Testing for stationary dynamics in the Barro Colorado Island forest

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A B S T R A C T

We analyse population dynamics in Barro Colorado Island (Panama) using census data of a 50 ha forest plot spanning 35 years, and address the question whether this community is in a stationary state. Individual species abundances show large fluctuations, but assessing stationariety requires discriminating random fluctuations from actual trends. This requires evaluating mean quantities as well as the structure (i.e. the correlations) of the fluctuations around this mean. We argue that a species average is the best surrogate for the theoretically required but unfeasible history average. We define the overlap, a species-averaged measure of composition similarity, which reveals that the BCI population dynamics is stationary but not static, displaying fluctuations with a characteristic time of around 15 years, two orders of magnitude less than previously estimated.

1. Introduction

Ecological systems (May and McLean, 2007) are neither static nor in thermodynamic equilibrium (Michaelian, 2005), but nevertheless the question may be asked whether they reach a steady state (Hening and Li, 2021). Assessing whether a given ecosystem or ecological community is actually in such a steady, or stationary, state is difficult, and ecological theories often *assume* a stationary state (Missa et al., 2016; Ma et al., 2021). However, this assessment is important for theoretical as well as practical reasons, including understanding the long-term dynamics of ecological communities, sustainable management, biodiversity conservation, and forest restoration (Thompson et al., 2009; Rodríguez et al., 2016; Cetin, 2016; Cetin, 2019; Zeren Cetin et al., 2020).

Understanding an ecosystem's dynamics necessarily involves accounting for spatial and temporal fluctuations (Wu and Loucks, 1995). To ascertain whether the system is stationary, one needs to establish not only whether average quantities are changing with time, but also if the structure of the fluctuations around the mean is evolving or not (Priestley, 1981). Thus noise here is both a nuisance and a source of information (Boettiger, 2018). It is a nuisance because species' abundances will change in time due to stochastic fluctuations even when the system is actually stationary in the statistical sense, and so it hampers our access to the evolution of average abundances (such as would be

described by deterministic differential equations, like Lotka-Volterra). But it is also a source of information, because the correlations of these fluctuations encode properties of the system's dynamics, and can reveal signs of system evolution even when mean values are not changing in time (Cugliandolo, 2004).

Thus, to establish whether or not an ecological community is stationary, one must attempt to estimate both averages and correlations while making allowance for the presence of random fluctuations. This means, at least, being able to compute averages over the statistical ensemble, or probability distribution, that describes these fluctuations. From the theoretical point of view, a *history average* is required, i.e. an average over different realizations of a stochastic process: the composition of the local community's population fluctuates because of death, birth and immigration (from a larger regional community) processes (Hubbell, 2001; Vanpeteghem et al., 2008). But of course we do not have experimental access to such an ensemble, as history has happened only once. We must look for a proxy of the ensemble, as one must do to interpret experimental results in terms of statistical mechanical theories. Two often employed proxies are time averages (Allen and Tildesley, 1987) and space averages (Cavagna et al., 2018). However, in the present case both alternatives beg the question at least to some extent. If one can somehow assert that a stationary state has been reached (as e.g. in numerical simulation), a time average can approximate an ensemble

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average, but this is clearly out of the question here since the time series is too short to employ standard statistical tests of stationariety (Krauth, 2006). Alternatively, one can regard very distant individuals as belonging to independent populations and perform a space average, which should then be equivalent to a statistical average over many realizations of the stochastic process that gives rise to particular populations. The difficulty is that taking measurements far apart from each other may introduce unwanted environmental variations (e.g. in soil or resources), so that it is hard to estimate how large an area one should use, especially for the less abundant species.

In thermodynamic systems one may usually avoid dealing with fluctuations by considering intensive properties (i.e. per unit volume, area, or mass), because fluctuations grow with size more slowly than the average (Landau and Lifshitz, 1959), i.e. Taylor's law (Eisler et al., 2008) holds with exponent 1/2. However, this approach is no good in the case of ecological communities, not only because sizes are typically smaller and fluctuations grow faster with size [the Taylor's law exponent is larger than 1/2,] (Eisler et al., 2008; Giometto et al., 2015), but also because it amounts to performing a space average, and thus implicitly assumes homogeneity, which is in general not justifiable as discussed above.

Here we address these questions for the case of the Barro Colorado Island (Panama) rain forest. Past studies of rain forests population dynamics (Volkov et al., 2009; Azaele et al., 2006; Kalyuzhny et al., 2015) have assumed stationary conditions, perhaps due to the short temporal span of available time series, which hampers the empirical observation of dynamics of relatively slowly evolving systems. However, data from the Barro Colorado Island 50 ha permanent tree plot in Panama spanning eight population censuses over 35 years is now available Condit et al. (2019), allowing for a study of short- and mid-term dynamics. We argue (Section 2.1) that an average over species can act as suitable proxy for the history average, enabling us to deal with fluctuations without assuming homogeneity in space or time. We define a quantity, the overlap, related to a time correlation function, that allows us to probe whether the forest can be considered in a stationary state (Section 3), while mitigating the problems associated with estimating second moments in broad distributions (Section 4). In our approach, we use the census data, taking into account the available historical information [at variance with the snapshot proposal of]Rodríguez et al. (2016) but avoid any assumption of stationariety or homogeneity. Unlike previous studies [e.g. Azaele et al., 2006; Rodríguez et al., 2016] the metric we employ does not rely on a specific theoretical model of ecosystem dynamics, nor on general assumptions about dynamic interaction networks (May, 1972) or on inference or estimation of interaction matrices (Volkov et al., 2009).

