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“Biological Barter”: Patterns of Specialization Compared across Different Mutualisms

Jeff Ollerton

Obligate one-to-one mutualisms between species pairs are rare in practice and anomalous in theory.

—Howe (1984)

Specialization in interactions with other species is the root cause of why the world has millions of species rather than thousands.

—Thompson (1994)

It appears that we simultaneously know both a great deal and not very much at all about mutualism.

—Bronstein (1994a)

much information can be found in scattered form, and only awaits careful coordination in order to yield a rich crop of ideas. The various books and journals . . . are like a row of beehives containing an immense amount of valuable honey, which has been stored up in separate cells . . .

—Elton (1927)

Interactions between species are characterized by a continuum of evolutionary, functional, and ecological specialization (sensu Waser et al. 1996; Fenster et al. 2004; D. Vázquez et al., unpublished data; Ollerton et al., chap. 13 in this volume), ranging from obligate, two-species relationships to highly diffuse, opportunistic, multispecies associations. It should be clear from the preceding chapters that an important task of biologists is to characterize the nature of these interactions and to ask questions regarding their origin, maintenance, and stability. Although the main focus of this volume is on plant–pollinator interactions, cross-comparison with other types of interactions may yield insights that are of value to biologists interested in different types of interspecific associations, especially those searching for general laws and trends concerning mutu-

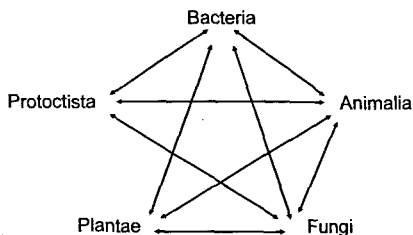


Figure 18.1 Mutualism connections between the five kingdoms of life. The connecting arrows indicate known examples of mutualistic relationships between members of each kingdom. There are in fact mutualisms between all possible pairwise combinations of kingdoms, with the exception of Plantae–Protocista (see text). Data from Batra (1979), Boucher (1985), Smith and Douglas (1987), Reisser (1992), Douglas (1994), Jolivet (1996), Nash (1996), Paracer and Ahmadjian (2000).

alistic interactions. This chapter, therefore, addresses broader questions of patterns of specialization and generalization across mutualisms.

Plant–pollinator interactions are largely mutualistic interactions (but see Renner, chap. 6 in this volume), which are defined as relationships between species that result in reciprocal benefits. Benefits in the short term may include trophic gain, physical protection, and dispersal of gametes or propagules. One can consider the exchange of resources and services a form of “biological barter” (see following discussion); ultimately, this barter is expected to result in increased fitness for both participants (Boucher 1985).

The range of organisms involved in mutualistic interactions spans all five kingdoms (as conservatively defined) and most groups within (fig. 18.1). The absence of any known mutualisms between the kingdoms Plantae and Protocista is an interesting anomaly and may be due to two factors relating to the autotrophic and heterotrophic members of the Protocista. All plants and the algal protocists are essentially autotrophic; therefore, there may be no resource basis for bartering, that is, mutual carbon exchange is unlikely to benefit either partner (see also fig. 18.2, and discussion following). The heterotrophic protocists are not as abundant as bacteria or fungi and, therefore, are less promising partners within a mutualism; in addition, heterotrophic protocists tend to be single celled and feed by endocytosis rather than by absorption (following production of exogenous enzymes) as in fungi and bacteria. Their solitary habits and mode of feeding may, therefore, make them less efficient than fungi and bacteria at obtaining inorganic nutrients en masse.

The partners involved in a mutualism directly exchange physical resources and services (Janzen 1985; Noë and Hammerstein 1995)—it truly is “biological barter” (fig. 18.2). Physical resources are largely concerned with nutritional gain (e.g., carbohydrates, inorganic nutrients, and water). Services range widely in their scope and include transport of propagules (e.g., seed and spore dispersal), movement of gametes (most familiarly in pollination, but also dispersal of fungal spermatia by Diptera; see Bultman and White 1988), bioluminescence,

cleaning, and physical protection. Of course, as in all generalizations concerned with the natural world, the physical resources/services dichotomy is simplistic and in reality it comprises a complex, multidimensional continuum. For example, nectar contains a mix of sugars (carbohydrate resource) and amino acids (inorganic nutrient resource; see, e.g., Gardener and Gillman 2001), among other things. In addition, physical resources are occasionally nonnutritional, for example, production of resins for nest construction by pollinating bees in genera such as *Dalechampia* (Euphorbiaceae) and *Clusia* (Clusiaceae; Armbruster 1984). In such cases, the plant initially provides a physical resource that ultimately supplies a service (physical protection of the bee offspring). Occasionally, mutualistic interactions are characterized by the conferment of both services and physical resources; for example, in some ant-*Acacia* relationships, the *Acacia* provides both domatia in which the ants can build nests (a service) and food bodies on which the ants feed (a physical resource; Seigler and Ebinger 1995). A second example is plant-fungus mycorrhizal relationships in which the fungus, in addition to providing water and inorganic nutrients to the plant, also reduces the risk of it becoming infected by pathogenic fungi and may produce secondary compounds that deter herbivores (Newsham et al. 1995). Biological barter, like barter in human societies, is complex and contingent upon the abilities and requirements of both partners. Thus, the representation of mutualistic associations in the two-dimensional format of figure 18.2 loses some of the complexity of what is often a multidimensional interaction, involving the exchange of multiple resources or services. I have tried to express this by including examples where an interaction involves exchange of a minor resource or service by mentioning that a particular barter occurs "in part."

