THE TEMPORAL DYNAMICS OF RESOURCE USE BY FRUGIVOROUS BIRDS:

A NETWORK APPROACH

JOFRE CARNICER1, PEDRO JORDANO1, AND CARLOS J. MELIÁN2

1Integrative Ecology Group, Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas, Pabellón del Perú, Av. María Luisa s/n 41013, Sevilla, Spain

2National Center for Ecological Analysis and Synthesis, 735 State St, Santa Barbara, CA 93101, USA

3Email: jofrecarnicer@ebd.csic.es
Abstract. Ecological networks patterns are influenced by a diverse array of ecological processes that operate at different temporal scales. Here we analyzed if the coupled effect of local abundance variation, seasonally phenotypic plastic responses and species evolutionary adaptations might act in concert to shape network patterns. We studied the temporal variation in three interaction properties of bird species (number of interactions per species, interaction strength and asymmetry) in a temporal sequence of 28 plant-frugivore interaction networks spanning two years in a Mediterranean scrub community. Three main hypotheses dealing with the temporal variation of networks properties were tested, examining the effects of abundance, switching behavior between alternative resources and morphological traits in determining consumer interaction patterns. Our results demonstrate that temporal variation in consumer interaction patterns is explained by short-term variation in resource and bird abundances and seasonal dietary switches between alternative resources (fleshy fruits and insects). Moreover, differences in beak morphology are associated with differences in switching behavior between resources, suggesting an important role of foraging adaptations in determining network patterns. We argue that beak shape adaptations might determine generalist and specialist feeding behaviors and thus the positions of consumer species within the network. Finally, we provide a preliminary framework to interpret phylogenetic signal in plant-animal networks. Indeed, we show that the strength of the phylogenetic signal in networks depends on the relative importance of abundance, behavioral and morphological variables. We show that these variables strongly differ in their phylogenetic
conservatism. Consequently, we suggest that moderate and significant phylogenetic
2effects should be commonly observed in networks.

Key words: abundance, bird, morphological trait, network, phylogeny, switching
4behavior.

INTRODUCTION

6Ecological communities are complex and dynamic phenomena, composed by
temporally variable populations that interact in very diverse ways (e.g. competence,
8predation, herbivory, dispersal, pollination, parasitism, among others) causing
continuous changes on the architecture of energetic and material fluxes over space and
time. Such overwhelming complexity can be simplified representing communities as
networks, in which basically species are represented as nodes and energetic fluxes

Network approaches have a long tradition in ecological research (Pimm 1982, Cohen et
al. 1990, Polis and Winemiller 1996) and have provided an appealing way to visualize
and synthesize the structure of ecological interactions (Guimerà et al. 2005, Olesen et
al. 2007, Rooney et al. 2008, Clauset et al. 2008), to study emergent and invariant
properties (Jordano et al. 2003, Bascompte et al. 2003), and to analyze the stability and

However, network approaches have been usually hampered by the inexistence of both
spatially and temporal explicit analyses (Winemiller 1990). Fortunately, an increasing
number of studies are progressively filling these gaps by providing both improved
spatially-explicit approaches (Holt 2002, McCann et al 2005, Rooney et al. 2008) and
empirically-exhaustive descriptions of the temporal dynamics of networks (Winemiller
241990, Olesen et al 2008). Similarly, another unsolved challenge is to identify and
quantitatively assess the relative importance of the diverse ecological and evolutionary processes that ultimately shape network structures (Jordano et al. 2003, Cattin et al. 2004, Jordano et al. 2008, Rooney et al. 2008). Indeed, most ecological networks share some invariant structural properties but the relative importance of the evolutionary and ecological processes that mold these emergent patterns is usually not well understood. For instance, networks are characterized by a low number of strong interactions and a much greater number of weak interactions (Paine 1992, McCann et al. 1998). Interactions tend to be asymmetric, in both the number of links per species and the strength of the interaction (Jordano 1987b, Jordano et al. 2003, Vázquez and Aizen 2004, Bascompte et al. 2006). More generally, networks are characterized by a few species that concentrate most of the interactions and usually exert a strong influence in most of the species (Jordano 1987b, Bascompte et al. 2003). However, and despite the importance of the issue, which are the underlying mechanisms that generate such asymmetric relationships in the number and strength of interactions between species in ecological networks is yet an unresolved debate (Thompson 2005, Lewinsohn et al. 2006, Jordano et al. 2006, Stang et al. 2006, Bascompte et al. 2007, Vázquez et al. 2007).