We find that the census data are consistent with an ecosystem in a stationary state, although far from static, and obtain a characteristic time for the composition fluctuations.

2. Methods

2.1. Observables

The crucial idea is that the choice of an ensemble proxy is based on known or postulated *invariances* of the system under study: if the system is stationary, all times are statistically equivalent; if the system is homogeneous, all positions are statistically equivalent. Then a time or space average, respectively, can replace a history average. Here we propose an ensemble proxy based on *species invariance:* we assume that all species are statistically equivalent, and that the variations in their abundances are due to random fluctuations. The idea of species equivalence is shared with the "neutral" theories of Caswell (1976) and Hubbell (2001), but here we are merely proposing an invariance, not formulating a new theory. Averaging over different species is then approximately equivalent to averaging a single species over many (experimentally inaccessible) realizations of the stochastic process. In

other words, we propose to use *species averages* as a proxy for history averages.

2.1.1. The overlap

The quantity we propose to compare the states of the forest at two different times is the *overlap*. Letting $n_\sigma(t)$ be the abundance of species σ at time t, the overlap is

$$Q\left(t_1, t_2\right) = \frac{1}{N_S} \sum_{\sigma=1}^{N_S} \frac{n_\sigma(t_1) n_\sigma(t_2)}{[\max(n_\sigma(t_1), n_\sigma(t_2))]^2}, \quad (1)$$

where N_S is the total number of species recorded in the full set of censuses. The overlap is a measure of the similarity of two configurations (Fig. 1b): identical configurations have overlap unity (in particular $Q(t, t) = 1$), while two configurations with very different composition have a low overlap (see A for a discussion of the asymptotic overlap). The denominator of each term serves to express both increase and decrease of abundance as a number less than 1.

The definition regards all trees of the same species as indistinguishable: two configurations with the same set of $\{n_\sigma(t)\}$ are considered identical even if the identities of all trees are different. A measure of similarity that flagged two configurations with identical abundances but different individuals as different is not desirable, because since individuals eventually die, no ecosystem could possibly be stationary in that sense. The definition of the overlap is thus consistent with a statistical interpretation of population data. A consequence of (1) is that if an individual dies in some position and another of the same species is born elsewhere, this change is not detected, i.e. the overlap is insensitive to spatial structure.

Although it is reasonable to dispense with individual identities, one may wonder about possible effects of spatial heterogeneities. We thus also explore a local version of the overlap, defined as

$$Q\left(t_1, t_2; \mathbf{r}\right) = \frac{1}{N_S} \sum_{\sigma=1}^{N_S} \frac{n_\sigma(t_1; \mathbf{r}) n_\sigma(t_2; \mathbf{r})}{[\max(n_\sigma(t_1; \mathbf{r}), n_\sigma(t_2; \mathbf{r}))]^2}, \quad (2)$$

where $\mathbf{r}$ indicates the position of a small quadrat within which the abundances are computed (we have used here quadrats of size $l^2 = 10$, m $\times$ 10,m). $Q(t_1, t_2; \mathbf{r})$ detects variations in species composition within quadrat $\mathbf{r}$. It is insensitive to changes outside the quadrat, but will decrease whenever a species' abundance changes in the quadrat, even if it is compensated by an opposite change elsewhere in the census plot.

2.1.2. Alternative measures of similarity

Below we compare the results from using the overlap to those obtained with other measures of similarity, namely the Jaccard index and the normalised time correlation function. The Jaccard index (Jaccard, 1902; Koch, 1957), often employed to compare ecological data is defined as

$$J\left(t_1, t_2\right) = \frac{\sum_\sigma \min\left[n_\sigma\left(t_1\right), n_\sigma\left(t_2\right)\right]}{\sum_\sigma \max\left[n_\sigma\left(t_1\right), n_\sigma\left(t_2\right)\right]}. \quad (3)$$

As the overlap, the Jaccard index is bounded, $0 \leqslant J(t_1, t_2) \leq 1$, and $J(t_1, t_1) = 1$. Another similarity measure sometimes employed, the Sørensen-Dice coefficient, is directly related to the Jaccard index by $S = 2J/(1 + J)$, which thus displays the same qualitative behaviour.

