The curious case of Skokholm: equilibrium, non-equilibrium and phase shifts in an island landbird assemblage

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Abstract

Previous work has indicated that the landbirds of Skokholm island (Wales) are not in equilibrium as defined in MacArthur-Wilson's classic theory of island biogeography. This study takes a new dataset with over six decades of data and investigates equilibrium on Skokholm using cluster analysis to identify periods of turnover stability. The attributes of the identified periods were investigated in relation to the MacArthur-Wilson model using analyses of change in numbers of species, S, from one year to the next and measures of variability in S quantified for each of the periods identified together with a consideration of the dynamics in the numbers of species by habitat groupings. Cluster analysis identified four main periods of which two middle periods appeared to be in equilibrium but with a phase shift in-between. The first and last periods showed non-equilibrium dynamics but plots of species by habitat groupings suggested that this was due to habitat changes going on at those times. This decadal long dataset indicates that the landbirds of Skokholm exhibit periods of both equilibrium and non-equilibrium with the latter attributable to habitat change. The apparent phase shift in the equilibrium number of species was unexpected within the framework of island biogeographic theory and not easily explained using the current MacArthur-Wilson framework. There is a need to integrate the theory of island biogeography with more recent work on alternative stable states, tipping points, and phase (or regime) shifts, together with equilibrium and non-equilibrium dynamics, into a single framework.

Key words: island biogeography, equilibrium, phase shift

INTRODUCTION

The theory of island biogeography ('ETIB') (MacArthur and Wilson 1967) is an equilibrium model in which the number of species on an island arises from a balance between the opposing rates of immigration and extinction with the equilibrium number being dependent upon island size and isolation from the mainland (or source pool for archipelagos). Although ETIB is a dynamic model which recognises that colonisation and local extinction on islands will be ongoing it may be seen in the light of a strong tradition in ecology of equilibrium-thinking particularly with respect of the balance of nature paradigm (Connell 1978, Reice 1994, Rohde 2005). Equilibrium concepts have been questioned particularly in marine and aquatic environments with tipping points and regime shifts being features of systems undergoing over-exploitation and subject to climate instability (Gido et al. 2000, Collie et al. 2004, Weijerman et al. 2005, deYoung et al. 2008). In terrestrial environments, whilst non-equilibrium ideas have been addressed in relation to the role of disturbance in the maintenance of species richness of woody species in tropical rainforests (Connell 1978, Sousa 1984, Wu and Loucks 1995), little work has been done on animals (Sousa 1984).

Given sufficiently long-term data, ideas central to ETIB concerning for example, the shape of the relationships between the rates of immigration and extinction, respectively, and the number of species are testable and a number of studies have attempted to do this (see for example, Reed 1980, Williamson 1981, 1983, Nilsson and Nilsson 1982, Simberloff 1976, 1983, Pimm et al. 1988, Whittaker et al. 1989, Bush and Whittaker 1991, Russell et al. 1995, Manne et al. 1998). Here I take a recently updated long-term dataset for Skokholm (McCollin 2014a, 2014b), previously used in a shorter form by a number of workers (e.g., Abbott and Grant 1976, Williamson 1981, 1983, Simberloff 1976, 1983, Pimm et al. 1988, Russell et al. 1995, Manne et al. 1998, Philippi et al. 1998, Russell et al. 2006, Stracey and Pimm 2009), and test for the presence of equilibrium by considering how the numbers of species vary over time. Although one other island, Krakatau, has featured greatly in discussions of equilibrium (e.g., Thornton et al. 1990, 1993), Skokholm was chosen here since this is one of the longest near-continuous datasets of its type plus various authors have questioned whether the landbirds of the island are in equilibrium (Abbott and Grant 1976, Williamson 1981, 1983, Simberloff 1983, Russell et al. 2006, Golinski and Boecklen 2006).

MATERIALS AND METHODS

Study Site

Skokholm is a 96ha island lying c. 3.5km off the coast of Pembrokeshire, Wales and is a nature reserve of the Wildlife Trust of South and West Wales. The island has internationally important seabird populations such as Manx Shearwater *Puffinus puffinus* but here I focus on the landbirds, breeding records for which date back to 1928 (Lockley 1938, Lack 1969, Williamson 1981, Thompson 2007).

