REPORT

Intraguild predation: a widespread interaction related to species biology

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Abstract

Intraguild predation (IGP), defined as killing and eating among potential competitors, seems to be a ubiquitous interaction, differing from competition or predation. In the present study we assess the frequency of IGP among 763 potential intraguild prey and 599 potential intraguild predators. Our results indicate that IGP is common in nature, reaching frequencies between 58.4 and 86.7%. A null model suggests that IGP in different groups of predators and prey (i.e. carnivores, omnivores, herbivores, detritivores, or top and intermediate species) have different deviations from a chance expectation, indicating these attributes of species biology as main determinants of IGP persistence. We suggest that IGP satisfies two basic requirements to be considered as important to the trophic structuring of communities. First, its occurrence is not random, rather it is associated with well-defined attributes of species biology, and secondly, it is a widespread interaction.

Keywords

Community modules, food webs, intraguild predation, null model, omnivory, species interaction.

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INTRODUCTION

Intraguild predation (IGP), defined as killing and eating among potential competitors, has gained relevance since Polis *et al.* (1989) pointed out its ecological and evolutionary implications. These authors showed that IGP is a taxonomically widespread interaction within communities which can occur at different trophic levels, and has the potential to affect the distribution, abundance and evolution of the species involved (Polis *et al.* 1989; Holt & Polis 1997). However, despite the apparent commonness of IGP (Morin 1999), no quantitative assessment of its incidence has been attempted, as is the case for other interactions such as competition and predation (e.g. Connell 1983; Schoener 1983; Sih *et al.* 1985; Marquet 1990).

In IGP interactions at least three species are involved, an IGPredator, an IGPrey, and a resource or prey species which is shared by both of them. Theoretical evidence suggests that the transformation from a purely competitive or predator–prey interaction to an IGP interaction could entail changes in the equilibrium condition for species coexistence (Schoener 1976; Pimm & Lawton 1978; Morin & Lawler 1996; Holt & Polis 1997; McCann & Hasting 1997). A consistent theoretical prediction is that persistence

of IGP depends on the existence of differences in the efficiency of resource exploitation between the IGPredator and the IGPrey, being lower in the former than in the latter (Holt & Polis 1997; Diehl & Feissel 2000, 2001; Mylius *et al.* 2001). In a similar vein, weak competition between IGPredators and IGPrey has also been suggested as a requirement for their coexistence (Mylius *et al.* 2001). In spite of these theoretical developments, empirical evidence for the effects of IGP on species coexistence and dynamics are mainly limited to microcosm experiments and parasitoid systems (Morin & Lawler 1996; Morin 1999; Amarasekare 2000; Borer *et al.* 2003). An analysis of the incidence of IGP interactions in food webs can potentially complement available studies and provide key evidence, for or against, theoretical models. Topological descriptions of food webs focus on connection patterns without considering either the magnitude (i.e. interaction strength), or the population dynamics of the interacting species; an aspect that has generated doubts regarding their validity (e.g. Paine 1988; Polis 1991, 1994). However, the observed topology of a food web is a consequence of stabilizing and destabilizing ecological processes related to population dynamics, interaction strength, diet selection, and enemy avoidance, furthermore, observed topological patterns depart

significantly from null model expectations (Gotelli & Graves 1996; Milo *et al.* 2002).

In the present paper we re-analyse published data (Cohen *et al.* 1990) on 113 food webs in order to assess the frequency of IGP in nature. The approach used here differs from previous studies oriented towards detecting patterns in food web parameters (e.g. connectance, chain length, species and links distribution among 'trophic groups'), in that we use individual species information from food web collections. The database made available by Cohen *et al.* (1990) provides the opportunity to test how common IGP is among 763 potential IGPrey and 599 potential IGPredators species, allowing us to estimate the frequencies of IGPredators and IGPrey, and to relate them with biological characteristics of species. Furthermore, food web matrices provide a conservative estimation of IGP frequencies and sufficient information for developing a robust null model to contrast against observed values. This makes it possible to know whether the observed frequencies of IGP are unusually large or small, and to have an assessment of its ecological significance (Gotelli & Graves 1996).

