FIG–FRUGIVORE INTERACTIONS FOLLOW A CONSTRAINED BROWNIAN MOTION MODEL OF EVOLUTION IN AN IMPORTANT BIRD AREA, WEST AFRICA

Kowiyou Yessoufou,[a] Michelle van der Bank,[a] Jacinta Abalaka,[b] and Barnabas H. Daru[a,c,]*

[a]*African Centre for DNA Barcoding, University of Johannesburg, P.O. Box 524 Auckland Park, 2006 Johannesburg, South Africa*
[b]*A.P. Leventis Ornithological Research Institute, Laminga, P.O. Box 13404 Jos, Nigeria*
[c]*Department of Zoology, University of Jos, P.M.B. 2084 Jos, Nigeria*

ABSTRACT

Understanding how ecosystems function is critical in order to shed light on processes that lead to species coexistence. *Ficus* species provide highly specialized niches for frugivores in tropical forests, but little is known about how *Ficus*–frugivore interactions evolve over time. Here we applied three approaches to investigate these interactions based on key parameters. We tested for a model of evolution that could explain interaction patterns, evaluated the phylogenetic signal, and assessed the evolutionary rate of niches generated by *Ficus* species. We showed that interactions are best explained by a Brownian motion model, indicating a random walk. However, the signal observed is lower than expected under this model, and at the same time the evolutionary rate provides evidence for niche conservatism. Such findings are incompatible with an unbounded Brownian process. We therefore propose that a random walk constrained by ecological forces towards a stabilizing selection could better explain fig–frugivore interactions in tropical forests.

Keywords: Bounded Brownian model, felsen, niche evolutionary rate, phylogenetic signal, Ornstein–Uhlenbeck stabilizing selection model, plant–animal interactions

1. INTRODUCTION

Understanding plant–animal interactions is key to disentangling ecosystem function in tropical forests (Price, 2002). Recent studies shed light on several plant–animal relationships, of which *Ficus*–frugivore interactions are one of the best well-known (Shanahan et al., 2001; Bleher et al., 2003). *Ficus* species provide "backup" resources for frugivores, especially during period of fruits scarcity (Poonswad et al., 1998; Shanahan et al., 2001; Bleher et al., 2003). *Ficus* is the most widely consumed plant genus, providing food resources for over 10% of the world's birds and 6% of the world's mammals (Sha-

nahan et al., 2001). As such, a loss of *Ficus* species in forests could drive a dramatic decline in frugivore populations (Lambert and Marshall, 1991; Kinnaird and O'brien, 2005). In turn, such decline could further lead to an eventual loss of plants that are dependent on frugivores for seed dispersal.

Therefore continued commitment is necessary to uncover how animals and plants interact, especially how the interactions evolve over time. This understanding is critical to predict the future of Earth's biodiversity especially in the face of global change (Cavender-Bares et al., 2009). Disentangling the dynamic of plant–animal interactions is also a powerful way of predicting the diversity pattern of each partner, especially when prior information is lacking (Githiru et al., 2002; Kissling et al., 2007). For instance, because of the high specialization of fig–wasps interactions, information on fig diversity is enough to predict wasp diversity in a given ecosystem, and vice-versa (Rønsted et al., 2005).

Previous works revealed that *Ficus* species may provide specific niches for frugivores (Lord, 2004; Kissling et al., 2007). However, it remains unclear how these niches have evolved over evolutionary history. Phylogenetic relatedness is currently acknowledged as promising in ecological investigations (Proches et al., 2008; Schaefer et al., 2011). Such an approach can reveal important traits that exhibit significant phylogenetic signals, which is critical in various ways. For instance, the presence of a signal may be useful in detecting shifts in correlation patterns on a phylogeny (Revell and Collar, 2009), and in uncovering the predominance of specific selective regimes (Hansen, 1997; Butler and King, 2004; Hansen et al., 2008). It also proves essential in addressing changes in evolutionary rates (O'Meara et al., 2006; Ackerly, 2009; Jombart et al., 2010).

Generally, most studies of phylogenetic signal assume the Brownian motion as null expectation, without prior investigation (Harvey and Pagel, 1991; Hansen, 1997; Freckleton and Harvey, 2006). Recent studies have revealed limits of this assumption (Freckleton and Harvey, 2006; Ackerly, 2009), raising the need of using the weight-of-evidence approach in comparative data analyses (Krasnov et al., 2011). Here we investigate the patterns of evolutionary history of fig–frugivore interactions in a West African forest, combining model fitting, tests of phylogenetic signal, and quantification of the rate of niche evolution. Our major expectation is that closely related *Ficus* species (host species) provide similar niches to frugivores. We therefore predict a significant phylogenetic signal and a low radiation rate of niches generated by host species. Our results provide instead evidence that fig–frugivore interactions evolve under a constrained Brownian-like fashion, suggesting a trend towards the Ornstein–Uhlenbeck stabilizing selection model. We therefore conclude that the assumption of a Brownian model should be made with caution.

