


# The characteristic time of ecological communities

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**Abstract.** A simple description of temporal dynamics of ecological communities may help us understand how community assembly proceeds, predict ecological responses to environmental disturbances, and improve the performance of biological conservation actions. Although community changes take place at multiple temporal scales, the variation of species composition and richness over time across communities and habitats shows general patterns that may potentially reveal the main drivers of community dynamics. We used the simplest stochastic model of island biogeography to propose two quantities to characterize community dynamics: the *community characteristic time*, as a measure of the typical time scale of species-richness change, and the *characteristic Jaccard index*, as a measure of temporal  $\beta$  diversity, that is, the variation of community composition over time. In addition, the community characteristic time, which sets the temporal scale at which null, noninteracting species assemblages operate, allowed us to define a relative sampling frequency (to the characteristic time). Here we estimate these quantities across microbial and macroscopic species assemblages to highlight two related results. First, we illustrated both characteristic time and Jaccard index and their relation with classic time-series in ecology, and found that the most thoroughly sampled communities, relative to their characteristic time, presented the largest similarity between consecutive samples. Second, our analysis across a variety of habitats and taxa show that communities span a large range of species turnover, from potentially very fast (short characteristic times) to rather slow (long characteristic times) communities. This was in agreement with previous knowledge, but indicated that some habitats may have been sampled less frequently than required. Our work provides new perspectives to explore the temporal component in ecological studies and highlights the usefulness of simple approximations to the complex dynamics of ecological communities.

**Key words:** community composition; community ecology; island biogeography; microbial communities; microbial ecology; stochastic models; temporal dynamics; turnover.

## INTRODUCTION

A central goal of community ecology is to understand temporal dynamics in species diversity and composition. Temporal dynamics are essential to gain a mechanistic comprehension of the drivers of community assembly, improve conservation and management measures, monitor the effect of disturbances, forecast the consequences of climate change, or even design and control microbial communities (Fisher et al. 2010, Supp and Ernest 2014, Warren et al. 2015, Gonze et al. 2018). Although this body of knowledge is still limited (Dornelas et al. 2014, Hortal et al. 2015), its importance in ecology has been increasingly acknowledged (Levin 1992, White et al.

2006, Dornelas et al. 2013). Deeply related to community dynamics, a central issue is to establish the temporal scale at which communities function. Previous research has established that temporal changes operate at multiple scales, as biotic and abiotic drivers of community change can interact in different complex, scale-dependent ways (Levin 1992). However, community ecologists still aim to describe temporal dynamics with simple measures that summarize the inherent dynamics of ecological communities. These measures may help address relevant questions in ecology, such as the search for general patterns in community dynamics or the identification of baselines for detecting ecological changes (Sutherland et al. 2013).

Although the importance of temporal dynamics was hinted already by Darwin (Magurran 2008), it can be considered that Preston was the first to study temporal scales in ecological communities. Preston (1960) introduced the concept of species-time relationships (STR),

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the relationship between time and the number of species we find in a sample as time increases. Other measures of richness or compositional change have been used since then, as species turnover (Diamond and May 1977, Russell et al. 1995, Hallett et al. 2016, Hillebrand et al. 2018), or the slope of similarity indices (such as the Jaccard index) as function of time (Dornelas et al. 2014). Moreover, some of these works (Diamond and May 1977, Russell et al. 1995, Dornelas et al. 2014) also try to compare turnover or community similarity with models rooted in the equilibrium theory of island biogeography (ETIB).

The ETIB developed by MacArthur and Wilson (1967) can be considered as the first mechanistic attempt to understand community dynamics (May 2010). ETIB is a neutral theory that focuses on how a dynamic equilibrium between colonization and extinction determines both the average number of species at the steady state and community temporal turnover even after this equilibrium has been attained (Simberloff 1969). Because censuses apart in time might underestimate repeated colonization and extinction events, Diamond and May (1977) introduce the term *uncertainty principle* to describe the problem of the choice of the optimal time interval between censuses. They built on ETIB to define a species-specific turnover index as a function of census interval. Further exploration of a similar community turnover index indicates that a simple measure of mean turnover is not enough for comparisons among communities (Russell et al. 1995). Recently, Dornelas et al. (2014) measured how diversity varies in time by comparing the observed slopes of the Jaccard index with the ones obtained for a null model based on random colonizations and extinctions. This random null model was not fitted to data, though. Other approaches try to understand diversity temporal change in ecological communities, based on either niche (Chisholm et al. 2014) or neutral (Azzele et al. 2006, Allen and Savage 2007, Kalyuzhny et al. 2015) community dynamics, but require variability in species abundances. However, long temporal data on species abundances across whole communities are expensive to obtain and maintain (although Condit 1998; Dornelas et al. 2018 constitute remarkable exceptions of this). In addition, these methods do not apply when species presence and absence are the only data available.

