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Pitfalls in quantifying species turnover: the residency effect

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Abstract. The composition of ecological communities changes continuously through time. Understanding this turnover in species composition is a central goal in biogeography, but quantifying species turnover can be problematic. Here, I describe an underappreciated source of bias in quantifying species turnover, namely 'the residency effect', which occurs when the contiguous distributions of species across sampling domains are small relative to census intervals. I present the results of a simulation model that illustrates the problem theoretically and then I demonstrate the problem empirically using a long-term dataset of plant species turnover on islands. Results from both exercises indicate that empirical estimates of species turnover may be susceptible to significant observer bias, which may potentially cloud a better understanding of how the composition of ecological communities changes through time.

Keywords. Extinction, immigration, island biogeography, methods, plants, sample bias

Introduction

Understanding how ecological communities change through time is a central goal in biogeography (see Magurran et al. 2010). Species turnover is an important attribute of biogeographic theory (e.g., Rosindell and Harmon 2013) and a key prediction of the theory of island biogeography (MacArthur and Wilson 1967). As a result, hundreds of empirical studies have quantified turnover in the composition of ecological communities through time using long-term field observations (e.g., Aggemyr and Cousins 2012, Pergl et al. 2012, Stegen et al. 2013). Given the importance of understanding how life on earth will respond to accelerating environmental change, scientific interest in species turnover is likely to increase substantially in the future (Dornelas et al. 2013).

Despite its importance, quantifying species turnover accurately can be problematic. One potential source of bias is 'crypto-turnover' (Lynch and Johnson 1974). When time intervals separating censuses are long, changes in species composition will go unnoticed when species immigrate and then go extinct (or vice versa) in between censuses. The severity of crypto-turnover bias is known to increase with sampling intervals and can lead to spuriously low estimates of species turnover (Simberloff 1976, Diamond and May 1977, Whittaker and Fernández-Palacios 2007, Magurran et al. 2010, Thomašovỳch and Kidwell 2010). Although crypto-turnover was originally described in the context of censuses separated by time, it could also arise through space when sampling points along spatial gradients are positioned too far away from one another to detect species with small distributional ranges.

Here, I highlight an additional factor affecting crypto-turnover bias. I demonstrate that when species appear and disappear quickly from sampling gradients, they are more likely to be missed in widely-dispersed censuses across the gradient. First, I conducted a simple simulation model to illustrate the problem theoretically. I then demonstrate the problem empirically by analysing a dataset of long-term observations of plant species turnover in an island archipelago. Both results indicate that when the average lengths of residency of species across sampling gradients are shorter than census intervals, it can lead to biased estimates of species turnover.

Methods

Simulation model

I first explored how lengths of residency might affect crypto-turnover bias by conducting a simple simulation exercise. During each iteration of the simulation, the average position of 30 hypothetical species was chosen at random across a domain of 100 arbitrary units, which can be conceptualised as either time or space. Each species was then assigned a length of residency (r), namely a contiguous interval across the domain representing its realised distribution. In the context of time, length of residency refers to how long a species maintains a viable population at a single locality (e.g., the length of time a species inhabits an oceanic island). In the context of space, length of residency refers to the distribution of species along spatial gradients (e.g., elevational range). During each iteration, each of the 30 hypothetical species was assigned a length of residency from one of 19 probability density functions, which represented their duration of residency through time or their contiguous distance of residency in space. Probability density functions were normally distributed and had a standard deviation of one. Mean values (mean r = 5 to 95 in five-unit intervals) were chosen to investigate the behaviour of the model at even intervals across the entire the sampling domain. Mean length of residency values outside this range (mean r < 5, mean r > 95) are problematic. As the mean of length of residency functions get closer to the boundaries of the domain, they begin to generate values that are either less than zero, which is impossible (species cannot have negative ranges), or bigger than the specified domain, which is also impossible (species cannot have distributions that are larger than the spatial and temporal boundaries within which they exist). SigmaPlot (2008) was used to interpolate results for intervening values for illustrative purposes.

