



# A model-independent test for the presence of regulatory equilibrium and non-random structure in island species trajectories

Michael Golinski\* and William J. Boecklen

Department of Biology, Box 30001, New Mexico State University, Las Cruces, NM 88003, USA

## ABSTRACT

**Aims** To test a key prevision of the dynamic equilibrium theory of island biogeography, namely that changes in species numbers on islands over time (hereafter, species trajectories) are equilibrated, and to characterize aspects of the dynamical properties of species change over time using a model-independent test.

**Methods** We tested for regulatory equilibrium and non-random structure in species numbers through time by comparing observed correlation coefficients at lag- $k$  for species trajectories from four true islands and two habitat islands. First, we estimated the shape of the autocorrelation function for each observed species trajectory by calculating correlation coefficients of the observed data between pairs of values  $N_{t-k}$  and  $N_t$  separated by lag- $k$  ( $k = 1, 2, \dots, N - 1$ ). Second, we tested the observed correlation coefficients at each lag against a distribution of correlation coefficients generated by randomly ordering observed numbers in the species trajectories.

**Results** The patterns of autocorrelation functions for all but one of the observed species trajectories did not exhibit evidence of regulatory equilibrium, and, in fact, closely matched what would be expected from a non-stationary or 'random walk' process. The majority of the correlation coefficients generated from the observed species trajectories did not deviate significantly from correlation coefficients produced by the randomized trajectories. However, there was strong evidence of unusual positive autocorrelation at small time lags for birds on islands measured annually (2- to 4-year lags) and for arthropods on islands measured weekly (7- to 8-week lags), suggesting some degree of structure in change in species richness over time.

**Main conclusions** The autocorrelation function patterns for all but one of the observed species trajectories showed various forms of non-stationarity. These types of patterns suggest that the numbers of species through time gradually wandered away from their initial sizes. Our model-independent test of individual correlation coefficients revealed significant structure in the observed species trajectories. These trajectories appear to be non-random at relatively short lag intervals, indicating a process with short memory.

## Keywords

Autocorrelation function, correlation coefficient, dynamic equilibrium theory, island biogeography, non-stationarity, regulatory equilibrium, species trajectory, stationarity.

\*Correspondence: Michael Golinski, Department of Biology, Box 30001, New Mexico State University, Las Cruces, NM 88003, USA. E-mail: mgolinsk@nmsu.edu

## INTRODUCTION

The dynamic equilibrium theory of island biogeography predicts that the species numbers on islands remain constant

over time (MacArthur & Wilson, 1963, 1967; Simberloff, 1974). Islands are colonized by immigrant species at a rate proportional to the number of extinctions of species on that island. While the composition of species changes, the

overall number remains constant. A slight variation about equilibrium in species numbers over time is determined by the probabilistic nature of extinction and immigration events.

There have been two major approaches to determining whether species numbers on islands exhibit equilibrium as predicted by the dynamic equilibrium theory of island biogeography. The first approach relies on fixed criteria such as mean-to-variance ratios in species numbers over time (MacArthur & Wilson, 1963), percentage difference in species numbers over time (Diamond, 1969), and a coefficient of variation in species numbers over time (Diamond & May, 1977; Abbot & Black, 1980). Simulated analyses have shown that such fixed criteria have limited utility (Boecklen & Nosedal, 1991).

The second approach is to use statistical tests based on Markov models. This approach is used to determine how much variation in species number is inconsistent with an equilibrium number of species (Simberloff, 1983b; Boecklen & Nosedal, 1991). The construction of the Markov models in these studies was based on the following rules: (1) the transition probabilities (i.e. species absence to presence, presence to absence, absence to absence, and presence to presence) were estimated directly from the data; and (2) changes in the state of a species at  $t$  to that at  $t + 1$  (present/absent) were determined by refereeing a pseudo-random deviate to the estimated transition probabilities. Using this approach, Simberloff (1983b) determined that none of three species trajectories for Farne Island, Skokholm Island, and Eastern Wood differed significantly from those generated by the Markov model. However, Boecklen & Nosedal (1991) contended that interpretation of the results generated from Markov models might produce Type I and Type II statistical errors. They caution that one does not know if the close agreement between the null model and actual species trajectory data results because the Markov model parameters are estimated from the data and so the model describes the data well, or because changes in species numbers through time are random.

