Invasions cause biodiversity loss and community simplification in vertebrate food webs

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Global change is increasing the occurrence of perturbation events on natural communities, with biological invasions posing a major threat to ecosystem integrity and functioning worldwide. Most studies addressing biological invasions have focused on individual species or taxonomic groups to understand both, the factors determining invasion success and their effects on native species. A more holistic approach that considers multispecies communities and species' interactions can contribute to a better understanding of invasion effects on complex communities. Here we address biological invasions on species-rich food webs. We performed in silico experiments on empirical vertebrate food webs by introducing virtual species characterised by different ecological roles and belonging to different trophic groups. We varied a number of invasive species traits, including their diet breadth, the number of predators attacking them, and the bioenergetic thresholds below which invader and native species become extinct. We found that simpler food webs were more vulnerable to invasions, and that relatively less connected mammals were the most successful invaders. Invasions altered food web structure by decreasing species richness and the number of links per species, with most extinctions affecting poorly connected birds. Our food web approach allows identifying the combinations of trophic factors that facilitate or prevent biological invasions, and it provides testable predictions on the effects of invasions on the structure and dynamics of multitrophic communities.

Biological invasions are one of the major threats to biodiversity worldwide, with enormous ecological and economic costs associated (Vitousek et al. 1996). Research on biological invasions has focused on the impact and distribution of individual invaders (Clavero and García-Berthou 2005, Kumschick and Nentwig 2010, Wardle et al. 2011), and on identifying and predicting the factors that facilitate invasions, including which traits predispose species to become successful invaders (Kolar and Lodge 2001, Cassey et al. 2004, Sol et al. 2005, Romanuk et al. 2009). Propagule pressure, habitat suitability, and previous success of other invasion events are among the best predictors of invasion success (Williamson and Fitter 1996). For vertebrates, human affiliation, population growth rates, and the capacity to cope with novel environments are also important predictors of successful invasions (Jeschke and Strayer 2006, Vall-llosera 2012).

However, most studies have neglected how interactions between species in the recipient community could affect invasion success. When interactions were considered, they only included the subset of species directly interacting with the invasive (Sih et al. 2010, Jones and Gomulkiewicz 2012), or have used modelled food webs (Romanuk et al. 2009). There is a lack of studies on invasions and their consequences for the whole community using empirical food webs. These previous studies have shown that variables that reflect the interaction between the invader and its new community, such as trophic generality or trophic position, are the most important predictors for invasion success. They also reveal that food web structure influences invasion success. For instance, Romanuk et al. (2009) showed that communities with lower connectance values are more likely to be invaded than those with higher connectance.

A food web approach allows generating testable predictions on the consequences of different types of environmental changes on the arrangement of interactions in multitrophic communities. For example, the removal of the most highly-connected prey species in a food web can have catastrophic effects by triggering a cascade of extinctions of those predators specialized on that particular prey (Solé and Montoya 2001, Dunne et al. 2002, Montoya et al. 2006, Stouffer et al. 2012). This network approach offers insights if we aim at addressing the overall effect of both species gain and loss in an increasingly modified world. However, food web research has paid more attention to the effects of species losses/extinctions (Visser et al. 2011)

rather than species gains via invasions or (re-)introductions (Romanuk et al. 2009, Wardle et al. 2011) or to geographical distribution shifts, an universal phenomenon as climatic conditions change (Lurgi et al. 2012a, b, Walther 2010).

We adopt a theoretical approach for the study of biological invasions in empirical food webs. We focus on the importance of trophic interactions to elucidate the processes governing biological invasions in complex communities by simulating species invasions in nine alpine vertebrate food webs comprising a total of 493 species. We study the effects of invaders on the native community by introducing artificially generated species with different traits which belong to different trophic groups, and by modifying their diet breadth, number of predators and extinction thresholds. The aim is to answer the following questions: 1) Which food web properties make communities more vulnerable to invasion? 2) Which invader's traits are good predictors of invasion success? 3) What are the effects of invasions on network properties and, are these effects consistent for invaders with different traits? And 4) what are the differences between the native species that survive and those that get extinct after a successful invasion?

We hypothesise that food web complexity prevents successful biological invasions. More complex communities, with high species richness and connectance, provide less available niche spaces and generalist predators are more common than in simpler communities. Invaders will face higher rates of competition and will also have a larger predation pressure, which would prevent their establishment in the community (Case 1990, Pimm 1991, Kennedy et al. 2002). We also expect that generalist consumers will be more successful invaders because they can obtain energy from different sources and consequently they will be able to persist even if some of their prey get extinct (Romanuk et al. 2009).

