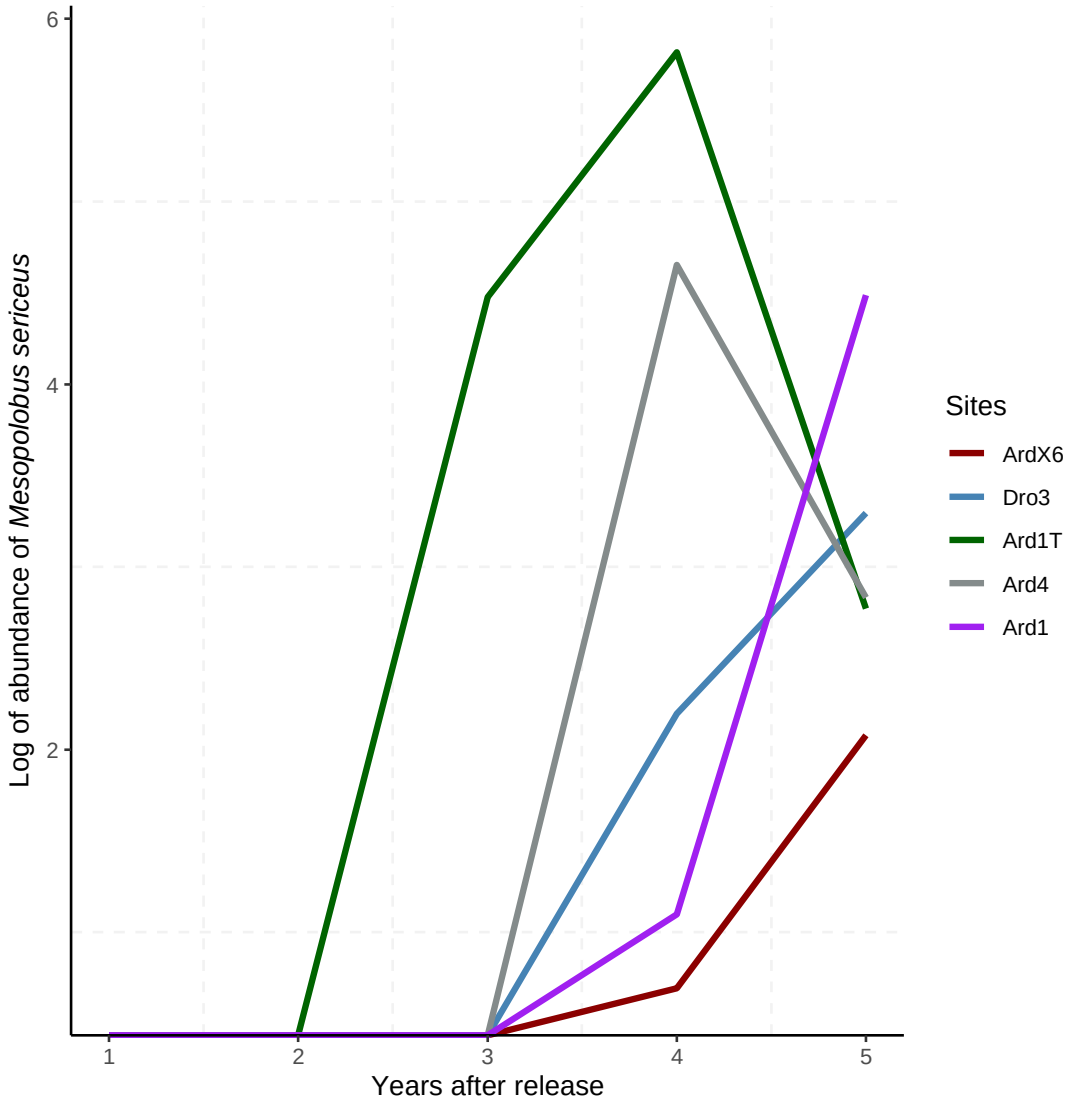

Figure 7 -Log of abundances of M. sericeus in five continental sites during the whole survey.