Our main objectives were to analyse the prevalence of IGP in nature and to relate its occurrence with the biology of the species involved in IGP interactions, so as to have an assessment of the potential contribution of IGP interactions to community structure. We found that IGP is a common pattern in food web topology and that its occurrence cannot be explained by chance alone. Furthermore, carnivores, herbivores and detritivores, and top and intermediate predators, differ in their propensity to engage in IGP interactions. To our knowledge this is the first study in which the incidence of IGP has been quantified across a large set of communities and in which deviations in expected occurrences from a specific null model of IGP have been assessed.

METHODS

Food web database and its suitability for the study of IGP interactions

Community food webs describe the binary feeding relationships between trophic species in a community (Cohen *et al.* 1990). A trophic species, or trophospecies, is a set of one or more biological species that share the same predators and prey (Cohen *et al.* 1990). We extracted information on trophospecies (hereafter species) from the 113 food webs published by Cohen *et al.* (1990). Previous analyses of this database, although not exempt from criticisms, have proven to be of great importance in deepening our understanding of food web patterns (e.g. Garlaschelli *et al.* 2003).

A key consideration in a study that uses the food web data in Cohen *et al.* (1990) is the existence of potential biases that might affect the results. It is known that this data set has several problems associated with trophic resolution, species aggregation, and with the species considered in the webs as compared with all the species present in the communities they are derived from (e.g. Pimm 1982; Polis 1991, 1994; Morin & Lawler 1996), which could affect the estimation of some food web parameters (e.g. Polis 1991, 1994; Martinez 1992, 1993). In this regard, we assume that those species not included in the webs have the same propensity to engage in IGP as those included, as there is no *a priori* reason to expect a different tendency to IGP between included–not included, and aggregated–not aggregated species.

Working with trophospecies can alter the interpretation of results; however, it should be considered that some of the empirical observations of IGP (Schoener 1989; Spiller & Schoener 1994, 1998) and related theoretical predictions (Courchamp *et al.* 1999) are based on aggregated species (e.g. birds, spiders, lizards, insects). Hence, from this perspective, IGP can be considered as an interaction among species or among 'trophic groups' engaged in IGP, where the effect of the group reflects a statistical tendency of its component species (see Spiller & Schoener 1998).

Our work does not estimate a food web parameter for IGP. We analysed the incidence of IGP for different types of species, excluding those that might introduce bias into our analysis (see below). We agree with the claim that the database by Cohen *et al.* (1990) lacks enough resolution so as to make a safe estimation of food web parameters possible (but see Garlaschelli *et al.* 2003). However, the biological information it contains does allow insights into food web structure (e.g. body size differences between predators and prey; Cohen *et al.* 1993). Furthermore, potential biases can be accounted for and, as we show, this renders our estimates of IGP in nature as conservative (see Discussion). Finally, it should be noticed that well-defined food webs also have problems, such as the likely accumulation of spurious links between species (Kondoh 2003).

Species classification

Traditionally, species in food webs have been classified as top (no other species in the food web prey upon them), intermediate (at least one species prey upon them, and they prey upon at least one other species), and basal (they do not prey upon other species) (Cohen *et al.* 1990). We changed the above classification to emphasize the biological attributes and functional roles of species within food webs. Thus, in addition to distinguishing among top, intermediate and basal species, we also identified whether the species was a carnivore, herbivore–detritivore, or an omnivore By omnivorous we refer to an animal that can feed on both animals and plants (Lincoln *et al.* 1998), which differs from

the definition of 'omnivorous' used by Pimm & Lawton (1978), i.e. 'a species that feeds on more than one trophic level'. Therefore, we expanded the classification, following the logical assumption that basal species are plants or detritus and intermediate species are animals. We considered that species eating only basal organisms were either herbivores or detritivores; species eating basal and intermediate organisms were omnivores; and species consuming only intermediate organisms were carnivores. Putting both classifications together, the organisms with potential to be an IGPrey or an IGPredator, were: top carnivorous (Tc), top omnivorous (To), intermediate carnivorous (Ic), intermediate omnivorous (Io), or intermediate herbivores or detritivores (Ih-d). We refer to this classification as 'trophic groups' (see Fig. 1). A few 'basal' species in the database were animals, and these species were classified as 'intermediate'.