Analysis

Here, I use the extended dataset for Skokholm 1928-2002 (McCollin 2014a, 2014b). These data comprise numbers of breeding pairs of landbirds on the island with data being derived from counts, territory mapping and, for more common species, estimates, undertaken by wardens present during the breeding season each year. There is a hiatus in the time series as no surveys were done in the war years between 1940-1945. The abundance data were tested for reliability by McCollin (2014a) and no bias in numbers could be detected when tested against randomised draws of data. In order to identify periods of relative stability, these data were entered into an agglomerative cluster analysis using minimum variance or error sum of squares (Ward’s method) and a Bray-Curtis similarity measure using CAP4 software (Pisces Conservation Ltd, no date). The periods thus identified are mapped onto the numbers of species by years graph. Although the data form a time series, it is implicit in the MacArthur-Wilson model that numbers of species depend on a balance between the rates of immigration and extinction on individual islands thus the assumption is that the data are non-independent. In practice, as the assemblage comprises a number of species, each of which comprises populations – some of which are resident year-round - the data from one year to the next may not be independent. The potential for immigration to occur depends on whether species are present in the species pool on the nearby mainland. Over long timescales the avifauna of the mainland may also be subject to turnover such that species like Corncrake *Crex crex*, which had a breeding pair on Skokholm in 1930, had almost disappeared from the nearby mainland by 1961 (Lockley 1961) despite being common and widespread on the adjoining mainland in the late 19th Century (Mathew 1894). Such species would be highly unlikely to recolonise once lost.

For each of the four periods identified by cluster analysis, equilibrium is tested for by correlating the change in the numbers of species from one year to the next (ΔS) against the number in the first of these years (Williamson 1987). These correlations show the strength of the return tendency in the time series akin to a 'ball and valley' equilibrium model (DeAngelis and Waterhouse 1987). No assumptions are made about the causal nature of this return tendency hence these plots are tested using a Spearman's rank correlation coefficient, r_s.

At equilibrium the number of species, S, on an island should remain relatively constant through time although some variability in S is to be expected due to the stochastic nature of extinctions and colonisations (Diamond and May 1977, Gotelli and Graves 1996). However, little guidance exists in terms of how much variability to allow around the mean S although MacArthur and Wilson (1967) suggested that the variance to mean ratio for S should attain a value of 0.5 at equilibrium. Simberloff (1983) noted the arbitrary nature of particular values proposed with a coefficient of variation of less than 0.2 (Diamond and May 1977) or less than 0.05 (Abbott and Black 1980) and variation in species numbers less than 16% all being classed as equilibrial (Diamond 1969). Here, measures of variation, including the coefficient of variation (CV) and the variance to mean ratio, are used to gauge the variability in numbers of species over time, and both measures are used to allow comparison to the literature.

Finally, to help interpret change the species were classified into ecological groups and numbers of species in each group are plotted by time. The species and their habitat requirements are well known (e.g., Fuller 1982) and species were classified according to habitat use and refined by expert judgement (Graham Thompson, warden on Skokholm from 1995 for c. 10 years, pers. comm.).

RESULTS

The cluster analysis divided the landbird data into four distinct periods: 1928–1947; 1948–1962; 1963– 1979; and 1980–2002 (Appendix 1, Fig. A1; Fig 1). The periods identified by cluster analysis (Appendix 1, Fig. A1) conform to a visual inspection of the data (Fig. 1): 1928–1947 being a decline from 19 down to 10 breeding bird species; 1948–1962 being a period of stability with a mean of 10.1 breeding species and low variability; 1963– 1979 being another period of stability with a mean of 13.5 species and slightly higher variability; and 1980–2002 showing an increase with a minimum of 12 and a maximum of 24 species. Compared to the two middle periods, the CVs and the variance/mean ratios for the first and last periods were highest at 0.18 and 0.15, and 0.49 and 0.69, respectively. Further, the numbers of years in which S was ± 10% was highest for the first and last periods (Table 1). Although the mean numbers of species in the middle periods showed greater stability, there was a very highly statistically significant difference between the mean number of species in these two periods ($t = 4.1$, $p < 0.001$, $df = 28$). The analysis of change in numbers of species (ΔS) versus S showed statistically significant and correspondingly higher r_s and lower p-values for the Spearman rank correlation coefficients for the two middle periods when compared to the outlying periods (Table 1). Fig. 2 shows the change in numbers of species by habitat groupings. This plot highlights the differences in stability between different groups of species and point to the role of habitat change (see Discussion).