Material and methods

Food web construction

We used a dataset from the south-eastern slopes of the Pyrenees, covering a region of ca 900 000 ha with contrasting relief and elevations (between 255 and 3140 m a.s.l.). Food webs were constructed from public databases and extensive bibliography search. Species co-occurrence was dependent upon four factors: coincidence in 1) space, in a grid of 92 cells of 10×10 km, 2) elevation, where three elevational ranges were differentiated: low, intermediate, and high (as done in Lurgi et al. 2012b for the same data set), 3) habitat type, and 4) season (spring–summer SS, autumn–winter AW, and all year ALL). If a species pair matched these criteria, and the literature reported a trophic relationship among them, then a link was added to the food web. Species interaction strength was derived from body size, following evidence suggesting that interaction strength is determined by predator:prey body size ratios (Berlow et al. 2004, 2009, Emmerson and Raffaelli 2004, Emmerson et al. 2005, Brose et al. 2006). In particular, we used the theoretical derivation of Emmerson et al. (2005), where predator–prey interaction strength was predicted as predator body size $^{0.75}$/prey body size. Body sizes were obtained from an exhaustive literature search and refer to average adult body sizes. One food web per season per elevation was constructed, yielding a total of nine food webs. Supplementary material Appendix 1 contains detailed information on food web construction.

Food web properties

We calculated and analysed several food web and node properties (Table 1). Food web properties included connectance (C, number of realised trophic links), the standard deviation of generality ($GenSD$, a measure of the variability of diet breadth among species), the standard deviation of vulnerability ($VulSD$, that measures the variability of predator pressure on species), mean food chain length ($MFCL$, that measures the vertical diversity of the network) (Williams and Martinez 2000), and modularity (M, which indicates the presence of densely linked groups within a network) (Guimerà and Amaral 2005). All these structural properties provide information about network complexity. More complex communities are, for example, those with more species, more links per species, higher connectivity and higher values of mean food chain length.

Node properties included indegree (number of prey), outdegree (number of predators), body size and role. Roles are classified depending on how species connectance within the compartment as non-hub nodes (poorly connected) or hub nodes (well connected). Roles R1, R2, R3 and R4 are non-hub nodes with many links to other food web compartments; Roles R5, R6 and R7 are hub nodes with

Table 1. Values of network properties of the 9 original food webs (by elevations and seasons; ALL: all year season, SS: spring–summer season, AW: autumn–winter). *S*: number of species; *L*: number of links; *L/S*: number of links per species; *C*: connectance; *GenSD:* standard deviation of generality; *VulSD:* standard deviation of vulnerability; *MFCL:* mean food chain length; *M:* modularity.

Season	Low elevation			Intermediate elevation			High elevation		
	ALL	SS	AW	ALL	SS	AW	ALL	SS	AW
S	223	214	125	202	199	125	82	82	51
L	875	851	506	799	791	506	179	179	119
L/S	3.924	3.977	4.048	3.955	3.975	4.048	2.183	2.183	2.333
C	0.018	0.019	0.032	0.02	0.02	0.032	0.027	0.027	0.046
VulSD	0.951	0.952	0.87	0.955	0.956	0.87	0.656	0.656	0.616
GenSD	3.224	3.124	2.736	3.067	3.03	2.736	2.845	2.845	2.43
MFCL	2.731	2.738	2.521	2.793	2.793	2.521	2.171	2.171	2.115
M	0.307	0.304	0.265	0.302	0.303	0.265	0.361	0.361	0.304

few connections to other compartments (Guimerà and Amaral 2005). Supplementary material Appendix 2 provides a detailed description of these properties.

Invasion experiments

We performed in silico invasions by introducing species that belong to one of the following trophic groups: birds of prey (BP), other birds (BI), mammal carnivores (MC), other mammals (MM), reptiles (RE) and amphibians (AM). The body size of the introduced species (the invader hereafter) was calculated by averaging the body size of its trophic group.

Due to changes in trophic group composition across our nine empirical food webs, invader's body size varied within each trophic group. For instance, mammal invaders' body size ranged from 4196.5 g to 7664.7 g across the food webs analysed. The exact body size value of the invader was therefore determined for each food web.

For each invasion event, several scenarios were analysed in our model, based on the combination of three parameters. Firstly, the fraction of generality, $FrGen$, which corresponds to diet breadth, and determines the fraction of links to prey species that are randomly assigned to the invader from the set of prey present within the same trophic group. Secondly, the fraction of vulnerability ($FrVul$), which determines the fraction of links to predators that are randomly assigned to the invader from the set of predators belonging to the same trophic group. Thirdly, an extinction threshold ($ExtThr$), ranging from 0 to 1, which reflects the fraction of the sum of predator–prey interaction strengths that a species can lose or gain before getting extinct after the invasion event. In the case of predators, this threshold determines the maximum fraction of prey consumption that the predator can lose before extinction. For preys, this threshold corresponds to the maximum predator consumption it can tolerate. In both cases interaction strengths between the invader and its predators and prey are updated as illustrated in Fig. 1a.

