Functional equivalence in plant-animal interactions: ecological and evolutionary consequences

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There may be ten million species of plants and animals on earth; are there really ten million kinds of population dynamics? (Lawton 1992)

Anyone who begins to analyse ecological interactions has no doubt felt the sensation that each new interacting pair of species will offer a new outcome, so that such interactive results will invariably be species-specific. Embedded in the Linnean taxonomic tradition, the general tendency in studies on the ecology of interspecific interactions has narrowed down to a search for differences between species, more than a search for similarities that might be evident if consideration were given to shared traits, such as body size, ecophysiological responses, or life-history traits (Hay 1994, Steneck and Dethier 1994, Duarte et al. 1995). On the other hand, the study of ecological interactions has been fuelled by optimality-guided theoretical approaches predicting that evolution results in the most efficient phenotype in each environment (Solbrig 1993). Thus, the interactions where these optimal phenotypes are involved should in turn be well-adjusted and optimized, tending towards specialization and coevolution. The upshot of these views is that the uniqueness of taxonomic entities translates to the uniqueness of interactive outcomes.

To these conceptually constrained viewpoints, we must add a methodological limitation, bound by budget and time of research grants, and thus most studies on interspecific interactions focus largely on selected species assemblages containing only a few species found in a given location during a short period of time (Hairston 1989, Kareiva 1994, Zamora et al. 1999). The result is that today, very few broad generalizations on the ecology and evolution of interspecific interactions have been ventured, in contrast with the very large number of studies published.

Prevalence of generalist assemblages in plant-animal interactions

Most research has been devoted to the study of highly simplified interactive systems (even as few as two species). In contrast, the empirical evidence gathered during the last few years has shown that many of the interactive systems known are generalist and dynamic, often an animal interacting with many plant species and vice versa (Jordano 1987, Thompson 1994, Herrera 1995, 1996, Romeo et al. 1996, Waser et al. 1996). Even some of the traditionally considered obligate interactions, such as those existing between figs or yuccas and their pollinators, may not be so absolutely obligate as previously thought (Pellmyr et al. 1996, Waser et al. 1996). Therefore, generalization in ecological interactions is common throughout nature in plant-animal interactions, being a rule also when considering trophic webs as a whole (Polis and Strong 1996, Polis and Winemiller 1996).

Recently, Ollerton (1996) outlined a major paradox in plant-pollinator systems: how to reconcile the widespread existence of generalism with the evidence of consistent, directional selection? Consistency may come from well-differentiated selective pressures, which are easily derived from predictable, specialized interactive systems comprised of few species. But how might consistency come from spatio-temporally variable, generalized, multispecific systems?

In multispecific systems, there is an opportunity for species-specific specialization only when species, due to interspecific differences, bring about different interactive outcomes. It can happen that selective pressures exerted by the various species go in different, even opposite directions. The final result can be a dilution of all selective pressures, because the pressure of one species is often opposed, constrained, or modified by

pressures of other species. In the overall result, *the noise overwhelms the pattern*. The resulting "Diffuse coevolution" process has been more successful in drawing attention to the complexity of interactions in a multispecific context than in producing clear predictions of outcomes (Fox 1988, Thompson 1994, 1999a, b). In fact, only recently have formal criteria been developed to differentiate diffuse from pairwise coevolution (Hougen-Eitzman and Rausher 1994, Iwao and Rausher 1997).

Thompson (1994, 1999a, b) recently proposed that, because of geographical variation within species, many species are composed of populations specialized to different interactions. Thus, considering populations together in a species-level analysis can provide a misleading idea of generalism, when in fact there is a complex population-level mosaic of interactions, with some populations becoming a "hot spot" for specialization and potential coevolution. However, this population-based approach only reduces the magnitude of the problem when considering multispecific assemblages, but does not eliminate it. This is because, on a local basis, a given plant or animal at any one life-history stage can interact with a subset of the total geographical assemblage, which is composed of populations of many species (Herrera 1988, 1995, Jordano, 1995a, Waser et al. 1996, Gómez and Zamora 1999, Zamora 1999).

One possibility is that, despite a wide spectrum of species locally interacting, there are only a few strong interactions, and a large network of weak relationships (Jordano 1987, Ollerton 1996, Waser et al. 1996, Waser 1998). In this case, an apparently generalist system may prove to be specialized because only one or a few key species in the interactive assemblage actually drive the system.