Statistical errors associated with model-dependent approaches can be avoided by using model-independent methods. In this paper, we introduce a model-independent test for determining if species trajectories are non-equilibrium or equilibrium, and if they exhibit non-random structure. We examined species trajectories in two ways. First, we used traditional time-series analysis to test for the presence of regulatory equilibrium in species trajectories. We examined the autocorrelation function (ACF) (Box & Jenkins, 1976; Finerty, 1980; Nisbet & Gurney, 1982) of lag- $k$  autocorrelated species trajectories to measure the extent to which change in species numbers over time showed an equilibrium or non-equilibrium pattern. Second, we compared the autocorrelation coefficients of observed species trajectories with those generated by randomizing the order of species richness. Our test detected little evidence of strong regulatory equilibrium, but did detect non-random structure

in the observed species trajectories at short and long time lags.

## MATERIALS AND METHODS

We analysed six species trajectories from the literature (Table 1). Four of these trajectories represent true islands, while Farne and Eastern Wood are habitat islands. The number of censuses for annual data (Skokholm, Farne, and Bardsey) ranged from 16 years for Bardsey Island to 34 years for Skokholm Island. Weekly census data were collected on *Spartina* islets CI and CJ for 53 weeks.

### Test for regulatory equilibrium

The ACFs for observed species trajectories were estimated by calculating correlation coefficients ( $r_k$ s) between pairs of values  $N_{t-k}$  and  $N_t$  separated by lag- $k$  ( $k = 1, 2, \dots, N - 1$ ). Values of  $r_k$  were then plotted as a function of lag- $k$ . We then compared observed ACFs with those produced by both stationary and non-stationary processes (see Turchin & Taylor, 1992). For example, a non-stationary time series, such as that produced from a random walk, shows increases or decreases in a running average of species numbers over time. The ACF for a non-stationary time series decays more slowly than exponentially, and can show a pattern of negative or positive autocorrelation at short or long lags (Fig. 1a). Alternatively, a stationary time series, such as that produced from a white-noise process, shows no increase or decrease in a running average of species numbers over time, and has an ACF that decays to zero in a monotonic or oscillatory pattern (Fig. 1b).

### Test for non-random structure

To determine if an observed species trajectory exhibited non-random structure, we compared that trajectory with tract-

**Table 1** Species trajectories examined for regulatory equilibrium and non-random structure

Island	Taxa	Time period	Source
Bardsey	Birds	16 years	Diamond (1984)
Eastern Wood	Birds†	26 years	Williamson (1981)
Farne	Birds†	29 years§	Diamond & May (1977)
Skokholm	Birds*	34 years¶	Abbot & Grant (1976)
<i>Spartina</i> islet CI	Arthropods‡	53 weeks	Rey (1981)
<i>Spartina</i> islet CJ	Arthropods‡	53 weeks	Rey (1981)

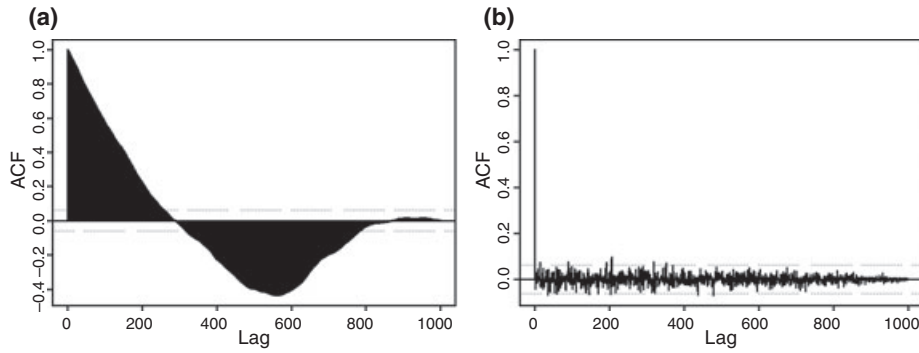
\*Passerine birds.

†Land birds.

‡Two species on islet CI went into diapause. Four species on islet CJ went into diapause. All were considered present until the end of the time series.

§There is a gap of 6 years (1940–45). The randomization algorithm ignored this gap.

¶There is a gap of 1 year (1957). The randomization algorithm ignored this gap.