Network patterns are the result of a diverse array of ecological and evolutionary processes that operate along a wide range of temporal scales (Johnson and Stinchcombe 2007). On one hand, at short ecological time-scales, communities vary in species composition due to processes of birth, death, migration, and dispersal, among others. All these processes cause abundance and composition variation and might alter the type, number and strength of interactions observed (Jordano 1984, 1985, 1994, Herrera 1984, Vázquez et al. 2007). Similarly, at short ecological time-scales species might respond
to changes in the environmental conditions by phenotypic plastic responses (Agrawal 2001, Price et al. 2003). For instance, consumer species may seasonally switch the resources used, thus modifying the interactions exerted and causing variation in network properties at short-time scales (Rooney et al. 2006). On the other hand, at much longer time scales, species evolve or coevolve in a set of morphological and behavioral traits (adaptations) that might determine the species with whom they interact (Thompson 2005). Such evolutionary processes may imply the generation of geographical mosaics of selection, coevolutionary hot-spots, and trait remixing processes (Thompson 2005, Gomulkiewicz et al. 2007). All these processes may require a considerable number of generations and thus are thought to operate at longer temporal scales (Johnson and Stinchcombe 2007).

Here we studied the temporal variation in three network properties of consumer frugivorous bird species (number of interactions per species, interaction strength and asymmetry) in a temporal sequence of 28 networks spanning two years. The mutualistic plant-animal network analyzed was composed by 24 frugivorous bird species and 15 plants that produce fleshy fruits and is located in a Mediterranean shrub community in Southern Spain (Jordano 1984). Three main hypotheses dealing with the temporal variation of consumer interaction properties were tested (table 1). The three hypotheses examine the effect of bird abundance, bird foraging behavior and morphology in determining network patterns.

The abundance hypothesis (Jordano 1987b, Vázquez and Aizen 2004, Vázquez et al. 2007) states that short-term variation in local population abundance is the principal factor that determines the variation in the number and strength of interactions in ecological networks. It predicts that the greater the abundance of a species, the
greater will be both the number of interactions established and the interaction strength produced in the rest of the species (Vázquez et al. 2005, Stang et al. 2006, Vázquez et al. 2007).

The switching behavior hypothesis states that consumer species will show increased number of interactions and higher interaction strengths in the resource-channel that use preferentially during an elapse of time (Murdoch 1969, Berthold 1976, Abrams 2006, Rooney et al. 2006). Resource channels (Rooney et al. 2006) are composed by two or more sets of species that are usually unrelated at high taxonomic levels (i.e. fungi versus bacteria, invertebrates versus fleshy fruits), that show specific turnover rates (production:biomass ratios), and share common top-consumer species (Rooney et al. 2006). In our study system, top-consumers are bird species that alternate between two resource-channels: fruits \( R_1 \) and invertebrates \( R_2 \) (Jordano 1984, 1985, 1987a).

The species trait hypothesis states that evolutionary processes had produced unique morphological, behavioral and life-story traits that determine the type, number and strength of the interactions exerted by species (Thompson 2005, Stang et al. 2006, Björklund 2006). The species trait hypothesis predicts the existence of a limited set of morphological, behavioral or life-story traits that explain interspecific differences observed between species in the number and strength of interactions (Stang et al. 2006).

Similarly, according to the species trait hypothesis, the identity of a species (used as a proxy of their unique evolutionary history) is expected to be a fundamental variable explaining the temporal variation in the type, number and strength of its interactions with other species. If adaptation strongly determines network patterns, we predict that species would maintain consistently a different number and strength of interaction along
the whole temporal sequence examined here (two years), irrespective of temporal
changes in abundance or species switching behavior.

Overall, our main aim here is to contrast the abundance, the switching behavior
and the species trait hypotheses, to evaluate if these three mechanisms are active and
assess their relative importance.

8 MATERIAL AND METHODS

Study site

Field work was conducted in Hato Ratón, an area located at the northeast border of the
Doñana National Park, Huelva province, SW Spain (Jordano 1984). The study period
extended from early 1981 throughout April 1983, encompassing two consecutive
fruiting seasons. The study site is a medium to high (2.5-5 m) dense sclerophyllous
shrubland growing on sandy soils at 13 m of elevation. Vegetation was dominated by
tall shrubs and treelets of *Pistacia lentiscus* (Anacardiaceae), *Olea europaea var.*
*sylvestris* (Oleaceae), *Phillyrea angustifolia* (Oleaceae) and *Rhamnus lycioides*
(Rhamnaceae). The shrubland is characteristic in having a great cover and diversity of
plants producing fleshy fruits (72,2% cover, n=21 species), but is dominated by *P.
lentiscus* (33,4 %cover).