There is an alternative and/or complementary, barely explored possibility – namely that, although different species may interact on a local basis, most of these species bring about similar interactive outcomes. In this case, different species might be functionally equivalent. The resulting cumulative contributions from different species interacting in a similar way might be expected to result in responses to whole groups of species. In the overall result, *the pattern overwhelms the noise*. This possibility, however, has been largely disregarded despite that the ideas that species can be ecological equivalents in different communities (e.g. Odum 1959), or that different species can exploit a similar resource in a similar manner (e.g. the guild concept of Root 1967), are very old. As a result, we seldom know whether different interacting species are functionally equivalent, exerting similar effects both on populations and on community organization, or whether they are functionally distinct, with unique or non-substitutable roles. Here, I will explore this latter possibility, analysing the ecological setting that might promote functional equiv-

alence in multispecific plant-animal systems (see related approaches in Hougen-Eitzman and Rausher 1994, Romeo et al. 1996 and Iwao and Rausher 1997 for plant-herbivore interactions; Gómez and Zamora 1999 for plant-pollinator interactions; Morin 1995, Kurzava and Morin 1998 and Sih et al. 1998 for predator-prey relationships; and Callaway 1998 for plant-plant interactions).

Much effort is being concentrated on approaching ecological interactions from a reductionistic perspective, often based on genetic studies. This approach is proving particularly effective in the analysis of stepwise, gene-for-gene models, including two species (or lineages) maintaining a high level of mutual dependence (e.g. host with parasites and/or obligate mutualists, see Thompson 1994, 1999a, b). However, this approach may be inadequate to explain the ecological and evolutionary organization of the multispecific, facultative system, where the degree of mutual dependence and reciprocity between interacting species diminishes dramatically. In this context, the analysis of the mechanisms involved in the maintenance of these generalist, facultative systems, and their ecological and evolutionary consequences merit attention from ecologists in order to gain a balanced view of the big picture of ecological interactions.

Here, from the standpoint of the functioning of interactive assemblages, the question is whether changes in taxonomic identity of the interacting species affect the outcomes of the interactions. Certainly, there are millions of species interacting in nature, but, paraphrasing Lawton (1992), we might ask: Are there as many different outcomes of interactions as interacting pairs of species? Does a plant have as many forms of defence as it has herbivore species? Are there as many ways to eat a leaf as a plant has herbivore species? Are there as many ways to make contact with anthers of stigmas as a plant has pollinator species?

Of course, at the most detailed level, the answer is likely to be yes. However, differences may not be significant in ecological and evolutionary terms.

Ecological characteristics driven to functional equivalence

The outcomes of some plant-animal interactions pivot on unusual traits in either the plants and/or the animals that confer a high degree of specificity (e.g. the Beltian bodies and extrafloral nectaries allowing the acacia-ant mutualism). However, it seems obvious that not all attributes of plants and animals are relevant to the outcome of an interaction. For example, the number of setae on a femur, which enables taxonomic distinction between two species of insect herbivores would not necessarily be relevant when considering the interaction

of those two species and a given plant or a given predator. Contrarily, these two species can share critical qualitative and/or quantitative traits that are relevant to the interaction, such as: size, shape, chemical composition, nutritive and/or energetic value, ecophysiological responses, behaviour, life-history stage, abundance, etc., and all of these shared traits can lead to similar interactive outcomes irrespective of the species' taxonomic affinities. In this case, the resulting outcome of interactions should be trait-specific instead of taxon-specific. For example, different generalist predators of similar size might affect communities in similar ways, as long as they consume similar sets of prey species at comparable rates (Morin 1995, Kurzava and Morin 1998).

Formally speaking, functional equivalence may appear in the qualitative and quantitative aspects of ecological interactions, or both. Populations of different species can generate similar frequencies of occurrence of the interaction by having, for example, similar population abundance and/or frequency of visits. On the other hand, different species, by sharing similar qualitative traits, can exert similar per capita effects on the proportional change in the population size of a target species. In this case, the individuals of different species are interchangeable (with regard to this interaction, although not necessarily interchangeable with respect to the interactions with other species of the ecosystem). These shared traits may be:

1) *Unspecialized traits*: of plants, animals, or both, which might foster both generalism and functional equivalence. For example, a simple actinomorphic flower can allow taxonomically distant flower visitors to act as pollinators by contacting anthers and stigma when collecting pollen or nectar, and depositing pollen enough for seed production.

2) *Fixed traits*: shared traits may be relatively invariant, and thus may bring about similar outcomes in different times and/or places. For example, body size can account for much of the variation in pollinator behaviour at flowers (Herrera 1997).

3) *Plastic traits*: contrarily, shared traits may have a high degree of phenotypic plasticity (e.g. foraging behaviour, ecophysiological responses), in such a way as to develop the same kind of phenotypic response when appearing in the same kind of environmental setting. For example, different species of flies and ants develop similar behaviour at the flowers of a mass-flowering plant, thereby unfolding similar, predictable patterns of interactions despite the high diversity of species involved (Gómez and Zamora 1999).