DISCUSSION

Using a variety of approaches previous analyses have found that the landbirds on Skokholm are not in equilibrium (Abbott and Grant 1976, Williamson 1981, 1983, Russell et al. 2006). In the approach taken here, the time series has been divided up according to an objective method and the overall dynamics of S over time is characterised by these four distinct periods including two distinct periods of equilibrium: 1948–1962, and 1963– 1979. Whilst, the analysis of ΔS versus S indicates that for all years taken together, it appears that the number of breeding landbird species is not in equilibrium due to the variability in the time series (Table 1). However, this variability is attributed particularly to the first and last phases in which species are declining and increasing, respectively whereas the two middle periods appear to show attributes consistent with dynamic equilibria with both periods having little variability and with statistically significant relationships between ΔS and S indicating a strong return tendency. Nonetheless, these two equilibrium periods appear to be separated by a phase shift with an increase in numbers of species, S, from a mean of 10.1 to 13.5 species. Whittaker (1998, 2000) proposed a model in which single taxon island assemblages are envisaged as being in one of four possible states depending upon dynamic or static equilibriums and equilibrial or non-equilibrial states. In terms of Whittaker’s model, the dynamics of the landbirds on Skokholm appear to be consistent with shifts from non-equilibrium to equilibrium dynamics. The dynamic equilibria lasted 32 years out of 68 years in total (i.e., just under half the time) but consisted of two distinct periods of 15 and 17 years respectively with statistically significant differences in the mean numbers of species (Table 1). Whittaker (2000) suggested that some authors tend to find for one particular state whereas within a single island different taxa may simultaneously occupy different states or a single taxon may occupy different positions for different islands. One novel finding here in relation to Whittaker's model is that a single taxon appears to move from one state to another whilst different groups of species within the taxon show differing responses according to their habitat use.

One reason for the apparent phase shift may be due to habitat change. The plot of species by habitat groupings (Fig. 2) suggests changes to habitats may have been taking place such that the numbers of species by habitat groupings changed according to habitat availability. Since being first described (Conder and Keighley 1947, Goodman and Gillham 1954) there have been changes in the cover and distribution of vegetation types on Skokholm. Latterly, Ninnes (1998) stated that possibly the most important changes in conservation terms (i.e., for burrowing seabirds), have been shifts in the area dominated by the herb Sea Campion *Silene maritima*, which had increased from 1% to 15% of the land area over the period 1948-1997, and over half of the thrift *Armeria maritima* dominated turf which had been lost to grassland (although it had also spread into new areas). (Thrift, a herb, forms a burrowing medium for internationally important populations of Manx Shearwaters and Puffins *Fratercula arctica*). Other changes include loss of heather *Calluna vulgaris* heath and eutrophication of wetlands. Ninnes (1998) suggested the main underlying factors in these changes were related to grazing, past landuse, and changes in the abundance and distribution of seabirds. Commercial sheep grazing ceased in 1935 although hardy Soay continued to be maintained and Lockley, and Buxton (1946) reported a population of 25 rising to 35 in the autumn of 1946. Thompson (2007) stated that Soay sheep were on the island until shortly after 1964. Rabbit *Oryctolagus cuniculus* grazing continued even after concerted, yet ultimately unsuccessful, attempts to exterminate them from the island by introducing myxomatosis in the late 1930s and by using using cyanogas in 1939 and 1940 (Lockley and Buxton 1946, Lockley 1947). Goodman and Gillham (1954) reported that the rabbit population was around 10,000 and that a few goats and a pony also lived on Skokholm at that time.