2. MATERIALS AND METHODS

2.1. STUDY SITE

The study was conducted in the Amurum forest reserve (300 ha) on the Jos Plateau in north-central Nigeria, located at latitude 09°53′N, longitude 08°59′E, and at an alti-

tude of 1280 m (Vickery and Jones, 2002). Amurum forest is a key biodiversity hotspot in West Africa and also an Important Bird Area (IBA) with at least 278 bird species (Ezealor, 2001). Vegetation comprises gallery forests, savanna woodlands, and rocky outcrops, all of which differ greatly in floristic composition. Temperature ranges from 8° to 38 °C, whereas mean annual rainfall is 1411 mm (Payne, 1998).

2.2. MATERIALS

Two types of materials were used. Firstly, we used molecular data. From GenBank/ EBI we retrieved DNA sequences (ITS, ETS; *G3pdh* and *trnL-F*) for 65 African *Ficus* (SI Table S1) based on availability of DNA sequences. Secondly, seven *Ficus* species were monitored in the forest. These include *F. lutea* Vahl, *F. sycomorus* L., *F. abutilifolia* (Miq.) Miq., *F. thonningii* Blume, *F. ingens* (Miq.) Miq., *F. ovata* Vahl, and *F. platyphyl-la* Del. The sampling was limited to these seven species because we considered species that were fruiting during the period of study.

2.3. FRAMEWORK AND DATA COLLECTION

The principle guiding our data collection is that each *Ficus* species offers a unique niche to frugivores, and frugivore interactions with *Ficus* species reflect this uniqueness. Therefore, we expect that, for more closely related *Ficus* species, factors that capture this uniqueness should be similar, as a result of niche conservatism (Wiens et al., 2010).

We therefore observed and recorded major frugivore interactions with the seven *Ficus* tree species. These data were collected for almost three years during the peak fruiting period of *Ficus* species in the forest (June 2007–March 2009). Data collected include four parameters commonly used to assess the extent to which frugivores interact with *Ficus* trees (Coates-Estrada and Estrada, 1986): (i) the number of frugivore species (referred to as visitors) observed on each *Ficus* tree species, (ii) the length of the visit (i.e., the time visitors spent on the tree), (iii) the number of figs eaten, and (iv) the number of figs dropped from the tree (due to presence of frugivore on the tree). Information on all frugivores, visited *Ficus*, and all parameters are available in Supplementary Information (SI Table S2). Observations were made using binoculars and telescope from a concealed position on the ground from which as much of the focal plant canopy as possible was viewed, and from a distance that avoids disturbance of the foraging species. Sampling efforts were limited to only seven species, since we only considered species that were fruiting during the study period. All frugivores considered in this study are birds. Because we did not monitor *Ficus* species at night, nocturnal frugivores are excluded from the study. Taxonomic nomenclature of birds followed Borrow and Demey (2004).

2.4. DIVERGENCE TIME ESTIMATION

Divergence times were estimated using a Bayesian MCMC approach implemented in BEAST vs 1.4.8 (Drummond and Rambaut, 2007), which allows simultaneous estimation of the topology, substitution rates, and node ages (Drummond and Rambaut, 2007). The dataset was divided into four partitions according to the gene regions used in this study (ITS, ETS, *G3pdh* and *trnL-F*). We implemented the GTR + Γ + I model of

sequence evolution for each partition based on the Akaike Information Criterion (AIC) scores for substitution models evaluated using jModeltest vs 0.1.1 (Posada, 2008) with a gamma-distribution and four rate categories. A speciation model following a Yule process was selected as the tree prior, with an uncorrelated lognormal (UCLN) model for the rate variation among branches, and the mean rate was fixed at 1.0. A uniform prior with lower bounds of 40, 38, 35, and 37 Myrs was used as minimum age constraint for the *Galoglychia*, *Urostigma*, *Sycidium*, and *Sycomorus* clades, respectively, based on fossil information (Rønsted et al., 2005). These calibrating points were based on the old fossilized achenes assigned to *Ficus* (Collinson, 1989). Metropolis-coupled Monte Carlo Markov Chains were run for 20 million generations, sampling every 1000th generation. The adequacy of sampling was assessed using the Effective Sample Size (ESS) diagnostic with Tracer v.1.5 (Rambaut and Drummond, 2007). Of the 10,001 posterior trees we obtained, the first 1,000 were discarded as "burn-in" before combining all runs to build the maximum clade credibility tree (MCMC tree; SI Fig. S1) using TREEAN-NOTATOR vs. 1.4.8 (Drummond and Rambaut, 2007). All our comparative analyses were based on the MCMC tree assembled using BEAST.

