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Author(s): Ian Abbott and Robert Black

Source: *Journal of Biogeography*, Vol. 7, No. 4 (Dec., 1980), pp. 399-410

Published by: Wiley

Stable URL: <https://www.jstor.org/stable/2844658>

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## Changes in species composition of floras on islets near Perth, Western Australia

IAN ABBOTT\* and ROBERT BLACK    Department of Zoology,  
University of Western Australia, Nedlands 6009, Western Australia

**ABSTRACT.** Seventy-six aeolianite limestone islets were visited at least twice between 1975 and 1978, and their floras were recorded. 38% (twenty-nine of the islets) remained unvegetated; they had a smaller area and lower maximum elevation than islands that were vegetated. 55% (forty-two) of the islets showed no change in plant species composition, were smaller, and had fewer plant species than islands that did show change in species composition over time.

Comparisons with the same islets sampled in the 1950s show that turnover of species is 3 times higher for long census intervals (~ 20 years) than for short census intervals (1–3 years). For those islets censused in 1975, 1977 and 1978 there was a significant difference between 1975–77 and 1977–78 in the proportion of islands showing only extinctions or immigrations of species; this may be related to an increase in rainfall or a cyclone in 1978.

Physically stable islands such as we studied seem to be more relevant in assessing the extent of plant species turnover on islands than cays, which tend to be physically unstable.

### Introduction

Since the publication (1967) of MacArthur & Wilson's equilibrium model of island biogeography, much research aimed at testing the model has been done (Simberloff, 1974). Comparatively little effort has been devoted to testing it on real islands, especially with plant species (Heatwole & Levins, 1973; Abbott, 1977). Instead, students have chosen artificial islands, in effect habitat islands, for the convenience of experimentally manipulating critical variables such as area or isolation (e.g. Molles, 1978; Schoener, Long & De Palma, 1978). How relevant their findings are to land masses surrounded by water (i.e. islands in the conventional sense) has not been established. Indeed, there is a need to test the equilibrium model on a biogeographical scale (Brown & Kodric-Brown, 1977).

Probably the easiest way of testing the equilibrium theory on islands is to record the species present of some taxonomic group of interest at two different censuses, preferably 1 year apart (Jones & Diamond, 1976). If the size of an insular fauna or flora is at a dynamic equilibrium, then there should be only slight changes from year to year in the kinds of species present; the numbers of extinctions and immigrations should balance. Constancy of species number over time, although consistent with the equilibrium model, may instead support an hypothesis of non-equilibrium: species that become extinct on or are absent from an island may have difficulty in recolonizing because of poor dispersal ability, and species may persist for long periods on islands irrespective of the presence of other species. On the other hand, constancy could be effected by the so-called rescue effect (Brown & Kodric-Brown, 1977): species may become extinct regularly but just as frequently immigrate to islands. Constancy

\*Present address: Institute of Forest Research and Protection, Hayman Road, Como 6152, Western Australia.