Once the invader's links were established, we performed a two-step process to recalculate the interaction strengths between the set of species directly connected to it, and the predators and prey connected to this set. In a first step, interaction strengths of invader's prey and their predators is reduced by an amount proportional to the strength of the new interaction of these prey with the invader, corrected by the number of predators each prey had before the invasion. In a second step, the interaction strengths of these predators with their remaining prey were increased in proportion to the reduction caused by the invader attacking one of their prey and corrected by the number of prey species (see example in Fig. 1b). Finally, if the new sum of interactions strengths was higher for a given prey, or lower for a given predator, than some fraction of the sum -determined by the extinction threshold- before the invasion, that species was considered extinct (Fig. 1c). For each invasion event, we followed this process only once (see Fig. 1 and Supplementary material Appendix 4 for further details). Since empirical evidence suggests that perturbations rarely propagate through food webs more than three links away from the initial perturbation (Abrams

et al. 1995, Menge 1995), this process only involved the recalculation of the interaction strength between the set of species directly connected to the invader, and the predators and prey in turn connected to these set of species.

Invaders varied in their values of $FrGen$, $FrVul$ and $ExtThr$, all ranging from 0.1 to 0.9, with an increment of 0.2. Each invasion attempt was analysed on each of our nine empirical food webs. A total of 5625 invasion attempts were simulated, because some of the scenarios were not feasible due to the lack of some trophic groups in a given elevation or season.

Statistical analyses

For each invasion event, we analysed: 1) food web and node properties from the community before invasion, 2) invader's traits at the moment of introduction, and 3) food web and node properties, including those of the invader, after extinctions. When necessary, we controlled for the variation in the number of species (S) across food webs, because some food web properties co-vary with S (Bengtsson 1994). All analyses were done with R ver. 2.5. Supplementary material Appendix 3 provides details of the statistical analyses.

Results

Network resistance

From the total number of invasion attempts, 4247 (75%) failed and 1378 (25%) were successful. Reasons for failure included too large predation pressure (2485 cases, 59%) and a lack of enough resources for the invader (1762 cases, 41% of failures).

To determine which food web properties made communities more vulnerable to invasions, we compared food webs with successful and unsuccessful invasions. In general, food web complexity conferred resistance to invasions. Successful invasions occurred in networks with less species (t = −5.866, p < 0.001, DF = 5624), less links (t = −6.354, p < 0.001, DF = 5624) and less links per species (t = −5.653, p < 0.001, DF = 5624). We also observed that more vulnerable networks had lower values of mean food chain length (MFCL) (t = −12.04, p < 0.001, DF = 5624), lower standard deviation of vulnerability (VulSD) (t = −5.012 p < 0.001, DF = 5624), and lower standard deviation of generality (GenSD) (t = −6.613, p < 0.00198, DF = 5624). Unexpectedly, successful invasions occurred in food webs with relatively large connectance values (t = 6.19, p < 0.001, DF = 5624).

Determinants of successful invaders

Invasion success relied upon all of the invader's traits we expected, namely the invader's trophic group, its role within the network, the predation it suffered and its diet breadth.

First, mammals (MC and MM) were the most successful invaders, with only 49.5% and 63.2% of failed attempts, respectively. This was also reflected by the total number of successful invasions (1378), from which a 30% of the total corresponds to mammal carnivores and a 27.5% to
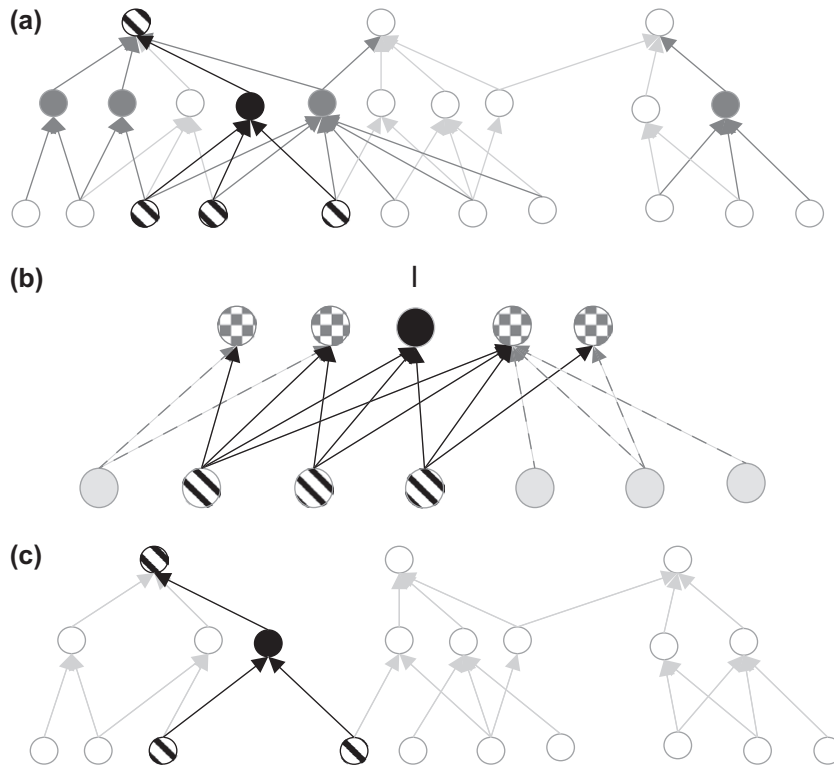
Figure 1. Illustration of the in silico invasion experiments performed in the food webs. Nodes correspond to species and links point from prey to predators. (a) An invasive species (black node) is introduced. Invader's outgoing (predators) and ingoing (prey) links are chosen from the set of outgoing and incoming links (dark grey arrows) from the set of species belonging to its trophic group (dark grey nodes). Only a fraction of the links from this set is chosen (black arrows) based on the 'fraction of vulnerability' and the 'fraction of generality' used, respectively. If the fraction of vulnerability is 0.3, only 30% of the possible links are assigned to the invader, and likewise for the fraction of generality. Invader's link strengths are calculated from predator-prey mass ratios between the invader and its interacting partners (line-patterned nodes). A recalculation of the strengths of the remaining trophic interactions of invader's part- ners is required and an example provided in (b) only for invader's (indicated by I) prey. A two-step process is performed. First the links (black arrows) connecting invader's prey (line-patterned nodes) with their predators (square-patterned nodes) are recalculated. In the second step, the links (dashed arrows) connecting these predators to their remaining prey (light grey nodes) are recalculated (see main text and appendix D for quantitative details). (c) This process can trigger direct and indirect extinctions (nodes present in (a) but absent in (c)). Direct extinctions are those caused directly by the predation pressure exerted by the invader while the indirect ones are those caused, for example, by the increase of the predation pressure on a prey as a result of the direct extinction of another prey that the invader and another predator shared. Species extinction may occur due to any of the following situations: 1) a prey gets extinct if the new sum of interaction strengths is higher than the sum given by the extinction threshold before the invasion; 2) a predator gets extinct if the new sum of interaction strengths is lower than the sum given by the same extinction threshold (see main text and appendix D for further details).