The aim of this contribution is to characterize temporal scales for species composition and richness across communities based only on species presence–absence data consistently. These two features of community dynamics, that is, the representative temporal scale that drives species richness temporal change, as well as the variation of community composition over time, are intertwined and, together, provide an overall picture of community change over time. To conduct this study, we make use of the stochastic formulation of ETIB as a Markovian birth–death process in continuous time (Alonso et al. 2015, Ontiveros et al. 2019). Under this approach, species colonization and extinction rates are estimated via species presence and absence from sampled

communities at different time intervals. Based on these estimates, here we propose two quantities to characterize community dynamics globally: the *community characteristic time*, as a measure of the typical time scale of species richness change, and the *characteristic Jaccard index*, as a representative measure of the variation of community composition over time. Therefore, it can be regarded as an alternative measure of stability or temporal beta diversity. As a benchmark, we use first three well-studied, classic data sets (Table 1). Then, we also examine the ability of the model to characterize temporal scales of community variation, and their relation to composition temporal patterns, for a variety of community data sets spanning from micro- to macro-organisms, aiming to represent a wide range of communities, taxa, and habitats (Table 1).

Our main findings are twofold. First, we found a very good analytical approximation for the decay of the Jaccard index over time. In terms of sampling frequency, the most thoroughly sampled communities, relative to their characteristic times, were more similar, according to the mean Jaccard index measured between consecutive samples. Second, using an array of different communities, including both macroscopic and microbial taxa, we studied whether actual sampling times were comparable to each community characteristic time. This quantity, as a measure of a typical temporal scale of community variation, can be used to inform about the optimal frequency at which communities should be sampled, thus solving the *uncertainty principle* (Diamond and May 1977).

## MATERIALS AND METHODS

### *Data samples*

Table 1 summarizes the data sets used in this study. We included three classic data sets that studied temporal aspects of ecological communities originally. Preston (1960) used Neotoma birds to first quantitatively describe STRs, whereas Simberloff and Wilson (1969) validated ETIB dynamics with island arthropods, and Diamond and May (1977) studied turnover rates for the Farne Islands bird communities. This allowed us to validate model performance in reproducing time variation in community composition as well as transient dynamics. We then used community data sets from bacteria, fishes, and plants, which represent a wide range of communities, taxa, and habitats. Most data sets were used to estimate the typical timescale of the associated communities. However, in order to study average community compositional change and its relation to characteristic and sampling times, we could only use the data sets that provided a larger number of sites.

### *Equilibrium theory of island biogeography*

In the 1960s, MacArthur and Wilson (1967) proposed the theory of island biogeography with the ultimate goal

TABLE 1. Data sets used in this study.

Habitat	Taxa	Location	Duration	Reference
Islands	Arthropods	Florida Keys, USA	1.5	Simberloff and Wilson (1969)
Deciduous forest	Birds	Neotoma, Ohio, USA	17	Preston (1960)
Island	Birds	Farne Islands, England	28	Diamond and May (1977)
Human	Bacteria	–	0.5–1.5	Caporaso et al. (2011)
Marine	Bacteria	English Channel	6	Gilbert et al. (2012)
Soils	Bacteria	Switzerland	4	Hartmann et al. (2014)
Aeroplankton	Bacteria	Pyrenees, Spain	7	Caliz et al. (2018)
Shallow saline lakes	Bacteria	Monegros desert, Spain	2	Triado-Margarit et al. (2019)
Alpine lakes	Bacteria	Pyrenees, Spain	1	PRJNA566370†
Coral reef	Fishes	Lakshadweep Archipelago, India	11	Alonso et al. (2015)
Sagebrush steppe	Plants	Idaho, USA	50	Zachmann et al. (2010)

*Notes:* The three first data sets were also used for model validation purposes. Duration expressed in years. Different sites were considered separately. The two hydroperiods of the shallow saline lakes were considered separately, as the lagoons dried in summer, restarting the dynamics.