After all 30 species were assigned a length of residency value and then randomly positioned within the domain, the number of crypto-turnover events (number of species that appeared in the domain and then disappeared between the two censuses) was tallied. Simulations were conducted for 19 census intervals, ranging from 5 to 95 sampling units in five-unit intervals, whose positions were chosen at random from within the domain. This process was iterated 1000 times for each of the 361 combinations of parameter settings (19 average length of residencies x 19 census intervals) and an average number of crypto-turnover events was obtained (code supplied in the supplemental material).

Empirical analyses

To test whether this 'residency effect' can be observed empirically, I analysed a long-term dataset on temporal turnover of plant populations in an island archipelago. I recorded the identity of all plant species present on 41 small, rocky islands located off the southern tip of the North Island of New Zealand (41°20'S, 174°47'E) for eight consecutive years (2004-2011), yielding a continuous annual record of immigrations and extinctions. Identical censuses were conducted twice during each growing season to ensure a thorough and accurate record of all species present each year (i.e. to minimise 'pseudo-turnover', see Nilsson and Nilsson 1985). Islands in the archipelago were very small (average = 98 m^2, range = 7–670 m^2) and heavily influenced by ocean-born disturbances (*sensu* Burns and Newfield 2009, Morrison and Spiller 2008). They supported only sparse plant communities (average species richness = 5, range = 1–14) with very rapid turnover rates (i.e. short lengths of residency). A more detailed description of the study site, sampling protocol and spatial patterns in diversity are described elsewhere (Burns et al. 2009).

First, I conducted an ordinary least-squares (OLS) regression to test whether rates of crypto-turnover declined with the average length of residency of species on each island. I began by calculating the length of residency for all species occurring on each island as duration of time (i.e., total number of years, 0–8) when they were observed. Length of residency values were then averaged among species to obtain a single value for each island, which were then regressed against crypto-turnover rates for each island. A crypto-turnover event occurred when a species immigrated and then went extinct, or conversely when it went extinct and then re-immigrated, between the second and seventh year of study, such that it would not have been observed if sampling was restricted to just the first (2004) and last (2011) year of sampling (i.e., the longest hypothetical census interval). However, the total number of crypto-turnover events registered on each island will co-

