# Variation in seed dispersal effectiveness: the redundancy of consequences in diversified tropical frugivore assemblages

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Plant–frugivore mutualistic assemblages frequently combine multiple, complementary or not (i.e. redundant), distinct effects of animal species. To a large extent, the outcomes of these interactions crucially depend on the delayed consequences of frugivore effectiveness on plant recruitment. We evaluated seed dispersal effectiveness for three plant species in a Brazilian Atlantic forest with a marked habitat heterogeneity defined by bamboo and non-bamboo patches. Twenty one, 23 and 14 bird species ate fruits of *Euterpe edulis, Sloanea guianensis* and *Virola bicuhyba* trees, respectively. For both *Euterpe* and *Virola*, visitation rate was the variable contributing for most variance across frugivore species in the quantitative component of effectiveness (QC, which depends on the combined effects of interaction frequency and per-interaction effect), while the number of fruits manipulated/visit had the greatest contribution in *Sloanea*. By combining observational data and experimental seed addition for *Euterpe* we tested for consistent functional patterns among species in the frugivore assemblage, extending beyond the fruit removal stage. Rankings of QC across *Euterpe* frugivores remained consistent with their relative contributions to fruit removal and, importantly, with their contributions to seedling establishment. Yet, QC of effectiveness across *Euterpe* frugivores were more homogeneous at the fruit removal and dispersal stages (contribution to seed dispersal) than for the delayed, dissemination and post-dispersal effects on recruitment. High complementarity of diversified frugivore assemblages may increase through added variance in their delayed effects related to qualitative components of effectiveness. Our results underscore the importance of assessing how dispersal services provided by mutualistic frugivores play complementary, rather than redundant, roles in seed dispersal within heterogeneous landscapes. Such ecological outcomes highlight the value of combining observational and experimental field designs to assess functional diversity patterns of tropical frugivore assemblages and delayed effects of their interactions with plants.

A central issue in the analysis of highly diversified mutualistic systems, such as those involving frugivorous animals and the plants they disperse, is to understand the functional consequences of interaction outcomes in terms of dispersal effectiveness. Both the quantitative (numerical aspects related to visitation and feeding rates) and qualitative (seed treatment, dissemination, post-dispersal prospects for establishment) components of effectiveness typically show ample variation across frugivore species within assemblages (Schupp et al. 2010). Given the multiplicative nature of both components, compensatory effects among them may occur so that a frequent but relatively inefficient visitor to a plant might result in similar overall effectiveness to a less common but reliable frugivore that gives adequate treatment to ingested fruits. Few previous studies have linked variation in effectiveness across frugivore species with the resulting pattern of seed dissemination in heterogeneous landscapes (Jordano and Schupp 2000, Calviño-Cancela 2002), i.e. how seeds actually reach microsites of variable prospects

for early plant recruitment and how variation in effectiveness translates into distinct contributions of each frugivore species to plant recruitment. When variation across species occurs within diversified mutualistic assemblages, the net effect of differences on effectiveness may render species as redundant or complementary in terms of their interaction outcomes (Carlo and Yang 2011). Recent work by Schleuning et al. (2015) establishes an explicit link to disperser effectiveness, through the consideration of quantitative and qualitative effects of seed dispersal within a functional framework. Schleuning et al. (2015) define seed disperser species as redundant or additive, depending on their contribution to the increase of seed dispersal function along a gradient of disperser richness. Additive are those species functionally singular, whereas redundant species are those leading to asymptotic trends in seed dispersal along the disperser richness gradient, as new added species do not contribute new, distinct ecological functions. When frugivores are complementary they provide complementary

(distinct) ecological functions, and thus a positive response in the seed dispersal function is expected when adding seed dispersers to the community.

A fundamental property of complex mutualistic assemblages seems to be a high functional redundancy, contributed by coevolutionary convergence and trait matching among component species (Bascompte and Jordano 2014). However, we still have a limited understanding of how variation in the quantity and quality components of seed dispersal effectiveness translates into functional equivalence of species in mutualistic assemblages (Zamora 2000). Low redundancy in frugivore assemblages may lead to increased and more thorough seed rain patterns, reaching a wider range of microhabitat types, and resulting in complementary dispersal services (McConkey and Brockelman 2011, Bueno et al. 2013). Yet the net effects of variation in disperser effectiveness on seed deposition patterns and the resulting seedling recruitment remain understudied for highly diversified frugivore assemblages. For example, variation and ranking in quantitative importance among frugivore species would not necessarily translate into a consistent rank in terms of the magnitude of effects on early stages of seedling establishment. We might expect markedly uncoupled effects of frugivores across dispersal stages (Jordano and Herrera 1995) whenever their dispersal services are complementary rather than redundant. Thus, Schleuning et al. (2015) suggested that a negative correlation between quantitative and qualitative aspects of disperser effectiveness actually leads to an increase in species complementarity among dispersers (and thus, additivity of their effects).