We also consider the normalised (or Pearson) time correlation, defined as

$$\rho\left(t_1, t_2\right) = \frac{C(t_1, t_2)}{\sqrt{\mathrm{Var}_{n(t_1)} \mathrm{Var}_{n(t_2)}}}, \quad (4)$$

where $C(t_1, t_2)$ is the species-averaged connected time correlation,
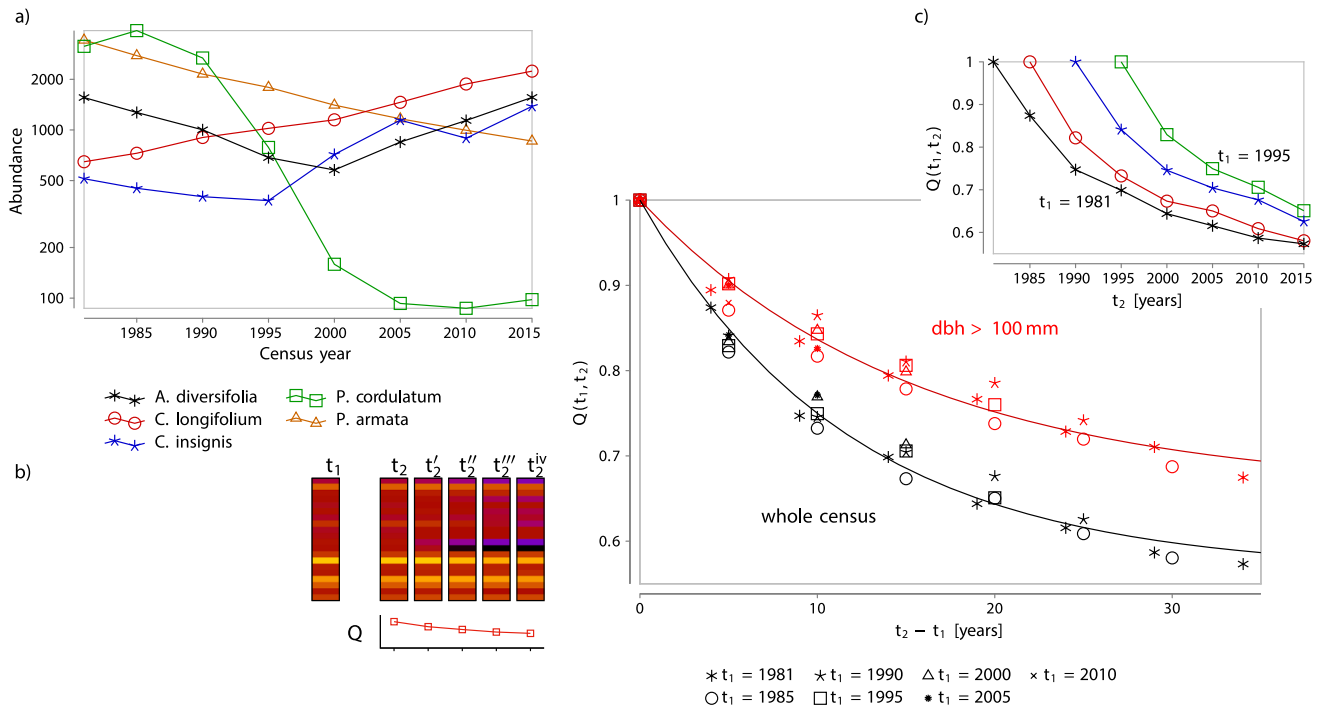
Fig. 1. Abundance fluctuations of the whole Barro Colorado Island forest are compatible with a stationary state despite strong fluctuations in individual species' abundances. **Panel a:** Abundances of individual tree species as recorded in the Barro Colorado Island censuses fluctuate considerably in time, seemingly contradicting the hypothesis of a stationary ecosystem. However, a system can be both stationary *and* fluctuating, and only appropriately averaged quantities can be used to establish whether it is actually stationary. **Panel b:** We define a quantity to compare the state of the forest at two times t_1 and t_2, based on an average over species, which we argue is the best surrogate for the theoretically required history average. The quantity is the *overlap* (1), graphically depicted here: each vertical bar represents the forest population, where each species is assigned to a small rectangle, color-coded with the respective abundance. The reference census (t_1) is successively compared species by species to the more recent ones; the overlap slowly decays from the value 1 corresponding to identical configurations. Note that the overlap includes data from all species, not just the examples chosen for panel a. **Panel c:** Overlap $Q(t_1,t_2)$ vs. t_2 using the first four censuses as reference (t_1). **Main panel:** Overlap plotted against the time *difference* $t_2 - t_1$: the decay has the same shape for all reference configurations, showing that the BCI forest is in a stationary state despite the considerable fluctuations in individual species abundance.

$$C\left(t_1,t_2\right) = \frac{1}{N_S}\sum_{\sigma=1}^{N_S}[n_\sigma(t_1) - \overline{n(t_1)}][n_\sigma(t_2) - \overline{n(t_2)}], \tag{5}$$

where $\overline{n(t)}$ is the species-averaged abundance,

$$n\left(t\right) = \frac{1}{N_S}\sum_{\sigma=1}^{N_S}n_\sigma\left(t\right), \tag{6}$$

and the variance is $\mathrm{Var}_{n(t)} = C(t,t)$.