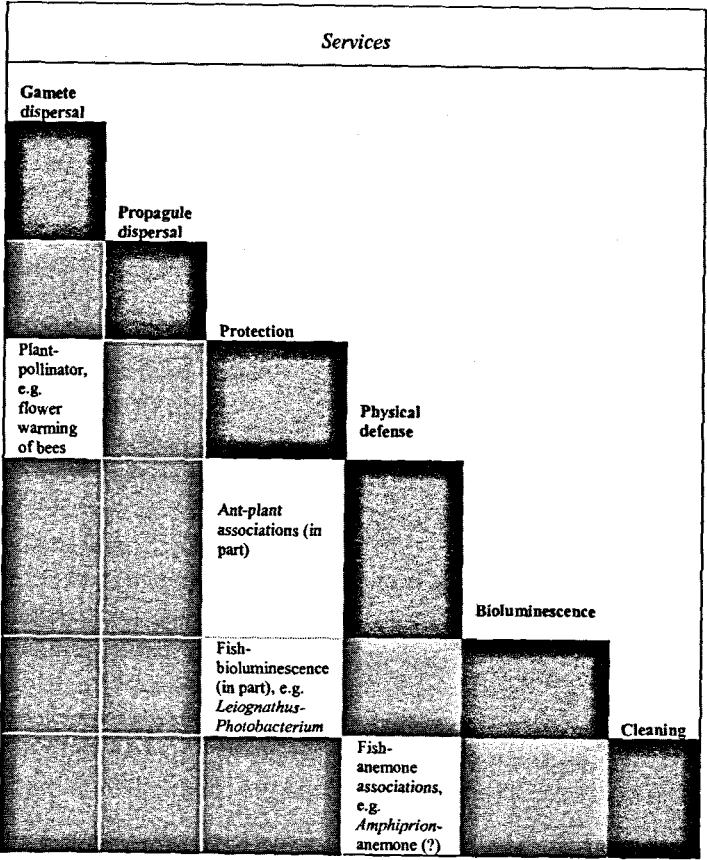
Direct mutualism (sensu Boucher et al. 1982) takes many forms, but it is clear from figure 18.2 that there is not a limitless set of permutations of resource and service barter. For instance, there are no known examples of mutualism in which partners trade the same resource or service (represented by the black cells on the diagonal in figure 18.2). This makes perfect biological sense: why should an organism barter something that it can make, obtain, or do itself? The gray cells within figure 18.2 are situations in which different resources or services could potentially be bartered but which are not documented in the literature, as far as I have been able to discover. As research progresses, such examples may come to light: suspected or confirmed mutualistic interactions new to science are discovered with almost annual predictability (Compton and Ware 1991; Grange 1991; Ellis and Midgley 1996; Ross and Newman 1996; Bultman et al. 1998; Stewart 1998; Naoki and Toapanta 2001; Brown et al. 2002; Corallini and Gaino 2003). But if they do exist, they are probably not common.

It is notable that mutualisms based on service-service bartering are rather rare and usually involve resources at some level (e.g., cleaning-physical defense associations in which the cleaner's reward includes food items as well as defense).

Resources

		Resources					
		Carbohydrate	Nitrogen	Inorganic compounds	Proteins, amino acids, etc.	Complex organic compounds	Water
Resources	Carbohydrate	Legume-rhizobia, Actinorhizae, etc. e.g. <i>Lotus-rhizobium</i> , <i>Alnus-Frankia</i> , <i>Gunnera-Nostoc</i>					
	Nitrogen	Lichens, mycorrhizae, metazoan-algae, etc. <i>Anzia-Trebouxia</i> , <i>Geosiphon-Nostoc</i> , <i>Pinus-fungi</i> , <i>Hydra-algae</i>					
	Inorganic compounds	Ant and termite fungal associations, e.g. <i>Cyphomyrmex-fungus</i> , <i>Odontotermes-fungus</i>					
	Proteins, amino acids, etc.						
	Complex organic compounds						
	Water	<i>Mycorrhizal</i> associations (in part)					
Services	Gamete dispersal	Plant-pollinator, e.g. <i>Asclepias</i> -pollinator		Plant-pollinator – (in part) calcium in nectar	Plant-pollinator – protein in pollen, amino acids in nectar	Plant-pollinator, e.g. oil, scent and resin rewards	Plant pollinator (in part) – water in nectar
	Propagate dispersal	Plant-disperser, fungus-disperser, e.g. <i>Viburnum</i> -birds, <i>Viola</i> -ants, <i>Phallus</i> -fly			Plant-disperser, fungus-disperser (in part) – proteins etc.		
	Protection	Animal gut microbes, e.g. <i>Lasioderma-Symbiotaphrina</i>			Insect mycetocyte (?) e.g. <i>Acyrtosiphon-Buchnera</i>		
	Physical defense	Plant-fungal associations, plant-ant relationships, ant-homoptera, e.g. <i>Lolium</i> -endophyte, <i>Passiflora</i> -ants, <i>Lasius</i> -homoptera					
	Bioluminescence	Fish-bioluminescence, e.g. <i>Leiognathus-Photobacterium</i>					
	Cleaning	Metazoan cleaning relationships (in part), e.g. <i>Buphagus</i> -mammal			Metazoan cleaning relationships (in part), e.g. <i>Buphagus</i> -mammal		

Figure 18.2 "Biological barter": examples of the range of physical resources and services offered for exchange in mutualistic relationships. The specific examples have been drawn from the studies used in the analyses in this chapter (see appendix 18.1). The black cells on the diagonal represent situations in which the same resource or service would be bartered; there are no known examples of this. The gray cells are situations in which different resources or services are bartered, but which are not documented in the literature. Data from Batra (1979), Boucher (1985), Smith and Douglas (1987), Reisser (1992), Douglas (1994), Jolivet (1996), Nash (1996), Paracer and Ahmadjian (2000).



Another very obvious trend within figure 18.2 is the dominance of carbohydrate exchange in mutualistic associations, emphasizing the fundamental role of primary productivity within ecosystems.

Mutualisms are among the most ubiquitous of interactions in nature, but also the least well understood, in comparison to, say, predator-prey or parasite-host interactions. As the quote from Bronstein (1994a) suggests, whereas a great deal of effort has gone into exploring the ecology and evolution of mutualisms, their enormous variety has meant that there has only been a limited attempt to synthesize these studies to search for broad-scale generalizations about the ecology and evolution of such interactions. Indeed, it could be argued that because of their diverse nature, there are no generalizations to discover beyond the fact that these relationships benefit all participants (and even that is far from proven in many cases).

Within the published literature there exists an enormous, diffuse, scattered dataset of observations on the diversity and specificity of mutualistic relationships. The purpose of this chapter is to draw together a fraction of these data to address questions regarding the relationship between interspecific biological intimacy and ecological specialization in mutualistic interactions. In particular, I wish to address a very specific hypothesis:

As mutualistic relationships become increasingly biologically intimate through trophic, physiological, and/or physical integration, they become increasingly exclusive.

The basis of this hypothesis is that the high degree of morphological and/or biochemical specialization required to maintain very close mutualistic relationships between species precludes their usurpation by other taxa (see Borowicz and Juliano 1991 for a similar argument applied to plant-fungus interactions). Therefore, there should be a negative relationship between the number of species involved in a relationship and the level of biological intimacy displayed by that interaction. This is represented by an informal model (fig. 18.3).