†Data set available in GenBank.

of explaining the geographical distribution of diversity. This theory was denominated equilibrium theory of island biogeography after the works by Simberloff (1969) and Simberloff and Wilson (1969). The basic equation underlying ETIB can be expressed as

$$\frac{dS}{dt} = c(S_P - S) - eS, \quad (1)$$

where  $S$  stands for the species richness in a site,  $S_P$  for the number of species in the regional pool, and  $c$  ( $e$ ) for the colonization (extinction) rate, which in the original theory were related to distance to the mainland and area of the island, respectively. The rates represent the proportion of sites where species colonize or undergo extinction per unit of time, but as only one site is considered here (as well as in the original formulation), the rates indicate the pace at which species enter or leave the site, or in the specific case of microbial communities, how the species rise or fall over the detection limit (Alonso et al. 2015, Ontiveros et al. 2019).

It is possible to easily calculate overall, community-aggregated estimates for colonization and extinction rates, assuming species independence in the dynamics, that is, absence of interspecific interactions, as well as species equivalence in their rates, that is, uniformity colonization and extinction rates across species (Alonso et al. 2015). As a consequence, community dynamics can be assumed to be governed by these two overall rates. These temporal rates yield an approximation to the diversity dynamics in the site. Estimation of the rates is detailed in Appendix S1, following Alonso et al. (2015) and Ontiveros et al. (2019).

#### Community characteristic time

Through these colonization and extinction rates, we can define a representative time scale at which species richness and composition typically vary in a community. The solution of classical ETIB model, as well as its

stochastic formulation (Alonso et al. 2015), shows clearly that the temporal evolution is governed by the combination  $c + e$  (see Appendix S1: Eq. S6). Therefore, we can define a temporal scale at which diversity changes significantly, that we denominate *community characteristic time*,  $T_c$ , and its confidence interval length,  $\Delta T_c$ , via the following equations:

$$T_c = \frac{1}{c + e},$$

$$\Delta T_c = \frac{|\Delta c| + |\Delta e|}{(c + e)^2}, \quad (2)$$

where  $\Delta c$  ( $\Delta e$ ) corresponds to the confidence interval of  $c$  ( $e$ ). As shown in Alonso et al. (2015), in the case of regular sampling schemes, characteristic time depends directly on the time interval among samples,  $\Delta t$ , as well as on the colonization and extinction transition probabilities (see Appendix S1: Eq. S24). With all these elements, we define the number of samples taken in a characteristic time as  $\nu_s$ , the *relative sampling frequency*, as

$$\nu_s = \frac{T_c}{\Delta t}. \quad (3)$$

If  $\nu_s \approx 1$ , communities are sampled between intervals comparable to the representative timescale of the system. Therefore,  $\nu_s$  can be used as an indicator of how thoroughly the community is sampled to estimate community dynamics.

Estimated colonization and extinction rates also allow us to simulate the dynamics of the communities for model validation. We have done so for three classic examples of community dynamics, Neotoma birds, Farne Islands birds, and Florida Keys arthropods (see Appendix S1: Fig. S2). For Neotoma birds, the model was also validated by comparing with the STR (obtained accumulating the richness of consecutive samples) that

our simulations produced. We obtained all estimates using the function `irregular_single_dataset` of package “island” (Ontiveros et al. 2019), which allows calculating colonization and extinction rates for irregular sampling schemes, and simulations were performed using function `PA_simulation`.

#### Temporal $\beta$ diversity: characteristic Jaccard index

The characteristic time defines a typical time scale for ecological community dynamics. To measure temporal  $\beta$  diversity or species compositional change over time, we

used the Jaccard index, which accounts for richness but is invariant to abundance, being the perfect match for our measures. We also explored turnover (Diamond and May 1977, Russell et al. 1995), as it is an almost complementary measure to Jaccard’s index. We define both measures and find approximate expressions for their variation over time in Box 1. We defined the *characteristic Jaccard index* as the Jaccard index evaluated at the characteristic time  $T_c$  (see Box 1). Additionally, we tested how well our measures of temporal scale related to compositional change. Compositional change not only depends on characteristic time, but also on its