2.2. Data

We used data from the Barro Colorado Island 50 ha permanent tree plot in Panama (Condit, 1998; Condit et al., 2012), which has been made publicly available (Condit et al., 2019). The data consists of eight population censuses, carried out in 1981 and every five years since 1985. Data collection for each census except the first took 10–11 months to complete (Condit et al., 2017), we ignore this interval and take each census as an instantaneous snapshot. The first census, started in March 1981, took two years to complete, however the bulk of individuals (95%) was censused before August 1982 (Condit et al., 2017), so we take 1981 as the first census' date.

The species, position and other information of individual trees with diameter at breast height larger than 10,mm is recorded in each census. For this study, we only need the individual's species (to compute the global overlap) and the positions (for the local overlap). A total of 328 different species were identified across the 8 censuses; all of these were used for the computation of the overlap (i.e. N_S in Eqs. (1) and following is equal to 328).

3. Results

Abundances of individual species show sizeable fluctuations (Condit et al., 2017). While the total population shows fluctuations of less than 5%, there are some species with very large population fluctuations: we have identified 55 species that show more than 20% abundance change between consecutive censuses (considering only species with more than 100 individuals, see Fig. 1a). Some of them display considerable growth (*Calophyllum longifolium, Cecropia insignis*), others a catastrophic decrease (*Piper cordulatum,* which drops from more that 3100 individuals to less than 100, or *Poulsenia armata*), and yet others exhibit large oscillations (like *Acalypha diversifolia,* which starts and ends the period with about 1500 individuals, but hits a low of 578 in census 5). In a few cases, the relative variation between consecutive censuses is close to 1 (e.g. *Cecropia insignis, Croton bilbergianus, Palicourea guianensis*, not shown).

To analyse these fluctuations we compare censuses using the overlap (1), which definition is depicted graphically in Fig. 1b. In Fig. 1c we plot the overlap between the first census and all the others, i.e. $Q(1981,t)$ for $t = 1981, 1985, 1990, \ldots, 2015$ We have done this for two sets: the whole census population and the population with diameter at breast height (dbh) larger than 100,mm (i.e. excluding saplings). Note that to compute the overlap we have used abundances for all the 328 recorded species, not just those shown as an example in Fig. 1a. In both cases we observe that the overlap decays monotonically from 1, indicating that the composition of the population is evolving, and that as time passes the state is less and less similar to the reference configuration. We observe that a simple exponential function,

$$Q(t_1, t_2) = (1 - Q_\infty)e^{-(t_2 - t_1)/\tau} + Q_\infty, \tag{7}$$

can adequately fit the decay of the overlap. Note that since $Q(t_1, t_1) = 1$, the asymptotic overlap and the amplitude of the decay are related, so that there are only two independent parameters, τ and Q_∞. The asymptotic overlap measures how different from the reference the system becomes for very long times. The measured values of Q and the fitted values of Q_∞ indicate significant changes in the species distribution over time, although Q_∞ is higher than the value expected for a completely different composition (see Appendix A). The time scale for the decay is given by the characteristic time τ, found to be around 12 years (15 y for dbh > 100 mm). Note however that slower processes could exist, undetectable with a time series of the length available, that could bring Q_∞ down to lower values. The set of larger trees (dbh > 100 mm) appears to be slightly more stable that the full set, with a larger asymptotic overlap and slightly larger relaxation time. This higher variability in the population of smaller trees has been already observed before (Condit et al., 2017).

The fact that the overlap decays indicates that the forest is not static but evolving. However, this does imply that the system is not stationary: a system can be statistically stationary, even while fluctuating, if any configuration can be considered as good a starting point to measure the dynamic evolution as any other (Priestley, 1981). In terms of the overlap, we want to know if the evolution (as measured by the decay of Q) is different if we take a different census as reference. This is what we do in Fig. 1 (main panel), where, to compare different origins, we have plotted in the abscissas the time *difference* with respect to the census used as reference. Remarkably, the decay with respect to the reference census is very similar in all cases. This finding means that the decay of the overlap is compatible with a dynamics where all the observed configurations (censuses) are statistically equivalent, i.e. a *stationary dynamics*.

Possible effects of spatial heterogeneity can be studied by considering the local version of the overlap (2). Fig. 2 show maps of the local overlap between the 1981 census and four later ones. It is seen that the local overlap is rather heterogeneous, with some spots showing rapid pronounced decrease. In other words, the decay of the global overlap does not happen through gradual global change, but through sudden spatially localized events.

To check whether spatial heterogeneity affects our analysis of a stationary state using the global overlap, we compute the local overlap averaged over the whole plot,

$$Q_{SA}\left(t_1, t_2\right) = \frac{1}{N_q} \sum_{\mathbf{r}} Q\left(t_1, t_2; \mathbf{r}\right), \tag{8}$$

where $N_q = 50 \cdot 10^4 \, \mathrm{m}^2/l^2$ is the number of quadrats and SA stands for space average. We show Q_{SA} in Fig. 3. As expected, the values attained by Q_{SA} are higher than those of $Q(t_1, t_2)$ due to the lower number of species per quadrat ($N(100, \mathrm{m}^2) \approx 23$ for dbh > 10 mm and ≈ 4 for dbh > 100 mm, see Appendix A).