It is unclear whether the predicted relationship between biological intimacy and ecological specialization should be a simple linear function (fig. 18.3, line a) or a more complex function, in which the taxonomic exclusivity of the relationship is reached after a relatively high (line b) or comparatively modest (line c) level of intimacy. The different shapes of these curves imply disparate trajectories in the evolution of ecological specialization in mutualistic interactions.

Methods

From a broad survey of the relevant literature, I have compiled a database of mutualistic interactions, which I have used to test the intimacy-specialization hypothesis. This dataset is not random (in a statistical sense) because certain classes of mutualism (and within these classes, particular systems) have been much more comprehensively studied than others; however the data are representative of the diversity of mutualisms, as presented in figure 18.2.

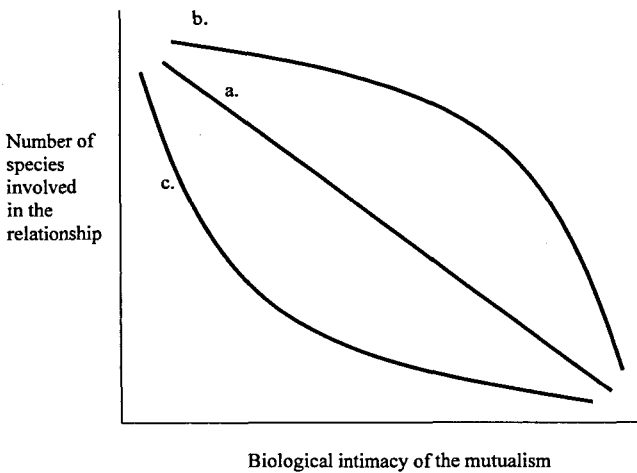


Figure 18.3 An informal graphical model of the predicted relationships between the biological intimacy of a mutualism and the number of partner species of a given mutualist (see text for a description of lines a, b, and c).

Using published sources, I compiled information regarding the ecological specificity of the relationships from studies of mutualistic associations that covered the full range of these interactions as they are currently known. The inclusion of a particular mutualistic relationship was determined by how well studied the system has been and, hence, the availability of the pertinent information (see following discussion). The dataset used for the following analyses is presented in appendix 18.1.

There is a clear problem with counting the number of species involved in an interspecific relationship: species concepts vary systematically and are particularly difficult to pin down for microorganisms. In addition, variation in observation effort between studies can be problematic (Ollerton and Cranmer 2002; Ollerton et al., chap. 13 in this volume). Therefore, to provide a degree of robustness within the data, I began by identifying “focus” genera. As the term implies, a *focus genus* is one that acts as the “focus of attention” for other species in a mutualistic interaction. For example, in a plant–mycorrhizal interaction, the focus genus is that of the plant; in a fish–fish cleaning relationship, the focus genus is that of the fish being cleaned; and so forth. I deliberately use this phraseology to avoid using the term *host*, because that word implies a large degree of physical intimacy, which in fact is one of the variables being assessed in this analysis.

For each focus genus, I recorded the number of partner genera associated with that mutualism. For example, from appendix 18.1 it can be seen that the focus genus *Asclepias* (Apocynaceae) is known to be pollinated by 150 genera of animals. The taxonomic level of genus is a more conservative one than that of species, although I accept there are still problems with comparing, for example, a

“genus” of bacteria with a “genus” of flowering plants. In addition, recent molecular phylogenetic investigations have uncovered surprising levels of microbial symbiont diversity (see review by Herre et al. 1999). Nonetheless, if synthetic analyses such as this are to be conducted at all, it is necessary for us to take a robust, but honest, approach to the problems inherent in these kinds of datasets. Perhaps future analyses will incorporate less subjective measures, for example genetic diversity.

The identity of the focus genera I surveyed was determined in part by the body of work available. For example, the pollinators of the genera *Asclepias* (Apocynaceae) and *Ficus* (Moraceae) have been quite well studied compared to many other plants, and mycorrhizal associations between *Pinus* (Pinaceae) and fungi have been thoroughly documented. The criteria for including a focus genus were that (1) there was at least 10 years worth of literature available, (2) at least five species of the genus had been researched, and (3) there was some geographical diversity to these studies. To provide some balance within the dataset (i.e., to not swamp the study with plant–pollinator relationships) no more than five focus genera were included for each broad category of mutualism (e.g., mycorrhizae, endophyte, seed dispersal, pollination, etc.).

These data have been gleaned from a huge range of sources. To save space, the original references are not presented here, but a full list of sources is available upon request from the author.

In addition to recording the numbers of partner genera associated with the focus genus in that particular relationship, an “index of biological intimacy” was calculated for the relationship (independent of the number of partner genera recorded). Each mutualism was scored for the following criteria.

1. Physical dependence of the mutualism:

- 0 = none of life cycle
- 1 = part of life cycle
- 2 = all of life cycle

2. Trophic dependence:

- 0 = wholly independent
- 1 = *partially dependent*
- 2 = wholly dependent

3. Physiological integration:

- 0 = no integration (extracorporeal)
- 1 = integrated for part of life cycle or intercellular
- 2 = wholly integrated/intracellular

4. Vertical transmission:

- 0 = *no vertical transmission of partner mutualist from parent to offspring*
- 1 = transmission of mutualist from parent to offspring

Of course there is no single metric of “biological intimacy” that could represent the whole diversity of mutualisms in all of their many forms; therefore, the preceding criteria were selected to represent the most biologically meaningful measures of intimacy and to provide an additive, multitrait representation. The index of biological intimacy is the sum of the scores for the individual criteria and, therefore, potentially ranges from 0 (a very low level of biological intimacy) to a maximum of 7 (a very high level of biological intimacy). As might be expected, there is considerable intercorrelation of traits (data not presented).

Comparative analyses such as this suffer from the problem that species are not statistically independent units but are linked by their phylogeny, and possible phylogenetic biases must be taken into consideration in any comparative analysis (Harvey and Pagel 1991). However, because the dataset used in these analyses spans all five kingdoms, and a wide range of genera, orders, and classes, a formal phylogenetically corrected regression is not possible—whether it is required for such a phylogenetically broad spread of taxa is arguable.

Results and Discussion

The level of biological intimacy of a mutualistic relationship has a strong effect on the degree of specialization of that relationship (fig. 18.4A). These data are strongly right skewed and nontransformable; however, there is a statistically significant, negative correlation between the index of biological intimacy and the number of partner genera associated with the focus genus (Spearman rank correlation, $r_s = -0.59$, $N = 39$, $P < .001$). Sensitivity analyses show that this is a statistically robust conclusion (see appendix 18.2).

It is clear that, as mutualistic relationships become more biologically intimate, the number of genera involved in that relationship is rapidly reduced; that is, the response function fits the line c model of figure 18.3 (concave and steeply declining).