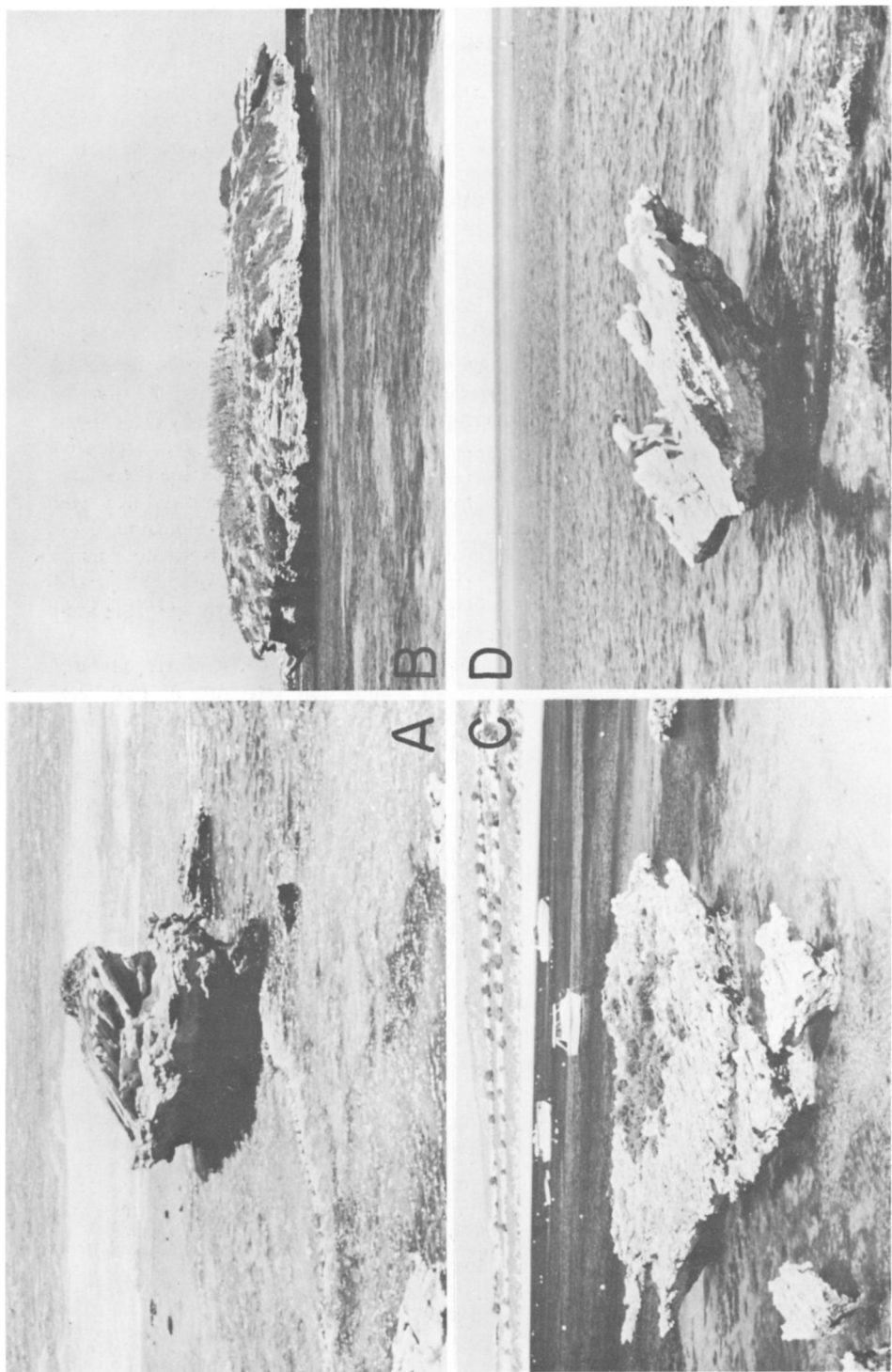


FIG. 1. Photographs of four of the islets studied near Rottneest Island. Code numbers refer to map in Abbott (1977). (A) No name, code number 15, showing undercut sides and exposed reef platform linking islet to Rottneest Island. Area  $70\text{ m}^2$ , elevation 6 m, and distance from Rottneest I. 20 m. The islet supports three to five plant species. Note osprey nest. (B) Green I, code number 19, showing steep sides. Area  $1200\text{ m}^2$ , elevation 6 m, and distance from Rottneest I. 60 m. This islet supports seventeen to twenty plant species. Note gulls hovering over the island. (C) No name, code number 38. Area  $140\text{ m}^2$ , elevation 4 m, distance from Rottneest I. 4 m. This islet supports thirteen to twenty plant species. (D) Mushroom Rock, code number 47. Area  $30\text{ m}^2$ , elevation 2.5 m, distance from Rottneest I. 17 m. This islet supports one or two plant species.

of species over time can therefore arise from other causes than those postulated by the equilibrium theory.