Data

Quantitative data about the interactions between birds and fleshy-fruiting plants were
derived from faecal samples of birds captured in mist-nets (Jordano 1984). A total of 10
mist-nets were operated weekly, 2 days per week. The nets were opened from down to
dusk and checked at hourly intervals. The relative importance of animal prey (mostly
arthropods) and vegetable remains (mostly fruits) in bird faeces was assessed. The
2percent volume occupied by each fraction (to the nearest 10%) was estimated visually.
These measures were used as an estimate of the relative resource-channel use (fruits,
4% \( R_1 \), and invertebrates, \( \%R_2 \)). Faecal samples were mostly composed by fruits and
invertebrates. Flowers or other resources were very infrequently consumed by a few
species and occupy negligible fractions of the samples. Thus, for all the samples, \( \%R_1 \approx
100 - \%R_2 \). Both seeds and pulp remains in the faeces were identified, the latter by
microscopic inspection of the pericarp tissue. The analyses were carried out from July
to November, covering a total of 28 periods of 15 days in 1981-1983. This resulted in a
temporal sequence of 28 networks, with 13 and 15 networks per year respectively.
During the spring period (April-June), birds totally switched to an insectivorous diet due
to the high availability of insects and the nearly absence of fruits in the environment
(Carnicer et al. 2008). On spring fruit-bird interactions were occasional and rare
phenomena. For instance, on May-June of 1981, and after two months of intensive mist-
net sampling, a single fruit-bird interaction was detected. Therefore, we excluded April-
June data and restricted the analyses to the fruiting peak period (July-March).
Networks were examined grouping by 15 day, monthly and two-month periods. We
observed a high temporal turnover in the type and number of interactions (Appendix A)
and a great weekly variation in bird densities, fruit abundances and percentages of fruits
consumed in the diet (Appendix B). Therefore, we opted for the higher scale of
resolution (15- days) in order to more precisely quantify and analyze the temporal
variation of interactions.
Bird abundance data was obtained by performing weekly counts along a permanent 1-
24km-length transect following the procedure of Emlen (1981).
Variation in fruit production was estimated by transect counts of the total number of ripe fruits per unit area that were checked every 15 days in 15 replicate plots 30 m x 1.5 m (Jordano 1984). Relative variation in invertebrate abundance was calculated using 4 adhesive traps that were set hanging from vegetation and on the ground (Jordano 1984); these traps were monitored weekly. Bird morphological measures used (wing, tail, body size, gape width, tarsus, culmen) were obtained from birds captured in the mist-nets using standard procedures (Jordano 1984, 1987a&c). Previous studies with frugivorous Mediterranean birds have documented the relevance of these morphological traits on fruit and insect consumption (Jordano 1987a,c).

The sampling effort applied was constant along the study period, and this allowed the quantitative assessment of the temporal dynamics of interaction networks. However, it is important to bear in mind that temporal two-week slices are not to be interpreted as fully resolved networks: the number of interactions observed is surely limited by the strength of the sampling effort applied (20 mist-nets per week; mean= 7.78 captures per species per time period). No doubt, increasing sampling effort per time unit (e.g. 40 mist-nets per week) would surely provide an increase in the number of interactions per time unit detected and a better resolution of network structures showed.

**Network properties measured**

The three hypotheses were examined on three network properties for consumer bird species (the number of interactions per species or degree, interaction strength and asymmetry). Therefore, we restricted our analysis to consumer bird species in the mutualistic plant-animal network (fleshy-fruited plant species and frugivorous birds). This restriction allowed us to focus on hypotheses based on bird natural history.
Arthropod-bird interactions were not included in the analyses because taxonomic resolution was much lower (order level) and produced coarse and very imprecise networks. Pajek software was used to calculate species degree and interaction strength for each bird (de Nooy et al. 2005; http://vlado.fmf.uni-lj.si/pub/networks/pajek/). The use of this software facilitated calculation without implying any special mathematical assumption. Bird species degree \((k_m)\) was defined as the number of interactions of a focal bird species \(m\) with other plant species in each temporal sequence (see Brandes and Erlebach 2005 for an introduction to the term degree and their use in graph theory).

Interaction strength \((IS_{mn}, \text{hereafter})\) was estimated as the total number of fruits described for a plant-animal interaction during two weeks (Vázquez et al. 2005, Vázquez et al. 2007). Interaction strength for a bird species \(m\) \((IS_m)\) was calculated as the sum of all the interactions strengths with \(n\) interacting plants \((IS_m = \Sigma IS_{mn})\) (Bascompte et al. 2006). Note that this measure of interaction strength does not measure the relative impact of consumer species on plant demography (Sabo et al. 2005), and thus clearly differs from other system-level measures of interaction strength usually used in microcosm and experimental field approaches (Paine 1992, Sabo et al. 2005).

Ideally, interaction strength measures should integrate also the fate of seeds once the disperser leaves the mother plant. This should require an evaluation of: 1) the treatment the disperser gives to the seeds (digestive tract passage can destroy seeds or enhance germination) 2) the quality of deposition that is associated with spatial movement of dispersers 3) the demographic fate of dispersed seeds. However, due to practical reasons, the demographic consequences are only evaluated at the first stage of the dispersal cycle (e.g. amount of fruit consumed by dispersers during an elapse of time).
Following Vázquez and collaborators (2007), we defined asymmetry ($A_m$) as a species-level property that evaluates the relative difference between the number and strength of interactions exerted by a focal species on their partner species versus the number and strength of interactions exerted by partner species on the focal species. A detailed mathematical description is provided in Vazquez et al. (2007). Asymmetry values range between $-1$ and $1$. Positive values indicate that the number and strength of the interactions with partner species is quantitatively more important than the reciprocal effect exerted by the interaction partners on the focal species (Vázquez et al. 2007). Negative values indicate the reversed situation, in which the number and strength of interactions of partner species on the focal species is more important than the effect of focal species on them. 0 values indicate that the interactive relationships are symmetrical (Vázquez et al. 2007). Again, note that this asymmetry measure is not evaluating the demographic effects of fruit consumption on plant populations, and therefore clearly differs from system-level measures that experimentally estimate this effect (Paine 1992).