Displaying the y axis of figure 18.4A on a log scale allows the pattern of the data to be seen more clearly (fig. 18.4B). The data points have been coded with respect to whether the mutualism would normally be considered closely symbiotic or nonsymbiotic, defined by Boucher et al. (1982, 316) as “using physiological integration as the basic criterion.” In figure 18.4B, there is no clear distinction between symbiosis and other types of relationship in terms of the degree of biological intimacy of the relationship, as defined by this index: “nonsymbiotic” relationships can be as biologically intimate as symbiotic interactions. The highest scores for nonsymbiotic mutualisms were achieved by the *Cyphomyrmex*-fungus, *Odontotermes*-fungus, *Ficus*-fig wasp, *Cecropia*-ant, *Xyleborus*-fungus, *Sirex*-*Amylostereum*, and *Acacia*-ant mutualisms. Low scores (3 or less) for mutualisms traditionally classed as symbiotic were found for *Geosiphon*-*Nostoc*, *Sphagnum*-cyanobacteria, *Pinus*-fungus, *Lotus*-*Rhizobium*, *Alnus*-*Frankia*, and

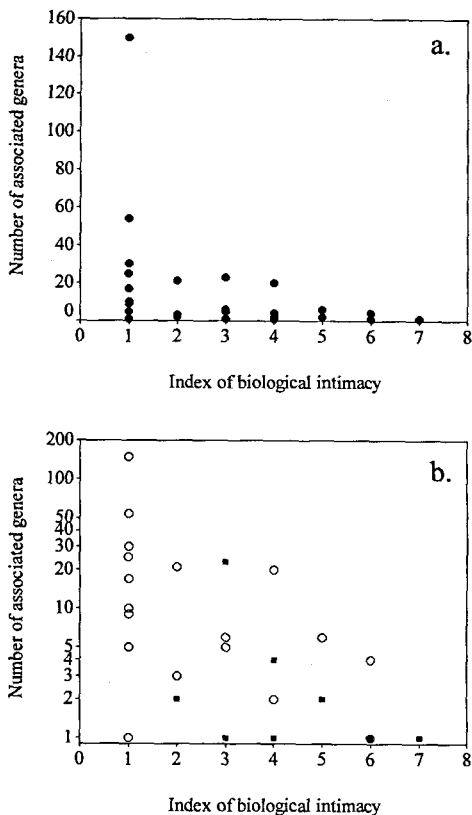


Figure 18.4 (A) The relationship between biological intimacy and number of partner genera associated with a focus genus for the mutualistic associations in appendix 18.1. Some data points represent multiple examples. (B) The relationship in (A), with the y axis as a log scale. The data points have been classified as representing the symbiotic (solid squares) and nonsymbiotic (open circles) interactions in appendix 18.1.

Blasia-Nostoc (see appendix 18.1). Boucher et al. (1982, 316) stated quite reasonably that the symbiotic-nonsymbiotic dichotomy was “artificial but convenient.” I would go further and suggest that the symbiosis-nonsymbiosis dichotomy may be too artificial to use if we wish to study the true biological nature of mutualistic associations, especially in relation to the biological intimacy of the relationship.

The steeply declining relationship between biological intimacy and number of associated genera suggests that mutualisms can evolve to be comparatively exclusive (at a generic level) at a relatively modest level of biological intimacy (fig. 18.4A). The mutualisms at the very highest level of intimacy (index of 7) are represented by single-genus relationships (fig. 18.4B, appendix 18.1), for example, the *Azolla-Anabaena* and *Lolium-Neotyphodium* interactions. However, it is also clear that exclusivity is not a certainty at higher levels of intimacy and

that, even with an index of greater than or equal to 5, relationships can be surprisingly nonspecific (e.g., the *Xyleborus*-fungus and *Cecropia*-ant mutualisms). Conversely, relationships characterized by low levels of intimacy can also be quite specialized: for example, the *Epichloe*-*Phorbia* and *Sphagnum*-cyanobacteria interactions.

The results obtained from this analysis are biological trends rather than fixed rules, but there is certainly a trend toward taxonomic exclusivity at higher levels of biological intimacy, which supports the original hypothesis set out in the beginning of this chapter.

What are the mechanisms governing the relationship between intimacy and specialization? There are broadly two factors that are important. The first is the *physical* fit between the organisms; for example, short-tongued animals cannot access nectar in long-tubed flowers, and small birds are unable to ingest large fruit (Jordano 1987). The second is the *biochemical* fit between the organisms. This is less straightforward than the former and relates to the ability of the two organisms to recognize, communicate with, and tolerate one another at a molecular level. This could be as intimate as the recognition/rejection systems in legume-rhizobia and plant-mycorrhizal relationships (Lum and Hirsch 2002); less intimate, but just as specific, olfactory signaling between a flower and its pollinators (Kite et al. 1998); or more diffuse, such as the correlation between nectar composition and pollination systems found in some plant groups (Perret et al. 2001) and identification of myrmecophilic plants by ants.

It is tempting to assume that it is the biochemical fit between organisms that governs highly specialized relationships such as microbial-plant and -animal mutualisms. However, there is clearly an important *physical* component to these interactions: bacteria and fungi are sufficiently small that they become intimately associated with the roots of the plants that they service, whereas fig wasps are tiny compared to most other insect pollinators yet need to be small to interact with *Ficus* syconia. Both the physical and biochemical "fit" of the organisms concerned are required if the relationship is to be successful.

Boucher et al. (1982) reviewed the literature on the strength of mutualistic interactions (obligate vs. facultative) and the range of partners involved in the relationship: a single partner (monophilic), a restricted range of partners (oligophilic), and a wide range of partners (polyphilic). Their findings are summarized in table 18.1, which shows that some classes of interaction within this matrix of possibilities are more probable than others. But the main finding is that, if an interaction is obligate, it usually involves a very limited set of partners, whereas facultative interactions tend to have a wider range of partners. The facultative-obligate dichotomy is inherent within the index of biological intimacy used in the analyses presented in this chapter (especially the "physical dependence" and "trophic dependence" factors; see Methods). Therefore, my find-

Table 18.1 The relationship between the strength of a mutualistic interaction and the number of partners involved, in terms of the relative rarity and commonness of those interactions in nature

Strength of relationship	Number of partners involved		
	Monophilic	Oligophilic	Polyphilic
Facultative	Unknown	Common	Common
Obligate	Common	Common	Rare

Source: Based on Boucher et al. 1982.

ings are in broad agreement with those of Boucher et al. (1982): at low levels of biological intimacy, generalization is the norm, and at higher levels of biological intimacy, specialization becomes more common.

