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1 The curious case of Skokholm: equilibrium, non-equilibrium and phase shifts in an island landbird
2 assemblage
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13
14
15   Abstract
16
17   Previous work has indicated that the landbirds of Skokholm island (Wales) are not in equilibrium
18   as defined in MacArthur-Wilson's classic theory of island biogeography. This study takes a new
19   dataset with over six decades of data and investigates equilibrium on Skokholm using cluster
20   analysis to identify periods of turnover stability. The attributes of the identified periods were
21   investigated in relation to the MacArthur-Wilson model using analyses of change in numbers of
22   species, S, from one year to the next and measures of variability in S quantified for each of the
23   periods identified together with a consideration of the dynamics in the numbers of species by
24   habitat groupings. Cluster analysis identified four main periods of which two middle periods
25   appeared to be in equilibrium but with a phase shift in-between. The first and last periods showed
26   non-equilibrium dynamics but plots of species by habitat groupings suggested that this was due to
27   habitat changes going on at those times. This decadal long dataset indicates that the landbirds of
28   Skokholm exhibit periods of both equilibrium and non-equilibrium with the latter attributable to
29   habitat change. The apparent phase shift in the equilibrium number of species was unexpected
30   within the framework of island biogeographic theory and not easily explained using the current
31   MacArthur-Wilson framework. There is a need to integrate the theory of island biogeography with
32   more recent work on alternative stable states, tipping points, and phase (or regime) shifts, together
33   with equilibrium and non-equilibrium dynamics, into a single framework.
34
35
36
37   Key words: island biogeography, equilibrium, phase shift
38
39

40   INTRODUCTION

41

42   The theory of island biogeography ('ETIB') (MacArthur and Wilson 1967) is an equilibrium model

43   in which the number of species on an island arises from a balance between the opposing rates of

44   immigration and extinction with the equilibrium number being dependent upon island size and

45   isolation from the mainland (or source pool for archipelagos). Although ETIB is a dynamic model

46   which recognises that colonisation and local extinction on islands will be ongoing it may be seen in

47   the light of a strong tradition in ecology of equilibrium-thinking particularly with respect of the

48   balance of nature paradigm (Connell 1978, Reice 1994, Rohde 2005). Equilibrium concepts have

49   been questioned particularly in marine and aquatic environments with tipping points and regime

50   shifts being features of systems undergoing over-exploitation and subject to climate instability

51   (Gido et al. 2000, Collie et al. 2004, Weijerman et al. 2005, deYoung et al. 2008). In terrestrial

52   environments, whilst non-equilibrium ideas have been addressed in relation to the role of

53   disturbance in the maintenance of species richness of woody species in tropical rainforests (Connell

54   1978, Sousa 1984, Wu and Loucks 1995), little work has been done on animals (Sousa 1984).

55

56   Given sufficiently long-term data, ideas central to ETIB concerning for example, the shape of the

57   relationships between the rates of immigration and extinction, respectively, and the number of

58   species are testable and a number of studies have attempted to do this (see for example, Reed

59   1980, Williamson 1981, 1983, Nilsson and Nilsson 1982, Simberloff 1976, 1983, Pimm et al.

60   1988, Whittaker et al. 1989, Bush and Whittaker 1991, Russell et al. 1995, Manne et al. 1998).

61   Here I take a recently updated long-term dataset for Skokholm (McCollin 2014a, 2014b),

62   previously used in a shorter form by a number of workers (e.g., Abbott and Grant 1976, Williamson

63   1981, 1983, Simberloff 1976, 1983, Pimm et al. 1988, Russell et al. 1995, Manne et al. 1998,

64   Philippi et al. 1998, Russell et al. 2006, Stracey and Pimm 2009), and test for the presence of

65 equilibrium by considering how the numbers of species vary over time. Although one other island,

66 Krakatau, has featured greatly in discussions of equilibrium (e.g., Thornton et al. 1990, 1993),

67 Skokholm was chosen here since this is one of the longest near-continuous datasets of its type plus

68 various authors have questioned whether the landbirds of the island are in equilibrium (Abbott and

69 Grant 1976, Williamson 1981, 1983, Simberloff 1983, Russell et al. 2006, Golinski and Boecklen

70 2006).