Although some brief descriptions of the vegetation were made in the early years (e.g., Conder and Keighley 1947) little information was presented about habitat change at this time period. Before Lockley arrived, Skokholm was last farmed in 1912. Other than grazing by rabbits, and by a couple of horses and a donkey from 1916 there was no attempt to farm the island until Lockley took out a lease in 1927 (Howells 1968). Undoubtedly the abandonment would have led to some successional change which would have been reversed when farming resumed. Conder and Lockley (1947) reported that heather was invading parts of the grassland and bracken *Pteridium aquilinum* was invading heather, thrift and pasture, the latter at a rate of about a metre per year. They also reported the bog had increased in the past 10-15 years and the pasture, in some parts, was reported to be heavily grazed by rabbits. By 1932 Lockley had established a sheep herd of about 100 ewes and in 1939 and 1940 Lockley reduced the rabbit population on the island down to about 400 (Thompson 2007). Hence, although there is little information about vegetation change in the early years of the survey there is little doubt that the combined grazing pressure of both rabbits and sheep would have been heavy and the introduction of Soay sheep in particular (being partial to woody vegetation) could have led to a decline of shrub and associated bird species in the early years. The decline in species in the early years (1928-1947) is characterised most notably by the loss of regular breeders Common Blackbird and Dunnock along with intermittent breeders, Robin, Sedge Warbler, and Common Whitethroat, all species associated with woody cover (Fig. 2)(see Appendix 1, Table A1 for scientific names of birds).

Occasional attempts have been noted to encourage nesting by providing suitable habitat. Thompson and Purcell (1997) reported on Common Linnets which nested in a gorse *Ulex europaeus* bush, and an unsuccessful attempt to encourage overwintering Blue Tits *Cyanus caeruleus* to nest by erecting a box. A nest box was also provided for Red-billed Chough in 2005. The gorse had been planted deliberately to increase bird diversity and many shrubs and trees were planted around the observatory buildings in the 1980s and 1990s providing cover that was previously lacking. Common Blackbird and Sedge Warbler benefitted from this. Further, elder (*Sambucus nigra*) and bramble (*Rubus fruticosus*) were planted in the east of the island which may also provide a food resource, song-posts and potential nest sites (Graham Thompson, pers. comm.). These all undoubtedly led to an increase in species associated with shrub and other three-dimensional habitats in the final period and the single group changing most in both the first and last periods were the species of three-dimensional habitats including shrub. This group declined the most in the first period and increased the most in the last period (Fig. 2).

The apparent phase shift between the second and third periods was accompanied by increases in both shrub species and also in both raptors and corvids, as well as water, wetland and marsh species. I.e., these suggest habitat changes taking place, and in the case of corvids, there may have been a relaxation in persecution by wardens (particularly of Carrion Crows and also of predators such as Little Owl as occasionally noted in annual reports)(n.b., no mammalian predators have ever been recorded on Skokholm (Thompson 2007)). Other localised habitats include the pond and its associated wetland vegetation, used intermittently for nesting by Mallard, Common Moorhen and Water Rail. As a group these wetland species were largely missing from the second period, but began to recover in the third period and to be well established by the final period.

Hence, in terms of equilibrium and non-equilibrium dynamics there is a strong argument for the effects of habitat change on the island affecting nesting and feeding opportunities and being influential in species' turnover over time. The question of whether communities are in equilibrium or not remains controversial although perturbation due to human influence is often a factor that affects ecosystem dynamics (Rohde 2013). Here, the differences between equilibrium and non-equilibrium reflect periods when humans directly or indirectly affected habitats on Skokholm by altering grazing regimes and establishing more woody plant species, respectively. Thus, periods of non-equilibrium probably reflect periods of adjustment due to successional change.