Law and Koptur (1986) reviewed the earlier literature on the evolution of specificity in mutualisms. They noted that most mutualisms, of all persuasions, tend to be nonspecific, certainly in comparison to antagonistic relationships. For instance, they noted that host–parasite systems can be specific at the level of genotype (though the same is true for the legume–rhizobium symbiosis and may also apply to other, less-well-studied microbial mutualisms; see Young and Johnston 1989). Law and Koptur argued that intimacy of the relationship does not explain this disparity, because mutualisms can be, and often are, just as intimate as antagonistic relationships. To explore the circumstances under which specialized mutualisms could evolve, they developed a simple model of guild–guild coevolution. One of the surprising outcomes of this model was that it was theoretically possible for strong natural selection to favor nonspecificity at the guild level, thereby eradicating specialized phenotypes from the community. This contrasts strongly with a traditional view that evolution drives interacting species toward specialization (see also Armbruster and Baldwin 1998; Waser, chap. 1 in this volume).

Patterns of ecological specialization in pollination systems versus vertebrate seed dispersal systems were compared by Jordano (1987), who found that pollination systems of plants were, on average, a third more ecologically specialized than plant seed dispersal systems. Jordano argued that this pattern is likely to be caused by the greater requirement of a physical fit (“morphological coupling”) between flowers and pollinators than between fruit and seed dispersers. This remains an intriguing possibility which has never been properly tested.

Comparisons with Nonmutualistic Interactions

Mutualism is only one category of interspecific relationship, and, in places, it blends with other types of interaction such as predation, parasitism, and commensalism. How do the patterns of specialization and biological intimacy apparent in mutualisms compare with other types of interaction? Borowicz and Juliano (1991) compared levels of host specificity between mutualistic (ecto-

mycorrhizal), shoot parasitic, and root necrotrophic fungi and their north temperate tree and shrub hosts. These three fungal life styles show a range of physical intimacy/integration with their hosts, with shoot parasites being more intimate than ectomycorrhizal associations, which in turn are more intimate than root necrotrophs. The authors predicted that there should be a negative correlation between the level of intimacy of the relationship and the host ranges of fungi in each group: root necrotrophs being the most broadly associating and shoot parasites the least broadly associating. Their analysis showed this not to be the case, and in fact the mutualistic ectomycorrhizal fungi were the most host specific. Therefore, the authors concluded that it was the type of species interaction (mutualistic vs. antagonistic) that determined host specificity in these fungi, rather than level of physical intimacy per se. This is in disagreement with the analysis presented in this chapter, but it may be that such patterns, if present at a smaller scale, are masked by a larger-scale analysis.

Studies which attempted to synthesize plant-microbe interactions using combinations of partners that are not normally found in nature were reviewed by Law (1985). He concluded that mutualistic relationships such as rhizobia and mycorrhizae are much less specific at a genotype level than equivalent antagonistic relationships, as expected from theory. Is this true only for biologically intimate comparisons (e.g., bacterial pathogens vs. bacterial mutualists) or is it also true for less-intimate associations (e.g., insect herbivores vs. insect pollinators)? There are certainly many examples of plants which, following their introduction to an area, can utilize the local pollinators, seed dispersers, and even mycorrhizal fungi (Richardson et al. 2000).

Thompson (1994) reviewed the literature on the relationship between physical intimacy and ecological specialization in parasitic and herbivorous interactions and concluded that a diversity of taxa, from a range of habitats and involved in different kinds of interactions, tends to be more ecologically specialized when they are more physically intimate with their hosts. This holds true for ectoparasites of birds and mammals, microlepidoptera and their larval food plants, marine limpets and the seagrasses on which they feed, and seaslugs, crabs, and amphipods in their seaweed habitats. These results further support the generality of the finding that mutualisms become much more ecologically specialized as the biological intimacy of the relationship increases and suggests that the trend may extend beyond mutualistic associations to include parasitism, herbivory, predator-prey interactions, and commensalism.

Some Evolutionary Considerations

The analyses presented in this chapter, in addition to the previous outlined studies, support the hypothesis that the taxonomic exclusivity of a mutualistic relationship is governed to some extent by the biological intimacy of that interaction. But what are the conditions under which highly exclusive interactions

can evolve? For example, is it possible for an interaction to evolve from low biological intimacy to high biological intimacy (i.e., shift from, say, an index of 1 or 2 to an index of 6 or 7 in fig. 18.4)? Such extreme evolutionary shifts are known from free-living to parasitic lifestyles (e.g., *Cuscuta* compared to other Convolvulaceae; see Neyland 2001), within parasite lineages (e.g., Microsporida compared to more typical Fungi; see Keeling and Fast 2002), and even within species, in the case of gender dimorphism in deep sea anglerfish (e.g., Munk 2000). Are such extreme shifts possible within mutualistic relationships? Or is it more likely that the starting conditions of the relationship are what determines the level of intimacy and, hence, exclusivity? One way to address this question is to map organism traits, including interactions, onto independently derived (preferably molecular) phylogenies. This has been done for plant–pollinator interactions in a range of families and genera (see review by Weller and Sakai 1999) and less often for other mutualisms. The results support the notion that the functional and ecological specificity of interactions can readily evolve, perhaps even quite rapidly, and that clades do not always evolve toward specialization (Armbruster and Baldwin 1998; Machado et al. 2001; Armbruster, chap. 12 in this volume). To my certain knowledge, biological intimacy per se has never been mapped in this way and it remains a largely unexplored area.

The fitness advantage of generalizing on multiple pollinators, versus specializing on one or a few pollinators, was explored by using a simple model by Waser et al. (1996). There are clear benefits of risk-spreading when pollinators vary spatially and temporally (as they often do in nature; e.g., Herrera 1988; Lamborn and Ollerton 2000). Interactions between microbes such as fungi and algae and their animal or plant hosts are often characterized by colonization by multiple species or genotypes (Douglas 1994). Even in quite functionally specialized, biologically intimate relationships, the hosts can effectively generalize at the genotype level, and there exists evidence that this can benefit the host because different genotypes contribute different resources or services to the relationship (Newsham et al. 1995).

An extreme category of specialization involves the loss by a species of its mutualistic partner(s). In many cases, this is associated with habitat specialization by the host, for example, among those few angiosperm lineages that no longer form mycorrhizal associations (Fitter and Moyersoen 1996). In other cases, this may relate to the unpredictability of the other partner, such as obligate self-pollination in plants that grow in extreme environments (Proctor et al. 1996), or, simply, to efficiency gains in a particular environment, as in the evolution of wind pollination (Linder 1998; Wallander 2001). Loss of mutualistic partners has also been documented in an ant–plant system (Blattner et al. 2001).