2.5. DATA ANALYSIS

All parameter values were averaged and $\log_{10}$-transformed, but number of figs dropped was rather $\log_{10}(y + 1)$-transformed instead because this parameter has the value of 0 (zero) for some *Ficus* trees. Data analysis comprised three steps.

Firstly, we compared the fit of several models of evolution, each depicting a different selective regime on the data of fig–frugivore interactions. Six models were compared (Table 1), and the best model was selected using the bias-corrected version of the Akaike Information Criterion AICc (Sugiura, 1978; Hurvich and Tsai, 1989). AICc is more suitable than AIC in model selection for relatively small data sets (Bedrick and Tsai, 1994; Wong and Li, 1998). We then calculated the difference (Δ_i) between AICc of a given model i and that of the best-fit model. Such analysis is indicated for model ranking. Model ranking was interpreted using Burnham and Anderson's (2003) framework. They suggest that, if $\Delta_i \leq 2$ for a model, this indicates that the model is suitable for the data; if $4 \leq \Delta_i \leq 7$, the model is less adequate, and $\Delta_i > 10$ is indicative of the least fit model.

Secondly, we evaluated the degree of evolutionary conservatism in *Ficus*–frugivore interactions by conducting two phylogenetic signal tests: K-statistics test (Blomberg et al., 2003) implemented in PICANTE vs 1.2 (Kembel et al., 2010), and Abouheif's test (Abouheif, 1999) implemented in ADEPHYLO vs 1.1 (Jombart et al., 2010). The K statistic evaluates the signal in a trait against a Brownian motion (BM) model. If K is near 0, it means that there is no phylogenetic signal. If K = 1, the trait follows a Brownian character evolution, but K > 1 indicates that closely related species shared similar characters more than expected. The statistical significance of the K values was evaluated by randomly shuffling values of interaction parameters among *Ficus* species 1000 times and calculating 95% confidence intervals (CI). We also reconstructed a traitgram for each parameter to show the arrangement of *Ficus* species along a continuous trait axis and their connection to the underlying phylogeny. This helps provide better interpreta-

Table 1

Models comparison of trait evolution of fig–frugivore interactions. Values indicated are the bias-corrected version of the Akaike Information Criterion AICc. Values in bold are the lowest AICc scores for each parameter indicating the best fit of BM model. Values underlined indicate the second lowest AICc scores

Models	Indications of the models	Parameters of fig-frugivore interactions			
		Time spent	Number of figs eaten	Number of figs dropped	Number of visitor species
Lambda	When close relatives are less similar than expected, it stretches terminal branches relative to deep branches to fit	30.7737	24.0741	43.33476	41.39157
Delta	When Brownian rate parameter speeds up or slows down over time	31.0125	24.1304	44.39564	42.21997
Kappa	When change occurs with each speciation event, but is not proportional to branch length	32.1161	25.0862	46.94018	44.56616
Early Burst (EB)	When there is an initial burst of trait diversification but less later	32.1209	25.3119	47.21171	44.70513
Ornstein–Uhlenbeck (OU)	When taxa diverge less on long branches than expected, due to stabilizing force pulling towards center	<u>30.7736</u>	<u>24.073</u>	<u>43.33474</u>	<u>41.39157</u>
Brownian motion (BM)	Trait diverge indefinitely, random walk	**22.1209**	**15.3119**	**37.21171**	**34.70513**

tion of the K values (Ackerly, 2009).

Abouheif's test uses a nonparametric test to evaluate signal based on the Moran's index (Pavoine et al., 2008). This test first calculates a C-statistic, $C = 1-\eta/2$, with η as the ratio of the sum of squared differences between successive observations (i.e., the trait values of successive taxa on the phylogeny) to the sum of the squares for each observation. The mean of the observed C-values is then compared to the mean of randomized C-values estimated by randomly shuffling the tips of the phylogeny. We used 999 random permutations to obtain *p*-values.

Finally, we assessed the evolutionary rate of niche radiation using Ackerly's (2009) felsen metric. A felsen indicates an increase of one unit per million years in the variance among sister taxa of ln-transformed trait values. High felsen indicates adaptive radiation while low felsen suggests niche conservatism (Ackerly, 2009).

3. RESULTS

The phylogeny, reconstructed using multigene sequence data and BEAST techniques, is in agreement with the latest phylogenetic studies of Afrotropical *Ficus* (SI Fig. S1), and could therefore be reliably used in our analyses.

We found that the BM model exhibits the lowest AICc score, suggesting that param-

Table 2

Comparisons of AICc values of all models to the best model of fig-frugivore interactions. Values indicated are the differences between the AICc of each model and that of the best.