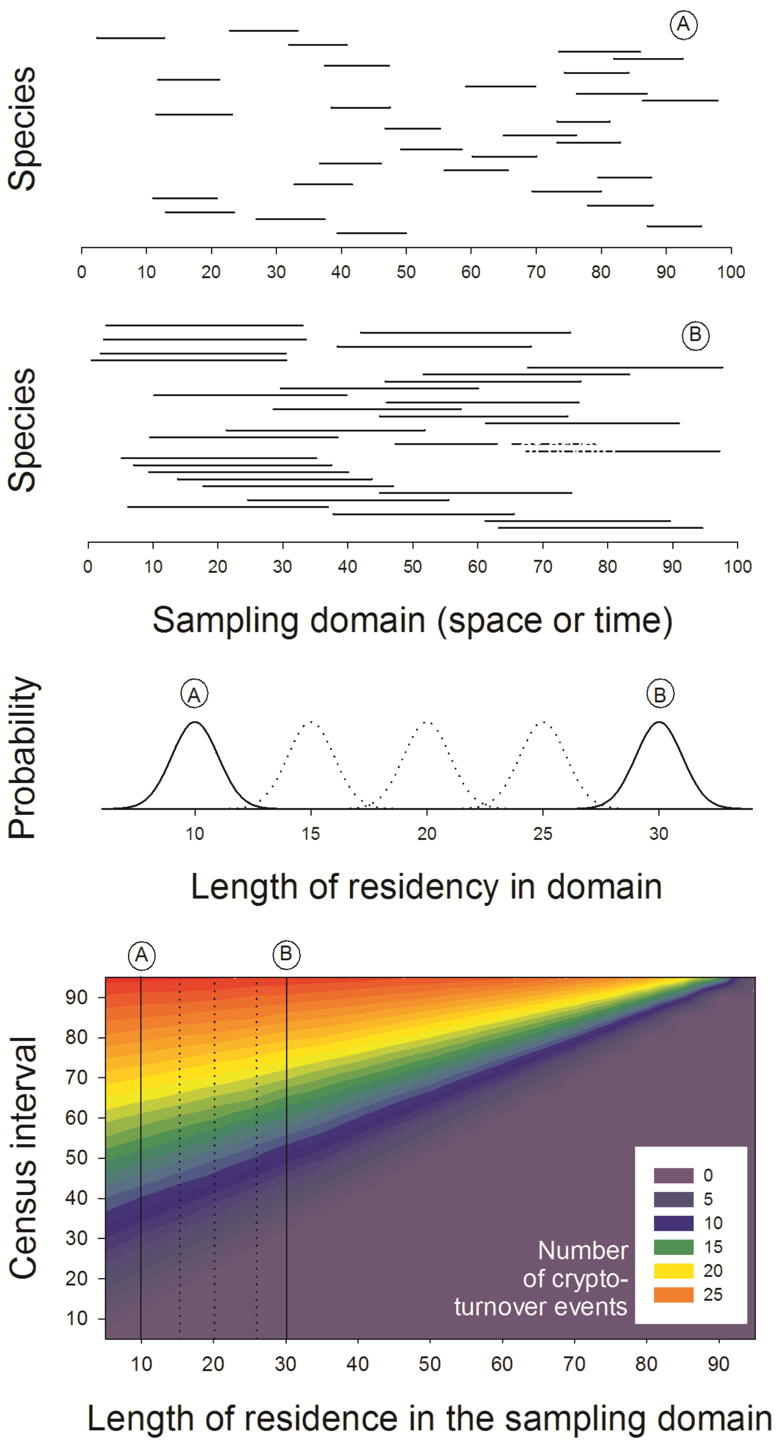

Figure 1. Results of a simple simulation demonstrating the relationship between crypto-turnover and the average length of residency of species across sampling domains in space or time. The top two panels illustrate two simulation replicates. (A) illustrates randomly situated ranges of 30 species whose average length of residency along the sampling domain is 10, while (B) illustrates 30 species with an average length of residency of 30. The third panel illustrates probability density functions for five length of residency settings from which lengths of residency were drawn randomly for each species. The two functions in the third panel with solid curves, which are labelled 'A' and 'B', correspond with the simulation replicates in the top two panels labelled 'A' and 'B'. The bottom panel depicts the results of simulations across a wide range of census intervals (y-axis: 5–95) and lengths of residency (x-axis: 5–95). Coloured contour lines illustrate the severity of crypto-turnover bias. Vertical lines represent the five lengths of residency illustrated in the third panel (10–30 in five unit intervals). Solid lines refer to the two length of residency values labelled 'A' and 'B' in the top three panels. Crypto-turnover bias increases with census intervals, declines with the average length of residency across the sampling domain and becomes negligible when length of residency exceeds census interval.

vary passively with the total number of species present; all else being equal, islands housing four species are four times more likely to experience a crypto-turnover event than an island housing only a single species. To remove this confounding effect, the total number of crypto-turnover events was divided by the total number of species registered on each island across the 8-year sampling period. Islands that failed to register a single immigration or extinction event were removed because they were uninformative. Data conformed to assumptions of OLS without transformation.

Second, I conducted reduced major axis regression (RMA) to test whether long-interval estimates of extinction and immigration accurately predicted true rates of immigration and extinction. Long-interval estimates of extinction and immigration were calculated as the number of events that occurred between only the first (2004) and last (2011) census. True rates of immigration and extinction were calculated as the total number of events that occurred on each island across all eight years of sampling. Slope and intercept parameters and their 95% confidence limits (CI) were calculated using the 'lmodel2' (Legendre 2013) package in R (R Development Core Team 2012) to test for differences from isometry (a relationship with a slope of one and intercept of zero). Data conformed to assumptions of RMA without transformation.