Such examples may provide an insight into the relationship between specialization and the stability of mutualisms. Recent models of the evolution of mutualistic interactions have emphasized that mutualisms are inherently unstable

and that they will evolve toward exploitative interactions (i.e., parasitism in its many forms) if a mutation emerges that can gain the fitness benefits of the relationship without the associated resource cost (see references in Pellmyr and Huth 1994). There certainly are a number of studies that have shown that some species can evolve as parasitic members of otherwise mutualistic interactions (see review by Yu 2001): for example, interactions between *Yucca* and yucca moths (Pellmyr 2003), *Ficus* and fig wasps (Lopez-Vaamonde et al. 2001), and some between lycaenid butterflies and their ant hosts (Fiedler 1998). Freeman and Rodriguez (1993) showed that the genetic difference between a pathogenic and a mutualistic fungus could be as small as a single gene mutation, suggesting the possibility of rapid shifts between parasitism and mutualism in these organisms. Therefore, mutualistic interactions between organisms may be very evolutionarily dynamic and fluctuate rapidly in time and space. According to Thompson's (1994) Geographic Mosaic Theory of Coevolution, this is probably true of most close biotic interactions.

Mutualistic interactions are incredibly diverse in their nature, involving organisms from all of the five kingdoms, with an almost perfectly symmetrical set of documented interactions (see beginning of chapter and fig. 18.1). Models that predict instability in mutualistic interactions, and their subsequent evolution into exploitative interactions, may hold for a subset of mutualisms, but we cannot assume that all (or even the majority?) of mutualisms can be invaded by parasitic mutations. For many mutualisms, it is extremely difficult to envision how they could be "invaded" by parasitic exploiters; in such circumstances, the mutualism itself is inherently stable. For example, most plant-pollinator interactions are ecologically generalized: flowers are visited by a number of potential pollinators, and most pollinating insects visit a wide range of flowers, which gives these relationships an element of risk-spreading stability (Waser et al. 1996 and references therein; but, for a different perspective, see Johnson and Steiner 2000). Plant-pollinator interactions have provided us with a few good examples of situations in which the interaction has been exploited by parasites (see earlier discussion) but I would argue that these are exceptional and nontypical examples.

It is well documented that not all flower visitors are pollinators. The exploitation of nectar resources without performing pollination ("nectar thieving" sensu Irwin et al. 2001; see also the review of "nectar robbery" by Maloof and Inouye 2000) appears to be mainly determined by the mechanical and behavioral fit between the flower and the visitor. Flower visitors are typically too small to contact the sexual parts of the flower, and so they take nectar without picking up or depositing pollen. But this is not an evolved interaction—the nectar robbers have probably not evolved small size to allow them to rob nectar. The situation has arisen simply as a result of the wide range of sizes of flowers and their visitors. Nectar robbery would only evolve as a specific strategy if there was a fitness cost

of transferring pollen. In that case, one could imagine that a mutant which could exploit the nectar resource without contacting the anthers of the flower and picking up pollen, would be at a great advantage compared to the typical flower visitor. As far as I am aware, it has never been demonstrated that there is a fitness cost for an animal which transfers pollen, despite the often very large pollen loads that pollinators can carry. Such mutualisms are noninvasive simply because there is no opportunity for a mutant to gain a fitness advantage. It is notable that the aforementioned examples of invaded pollination mutualisms are all of relationships in which the plant offers a proportion of its ovules as the resource for the pollinator to use as larval food, and which may themselves have evolved from interactions that were originally parasitic in nature. In these examples, the fitness of the pollinator is intimately bound to the fitness of the plant.

What does this tell us about the relationship between the level of specialization of a mutualistic interaction and its evolutionary stability? It is intuitive to imagine that more evolutionarily, functionally, or ecologically generalized relationships are more stable due to risk-spreading. In the case of plant–pollinator interactions, this may be responsible for the nested pattern of interactions that appear to be commonly found in plant–pollinator and plant–seed disperser networks, in which ecologically specialized animals tend to interact with ecologically generalist plants, and specialized plants interact with generalist animals (Petanidou and Ellis 1996; Bascombe et al. 2003; Dupont et al. 2003; Jordano et al., chap. 8 in this volume; Vázquez and Aizen, chap. 9 in this volume). Ollerton et al. (2003) have suggested that long-term climatic instability has often altered the community context in which organisms find themselves, thereby filtering out specialist–specialist interactions and leaving the pattern of nestedness that we observe.

In more ecologically or functionally specialized mutualistic interactions, we may, therefore, expect to find that the relationships are less evolutionarily stable. Is there any evidence for this? Many reef animals, including corals, form mutualistic associations with photosynthetic algae (collectively termed *zooxanthellae*). These associations are the basis for some 90% of the primary productivity of reef environments (Cowen 1988). In reef-building corals, the interaction is functionally specialized and was originally also thought to be highly ecologically specialized, the photosynthetic partner being only a single species/genotype of the dinoflagellate genus *Symbiodinium* (Rowan and Powers 1991). It is now known that single species of coral, and even individual colonies, can host multiple *Symbiodinium* “species” (see review by Rowan 1998). The persistence of this relationship has been the subject of much discussion and Cowen (1988) has suggested that the slow reestablishment of reef communities following mass extinction events was constrained by the need to reestablish the coral–alga symbiosis. Rowan and Powers (1991) proposed that the relationship between the corals

and algae is evolutionarily very labile, and there is little evidence for codiver-sification of the two groups. It is unknown if the relationship has always involved *Symbiodinium* (zooxanthellae do not fossilize), but the available evidence suggests that even an interaction as biologically intimate as this can be evolutionarily stable, and persistent to the point of reestablishing itself following mass extinction.

In another functionally specialized interaction, Piercey-Normore and De-Priest (2001) documented multiple examples of switching of *Trebouxia* algal partners by lichenized fungi in the family Cladoniaceae, suggesting that although these interactions are biologically intimate (the comparable *Anzia-Trebouxia* association scores a 6; see appendix 18.1) they are nonetheless evolutionarily labile.

Other specialized examples are provided by *Ficus*-fig wasp and *Yucca*-yucca moth interactions, which are thought to have evolved 90 and 40 million years ago, respectively, again suggesting that highly specialized interactions can be remarkably persistent (Pellmyr and Leebens-Mack 1999; Machado et al. 2001). Similarly, the association between *Macaranga* (Euphorbiaceae) and *Crematogaster* ants is highly species specific and is thought to be at least seven million years old (Itino et al. 2001).