### Box 1: Community composition dynamics: Characteristic Jaccard Index

One of the most used indices to study the change in community composition is the Jaccard index. This index allows to compare sites using presence–absence data, and it is defined as follows:

$$\mathcal{J}_{ij} = \frac{C}{A + B + C}, \quad (4)$$

where  $A$  is the number of species present at time  $t_i$  and not at time  $t_j$ ,  $B$  the number of species present at time  $t_j$  and not at  $t_i$ , and  $C$  the number of species present at both times. Now, let  $p_i$  be the proportion of species present at time  $t_i$  and  $\Delta t = t_j - t_i$  the interval of time between samples. As shown in Appendix S1, we can approximate the variation of the Jaccard index, for a relatively high number of species, in terms of colonization and extinction rates as

$$\mathcal{J}_i(\Delta t) \approx \frac{p_i[c + e \exp(-(e+c)\Delta t)]}{p_i[e + c \exp(-(e+c)\Delta t)] + c[1 - \exp(-(e+c)\Delta t)]} \quad (5)$$

Therefore, the characteristic Jaccard index is defined as the value of the expression above when  $\Delta t = T_c$ . Eq. 5 also hints that the Jaccard index reaches an asymptote after some time. Therefore, we have defined an asymptotic Jaccard index,  $\tilde{\mathcal{J}}_i$ :

$$\tilde{\mathcal{J}}_i = \lim_{\Delta t \rightarrow \infty} \mathcal{J}_i(\Delta t) \approx \frac{p_i c}{p_i e + c}, \quad (6)$$

which reduces to  $\tilde{\mathcal{J}}^* \approx c/c + 2e$  starting from the occupancy at equilibrium,  $p_i = c/(c + e)$ .

We calculated bounds of the ratio  $\Delta t/T_c = 1/\nu_s$  for the system to reach approximately the asymptotic Jaccard index (see Appendix S1). Specifically, for  $0.22 \leq e/c \leq 2.31$ , the relative error  $|J^*(\Delta t) - \tilde{\mathcal{J}}^*|/\tilde{\mathcal{J}}^*$  equals  $10^{-2}$  if  $\Delta t$  satisfies the bounds  $3.6 \leq \Delta t/T_c \leq 5.6$ . This means that, for a wide range of extinction to colonization ratios, the system takes from about 4–5 characteristic times to reach the asymptotic compositional state starting from an initial proportion of species  $p_i = c/c + e$ .

The same reasoning can be extended to turnover,  $\mathcal{T}$ , as defined by Diamond and May (1977). Translating this definition to the same components  $A$ ,  $B$ , and  $C$  as above, we have that

$$\mathcal{T}_{ij} = \frac{A + B}{A + B + 2C} \quad (7)$$

from which we obtain a similar expression for the evolution of turnover over time:

$$\mathcal{T}_i(\Delta t) \approx \frac{[\exp(\Delta t(e+c) - 1)][(1-p_i)c + p_i e]}{c[\exp(\Delta t(c+e))(p_i + 1) + p_i - 1] + p_i e[\exp(\Delta t(c+e)) + 1]}. \quad (8)$$

The derivation of these and additional metrics can be found in Appendix S1.

relationship with the mean time among samples, that is, how often the community has been sampled, so we studied the variation of the Jaccard index with  $\nu_s$ , the relative sampling frequency; see Eq. 3. We only calculated the mean Jaccard index between consecutive samples for habitats with enough replicates reported (arthropod communities in mangrove islands and shallow saline lakes from the Monegros desert).

## RESULTS

### Model validation

The first question we asked is whether the model can reproduce, at least qualitatively, the temporal dynamics of ecological communities. To answer that question, we revisited three classic studies on community dynamics, namely: arthropod recolonization in island E3 of the Florida Keys, Farne Island birds, and *Neotoma* birds. First, we estimated colonization and extinction rates in the three communities, obtaining colonization rates of  $5.64 \times 10^{-3}$ ,  $2.04 \times 10^{-4}$  and  $7.47 \times 10^{-4} \text{ d}^{-4}$ , and extinction rates of  $1.14 \times 10^{-2}$ ,  $4.10 \times 10^{-4}$ ,  $2.84 \times 10^{-5} \text{ d}^{-1}$ , for arthropods, island birds, and deciduous forest (*Neotoma*) birds, respectively. These rates allowed us to simulate the dynamics of the communities. In Appendix S1: Fig. S1 we show the performance of our model for these classic data sets. The observed richness, as a function of time, is inside the 95% confidence interval of the simulations in the three communities.