71

72 MATERIALS AND METHODS

73 Study Site

74 Skokholm is a 96ha island lying c. 3.5km off the coast of Pembrokeshire, Wales and is a nature

75 reserve of the Wildlife Trust of South and West Wales. The island has internationally important

76 seabird populations such as Manx Shearwater *Puffinus puffinus* but here I focus on the landbirds,

77 breeding records for which date back to 1928 (Lockley 1938, Lack 1969, Williamson 1981,

78 Thompson 2007).

79

80 Analysis

81 Here, I use the extended dataset for Skokholm 1928-2002 (McCollin 2014a, 2014b). These data

82 comprise numbers of breeding pairs of landbirds on the island with data being derived from counts,

83 territory mapping and, for more common species, estimates, undertaken by wardens present during

84 the breeding season each year. There is a hiatus in the time series as no surveys were done in the

85 war years between 1940-1945. The abundance data were tested for reliability by McCollin (2014a)

86 and no bias in numbers could be detected when tested against randomised draws of data. In order

87 to identify periods of relative stability, these data were entered into an agglomerative cluster

88 analysis using minimum variance or error sum of squares (Ward's method) and a Bray-Curtis

89 similarity measure using CAP4 software (Pisces Conservation Ltd, no date). The periods thus

90   identified are mapped onto the numbers of species by years graph. Although the data form a time

91   series, it is implicit in the MacArthur-Wilson model that numbers of species depend on a balance

92   between the rates of immigration and extinction on individual islands thus the assumption is that

93   the data are non-independent. In practice, as the assemblage comprises a number of species, each of

94   which comprises populations – some of which are resident year-round - the data from one year to

95   the next may not be independent. The potential for immigration to occur depends on whether

96   species are present in the species pool on the nearby mainland. Over long timescales the avifauna

97   of the mainland may also be subject to turnover such that species like Corncrake *Crex crex*, which

98   had a breeding pair on Skokholm in 1930, had almost disappeared from the nearby mainland by

99   1961 (Lockley 1961) despite being common and widespread on the adjoining mainland in the late

100   19th Century (Mathew 1894). Such species would be highly unlikely to recolonise once lost.

101

102   For each of the four periods identified by cluster analysis, equilibrium is tested for by correlating

103   the change in the numbers of species from one year to the next (ΔS) against the number in the first

104   of these years (Williamson 1987). These correlations show the strength of the return tendency in

105   the time series akin to a 'ball and valley' equilibrium model (DeAngelis and Waterhouse 1987). No

106   assumptions are made about the causal nature of this return tendency hence these plots are tested

107   using a Spearman's rank correlation coefficient, r_s.

108

109   At equilibrium the number of species, S, on an island should remain relatively constant through

110   time although some variability in S is to be expected due to the stochastic nature of extinctions and

111   colonisations (Diamond and May 1977, Gotelli and Graves 1996). However, little guidance exists

112   in terms of how much variability to allow around the mean S although MacArthur and Wilson

113   (1967) suggested that the variance to mean ratio for S should attain a value of 0.5 at equilibrium.

114   Simberloff (1983) noted the arbitrary nature of particular values proposed with a coefficient of

115   variation of less than 0.2 (Diamond and May 1977) or less than 0.05 (Abbott and Black 1980) and

116   variation in species numbers less than 16% all being classed as equilibrial (Diamond 1969). Here,

117   measures of variation, including the coefficient of variation (CV) and the variance to mean ratio,

118   are used to gauge the variability in numbers of species over time, and both measures are used to

119   allow comparison to the literature.

120

121   Finally, to help interpret change the species were classified into ecological groups and numbers of

122   species in each group are plotted by time. The species and their habitat requirements are well

123   known (e.g., Fuller 1982) and species were classified according to habitat use and refined by expert

124   judgement (Graham Thompson, warden on Skokholm from 1995 for c. 10 years, pers. comm.).

