

Sampling completeness in seed dispersal networks: When enough is enough



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Abstract

Ecological networks are an increasingly popular tool to explore community assembly rules and frame practical conservation issues. However, most described networks vary largely in sampling effort, hampering the distinction of true biological patterns from artefacts caused by poor sampling. Identifying entire seeds in the droppings of mist-netted birds is generally considered a preferred sampling method for building unbiased, quantitative seed dispersal networks. We retrieved seeds from the droppings of 936 mist-netted birds captured during five days in seven sites in Portugal and estimated sampling completeness as the diversity of seed species, disperser species, and links detected with respect to those predicted by Chao 2 estimator. In one of those sites, sampling effort was extended to 25 days to evaluate the sensitivity of ten network structure descriptors to increasing sampling effort. After five sampling days we detected 93% of the seed species, 97% of the disperser species, and 79% of the links predicted by Chao 2, however sampling for 25 days resulted in the detection of more seeds, dispersers, and links than those estimated at day 5. Most network descriptors only began to stabilize around day 8, except for Connectance and Weighted Connectance that stabilized earlier. Similarly, only after 8 days most networks descriptors significantly departed from the confidence interval estimated by null models exclusively constrained by species abundances, thus reflecting independent ecological patterns. Nestedness was the only exception, as it never departed from the null models. We suggest that Chao 2 may slightly underestimate the real diversity and that in our case at least eight sampling days were needed to build a sound seed dispersal network as 67% of the seeds, 88% of the dispersers, and 71% of the links were detected. Our results have important implications for the interpretation of seed dispersal networks because under-sampled networks may produce biased descriptors that do not suitably characterize the focal communities.

Zusammenfassung

Ökologische Netzwerke werden immer beliebter als eine Methode, um die ‘assembly rules’ für Gemeinschaften zu untersuchen und praktische Naturschutzregeln zu entwerfen. Indessen variieren die meisten Netzwerke erheblich hinsichtlich des Probenahmeaufwandes, was die Unterscheidung zwischen tatsächlichen biologischen Mustern und Artefakten, die sich aus unzureichender Probenahme ergeben, erschwert. Die Bestimmung von Samen aus dem Kot von Vögeln aus Japannetzfängen gilt als eine bevorzugte Sammelmethode, um unverfälschte, quantitative Samenausbreitungsnetzwerke zu konstruieren. Wir separierten Samen aus dem Kot von 936 gefangenen Vögeln (sieben Fangplätze in Portugal; Fangzeitraum: i.d.R. fünf Tage)

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und bestimmten die Vollständigkeit der Erfassung als die Diversität der festgestellten Samenarten, Vogelarten und Verbindungen in Relation zum nach Chao 2 berechneten Schätzwert. An einem der Fangplätze wurde die Probenahme auf 25 Tage ausgedehnt und die Reaktion von zehn Netzwerkdeskriptoren auf die zunehmende Stichprobengröße ermittelt. Nach fünf Probetagen erhielten wir 93% der Samenarten, 97% der Vogelarten und 79% der vorhergesagten (Chao 2) Interaktionen. Der Fangzeitraum von 25 Tagen erbrachte indessen noch mehr Samenarten, Vogelarten und Interaktionen. Die meisten Netzwerkdeskriptoren begannen sich nach etwa acht Tagen zu stabilisieren. Nur Konnektanz und gewichtete Konnektanz stabilisierten sich früher. In gleicher Weise wichen die meisten Netzwerkdeskriptoren erst nach acht Tagen signifikant von den Vertrauensbereichen ab, die für Nullmodelle mit limitierten Artenabundanzen berechnet wurden, was unabhängige ökologische Muster anzeigt. Die ‘nestedness’ war die einzige Ausnahme und wich in keinem Fall von den Nullmodellen ab. Wir meinen, dass Chao 2 die tatsächliche Diversität leicht unterschätzen könnte und dass in unserem Fall mindestens acht Fangtage benötigt wurden, um ein vernünftiges Ausbreitungsnetzwerk zu konstruieren, da 67% der Samenarten, 88% der Vogelarten und 71% der Interaktionen (bezogen auf den 25-tägigen Fangzeitraum) entdeckt wurden. Unsere Ergebnisse haben wichtige Konsequenzen für die Interpretation von Samenausbreitungsnetzwerken, weil unzureichend beprobte Netzwerke verfälschte Deskriptoren hervorbringen können, die zu unbrauchbaren Beschreibungen der untersuchten Gemeinschaften führen.