Now, we turn to richness and community composition patterns. Fig. 1 presents the different patterns studied for the three classic data sets used in this contribution. We satisfactorily recovered the STR for *Neotoma* birds, turnover over time for the transient species in the Farne Islands, and the evolution of the Jaccard index over time for island E3 of the Florida Keys. We tested the performance of the stochastic ETIB model in reproducing the temporal change in  $\beta$  diversity over time in Fig. 1c. We also calculated the characteristic Jaccard index for island E3, that is, the expected Jaccard index after a characteristic time, yielding a value of 0.406. Simulations also validate our estimation of the variation of the Jaccard index over time (i.e., Eq. 5 in Box 1), as can be checked in Appendix S1: Fig. S2. In sum, observational patterns are overall reasonably well reproduced by theoretical predictions.

### Characteristic time and sampling frequency

We examined the temporal scales of different communities estimating their colonization and extinction rates, as well as their associated characteristic times. Fig. 2 represents the characteristic time,  $T_c$ , as function of the mean sampling time interval for each data set. Among microbial communities, soils had the slowest dynamics with a characteristic time of above seven months, while the communities found in humans, especially those on

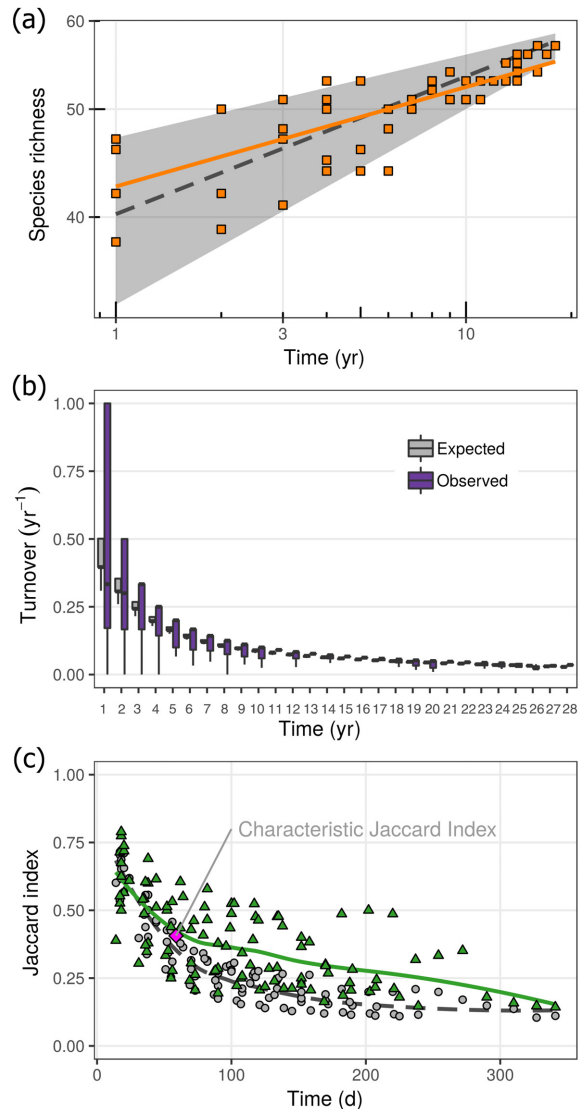


FIG. 1. Richness and community composition patterns recovered by a simple stochastic model of island biogeography. (a) Species–time relationship of deciduous forest birds community at *Neotoma*. Estimated accumulating species richness over all possible consecutive samplings, yields a power-law relation  $S \sim t^w$ ,  $S$  being the species richness and  $t$  the time in years, where  $w = 0.089$  ( $P$  value  $< 0.001$ ). (b) Turnover rate of island birds in the Farne Islands. Four species were always present and subsequently excluded. (c) Community similarity measured with the Jaccard index, calculated between consecutive samples, for arthropods in the Florida Keys. In all panels, colored elements correspond to the observed community measures. Gray elements (shaded areas, boxplots, or circles) correspond to model simulations. In (c), both lines are moving averages of data (green) and simulations (dashed gray).

hands, had a faster characteristic time—about a few days. The macroscopic communities presented longer characteristic times of years, except the macroinvertebrates that yielded several weeks as the community characteristic time (Fig. 2). Therefore, our characteristic