The one peculiarity of the data is the apparent phase shift between the second and third periods. Although habitat change and/or changes in management may be the ultimate cause of this, it is apparent that the numbers of species remained relatively constant during each of these periods but with statistically significant differences in the mean number of bird species between them. This is the first time this phenomenon has been described in relation to the theory of island biogeography. One possible reason for this is a switch to an alternative equilibrium state after perturbation (Collie et al. 2004). One candidate forcing variable for such a shift is the severe winter of 1962-63, the coldest in England in the twentieth century (Parker and Horton 2005), and which caused population crashes in resident species such as Robin and Wren in southern England (Beven 1976, Dhondt 1986). Winter climate variables (duration of winter frosts, snow periods, and occurrence of cold, wet days) have been shown to affect survival of resident bird species (Robinson et al. 2007) and elsewhere climate-related perturbances have been shown to give rise to different communities which may be stable at least in the short term (Letnic and Dickman 2010). However, given that the increase in numbers of species in the third period was primarily due to those associated with 3-dimensional habitats (bushes, trees, buildings) and species associated with water, wetland and marsh (Fig. 2.), it seems more likely that the phase shift was endogenic rather than exogenic in origin.

Previously, the non-equilibrium dynamics of breeding landbirds and the associated high variability in S on Skokholm have been attributed both to the high extinction rate of small populations on a “very small island” (Schoener 2010) and changes due to the weather, acting through food supply (Abbott and Grant 1976). However, these arguments also apply to other small offshore UK islands yet in a sample of 16 islands Manne et al. (1998) found that Skokholm was one of only two islands not conforming to the MacArthur-Wilson model. In all other respects the islands would have similar climates and were all similarly small. Notwithstanding this, Abbott and Grant (1976) did recognise that Skokholm landbirds were apparently at equilibrium during the period 1946-1962, a period corresponding to the second period in this study. Further, the two periods of equilibrium identified in this study are consistent with two out of the three periods of stability identified by Williamson (1983) using an ordination approach.

MacArthur and Wilson (1967) themselves recognised that non-equilibrium dynamics potentially play a role in ecological communities and that even at equilibrium some turnover may be due to successional change. The effects of habitat change on the assemblage here have been detected by analysing the species by habitat-based groupings – a novel approach to analysing environmental change when the data on vegetation change might not be there to match. This study illustrates the value of long-term data and there is a need to continue monitoring island populations and extend previous analyses since greater insight may be gained using longer time series. In conclusion, there is a need to integrate the theory of island biogeography into models of ecology encompassing alternative stable states, tipping points, and phase (or regime) shifts together with equilibrium and non-equilibrium dynamics into a single framework (see, for example, Ward and Thornton 1998).

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Supplementary material (Appendix 1 at <www.oikosoffice.lu.se/appendix>). Appendix 1.

Table 1. Attributes of the four periods identified by cluster analyses and that of the whole dataset 1928-2002 (All years). Significance: *** p < 0.001; ** p < 0.01; ns not significant.

Years	***Number of years***	***Mean number of species***	***CV***	***Var/ mean ratio***	***10% range around the mean***	***No of years above 10% (% of total)***	***No of years below 10% (% of total)***	**r_s *ΔS vs S***
1928–1947	14	13.5	0.18	0.49	12.15 - 14.85	4 (29)	6 (43)	-0.47 ns
1948–1962	15	10.1	0.04	0.04	9.09 - 11.11	0 (0)	2 (13)	-0.83***
1963–1979	17	13.5	0.08	0.14	12.15 - 14.85	1 (6)	3 (18)	-0.68**
1980–2002	23	18.4	0.15	0.69	16.56 - 20.24	7 (30)	8 (35)	-0.24 ns
All years	69	14.3	0.06	1.10	12.87 - 15.73	20 (29)	26 (38)	-0.24 ns

Figure legends

Figure 1. Numbers of breeding landbird species on Skokholm 1928-2002. Note the hiatus between 1940-1945 due to WWII. The shading represents the four main clusters identified in the cluster analysis (Appendix 1, Fig. A1).

Figure 2. Numbers of species by habitat groupings:- interrupted line: grassland and other open habitats; solid line: three-dimensional habitats (inc. bushes, trees, buildings); dashed line: raptors and corvids; dotted line: water, wetland and marsh species. Species' habitat groupings are listed in Appendix 1 Table A1.