The species classification introduced herein attempts to include more biological realism to topological food web studies. Our classification is no more susceptible to biases than any other classification. Our categorization does not alter the topology of the analysed food webs. Instead, our categories provide a biologically meaningful way of analysing IGP, without altering its incidence. Species engaged in IGP interactions under classical definition remain so after the application of our classification, and no new IGP links are added as a consequence of using our classification.

Intraguild predation in food webs

IGP occurs when a predator–prey pair share at least one prey resource (Polis *et al.* 1989). Relative frequencies of predator and prey IGP were calculated for each of the trophic groups (see above) as the proportion of the total species in the group engaged in IGP, regardless of the food web from which they came.

Not all species can engage in IGP interactions; in order to be an IGPrey, the species should have at least one prey and one predator; this implies that only intermediate organisms can be an IGPrey. Basal species and intermediate herbivores or detritivores cannot be IGPredators because they cannot feed on the prey of their prey. Similarly, to be an IGPredator, an organism has to eat more than one prey, because otherwise it would not be possible to share a prey with its prey. This implies that monophagus species cannot be IGPredators, and their prey cannot be IGPrey unless preyed upon by another, non-monophagus, IGPredator. As one of the principal problems with food web data is the resolution of trophic links within the food web, it is possible for monophagy to be an artefact of resolution (Polis 1991, 1994; Martinez 1993). To control for this potential bias, species falling under this category were removed from the analysis. Using this procedure, some real monophagus species were eliminated, but given the resolution of the data a large number of falsely accused monophagus species were removed. Thus, the net effect is a reduction in the bias associated with estimating the frequency of IGP among and within trophic groups.

Other trophic restrictions to IGP takes place when the candidate for IGPrey is a herbivore. These species can only be an IGPrey when their predator is an omnivore, because otherwise, the predator could not feed on the herbivores resource. This means that a carnivorous predator with an herbivorous prey has no chance of being engaged in IGP interactions. We took into account this restriction and calculated the IGP frequencies without considering carni-
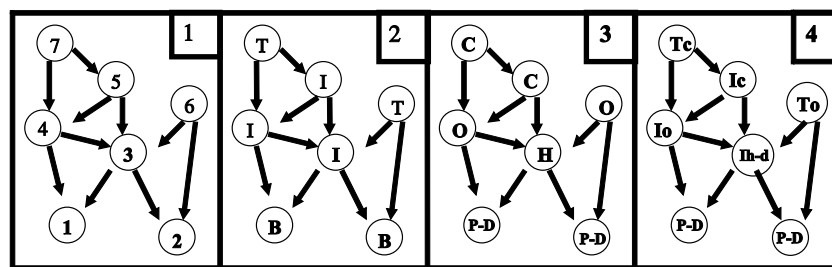

Figure 1 Classification of species within food webs as used in this study. Box 1 shows a food web without classification. In box 2, species are named according to the classical view as basal (B) species that eat no other species; intermediate (I), at least one species eats them and they eat at least one species; and top (T), no other species in the web eats them. In box 3 it is assumed that basal individuals are plants or detritus (P-D), and intermediate and top species are animals. Thus, the species that only eat intermediate organisms are considered to be carnivorous (C); those that eat intermediate and basal species are considered as omnivorous (O), and when they only eat basal organisms they are considered herbivorous or detritivorous (H-D). Our study combines the classifications shown in boxes 2 and 3. The results are shown in box 4. Using the species number shown in box 1 the classification is as follows: species 1 and 2 are plants or detritus (P-D), 3 is an intermediate herbivore–detritivore (Ih-d), 4 is intermediate omnivorous (Io), 5 is intermediate carnivorous (Ic), 6 is top omnivorous (To), and 7 is top carnivorous (Tc). Notice that the first character corresponds to the classical classification and is followed by a one letter referring to the classification herein proposed [herbivorous–detritivorous (h-d), carnivorous (c) or omnivorous (o)].

vore–herbivore pairs as potential IGPredators and IGPrey. However, to assess the extent to which our results depended on the exclusion of monophagous and carnivorous–herbivorous pairs, IGP frequencies were also calculated for the complete database without excluding any species.