125

126   RESULTS

127

128   The cluster analysis divided the landbird data into four distinct periods: 1928–1947; 1948–1962;

129   1963– 1979; and 1980–2002 (Appendix 1, Fig. A1; Fig 1). The periods identified by cluster

130   analysis (Appendix 1, Fig. A1) conform to a visual inspection of the data (Fig. 1): 1928–1947 being

131   a decline from 19 down to 10 breeding bird species; 1948–1962 being a period of stability with a

132   mean of 10.1 breeding species and low variability; 1963– 1979 being another period of stability

133   with a mean of 13.5 species and slightly higher variability; and 1980–2002 showing an increase

134   with a minimum of 12 and a maximum of 24 species. Compared to the two middle periods, the CVs

135   and the variance/mean ratios for the first and last periods were highest at 0.18 and 0.15, and 0.49

136   and 0.69, respectively. Further, the numbers of years in which S was ± 10% was highest for the first

137   and last periods (Table 1). Although the mean numbers of species in the middle periods showed

138   greater stability, there was a very highly statistically significant difference between the mean

139   number of species in these two periods ($t = 4.1$, $p < 0.001$, $df = 28$). The analysis of change in

140   numbers of species (ΔS) versus S showed statistically significant and correspondingly higher r_s and

141   lower p-values for the Spearman rank correlation coefficients for the two middle periods when

142   compared to the outlying periods (Table 1). Fig. 2 shows the change in numbers of species by

143   habitat groupings. This plot highlights the differences in stability between different groups of

144   species and point to the role of habitat change (see Discussion).

145

146   DISCUSSION

147

148   Using a variety of approaches previous analyses have found that the landbirds on Skokholm are not

149   in equilibrium (Abbott and Grant 1976, Williamson 1981, 1983, Russell et al. 2006). In the

150   approach taken here, the time series has been divided up according to an objective method and the

151   overall dynamics of S over time is characterised by these four distinct periods including two

152   distinct periods of equilibrium: 1948–1962, and 1963– 1979. Whilst, the analysis of ΔS versus S

153   indicates that for all years taken together, it appears that the number of breeding landbird species is

154   not in equilibrium due to the variability in the time series (Table 1). However, this variability is

155   attributed particularly to the first and last phases in which species are declining and increasing,

156   respectively whereas the two middle periods appear to show attributes consistent with dynamic

157   equilibria with both periods having little variability and with statistically significant relationships

158   between ΔS and S indicating a strong return tendency. Nonetheless, these two equilibrium periods

159   appear to be separated by a phase shift with an increase in numbers of species, S, from a mean of

160   10.1 to 13.5 species. Whittaker (1998, 2000) proposed a model in which single taxon island

161   assemblages are envisaged as being in one of four possible states depending upon dynamic or static

162   equilibriums and equilibrial or non-equilibrial states. In terms of Whittaker's model, the dynamics

163   of the landbirds on Skokholm appear to be consistent with shifts from non-equilibrium to

164   equilibrium dynamics. The dynamic equilibria lasted 32 years out of 68 years in total (i.e., just

165 under half the time) but consisted of two distinct periods of 15 and 17 years respectively with

166 statistically significant differences in the mean numbers of species (Table 1). Whittaker (2000)

167 suggested that some authors tend to find for one particular state whereas within a single island

168 different taxa may simultaneously occupy different states or a single taxon may occupy different

169 positions for different islands. One novel finding here in relation to Whittaker's model is that a

170 single taxon appears to move from one state to another whilst different groups of species within the

171 taxon show differing responses according to their habitat use.

172

173 One reason for the apparent phase shift may be due to habitat change. The plot of species by habitat

174 groupings (Fig. 2) suggests changes to habitats may have been taking place such that the numbers

175 of species by habitat groupings changed according to habitat availability. Since being first

176 described (Conder and Keighley 1947, Goodman and Gillham 1954) there have been changes in the

177 cover and distribution of vegetation types on Skokholm. Latterly, Ninnes (1998) stated that

178 possibly the most important changes in conservation terms (i.e., for burrowing seabirds), have been

179 shifts in the area dominated by the herb Sea Campion *Silene maritima*, which had increased from

180 1% to 15% of the land area over the period 1948-1997, and over half of the thrift *Armeria maritima*

181 dominated turf which had been lost to grassland (although it had also spread into new areas).