These ideas were examined since 1975 with the floras of islets adjacent to Rottnest Island, itself 18 km from the mainland coast at Fremantle, Western Australia. The islets are in general quite small stacks of aeolianite with planar area less than 1000 m<sup>2</sup>; most can be easily reached by wading across reefs at low water from Rottnest Island. Other islets farther south have also been studied, but less frequently because a boat is needed to reach them. In all over seventy islands have been revisited at least once since 1975. (For a map of the islands, see Abbott, 1977.)

Very few of the islets have beaches; most have undercut cliffs (Fig. 1) so that it would be extremely difficult for fruits or seeds of plants from nearby source areas to be washed onto the islands. Small, light seeds could be blown onto the islets, and still others could be introduced by nesting Silver Gulls (Abbott, 1977) or Ospreys (pers. obs.). These islets hence offer marked differences from cay islands with their extensive beaches to receive flotsam (Heatwole & Levins, 1973), and are typical of cliff-bound continental islands, more common around Australia than cays.

## Methods

As the climate near Perth is Mediterranean, with the rainfall concentrated in winter, annual plants germinate in late autumn/winter and die in December/January. We therefore visited the islands towards the end of spring or the middle of summer so that all annual plants could be identified to species. Islands were visited as follows: Rottnest stacks in December 1975, 1977 and 1978; those in and south of Shoalwater Bay in October 1975 and September 1977, and Carnac I. and some adjacent stacks in December 1975 and November 1976.

Each island was visited for long enough that all parts were carefully searched. This time ranged from 5 min (small rocks) to 1 week (16 ha island). We wish to emphasize our care in searching for plant species, because superficial examination will tend to exaggerate changes in plant species compo-

sition. One of us was familiar with all the plant species, and was able to identify recently dead and dying annuals. Care was taken to collect only small portions of plant species in 1975 so as not to deplete any populations. As a boat was available at Rottnest only in 1975, several islands offshore were not subsequently revisited; they are not considered in this paper.

## Results

### *Changes in plant species richness with time*

Twenty-nine islets remained unvegetated over the period of study (1975–77–78 for those near Rottnest; 1975–77 or 1975–76 for those elsewhere). Thirteen of the vegetated islands had the same species during the study. The remaining thirty-four islands did not have constant species composition over time. Thus 55% of all islets studied showed no change in plant species composition over the period of sampling, but only 28% of the vegetated islands had unchanging floras.

Most of the islands whose floras changed during the study fell into one of two categories. Either the change involved extinctions only or immigrations only (Table 1). Of the eleven cases of extinctions only (Rottnest islets), nine occurred in 1977–78 and only two in 1975–77. The eleven cases comprise eight islands having one extinction, two with two extinctions and one with three extinctions. Of the fourteen immigrations, eleven occurred in 1975–77 and three in 1977–78. These were of seven islands with one species immigrating, five with two species immigrating and one each with three or four species immigrating. The remaining islets agreed reasonably well with those near Rottnest for the same census interval. Immigrations predominated. Of the seven cases of immigrations only, five islands involved one species immigrating and two others had two species immigrating. However, of the seven cases involving both immigrations and extinctions, extinctions predominated on four islands; the total number of local extinctions far exceeded local immigrations.

For the twenty-five islets near Rottnest Island with extinctions or immigrations only since 1975, immigrations predominate in

TABLE 1. Extinctions, immigrations, or both of plant species on islets studied, 1975–78

A. Islets near Rottnest (1975–77, 1977–78)	No. islets	Total changes		Total
		1975–77	1977–78	
Extinctions only	11	3	12	15
Immigrations only	14	20	4	24
Both	3	2(E), 1(I)	4(E), 5(I)	6(E), 6(I)
B. Other islets (1975–77 unless otherwise noted)	No. islets	Total changes		
Extinctions only (1975–76)	1	1		
Immigrations only	7	9		
Both	7 (2 of these 1975–76)	38(E), 7(I)		

1975–77, whereas extinctions predominate in 1977–78 (Table 1, a significant difference  $\chi^2 = 13, P < 0.001$ ).