Null model

A complete treatment of macroscopic patterns (like IGP frequencies) necessarily requires establishing that the pattern is different from what would be expected by chance alone, and to understand the nature of the small-scale processes involved in their generation (Maurer 1999). Null models appeared early on the food web literature, and they could be crucial to the interpretation of results, because 'only by comparison with a null model can we decide if a certain web metric is unusually large or small' (Gotelli & Graves 1996).

In this case a possible null model is to take the frequencies of IGP observed in empirical food webs, and to contrast them with the values registered in webs generated by random procedures subjected to some biological restrictions (Pimm 1980, 1982). However, empirical food webs differ from randomly generated webs in many aspects other than IGP. The objective of null models is to generate the pattern that would be expected in the absence of a particular ecological mechanism (e.g. Pimm 1980, 1982; Gotelli & Graves 1996; Arim & Barbosa 2002). Nevertheless, food web randomization generates a pattern in the absence of many ecological mechanisms (e.g. Pimm 1980), so we looked for a null model that was more specific to IGP.

The model employed was based on the estimation, of the probability that any predator–prey pair (hereafter pair), shared a resource by chance alone (see Fig. 2). That is, the probability of being an IGpredator or an IGprey by chance. To do this we started by estimating the probability that the pair did not share resources by chance. We assumed that the predator takes a random sample from all the available prey to which it has access. Given that our null model involves sampling without replacement, and that the prey pool is finite, a hypergeometric distribution shall be used (Feller 1968).

$$P(X = 0) = \frac{\binom{\mathrm{Pr} - R}{Z}}{\binom{\mathrm{Pr}}{Z}} \tag{1}$$

where $P(X = 0)$ is the probability that the predator–prey pair shares zero resources by chance. Pr, or *prey pool* is the number of basal and intermediate species that are available to the predator. Carnivores cannot eat basal organism, so their prey pool is restricted to intermediate species. As we are evaluating the probability that a fixed pair does not share resources, they are not part of the pool, hence the prey of the
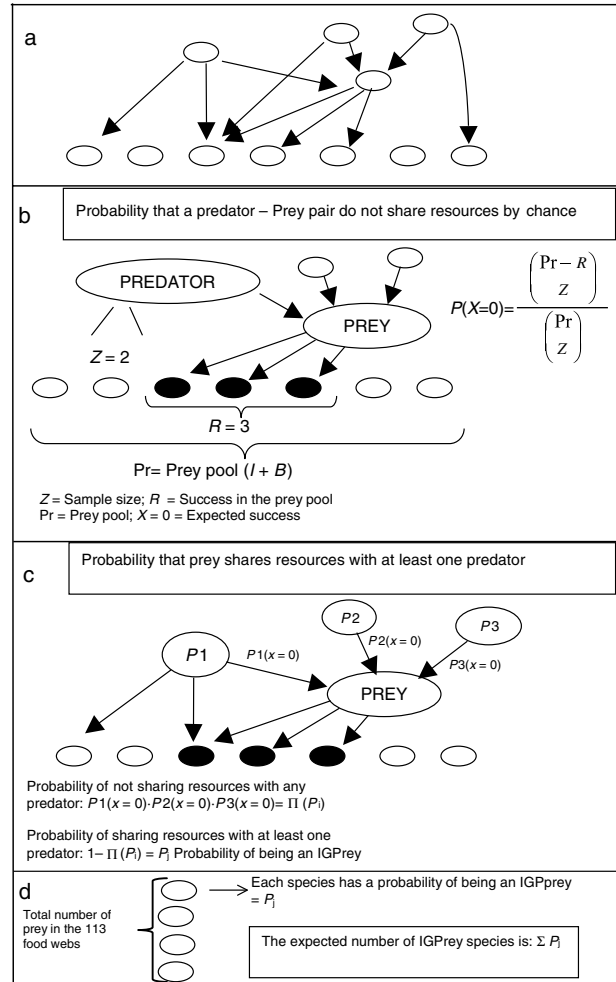
pair should always be subtracted from the pool and when the predator is intermediate it should be subtracted as well. R, represents the number of species in the prey pool (Pr) that are resource for the prey. If at least one of these is consumed by the predator then IGP occurs. If the predator was carnivorous, only the number of intermediate species that were resources of the prey were considered, otherwise all the species that were resources of the prey were included. Z, is the actual number of prey in the predator's diet minus 1 (because the prey in the pair has to be subtracted). When $Z > (\mathrm{Pr} - R)$ then $P(X = 0) = 0$ by definition, as there is no way of sampling without success (i.e. in this case the relation $P(X = 0) = 0$ is interpreted as impossibility, see Feller 1968 p. 44).