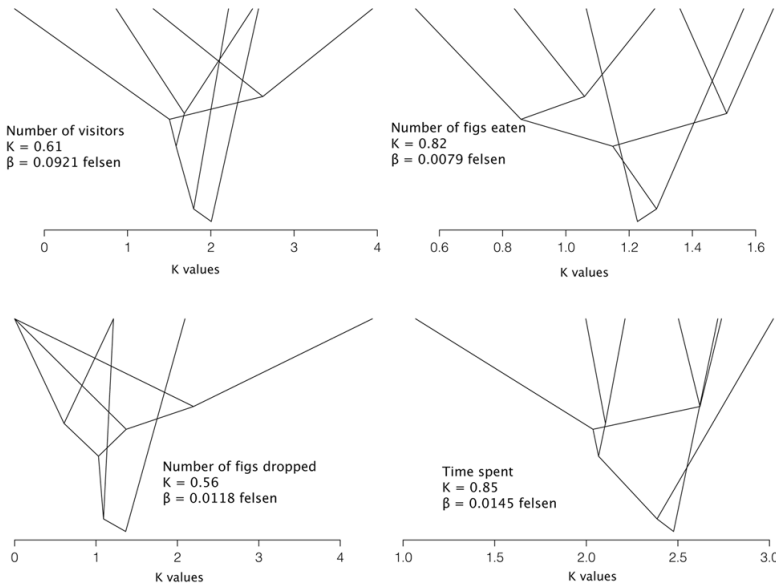| Models	Parameters of fig–frugivore interactions			
	Time spent	Number of figs eaten	Number of figs dropped	Number of visitor species
Lambda	8.6528	8.7622	6.12305	6.68644
Delta	8.8916	8.8185	7.18393	7.51484
Kappa	9.9952	9.7743	9.72847	9.86103
Early Burst (EB)	10	10	10	10
Ornstein-Uhlenbeck (OU)	8.6527	8.7611	6.12303	6.68644

Fig. 1. Phylogenetic traitgrams illustrating values of the K statistic for phylogenetic signal. Tips of the phylogenies (not shown) are arrayed along the *x* axis, showing the species trait values, and internal node positions correspond to ancestral states obtained by phylogenetic independent contrast approach. Node depths reflect phylogenetic branch lengths. Traitgrams with more branches crossing indicate greater convergent evolution. The parameter corresponding to each traitgram is indicated as well as K values and rate of evolution (in felsen).

eters of frugivore–*Ficus* interactions are best explained by this model of character evolution. We also found that the Ornstein–Uhlenbeck stabilizing (OU) selection model is the second best model (Table 1). Comparing all models to the BM model (the best model), we found $\Delta_i < 7$ for number of figs dropped and number of visitors, but $\Delta_i > 7$ for the rest of the parameters when considering OU model (Table 2). Also, we found $6.69 \leq \Delta_i \leq 10$ for the rest of the model. However, OU model has always a lower Δ_i value for all parameters compared to the rest of the models, except that it has similar Δ_i value with the model lambda for number of visitors (Table 2).

Consequently, we evaluated the quantity of signal in each parameter, and compared it to expectation under the BM model. The traitgrams (Fig. 1) and K distribution (Fig. 2) indicate that K values for all parameters are <1, indicating an absence of significant signal and a non-Brownian model: Number of visitors ($K_{observed} = 0.61$; $K_{random.mean} = 0.85$, 95% CI = 0.572 – 1.196), time spent ($K_{observed} = 0.85$; $K_{random.mean} = 0.86$, CI = 0.575 – 1.353), number of figs eaten ($K_{observed} = 0.82$; $K_{random.mean} = 0.85$, CI = 0.589–1.320), except that the phylogenetic signal in number of figs dropped is significantly lower than expected ($K_{observed} = 0.56$; $K_{random.mean} = 0.88$, CI = 0.585–1.495) (although it was not significantly different from the expectation when we applied the Bonferroni multiple comparisons correction; results not shown). In addition, the Abouheif's test also provides evidence
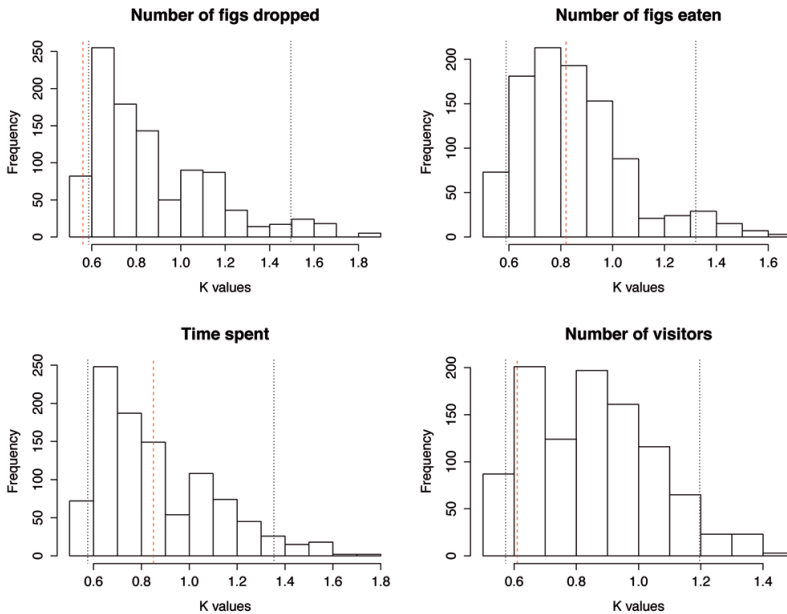

