A nagging, the field of frugivory and
courtship to frugivory is the ability to track
abundance of fruits. S. atrocapilla were
more abundant in years when Phillyrea
latifolia mast fruited. Otherwise, popu-
lations of frugivorous species were no
more variable than populations of
nonfrugivorous species.

The ‘remarkable indifference’ of fru-
givores 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 abundant13, which has led to
the generalization that an important adap-
tation to frugivory is the ability to track
flushes of fruit that are often asynchronous
in space and time12. Balancing this view is
the frequent observation of enormous dis-
cordance in fruit-frugivore interactions;
clear patterns in one year disappear the
next or are not present at a different site11.

Which view of fruit-frugivore interac-
tions is more likely to be accurate? It has
variables, whereas studies examining dis-
cordance to frugivores to variation is the ability to track
abundance of fruit. Such data are necessary to gauge
variation in one was linked to variation in the
lations and to determine whether vari-
ation in fruit and frugivorous bird popu-
larization was the goal to quantify the extent of vari-
ability. In fact, populations of frugivorous

New frameworks have been suggested
but have generally failed to unite interest
among the more and more disparate ap-
proaches to the field14. Where does one
turn for guidance? Enter a recent paper
by one of the most prolific and influential
workers in the field, Carlos Herrera15. 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 composi-
tion and abundance of ripe fruit and frut-
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,
these data allow us to gauge the extent of vari-
ation in fruit and frugivorous bird popu-
lations and to determine whether vari-
ation within a site will detect correlations
between frugivore abundance and abiotic
variables, whereas studies examining dis-
cordances between sites will detect re-
source tracking. Nevertheless, the conclu-
sion 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 ‘syn-
chronous production of large seed crops
within a species pair’12) has been
realized the importance of acorn abun-
dance in oak species16, mainly because long-term studies were initiated decades ago by wildlife managers who
realized the importance of acorn abun-
dance to game species. Masting is usually
thought to be associated with dry-fruited
species17. Despite frequent claims of supra-
annual variation in fleshy-fruited species13,
lack of long-term data has apparently
hid lack of such studies from looking for
masting cycles. In fact, masting in fleshy-fruited
species is rarely even considered. Herrera’s
data resolved the issue regarding temporal
variation in frugivore niche at seven out of
13 species should start to change that.
NEWS & COMMENT

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 mast events in dry versus fleshy fruits because consumption of the former is generally detrimental to plant fitness, whereas consumption of the latter is not. 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 mast events 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 cost hypothesis’). How common is masting in fleshy-fruited species? Herrera knows of only one other report of significant periodicity in fruit abundance of a fleshy-fruited species. Based on a literature search of our own, we agree that rigorous demonstration of masting in fleshy-fruits is extremely rare. However, there are numerous studies that, although not convincing when considered individually, certainly are when viewed collectively. 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 frugivores in many other communities and, unlike the case in Herrera’s study site, in fleshy-fruited species appears common when viewed collectively. Masting when considered individually, certainly extremely rare. However, there are numerously foraged nonrandomly. Interestingly, they significantly preferred fruits either high in lipids or high in carbohydrate hydrates; 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 frugivores 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? 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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Doug J. Levey
Dept of Ecology and Evolutionary Biology, Brown University, Providence, RI 02912 and Dept of Zoology, University of Florida, Gainesville, FL 32611, USA
(doug_levey@brown.edu)

Craig W. Benkman
Dept of Biology, New Mexico State University, Las Cruces, NM 88003, USA (benkman@nmsu.edu)

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Complex dynamics in ecology

Ecological systems are complex, and the complexity has two principal forms: intricate interactions among numerous species (ecosystem complexity) and changing patterns of observed abundances (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 (Milano, Italy) was devoted to the origins of a mast-fruiting, bird-dispersed tree: bridging frugivorous activity and seedling establishment, Ecol. Monogr. 64, 315–344.

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, but the population dynamics of many species are more complicated. Temporally, some populations show cyclical trends, whereas others can even be chaotic. Spatially, populations undergo frequent, local extinctions and recolonizations, and some seem to show coherent spatial patterns. 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. The overall theme of his review was 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 Schaller (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 analogous to predator-prey systems. 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. Schaller 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). 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 Aucioli, 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, whereas others predict evolution to stability. Karin Jönsson (Center 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. 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, 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 ‘invasibility’ 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 defined fitness as the deterministic average relative rate of increase of a population.