Fruit–seed disperser interactions: timely insights from a long-term perspective

Arguably, the field of frugivory and seed dispersal is stuck. After a steep and almost continuous rise in the number of papers published per year between 1973 and 1994, interest in the field seems to have reached an asymptote (Fig. 1). Perhaps it has even started to decline.

More unsettling is a vague uncertainty about where the field is headed[1]. In the 1980s, it was propelled into the mainstream of evolutionary ecology through a collective focus on a central paradigm. This paradigm[2], developed in the 1970s, held that coevolution between fruit-eating vertebrates and fruiting plants would lead to suites of characters, ranging from 'specialized' morphological, physiological or ecological matches between species pairs to 'generalized' or 'diffuse' matches between groups of species. Assumptions and predictions of this paradigm were quickly tested and usually rejected[3]. Consequently, workers in the 1990s have started to place their focus elsewhere[4]. The problem is that their new foci are generally narrower and largely disjointed. An all-encompassing framework has been lost. Even more alarming, rigorous phylogenetic analyses have raised numerous doubts about whether seed dispersers even matter (in an evolutionary sense) to fruiting plants[5].

New frameworks have been suggested but have generally failed to unite interest among the more and more disparate approaches to the field[4]. Where does one turn for guidance? Enter a recent paper by one of the most prolific and influential workers in the field, Carlos Herrera[6]. The paper offers what is sorely needed and yet, by definition, so rare in any young field – a long-term data set. Herrera summarizes 12 years of data from a sclerophyllous-scrub site in southern Spain. This is almost certainly the longest-term data set on a plant-disperser system yet published.

Herrera monitored species composition and abundance of ripe fruit and fruit-eating birds in autumn. Fruit preferences, diet composition and recapture rates of the two most common seed dispersers, the robin (*Erithacus rubecula*) and the blackcap warbler (*Sylvia atricapilla*), were also monitored. At the most basic level, the goal was to quantify the extent of variation in fruit and frugivorous bird populations and to determine whether variation in one was linked to variation in the other. Such data are necessary to gauge the degree of mutual dependence between birds and fruiting plants. If, for example, variation in fruit abundance has little effect on the behavior and ecology of fruit-eating birds or if variation in fruit-eating bird abundance has little effect on plant reproduction, then any dependency of one group on the other would be unpredictable and cause re-evaluation of the classic view of seed-dispersal systems.

Despite large supra-annual variation in fruit supply and fruit-eating bird abundance, there was generally no correlation between the two. In only one species pair was there any hint that birds tracked abundance of fruits: *S. atricapilla* were more abundant in years when *Phillyrea latifolia* mast fruited. Otherwise, population sizes of fruit-eating birds were best explained by autumn weather patterns. These results, combined with very low return rates that were unrelated to fruit abundance, strongly suggest that fruit-eating birds were not tracking fruit availability. In fact, populations of frugivorous species were no more variable than populations of nonfrugivorous species.

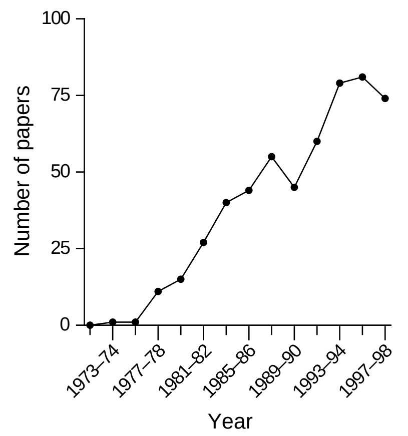

Fig. 1. Number of citations in the BIOSIS data base from a search of '(frugivor* or fruit*) and seed dispersal' as a function of year of publication. The '*' denotes a 'wildcard' character to retrieve all possible suffix variations of a given word. Number of citations for 1998 estimated by extrapolation from 36 weeks of data.

The 'remarkable indifference'[6] of frugivores to variation in their major food supply seems incongruous with results of many previous studies. In numerous places and on diverse scales, fruit-eating birds tend to be most abundant when and where fruit is most abundant[7–9], which has led to the generalization that an important adaptation to frugivory is the ability to track flushes of fruit that are often asynchronous in space and time[7,9]. Balancing this view is the frequent observation of enormous discordance in fruit–frugivore interactions; clear patterns in one year disappear the next or are not present at a different site[10].

Which view of fruit–frugivore interactions is more likely to be accurate? It has been difficult to judge because authors inevitably stress the first view whenever they find any coupling between fruits and frugivores and the second view if they fail to find such coupling. The major problem is that practically all studies lack the clout of a long-term data set to distinguish between normal and abnormal years or to minimize type II error in the case of failure to find pattern. Herrera's data are the best available and argue strongly for a system in disequilibrium. Normal years at his site are those in which fruit-eating birds pay little attention to the abundance of all fruit crops combined or to the fruit crops of any single species. As in all studies, however, our interpretation is constrained by the types of data gathered; some of the variation between studies could be the result of focusing on different spatial and temporal scales. For example, variation in the average migration distance might be most strongly tied to abiotic factors, such as temperature, but the distribution of migrants within a region might be correlated with large-scale patterns of food availability. If so, studies focusing on annual variation within a site will detect correlations between frugivore abundance and abiotic variables, whereas studies examining distributions between sites will detect resource tracking. Nevertheless, the conclusion remains the same: abiotic variables are very important and might overwhelm the extent of coupling between frugivores and fruits.