Discussion

Classical biological control offers an exciting frame to investigate real-time population dynamics during invasive processes. Yet, the opportunities remain rare because of various reasons including (i) the quite high rate of establishment's failure, (ii) the temporal frame required for the observation of significant patterns and (iii) the lack of funding for post-release surveys. With regard to this context, the deliberate introduction of *T. sinensis* against *D. kuriphilus* in France thus represents a unique opportunity. Indeed, *T. sinensis* has been proven to establish very easily and to drastically reduce *D. kuriphilus* populations after only few years (Borowiec et al 2018). From an ecological point of view, this "boom and bust" of *D. kuriphilus* provides a transient bonanza. Everywhere *D. kuriphilus* was introduced, it has become the trophic subsidy of a number of native parasitoids (Matosevic & Melika 2013, Panzavolta et al. 2013).

Among the nine native parasitoids that appeared to use *D. kuriphilus* as a trophic subsidy in our survey, most of them are related to oak gall-wasps and behave as generalists. However, their degree of generalism markedly varies, from extremely polyphagous like *Eupelmus kiefferi* and *E. urozonus* to tribe-specific species like *Mesopolobus sericeus*. The main results of the cooccurrence null model analyses is the increasing exclusive competition through time (Figure 3). This means that the native community undergoes a significant restructuration because of *D. kuriphilus* rarefication. We are not surprised to initially see high abundances of *E. urozonus* and *E. azureus* which are generalist parasitoids and can therefore shift hosts more easily and thus are more successful in colonizing invasive host (Cornell and Hawkins 1993, Hawkins 2005). However, in the following years, *Mesopolobus sericeus* was the main species able to persist on this trophic subsidy (Figure 4). And this, despite the fact that it was not detected once at the beginning of the survey in any site (Figure S1). It seems to be the same for *Aulogymnus* spp. except that they are very less abundant and this includes all species from the *Aulogymnus* genus. The examples of native species displaced by invasive species are numerous (e.g. Rowles and O'Dowd 2007, Bohn et al 2008, Inoue et al 2008, Sebastian et al 2015) therefore we are not surprised to observe such outcome for most of our native species, which are outcompeted by the introduced specialist *T. sinensis*. *Mesopolobus sericeus* appears to be able to coexist with *Torymus sinensis* on *Dryocosmus kuriphilus*.

This persistence of *M. sericeus* was however modulated by the local environment (Figure 5). Among the seven sites showing a marked domination of *M. sericeus* (Figure 4), six are indeed located in Corsica. A first hypothesis would be that community restructuration due to trophic interactions happens with more amplitude in an island context. Due to their smaller size (Cassey 2003) and their reduced diversity (Williamson 1981), islands are indeed more subject to destructive oscillations (Elton 1958). Nonetheless, five continental sites (i.e. ArdX6, Dro3, Ard1T, Ard4, Ard1; assigned with stars in Figure 4) also exhibits a less marked but similar increase of *M. sericeus* (Figure 7), four of them being in semi-natural landscapes (Figure 1). We thus think that the final dominance of *M. sericeus* towards other native species is rather explained by differences in the landscape rather than a "mainland *versus* island" dichotomy. In fact, most of the known host of *M. sericeus* are oak gall-wasps (Noyes 2019), oak trees being rarer in agricultural landscapes than in semi-natural ones. Large

populations of *M. sericeus* acting like sources for the colonization of chestnut orchards are consequently more likely to be sustained in this latter habitat.

Nonetheless, we need to point out that although our study contains insightful information on how our native parasitoid community structure evolves, species dynamics we observed the last year of the survey are not fixed but quite the opposite. Species dynamics are most probably still evolving towards a, yet unknown, state of equilibrium. We are still not in measure to predict with certainty what will happen when *D. kuriphilus* will become even rarer. Maybe *T. sinensis* will remain the dominant species or maybe because of the presence of its native hosts, *M. sericeus* will outperform *T. sinensis* at least in semi-natural habitats. Furthermore, although we evidenced a successful host range expansion from the majority of these native parasitoids, nothing is known about how their populations evolved on their native hosts. A main open perspective of this work is thus to analyze how the structure of native parasitoids evolves within the oak gall-wasp's community.

In conclusion, our work sheds a new light on how the "boom-and-bust" dynamics of an invasive pest can impact the structure of native communities of potential antagonists. Our results evidence a site-specific scenario where a sole native species, *M. sericeus*, dominates the native community on the trophic subsidy and is able to co-exist with the exotic and specialized competitor, *T. sinensis*. Of particular interest would be the long-term survey of these two species. Indeed, *M. sericeus* is now able to exploit both the native gall-wasps and *D. kuriphilus*. This extended host range may have lasting impacts on *T. sinensis* populations, all the more so *D. kuriphilus* will reach a low density at a global scale. In turn, the rarefaction of *D. kuriphilus* and the competition with *M. sericeus* might constrain *T. sinensis* to exploit new hosts.