Asymmetry values along the temporal sequence for each species were calculated using a MatLab code that is available upon request to the authors. Additionally, we measured other network traits: maximum and minimum interaction strength for each species and period time, core, and centrality. A description of these network measures is provided in de Nooy et al. (2005).

**Temporal trends in network structure, switching and abundances**

We studied the temporal variation of three variables: plant-bird interactions (1), bird switching behavior between invertebrates and fruits (2), and bird abundance (3). First, we analyzed faecal samples collected along two years and obtained a temporal sequence
of the variation of plant-bird interactions. This sequence was graphed using Pajek software (de Nooy et al. 2005). Secondly, faecal samples were used to assess the proportion of fruits and invertebrates used by each species along the temporal sequence (switching behavior). Differences in switching rates between species were quantified by plotting the percentage of fruits in the diet ($R_1$) against the resource ratio in the environment (calculated as $R_1 / (R_1 + R_2)$; or $R_1 / R_2$) for each species (Carnicer et al. 2008). Sigmoid curves (four-parameter logistic equations) were fitted using non-linear regression methods. We estimated switching delay for each species by calculating the relative environmental resource ratio at which 25% of fruits in species’ diet was achieved [$R_1 / (R_1 + R_2)$]. PRISM software (version 5.0) was used to interpolate values from the sigmoid curves fitted. In addition to sigmoid fits, we explored and applied linear fits using standard least squares models. These analyses allowed the evaluation of switching behavioral responses in relation to the changes in the relative proportion of resources in the environment for each species.

Thirdly, census data were used to estimate the temporal variation in bird abundances.

Hypothesis testing

To assess the relative support for each of the hypotheses examined, we modelled bird interaction properties as a function of the variables associated with each hypothesis (table 1). The abundance hypothesis predicts that bird interaction properties ($k_m, IS_m, A_m$) would be positively related with the temporal variation of bird abundance ($N_m$) and/or resource abundance ($R_1, R_2$). If both bird and resource abundance increase the probability of interaction, an increased number and stronger interactions should be observed when both birds and resources are very abundant. This was tested introducing the interactions $N_m^* R_1$ and $N_m^* R_2$ in the models. The switching behavior hypothesis
predicted a positive and significant association between the temporal variation in the percentage of fruits used in the diet ($%R_i$) and network properties measured ($k_m$, $IS_m$, $A_m$). Finally, the species trait hypothesis predicts that species identity ($Sp$) will be associated with significantly different values of network properties ($k_m$, $IS_m$, $A_m$) along all the temporal sequence. We used generalized linear mixed models with node identity ($Sp$), percentage of fruits in the diet ($%R_i$), bird abundance ($N_m$), fruit abundance ($R_i$), invertivore abundance ($R_2$) and the interactions ($N_m*R_i$; $N_m*R_2$) as independent variables (Table 1) (Wolfinger and O’Connell 1993).

Sampling effort was maintained constant along the whole study period and therefore number of bird captured in mist-nets was proportional to local species’ abundance ($R^2 = 0.57$; $p<0.0001$). This abundance effect on sample size and therefore on the number of interactions was captured in the models by introducing the density variable ($N_m$).

However, some species were possibly undersampled due to their idiosyncratic mobility behavior or by stochastic sampling effects. To quantitatively account for such deviations, we estimated sampling error (SE) by regressing for each species the number of captures against the local abundance estimates derived from transect counts. The residuals of this regression assessed the observed difference between local abundance and realized sample size for each species and time period and thus provided a reasonable estimate of the sampling error. Sampling error (SE), time period (15 days) and year were introduced in the models as random variables. We used the Glimmix procedure of SAS 9.1.3 and JMP 5 to perform the analyses. Species with no fruit in the diet were excluded from the analyses.

Obviously, other complementary processes might be influencing the interaction patterns but are not examined here. Likely candidates could be geographic variation and scale-
dependence in the patterns of foraging (Telleria and Carbonell 1999, García and Ortiz-Pulido 2004), group feeding behavior, and heterospecific attraction among birds (Mönkkönen and Forsman 2002).