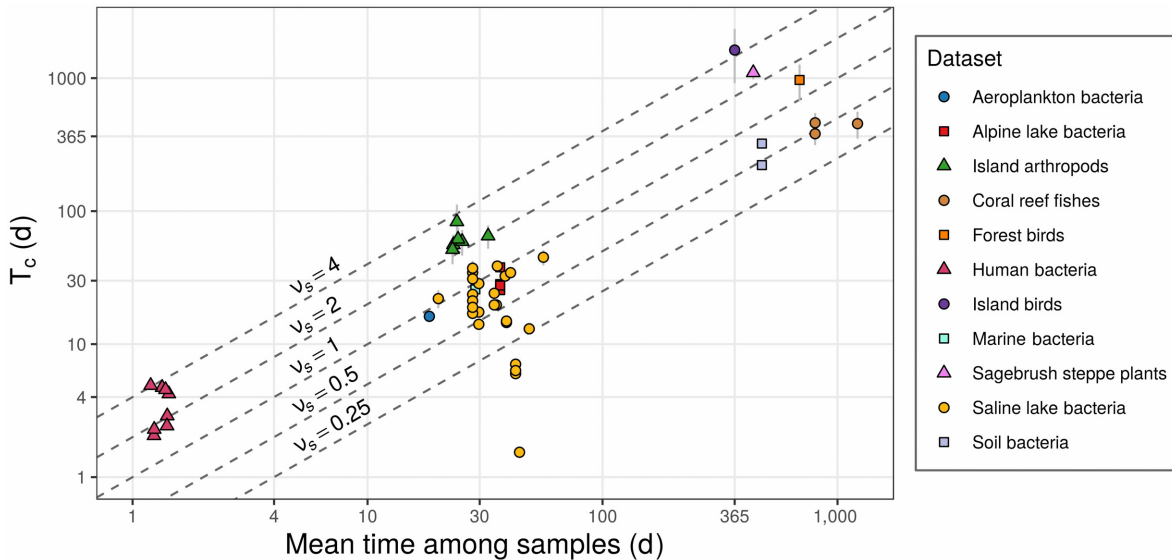


FIG. 2. The characteristic time of different communities.  $T_c$ , characteristic time;  $\nu_s$ , relative sampling frequency. We found that birds and plants had the slowest dynamics, and the fastest habitat is found in humans, especially in hands. Each point represents a site, and error bars (gray) indicate the characteristic time error estimation. Along the dotted lines, the relative sampling frequency is constant.

time estimates were consistent with the expected typical time that should drive community dynamics emerging from different taxa assemblages, ranging from bacteria to macro-organisms. Even among bacterial communities, our time estimates were consistent; compare soils (slow dynamics) vs. human (fast dynamics).

Communities lying close to the line  $\nu_s = 1$  were sampled in a timescale comparable with the characteristic time. Among the 11 studied data sets, five of them (humans, invertebrates, plants, birds) were sampled more frequently than the inferred characteristic time, whereas coral reef fishes, soil microbes, and some saline lakes were slightly undersampled (Fig. 2).

#### Community composition temporal change

We investigated how community composition depended on the relative sampling frequency  $\nu_s$  (i.e., how often the community was sampled relative to the characteristic time of the system). Using the two data sets that comprised a larger number of sites, we found that community similarity increased with  $\nu_s$ , as demonstrated by the Spearman's  $\rho$  of this relation:  $\rho = 0.976$ ,  $P$  value  $< 0.001$  for saline lakes;  $\rho = 0.881$ ,  $P$  value  $< 0.001$  for arthropods (note that arthropods data were subsampled to improve statistics; see Fig. 3). This result implies that oversampled communities exhibited a higher similarity in community composition.

#### DISCUSSION

The current study has found that the simplest stochastic model of equilibrium island biogeography theory can

recover richness and composition patterns such as the STR, turnover, or Jaccard index. Moreover, we have shown that the observed patterns depended on an inherent temporal scale, which we have called characteristic time. This measure may not only help us compare compositional change among different communities through the characteristic Jaccard index, but it also aids in assessing whether we are sampling a community frequently enough to capture meaningful temporal variations and properly describe its dynamics. As our characteristic time sets up a typical scale of community change, the ambiguity in the choice of the time interval between censuses, that is, the *uncertainty principle* posed originally by Diamond and May (1977), is effectively solved. In this sense, the results shown in Fig. 2 give a precise hint of the communities that have been oversampled, in comparison with those undersampled. This emphasizes the importance of an accurate estimation of the time between samples. We suggest using the characteristic time  $T_c$  as a typical measure of community change, as well as the relative sampling frequency,  $\nu_s$ , as an indicator of the proximity between community sampling times and the typical scale estimated by  $T_c$ . From our analysis, it is clear that undersampled communities exhibiting  $\nu_s < 1$  must to be sampled more often to improve their dynamical description as well as proper estimates of the characteristic time (see Appendix S1: Fig. S5).