4) *Trophic habit*: unrelated, polyphagous species can also share similar trophic criteria (basically, to take the most nutritive meal and to avoid the most unpalatable or poisonous tissues) and provoke similar selective pressures. Even monophagous insects do not search for plants that have been classified by us into a particular taxon, but rather hunt for a plant with a chemical profile that fits their search. This profile may be rather specific, and restricted to a single species, or broader, and characteristic of a plant genus or family (Schoonhoven et al. 1998).

5) *Similar responses*: plant responses to animals are physiologically and genetically correlated and/or constrained (Gould 1988, Pilson 1996), and are mostly non-specific, but directed to any kind of damage. For example, the ability of plants to produce regrowth shoots from dormant buds is a clear response to herbivory as well as abiotic damage (fire, drought, frost; see Tuomi et al. 1990, Zamora et al. 1999). Furthermore, responses may be exclusively quantitative, because the plant can vary the quantity of resource used to avoid or attract animals more easily than produce a new product.

Examples of functional equivalence

There is no doubt that some interactions are simply the result of the coincidental congruence of traits possessed by the interacting organisms. Even plant-animal interactions for reproduction may successfully persist in the absence of mutual adaptation and a shared history of interaction between counterparts (Herrera 1996). For example, any plant species bearing fleshy fruits can be effectively dispersed, so long as an animal is large enough to swallow the fruit, and then expel the seeds in faeces. Furthermore, plant and animal species introduced by humans and coming from exotic fauna and flora can maintain interactive systems (pollination, seed dispersal, herbivory) similar to those of native species, thereby providing an example of "ecological fitting" without a common evolutionary history (Janzen 1985).

Below, I will provide some examples of plant-animal interactions supporting the idea of functional equivalence.

1) Plant-herbivore systems

Plants may interact simultaneously or sequentially with a wide variety of herbivores (both monophagous and polyphagous), which can produce synergistic reductions of plant fitness (i.e. the damage by a herbivore predisposes plants to the damage by another herbivore). In these cases, more general plant defences would be favoured that reduce damage by the entire herbivore assemblage (Gould 1988). In this way, most secondary plant compounds are inhibitory both to herbivores and to pathogens, suggesting that certain highly toxic plant chemicals are of a generalized nature and affect multiple species (see Romeo et al. 1996 for a recent review).

Possible synergistic effects can arise from the confluence of different mechanisms as for example occur in the defence of marine algae against herbivores (Hay et al. 1994). Furthermore, secondary metabolites may also directly increase competitive ability through allelopathic effects on neighbouring plants. For example, Schmitt et al. (1995) showed that the secondary metabolites that defend the brown alga *Dyctiota menstrualis* (Dyctiotales) against herbivores also have the allelopathic function of eliminating competitors.

2) Plant-pollinator systems

Very different pollinator species can select floral features in parallel directions (Waser and Price 1981). Furthermore, taxonomically unrelated pollinators can forage at plants in similar ways, and thereby have similar individual effectiveness (Feinsinger 1983, Pettersson 1991, Vaughton 1992, Conner et al. 1995, Fishbein and Venable 1996). For example, the mass-flowering strategy of *Hormatophylla spinosa* channels pollinator movements between flowers in such a way that most taxonomically unrelated pollinators (e.g. nectarivorous ants and small flies) behave similarly at flowers, even depositing a similar number of pollen grains. As a result, all species belonging to the same guild (nectarivorous or pollinivorous) are functionally equivalent from the plant's viewpoint, exerting comparable selective pressures (Gómez and Zamora 1999).

Also, a coarse fitting above the level of species for higher taxa (order, family) can appear, instead of specialization on particular species. For example, feeding specialization in most bee species appears at the taxonomic level of plant tribe, subfamily, or family, but not at the level of plant species (Müller 1996). In the same way, Herrera (1987) indicated that major pollinator groups (e.g. order) may differ more consistently in aspects of pollinator effectiveness than particular species belonging to these groups. In fact, most of the variation in traits within lineages occurs at the genus and higher taxon levels (Jordano 1995b).

3) Plant-seed-dispersal systems

Many plants can be dispersed by numerous bird species, and many birds can consume the fruits of numerous plant species (Jordano 1987, Herrera 1995). Despite this, most plant-seed-dispersal systems exemplify an efficient, ecologically based mutualism, in which there appears a clear mismatch between evolutionary stability (or stasis sensu Stanley 1979, Gould 1982) of the plants, and the high evolutionary rate of animals with which the plants interact (Herrera 1995, García et al. 1999). The stability of major traits (e.g. fruit size) of tree and shrub species over millions of years, as compared with a rapid succession of bird and mammal extinctions (Herrera 1985, Jordano 1995b), supports the hypothesis of replacement of ecologically equivalent seed-dispersal species. Functional equivalence can thus account for the fact that plant-animal interactions can continue to function with demographic consequences (i.e. changing the distribution and abundance of interacting species), without the necessity of genetic changes. As a result, the match between fruiting plants and the abundance of seed-dispersal birds will not be an adaptive process at the population level, but a demographic sorting process at the community level (Jordano 1987, Herrera 1992).