4

Testing for the independence of the hypotheses

6The hypotheses examined (abundance, switching behavior and species trait) are likely to be not independent. Indeed, life-story and morphological traits are known to affect both bird abundance and resource choice behavior (Böhning-Gaese and Oberrath 1999, 2001, Stang et al. 2006). To assess if morphological traits were effectively associated with bird abundance and interspecific differences in switching behavior (Fig. 1), we applied two different approaches. First, we modelled the percentage of fruits in the diet (%Rm) and abundance (Nm) as a function of 9 morphological traits (body mass, wing length, tail length, tarsus length, culmen length, culmen2, wide, height, gape width).

Specifically, traits were measured in 2028 birds captured in the mist-nets during along the whole study period. These models allowed us to evaluate if abundance variation and switching behavior were associated with interspecific differences in these morphological traits.

Secondly, we conducted a path analysis to assess the existence of significant direct and indirect effects of morphological traits on the percentage of fruits in the diet (%Rm), bird abundance (Nm) and bird interaction properties (km, ISm, Am) (Fig. 1). Phylogenetic contrasts were applied to estimate the influence of phylogenetic conservatism in the path coefficients (Felsenstein 1985, Midford et al. 2002, Martins 2004).

Testing for phylogenetic conservatism in the variables used
The coupled effect of population abundance variation, switching adaptive behavior and morphological traits might determine to some extent bird interaction patterns (Jordano 1987, Jordano et al. 2003, Stang et al. 2006, Vázquez et al. 2007). Interestingly enough, abundance, behavioral and morphological variables are expected to differ in the degree of phylogenetic signal showed. For instance, local bird abundances have been found to exhibit low or no significant phylogenetic signal (Cofre et al. 2007), and behavioral traits usually exhibit less phylogenetic signal than morphological traits (Wcislo 1989, Blomberg et al. 2003). Thus network properties might rely on a set of variables or specific traits that evolve at different rates and strongly differ in their phylogenetic conservatism (Böhning-Gaese and Oberrath 1999, Blomberg et al. 2003, Cattin et al. 2004, Cofre et al. 2007). Overall, we point that the phylogenetic signal observed in network properties should be quite variable depending on the relative importance of abundance, behavioral and morphological traits implied (Fig. 1, table 1). Therefore, phylogenetic signal in networks should be expected to reach intermediate $K$ values between those observed for abundance (low or non significant) and morphological traits (high).

To assess the degree of phylogenetic conservatism in bird consumer interaction properties ($k_m$, $IS_m$, $A_m$) we applied a randomization test for phylogenetic signal to degree variables under study (degree, interaction strength and asymmetry) (Blomberg et al. 2003). The means of the values in $k_m$, $IS_m$, $A_m$ for all the temporal sequence were used for each species. We used the MatLab program PHYSIG.m to calculate the statistic $K$ (Blomberg et al. 2003). A $K$ less than one implies that species resemble each other less than expected under Brownian motion evolution along the candidate tree. A $K$ greater than one implies that close relatives are more similar than expected under Brownian
motion evolution, and thus indicates strong phylogenetic conservatism (Blomberg et al. 2003). K values obtained for the dependent variables studied ($k_m$, $IS_m$, $A_m$) were compared to those observed for bird abundance ($N_m$), switching behavior ($%R_1$) and nine morphological traits (body size, wing length, tail length, culmen height, tarsus length, culmen length (to skull base), culmen length (exposed culmen, to feathers edge, gape width and intestine length). These comparisons allowed us to assess the relative phylogenetic conservatism of network traits relative to abundance, behavior and morphological traits.

RESULTS

Temporal trends in abundance, resource switching and network interactions

The two resource-channels (fruits and invertebrates) varied asynchronously with contrasting peaks. Fruits presented a maximum abundance in autumn, whereas the invertebrate abundance maximum was in spring, with a secondary peak in early autumn (Appendix B). Bird species abundance varied temporally, by the effect of autumn and spring passes, migration of wintering and breeding species, and variation in local resident abundance. Overall, bird abundances were greater in autumn and winter, matching the temporal pattern of fruit abundance (Appendix B).

The bulk of the species presented seasonal shifts in the proportion of fruits ($%R_1$) and invertebrates ($%R_2$) in the diet. Switching behavior was observed in 14 out of 24 species. We could differentiate three basic types of switching behavior: fast switchers, delayed switchers, and invertebrate specialists (Appendices B, C and D). Fast switchers were species that increased very rapidly the proportion of fruits in the diet with relatively small increases in the ratio of fruits/invertebrates in the environment. Delayed
switchers demanded a much greater asymmetry in the ratio of fruits/invertebrates to start switching to the fruit resource channel (Appendix C). When finally switched, they switched to a less extent, thus conserving a relatively high proportion of invertebrates in the diet. Finally, invertebrate specialists were those species that were insensible to the changes in the environmental ratio of fruits/invertebrates and maintained consistently an invertivorous diet coupled with the occasional ingestion of some fruits. 10 out of 20 species species behaved as fast switchers (Erithacus rubecula, Phoenicurus phoenicurus, Sylvia atricapilla, S. borin, S. cantillans, S. communis, S. hortensis, S. melanocephala, Turdus merula and T. philomelos), 4 species behaved as slow switchers (Luscinia megarhynchos, S. undata, Muscicapa striata, and Ficedula hypoleuca), and 5 as invertivore specialists (Hippolais polyglotta, Phylloscopus collybita, P. bonelli, P. trochilus, Regulus ignicapillus). Finally, for 6 species interaction data was to scarce to evaluate any temporal tendency in resource-channel use (Parus caeruleus, P. major, P. cristatus, Phoenicurus ochrurus, Saxicola torquata, and Turdus iliacus). When analyzing the variation of the percentage of fruits in the diet as a function of the relative resource supply (calculated as R1 / R1 + R2; or R1 / R2), significant fits were obtained applying both sigmoid non-linear fits and linear least square models. Responses of fast switchers (the most numerous group) consisted in an initial linear response that accounted for the bulk of the variation and a subsequent saturation phase (at 80-100% of fruits in the diet) in which the percentage of fruits was independent of the relative quantity of fruits in the environment (Appendix C and D).