182 (Thrift, a herb, forms a burrowing medium for internationally important populations of Manx

183 Shearwaters and Puffins *Fratercula arctica*). Other changes include loss of heather *Calluna*

184 *vulgaris* heath and eutrophication of wetlands. Ninnes (1998) suggested the main underlying

185 factors in these changes were related to grazing, past landuse, and changes in the abundance and

186 distribution of seabirds. Commercial sheep grazing ceased in 1935 although hardy Soay continued

187 to be maintained and Lockley, and Buxton (1946) reported a population of 25 rising to 35 in the

188 autumn of 1946. Thompson (2007) stated that Soay sheep were on the island until shortly after

189 1964. Rabbit *Oryctolagus cuniculus* grazing continued even after concerted, yet ultimately

190 unsuccessful, attempts to exterminate them from the island by introducing myxomatosis in the late

191 1930s and by using using cyanogas in 1939 and 1940 (Lockley and Buxton 1946, Lockley 1947).

192 Goodman and Gillham (1954) reported that the rabbit population was around 10,000 and that a few

193 goats and a pony also lived on Skokholm at that time.

194

195 Although some brief descriptions of the vegetation were made in the early years (e.g., Conder and

196 Keighley 1947) little information was presented about habitat change at this time period. Before

197 Lockley arrived, Skokholm was last farmed in 1912. Other than grazing by rabbits, and by a couple

198 of horses and a donkey from 1916 there was no attempt to farm the island until Lockley took out a

199 lease in 1927 (Howells 1968). Undoubtedly the abandonment would have led to some successional

200 change which would have been reversed when farming resumed. Conder and Lockley (1947)

201 reported that heather was invading parts of the grassland and bracken *Pteridium aquilinum* was

202 invading heather, thrift and pasture, the latter at a rate of about a metre per year. They also reported

203 the bog had increased in the past 10-15 years and the pasture, in some parts, was reported to be

204 heavily grazed by rabbits. By 1932 Lockley had established a sheep herd of about 100 ewes and in

205 1939 and 1940 Lockley reduced the rabbit population on the island down to about 400 (Thompson

206 2007). Hence, although there is little information about vegetation change in the early years of the

207 survey there is little doubt that the combined grazing pressure of both rabbits and sheep would have

208 been heavy and the introduction of Soay sheep in particular (being partial to woody vegetation)

209 could have led to a decline of shrub and associated bird species in the early years. The decline in

210 species in the early years (1928-1947) is characterised most notably by the loss of regular breeders

211 Common Blackbird and Dunnock along with intermittent breeders, Robin, Sedge Warbler, and

212 Common Whitethroat, all species associated with woody cover (Fig. 2)(see Appendix 1, Table A1

213 for scientific names of birds).

214

215   Occasional attempts have been noted to encourage nesting by providing suitable habitat. Thompson

216   and Purcell (1997) reported on Common Linnets which nested in a gorse *Ulex europaeus* bush, and

217   an unsuccessful attempt to encourage overwintering Blue Tits *Cyanus caeruleus* to nest by erecting

218   a box. A nest box was also provided for Red-billed Chough in 2005. The gorse had been planted

219   deliberately to increase bird diversity and many shrubs and trees were planted around the

220   observatory buildings in the 1980s and 1990s providing cover that was previously lacking.

221   Common Blackbird and Sedge Warbler benefitted from this. Further, elder (*Sambucus nigra*) and

222   bramble (*Rubus fruticosus*) were planted in the east of the island which may also provide a food

223   resource, song-posts and potential nest sites (Graham Thompson, pers. comm.). These all

224   undoubtedly led to an increase in species associated with shrub and other three-dimensional

225   habitats in the final period and the single group changing most in both the first and last periods

226   were the species of three-dimensional habitats including shrub. This group declined the most in the

227   first period and increased the most in the last period (Fig. 2).