Fig. 2. Values of Blomberg's K (dashed red line) for parameters of fig-frugivore interactions. Histogram bars represent K-values based on 1000 randomizations. None of the parameters show significant signal. Dotted lines give the 95% confidence interval.

for absence of significant signal in all parameters characterising fig–frugivore interactions (Fig. 3).

Meanwhile, across all interaction parameters and all *Ficus* species, diversification rates of all parameters exhibited 15-fold range of variation, from 0.00799 to 0.11762 felsen (Fig. 1). Average rates increased in the order: number of figs eaten > length of visit > number of visitors > number of figs dropped (SI Fig. S2). We observed a strong negative relationship between Ackerly's niche diversification rate and Blomberg's K values (SI Fig. S3).

4. DISCUSSION

Model fitting reveals that the evolution of fig–frugivore interactions is best explained by a BM model. This model suggests that the evolution of parameters characterizing *Ficus*–frugivore interactions is gradual, with no specific trends over time, characteristics which agree with a random walk through evolutionary history. Further to this, the fit of
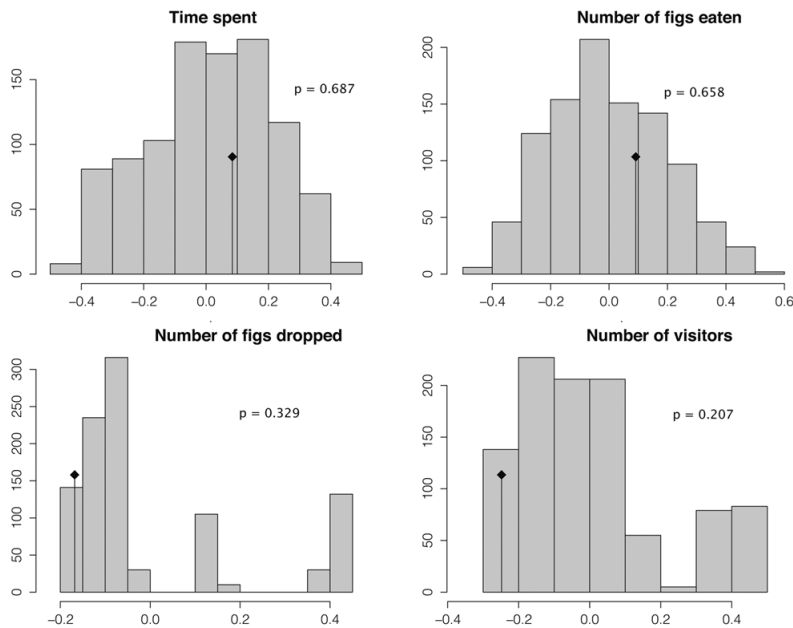

Fig. 3. Abouheif's test of phylogenetic signal in the fig–frugivore interactions. Histogram indicates the frequency distribution of the mean C-statistics calculated from the traits data along the tips of the phylogeny (tips). The vertical line holding a rectangular black dot indicates the position of the observed mean C-statistic relative to the null hypothesis sampling distribution of randomized mean C-statistics. None of the parameters exhibit signal; significance is also indicated as p values on the figure.

BM also suggests that the interaction parameters evolve under absence of ecological constrains, implying that fig–frugivore interactions are evolutionarily labile. The evolutionary lability suggests that adaptive radiation may be playing a critical role in explaining the fig–frugivore dynamic (Schluter, 2000).