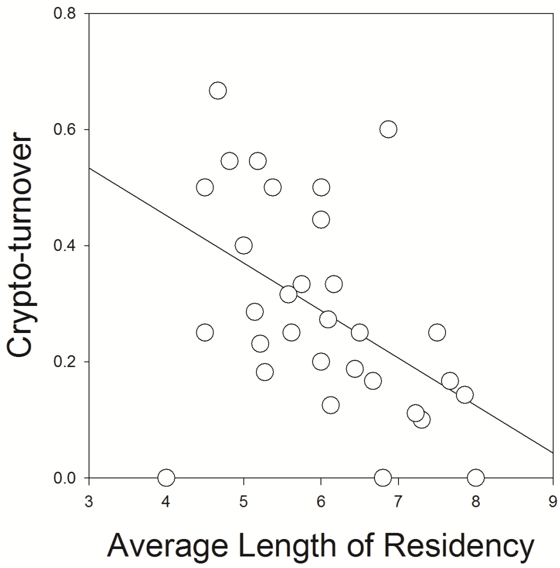

Figure 2. Relationship between the length of residency (average number of years that species occured on a given island) and rates of crypto-turnover for 36 small islands. Rates of crypto-turnover were defined as the number of species that immigrated and then went extinct between the first (2004) and last (2011) years of the study (and vice versa) divided by the total number of species present.

Results

The simulation model illustrates that when species appear and disappear from the sampling domain quickly, or in other words when they have small lengths of residency, they are more likely to be missed in disparate censuses (Figure 1). Species also are more likely to go unnoticed when census points are widely scattered across the domain. When both factors are viewed jointly, crypto-turnover bias increases when the ratio of census intervals to lengths of residency increases above one, and it becomes negligible when lengths of residency exceed census intervals.

Empirical analyses showed that rates of crypto-turnover declined with average lengths of residency (R^2 = 0.214, p < 0.003; Figure 2), as predicted by the simulation model. Results also showed that long-interval estimates of turnover provided a biased representation of true rates of turnover (Figure 3). The number of immigration events that were tallied between just the first and last census were correlated with the total number of immigration events that were registered throughout the study period (R^2 = 0.342, p < 0.001). However, the intercept parameter was greater than zero (1.489; 95% CI = 0.902, 1.926) and the slope was greater than one (2.031; 95% CI = 1.515, 2.722). Similar results were observed for extinction. Although long-interval estimates of extinction events scaled positively with the total number of extinction events (R^2 = 0.189, p = 0.011), the intercept was greater than zero (1.334; 95% CI = 0.696, 1.795) and the slope was greater than one (2.749; 95% CI = 1.988, 3.081). Therefore, crypto-turnover bias increased on islands that experienced higher actual rates of turnover, or in other words, shorter durations of residency.