*Floristic changes relative to physical features of islets*

The influence of the physical features of the islets on changes in composition of these floras was examined for the three groups recognized in Table 2. Islands that were unvegetated for the period of study had a significantly smaller area than the vegetated islands that showed no changes in species composition (Mann-Whitney U test, two-tailed  $P = 0.002$ ). Vegetated islands showing no turnover in plant species also had a significantly smaller area than the vegetated islands showing turnover ( $P = 0.002$ ). The corresponding levels of probability for the respective comparisons of elevation were 0.0001 and 0.44. Vegetated islands not showing turnover also had significantly fewer plant species (in 1978) than vegetated islands that did show turnover during the period of study ( $P = 0.004$ ).

*Turnover of plant species in relation to census interval*

Turnover is the number of extinctions ( $E$ ) and immigrations ( $I$ ) relative to the number of species comprising the flora on the two separate censuses ( $S_1, S_2$ ). It equals  $(E + I) / \frac{1}{2}(S_1 + S_2)$  [slightly modified after Diamond, 1969].

Although turnover rate (i.e. turnover  $\div$  census interval) can be related successfully to census interval, Abbott (1980) has argued that it is more appropriate to consider turnover *per se* in relation to census interval. There is little tendency for turnover to vary with census interval (Table 3). It has been argued that censuses should be annual otherwise changes will be missed, therefore underestimating turnover (Jones & Diamond, 1976; Diamond & May, 1977, considering birds). Our data do not support this idea. On the other hand, when censuses performed by G. M. Storr in 1956 or 1959 for islets near Rottnest Island and in Shoalwater Bay respectively are compared (Table 4) with ours

TABLE 2. Physical and biological features of islands, classified into three groups

Type of islet	Median area (m <sup>2</sup> ) (range)	Median elevation (m) (range)	Median number of plant species (range)	No. of islets
Islets showing no change in floras with time				
(a) Islets unvegetated throughout study	20 (2–1300)	3 (1–6)	0 (0)	29
(b) Islets vegetated throughout study	110 (10–560)	5 (5–13)	2 (1–5)	13
Islets showing change in floras with time	170 (4–160, 900)	5 (2.5–20)	6 (0–86)	34

TABLE 3. Species turnover on islets adjacent to Rottnest Island

	Census interval (years)		
	1 (1977–78)	2 (1975–77)	3 (1975–78)
Median turnover	0.22	0.16	0.16
<i>N</i>	21	20	20

TABLE 4. Species turnover for islets visited in the 1950s near Rottnest Island or in Shoalwater Bay

A	Census interval	
	Short (1–3 years: 1975–77–78)	Long (19–22 years: 1956–75–77–78)
Median turnover for same five islets near Rottnest	0.14	0.46
<i>N</i>	15	15

B	Census interval	
	Short (2 years: 1975–77; 1975–76 for Carnac I.)	Long (16–18 years: 1959–75–77)
Median turnover for same eight islets in Shoalwater Bay and Carnac I.	0.16–0.22	0.44–0.52
<i>N</i>	9	18

for the same islands in 1975–77–78 and 1975–77 respectively, turnover is about 3 times as great for long census-intervals (16–22 years) as against short census-intervals (1–3 years).

These findings suggest that over a short period of about 3 years the bulk of the islets change little in plant species number, whereas over a longer period (~20 years) there is a marked change in species composition. A similar idea was supported with changes in avifaunas on islands round South-western Australia (Abbott, 1978).