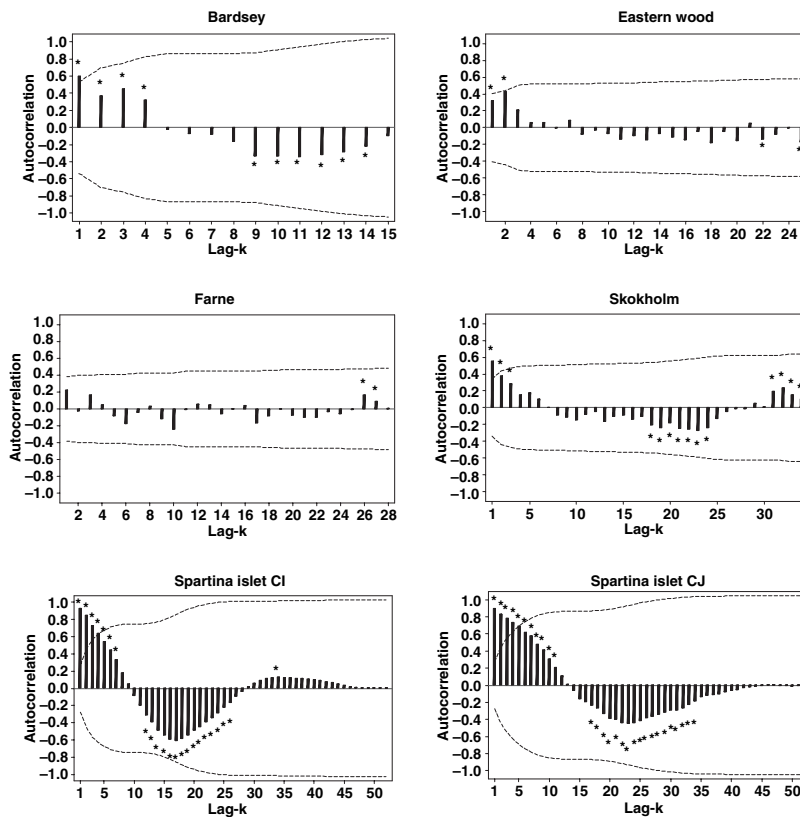
**Figure 1** Autocorrelation functions for (a) a simulated random-walk time series ( $N = 1000$ ) with non-stationary mean and no periodicity, and (b) a simulated white-noise time series ( $N = 1000$ ) with stationary mean and constant variance. The time unit for each time series is arbitrary, with lag- $k = 1, 2, \dots, N - 1$ . The dotted lines indicate the 95% confidence limits for significant autocorrelation. Note that there is always positive autocorrelation at lag- $k = 0$ .

ories produced by randomizing the order of observed species numbers. In particular, for each species trajectory, we generated 5000 random trajectories, and at each lag, we compared the observed  $r_k$  (lag- $k$  autocorrelation coefficient) with the 5000 randomized trajectories ( $r'_k$ ). The significance level of  $r_k$  was determined to be the proportion of values that were as extreme as or more extreme than the values of  $r'_k$  in the randomized distribution. If  $r_k$  was positive and greater than 95% of  $r'_k$ , it provided evidence of significant positive autocorrelation, whereas if  $r_k$  was negative and less than 5% of  $r'_k$ , it provided evidence of significant negative autocorrelation.

**RESULTS**

**Evidence of regulatory equilibrium and non-random structure**

Evidence of regulatory equilibrium in observed species trajectories was determined by observing the shape of the ACF for each observed species trajectory. ACF plots were constructed by calculating correlation coefficients of the observed data between pairs of values  $N_{t-k}$  and  $N_t$  separated by lag- $k$  ( $k = 1, 2, \dots, N - 1$ ) (Fig. 2). Five of the observed species trajectories did not exhibit strong evidence of regula-



**Figure 2** Autocorrelation function plots. Values with \* denote values for observed  $r_k$  that deviate significantly from those produced by randomizing species order (see text for details). Dashed lines indicate 95% confidence intervals for the observed autocorrelation function.