References

Al Khatib, F. *et al.* An integrative approach to species discrimination in the *Eupelmus urozonus* complex (Hymenoptera, Eupelmidae), with the description of 11 new species from the Western Palaearctic. *Syst. Entomol.* **39**, 806–862 (**2014**).

Al khatib, F. *et al.* Multilocus phylogeny and ecological differentiation of the '*Eupelmus urozonus* species group' (Hymenoptera, Eupelmidae) in the West-Palaearctic. *BMC Evol. Biol.* **16**, (2016).

Bennett, F. D. Do Introduced Parasitoids Displace Native Ones? *Florida Entomol.* **76**, 54–63 (**1993**).

Bernardo, U. *et al.* Description of *Synergus castaneus* n. sp. (Hymenoptera: Cynipidae: Synergini) Associated With an Unknown Gall on *Castanea* spp. (Fagaceae) in China. *Ann. Entomol. Soc. Am.* **106**, 437–446 (**2013**).

Blackburn, T. M., Cassey, P., Duncan, R. P., Evans, K. L. & Gaston, K. J. Avian extinction and mammalian introductions on oceanic islands. *Science (80-.).* **305**, 1955–1958 (**2004**).

Bøhn, T., Amundsen, P. A. & Sparrow, A. Competitive exclusion after invasion? *Biol. Invasions* **10**, 359–368 (**2008**).

Borowiec, N. *et al.* Early population dynamics in classical biological control: establishment of the exotic parasitoid *Torymus sinensis* and control of its target pest, the chestnut gall wasp *Dryocosmus kuriphilus*, in France. *Entomol. Exp. Appl.* **166**, 367–379 (**2018**).

Brussino, G. *et al.* Pericoloso insetto esotico per il castagno europeo. *Avversità delle piante.* 59–62 (**2002**).

Carlsson, N. O. L., Bustamante, H., Strayer, D. L. & Pace, M. L. Biotic resistance on the increase: Native predators structure invasive zebra mussel populations. *Freshw. Biol.* **56**, 1630–1637 (**2011**).

Carroll, S. P. Natives adapting to invasive species: Ecology, genes, and the sustainability of conservation. *Ecol. Res.* **22**, 892–901 (**2007**).

Cassey, P. A comparative analysis of the relative success of introduced land birds on islands. *Evol. Ecol. Res.* **5**, 1011–1021 (**2003**).

Cooper, W. R. & Rieske, L. K. Community Associates of an Exotic Gallmaker, *Dryocosmus kuriphilus* (Hymenoptera: Cynipidae), in Eastern North America. *Ann. Entomol. Soc. Am.* **100**, 236–244 (**2007**).

Cooper, W. R. & Rieske, L. K. A native and an introduced parasitoid utilize an exotic gall-maker host. *BioControl* **56**, 725–734 (**2011**).

Cornell, H. V & Hawkins, B. A. Accumulation of Native Parasitoid Species on Introduced Herbivores : A Comparison of Hosts as Natives and Hosts as Invaders. *Am. Soc. Nat.* **141**, 847–865 (**1993**).

Cox, J. G. & Lima, S. L. Naiveté and an aquatic-terrestrial dichotomy in the effects of introduced predators. *Trends Ecol. Evol.* **21**, 674–680 (**2006**).

Crawley, M. J. & Schonrogge, K. Quantitative webs as a means of assessing the impact of alien insects. *J. Anim. Ecol.* **69**, 841–868 (**2000**).

Daszak, P., Cunningham, A. A. & Hyatt, A. D. Emerging infectious diseases of wildlife - Threats to biodiversity and human health. *Science,* **287**, 443–449 (**2000**).

Diamond, J. Assembly of species communities. in *Ecology and Evolutioin of Communities* (eds. Cody, M. & Diamond., J.) 342–444 (**1975**).

Eilenberg, J., Hajek, A. & Lomer, C. Suggestions for unifying the terminology in biological control. *BioControl* **46**, 387–400 (**2001**).

Elton, C. The ecology of invasions by plants and animals. (**1958**).

Francati, S., Alma, A., Ferracini, C., Pollini, A. & Dindo, M. L. Indigenous parasitoids associated with *Dryocosmus kuriphilus* in a chestnut production area of Emilia Romagna (Italy). *Bull. Insectology* **68**, 127–134 (**2015**).