#### *Turnover of plant species in relation to island area*

The thirty-eight islets adjacent to Rottnest Island were categorized as small if they were < 100 m<sup>2</sup> in area or large if they were > 100 m<sup>2</sup>. Eight of the twenty-five islets had a change in

number of plants while the remaining ones did not. This was significantly fewer than the ten of thirteen large islets with a change in number of plant species ( $\chi^2_{1df} = 5.2$ ,  $P < 0.05$ ).

As suggested earlier for all islets, small islets tend to change little in species number whereas large ones change more. In this sense small islets have more stable floras than large islets.

#### *Extinction and immigration of annual, succulent and alien plant species*

Most of the plant species that become extinct or immigrate are annuals (Table 5). None of the differences between short and long census intervals in the number of: (a) annual species, (b) succulent species, (c) alien species that become extinct or immigrate compared with the numbers that do

TABLE 5. Comparison of proportion of annual, succulent and alien plant species comprising species extinctions and immigrations between short or long census intervals

	Census interval	
	Short (1–3 years: 1975–77–78)	Long (19–22 years: 1956–75–77–78)
<b>A. For same five islets near Rottneest</b>		
1. Total no. extinctions and immigrations	16	19
(a) of annuals (%)	69	68
(b) of succulents (%)	44	26
(c) of aliens (%)	50	53
2. Total no. extinctions	8	7
(a) of annuals (%)	63	71
(b) of succulents (%)	50	14
(c) of aliens (%)	50	57
3. Total no. immigrations	8	12
(a) of annuals (%)	75	67
(b) of succulents (%)	38	33
(c) of aliens (%)	63	50
<b>B. For same eight islets in Shoalwater Bay and Carnac Island</b>		
	Census interval	
	Short [2 years: 1975–77 (1975– 76 for Carnac I.)]	Long (16–18 years: 1959–75–77)
1. Total no. extinctions and immigrations	47	118
(a) of annuals (%)	66	71
(b) of succulents (%)	15	23
(c) of aliens (%)	60	59
2. Total no. extinctions	36	49
(a) of annuals (%)	64	63
(b) of succulents (%)	8	20
(c) of aliens (%)	58	47
3. Total no. immigrations	11	69
(a) of annuals (%)	73	77
(b) of succulents (%)	36	25
(c) of aliens (%)	64	68

not become extinct or immigrate are significant ( $\chi^2$  for independence or Fisher's exact test). Alien plant species are those that are not native to Australia; most are annuals (Abbott, 1977). All but one of the succulent species are native to Australia.

### Discussion

Much of the testing to date of the MacArthur–Wilson equilibrium theory with island floras has been attempted by Heatwole & Levins (1973), Heatwole (1976) and Abbott (1977).

This involves examining the predictions

that: (1) species number on islands should be predictable and constant, despite: (2) changes in species composition (i.e. some species immigrate, the same or others become extinct). The latter clause is a necessary but not sufficient condition for the validation of the equilibrium theory, and is the easier of the two predictions to falsify because only two consecutive censuses are required.

It is difficult to decide, from a series of censuses of an island flora, just what is meant by constancy of species number. Some authors (Heatwole & Levins, 1973, p. 1045) calculate the mean of species number from the available series of censuses. This pro-

cedure seems insufficient because a mean can be constructed for any series of numbers and need not have biological meaning. Some operational definition of constancy is necessary; we therefore propose that if the coefficient of variation of species number over a series of censuses is less than 5%, then this may be called constancy.

The rival hypothesis to the equilibrium theory is the non-equilibrium one (Brown, 1971; Abbott & Grant, 1976). By the equilibrium hypothesis, islands support as many plant species as possible, given their area, elevation, distance from the source area, etc. The non-equilibrium hypothesis instead is based on the premise that islands are under-saturated with species, and could hold more. Dispersal difficulties or historical factors or both are responsible for preventing certain species from establishing on islands. It seems the only way to support conclusively the non-equilibrium hypothesis is to show that: (1) propagules quite infrequently reach the island and those that do fail to establish due to random extinction alone, (2) when such species are introduced deliberately, they persist for a defined period (see later).