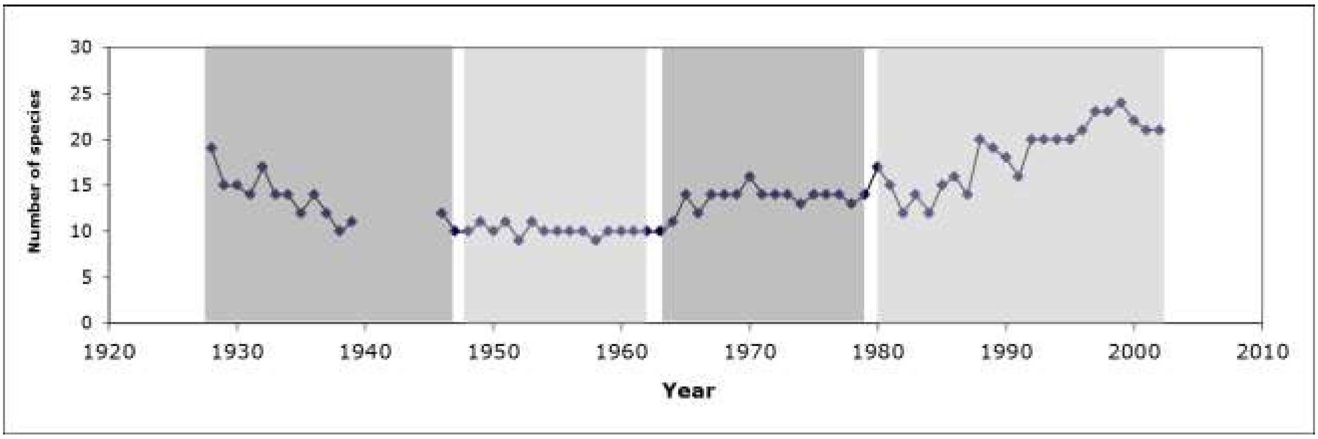
Number of species
0
5
10
15
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Figure 1.

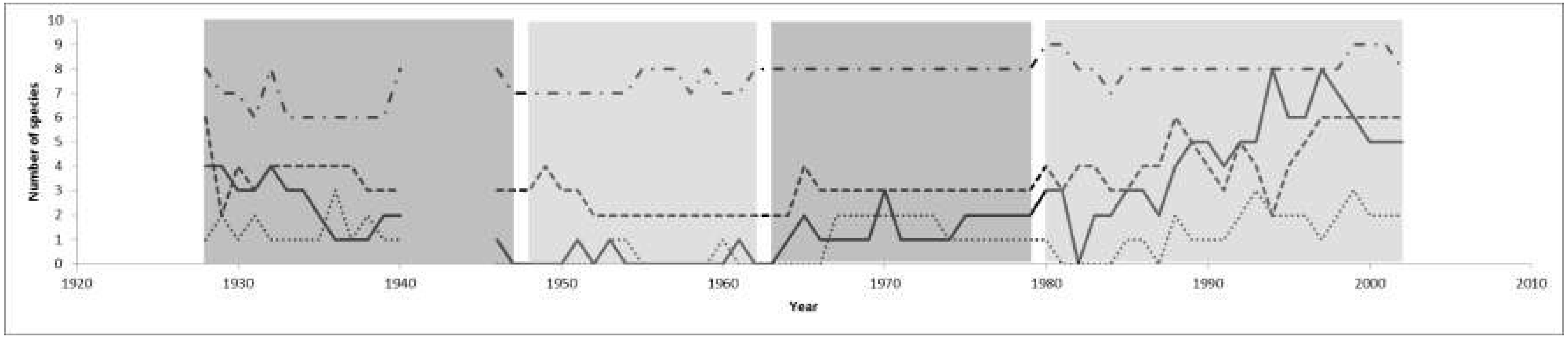
Number of species
0
1
2
3
4
5
6
7
8
9
10
1920
1930
1940
1950
1960
1970
1980
1990
2000
2010
Year

Figure 2.