Gotelli, N. Null model analysis of species co-occurrence patterns. *Ecology* **81**, 2606–2621 (**2000**).

Gotelli, N., Hart, E. & Ellison, A. Package ‘ EcoSimR ’. *R Packag.* (**2015**).

Grosholz, E. Ecological and evolutionary consequences of coastal invasions. *Trends Ecol. Evol.* **17**, 22–27 (**2002**).

Gyotoku, Y. & Uemura, M. Ecology and biological control of the chestnut gall wasp, *Dryocosmus kuriphilus* Yasumatsu (Hymenoptera: Cynipidae), 1: Damage and parasitization in Kumamoto prefecture [Japan]. *Proc. Assoc. plant Prot. kyushu* (**1985**).

Hamilton, J. G., Holzapfel, C. & Mahall, B. E. Coexistence and interference between a native perennial grass and non-native annual grasses in California. *Oecologia* **121**, 518–526 (**1999**).

Hawkins, B. Pattern and process in host-parasitoid interactions. (**2005**).

Haye, T., Fischer, S., Zhang, J. & Gariepy, T. Can native egg parasitoids adopt the invasive brown marmorated stink bug, *Halyomorpha halys* (Heteroptera: Pentatomidae), in Europe? *J. Pest Sci. (2004).* **88**, 693–705 (**2015**).

Herlihy, M. V., Talamas, E. J. & Weber, D. C. Attack and Success of Native and Exotic Parasitoids on Eggs of *Halyomorpha halys* in Three Maryland Habitats. *PLoS One* **11**, e0150275 (**2016**).

Howarth, F. G. Classical biocontrol: panacea or Pandora's Box. *Proc. Hawaiian Entomol. Soc.* **24**, 239–244 (**1983**).

Howarth, F. G. Environmental Impacts of Classical Biological Control. *Annu. Rev. Entomol.* **36**, 485–509 (**1991**).

Husson, A. F., Josse, J., Le, S., Mazet, J. & Husson, M. F. Package ' FactoMineR '. *R Packag.* (**2019**).

Inoue, M. N., Yokoyama, J. & Washitani, I. Displacement of Japanese native bumblebees by the recently introduced *Bombus terrestris* (L.) (Hymenoptera: Apidae). *J. Insect Conserv.* **12**, 135–146 (**2008**).

Jehl, J.R.Jr & Everett, W.T. History and status of the avifauna of isla Guadalupe, Mexico. *Trans. san diego Soc. Nat. Hist.* **20**, 313–336 (**1985**).

Jones, A. L., Jennings, D. E., Hooks, C. R. R. & Shrewsbury, P. M. Sentinel eggs underestimate rates of parasitism of the exotic brown marmorated stink bug, *Halyomorpha halys*. *Biol. Control* **78**, 61–66 (**2014**).

Keitt, B. S., Wilcox, C., Tershy, B. R., Croll, D. A. & Donlan, C. J. The effect of feral cats on the population viability of black-vented shearwaters (*Puffinus opisthomelas*) on Natividad Island, Mexico. *Anim. Conserv.* **5**, 217–223 (**2002**).

Kolde, R. Package ' pheatmap '. *R Packag.* 1–8 (**2019**).

Lewi, S. & Alan, R. The checkerboard score and species distributions. *Oecologia* **85**, 74–79 (**1990**).

Louda, S. M., Pemberton, R. W., Johnson, M. T. & Follett, P. A. NONTARGET E FFECTS —THE ACHILLES ' HEEL OF BIOLOGICAL CONTROL ? Retrospective Analyses to Reduce Risk Associated with Biocontrol Introductions. *Annu. Rev. Entomol.* **48**, 365–396 (**2003**).

Lynch, L. D. & Thomas, M. B. Nontarget effects in the biocontrol of insects with insects, nematodes and microbial agents: the evidence. *Biocontrol News Inf.* **21**, 117N – 130N (**2000**).

Mallon, C. A. *et al.* The impact of failure: Unsuccessful bacterial invasions steer the soil microbial community away from the invader's niche. *ISME J.* **12**, 728–741 (**2018**).

Matošević, D. & Melika, G. Recruitment of native parasitoids to a new invasive host: First results of *Dryocosmus kuriphilus* parasitoid assemblage in Croatia. *Bull. Insectology* **66**, 231–238 (**2013**).