However, just like the global overlap, Q_S decays exponentially in the time difference between censuses, and independently of the census taken as reference. A simple exponential (Eq. 7) also fits $Q_s(t_1, t_2)$ rather well, with slightly higher values of τ (Table 1). The characteristic time is again longer for the set of larger trees. The most important feature of the overlap decay, namely that it depends only on the time difference $t_2 - t_1$ holds also for the space-averaged local overlap, so that even taking into account the heterogeneities of the population changes, the result is compatible with a stationary dynamics.

4. Discussion

The overlap we have defined is inspired in the quantity of the same name used in spin glass theory (Mézard et al., 1987) to compare states. Other measures of similarity, like the Jaccard index or the Sørensen-Dice
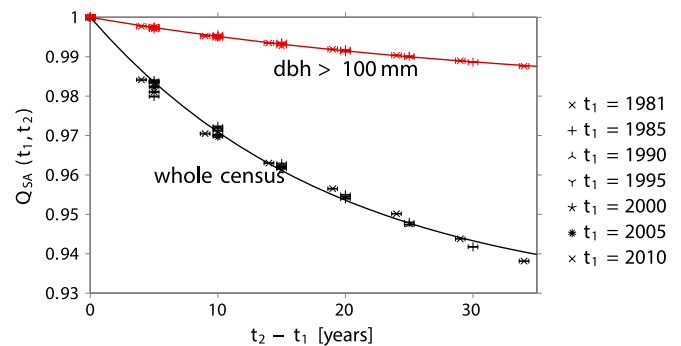
Fig. 3. Space-averaged local overlap, $Q_{SA}(t_1, t_2)$ vs. the time difference $t_2 - t_1$ for all pairs of censuses.
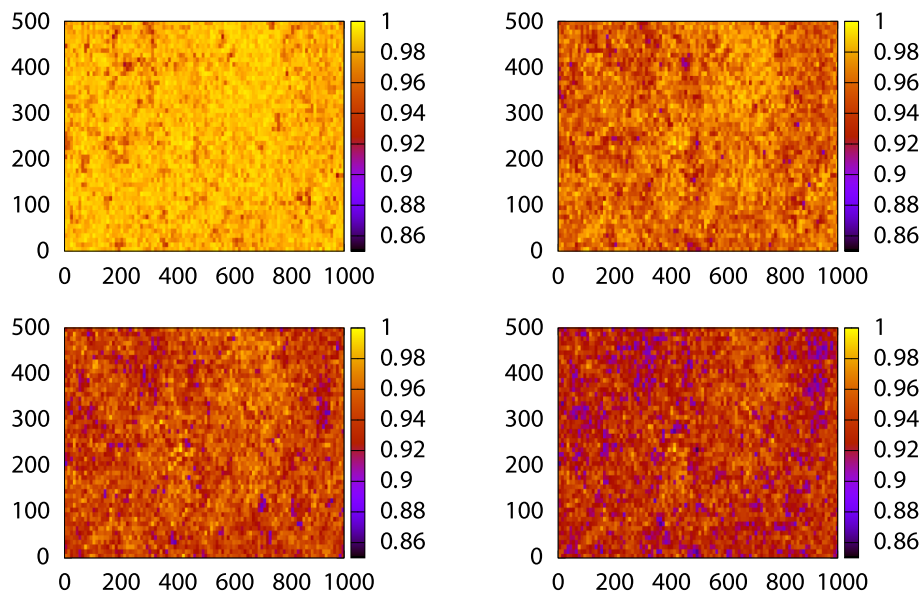
Fig. 2. Maps of local overlap, using quadrats of side $l = 10$, m. Colors indicate, as function of quadrat position, the value of the local overlap between the 1981 census and (from left to right and top to bottom) censuses of the years 1985, 1995, 2005, and 2015. The minimum expected overlap for quadrats of this size is $q_0 \approx 0.86$.

Table 1
Parameters of the exponential fit to the overlap in the different cases.

Overlap	Set	τ [y]	Q_∞
$Q(t_1, t_2)$	dbh$>$ 10,mm	11.7	0.565
$Q(t_1, t_2)$	dbh$>$ 100,mm	15.3	0.659
$Q_{SA}(t_1, t_2)$	dbh$>$ 10,mm	19.2	0.928
$Q_{SA}(t_1, t_2)$	dbh$>$ 100,mm	36.2	0.980

coefficient, yield qualitatively similar results (Fig. 5). However, the advantage of the overlap is conceptual. Apart from the normalisation of each term, our definition is that of a correlation function, $C(a, b) = \langle n(a)n(b) \rangle$, where the statistical ensemble average $\langle \ldots \rangle$ is replaced by an *average over species,* i.e. we use species as a proxy for the average over the actual statistical ensemble, much like time or space averages are commonly used in statistical physics. We are in effect saying that all species are equivalent to one another: in this sense our definition is species-neutral. Species equivalence is a basic assumption of "neutral" theories of biodiversity (Caswell, 1976; Hubbell, 2001; Volkov et al., 2003; Vanpeteghem et al., 2008; Chisholm, 2011), but we stress that here we are merely proposing an invariance that allows to use species averages as a proxy for history averages. In particular, unlike the mentioned approaches, we do not make additional assumptions (such as absence of interactions) or impose other constraints (like a constant total population). The observable we define is general, and not tied to a particular theory. Rather, it constitutes a tool to analyze the dynamics that can be applied to empirical or simulation data without assuming the validity of a particular theoretical hypothesis on the time evolution.