The temporal structure of plant-bird interactions is showed in Appendix E. The total number of interactions was higher during the fruit peak periods (September-
November), matching the trends of fruit resource variation and bird abundance
2(Appendix B).

Hypothesis testing

4The three hypotheses examined were empirically supported (Table 2). However, a
different pattern of response was observed for species degree and interaction strength
6patterns. Indeed, abundance variables were the best predictors for interaction strength
8patterns, but explained a lesser amount of variation in qualitative network patterns
degree) (Table 2, Fig. 2). The interaction among resource and bird abundance was
strongly significant for degree and interaction strength, indicating that both consumer
and resource abundances contribute to increase the probability of interaction. The
models explained between 64-71% of the variation in network properties (Table 2).

Testing for hypotheses independence

Models explaining the variation of bird abundances ($N_m$) and the percentage of fruits in
the diet ($\%R_1$) using morphological traits performed much better in the case of the
percentage of frugivory in the diet than with abundance (Appendix F). Indeed,
morphological traits explained only 6% of the variation in bird abundances ($p<0.05$)
but explained 43% of the variation between species in the percentage of fruits in the diet
($p<0.0001$). Beak morphology traits (gape width and culmen length) were strongly
associated with the percentage of fruits in the diet (Appendix F). In line with these
results, path analyses indicated significant indirect effects of gape width on the number
and asymmetry of bird interactions ($k_m, A_m$) through their effect on switching behavior
($\%R_1$) (Fig. 2). Overall, our results suggest that foraging morphological traits are
directly associated with switching behavior, being gape width the character more
strongly associated with this behavior.
Testing for phylogenetic conservatism

The three bird interaction properties examined \((k_m, IS_m, A_m)\) showed a significant phylogenetic signal \((p<0.05; \text{Appendix G})\). In contrast, other network measures (centrality and minimum interaction strength) did not show a significant phylogenetic effect. As was expected, morphological traits were characterized with the stronger phylogenetical signals and abundance was not significantly associated with phylogeny. Interestingly enough, we found intermediate \(K\) values for all network properties examined. Indeed, network \(K\) values were weaker than \(K\) values for morphological traits, similar to \(K\) values observed for behavioral traits and greater than \(K\) values observed for species abundance (Fig. 3).

DISCUSSION

Our results suggest that ecological networks patterns are influenced by a diverse array of ecological processes that may operate at different temporal time-scales (Hastings 2004). The coupled effect of local abundance variation, phenotypic plastic responses (switching behavior) and species evolutionary adaptive processes might be shaping network patterns. We showed that both species abundance and switching behavior vary at an ecological time-scale and determine bird interaction patterns. Our results supported also the existence of adaptations in ecomorphological and foraging traits that shape the architecture of network patterns (Stang et al. 2006). However, the importance of morphological constraints differed in the case of species abundance and switching behavior hypotheses. Morphological traits were weakly related with interspecific differences in bird abundance but strongly related to the percentage of fruits in the diet and the ability of switch among invertebrates and fruits. Thus, switching behavior varies
seasonally at an ecological time-scale but it depends on foraging morphological traits 
2 (beak shape) that might evolve at much more slower temporal rates.

These findings are consistent with the existing literature that suggests an important role 
4 of bird beak shape in: setting the type and number of interactions established by birds 
(Jordano 1987a & b, Benkman 1999, Böhning-Gaese et al. 2003); promoting diet 
6 diversification and speciation processes (Abzhanov et al. 2004, Wu et al. 2004, 
Fitzpatrick et al. 2005, Phillimore et al. 2006, Grant and Grant 2006) and that highlight 
8 a possible role of beak shape in driving the evolution of bird behavior (Podos 2001).