Close examination of how individual plant species contributed to community-level variation in annual fruit production yielded another surprise: masting (a 'synchronous production of large seed crops within a population or community of species every two or more years'[11]). In North America, masting is best known and documented in oaks (*Quercus* spp.), mainly because long-term studies were initiated decades ago by wildlife managers who realized the importance of acorn abundance to game species. Masting is usually thought to be associated with dry-fruited species[12]. Despite frequent claims of supra-annual variation in fleshy-fruited species[13], lack of long-term data has apparently inhibited researchers from looking for masting cycles. In fact, masting in fleshy-fruited species is rarely even considered. Herrera's documentation of significant supra-annual variation of fruit production in seven out of 13 species should start to change that.

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Such a broadening of perspective could provide new insights into evolutionary theories of masting. In particular, there is fertile ground in contrasting responses of consumers to masting events in dry versus fleshy fruits because consumption of the former is generally detrimental to plant fitness, whereas consumption of the latter is generally beneficial. In this context, note that one of the most widely accepted hypotheses for masting – that irregular mass fruiting events increase reproductive success by saturating local populations of consumers[12] – makes little sense for fleshy-fruited species. Because consumers of fleshy fruits are usually seed dispersers, saturating them would presumably be an inefficient strategy of reproduction. Alternative explanations of masting in fleshy-fruited species are needed.

Perhaps masting in fleshy-fruited species is best explained as a means of increasing attraction of frugivores and thereby increasing efficiency of seed dispersal (the 'animal fruit-dispersal' hypothesis[12]). Herrera's data do not support this hypothesis. The most common frugivores did not increase in abundance during mast years and there was remarkably little correlation between abundance of fruit species in their diets and relative availability of those fruit species in the field. Lack of both functional and numerical responses of frugivores to masting cycles suggests an explanation for masting based on plant physiological constraints. Herrera's data suggest that large fruit crops might require so many resources that they cannot be produced every year (the 'resource matching hypothesis'[12]).

How common is masting in fleshy-fruited species? Herrera knows of only one other report[14] of 'significant periodicity in fruit abundance of a fleshy-fruited species'. Based on a literature search of our own, we agree that rigorous demonstrations of masting in fleshy fruits are extremely rare. However, there are numerous studies that, although not convincing when considered individually, certainly are when viewed collectively[15]. Masting in fleshy-fruited species appears common and, unlike the case in Herrera's study site, frugivores in many other communities appear to respond in many ways to large-scale fluctuations in fruit abundance[7,9]. These responses may have 'chain reaction' effects on other plants and animals within the community. In eastern North America, for example, masting patterns of oaks are tied not only to populations of acorn consumers but also to tick and gypsy moth population cycles[16]. Given such pervasive effects of masting in hard-fruited species, it seems prudent to look for them in fleshy-fruited ones.

A final lesson from Herrera's paper represents a new twist on a familiar theme: the danger of generalizing from short-term studies. The two most common frugivores at his site typically focused their foraging on a single species of fruit, which constituted >50% of ingested pulp mass. The focal species changed from one year to the next and, more interestingly, the type of fruit also changed. In some years, a lipid-rich fruit was clearly preferred, whereas in other years a carbohydrate-rich fruit dominated diets. The significance of this observation relates to studies that have attempted to classify birds by the nutritional characteristics of fruits they eat. Such studies rarely consider year-to-year variation, relying instead on a single season or an average of several seasons. Because birds can switch from specializing on one type of fruit in one year to a very different type of fruit in another year, conclusions about dietary specialization in frugivores might need re-evaluation.

Despite often dramatic changes in the type of fruit dominating the diet, a more general analysis of rank preferences revealed consistent preferences among all fruit species in the community. Birds obviously foraged nonrandomly. Interestingly, they significantly preferred fruits either high in lipids or high in carbohydrates; species with intermediate levels of each were least consumed. This result, coupled with the observation that the dominant fruit species in the diet can change from being lipid-rich to carbohydrate-rich, suggests that Herrera's correlations of bird abundance and fruit abundance were perhaps too simplistic to detect patterns of covariation. If birds are responding to types of fruit (lipid-rich versus carbohydrate-rich) and their preferences for the most important fruit species shift, correlations involving the abundances of all fruits or of single fruit species are likely to be blind to such responses. Incorporating these complexities into analyses of frugivore and fruit abundances will undoubtedly increase our understanding of whether and how frugivore populations are coupled with fruit production.

In conclusion, Herrera presents a sobering demonstration of why studies at greater temporal scales are necessary to understand plant–disperser interactions. We emphasize, however, that a parallel argument can be made for studies that employ a greater spatial scale. More to the point, it remains unclear whether fruits and frugivores are typically decoupled at other sites to the extent that Herrera's analyses suggest they are in southern Spain. Numerous other studies present a very different view – albeit one based on short-term data sets – in other communities[17]. If Herrera's data turn out to be representative of other places, they will certainly force a change in our theoretical and empirical approaches to plant–disperser interactions.