At this point, one may ask two questions. First, in a stationary system, average quantities are independent of time. In particular, the average abundance must be time-independent; is it actually so in BCI? The practical problem is that, while the expectation of time-independence is true for the history average, we only have access to the species average, which, as a statistical estimate, is subject to fluctuations even under stationary conditions. We expect that relative fluctuations tend to zero as the size of the sample increases (where a larger sample means a sample with more species), but, unlike thermodynamic systems, the distribution of species abundances is much broader than Gaussian. The abundance distribution of BCI has been shown (Hubbell et al., 2008; Hubbell, 2013) to be broader than a lognormal distribution, and more similar to Fisher's logseries (Fisher et al., 1943). Estimating the moments of broad distributions is difficult, and one can expect significantly larger fluctuations than for a narrow, Gaussian-like distribution. We have computed the species-averaged abundance, Eq. (6), vs. time to check if it is consistent with a
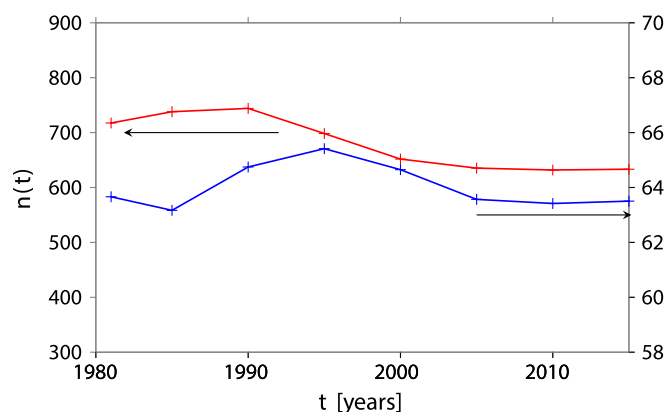

Fig. 4. Species-averaged abundance vs. time, $n(t)$ for the whole census (red) and dbh $>$ 100 mm (blue). $n(t)$ fluctuates much less than individual abundances: the maximum instantaneous deviation of from its time average is is slightly above 9% when considering all trees and approximately 2.2% for dbh $>$ 100 mm.

stationary forest (Fig. 4). We find quite moderate fluctuations, compatible with a stationary scenario. In the stationary state, the history-average abundance must be time-independent, but instead our estimate using an average over a finite number of species is bound to exhibit fluctuations. The absence of obvious long-term trends in the species-averaged abundance is consistent with the assertion that the BCI forest is stationary, as well as the observed fluctuations, which do not exceed 10%.

The second question is why use the overlap instead of the standard time correlation mentioned above. The answer again is the broad distribution of abundances. The time correlation $C(a, b)$ is the covariance of the abundance in a and b (variance when $a = b$), and the problem mentioned above for the average is aggravated for higher moments. Thus the time correlation is bound to be subject to stronger statistical fluctuations than the overlap, and can be expected to be rather difficult to estimate accurately. Instead, the individual normalisation of each term in the overlap makes it insensitive to fluctuations in the overall size of the population and in the estimated variance, while it can still detect dynamical processes involving taxonomic changes other than fluctuations of the overall community size. Computing the Pearson correlation (see Section 2.1.2 and Eq. (4)), which normalises the correlation with the product of the standard deviation at each time, yields results similar to the overlap (Fig. 5).