Our results provide a preliminary framework to interpret consumer 
10 specialization and generalization patterns in bird-fleshy fruiting plants networks. First, 
three main types of specialization-generalization behaviors were found in birds: fast 
12 switchers (generalists), slow switchers (circumstantial generalists) and invertebrate 
specialists. Only fast switchers play a significant role shaping the architecture of plant- 
14 bird network in terms of degree and interaction strength because they become central in 
the network, i.e., concentrate a high number of interactions. Thus, bird species 
16 characterized with a low number of plant-bird interactions and weak interactions 
strengths were invertebrate eaters that only feed on fruits when they were extremely 
18 abundant (slow switchers) or invertebrate eaters that only occasionally rely in fruits 
(invertebrate specialists). Interestingly enough, these findings are consistent with the 
20 predictions of optimal foraging theory. Optimal foraging theory (Charvov 1976, 
Stephens and Krebs 1986, Berec et al. 2003) predicts that species with higher handling 
22 times (smaller gape widths) would only use to the less profitable prey (fruits) when the 
rate of encounter with the more profitable prey (insects) falls below a critical value (i.e. 
24 when fruits are very abundant and insects are scarce) (Berec et al. 2003, Berthold 1976).
Thus, switching in invertebrate species should be more prone to occur in the autumn 2fruiting peak, when fruits are abundant and invertebrates scarce. This is consistent with the trends described for slow switching species. We suggest that optimal foraging theory might be applied to understand and predict bird specialization-generalization network patterns (Beckerman et al. 2006, Eveleigh et al. 2007).

The patterns shown highlight that bird interaction strength patterns are strongly associated with abundance variation. Indeed, abundance was found to be the best predictor of interaction strength variation. The interaction of resource and consumer abundance was highly significant, suggesting that the coupled phenomena of high consumer and resource abundances increases the probability of interaction. Abundance was weakly related with the variation in morphological traits and no phylogenetic signal was observed in bird abundance. All these evidence imply that frugivorous birds interaction strength patterns might be much less constrained by evolutionary constraints. This assertion is strongly supported by recent findings of Rezende et al. (2007), who reviewed 36 plant-pollinator and 23 plant-frugivore mutualistic networks and found that the amount of phylogenetic signal for interaction strength was significantly lower than for estimates of species degree. Overall, we suggest that switching behavior and morphological constraints play a greater role in determining the type and number of interactions exerted by bird species whereas abundance variation plays a more active role in determining bird interaction strength patterns.

Our results also provide some new insights to the question of what determines the strength of phylogenetic signal in network patterns. We showed that bird interaction properties depend on species abundance, behavioral and morphological traits. All these types of properties strongly differ in their phylogenetic conservatism (Blomberg et al.
Therefore, the strength of phylogenetic signal observed in network patterns might be explained by the relative importance of abundance, behavioral and morphological variables and should usually take intermediate K values. Accordingly, we should expect that interaction strength patterns would be characterized by weaker phylogenetical signals because they are more influenced by abundance variation. Empirical evidence available supports this assertion (Rezende et al. 2007).

Overall, we point that network patterns are determined by short-term variation in abundance and seasonal variation in resource switching behavior. Nevertheless, acting at slower temporal rates of variation, the adaptive processes shaping foraging morphological traits seems to play also a very important role in defining global network architecture. Evolutionary adaptive processes acting on beak morphology and other traits may establish the ability of bird species to switch to fruits and the relative percentage of fruits in the diet for each species (Jordano 1987, Thompson 2005, Abzhanov et al. 2004, Wu et al. 2004) and thus largely shape degree patterns.

Therefore, adaptive processes acting on bird foraging traits possibly define the roles of bird generalist and specialist species and the whole network architecture (Stang et al. 2006). Within this network architecture, however, other variables such as local abundance may determine the short term responses that result in varying degrees of interaction strength among species.

ACKNOWLEDGMENTS

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4LITERATURE CITED


APPENDIX A

Variation of the number of interactions observed at different time-scale resolutions (Ecological Archives).

APPENDIX B

Temporal trends observed in the studied variables $R_1$, $R_2$, $\%R_1$, $N_m$ (Ecological Archives).

APPENDIX C

Switching behavior trends observed (Ecological Archives).

APPENDIX D

Switching behavior classification (Ecological Archives).

APPENDIX E

Temporal changes in network structure in 1981-83 (Ecological Archives).

APPENDIX F

Test effects for 9 morphological variables predicting the variation in the proportion of fruits in the diet (Ecological Archives).
APPENDIX G

Values and significance of the statistic K for the variables under study (Ecological Archives)
TABLE 1 Hypotheses and predictions tested. \( N_m \) bird abundance, \( R_1 \) fruit abundance, \( R_2 \) invertebrate abundance, \( \%R_1 \) percentage of fruits in the diet, \( \%R_2 \) percentage of invertebrates in the diet, \( Sp \) species identity.