To further test the validity of this model, we conducted two tests of phylogenetic signal using Blomberg's K and Abouheif's tests. The presence of signal or niche conservatism is indicated by K > 1 (Losos, 2008). For all parameters, we observed K < 1, giving support to the absence of significant signal (Blomberg et al., 2003). Also, Abouheif's test provides further evidence of a random walk through evolutionary time. The absence of signal we observed in fig–frugivore interactions contradicts our expectations, given the specialization in such interactions reported elsewhere (Kissling et al., 2007). What factors could underlie this? There are three main categories of frugivores based on frugivory regime: obligate frugivores primarily feeding on fruits; partial frugivores, which have, beside fruits, other major food items; and opportunistic frugivores, which occasionally eat fruits as supplementary foods (Kissling et al., 2007). The interaction parameters reported here were recorded irrespective of frugivory regimes. Although we did not explicitly consider fig–frugivore interactions based on frugivory regimes, we expect interactions between figs and obligate frugivores to exhibit significant signal. In contrast, partial and especially opportunistic frugivores are expected to show random interactions with *Ficus*, since figs are not their primary food resource. Because we combined partial, opportunistic, and obligate frugivores in our data analysis, this might blur a net departure from random interactions such that a BM model could fit the data.

Meanwhile, values of Ackerly's felsen metric (Ackerly, 2009) are very low, varying from 0.00799 to 0.11762 felsen. These low values are unexpected when signal is absent, contradicting a pattern of Brownian evolutionary fashion (Ackerly, 2009). In addition, we found a strong negative correlation between K and felsen values ($r^2 = 0.98$, SI Fig. S2), again giving strong support to a non-Brownian evolution (Ackerly, 2009). What could underlie such contrast? Metrics of phylogenetic signal are excellent measures of the overall evolutionary pattern of a trait, but can be driven by only a specific conserved clade on the phylogeny (Ackerly, 2009). As such, information related to diversification rate is not captured, causing limitation in the use of phylogenetic signal to detect conservatism (Ackerly, 2009). The non-Brownian model revealed by the K test and the niche evolutionary rate in fig–frugivore interactions could be explained by two major factors (Silvertown et al., 2006; Revell et al., 2008).

The first factor may be linked to adaptive evolution. There is a general tendency for specialization in animal-plant interactions (Price, 2002). For instance, *Treron waalia* (Bruce's green-pigeon) is reported to feed specifically on *Ficus platyphylla* only (Kissling et al., 2007). Each *Ficus* species may therefore provide a unique resource to which specific frugivores are adapted ("niche assembly theory"; Hutchinson, 1959). Such specialization would indicate a possible co-evolutionary history between *Ficus* species and frugivores. A co-evolutionary pattern suggests a strong adaptive radiation which can lead to the niche conservatism revealed by low rate of niche evolution.

The adaptive radiation in fig–frugivore interactions may have two main origins: fig

size and fig color. There is a great variation in fig size among the seven *Ficus* species we investigated. Previous works revealed specialization of frugivores relating to differently sized fruits (Githiru et al., 2002; Herrera, 2002; Lord, 2004). Fig color varies greatly to include red, brown, yellow, orange, green, and black figs. Some frugivores are reported to have specific color preferences (Gautier-Hion et al., 1985; Herrera, 2002; Voigt et al., 2004), an indication of possible adaptive evolution.

The second factor that can account for a non-Brownian model could be linked to a "bounded random walk" (Ackerly, 2009). The fact that model fitting reveals a best fit of the Brownian model gives support to the possibility of an "unbounded" random walk playing a critical role in fig–frugivore interactions. In the meantime, K values are lower than 1, and rates of niche evolution are low, indicating a bounded Brownian model, i.e., indicating that some forces (e.g., ecological) are limiting increasing fluctuations of the parameters measured (Freckleton and Harvey, 2006; Ackerly, 2009). Such constrains will eventually lead to a pattern similar to that of a stabilizing model (e.g., the Ornstein–Uhlenbeck model) that actually captures the evolution of a phenomenon that has been constrained around some equilibrium points. This view is supported by the fact that the the Ornstein–Uhlenbeck model is the second best model that fits the data (Table 2). It is also supported by the finding that the OU model has the lowest Δ_i value, i.e., the AICc value of OU model is the closest of all models tested to the AICc value of the best model. Given such ecological constrains, tests of phylogenetic signal, especially those assuming Brownian model without prior investigations, might be misleading (Freckleton and Harvey, 2006; Ackerly, 2009).

Crucially, our study shows not only that fig–frugivore interactions might follow a random walk through the evolutionary history of the genus *Ficus*, but that the evolution of the interactions is best explained by a bounded Brownian-like model, indicating a trend towards the Ornstein-Uhlenbeck model. Assumption of a Brownian model as reference model in comparative data analysis must therefore be done with caution. However, our analysis was based not only on a single study site (i.e., limited environmental conditions), but also on a limited sampling size. Such limitations make our finding not generalizable, although it clearly indicates that the BM model in comparative analysis should not be applied uncritically. We recommend that further analysis using larger sampling size from different environmental conditions is required to provide a more generalizable pattern of the evolution of *Ficus*–frugivore interactions. It is also possible that the reproductive strategies of *Ficus* spp. might be important in determining their interactions with frugivores. However, this is unlikely to affect our results since all seven *Ficus* species studied are monoecious, with only *Ficus platyphylla* being either mono- or dioecious.