228

229   The apparent phase shift between the second and third periods was accompanied by increases in

230   both shrub species and also in both raptors and corvids, as well as water, wetland and marsh

231   species. I.e., these suggest habitat changes taking place, and in the case of corvids, there may have

232   been a relaxation in persecution by wardens (particularly of Carrion Crows and also of predators

233   such as Little Owl as occasionally noted in annual reports)(n.b., no mammalian predators have ever

234   been recorded on Skokholm (Thompson 2007)). Other localised habitats include the pond and its

235   associated wetland vegetation, used intermittently for nesting by Mallard, Common Moorhen and

236   Water Rail. As a group these wetland species were largely missing from the second period, but

237   began to recover in the third period and to be well established by the final period.

238

239   Hence, in terms of equilibrium and non-equilibrium dynamics there is a strong argument for the

240   effects of habitat change on the island affecting nesting and feeding opportunities and being

241   influential in species' turnover over time. The question of whether communities are in equilibrium

242   or not remains controversial although perturbation due to human influence is often a factor that

243   affects ecosystem dynamics (Rohde 2013). Here, the differences between equilibrium and non-

244   equilibrium reflect periods when humans directly or indirectly affected habitats on Skokholm by

245   altering grazing regimes and establishing more woody plant species, respectively. Thus, periods of

246   non-equilibrium probably reflect periods of adjustment due to successional change.

247

248   The one peculiarity of the data is the apparent phase shift between the second and third periods.

249   Although habitat change and/or changes in management may be the ultimate cause of this, it is

250   apparent that the numbers of species remained relatively constant during each of these periods but

251   with statistically significant differences in the mean number of bird species between them. This is

252   the first time this phenomenon has been described in relation to the theory of island biogeography.

253   One possible reason for this is a switch to an alternative equilibrium state after perturbation (Collie

254   et al. 2004). One candidate forcing variable for such a shift is the severe winter of 1962-63, the

255   coldest in England in the twentieth century (Parker and Horton 2005), and which caused

256   population crashes in resident species such as Robin and Wren in southern England (Beven 1976,

257   Dhondt 1986). Winter climate variables (duration of winter frosts, snow periods, and occurrence of

258   cold, wet days) have been shown to affect survival of resident bird species (Robinson et al. 2007)

259   and elsewhere climate-related perturbances have been shown to give rise to different communities

260   which may be stable at least in the short term (Letnic and Dickman 2010). However, given that the

261   increase in numbers of species in the third period was primarily due to those associated with 3-

262   dimensional habitats (bushes, trees, buildings) and species associated with water, wetland and

12

263   marsh (Fig. 2.), it seems more likely that the phase shift was endogenic rather than exogenic in

264   origin.

265

266   Previously, the non-equilibrium dynamics of breeding landbirds and the associated high variability

267   in S on Skokholm have been attributed both to the high extinction rate of small populations on a

268   "very small island" (Schoener 2010) and changes due to the weather, acting through food supply

269   (Abbott and Grant 1976). However, these arguments also apply to other small offshore UK islands

270   yet in a sample of 16 islands Manne et al. (1998) found that Skokholm was one of only two islands

271   not conforming to the MacArthur-Wilson model. In all other respects the islands would have

272   similar climates and were all similarly small. Notwithstanding this, Abbott and Grant (1976) did

273   recognise that Skokholm landbirds were apparently at equilibrium during the period 1946-1962, a

274   period corresponding to the second period in this study. Further, the two periods of equilibrium

275   identified in this study are consistent with two out of the three periods of stability identified by

276   Williamson (1983) using an ordination approach.

277

278   MacArthur and Wilson (1967) themselves recognised that non-equilibrium dynamics potentially

279   play a role in ecological communities and that even at equilibrium some turnover may be due to

280   successional change. The effects of habitat change on the assemblage here have been detected by

281   analysing the species by habitat-based groupings – a novel approach to analysing environmental

282   change when the data on vegetation change might not be there to match. This study illustrates the

283   value of long-term data and there is a need to continue monitoring island populations and extend

284   previous analyses since greater insight may be gained using longer time series. In conclusion, there

285   is a need to integrate the theory of island biogeography into models of ecology encompassing

286   alternative stable states, tipping points, and phase (or regime) shifts together with equilibrium and

287   non-equilibrium dynamics into a single framework (see, for example, Ward and Thornton 1998).