Using this procedure, we can calculate the probability of not observing IGP between any species pair. To calculate the probability that one species was an IGPrey (or an IGPredator), we utilized the probability that the species does not share resources with every one of its predators (prey). It was assumed that these are independent events, so by multiplying their probabilities we found the probability

Figure 2 Calculation of the expected number of species engaged in IGP. (a) food web as reported in Cohen *et al.* (1990). (b) The calculation of the probability that a predator and a prey do not share resources by chance. Z, is the number of predator links that are assumed to be a random sample of the prey pool; R, is the number of successes in the prey pool, or the number of species that, when eaten by the predator, imply IGP (black dots in the prey pool); Pr, is the prey pool formed by all basal and intermediate organisms $(B + I)$. However the actual size of the prey pool depends on the predator–prey pair analysed. Carnivorous predators only eat intermediate preys so Pr $= I$. As the focal predator–prey pair analysed is not in the prey pool, one unit should be subtracted to account for the prey not being in the pool, so Pr $= B + I - 1$ for omnivorous predators and Pr $= I - 1$ for carnivorous predators. In the same vein, when the predator is intermediate it should be subtracted as well (Pr $= B + I - 2$ or Pr $= I - 2$). (c) Estimation of the probability that a species being an IGPrey. Using the probability that a prey does not share resources with each one of it predators, the product of these probabilities is the probability of not sharing resources with any predator. Subtracting this probability from 1 gives the probability of sharing resources with at least one predator. (d) The calculation of the expected number of IGPrey in the complete database. The example is focused on IGPrey, the calculation of the expected incidence of IGPredators follows the same logic, but the probability calculated in (c) is obtained by calculating the product of the probability of being an IGPredator with each one of its prey and subtracting this value from 1.

that the prey (predator) does not share resources with any of its predators (prey). If this probability is subtracted from 1, we obtain the probability that the prey (predator) share one or more resources with one or more predators (prey), this is the probability of the species being an IGPrey (IGPredator). That is,

$$P_j(\text{IGP}) = 1 - \left(\prod P_i \right) \qquad (2)$$

where P_i represents the probability that species j does not share resource with species i by chance. The sum of these probabilities for all the species in each trophic group gives the expected number of species with IGP in the trophic group (Denny & Gaines 2000), that is,

$$E(\text{IGP}) = \sum P_j(\text{IGP}) \qquad (3)$$

The null model proposed herein only assumes that predator diet selection is independent of the occurrence of IGP. The number of top, intermediate and basal species, number of prey for each species, as well as the total number of predators and prey in the system, and also food web connectance are retained in the null model. The model is only 'null' in relation to predator links that imply or not imply IGP among available prey. It is based in the distribution of reported links between the reported species.

Contrast between null model and data

Deviations of the observed IGP frequencies from the frequencies predicted by the null model reflect the relevance of the interaction (Gotelli & Graves 1996). As our species might share a common food web with other species in the collection, they cannot be considered as independent observations. To account for this lack of independence, we carried out a bootstrap procedure (Efron & Tibshirani 1993) according to the following steps. First, we had a population of observed values (occurrence of IGP in each species) with a paired population of expected values (probability of IGP for each species). Second, in order to have an independent group of observations, one individual was randomly selected from each food web. Food webs that were not independent, following Bengtsson (1994), were considered to be one web and only one individual was taken from the pair. Third, in the generated subsample, the expected percentage of species with IGP was subtracted from the observed percentage registering the resultant value. Fourth, this procedure was replicated for each group 10 000 times and a 95% confidence interval was constructed (Efron & Tibshirani 1993). If zero was within the 95% most frequent values, the difference between observed and expected frequencies was considered a matter of chance, otherwise a real difference was accepted.