<table>
<thead>
<tr>
<th>Hypotheses</th>
<th>Indep. Var.</th>
<th>Theory (T) and predictions (P)</th>
<th>Expected phylogenetic conservatism (K)</th>
</tr>
</thead>
<tbody>
<tr>
<td>( H_1 ) Consumer Abundance</td>
<td>( N_m )</td>
<td>T: Differences in local consumer and resource population abundance produce asymmetrical relationships in plant-animal interactions.</td>
<td>Non significant or low</td>
</tr>
<tr>
<td>Resource Abundance</td>
<td>( R_1 )</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>( R_2 )</td>
<td>P: Variation in bird population abundance, resource abundance, or their interaction will significantly predict bird interaction properties ( (k_m, IS_m \text{ and } A_m) ).</td>
<td></td>
</tr>
<tr>
<td>Consumer abundance &amp; Resource abundance</td>
<td>( N_m \times R_1 )</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>( N_m \times R_2 )</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( H_2 ) Switching behavior</td>
<td>( %R_1 )</td>
<td>T: Species seasonally switch the percentage of diet destined to different alternative resource-channels ( (R_1: \text{fruits;} R_2: \text{invertebrates}) ). Differences in the quantitative use of the channels shape asymmetrical relationships in plant-animal interactions.</td>
<td>Mid or high</td>
</tr>
<tr>
<td></td>
<td>( %R_2 )</td>
<td>P: The seasonal variation in the percentage of fruits in the diet will significantly predict bird interaction properties ( (k_m, IS_m \text{ and } A_m) ).</td>
<td></td>
</tr>
<tr>
<td>( H_3 ) Species trait</td>
<td>( Sp )</td>
<td>T: Bird species differ in life-story and morphological traits that are products of their unique evolutionary histories. Such differences between species determine specific interaction patterns and produce asymmetrical relationships.</td>
<td>High</td>
</tr>
<tr>
<td></td>
<td></td>
<td>P: Interespecific differences in bird morphological traits will be associated with differences between species in bird interaction properties ( (k_m, IS_m \text{ and } A_m) ) by direct or indirect causal paths (Fig. 1).</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>P: Bird species identity ( (Sp) ) will consistently predict differences in bird interaction properties ( (k_m, IS_m \text{ and } A_m) ).</td>
<td></td>
</tr>
</tbody>
</table>
TABLE 2 Effect tests for the independent variables. Dependent variables are the number of interactions or degree ($k_m$), interaction strength ($IS_m$) and asymmetry ($A_m$).

The total percentage of variance explained ($R^2_{adj}$, $p<0.0001$) is also provided for the three models ($k_m$, $IS_m$, $A_m$).

<table>
<thead>
<tr>
<th>Variables</th>
<th>$k_m$</th>
<th>$IS_m$</th>
<th>$A_m$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$R^2 = 0.69$</td>
<td>$R^2 = 0.62$</td>
<td>$R^2 = 0.76$</td>
</tr>
<tr>
<td>Test effect</td>
<td>SS</td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>$Sp$</td>
<td>128.13</td>
<td>3.76</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>$%R_1$</td>
<td>8.80</td>
<td>4.40</td>
<td>0.039</td>
</tr>
<tr>
<td>$N_m$</td>
<td>18.34</td>
<td>9.16</td>
<td>0.003</td>
</tr>
<tr>
<td>$R_1$</td>
<td>3.48</td>
<td>1.74</td>
<td>0.191</td>
</tr>
<tr>
<td>$R_2$</td>
<td>1.28</td>
<td>0.63</td>
<td>0.426</td>
</tr>
<tr>
<td>$N_m*R_1$</td>
<td>17.89</td>
<td>8.93</td>
<td>0.004</td>
</tr>
<tr>
<td>$N_m*R_2$</td>
<td>15.01</td>
<td>7.50</td>
<td>0.008</td>
</tr>
<tr>
<td>$SE$</td>
<td>7.31</td>
<td>3.65</td>
<td>0.060</td>
</tr>
</tbody>
</table>
FIG. 1. An illustrative scheme of the hypothesised causal relationships among abundance, behavioral and morphological traits, network properties and phylogenetic conservatism (measured by the statistic K).

FIG. 2. Path diagram of expected causal effects of gape width (gape), bird population density ($N_m$) and switching behavior ($%R_1$) on three network properties: (a) degree ($k_m$); (b) interaction strength ($IS_m$); (c) asymmetry ($A_m$)). Bold arrows indicate path coefficients that are significant at $p<0.05$. Values inside parenthesis are path coefficients corrected by phylogenetic contrasts.

FIG. 3. Comparison of the values of the statistic K in network properties (degree, interaction strength, asymmetry, maximum interaction strength, minimum interaction strength, centrality and core, white dots) and K values for abundance, behavioral and morphological traits ($N_m$, $%R_1$, gape width, body size, intestine length, culmen height, wing length, tail length, tarsus length and culmen length, black dots). A Tukey Kramer test is provided comparing the mean phylogenetic signal in network properties versus morphological traits ($p<0.0001$). The line across each diamond represents the group mean. The vertical span of each diamond represents the 95% confidence interval for each group.
Figure 1
Figure 2