Abbott & Grant (1976) pointed out, however, that the equilibrium and non-equilibrium theories are not strictly rivals, because the equilibrium theory actually incorporates non-equilibrium conditions as stages in the development of equilibrium. Equilibrium may not then be reached because of insufficient time or irregular environmental conditions. The danger here is that the equilibrium theory becomes all-embracing; even if non-equilibrium were demonstrated by the two criteria listed above, it seems unsatisfactory to conclude that the island flora under study has the potential to reach equilibrium.

There are impressive changes in island floras in the Caribbean and Great Barrier Reef region which are little disturbed by man. Most of the islets studied have been sand cays. We point out that such islands are not a strong test of the equilibrium model, and in particular the null hypothesis that there is no change in species number with time, for several reasons. First, these islands do not have a constant area or shape (Heatwole & Levins, 1973) because they consist wholly of sand and coral debris deposited by wave

action. Second, with extensive, gently sloping beaches such cays ought to receive large numbers of propagules in flotsam stranded by wave action. Third, as most cays occur in tropical regions, they are subject to frequent cyclonic or hurricane disturbances which often cause waves temporarily to inundate cays and wash vegetation away.

In contrast we think our studies of the floras of aeolianite stacks are more relevant. Cays and other oceanic islands are not a major component of the world's islands; most are continental, representing the remains of a now submerged landscape. To determine the usual situation, it is of course necessary to study the most common type of island. The islets we studied are physically stable and are rarely subject to cyclones (like much of the temperate parts of the world) and would seem to be more suitable objects for disproving the null hypothesis that there are no changes in the floras on islands over a period of time. Finally, most of the islets studied are close to the source area, so that immigration ought to be frequent. This is typical of continental islands around Australia (Abbott, unpubl.).

Probably the most important modifications so far proposed to MacArthur & Wilson's original formulation of their equilibrium model concern the demonstration of non-equilibrium (Brown, 1971; Abbott & Grant, 1976) and interaction between immigration and extinction, apparently reducing turnover ('rescue effect', Brown & Kodric-Brown, 1977). Our data are equivocal in their support of the equilibrium model. Both short-term extinctions and immigrations occur on the majority of vegetated islets. If, however, all islets are considered (including those bare of vegetation) then a majority of islets showed no change in species number during the period of study.

With annual species (which die in summer), it is impossible to rule out the rescue effect because some of the next generation plants may originate from seeds deposited on the islet by earlier generations (a buried seed-bank) rather than from fruits blown to the islet before the next winter. The infrequency of immigrations by perennial species seems to rule out a role for the rescue effect.

There are several explanations possible why small islands have more stable floras than large



ones, even though this finding seems intuitively wrong. (One of the postulates of the equilibrium model is that extinction rates of species decrease on large islands because population sizes can be larger.) On small islands, wave action may prevent establishment of plants, or the continual deposition of seaspray may limit the available niches to only the most salt-tolerant species (Whitehead & Jones, 1969), or the limited area of soil present may be a small target for propagules to reach. Possible reasons why large islands should be less stable are that large islands present a bigger target to propagules, some of which may survive 1 year but fail to set seed. Nesting seabirds, which form large colonies on the larger islands only, may introduce plant species and exterminate others (fully considered by Abbott, 1977). Thirdly, inter-specific competition may be more keen on large islands because there are more plant species present.

Our data hint at the importance of climate in affecting turnover of plant species on islands. It was shown for islets near Rottneest that there were more immigrations detected in 1975–77 but more extinctions inferred in 1977–78. The total annual rainfall at the Rottneest Island meteorological station for 1957, 1976, 1977 and 1978 was 542, 464, 333 and 696 mm respectively. (Mean annual rainfall = 736 mm between the years 1880 and 1978.) A cyclone passed close to the island on 4 April 1978, the effect of which was to raise sea level by about 1 m and generate a heavy sea. This information suggests that immigrations have been highest in the years of lowest rainfall and extinctions highest in the period that included a cyclone. Nonetheless this needs to be treated with caution as other factors, as yet unrecognized by us, may be responsible. We are unable to relate the differential proportion of immigrants or extinctions in the periods 1975–77 and 1977–78 to differences in usage of the islands by nesting seabirds.