Most ectomycorrhizal fungi are generalists, capable of colonizing a range of different plant hosts. Phylogenetic analysis by Hibbett et al. (2000) has shown that ectomycorrhizal associations by basidiomycete fungi are evolutionarily unstable, with repeated evolution of these relationships and frequent reversions of fungal lineages from a mutualistic to a free-living life style. This may be related to the more generalized associations between plants and ectomycorrhizal fungi, or it may be explained by the great age of this class of mutualism (at least 200 million years; see review by Cairney 2000).

The preceding examples suggest that there is no apparent trend for either generalized or specialized mutualistic interactions to be more or less evolutionarily labile. However, as shown by the coral-zooxanthellae example (Rowan and Powers 1991; Rowan 1998), we should be cautious about assessing the degree of specialization of mutualisms, particularly those involving microbes, until molecular phylogenetic analyses of symbiont diversity have been conducted (Herre et al. 1999).

Douglas (1994, 89-90) viewed the evolution of specificity in symbiotic (in fact, microbial) interactions as "the outcome of a trade off . . . between opposing selections pressures, one to broaden the range of acceptable partners, and the other to become increasingly specialized." Douglas argued that highly intimate associations involving vertical transmission of symbionts are more likely to be specialized than less intimate associations, in which fluctuations in the availability of the partner makes generalization a less risky host strategy. However, there are clearly many other factors which may influence specificity. Indeed,

interactions which are apparently specialized in the field sometimes prove to be more generalized in the laboratory, where hosts can form associations with partners with which they would not normally interact (Law 1985; Douglas 1994), suggesting a degree of lability that would only become manifest following the extinction of a host's normal symbiont or the dispersal of that host beyond its normal range (a common situation for introduced plant species; e.g., Chittka and Schürkens 2001).

Conclusions

The results presented here and the review of other relevant literature strongly support the hypothesis that biologically intimate interactions between species tend to be more ecologically specialized and taxonomically exclusive. Although the dataset used in these analyses is relatively small compared to the diversity of mutualistic interactions found in nature, it is nevertheless a representative sample. Future analyses could extend the range of mutualisms included within the dataset and more deeply explore the patterns within and between clades of taxa, and functional interactions.

Theoretical approaches to the evolution of specialization and generalization in mutualisms have begun to appear over the past 20 years or so and were reviewed by Hoeksema and Bruna (2000). Of particular interest are "virulence models," which predict that mutualistic partners should generalize because of a trade-off in ecological attributes important to the mutualism, such as the ability to colonize new hosts and vie against competitors. For example, mycorrhizal fungi, which are poor competitors, could possibly colonize the roots of young plants quite early but may be subsequently replaced by fungi that are slower colonizers but better competitors (Hoeksema and Bruna 2000; see also Hoeksema and Kummel 2003). A plant-pollinator example could involve two species of bee which show a trade-off between minimum flight temperature and aggressiveness. The less aggressive species can visit the flowers of a plant early in the morning, but it is excluded by its competitor's aggression later in the day. Although the timescales are different, in both of these examples, generalization (at some level) can be maintained by ecological trade-offs.

Howe (1984) has argued that "nonsymbiotic" mutualisms are rarely obligate, whereas "symbiotic" mutualisms (which the author argues are largely derived from host-parasite interactions) are more often highly specialized. This use of dichotomous terminology is commonplace in the mutualisms literature and is, I feel, misleading at best and divisive at worst. My analysis suggests that there is no dichotomy between "symbiotic" and "nonsymbiotic" relationships; rather there is a continuum of degrees of biological intimacy and that as the level of intimacy increases so does the exclusivity of that relationship.

The data used in these analyses were scored at the genus level for reasons of taxonomic and statistical robustness. Would the same results have been ob-

tained had the data been analyzed at the species level? That question awaits future analyses, but my reading of the literature suggests that the pattern would be the same. Interactions involving a single focus genus and a single partner genus may be specialized at a species–species level or at a species–genus level. In the latter case, a single species of the focus genus can form an association with any of the species in the partner genus. On the other hand, interactions involving a single focus genus and multiple partner genera tend not to be specialized at a species–genus level, but rather a single species can form associations with multiple genera, for example, plant–seed disperser relationships (although *Ficus*–fig wasp relationships are a notable exception to this generality). If this is indeed the case, then the greater the number of partner genera a focus genus is associated with, the greater should be the species-level generalization. Having said that, a large focus genus may contain species that are more or less specialized or generalized (for example, the genus *Xysmalobium* [Apocynaceae: Asclepiadoideae] in southern Africa; Ollerton et al. 2003). In this case, a representative sample of species from the whole range of specialized to generalized would have to be included in the analysis (perhaps another good reason for analyzing at a generic level—to give an “average” value for those taxa?). The paradox, of course, is that the level of biological intimacy is not expected to vary much within a genus, because it is controlled by biological attributes which are likely, by definition, to be similar within genera. What then controls the level of specialization exhibited by different species within a genus? Are ecological context and partner availability more important than morphological and biochemical “fit”? This promises to be a productive area for future research but requires some very detailed field and/or laboratory observations (Fox and Morrow 1981; Herrera 2005).

The benefits of mutualism to all parties involved in the interaction are often assumed rather than empirically measured (Douglas and Smith 1989; Cushman and Beattie 1991). Within the database I used for these analyses, I have no doubt that some of the interactions are not in fact mutualistic, or are at best conditionally mutualistic, varying over time and space (Bronstein 1994b). Only future analyses will reveal whether the results that I have presented are robust, though the sensitivity analyses in appendix 18.2 suggest that they are. It is worth noting that recent models of the evolution of mutualisms, using economic arguments about resource specialization, suggest that the benefits of mutualism may, in theory, be so small that they are undetectable (Schwartz and Hoeksema 1998). These emerging results, together with new findings regarding the cryptic diversity of mutualistic partners (Herre et al. 1999), are significant challenges to our current ideas about mutualisms and the ways in which we approach our research. But they also point to exciting future findings.

The quotations that open this chapter were chosen because they seem to reflect themes about the current debates regarding the commonness of highly specific plant–pollinator and other mutualistic associations (Howe 1984), the

importance of specialization in generating biological diversity (Thompson 1994), how little we truly understand about the ecology and evolution of mutualisms (Bronstein 1994a), and the fact that no one researcher can hope to collect all of the data required to address these important questions, highlighting the advantages of a synthetic, comparative approach (Elton 1927). Protection and management of biodiversity is a foremost conservation priority for humanity, and synthetic analyses of available data are required to scientifically underpin judgments regarding the ability of habitats to sustain the biodiversity of species interactions.