mammals. These percentages were larger to those corre- sponding to successful invasions of birds of prey (17.1%), amphibians (11.4%), birds (8%), and reptiles (6%).

Second invaders had different success rates depending on their role in the network. Species with only a few connec- tions within their compartment (e.g. roles R1 and R5) were the most successful invaders, with a mean success rate of 70%. Remaining species roles were only successful in 20% of the invasion events.

Third, invaders with fewer predators (i.e. less vulnerable) tended to be more successful (Fig. 2). In addition, for a given fraction of vulnerability, success was significantly dif- ferent depending on invader's body size and trophic group. The smaller the body size of the invader, the lower the $FrVul$ it could tolerate to succeed ($t = 20.05$, $p < 0.001$, DF = 1376), i.e. bigger invaders could tolerate higher preda- tion pressures. This was consistent across trophic groups, with the exception of mammals, non-carnivores in particular.

Finally, generalist invaders with broad diet breadths (i.e. high values of $FrGen$) were significantly more successful than specialists (Fig. 2). In all cases except for mammals, invasions failed if the $FrGen$ was 0.1. Maximum success rates occurred with $FrGen$ values higher or equal than 0.5. More- over, we found that larger invaders also needed a wider diet breadth to succeed ($t = 6.143$, $p < 0.001$, DF = 1376).

Effects of invasions on network properties

Invasions had significant effects on all analysed food web properties. Invasions significantly decreased on average several dimensions of food web complexity, including the number of links ($D = 0.1548$, $p < 0.001$), the number of species ($D = 0.1675$, $p < 0.001$), the mean food chain length ($D = 0.2765$, $p < 0.001$), the standard deviation of vulnerability ($D = 0.2235$, $p < 0.001$), and the standard deviation of generality ($D = 0.2708$, $p < 0.001$). On the
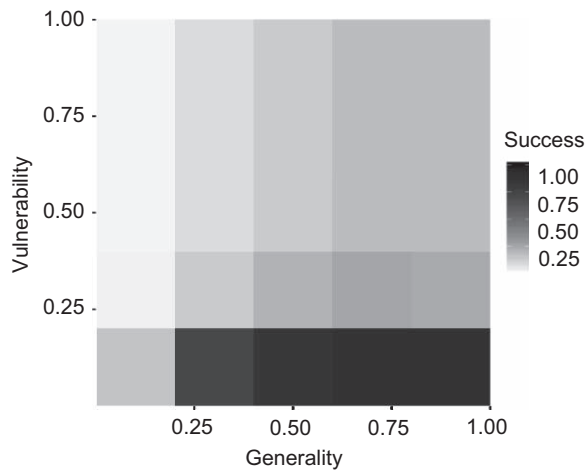
Figure 2. Heatmap for invasion success rate of the possible combinations between the fraction of vulnerability and the fraction of generality of the invader species. Higher success rates occur at low values of vulnerability and high values of generality.

contrary, invasions significantly increased on average the modularity of the network (D = 0.1916, p < 0.001), its connectance (D = 0.2301, p < 0.001), and the number of links per species (D = 0.209, p < 0.001). Invaded communities were, on the one hand, smaller and with less vertical diversity than their original counterparts, and on the other hand, more connected due to the major dominance of generalist and vulnerable species. Also, modularity increased after invasion, suggesting that the post-invasion tendency towards species with more connections is unbalanced towards within-compartment connections. These effects were more pronounced when the invader was a top predator (i.e. either BP or MC), which are amongst the largest species within the food web since species belonging to these trophic groups are larger than species from other groups. Globally, invader's role had a small effect on network properties. As expected, invaders with high roles (R6 and R7) significantly increased the number of links, and decreased the modularity and the standard deviation of vulnerability, whereas species with small roles had the opposite effect.