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Introduction

The study of community-wide species interaction networks experienced a tremendous growth in recent years and proved a powerful tool to explore many processes in ecology, being particularly valuable in disentangling the relationships between the structure and function of nature’s “entangled bank” (Heleno et al. 2014; Olesen, Dupont, Hagen, Rasmussen, & Trøjelsgaard 2012; Darwin 1859). The use of ecological networks deepened our understanding of important conservation issues such as environmental degradation (e.g. Traveset et al. 2013; Tylianakis, Tscharntke, & Lewis 2007) and ecological restoration (e.g. Heleno, Lacerda, Ramos, & Memmott 2010).

Seed dispersal is one of the research areas where ecological networks attracted greatest interest (e.g. Heleno, Olesen, Nogales, Vargas, & Traveset 2013; Carlo & Yang 2011; Donatti et al. 2011; Mello et al. 2011). The dispersal of seeds away from the mother plant is a key process, allowing plants to avoid competition, find suitable conditions for germination, and expand their distribution range (Traveset, Heleno, & Nogales 2014). Due to their high mobility, frugivorous birds are the main seed dispersers in most ecosystems (Herrera 1984; Traveset et al. 2014). Avian seed dispersal data can be collected by: (1) recording fruit consumption by birds on focal plants (Olesen et al. 2011), (2) identifying entire seeds in the droppings of mist-netted birds (Heleno et al. 2013), and (3) identifying seeds in droppings collected in the field and identifying the disperser species with molecular techniques (González-Varo, Arroyo, & Jordano 2014).

Most network structure descriptors are affected by sampling effort to some degree (Blüthgen 2010; Blüthgen, Fründ, Vázquez, & Menzel 2008; Rivera-Hutinel, Bustamante, Marín, & Medel 2012), with qualitative indices being more sensitive to sample size than quantitative analogues (Banasek-Richter, Cattin, & Bersier 2004). Specifically, poor

sampling underestimates the real diversity of links, truncating estimated trophic breath and leading to a biased network structure (Blüthgen et al. 2008). On the other hand, as implementing such a holistic approach is inherently highly labour-intensive, it is important to know when further effort will not significantly increase the accuracy of the community description, thus avoiding unnecessary work load (Hegland, Dunne, Nielsen, & Memmott 2010). This effort is of utmost importance to allow meaningful cross-study comparisons (Heleno et al. 2014).

Richness estimators based on species and link accumulation curves are a powerful way to evaluate sampling completeness (Chacoff et al. 2012; Olito & Fox 2015; Rivera-Hutinel et al. 2012), where the number of missing species is estimated as those needed to reach a theoretical asymptote (Chacoff et al. 2012). Although some statistical methods have been suggested to ease the problem (e.g. Bartomeus 2013), there are no satisfactory solutions for poor sampling, and the sampling effort needed to build comprehensive seed dispersal networks from which theoretical and applied conclusions can be drawn has not yet been evaluated. In this study we aim to evaluate (1) the effect of sampling effort on the completeness of seed dispersal networks based on the analysis of droppings from mist-netted birds, and (2) the sampling effort needed to build high quality seed dispersal networks so that reliable network descriptors can be calculated.

Materials and methods

Study sites and data collection

On five consecutive days in the first half of September 2012, birds were captured in seven sites throughout Portugal ranging from agro-forestry systems to secondary native forest (Fig. 1) (see Costa et al. 2014). In each site/day,

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