Here we studied the quantitative component (QC) of disperser effectiveness of frugivorous birds that feed on three plant species occurring syntopically at the Brazilian Atlantic forest but differing in fruit size: *Euterpe edulis* (Arecaceae), *Sloanea guianensis* (Elaeocarpaceae) and *Virola bicuhyba* (Myristicaceae). More specifically, we evaluated the relative influence of three subcomponents (rate of visits to fruiting plants, number of fruits manipulated per visit and dispersal probability) on QC and on disperser effectiveness.

By focusing on *Euterpe edulis*, a dominant subcanopy palm of the Atlantic forest, we combine QC with the abundances of bird species to further evaluate how the different bird species contribute to potential seed dispersal in two discrete habitats differing in vegetation structure: bamboo and non-bamboo patches (Rother et al. 2013a). We then ask how this translates in delayed consequences for early seedling recruitment in these two patch types.

Our ultimate goals are twofold: firstly, to understand which factors contribute to seed removal and how such factors vary among frugivore and plant species; second, to analyze the multiple factors influencing *E. edulis* seed removal to assess how complementary are the contributions of each disperser species to seed deposition and the resulting seedling establishment in different habitats. We use this approach to answer how complementary patterns in QC variation determine variation in effectiveness in highly diversified tropical disperser assemblages, with potential to influence forest dynamics through direct effects on recruitment.

## Methods

### Study site

The fieldwork was conducted at the lowlands of the Parque Estadual Carlos Botelho – PECB (24°00′–24°15′S, 47°45′–48°10′W), a reserve of over 37 000 ha of well-preserved Atlantic Rain Forest located in the State of São Paulo, SE Brazil (Supplementary material Appendix 1.1). Frugivory observations and bird censuses were made in a 10.24 ha permanent plot with approximately 3 ha dominated by *Guadua tagoara*, a large, semi-scandent woody native bamboo (culms may reach 10–15 m; Alves 2007) that forms patches of different shapes and sizes, ranging from 400 to 20 000 m². These patches are interspersed with areas lacking bamboos, forming a mosaic throughout the plot. Bamboo patches have a discontinuous canopy, with larger gaps between crowns, and thicker ground-litter than non-bamboo patches (Rother 2006). Although dominated by bamboos, some trees remained following the expansion of *G. tagoara* or managed to grow amidst it (Supplementary material Appendix 1.1).

### Frugivory

The three tree species studied are primarily bird-dispersed, whose fruits form a size-gradient (6 width × 10 mm length in *Sloanea guianensis*, 14.2 × 13.5 mm in *Euterpe edulis*, 15.0 × 21.4 mm in *Virola bicuhyba*; Supplementary material Appendix 1.2). From here on, these plant species are referred to only by their genera.

To quantify the visitation rates of potential seed dispersers, and the amount of seeds removed from plants, focal observations were made between 06:00 and 18:30 h for a minimum of 4 h on each tree at the permanent plot and in a trail crossing the forest. *Euterpe edulis* individuals were watched from April 2008 to August 2008, while *Sloanea* trees were watched on December 2007 and December 2008, and *Virola* trees from August 2008 to October 2008. The focal method comprised 276 h of observation on 46 individuals of *Euterpe*, and 77.3 h and 28 h of observation on five trees each for *Virola* and *Sloanea*, respectively. The sampling for the frugivory analysis was made during the fruiting period of each species in 2008 and 2009, with visitation data transformed to number of visits 10 h$^{-1}$. Fruit-eating birds were identified, counted and the number of fruits they removed (i.e. fruits ingested on the tree or carried in the beak when the bird left the tree), dropped or consumed only the pulp (leaving the seed attached to the tree) was recorded. From these records we calculated the number of fruits manipulated (i.e. ingested + dropped + fruits with pulp consumption only) per visit.