Although there were some clear patterns in the communities' response after invasion (i.e. decreased number of species, number of links, and standard deviation of generality and vulnerability; and increased connectance), there were properties that, even though they showed a significant trend, had a more irregular and unpredictable response (i.e. modularity and mean food chain length).

Extinctions triggered by successful invasions

Species that became extinct after invasions had specific traits: they were significantly smaller (z = −10.746, p < 0.001, DF = 6193), poorly connected (z = −6.07, p < 0.001, DF = 6193), with smaller roles, and mostly birds. Top predators (BP and MC) caused most of these selective extinctions. On the contrary, invaders belonging to other trophic groups promoted only a few extinctions, with extinct species not necessarily exhibiting the above-mentioned traits. In some cases, invaders mostly drove to

extinction species from the same trophic group (e.g. birds of prey and reptiles Fig. 3a), suggesting that in some cases invaders might replace natives within the same trophic group. Additionally, all the invaders, except those with roles R4 and R5, caused a large number of extinctions (Fig. 3b), but only invaders with R2, R3 and R6, markedly affected species with the specific traits mentioned above.

Discussion

Since biological invasions affect ecosystems at all levels of organization (Wardle et al. 2011), a holistic approach encompassing multiple species and their interactions is valuable to understand and predict community-level responses to invasions (Shea and Chesson 2002, Romanuk et al. 2009). We have presented a theoretical approach based on empirical data from alpine vertebrate food webs to investigate the importance of trophic interactions among species in the native community for assessing both invasion success and how invasions can disrupt biotic interactions within the food web. This complements previous theoretical works (Romanuk et al. 2009) and empirical studies focused on single species and/or small species subsets (Cassey et al. 2004, Sol et al. 2005, Vall-llosera 2012).

As observed in nature (Sax and Brown 2000, Vall-llosera 2012), most of our simulated invasions failed. Failures were mainly due to two mechanisms. First, to the lack of enough resources due to the under-exploitation of available resources by invaders (novelty disadvantage sensu Sih et al. 2010), or to niche overlapping between invasive and native species, provoking invasion failure by competitive exclusion. Second, to the overexploitation of invading prey by resident predators (Jones and Gomulkiewicz 2012).