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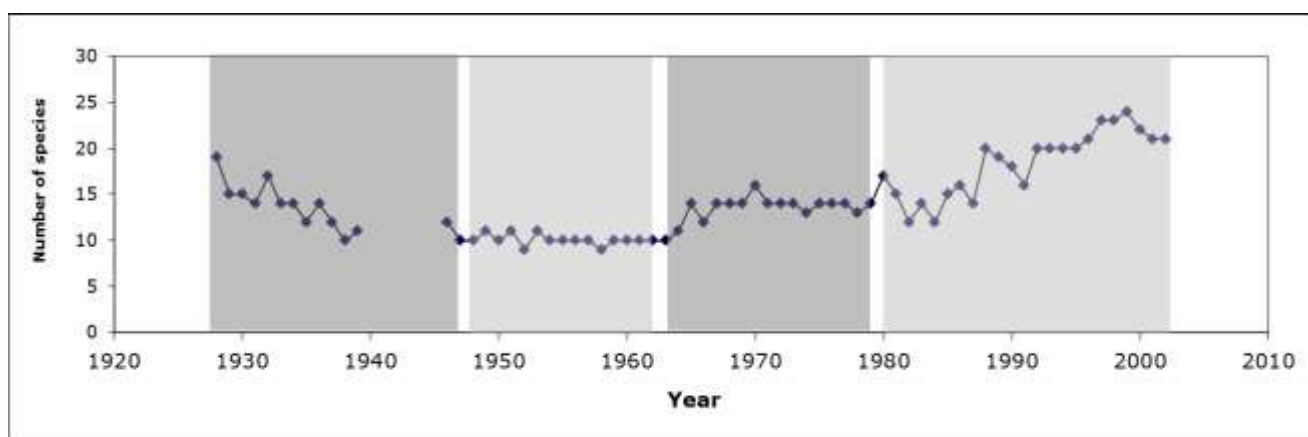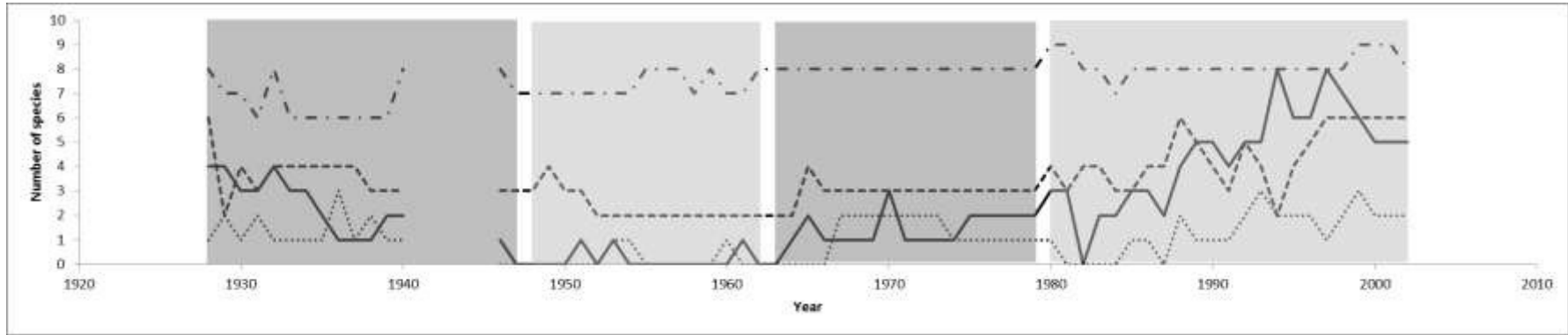
Figure 1.

Figure 2.