We used two complementary methods besides focal observations to increase sampling thoroughness and spatial extent. Spot censuses consisted of short (typically < 3 min) scans of tree canopies to record the activity of frugivorous birds while walking along trails crossing the forest. This method has the advantage of allowing the sampling of a large number of trees throughout the day (Howe and Vande Kerckhove 1981). Spot censuses yielded a total of 34 h of observation. In addition, non-systematic, haphazard recordings were made for all birds seen feeding on *Euterpe* fruits out of focal observations or spot census, totaling 1.45 h.

## Bird abundance

Birds were recorded using 10-min point counts with 30 m radius spaced at least 100 m from each other. This radius size allows accommodating a sampling point within the limits of the smallest bamboo patch sampled. Census points were randomly set in bamboo and non-bamboo habitats keeping the minimum distance between neighboring points. Each habitat received five points, which were sampled monthly, independently of the focal tree observations and spot censuses from May 2008 to April 2009 (except October 2008 due to bad weather conditions), between 06:00 to 09:00 h AM.

## Quantitative component

For each tree species, the number of visits 10 h$^{-1}$ of observations, the number of fruits manipulated/visit and the dispersal probability (removed fruits as a fraction of the total number of manipulated fruits) were used to calculate QC of seed dispersal. In order to graphically compare the QC profile among plant species, we constructed separate QC curves for *Euterpe*, *Sloanea* and *Virola* (Schupp et al. 2010, Jordano 2014). The QC values of each bird species were log-transformed and plotted in a bi-dimensional plane sorted from highest to lowest value (Magurran 1988). To evaluate the relative influence of each of the three subcomponents of the QC (number of visits 10 h$^{-1}$, fruits manipulated per visit and dispersal probability), we first estimated the relative dispersal contribution of each bird species as the proportion of the total QC contributed by each species (Vázquez et al. 2005). We then performed a multiple regression of each subcomponent on QC (lmg estimates, package relaimpo, Grömping 2006 in R package ver. 2.9.2 <www.r-project.org>). This procedure yields the fraction of variance in QC across frugivore species explained by each subcomponent and the bootstrapped confidence intervals for these relative contributions.

## Potential contribution to *Euterpe* dispersal (PCD)

We compared the potential contribution of each bird species to the dispersal of *Euterpe* seeds (seed rain) in bamboo and non-bamboo patches using the abundances of birds at each habitat, as revealed by the census data, and the species-specific estimates of QC. The contribution to seed dispersal (PCD) of each bird species to a given patch type was defined as PCD = QC × abundance, where abundance is given by the number of records of the bird species in a given patch type. To compare the rankings of PCD values between patches, we used a bi-dimensional plot, each dimension representing the PCD values in each patch type. Thus, PCD values indicate a weighted estimated contribution of each frugivore species to the total seed rain in each type of patch. A comparison of these ranks may help to better understand to what extent the frugivore assemblage is spatially complementary.

## Seed germination and potential contribution to *Euterpe* early seedling recruitment (PCR)

We combined the *Euterpe* PCD data with information on seed germination for the different frugivore species in order to obtain the potential contribution to recruitment (PCR), an estimate of the potential influence of variation in effectiveness on seedling establishment. PCR was calculated as PCR = PCD × GERM × TP, where GERM is the proportion of germinated seeds, and TP is the transition probability from emerging seedling to established seedling. We obtained the proportions of seed germination assigned to *Aburria jacutinga, Ramphastos vitellinus, Pteroglossus bailloni, R. toco, R. dicolorus* and *Turdus rufiventris* from data presented in Leite et al. (2012). With these data we estimated a linear regression including body mass (bm) and proportion of germinated seeds (pg) (pg = 0.533 − 0.000348 bm; r = 0.84, R$^2$ = 0.71, p = 0.03). Using this regression model equation we derived the proportion of seed germination that would be provided by the species not included in Leite et al. (2012), with the following exceptions: 1) for all *Turdus* species we used the original data presented in the paper for *T. rufiventris*. Given that the body mass of all *Turdus* species considered here do not differ greatly, we considered it was more realistic to use an actual data than the estimate obtained with the regression equation. 2) For *Pitangus sulphuratus*, whose body mass was under the minimum mass used in the regression, we also used the original data for *T. rufiventris*, since their body mass is also similar. 3) For all fruit thieves (i.e. birds that do not swallow the whole fruit but only pick pieces of the pulp) we used the value presented by Leite et al. (2012) for the germination of intact *Euterpe* fruits (i.e. fruits with pulp), which did not germinate at all.