Since the success of an invader might depend on the structure of the recipient community, it is important to identify community's properties that make them more susceptible to invasions. As expected, and in agreement with previous results by Romanuk et al. (2009), we showed that less complex communities were easier to invade. Food webs with more specialised predators and with prey attacked by fewer predators (i.e. with low values of *GenSD* and *VulSD*, together with a lower number of links per species) were more susceptible to invasions. These food webs are likely to offer wider niche opportunities for invasive predators, and for invasive prey that will suffer less predation. However, more connected food webs are less resistant to invasions than poorly connected ones. This seemingly contradictory result can be explained by the mathematical relationship between food web connectance and the number of species. We found that the most resistant networks were those with a higher number of species (S) and also with a higher number of links *(L)* per species (Case 1990, Kennedy et al. 2002). This increase in the number of links per species, however, is not enough to maintain or increase connectance given its quadratic relationship with S (i.e. $C = L/S^2$), whereas links per species only increases linearly. The link-species scaling hypothesis (Cohen and Newman 1985) states that, on average, the number of links per species in a web is scale-invariant at roughly two (i.e. $L/S = 2$ or $L = 2S$). In other words, species are linked to a
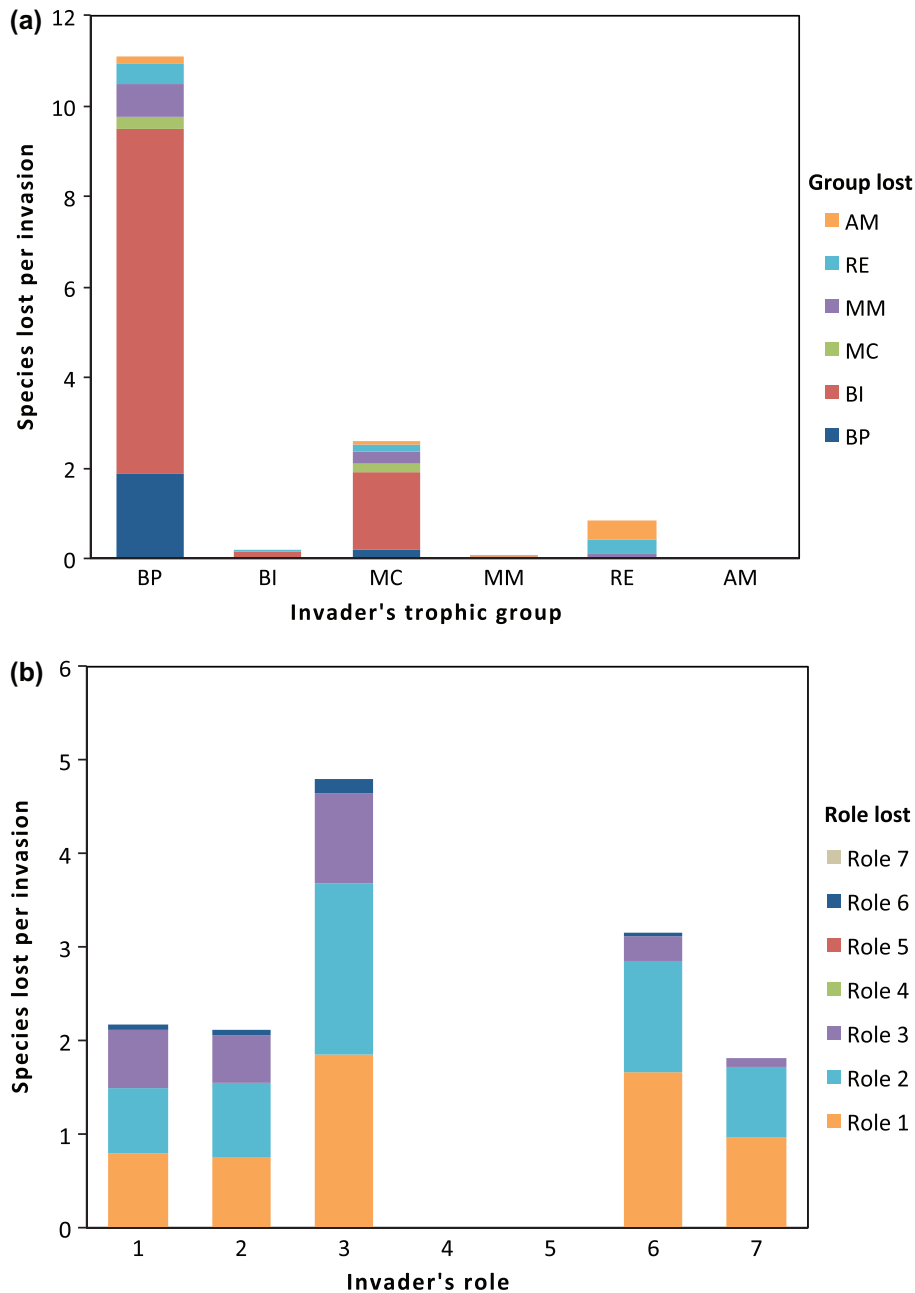
Figure 3. Number and type of lost species for each successful invasion event depending on the invader's type. (a) x-axis shows invader's trophic group (*AM*: amphibian, *BI*: bird, *MM*: mammal, *RE*: reptile, *MC*: mammal carnivore, *BP*: gird of prey). Each bar shows –for each invader's trophic group– the average number of species lost per invasion event by a species from that trophic group. Lost species are classified by their trophic group. (B) x-axis shows invader's role. Each bar shows – for each invader's role – the average number of species lost per invasion event by a species assuming the corresponding role. Lost species are classified by their role.

constant number of species independent of how many species are present in the community (Pimm 1982, Pimm et al. 1991). Alternatively, the constant connectance hypothesis (Martinez 1992), maintains that connectance is constant across food webs with different species richness. In our networks, we observe an increase in links per species with S, and a decrease in connectance with S, and hence they must lie somewhere in between these two hypotheses (as previously reported for other empirical food webs in Montoya and Solé 2003). Less connected networks can be harder to invade, but they actually have more links per species, which translates into higher complexity.

Identifying species' traits that are good predictors of invasion success is a central theme on biological invasions research. In our case, the invader's position within the network and its ability to extract energy from certain resources and to link different compartments within the community, are among the main determinants of invasion success. As expected, we found that more generalist invaders and those with a lower predation pressure (i.e. lower vulnerability)

were more successful (Romanuk et al. 2009). Interestingly, however, when invader's generality and vulnerability were considered together by means of the species' role in the food web, species with more links were not necessarily more successful. Most successful invaders were species with only a few links that connected otherwise disconnected species' compartments, or species that had most of their links within their compartment. Thereby, in order to be a successful invader, it is more important to avoid predators than to have a broad diet breadth.