REFERENCES

Abouheif, E. 1999. A method for testing the assumption of phylogenetic independence in comparative data. Evol. Ecol. Res. 1: 895–909.

Ackerly, D.D. 2009. Conservatism and diversification of plant functional traits: evolutionary rates versus phylogenetic signal. Proc. Nat. Acad. Sci. USA 106: 19699–19706.

Bedrick, E.J., Tsai, C.L. 1994. Model selection for multivariate regression in small samples. Biometrics 50: 226–231.

Bleher, B., Potgieter, C.J., Johnson, D.N., Bohning-Gaese, K. 2003. The importance of figs for frugivores in a South African coastal forest. J. Trop. Ecol. 19: 375–386.

Blomberg, S.P., Garland, T., Ives, A.R. 2003. Testing for phylogenetic signal in comparative data: behavioural traits are more labile. Evolution 57: 717–745.

Borrow, N., Demey, R. 2004. Birds of Western Africa. Christopher Helm, London.

Burnham, K.P., Anderson, D.R. 2003. Model selection and multimodel inference: a practical information-theoretic approach, 2nd ed. Springer-Verlag, New York.

Butler, M.A., King, A.A. 2004. Phylogenetic comparative analysis: a modelling approach for adaptive evolution. Am. Nat. 164: 683–695.

Cavender-Bares, J., Kozak, K.H., Fine, P.V.A., Kembel, S.W. 2009. The merging patterns of community ecology and phylogenetic biology. Ecol. Lett. 12: 693–715.

Coates-Estrada, R., Estrada, A. 1986. Fruiting and frugivores at a strangling fig in the tropical rain forest of Los Tuxtlas, Mexico. J. Trop. Ecol. 2: 349–357.

Collinson, M.E. 1989. The fossil history of the Moraceae, Urticaceae (including Cecropiaceae), and Cannabaceae. In: Crane, P.R., Blackmore, S., eds. Evolution, systematics, and fossil history of the Hamemelidae. Clarendon, Oxford, pp. 319–339.

Drummond, A.J., Rambaut, A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. BMC Evol. Biol. 7: 214.

Ezealor, A.U. 2001. Nigeria. In: Fishpool, L.D.C., Evans, M.I., eds. Important Bird Areas in Africa and associated islands: priority sites for conservation. Pisces Publications and BirdLife International (BirdLife Conservation Series No. 11), Newbury and Cambridge, UK.

Freckleton, R.P., Harvey, P.H. 2006. Detecting non-Brownian trait evolution in adaptive radiations. PLoS Biol. 4: e373.

Gautier-Hion, A., Duplantier, J.-M., Quris, R., Feer, F., Sourd, C., Decoux, J.-P., Dubost, G., Emmons, L., Erard, C., Hecketsweiler, P., Moungazi, A., Roussilhon, C., Thiollay, J.-M. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. Oecologia 65: 324–337.

Githiru, M., Lens, L., Bennur, L. A., Ogol, C.P.K.O. 2002. Effects of site and fruit size on the composition of avian frugivore assemblages in a fragmented Afrotropical forest. Oikos 96: 320–330.

Hansen, T.F. 1997. Stabilizing selection and the comparative analysis of adaptation. Evolution 51: 1341–1351.

Hansen, T.F., Pienaar, J., Orzack, S.H. 2008. A comparative method for studying adaptation to a randomly evolving environment. Evolution 62: 1965–1977.

Harvey, P.H., Pagel, M. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford, UK.

Herrera, C.M. 2002. Seed dispersal by vertebrates. In: Herrera, C. M., Pellmyr, O., eds. Plant–animal interactions—an evolutionary approach. Blackwell, Oxford, UK.

Hurvich, C.M., Tsai, C.L. 1989. Regression and time series model selection in small samples. Biometrika 76: 297–307.

Hutchinson, G.E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? Am. Nat. 93: 145–159.

Jombart, T., Balloux, F., Dray, S. 2010. *adephylo*: new tools for investigating the phylogenetic signal in biological traits. Bioinformatics 26: 1907–1909.

Kembel, S.W., Cowan, P.D., Helmus, M.R., Cornwell, W.K., Morlon, H., Ackerly, D., Blomberg, S.P., Webb, C.O. 2010. Picante: R tools for integrating phylogenies and ecology. Bioinformatics 26: 1463–1464.

Kinnaird, M.F., O'Brien, T.G. 2005. Fast foods of the forest: the influence of figs on primates and hornbills across Wallace's Line. In: Dew, D.L., Boubli, J.P., eds. Tropical fruits and frugivores: the search for strong interactors. Springer, Netherlands.

Kissling, W.D., Rahbek, C., Böhning-Gaese, K. 2007. Food plant diversity as broad-scale determinant of avian frugivore richness. Proc. R. Soc. Lond. B 274: 799–808.