TP values were estimated experimentally from a fully factorial seed addition experiment stratified in bamboo and non-bamboo patches and including a combination of replicated control plots and plots excluded from post-dispersal seed predators. Both seedling emergence and seedling survival up to the second year were recorded (Rother et al. 2013a). TP values indicate the probability that a *Euterpe* seedling emerging in a given patch type will result in an established seedling (> 2 years old). We used the specific TP values provided by Rother et al. (2013a) for bamboo and non-bamboo patches (see Supplementary material Appendix 1.3 for details).

## Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.3k8h7> (Rother et al. 2015).

## Results

### Quantitative component

The fruits of *Euterpe*, *Sloanea* and *Virola* were eaten by 21, 23 and 14 bird species, respectively (Supplementary material Appendix 1 Table A1). *Turdus flavipes* and *Trogon viridis* were the dominant species in relation to QC values, followed by *Turdus leucomelas*. Considering all bird species together for all three plant species studied, *T. flavipes* presented the greatest relative importance to the seed dispersal of *Euterpe* and *Virola* (Supplementary material Appendix 1 Fig. A1, Table A2). For both *Euterpe* and *Virola*, visitation rate

was the variable which contributed more strongly ($> 80\%$ and $> 60\%$, respectively) to variation in QC, while the number of fruits manipulated/visit had the greatest contribution to QC variation in *Sloanea* (Supplementary material Appendix 1 Fig. A2). The number of bird species with large QC was low, as observed in the last isoline of Fig. 1. These bird species, with a large number of fruits removed per visit and high visitation rate, contributed with high QC values (e.g. *Selenidera maculirostris* and *T. flavipes* for *Euterpe*; *Euphonia* sp., *E. pectoralis* and *Habia rubica* for *Sloanea*; *T. flavipes* and *T. viridis* for *Virola*; Fig. 1).

Visitation rate per bird species and fruits manipulated/visit are variables that significantly accounted for variation in the relative dispersal contribution, being positively related in the model. Dispersal probability also contributed to the quantitative component of *Sloanea* and *Virola* seed dispersal, but it did not so for *Euterpe* (Supplementary material Appendix 1 Table A3). Most frugivore species visiting *Euterpe* were highly reliable in terms of fruit handling, in contrast with *Sloanea* and *Virola* for which Thraupids, that frequently mash and drop fruits, were common visitors.

## Potential contribution to dispersal (PCD) and recruitment (PCR) in *Euterpe*

Ranking the bird species in relation to PCD and PCR resulted in a similar profile between bamboo and non-bamboo patches in PCD (test for differences in the coefficients of variation: $Z = 0.08$, $p = 0.93$) and PCR ($Z = 0.11$, $p = 0.91$). However, the PCR of bird species tended to be greater in bamboo than in non-bamboo patches. The among-species variation in PCD was lower (CV = 1.017 and 0.987, for bamboo and non-bamboo patches, respectively) than in PCR (CV = 1.337 and 1.498, respectively) (test for differences in the coefficients of variation PCD versus PCR, both stand types pooled: $Z = 3.23$, $p = 0.04$), indicating that birds effectiveness components are more homogeneous at the fruit removal and dispersal stages than when including also the delayed, dissemination and post-dispersal effects on recruitment. In addition, there was a decrease in the number of bird species potentially contributing to recruitment in relation to the bird species that potentially contributed to seed dispersal (Fig. 2). In order to test whether species in the assemblage performed consistently in terms of functional contributions
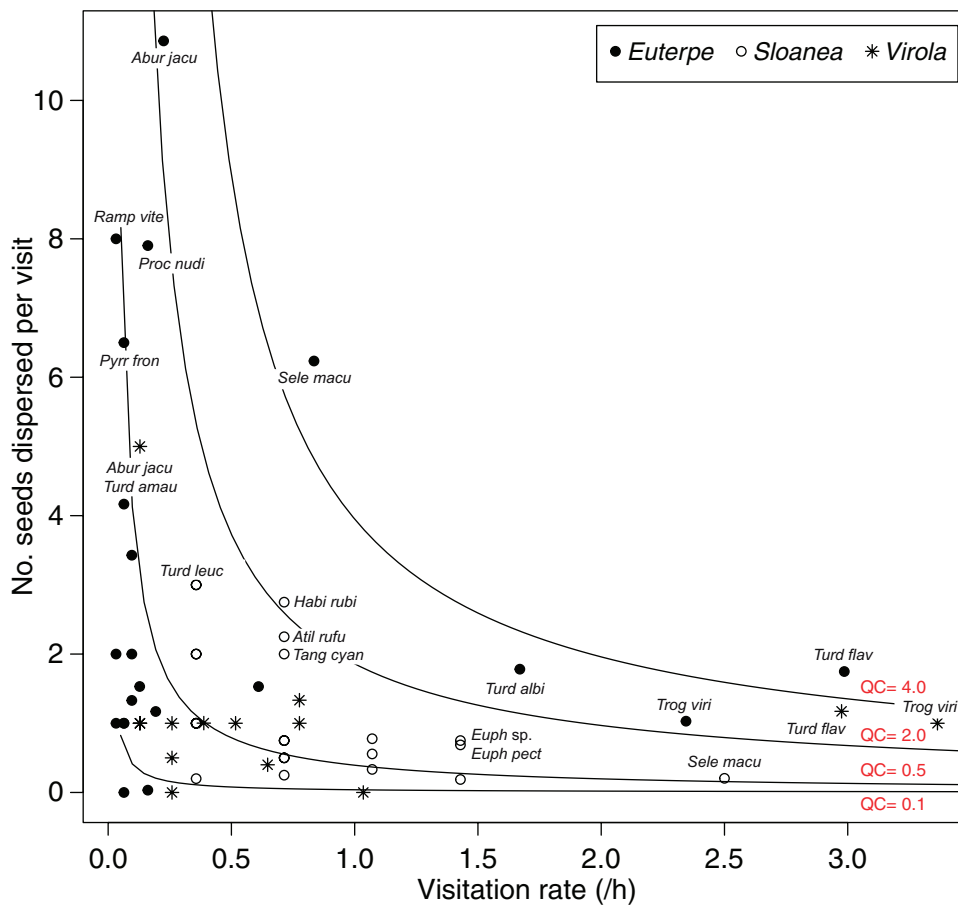