Some time ago, Azaele et al. (2006) found the hypothesis of a stationary state to be self-consistent within a theoretical data analysis of the
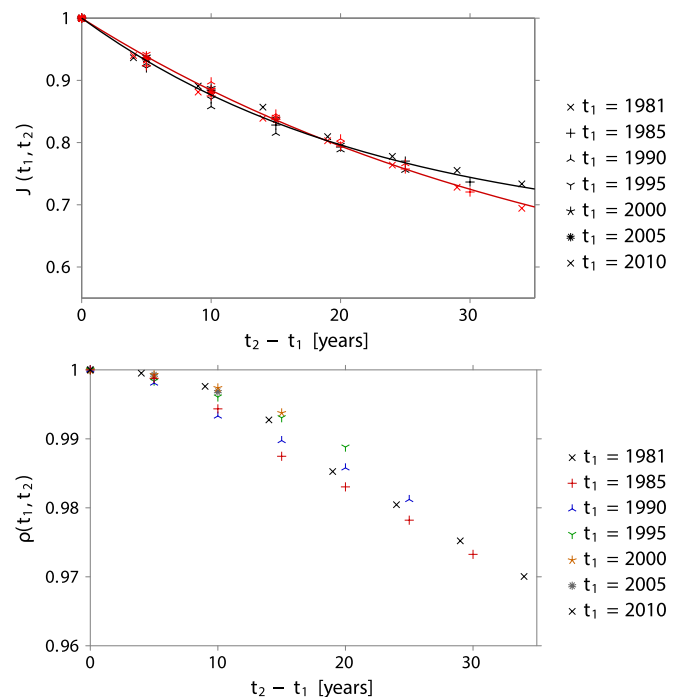
Fig. 5. The Jaccard index and normalised time correlation function are consistent with a stationary state. **Top:** Jaccard index $J(t_1, t_2)$ vs. $t_2 - t_1$ between all pairs of censuses, for trees with dbh > 10,mm (black) and dbh > 100,mm (red). Lines are fits to an exponential decay $J(t_1, t_2) = (1 - J_\infty)e^{(t_2 - t_1)/\tau_J} + J_\infty$. The values of the fit constants are $\tau_J = 23.2$,y, $J_\infty = 0.648$ for dbh > 10,mm and $\tau_J = 38.9$,y, $J_\infty = 0.489$ for dbh > 100,mm. The behaviour is qualitatively the same as that of $Q(t_1, t_2)$, displaying an exponential decay, albeit with slightly larger time constant. The plot shows that the $J(t_1, t_2)$, like the overlap, depends only on the time difference $t_2 - t_1$, i.e. it is also stationary. **Bottom:** Normalised (Pearson) time correlation $\rho(t_1, t_2)$ for all pairs of censuses and all trees. While the time correlation, being a second-order moment, is difficult to estimate when the distribution of n_σ is broad, the normalisation of the Pearson correlation compensates for fluctuations in sample size, similar to the term-by-term normalisation of the overlap. While its shape is different from an exponential, its decay is also compatible with a stationary scenario.

first three BCI censuses. At variance with our approach, these authors *assumed* the forest is stationary, and analysed the data using a particular theory (neutral theory). Our result significantly extends that work, not only because more censuses are now available, but moreover because ours is not a self-consistently check within a particular theory, but a data-based result that follows from the fact that the overlap depends only on the time elapsed between censuses.

From the exponential fits of the overlap decay, we obtain a characteristic time of about 15 years. This should be regarded as the characteristic time of processes happening within the available observational time window and sampling rate: possible processes with times faster that the 5 year interval between censuses cannot be detected with these data (Press et al., 1992). Similarly, it is impossible to measure processes with characteristic time much longer than the 35 year window of the time series. In particular, trends or fluctuations happening on the scale of centuries cannot be ruled out, so that processes much slower than those observable in the available time window could take the asymptotic overlap to much lower values. To our knowledge, the only other estimate of a characteristic time scale for the BCI forest is that Azaele et al. (2006), who obtained for the timescale of species turnover t_s a value $t_s \approx 3000$,years, using fits to detailed expressions following from neutral theory. This value is not necessarily incompatible with the present estimate, since our results do not rule out the presence of very slow processes causing fluctuations on the scale of centuries or milennia. However, detecting them in a time series spanning 30 years is tricky, and any attempt depends critically on the validity of the details of a particular theory.

Our treatment of fluctuations, and the fact that we find them compatible with a stationary state, says nothing about whether this community is near a critical or tipping point (Scheffer et al., 2009; Kéfi et al., 2011; Staal et al., 2016; Cetin, 2020; Li and Convertino, 2021). If the system is stationary, it will respond to a change in external conditions in the same way as it would have done in the past to the same change (Ma et al., 2021), but the present analysis does not inform us whether this response will be mild or catastrophic (Scheffer et al., 2001). For BCI, recent publications have discussed the issues of forecasting (Fort and Grigera, 2021) and early warnings (Fort and Grigera, 2021) at the level of individual species.

5. Conclusions

Our results show that (i) the BCI forest evolves, changing relative abundances over time, (ii) the evolution of larger trees (dbh > 100 mm) is slightly slower, (iii) the decay of the overlap has the same shape when choosing any of the censuses as reference, and (iv) the time scale for the decay is about 15 years.

Point (iii) is particularly important. A system in a stationary state is not the same as a static system. For example, a physical system in thermodynamic equilibrium is stationary but not devoid of dynamics: appropriate ensemble averages are time independent (or, equivalently, quantities such as density or energy per unit volume are constant if the size of the system is large enough), but there are observable fluctuations around this average value, and these fluctuations show a characteristic time (the *correlation time*), which is a measure of the time it takes for the quantity to "forget" the value it took at some earlier point in time. The relaxation time can be pretty large, even at equilibrium (Stanley, 1999), and can be determined by measuring correlation functions, which, like the overlap above, are stationary in the sense that they depend only on the difference between two times.