Invasions prompted significant changes on the native communities, beginning with a decrease in biodiversity. Most extinctions occurred when the invader was a top predator with a large to intermediate diet breadth. Due to the triangular shape of our vertebrate food webs and their low values of connectance, the invasion of a predator might generate a top–down effect (Eklöf and Ebenman 2006) where intermediate and basal species could not tolerate an increase in their predation pressure. It is expected that species that go extinct as a consequence of the invasion would be significantly smaller and poorly connected, and most of them birds (in agreement with Clavero and García-Berthou, 2005). Prey that have fewer predators are likely to suffer stronger interaction strengths, and thus be unable to support an increase on the predation pressure exerted by the invader. In the case of predators, those that are specialised will encounter more difficulties to compensate through prey switching the decreased energy input taken by the invader from the suite of preys they share. In terms of body size, it is expected that smaller species would be more vulnerable to extinctions since in our approach body size determines interaction strength.

Early studies by Pimm (1979, 1980), followed by others (Solé and Montoya 2001, Dunne et al. 2002, Montoya et al. 2006), showed that not all extinctions have the same effect on the community due to indirect effects that can eventually provoke indirect species loss. Indirect interactions can be almost as important as direct ones in regulating population dynamics (Menge 1995, Yodzis 1998, Montoya et al. 2009). Our approach allows measuring indirect effects of successful invaders and not only direct extinctions. Numerous extinctions resulted from increases of predation pressure over a given prey as a result of the direct extinction of another prey that served as food for both an invader and a shared predator (Fig. 1). Including these indirect extinctions allows for a better understanding of the effects caused by an invader on the native community in terms of biodiversity loss and changes in food web structure.

Post-invasion communities were smaller and more connected, not only due to the decrease in biodiversity but also to the specific traits of species that became extinct. Although the number of links decreased, this was counterbalanced by the fact that most of the species that were lost were poorly connected (lower *VulSD* and *GenSD*, and higher number of *L/S* in the invaded network). Even though it is generally recognised that networks composed of generalist species are more connected and more resistant against species loss (Dunne et al. 2002), the overall effect on the community still remains an open question. While invasions affected some food web properties in a predictable manner,

other properties showed a very variable response. Modularity and food chain length, for example, showed a very unpredictable response after invasions. Higher modularity and shorter food chain lengths reduce population abundance fluctuations and increase overall community stability (Pimm et al. 1991, Montoya et al. 2006, Stouffer and Bascompte 2011). Thus, invasions may affect positively or negatively community and population's stability, but it would do so in an unpredictable way (Sih et al. 2010).

We acknowledge the multiple limitations of our approach. The tradeoff between considering multiple interacting species and species-level details (e.g. demography) is always difficult when assessing the effects of global change on complex communities. We made a number of assumptions, including the calculations of how strongly species interact, the subset of native species an invader interacts with, the extinction criteria, or the exclusive consideration of trophic interactions. In spite of these limitations, the work presented here offers a predictive framework for the identification of key properties that make vertebrate communities more robust to biological invasions, and important traits that make species more successful invaders. Therefore, it is a comprehensive approximation to the study of biological invasions, since it not only takes into account the community context in which the invasions occur but also provides a systematic way of testing the ability of particular vertebrate species to invade natural communities that would otherwise not be considered as possible invaders.

References

Abrams, P. et al. 1995. The role of indirect effects in food webs. – In: Polis, G. A. and Winemiller, K. O (eds). Food webs: integration of pattern and dynamics. Chapman and Hall, pp. 371–396.

Bengtsson, J. 1994. Confounding variables and independent observations in comparative analyses of food webs. – Ecology 75: 1282–1288.

Berlow, E. L. et al. 2004. Interaction strengths in food webs: issues and opportunities. – J. Anim. Ecol. 73: 585–598.

Berlow, E. L. et al. 2009. Simple prediction of interaction strengths in complex food webs. – Proc. Natl Acad. Sci. USA 106: 187–191.

Brose, U. et al. 2006. Allometric scaling enhances stability in complex food webs. – Ecol. Lett. 9: 1228–1236.

Case, T. J. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. – Proc. Natl Acad. Sci. USA 87: 9610–9614.

Cassey, P. et al. 2004. Global patterns of introduction effort and establishment success in birds. – Proc. R. Soc. B 271 Suppl: S405–408.

Clavero, M. and García-Berthou, E. 2005. Invasive species are a leading cause of animal extinctions. – Trends Ecol. Evol. 20: 110.

Cohen, J. E. and Newman, C. M. 1985. A stochastic theory of community food webs. I. Models and aggregated data. – Proc. R. Soc. B 224: 421–448.

Dunne, J. A. et al. 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. – Ecol. Lett. 5: 558–567.

Eklöf, A. and Ebenman, B. 2006. Species loss and secondary extinctions in simple and complex model communities. – J. Anim. Ecol. 75: 239–246.

Emmerson, M. C. and Raffaelli, D. 2004. Predator–prey body size, interaction strength and the stability of a real food web. – J. Anim. Ecol. 73: 399–409.