Krasnov, B.R., Poulin, R., Mouillot, D. 2011. Scale-dependence of phylogenetic signal in ecological traits of ectoparasites. Ecography 34: 114–122.

Lambert, F.R., Marshall, A.G. 1991. Keystone characteristics of bird-dispersed *Ficus* in a Malaysian lowland rainforest. J. Ecol. 79: 793–809.

Lord, J.M. 2004. Frugivore gape size and the evolution of fruit size and shape in southern hemisphere floras. Austral. Ecol. 29: 430–436.

Losos, J.B. 2008. Phylogenetic niche conservatism, phylogenetic signal, and the relationships between phylogenetic relatedness and ecological similarity among species. Ecol. Lett. 11: 995–1003.

O'Meara, B.C., Ane, C., Sanderson, M.J., Wainwright P.C. 2006. Testing for different rates of continuous trait evolution using likelihood. Evolution 60: 922–933.

Pavoine, S., Ollier, S., Pontier, D., Chessel, D. 2008. Testing for phylogenetic signal in life history variable: Abouheif's test revisited. Theor. Pop. Biol. 73: 79–91.

Payne, R.B. 1998. A new species of firefinch *Lagonosticta* from northern Nigeria and its association with the Jos Plateau indigobird *Vidua maryae*. Ibis 140: 368–381.

Poonswad, P., Chuailua, P., Plongmai, K., Nakkuntod, S. 1998. Phenology of some *Ficus* species and utilisation of *Ficus* sources in Khao Yai National Park, Thailand. In: Poonswad, P., ed. The Asian hornbills. Ecology and conservation, Biodiversity Research and Training Program, National Center for Genetic Engineering and Biotechnology Bangkok, Thailand, pp. 227–252.

Posada, D. 2008. jModelTest: phylogenetic model averaging. Mol. Biol. Evol. 25: 1253–1256.

Price, P.W. 2002. Species interactions and the evolution of biodiversity. In: Herrera, C.M., Pellmyr, O., eds. Plant–animal interactions—an evolutionary approach. Blackwell, Oxford, UK.

Proches, S., Wilson, J.R.U., Richardson, D.M., Rejmanek, M. 2008. Searching for phylogenetic pattern in biological invasions. Global Ecol. Biogeogr. 17: 5–10.

Rambaut, A., Drummond, A.J. 2007. Tracer. [WWW document]. URL http://beast.bio.ed.ac.uk/Tracer.

Revell, L.J., Collar, D.C. 2009. Phylogenetic analysis of the evolutionary correlation using likelihood. Evolution 63: 1090–1100.

Revell, L.J., Harmon, L.J., Collar, D.C. 2008. Phylogenetic signal, evolutionary process, and rate.

Syst. Biol. 57: 591–601.

Rønsted, N., Weiblen, G.D., Cook, J.M., Salamin, N., Machado, C.A., Savolainen, V. 2005. 60 million years of co-divergence in the fig–wasp symbiosis. Proc. R. Soc. Lond. B 272: 2593–2599.

Schaefer, H., Hardy, O.J., Silva, L., Barraclough, T.G., Savolainen, V. 2011. Testing Darwin's naturalization hypothesis in the Azores. Ecol. Lett. 14: 389–396.

Schluter, D. 2000. The ecology of adaptive radiation. Oxford University Press, Oxford, UK.

Shanahan, M., So, S., Compton, S.G., Corlett, R. 2001. Fig-eating by vertebrate frugivores: a global review. Biol. Rev. 76: 529–572.

Silvertown, J., McConway, K., Gowing, D., Dodd, M., Fay, M.F., Joseph, J.A., Dolphin, K. 2006. Absence of phylogenetic signal in the niche structure of meadow plant communities. Proc. R. Soc. Lond. B 273: 39–44.

Sugiura, N. 1978. Further analysis of the data by Akaike's information criterion and the finite corrections. Comm. Stat. 7: 13–26.

Vickery, J., Jones, P.J. 2002. A new ornithological institute in Nigeria. Bull. Afr. Bird Club 9: 61–62.

Voigt, F.A., Bleher, B., Fietz, J., Ganzhorn, J.U., Schwab, D., Bohning-Gaese, K. 2004. A comparison of morphological and chemical fruit traits between two sites with different frugivore assemblages. Oecologia 141: 94–104.

Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Davies, T.J., Grytnes, J.A., Harrison, S.P., Hawkins, B.A., Holt, R.D., McCain, C.M., Stephens, P.R. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. Ecol. Lett. 13: 1310–1324.

Wong, C.S., Li, W.K. 1998. A note on the corrected Akaike information criterion for threshold autoregressive models. J. Time Ser. Analysis 19: 113–124.