Figure 1. Variation in the quantitative component (QC) of dispersal effectiveness among frugivorous bird species eating fruits of *Euterpe edulis*, *Sloanea guianensis* and *Virola bicuhyba*. Symbols represent individual bird species and their relative position in the plane defined by the variables determining the QC: visitation rate and the product of number of fruits consumed per visit and probability of dispersal. Isolines depict areas with the same QC value for the quantitative component. Only the most prominent bird species are mentioned by name in the figure. Codes for bird species: Aburjacu (*Aburria jacutinga*), Attirufu (*Attila rufus*), Euphpect (*Euphonia pectoralis*), Euph sp. (*Euphonia* sp.), Habirubi (*Habia rubica*), Procnudi (*Procnias nudicollis*), Pyrrfron (*Pyrrura frontalis*), Rampvite (*Ramphastos vitellinus*), Selemacu (*Selenidera maculirostris*), Tangcyan (*Tangara cyanocephala*), Turdalbi (*Turdus albicollis*), Turdflav (*Turdus flavipes*).
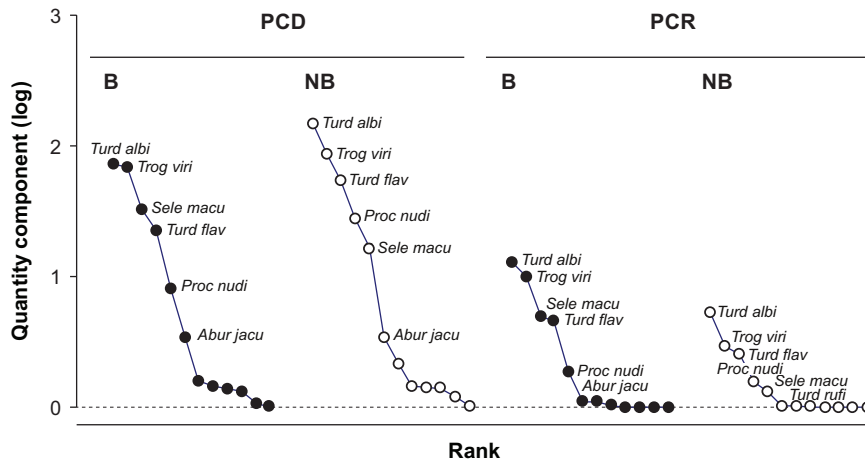
Figure 2. Bird species ranking according to their potential contribution to seed dispersal (PCD) and plant recruitment (PCR) for *Euterpe edulis* in bamboo (B) and non-bamboo (NB) stands. PCD and PCR values were transformed to log + 1.