Appendix 18.1

Table 18A.1 The dataset: A complete listing of the mutualistic associations used in the analyses in this chapter

Category of association	Genera (focus-partner[s]) ^a	Components of biological intimacy ^b					Total index score
		Number of genera	Physical dependence	Trophic dependence	Physiological integration	Vertical transmission	
Fungus–alga	<i>Anzia–Trebouxia</i>	1	2	2	2	0	6
Fungus–cyanobacteria	<i>Geosiphon–Nostoc</i>	1	1	1	1	0	3
Metazoan–alga	<i>Hydra–alga</i>	2	1	1	2	1	5
Metazoan–alga	<i>Convoluta–alga</i>	2	1	2	2	0	5
Metazoan–alga	<i>Porites–Symbiodinium</i>	1	1	1	1	1	4
Legume–rhizobia	<i>Lotus–Rhizobium</i>	1	0	1	2	0	3
Actinorhizae	<i>Alnus–Frankia</i>	1	0	1	2	0	3
Cycad–cyanobacteria	<i>Cycas–Nostoc</i>	1	1	1	1	0	3
Angiosperm–cyanobacteria	<i>Gunnera–Nostoc</i>	1	1	1	2	0	4
Liverwort–cyanobacteria	<i>Blasia–Nostoc</i>	1	1	1	1	0	3
Moss–cyanobacteria	<i>Sphagnum–cyanobacteria</i>	2	0	1	1	0	2
Fern–cyanobacteria	<i>Azolla–Anabaena</i>	1	2	2	2	1	7
Ectomycorrhizal–conifer	<i>Pinus–fungus</i>	23	1	1	1	0	3
VA mycorrhizal–angiosperm ^c	<i>Festuca–mycorrhizae</i>	4	1	1	2	0	4
Insect–gut fungus	<i>Lasioderma–Symbiotaphrina</i>	1	2	2	2	1	7
Ant–fungus	<i>Cyphomyrmex–fungus</i>	2	2	2	0	0	4
Termite–fungus	<i>Odontotermes–fungus</i>	2	2	2	0	0	4
Ascidian–Nephromyces	<i>Molgula–Nephromyces</i>	1	1	2	1	0	4
Insect–mycetocyte	<i>Acyrtosiphon–Buchnera</i>	1	2	2	2	1	7
Plant–endophyte	<i>Lolium–Neotyphodium</i>	1	2	2	2	1	7
Seed dispersal	<i>Viburnum–birds</i>	25	0	1	0	0	1
Pollination	<i>Ficus–fig wasp</i>	20	1	2	1	0	4
Pollination	<i>Asclepias–pollinator</i>	150	0	1	0	0	1
Pollination	<i>Erythrina–pollinator</i>	54	0	1	0	0	1
Ant–plant seed dispersal	<i>Viola–ant</i>	9	0	1	0	0	1

Table 18A.1 (continued)

Category of association	Genera (focus-partner[s]) ^a	Components of biological intimacy ^b					Total index score
		Number of genera	Physical dependence	Trophic dependence	Physiological integration	Vertical transmission	
Ant-extrafloral nectary	<i>Passiflora</i> -ant	17	0	1	0	0	1
Ant-plant	<i>Acacia</i> -ant	5	0	1	0	0	1
Ant-plant	<i>Cecropia</i> -ant	6	2	2	1	0	5
Ant-food body/dormatia	<i>Myrmecodia</i> -ant	3	1	1	0	0	2
Fungal spore dispersal	<i>Epichloe</i> - <i>Phorbia</i>	1	0	1	0	0	1
Fungal spore dispersal	<i>Phallus</i> -fly	30	0	1	0	0	1
Fish-biolum inescence	<i>Leiognathus</i> - <i>Photobacterium</i>	1	1	2	1	0	4
Bird-mammal cleaning	<i>Buphagus</i> -mammal	21	1	1	0	0	2
Anemone fish-anemone	<i>Amphiprion</i> -anemone	6	2	1	0	0	3
Shrimp-anemone	<i>Periclimenes</i> -anemone	5	2	1	0	0	3
Ant-hemipteran	<i>Lasius</i> -homoptera	9	0	1	0	0	1
Ant-hemipteran	<i>Oecophylla</i> -homoptera	10	0	1	0	0	1
Beetle-fungus	<i>Xyleborus</i> -fungus	4	2	2	1	1	6
Wood wasp-fungus	<i>Sirex</i> - <i>Amylostereum</i>	1	2	2	1	1	6

^aThe identity of the focus genus is given first, followed by the partner genus (if the relationship involves only a single genus of partner) or a collective term if there are two or more partner genera.

^bComponents of biological intimacy refers to the biological attributes of the partner genera in relation to the focus genus; see Methods for a description of each component of biological intimacy.

^cVA = vesicular-arbuscular.

Appendix 18.2

Sensitivity Analyses of the Dataset

I conducted three sets of analyses designed to test the sensitivity of the dataset in appendix 18.1 to (1) sample size, (2) accuracy of recording numbers of partner genera per host genus, and (3) accuracy of scoring the index of biological intimacy.

1. I randomly selected 50% of the dataset and in each case calculated a Spearman rank correlation between the number of partner genera and the index of biological intimacy. This was done for 25 iterations; 19 of the 25 iterations (76%) returned a statistically significant ($P \leq .05$) correlation, 2 of the iterations (8%) returned a marginally statistically significant ($P \leq .10$) correlation, and 4 of the iterations (16%) returned a nonsignificant ($P > .10$) correlation.
2. To a random selection of 50% of the dataset, I added one genus to the score for number of partner genera and in each case calculated a Spearman rank

correlation between the number of partner genera and the index of biological intimacy. I ran this for 20 iterations; 20 out of 20 iterations (100%) returned a highly statistically significant ($P \leq .001$) correlation.

3. Finally, I randomly selected 50% of the dataset and added 1 to the score of biological intimacy. I then calculated a Spearman rank correlation between the number of partner genera and the index of biological intimacy for 20 iterations. Once again, 20 out of 20 iterations (100%) returned a highly statistically significant ($P \leq .001$) correlation.

The results of these sensitivity analyses suggest that the dataset I used was robust to changes in sample size (up to 50%), to minor variations in the number of recorded genera, and to inaccuracies in scoring the index of biological intimacy.

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