High unpredictability and asymmetry of interactions, coupled with an important influence of abiotic factors, signal that mutual selection pressures between plants and seed dispersers are greatly constrained. There may be little point in looking for such selective pressures (a currently popular sport) or theorizing about them. In fact, this is Herrera's take-home message: the field of frugivory and seed dispersal will emerge from its slump only by 'an explicit consideration of plant–disperser systems as nonequilibrial, and the use of the corresponding conceptual tools'.

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Complex dynamics in ecology

Ecological systems are complex, and the complexity has two principal forms: intricate interactions among numerous species[1] (ecosystem complexity) and changing patterns of observed abundances[2] (dynamical complexity). What are the mechanisms that cause complex patterns? Which complexities are important? Does natural selection favour complexity? These are some of the fundamental questions that have attracted the attention of ecologists and evolutionary biologists for decades.

At the Seventh International Congress of Ecology last July (Florence, Italy) a full-day session organized by Charles Godfray (Imperial College at Silwood Park, Ascot, UK) and Marino Gatto (Politecnico di Milano, Italy) was devoted to the origins and forms of ecological complexity.

Dynamical complexity

Empirical data vary enormously in their degree of dynamical complexity. Some populations do not appear to change in size, apparently maintaining a stable equilibrium[3], but the population dynamics of many species are more complicated. Temporally, some populations show cyclic trends[4], whereas others can even be chaotic[5]. Spatially, some populations undergo frequent, local extinctions and recolonizations[6] and some seem to show coherent spatial patterns[7,8]. Explaining the mechanisms responsible for generating these observed patterns remains a major challenge for population biologists.

The source of dynamical complexity is an important and hotly debated subject. Complex ecological dynamics can arise from 'intrinsic' or 'extrinsic' influences on populations. The nonlinear response of population growth rate to increases in population density is an intrinsic feature, whereas the effects of the weather, for example, are extrinsic. Either intrinsic or extrinsic forces might be more important in given systems but commonly they interact; for example, seasonal changes in climate (or some other factor) might induce complex population dynamics in species that are intrinsically stable.

At the Intecol meeting, Robert May (University of Oxford, UK) introduced the subject of ecological complexity by reviewing how complex dynamics can often arise from extremely simple processes[2]. The overall themes of his review were that dynamical complexity in population fluctuations can arise from density-dependent population growth, simple rules can generate fractal patterns, and localized dispersal in a spatially homogeneous environment can give rise to spatially heterogeneous patterns.

William Schaffer (University of Arizona, Tucson, USA) presented a series of numerical analyses showing how dynamical complexity can arise in predator–prey systems as a consequence of seasonal forcing. This follows influential work on the effects of seasonality (in disease transmission rates) on the dynamics of host–parasite systems, which are strongly analagous to predator–prey systems[9,10]. Fundamental, qualitative features of real ecological dynamics are often exposed by very simple models, but such caricatures are unlikely to correspond quantitatively to any particular system. Schaffer presented some results of very detailed simulations, which are sometimes appropriate when they can be reliably parameterized using relatively high resolution data.

Marino Gatto argued that it might be most fruitful to study models incorporating some intermediate level of biological detail, because they capture the key features sufficiently well to be reasonably realistic without precluding rigorous analyses. Gatto's model predicts the mean and variance of population abundance in each occupied patch, not just the probability of occupation (as in the classic metapopulation model of Levins[11]). Related presentations considered the effects of local disturbances on the joint evolution of dispersal and reproductive effort (Ophélie Ronce, Université de Montpellier, France) and potential influences of ocean currents on marine predator–prey systems (Alfredo Ascioti, University of Reggio Calabria, Italy).

Evolutionary forces: simplicity or complexity?

A growing controversy concerns the influence of selective pressures on the character of population dynamics. Some models predict evolution to chaos[12], whereas others predict evolution to stability[13]. Karin Johst (Centre for Environmental Research, Leipzig, Germany) added to this debate, arguing that spatial structure, and perhaps age structure too, favours the evolution of chaotic dynamics.

In situations where population dynamics *are* complex, we may well ask whether there are any important biological implications[10]. Why should we care about chaos? Robert Holt (University of Kansas, Lawrence, USA) argued that chaotic dynamics favour high dispersal rates, even though dispersal is usually selected against[14], and chaos favours the persistent use of low quality (but stable) habitats. Greater dispersal implies a higher degree of global mixing, so chaos might resist the evolution of local adaptation. Régis Férrière (Ecole Normale Supérieure, Paris, France) noted that it is not clear how to define the meaning of 'fitness' and 'invasability' in populations with complex dynamics. Different types of mutant might be able to invade at different parts of a population cycle or on different dynamical attractors. Hans Metz (Institute of Evolutionary and Ecological Sciences, Leiden, The Netherlands) discussed a framework for dealing with these problems: he defines fitness as the asymptotic average relative rate of increase of a population[15].

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