across the stages of interaction (i.e. from QC - fruit removal, to PCD - seed dissemination and to PCR - lasting effects on recruitment), we compared the specific rank contributions across species at these three stages. Although there were significant correlations between the rank positions of each bird species across all the components (i.e. QC, PCD, PCR; all p < 0.01 in Kendall rank correlations), there were changes in the rank positions of bird species from QC to PCR, with some bird species (e.g. *Aburria*, *Ramphastos*, *Selenidera*) showing a sizeable reduction in rank importance (Supplementary material Appendix 1 Fig. A3).

## Discussion

### Assemblage diversity and variation in quantitative effectiveness components

The influence of three quantitative parameters of fruit removal upon QC varied among plant species, likely reflecting the variation in frugivore assemblages and its behavioral repertoire involved in fruit eating. The bird species richness recorded eating the three plant species followed the gradient of diaspore sizes, with the smallest seeds (*Sloanea*) being eaten by the largest assemblage, while *Virola*, with the largest seed, had the smallest assemblage of bird visitors. While *Euterpe* and *Virola* attracted large-sized birds (*A. jacutinga*, *P. nudicollis*, *S. maculirostris* and *Ramphastos* spp.), small birds predominated as visitors of *Sloanea*. These differences in assemblage composition determined different influences of foraging variables on the quantitative component of disperser effectiveness for the three plant species.

Variation in effectiveness across frugivore species in the more homogeneous assemblages of *Euterpe* and *Virola* was mainly driven by variation in visitation frequency (i.e. mainly along the x-axis of the effectiveness landscape in Fig. 1) rather than by differences in fruit handling (i.e. along the y-axis, Fig. 1). These assemblages were characteristically composed by large frugivores with low visitation rate but high foraging efficiency (i.e. *A. jacutinga* and *Ramphastos* spp.) or small thrush species with high visitation frequency but

reduced fruit handling efficiency. The most effective avian species in *Euterpe* and *Virola* assemblages were either large-bodied (e.g. toucans), largely dependent on fruit food (e.g. toucans, cotingids), consuming large quantities of fruits per visit, and efficiently swallowing most of the fruits handled or small thrushes with high visitation but limited fruit handling abilities. We expect variation in effectiveness among species in this type of assemblage to determine largely complementary seed dispersal services (McConkey and Brockelman 2011) mainly due to the fact of a reduced number of species being very effective but for different reasons (visitation or fruit handling) (also see Schleuning et al. 2015). Moreover, complementarity appeared to increase when considering the larger variation across *Euterpe* dispersers in effectiveness components related to recruitment of established seedlings. This is not unexpected and most likely generalizable to other assemblages combining large frugivorous birds showing similar fruit handling patterns in terms of a "per visit" efficiency (Levey 1987), and species with reduced handling effectiveness but high visitation (Jordano and Schupp 2000). Schleuning et al. (2015) have recently suggested that tradeoffs, i.e. negative correlations between quantitative and qualitative aspects of disperser effectiveness, may actually lead to an increase in complementarity (additive functional effects) among frugivores.

Comparative analyses of plant species with diversified frugivore assemblages (Vázquez et al. 2005) have shown that only a few frugivore species contribute most to overall dispersal, and many species have a very limited contribution. Our results indicate that reduced complementarity of dispersal services may arise in disharmonic assemblages where the main frugivore species show ample differences in visitation and fruit handling patterns (i.e. thrushes versus toucans or cotingids). Slight variation in visitation rate for any species in the *Euterpe* or *Virola* frugivore assemblage (e.g. *P. nudicollis*) may result in a similar effectiveness to the most effective *Turdus* species. Yet a much larger increase would be required for a less effective frugivore in *Sloanea* to replace an effective partner. The more ecomorphologically homogeneous *Sloanea* assemblage may show higher redundancy; no single species in this assemblage markedly diverged in visitation and most

variation in effectiveness was accounted for by differences in fruit handling. This resulted in *Sloanea* having a low QC range (0.08–1.07) compared to *Euterpe* (0.00–5.36) and *Virola* (0.00–3.49). Therefore, disharmonic frugivore assemblages may result in a high variance in effectiveness across frugivore species, mainly driven by variation in interaction frequency and/or fruit handling components. When species in the assemblage are relatively homogeneous in fruit handling, only slight variations in visitation frequency may drive dramatic changes in effectiveness.