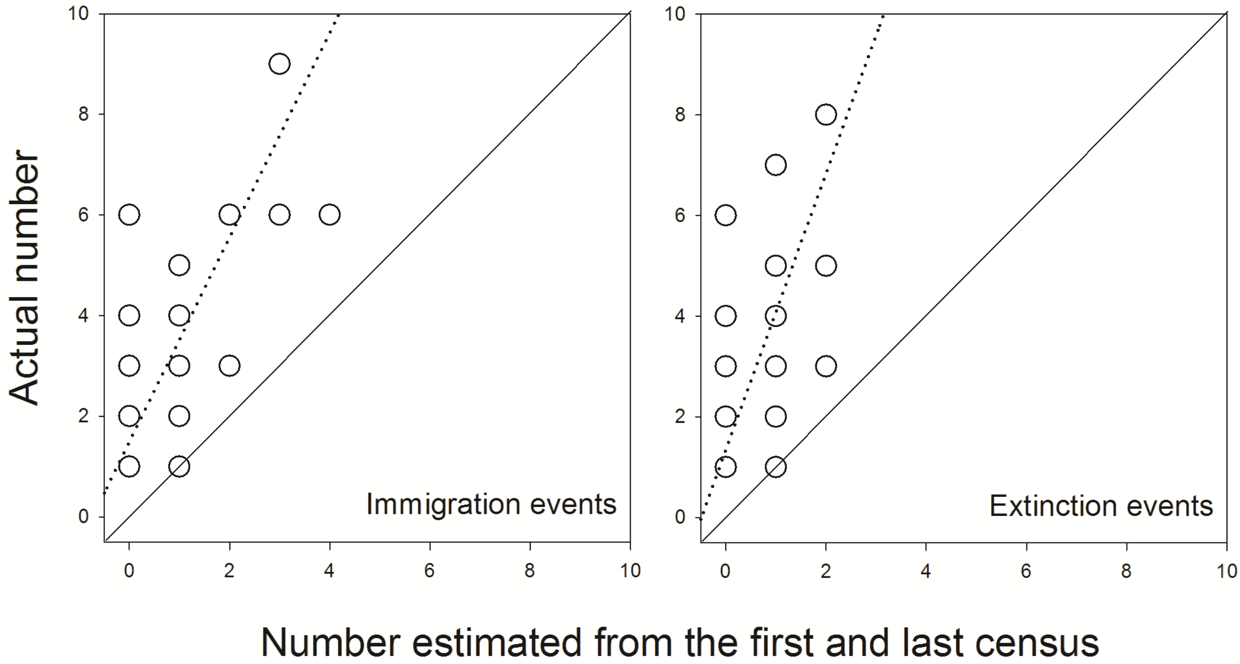

Figure 3. Relationships between the total (unbiased) number of immigration events (left) and extinction events (right) observed in eight consecutive years of censuses on 33 islands (y-axis) and the number of events estimated from just the first and last census (i.e. including crypto-turnover, x-axis). Solid lines represent isometry and dashed lines are the observed statistical relationships calculated with reduced major axis regression. Both relationships have slopes greater than one, indicating that crypto-turnover bias accelerates with actual turnover rates.

Discussion

Species turnover through time is a key prediction of biogeographic theory and studies testing this prediction often separate censuses widely through time (e.g., Burns and Newfield 2009). Results reported here demonstrate that crypto-turnover bias arising from long-interval censuses will be especially pronounced on islands with lower average lengths of residency, or in other words, higher actual rates of turnover. This 'residency effect' occurs only when census intervals are longer than lengths of residency and it increases as census intervals supersede residencies. Consequently, when lengths of residency are short relative to census intervals, true rates of species turnover may often be underestimated.

The severity of residency effects are likely to covary with both the physical characteristics of islands and the traits of the species they contain. Island attributes that increase turnover rates could predispose particular islands to greater residency effects. For example, islands that are more exposed to ocean-borne disturbances, which are known to increase turnover rates in some archipelagos (Burns and Newfeld 2009), could suffer greater rates of crypto-turnover bias relative to sheltered islands when observed across the same census intervals. Turnover rates are also known to vary among species, with longer-lived species displaying lower turnover rates than short-lived species (Schoener 1983). So islands housing greater numbers of short-lived species may suffer greater residency effects, all else being equal.

Analyses presented here focus on turnover through time, but the residency effect is equally plausible when space is used as a sampling domain (see also Soininen 2010). In this context, sampling points should be separated by distances that are smaller than the contiguous distributions of species. Minimising the residency effect and other potential sources of bias associated with measuring species turnover, both in space and in time, is likely to become increasingly important as biogeographers endeavour to understand how life on earth will respond to accelerating global environmental change.

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