Our study may help to address several aspects of interest. The most evident of them is the resolution of the uncertainty principle. The estimation of characteristic times across habitats and taxa might allow us to study changes in community composition and richness at appropriate timescales, for which theoretical frameworks

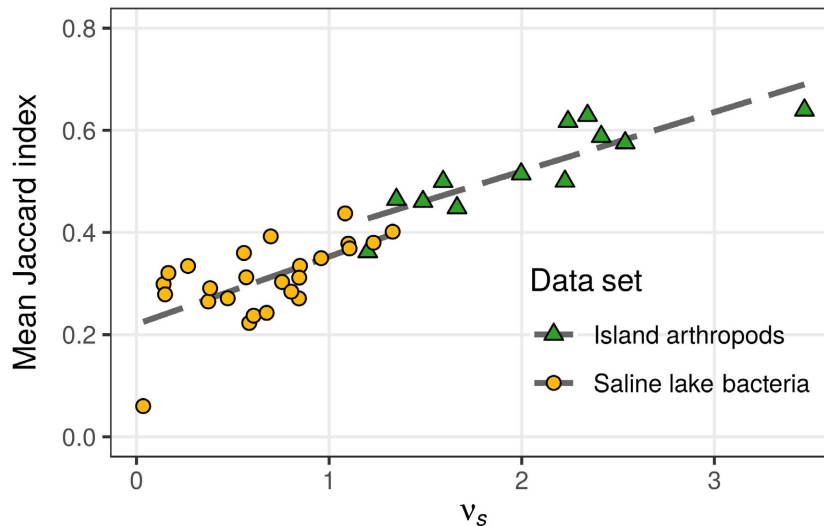


FIG. 3. Variation in community composition for multiple sites and two habitats.  $\nu_s$ , relative sampling frequency. Community similarity is larger for oversampled communities. Arthropod communities showed higher values of the mean of Jaccard indices between consecutive samples than shallow saline lakes, as the former were sampled more thoroughly. For saline lakes, each point represents a sampling site, whereas arthropods communities additionally were subsampled to improve statistics. Subsampling involved the second next sample to calculate the Jaccard index.

are currently lacking (Hastings 2010). Although characteristic times cannot be estimated a priori, wide application of the method might help ecologists to establish rules of thumb derived from our measures. Besides, we have shown that characteristic times are intimately associated with patterns of  $\beta$  diversity. We propose the characteristic Jaccard index as a good single measure to compare horizontal communities (sensu Vellend 2016), in contrast with previous studies indicating that single measures are not enough to characterize composition dynamics (Russell et al. 1995). At the very least, our simple stochastic model of ETIB can be used as a null model of community dynamics, estimated from presence–absence data, representing a baseline for detecting ecological change (Sutherland et al. 2013). Such a null model represents an improvement with respect to previous attempts that do not fit the parameters to the data (as in Dornelas et al. 2014).

Furthermore, our approach is relevant for monitoring and conservation, as it portrays random drift in community richness and composition (Hillebrand et al. 2018). Deviations from it may indicate departures of the two main hypothesis, *species equivalence* and *independence*, and/or the influence of abiotic factors on the community—we recall here that, in our model, species do not interact with each other (independence) and are characterized by equal colonization and extinction rates (equivalence). The influence of abiotic factors can also be modeled as previously demonstrated (Ontiveros et al. 2019), which potentially could help predict community dynamics under climate change, a much-needed venue of research (Fisher et al. 2010, Dornelas et al. 2013). Our model may also capture the effect of disturbances

(Alonso et al. 2015). Defaunation experiments (Simberloff 1969) and simulations (see Fig. 1c and Appendix S1: Fig. S2) indicate that, roughly after four characteristic times, a completely defaunated island reached equilibrium in composition and richness (this is consistent with our estimates in Box 1; see also Appendix S1: Fig. S1). Although there are few data monitoring community assembly from scratch, we conjecture that 4–5 characteristic times are a general rule of thumb for a community to reach dynamical equilibrium in species composition after a huge perturbation. A similar time is needed to approach the asymptotical baseline of the Jaccard index, as shown in Box 1 (see also Fig. 1c and Appendix S1: Fig. S2).