RESULTS

In general, in the subset of species analysed for IGP was observed in all the trophic groups reaching frequencies between 58.4 and 86.7% (Fig. 3a). When all the species in the database were considered, the incidence of carnivorous IGPredators was lower (Ic $= 29.7\%$ and Tc $= 30.3\%$; Fig. 3b).

For IGprey, the main results are a positive deviation from the model in the Ih-d group, and a negative one for Io and Ic species (Fig. 3a). The observed frequency of To as IGPredators was not different from that predicted by the null model, however, Tc species were observed as IGPredators less often than expected by the null model. Last but not least, Io and Ic species were observed as IGPredators more frequently than expected by chance (Fig. 3a). In spite of variations in the magnitude of the deviation from the null model, when the analysis is carried out using all the species available in Cohen *et al.* (1990) no major changes were observed (Fig. 3). The observed negative deviation from the null model in Tc species was marginally significant when all species where included.

DISCUSSION

Our results suggest that IGP satisfies two basic requirements to be considered as an important attribute of
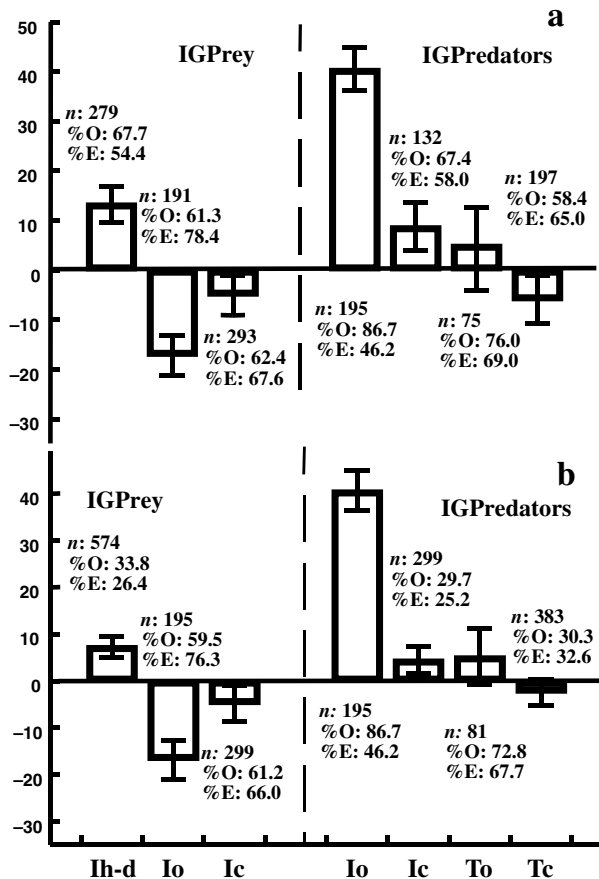
Figure 3 Deviations in the observed frequencies of IGP for different trophic groups, as compared with the expected frequencies under a null model. Error bars indicate the 95% confidence interval generated by a bootstrap procedure. *n*, number of species; %O, observed percentage of species involved in IGP interaction; %E, expected percentage of species involved in IGP interaction. (a) The observed pattern when a subset of the species is considered (see text). In this case only the top omnivorous species (To) show a frequency not different from the null model. In (b) all the species in the database are included. Note that the reported patterns are largely consistent in both figures, however two differences should be highlighted: (1) when all species are considered the magnitude of the deviations are reduced and (2) top carnivores [Tc in (b)] do not significantly deviate from the null model.

interacting species assemblages. First, its occurrence is not random, rather it is associated with well-defined attributes of species as captured in our classification. Secondly, it is a widespread interaction.

In general, large differences in the incidence of IGP were detected between IGPrey and IGPredators. Furthermore, carnivores (Ic, Tc), omnivores (Io), and herbivorous–detritivorous (Ih-d) species show significant deviations from the null model (Fig. 3). Therefore, IGP is unevenly distributed among different trophic groups in the food

webs. This represents a new pattern in IGP that could be a matter of future theoretical and experimental studies. Clearly, our trophic classification conveys more biological information than those distinguishing only basal, intermediate and top species, and allows for a better understanding of which species attributes are associated with the incidence of IGP in nature.