Our results underscore the importance of assessing the complementarity of dispersal services provided by mutualistic frugivores (Calviño-Cancela 2002, Carlo and Yang 2011, McConkey and Brockelman 2011, Montaño-Centellas 2012, Bueno et al. 2013). We expect many highly diversified frugivore assemblages to be disharmonic in terms of effectiveness components of the specific species, resulting in very limited functional equivalence and thus high complementarity of the seed dispersal mutualistic outcomes. Even assemblages with limited diversification, dominated by species of the same genus may show very high complementarity when patterns of seed deposition are combined with QC estimates to assess dispersal services, especially in heterogeneous landscapes (Morales et al. 2013, Schleuning et al. 2015). Increased variance in PCR across *Euterpe* frugivores relative to PCD supports this point.

### Functional effects of variation in effectiveness: complementarity and lasting consequences for recruitment in complex landscapes

How variation in the quantitative component of seed dispersal translates into consequences for plant recruitment to render estimates of actual effectiveness of seed dispersal has seldom been addressed for mega-diversified frugivore assemblages, with most previous studies dealing with relatively simple systems (Herrera et al. 1994, Jordano and Schupp 2000, Hampe et al. 2008). When considering multiple species, an immediate consequence is a marked pattern of complementary effects, where distinct species contribute to distinct parts of the seed shadow and, consequently, to regeneration. We addressed this question using *Euterpe*, for which data on the quantitative component of seed dispersal could be combined with estimates of species-specific contributions to 2nd-year seedling establishment. Highly effective frugivore species should have consistent positive effects throughout all the stages along the regeneration cycle of the plant (Jordano and Herrera 1995). We should expect therefore that the ranked effects of each partner species remain significantly consistent when considering the fruit removal stage (QC), the seed dissemination stage (PCD) and the delayed effects on early seedling recruitment (PCR).

Structural complexities of forest landscapes (i.e. the presence of bamboo patches) determine a marked variation in the outcome of interactions with frugivores. For instance, frugivores did not completely avoid bamboo patches, and some species seemed to be more prone to use them than non-bamboo patches (Rother et al. 2013b). For *Euterpe*, birds that most contributed to seed dispersal tended to occur in both patches. However, bamboo patches facilitate germination success and seedling emergence (Rother et al.

2013a), what explains why PCR of bird species tended to be greater in bamboo than in non-bamboo patches. For later stages, however, bamboo patches may impose a demographic bottleneck for *Euterpe* population recruitment, and in high densities bamboos may totally limit the recruitment of this palm species (Rother 2006).

Ecological redundancy is a frequent term in the ecological literature (Lawton and Brown 1993), yet the role of species is not, in technical terms, redundant. Technically, two complex systems are redundant when they are made of exactly the same functional components and have exactly the same function. This is clearly not the case in most biological systems where similar roles are played by distinctly different species: these systems made of different components that perform the same functional role are defined as degenerate (Tononi et al. 1999). Degeneracy is the ability of elements that are structurally different to perform the same function or yield the same output (Edelman and Gally 2001). In our study, frugivorous birds had complementary, rather than redundant (i.e. degenerate), roles in seed dispersal. Diversified interactions with multiple disperser species can be adaptive in complex landscapes, where the complementary action of different frugivores can enhance establishment success by disseminating seeds along non-overlapping seed shadows. We conclude that the functional diversity of avian frugivores at the fruit removal stage consistently translates into effective establishment at the late seedling establishment stage. Yet the relative contribution to recruitment (PCR) of some species (e.g. cracids, toucans, cotingids) is shaped by landscape heterogeneity, as revealed by the effects of bamboo stands, and increases the complementarity of their effects. Successful regeneration and local population persistence of tree species in tropical forests are closely linked to the effective conservation of their frugivorous bird assemblages and the maintenance of diversified seed dispersal services.

### References

Alves, G. T. R. 2007. Aspectos da história de vida de *Guadua tagoara* (Nees) Kunth (Poaceae: Bambuseae) na Serra dos Órgãos, RJ. – Dissertação, Univ. Federal de São Carlos, São Carlos, Brazil.

Bascompte, J. and Jordano, P. 2014. Mutualistic networks. Monogr. Popul. Biol. Ser., No. 53. – Princeton Univ. Press.

Bueno, R. S. et al. 2013. Functional redundancy and complementarities of seed dispersal by the last neotropical mega frugivores. – PLoS ONE 8: e56252.