Our results coincide with previous studies in several ways. First, we recovered richness and composition patterns, such as Preston’s original STR (Preston 1960), through simulation. Second, our approximation to turnover is analogous to that found in a previous study (Russell et al. 1995). Third, our estimates of temporal scales for different communities coincide with general intuition (Fig. 2). For example, we found slower dynamics for bacterial communities in soil than in aquatic environments, or birds compared with arthropods. Also, the characteristic time for the marine microbial community is comparable with the corresponding estimates in a previous study (Beninca et al. 2008). However, we also identified a contrasting result. A previous meta-analysis found that the dynamics of lacustrine assemblages is faster than the dynamics of marine ones for macroscopic species (Korhonen et al. 2010), whereas we observed the contrary in microbial communities. Further work is needed to discern if characteristic times differentiate



microbial communities from those of larger organisms. In any case, the lack of reliable estimates of timescales in ecology is striking, which may reflect unintentional biases towards evident natural cycles (i.e., seasonal or annual) or merely the lack of appropriate information on temporal trends of species richness (Hortal et al. 2015) because of long-standing institutional disincentives (Wolfe et al. 1987).

The study of microorganisms, which are inconspicuous but increasingly accessible, and their communities also suffer from this lack of information on temporal trends, and may prevent an adequate knowledge of the drivers of ecosystem functioning (Shade and Gilbert 2015). Probably, external drivers are behind the temporal dynamics of microbial communities, in general, and the observed patterns of characteristic time in this manuscript, in particular. Factors such as exposure to different types of food or travel for human-associated communities (Caporaso et al. 2011), seasonal nutrient cycles for aquatic communities (Tinta et al. 2015), or annual cycles of litter production or root exudation in the case of soil communities (Bardgett et al. 2005) are indicated as the main drivers of the dynamics of these communities. However, intrinsic factors such as differential generation times or interactions may also play a role in microbial community dynamics (Bucci et al. 2016). Nonetheless, as the relative sampling frequency indicates some slightly undersampled communities, we are convinced that more frequent surveys will improve our knowledge of the temporal dynamics of microbial communities.

We are also conscious of exceptions and limitations in our approach. A note of caution is due in the case of the estimation of turnover in the Farne Islands. When we considered all species in the community, our estimates of turnover were higher than the observed/predicted ones (Diamond and May 1977). We attribute this discrepancy to four species that were always present in the community, whereas the rest of the species were occasional, effectively violating the assumption of *species equivalence*. Excluding these species solved this discrepancy, although it left a small number of species in each sampling, producing fluctuations that account for the observed deviations. As a general rule, one has to be cautious with the model when its two main assumptions, species equivalence and independence, are clearly violated. Therefore, we recommend its application preferentially to horizontal communities (Loreau 2010, Vellend 2010). Mild deviations from these assumptions, like the ones reported for the arthropod data previously (Cirtwill and Stouffer 2016), are unlikely to affect much the estimates as can be observed here. Thus, the model acts as an *effective model* that integrates mild effects of interactions and niche differences in community dynamics. On the positive side, it is important to remark that the defaunation experiments performed by Simberloff and Wilson (1969) characterize the transient recolonization dynamics, so this data set is very well suited to study the

relaxation to equilibrium in community composition (Fig. 1c).

We have identified two additional issues when estimating characteristic times. The first one arises when we sample much less than characteristic times indicate. It might be happening for the less thoroughly sampled hydroperiods of shallow saline lakes. The second one evidences that characteristic time and temporal autocorrelation are associated, yielding a linear relationship between characteristic time and mean time between samples, which we have observed for bacterial communities in humans (Caporaso et al. 2011). We have devised procedures to identify these cases, as detailed in Appendix S1.

Temporal scales in ecology are seldom studied or characterized. In this contribution, we have shown the usefulness of a stochastic model of island biogeography and derived measures of timescale and compositional change to recover richness and community dynamics. This theoretical work sheds light on the inherent temporal scales of ecological communities. Further work is needed to understand the temporal aspects of different communities and habitats, and elucidate whether our conjecture, that is, that ecological communities require 4–5 characteristic times to reach a dynamic equilibrium in their diversity, hold as additional data sets are analyzed. Moreover, we expect that the approximations to community compositional change we have developed would allow us to compare it across habitats and groups, searching for generalities. We hope that putting the focus on dynamic patterns of community ecology will aid in improving our understanding of the processes and forces that drive diversity in any kind of community.

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