Our main results are in agreement with available theoretical predictions. IGPrey are observed less frequently than expected in omnivore and carnivore (Io, Ic) species, but more frequently than expected in herbivore–detritivore species (Ih-d). The former fits with the theoretical expectation that IGPrey are frequently excluded by the IGPredator (Holt & Polis 1997; Diehl & Feissel 2000; Mylius *et al.* 2001). Positive deviation from the null model in herbivore–detritivore species, is consistent with the prediction of more stable IGP when the shared resources is of lower quality to the IGPredator than is the IGPrey (Diehl 2003), as is the case in plant resources and animal IGPrey.

Among IGPredators, intermediate species (Io and Ic) presented greater and positive deviations from the null model than top species (To and Tc; Fig. 3). Predation experienced by intermediate IGPredators will likely reduce their ability to depress the resources shared with the IGPrey, stabilizing the IGP interaction. Predation implies a reduction in resource exploitation efficiency (Trussell *et al.* 2002), and a lowering in the intensity of competition (Gurevitch *et al.* 2000). In this way, intermediate IGPredators are limited, to some extent, by predation and therefore should be less likely to reach densities at which they exclude their own IGPrey. These patterns are in agreement with the theoretical claim that for IGP to persist, the IGPredator should have a lower efficiency in resource exploitation than the IGPrey (Holt & Polis 1997; Diehl & Feissel 2000; Mylius *et al.* 2001).

The incidence of IGP that we report represents a conservative estimation. The number of links in any real food web will be equal or, more likely, larger than the total numbers of links reported by Cohen *et al.* (1990). For the subset of species we worked with, the existence of more links could imply a reduction in observed IGP frequencies if new links are added to species previously classified as monophagous, without producing IGP. However, as previously stated, there is no *a priori* reason to expect that new links will add non-IGP species instead of IGP species to the subset. Furthermore, within the studied subset (all species except monophagous predators and carnivore–herbivore species pairs), it is valid to say that the addition of new links will only increase the number of species engaged in IGP. Our point is further supported by the results of carrying out our analysis using the complete set of species in Cohen's data set. In addition, supporting a conservative estimation of IGP frequencies in this study is the observed temporal variation of connections in natural food webs (Winemiller 1990;

Kondoh 2003), and species composition (Polis *et al.* 1997). The actual frequency of IGP can be thought of as the number of species engaged in IGP in a fixed lapse of time. This means that the real number of species that experience IGP would likely increase as the duration of the study increases. Finally, the aggregation of species could lead to incorrectly considering that a predator and its prey share a resource species, thus increasing the observed incidence of IGP. However, the null model detects both positive and negative deviations, demonstrating that this bias was not large enough to obscure the patterns.

Considering that the observed IGP frequencies are based on 763 potential IGPrey and 599 potential IGPredators species, and that these estimations are conservative, IGP appears to be a widespread interaction, even when all species in the database are included in the analysis, thus inflating biases that reduce IGP incidence (Fig. 3b). It should be noted that the high incidence of IGP was suggested, or suspected, elsewhere (e.g. Polis *et al.* 1989), but this is the first time that this claim has been statistically supported. Although IGP can be recognized as a common interaction, the question of the biological significance of the observed frequencies still remains open (Gotelli & Graves 1996). The significant and uneven deviation of IGP incidence from the null model predictions among trophic groups fosters our understanding of the ecological importance of IGP in nature, but additional work is necessary to assess its relevance for food web stability and persistence.

The relationship between diversity, trophic structure and the stability of ecological systems is an old and persistent focus of attention in ecology (e.g. McCann 2000). The present paper reinforces the vision that IGP is a widespread interaction that can be of paramount importance for the structure and stability of species communities. As in other approaches aimed at establishing the commonness of some biotic interactions, the relevance of the results admits some degree of inaccuracy (Connell 1983; Schoener 1983; Menge 1995). We hope, however, that our work will serve as motivation for further studies aimed at establishing the factors associated with the likelihood of observing IGP in nature, specially now that well-resolved food webs are becoming available (e.g. Dunne *et al.* 2002).

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