**Table 2** Summary of autocorrelation function (ACF) patterns for each observed species trajectory

Island	Structure	ACF	Regulatory equilibrium
Bardsey	Non-stationary	Positive autocorrelation ( $k = \text{years } 1\text{--}4$ )	No, non-periodic
Eastern Wood	Non-stationary	Positive autocorrelation ( $k = \text{years } 1\text{--}2$ )	No, non-periodic
Farne	Stationary	Positive autocorrelation ( $k = \text{years } 26\text{--}27$ )	No, non-periodic
Skokholm	Non-stationary	Positive autocorrelation ( $k = \text{years } 1\text{--}3$ and $31\text{--}34$ )	No or a very long cycle
<i>Spartina</i> islet CI	Non-stationary	Positive autocorrelation ( $k = \text{weeks } 1\text{--}7, 34$ )	No or a very long cycle
<i>Spartina</i> islet CJ	Non-stationary	Positive autocorrelation ( $k = \text{weeks } 1\text{--}11$ )	No or a very long cycle

tory equilibrium in species numbers. In fact, all of the observed ACF plots, with the exception of Farne, were suggestive of a non-stationary process. Such a process is observed in the ACF plots for Bardsey, the *Spartina* islets, Eastern Wood, and Skokholm, which do not decay to zero, either in a monotonically or in an oscillatory pattern (Box & Jenkins, 1976), but instead become progressively more negative as the lag increases. The pattern of change in species richness over time on Farne Island was similar to that expected from a non-periodic stationary process, in which species numbers decayed monotonically and oscillated around a constant mean and variance. This type of ACF pattern indicates a system dominated by white noise, rather than a system that is under regulatory equilibrium.

In order to determine if a given observed species trajectory exhibited non-random structure, we compared the  $r_k$  values generated from that trajectory with corresponding correlation coefficients in trajectories generated by randomizing the order of observed species numbers. Each ACF plot indicated  $r_k$  values that were significantly different from those generated by random (Fig. 2). The qualitative picture that emerges from each ACF plot is that the majority of  $r_k$  values generated from the observed species trajectories do not deviate significantly from those generated by the randomized trajectories. However, there was strong evidence of unusual positive autocorrelation at small time lags for birds on islands measured annually (2- to 4-year lags) and for arthropods on islands measured weekly (7- to 8-week lags), suggesting some degree of structure in the change in species richness over time. Table 2 summarizes the results obtained from tests for regulatory equilibrium and non-random structure.

## DISCUSSION

The focus of this study has been on testing for the presence of regulatory equilibrium in species trajectories. As discussed above, fixed-criteria methods for determining regulatory equilibrium are useless, and Markov models are problematic. To avoid these problems, we have used a traditional time-series analysis, with an emphasis on the form of the ACF, to test for regulatory equilibrium in species trajectories. Evidence of regulatory equilibrium in observed species trajectories was determined by comparing the shapes of the ACFs with the shapes of ACFs produced by stationary and non-stationary processes. The type of behaviour exhibited by five of the

species trajectories examined in this study was indicative of a non-stationary process (e.g. a random walk), whereby species numbers through time drifted (positively or negatively) away from the mean as the lag became larger. The use of a fixed-criteria test for regulatory equilibrium in species trajectories led MacArthur & Wilson (1963) to conclude that variance-to-mean ratios in species numbers vary between 0.25 and 0.75 for islands at or near equilibrium, while Diamond (1969) concluded that bird faunas of the Channel Islands (not analysed here) exhibited equilibrium, since species numbers differed by no more than 16% for surveys conducted in 1917 and 1968. Diamond & May (1977) viewed a coefficient of variation in species numbers less than or equal to 20% as evidence of equilibrium, while Abbot & Black (1980) required a coefficient of variation less than or equal to 5%. Boecklen & Nosedal (1991) point out that these types of fixed-criteria tests are not statistical, and therefore lack utility.

Based on the results of a Markov model, Simberloff (1983b) concluded that species trajectories for Farne Island, Skokholm Island, and Eastern Wood were non-equilibrial. We, similarly, found no strong evidence of regulatory equilibrium in the species trajectories for Skokholm Island and Eastern Wood. Neither did we find strong evidence for regulatory equilibrium in Bardsey Island, nor for the *Spartina* islets. Rey & Strong (1983) used the *Spartina* islet data to test the most basic assumptions of the MacArthur–Wilson model: extinction rates are positively correlated, and immigration rates negatively correlated with the number of species residing on a given island (MacArthur & Wilson, 1967). Their study found a significant correlation between change in number of species as a function of immigration and extinction rates, which led the authors to conclude that these correlations were in the direction predicted by the dynamic equilibrium model (i.e. changes in species numbers through time are equilibrial). We are unaware of studies testing whether species trajectories for Bardsey Island are equilibrial. While Abbot & Grant (1976) concluded that species trajectories for Farne Island are equilibrial, the ACF pattern for Farne Island indicates that species trajectories are stationary and non-periodic, which is suggestive of a system dominated by white noise. A potential significant constraint on using traditional time-series analysis is that avian data sets are of short duration and therefore do not lead to a powerful test. In the future, we hope to develop new model-independent approaches to circumvent this.