We turn now to the periods 1956–75, 1975–78 for the islets near Rottneest, and 1959–75, 1975–77 for the islets mainly in or near Shoalwater Bay. Species turnover was about 2–3 times greater over the long census interval than the short one (Table 4). Abbott (1977) suggested that the nesting

seabirds in the long term contribute most to turnover or plant species on certain islands, particularly those in Shoalwater Bay and Carnac Island.

There are several other factors that could account for high turnover during long census intervals. First, we would expect more extinctions and immigrations to occur over 16–22 years than over 1–3 years. Second, there have been four cyclones during the period 1956–75 (in March 1960, March 1961, April 1964 and February 1970), but only one in the period 1975–78 (in April 1978). Finally, the average annual rainfall at Rottneest Island over 1956–75 was 678 mm in contrast to 579 mm over 1975–78 (15% less). Wetter years may allow better germination of annuals than drier years, resulting in production of more seeds, perhaps increasing the chance of wider dissemination (and immigration?) in those years. In dry years more extinctions of plant species may result from increased physiological stress.

We emphasize that the three factors just outlined are speculative; our data are not sufficient to distinguish them. A long series of annual censuses (perhaps 10–20 years) may be necessary to do this more successfully.

Can studies of turnover in island floras be placed on an experimental footing? Experimental studies of insular insect faunas have been successful (Simberloff, 1976) but we doubt at present whether the same would apply to island floras. If plant species are to be removed, it would be necessary to be certain that no dormant seeds remained in the soil; to do this would require removal and treatment of the soil, during which the natural system will have been destroyed. One way to validate the non-equilibrium hypothesis is to add plant species to islands. Their survival and the continued persistence of the other plant species present would show that the flora was under-saturated with species, and hence would falsify the equilibrium hypothesis. If the added plant species survived and at least one of the original plant species became extinct, then this would be evidence for the equilibrium hypothesis. It is difficult to interpret the experiment if the plants added fail to survive even if none of the original plant species become extinct.

## Acknowledgments

We thank Paul Coster and John Scott for handling the boat when the islands in and near Shoalwater Bay were visited. Part of this research was financed by the Australian Research Grants Committee and the Zoology Department, University of Western Australia.

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## Appendix 1

### Occurrence of plant species on islets, 1956–78

The code numbers of islets refer to map in Abbott (1977). Islets near Rottnest Island with numbers 9–29, 31–37, 38–42 and 47 were visited in 1975, 1977 and 1978; those numbered 30, 37a and 39a were visited only in 1977 and 1978, and number 43 was visited in 1975 and 1978. Islets in or near Shoalwater Bay (numbers 84–120) were visited in 1975 and 1977. Carnac Island and surrounding islets (60, 65, 72) were visited in 1975 and 1976. Islets 121 and 121a were sampled in 1977 and 1978.

Islets with the following code numbers had no plant species present on any of the sampling dates: 9–12, 14, 16, 17, 21, 22, 25, 31, 32, 37a, 42, 84, 89, 90, 91, 100–102, 106–108, 112, 113, 117, 121a.

In the list below, the censuses of 1956, 1959, 1975, 1976, 1977 and 1978 are denoted as A, B, C, D, E and F respectively. \*Denotes species alien to Australia, now naturalized.