Calviño-Cancela, M. 2002. Spatial patterns of seed dispersal and seedling recruitment in *Corema album* (Empetraceae): the importance of unspecialized dispersers for regeneration. – J. Ecol. 90: 775–784.

Carlo, T. A. and Yang, S. 2011. Network models of frugivory and seed dispersal: challenges and opportunities. – Acta Oecol. 37: 619–624.

Edelman, G. M. and Gally, J. A. 2001. Degeneracy and complexity in biological systems. – Proc. Natl Acad. Sci. USA 98: 13763–13768.

Grömping, U. 2006. Relative importance for linear regression in R: the package relaimpo. – J. Stat. Software 17: 1–26.

Hampe, A. et al. 2008. Initial recruitment of vertebrate-dispersed woody plants: a spatially explicit analysis across years. – J. Ecol. 96: 668–678.

Herrera, C. M. et al. 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivory activity and seedling establishment. – Ecol. Monogr. 64: 315–344.

Howe, H. F. and Vande Kerckhove, G. A. 1981. Removal of wild nutmeg (*Virola surinamensis*) crops by birds. – Ecology 62: 1093–1106.

Jordano, P. 2014. Effectiveness landscapes in mutualisms: the analysis of quantity and quality components. – figshare. < http://dx.doi.org/10.6084/m9.figshare.971018 >.

Jordano, P. and Herrera, C. M. 1995. Shuffling the offspring: uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. – Écoscience 2: 230–237.

Jordano, P. and Schupp, E. W. 2000. Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. – Ecol. Monogr. 70: 591–615.

Lawton, J. H. and Brown, V. K. 1993. Redundancy in ecosystems. – In: Schulze, E. D. and Mooney, H. A. (eds), Biodiversity and ecosystem function. Springer, pp. 255–268.

Leite, A. B. et al. 2012. Differential seed germination of a keystone palm (*Euterpe edulis*) dispersed by avian frugivores. – J. Trop. Ecol. 28: 615–618.

Levey, D. J. 1987. Seed size and fruit-handling techniques of avian frugivores. – Am. Nat. 129: 471–485.

Magurran, A. E. 1988. Ecological diversity and its measurement. – Cambridge Univ. Press.

McConkey, K. R. and Brockelman, W. Y. 2011. Nonredundancy in the dispersal network of a generalist tropical forest tree. – Ecology 92: 1492–1502.

Montaño-Centellas, F. A. 2012. Effectiveness of mistletoe seed dispersal by tyrant flycatchers in a mixed Andean landscape. – Biotropica 45: 209–216.

Morales, J. M. et al. 2013. Frugivore behavioural details matter for seed dispersal: a multi-species model for Cantabrian thrushes and trees. – PLoS ONE 8: e65216.

Rother, D. C. 2006. Chuva de sementes e estabelecimento de plântulas em ambientes com bambus na Mata Atlântica. – Dissertação (Mestrado em Biologia Vegetal), Univ. Estadual Paulista, Rio Claro.

Rother, D. C. et al. 2013a. Demographic bottlenecks in tropical plant regeneration: a comparative analysis of causal influences. – Persp. Plant Ecol. Evol. Syst. 15: 86–96.

Rother, D. C. et al. 2013b. Avian assemblages in bamboo and non-bamboo habitats in a tropical rainforest. – Emu 113: 52–61.

Rother, D. C. et al. 2015. Data from: Variation in seed dispersal effectiveness: the redundancy of consequences in diversified tropical frugivore assemblages. – Dryad Digital Repository, < http://dx.doi.org/10.5061/dryad.3k8h7 >.

Schleuning, M. et al. 2015. Predicting ecosystem functions from biodiversity and mutualistic networks: an extension of trait - based concepts to plant–animal interactions. – Ecography 38: 380–392.

Schupp, E. et al. 2010. Seed dispersal effectiveness revisited: a conceptual review. – New Phytol. 188: 333–353.

Tononi, G. et al. 1999. Measures of degeneracy and redundancy in biological networks. – Proc. Natl Acad. Sci. USA 96: 3257–3262.

Vázquez, D. et al. 2005. Interaction frequency as a surrogate for the total effect of animal mutualists on plants. – Ecol. Lett. 8: 1088–1094.

Zamora, R. 2000. Functional equivalence in plant–animal interactions: ecological and evolutionary consequences. – Oikos 88: 442–447.