Emmerson, M. C. et al. 2005. Allometric scaling and body-size constraints in complex food webs. – In: Ruiter, P. C. et al. (eds), Dynamic food webs: multispecies assemblages, ecosystem development and environmental change. Academic Press, pp. 167–178.

Guimerà, R. and Amaral, L. N. 2005. Functional cartography of complex metabolic networks. – Nature. 433: 895–900.

Jeschke, J. M. and Strayer, D. L. 2006. Determinants of vertebrate invasion success in Europe and North America. – Global Change Biol. 12: 1608–1619.

Jones, E. I. and Gomulkiewicz, R. 2012. Biotic interactions, rapid evolution, and the establishment of introduced species. – Am. Nat. 179: E28–36.

Kennedy, T. et al. 2002. Biodiversity as a barrier to ecological invasion. – Nature 417: 636–638.

Kolar, C. S. and Lodge, D. M. 2001. Progress in invasion biology: predicting invaders. – Trends Ecol. Evol. 16: 199–204.

Kumschick, S. and Nentwig, W. 2010. Some alien birds have as severe an impact as the most effectual alien mammals in Europe. – Biol. Conserv. 143: 2757–2762.

Lurgi, M. et al. 2012a. Novel communities from climate change. – Phil. Trans. R. Soc. B. 367: 2913–2922.

Lurgi, M. et al. 2012b. Climate change impact on body size and food web structure on mountain ecosystems. – Phil. Trans. R. Soc. B. 367: 3050–3057.

Martinez, N. D. 1992. Constant connectance in community food webs. – Am. Nat. 139: 1208–1218.

Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. – Ecol. Monogr. 65: 21–74.

Montoya, J. M. and Solé, R. V. 2003. Topological properties of food webs: from real data to community assembly models. – Oikos 102: 614–622.

Montoya, J. M. et al. 2006. Ecological networks and their fragility. – Nature 442: 259–64.

Montoya, J. M. et al. 2009. Press perturbations and indirect effects in real food webs. – Ecology 90: 2426–2433.

Pimm, S. L. 1979. Complexity and stability: another look at MacArthur's original hypothesis. – Oikos 33: 351–357.

Pimm, S. L. 1980. Food web design and the effect of species deletion. – Oikos 35: 139–149.

Pimm, S. L. 1982. Food webs. – Chapman and Hall.

Pimm, S. L. 1991. The balance of nature? Ecological issues in the conservation of species and communities. – Univ. of Chicago Press.

Pimm, S. L. et al. 1991. Food web patterns and their consequences. – Nature 350: 669–674.

Romanuk, T. N. et al. 2009. Predicting invasion success in complex ecological networks. – Phil. Trans. R. Soc. B. 364: 1743–1754.

Sax, D. and Brown, J. 2000. The paradox of invasion. – Global Ecol. Biogeogr. 9: 363–371.

Shea, K. and Chesson, P. 2002. Community ecology theory as a framework for biological invasions. – Trends Ecol. Evol. 17: 170–176.

Sih, A. et al. 2010. Predator–prey naïveté, antipredator behavior, and the ecology of predator invasions. – Oikos. 119: 610–621.

Sol, D. et al. 2005. Big brains, enhanced cognition, and response of birds to novel environments. – Proc. Natl Acad. Sci. USA. 102: 5460–5465.

Solé, R. V. and Montoya, J. M. 2001. Complexity and fragility in ecological networks. – Proc. R. Soc. B. 268: 2039–2045.

Stouffer, D. B. and Bascompte, J. 2011. Compartmentalization increases food-web persistence. – Proc. Natl Acad. Sci. USA 108: 3648–3652.

Stouffer, D. B. et al. 2012. Evolutionary conservation of species' roles in food webs. – Science 335: 1489–1492.

Vall-llosera, M. 2012. Avian invasions : from basic to applied research. – PhD thesis, Univ. Autònoma de Barcelona.

Visser, S. N. et al. 2011. The Serengeti food web: empirical quantification and analysis of topological changes under increasing human impact. – J. Anim. Ecol. 80: 484–494.

Vitousek, P. M. et al. 1996. Biological invasions as global environmental change. – Am. Sci. 84: 468–478.

Walther, G. R. 2010. Community and ecosystem responses to recent climate change. – Phil. Trans. R. Soc. B 365: 2019–2024.

Wardle, D. et al. 2011. Terrestrial ecosystem responses to species gains and losses. – Science 332: 1273–1277.

Williams, R. J. and Martinez, N. D. 2000. Simple rules yield complex food webs. – Nature 404: 180–183.

Williamson, M. H. and Fitter, A. 1996. The characters of successful invaders. – Biol. Conserv. 78: 163–170.

Yodzis, P. 1998. Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. – J. Anim. Ecol. 67: 635–658.

Supplementary material (available online as Appendix oik-00859 at < www.oikosjournal.org/readers/appendix >). Appendix 1. Food web construction. Appendix 2. Food web and node properties. Appendix 3. Statistical analyses. Appendix 4. Recalculation of the interaction strength.