It must be stressed that the evidence obtained from the overlap is much stronger than simply the absence of an obvious trend in $n(t)$. The time-translation invariance of $Q(t_1, t_2)$, i.e. the fact that it depends only on the time difference $t_2 - t_1$, is a much more robust test of stationarity. It can indeed happen that single-time quantities (like $n(t)$) are almost constant, while correlation functions like the overlap are clearly non-stationary [an example of such a situation is the physical ageing of polymers and glasses, Struik, 1977; Cugliandolo, 2004].

Finally, the characteristic time of the exponential decay of the overlap is about 15 years. This can be interpreted as the time it takes to observe significant differences with respect to the reference configuration. A previous estimate (Azaele et al., 2006) found a much larger value (≈ 3000,years), assuming a stationary state and employing results from a particular theory. In contrast, our approach cannot probe fluctuations on scales much larger than the time span of available data, but the observable we used is free from strong theoretical assumptions (we have fitted an exponential function only as the simplest way to obtain a characteristic time), and can actually test whether the forest is stationary or not.

In summary, we have introduced the overlap as a dynamic observable to compare an ecosystem's taxonomic composition at different times and furnishing way to test whether the system is stationary. Applying this to the BCI forest community, we have for the first time obtained experimental evidence that the system is in a stationary state. The time decay of the overlap also shows that the system is not static, and that species abundances fluctuate on a time scale of ~ 15 years, two orders of magnitude faster than previously estimated.

CRediT authorship contribution statement

Andrea Cavagna: Conceptualization, Validation, Writing - review & editing, Funding acquisition. **Hugo Fort:** Conceptualization, Validation, Writing - review & editing, Funding acquisition. **Tomás S. Grigera:** Conceptualization, Validation, Writing - review & editing, Funding acquisition, Methodology, Software, Writing - original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data used has been made public prior to the writing of this article by the Smithsonian Tropical Research Institute

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Appendix A. The asymptotic overlap

The overlap is designed to attain a value of 1 for two configurations with identical taxonomic composition (i.e. with identical abundances for every species present). We must allow $n_\sigma(t) = 0$, because a species that is present at time t_1 and absent at time t_2 (or vice versa) must contribute a term smaller than 1 to the sum, to signal a difference in composition. Thus N_S is the total number of species ever recorded in any of the available censuses. It

can then happen that for some σ we have $n_\sigma(t_1) = n_\sigma(t_2) = 0$; In this case we have defined the corresponding term as 1, so that a species that is absent in both configuration does not spuriously lower the value of Q. A side effect of this choice is that the lowest possible value of the overlap, q_0, expected for two configurations with completely different composition, depends on the ratio of the total number of species recorded, N_S, and the typical number of species found in an area equal to the area occupied by the population being considered, $N(A)$.

Consider first the case when $N(A) \approx N_S$ (as in the main text, where the whole BCI plot is used). The overlap decrease is brought about by changes in the distribution, but it cannot happen that two configurations are completely disjoint, because that would require $N_S > 2N(A)$. To estimate q_0 in this case we assumed that both the total number of trees and the number of species remain constant (consistent with a stationary state), and we built a configuration by taking the abundances of the 1985 census (including the species with zero individuals) and exactly reversing the abundance rank (i. e. the most abundant species in 1985 was assigned lowest abundance, the second most abundant species was assigned the second lowest, etc). The overlap between this configurations and the 1985 census is $q_0 \approx 0.15$ (whole census) or $q_0 \approx 0.11$ (dbh > 100 mm).

On the other hand, if N_S is much larger than $N(A)$ (which is the case for the local overlap (2)), two disjoint configurations can nevertheless have a relatively high overlap. To see this, imagine that one takes a small $l \times l$ square within the BCI plot, and computes the overlap to compare the populations of only this square in two different censuses. The full BCI census recorded $N_S = 328$ different species, but in a l^2 area one finds on average $N(l^2)$ of those coexisting at any given time. If the two populations are identical, one gets $Q = 1$ because although $n_\sigma = 0$ for about $N_S - N(l^2)$ species, the species that have zero abundance in both censuses contribute a 1 to the sum, according to our definition. But if the two censuses record completely disjoint populations (i.e. none of the species found at $t = t_1$ is present at $t = t_2$ and vice versa), each census still has roughly $N(l^2)$ species in the area, so that the overlap will take a value

$$
\begin{aligned}
q_0 &\approx \frac{1}{N_S} \left[N(l^2)\cdot 0 + N(l^2)\cdot 0 + \left[N_S - N(l^2) - N(l^2) \right]\cdot 1 \right] \\
&= 1 - 2\frac{N(l^2)}{N_S}.
\end{aligned}
\tag{A.1}
$$

For example, if one uses the full list of $N_S = 328$ species but considers a square of $l = 50$,m, then, since for BCI $N(l^2) \approx 120$, the minimum value attained by the overlap will be $q_0 \approx 0.27$. For $l = 10$,m the average number of species is $N(l^2) \approx 23$ and the minimum overlap rises to $q_0 \approx 0.86$.

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