In conclusion, when interactive assemblages are diverse, functional equivalence can emerge as long as the relevant traits driving the outcomes of the ecological interactions are common to several species. The result is that we can have taxonomically diverse, but interactively limited assemblages, when considering the net outcomes of interactions. Generalist systems thus contain the seed of facultative systems, where a low level of mutual dependence may be linked to a high likelihood of species sharing a similar role. Generalization does not necessarily lead to erratic variation and/or unpredictability in the organization of multispecific systems (see also Waser 1998), nor does it necessarily lead to a melee of conflicting selective pressures. Contrarily, functional equivalence in multispecific, facultative systems is an ecological mechanism enabling the spatiotemporal replacement of equivalent species, maintaining a) an ecological interaction without any apparent species-specific coevolutionary consequences through time, b) an evolutionary process based on generalized pressures and/or responses to whole groups of species interacting in similar ways (Maddox and Root 1990). The result is ecological functionality, and evolutionary consistency, above the species level.

Defining criteria: How different? How similar?

Studies focusing on a few interactive species might represent a biased sample of real interactive systems. Thus, as an a priori selection of a couple or a few interacting species assures specificity, a preconceived taxon-biased view can provide an a priori unique view of interspecific outcomes. My proposal is not to replace this taxon-biased focus by an alternative functional-biased focus. Instead, I propose the usefulness of considering both views simultaneously. As a first step to define criteria and methods to detect functional equivalence in ecological interactions, below I provide some basic guidelines to analyse the possible degree of interspecific difference/equivalence in the outcomes of ecological interactions as the two sides of the same coin.

1) To work with the most complete possible interactive group of species (avoiding an automatic focus on the most obvious interactors, and including those that appear "inappropriate" to the interaction, as indicated by Waser et al. 1996).

2) To identify the qualitative and/or quantitative traits determining the outcomes of interactions. Some traits may be taxon specific (i.e. the length of the corolla spur of a flower), whereas others, such as size, chemical composition, trophic habit and ecophysiological responses, may be shared by many species.

3) To seek both the differences as well as similarities in the mechanism of interaction, and its ecological consequences. For this, I propose the null hypothesis of no difference between the interactive outcomes of different species, until the contrary is demonstrated. Studies with the appropriate design to examine potential species substitutability (Sih et al. 1998), and experiments and statistical protocols testing the additivity vs non-additivity effects in multispecific assemblages (see, for example, Strauss 1991, Hougen-Eitzman and Rausher 1994, Pilson 1996, Iwao and Rausher 1997) and the potential density dependence of interactive outcomes (Morin 1995) would be welcome.

4) To determine the level at which relevant differences and/or similarities may stand out. Differences could be more evident at higher taxonomic levels (genus, family). On the other hand, differences could be more evident when considering as a grouping criteria some relevant functional traits (see, for example, Morin 1995, Kurzava and Morin 1998, Gómez and Zamora 1999). This implies an a priori selection of functional traits as classification criteria, and an a posteriori statistical verification of the validity of that classification (Sullivan and Zedler 1999). Thus, grouping criteria should be based both on taxonomic affiliation as well as on functionality (Hay 1994).

5) To evaluate the same interactive assemblage across multiple communities in a long-term perspective (Thompson 1999b), and under varied abiotic conditions (Sullivan and Zedler 1999, Zamora 1999). The geographic level is ideal to test whether there may be a spatial variation in the outcomes of interactions as proposed in the theory of the geographic mosaic of interactions (Thompson 1994), or whether there are repeatable spatial and/or temporal patterns of interactive outcomes because different populations or species in different places and/or times, or under the same abiotic conditions, can share the relevant traits determining the outcomes of interactions.

Concluding comment

I hope that the ideas and evidence presented here serve to show that functional equivalence in ecological interactions is something more than an appealing theoretical possibility, but empirical oddity. In my opinion, functional equivalence in multispecific assemblages may represent, as other mechanisms well established in the mainstream of current ecological thinking (i.e. pairwise reciprocal specialization and systems dominated by keystone species), one of the possible pathways allowing consistency in both pressures and responses to selection in ecological and evolutionary arenas. To detect functional equivalence, however, it is necessary to concentrate more on the search for general patterns of interactive outcomes shared by many species than on the scrutiny of subtle differentiating details between selected species pairs/groups.

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