We conclude that the compelling result generated from this study is the presence of non-random structure in some of the species trajectories. To our knowledge, no studies have been undertaken to test for non-random structure in species richness over time. We attribute this to the fact that the fixed-criteria methods and Markov models used in previous studies were constructed to test only for regulatory equilibrium, and are not appropriate tests for detecting structure in species richness over time. To determine if an observed species trajectory exhibited non-random structure, we compared that trajectory with trajectories produced by randomizing the order of observed species numbers. While some values of  $r_k$  were positively correlated at short lags, there was considerable variation at longer lags. Our test showed that all of the observed species trajectories (with the exception of Farne) exhibited positive autocorrelation through the first few data points, and negative autocorrelation near the end of the time series. Only Skokholm Island and the *Spartina* islets exhibited negative autocorrelation near the middle of the time series. In a few cases, there was apparent structure at long lags. The *Spartina* islets, in particular, have a distinct pattern to their ACFs, and many of the  $r_k$  values are significant. However, it is perhaps difficult to ascribe biological importance to such results, since the pattern may be an artefact of short sampling intervals. One may ask if the type of structure in the observed species trajectories at different time lags is common in nature. We believe that the answer to this question requires a larger compendium of case studies and more theoretical work focusing on the mechanism responsible for the presence of pattern.

## REFERENCES

- Abbot, L. & Black, R. (1980) Changes in species composition of floras on islets near Perth, Western Australia. *Journal of Biogeography*, **7**, 399–410.
- Abbot, L. & Grant, P.R. (1976) Non-equilibrium bird faunas on islands. *The American Naturalist*, **110**, 507–528.
- Boecklen, W.J. & Nosedal, J. (1991) Are species trajectories bounded or not? *Journal of Biogeography*, **18**, 647–652.
- Box, G.E.P. & Jenkins, G.M. (1976) *Time series analysis: forecasting and control*. Holden Day, San Francisco.
- Diamond, J.M. (1969) Avifaunal equilibrium and species turnover rates on the Channel Islands of California. *Proceedings of the National Academy of Sciences USA*, **64**, 57–63.
- Diamond, J.M. (1984) 'Normal' extinctions of isolated populations. *Extinctions* (ed. by M.H. Nitecki), pp. 191–246. University of Chicago Press, Chicago.
- Diamond, J.M. & May, R.M. (1977) Species turnover rates on islands: dependence on census interval. *Science*, **197**, 266–270.
- Finerty, J.P. (1980) *The population ecology of cycles in small mammals*. Yale University Press, New Haven.
- MacArthur, R.H. & Wilson, E.O. (1963) An equilibrium theory of insular zoogeography. *Evolution*, **17**, 373–387.
- MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton.
- Nisbet, R.M. & Gurney, W.S.C. (1982) *Modelling fluctuating populations*. John Wiley & Sons, Chichester.
- Rey, J. (1981) Ecological biogeography of arthropods on *Spartina* islands in northern Florida. *Ecological Monographs*, **51**, 237–265.
- Rey, J.R. & Strong, D.R. (1983) Immigration and extinction of salt marsh arthropods on islands: an experimental study. *Oikos*, **41**, 396–401.
- Simberloff, D. (1974) Equilibrium theory of island biogeography and ecology. *Annual Review of Ecology and Systematics*, **5**, 161–179.
- Simberloff, D. (1983b) When is an island community in equilibrium? *Science*, **220**, 1275–1277.
- Turchin, P. & Taylor, A. (1992) Complex dynamics in ecological time series. *Ecology*, **73**, 289–305.
- Williamson, M. (1981) *Island populations*. Oxford University Press, Oxford.

## BIOSKETCHES

**Michael Golinski** has research interests that include the evolution of virulence in parasites, methods for endophyte classification, time-series analysis, fractals in nature, non-linear dynamics in ecology, island biogeography, and the role of mutualism in community stability.

**William J. Boecklen** has research interests in statistical ecology, conservation biology, community ecology, and insect–plant interactions, with particular emphasis on the role of endophytic fungi in mediating tri-trophic interactions involving plants, herbivores and natural enemies.

---

Editor: Nicholas Gotelli