McGeoch, M. A., Lythe, M. J., Henriksen, M. V. & McGrannachan, C. M. Environmental impact classification for alien insects: A review of mechanisms and their biodiversity outcomes. *Curr. Opin. Insect Sci.* **12**, 46–53 (**2015**).

Murakami, Y., Hiramatsu, T. & Maeda, M. Parasitoid complexes of the chestnut gall wasp (Hymenoptera: Cynipidae) in two localities before introduction of *Torymus* (*Syntomaspis*) *sinensis* (Hymenoptera: Torymidae), with special reference to prediction of results after release of the parasitoid. *Jap. Jour. Appl. Zool. Entomol.* **38**, 29-41 (**1994**).

Naranjo, S. E. Displacement of Native Natural Enemies by Introduced Biological Control Agents in Agro- Ecosystems: A Serious Non-target Effect or Not? in *Proceedings of the 5th International Symposium on Biological Control of Arthropods* 46–49 (**2017**).

Noyes, J.S. Universal Chalcidoidea Database. The Natural History Museum. Available at http://www.nhm.ac.uk/research-curation/projects/chalcidoids (**2019**, last access 2019-11).

Olabarria, C., Incera, M., Garrido, J., Rodil, I. F. & Rossi, F. Intraspecific diet shift in Talitrus saltator inhabiting exposed sandy beaches. *Estuar. Coast. Shelf Sci.* **84**, 282–288 (**2009**).

Panzavolta, T. *et al.* Native parasitoids associated with Dryocosmus kuriphilus in Tuscany, Italy. *Bull. Insectology* **66**, 195–201 (**2013**).

Pielou, D. P. & Pielou, E. C. Association among species of infrequent occurrence: The insect and spider fauna of *Polyporus betulinus* (Bulliard) Fries. *J. Theor. Biol.* **21**, 202–216 (**1968**).

Quacchia, A., Moriya, S., Bosio, G., Scapin, I. & Alma, A. Rearing, release and settlement prospect in Italy of *Torymus sinensis*, the biological control agent of the chestnut gall wasp *Dryocosmus kuriphilus*. *BioControl* **53**, 829–839 (**2008**).

Ricciardi, A. & Macisaac, H. J. Recent mass invasion of the North American Great Lakes by Ponto–Caspian species. **15**, 62–65 (**2000**).

Ricciardi, A. Facilitative interactions among aquatic invaders: Is an 'invasional meltdown' occurring in the great lakes? *Can. J. Fish. Aquat. Sci.* **58**, 2513–2525 (**2001**).

Robson, D. Appendix: statistical tests of significance. *J. Theor. Biol.* **34**, 350–352 (**1972**).

Rodriguez, L. F. Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. *Biol. Invasions* **8**, 927–939 (**2006**).

Rossi, F., Olabarria, C., Incera, M. & Garrido, J. The trophic significance of the invasive seaweed *Sargassum muticum* in sandy beaches. *J. Sea Res.* **63**, 52–61 (**2010**).

Rowles, A. D. & O'Dowd, D. J. Interference competition by Argentine ants displaces native ants: Implications for biotic resistance to invasion. *Biol. Invasions* **9**, 73–85 (**2007**).

Sax, D. F. & Gaines, S. D. Species invasions and extinction: The future of native biodiversity on islands. *Proc. Natl. Acad. Sci.* **105**, 11490–11497 (**2008**).

Schluter, D. A Variance Test for Detecting Species Associations , with Some Example Applications. *Ecology* **65**, 998–1005 (**1984**).

Sebastián, O. S., Navarro, J., Llorente, G. A. & Richter-Boix, Á. Trophic strategies of a non-native and a native amphibian species in shared ponds. *PLoS One* **10**, (**2015**).

Steadman, D. W. Extinction and biogeography of tropical Pacific birds. (University of Chicago Press, **2006**).

Suárez-Jiménez, R. *et al.* Importance of the invasive macroalga *Undaria pinnatifida* as trophic subsidy for a beach consumer. *Mar. Biol.* **164**, 1–9 (**2017**).

Suckling, D. M. & Sforza, R. F. H. What magnitude are observed non-target impacts from weed biocontrol? *PLoS One* **9**, (**2014**).

van Lenteren, J. C., Bale, J., Bigler, F., Hokkanen, H. M. T. & Loomans, A. J. M. Assessing Risks of Releasing Exotic Biological Control Agents of Arthropod Pests. *Annu. Rev. Entomol.* **51**, 609–634 (**2006**).

Williamson, M. Island populations. 300 (**1984**).