### JUNCAGINACEAE

*Triglochin trichophora* Nees 60 CD, 65 CD, 104 CE

### POACEAE

\**Avena barbata* Brot. 60 BCD, 104 BCE

\**Brachypodium distachyon* (L.) R. & S. 104 B

\**Briza minor* L. 60 B

*Bromus arenarius* Labill. 19 ACEF, 60 BCD, 65 CD, 88 BCE, 93 BE, 97 B, 104 B

\**B. diandrus* Roth 38 ACEF, 60 BCD, 93 BC, 104 BCE, 121 EF

\**Catapodium rigidum* (L.) C.E. Hubbard 38 F, 60 BCD

\**Cynodon dactylon* (L.) Pers. 104 CE

\**Ehrharta brevifolia* Schrad. 60 BCD

\**E. longiflora* Sm. 19 AC, 36 CF, 60 BCD, 104 BC

\**Hordeum leporinum* Link 19 ACEF, 37 A, 60 BCD, 88 BCE, 93 BCE, 97 B, 104 CE

\**Lagurus ovatus* L. 60 BCD, 104 C

\**Lolium loliaceum* (Bory & Chab.) Hand.-Mazz. 39a E, 60 BCD, 88 BC, 93 B, 104 BCE

\**Lopochloa cristata* (L.) Hylander 60 B

\**Parapholis incurva* (L.) C.E. Hubbard 38 CF, 60 BCD, 104 B

- \**Poa annua* L. 60 BCD, 65 CD, 88 BCE, 93 BCE, 97 E, 104 BCE  
*P. poliformis* (Labill.) Druce 38 ACEF, 60 BCD, 104 BCE  
 \**Polypogon monspeliensis* (L.) Desf. 60 D  
*Spinifex hirsutus* Labill. 60 B, 104 BCE  
*S. longifolius* R.Br. 60 BCD, 93 B, 104 BCE  
*Sporobolus virginicus* (L.) Kunth. 39 CEF, 93 BC, 97 C, 104 BCE, 121 EF  
 \**Stenotaphrum secundatum* (Walt.) Kuntze 104 BCE  
*Stipa elegantissima* Labill. 104 CE  
*S. flavesces* Labill. 60 BCD, 104 BCE  
 \**Vulpia myuros* (L.) Gmel. 60 CD, 104 B
- CYPERACEAE  
*Carex preissii* Nees 60 CD  
*Lepidosperma gladiatum* Labill. 60 BCD, 104 BCE  
*Scirpus antarcticus* L. 60 BCD, 104 BCE  
*S. nodosus* Rottb. 60 BCD, 104 BCE
- ARECACEAE  
 \**Phoenix canariensis* Hort. ex Chabaud 60 C
- LILIACEAE  
*Acanthocarpus preissii* Lehm. 60 BCD, 93 B, 104 BCE  
 \**Asphodelus fistulosus* L. 38 CEF  
*Thysanotus patersonii* R.Br. 38 CEF  
 \**Trachyandra divaricata* (Jacq.) Kunth. 60 BCD, 93 BE, 97 CE, 104 BCE
- IRIDACEAE  
 \**Romulea rosea* (L.) Eckl. 104 C
- HAEMODORACEAE  
*Conostylis candicans* Endl. 104 BCE
- ARACEAE  
 \**Zantedeschia aethiopica* (L.) Spreng. 60 CD
- URTICACEAE  
*Parietaria debilis* Forst. f. 19 ACE, 37 ACEF, 60 BCD, 65 CD, 88 BCE, 93 BCE, 97 B, 104 BCE  
 \**Urtica urens* L. 60 CD
- SANTALACEAE  
*Exocarpos sparteus* R.Br. 104 CE
- POLYGONACEAE  
*Muehlenbeckia adpressa* (Labill.) Meissn. 104 BCE  
 \**Rumex pulcher* L. 60 CD
- CHENOPODIACEAE  
*Atriplex cinerea* Poir. 19 C, 43 CF  
*A. isatidea* Moq. 93 B  
 \**A. patula* L. 60 BC, 88 E, 93 CE, 95 CE, 97 CE  
 \**Chenopodium album* L. 97 CE  
*C. glaucum* L. 19 CEF  
 \**C. murale* L. 27 F, 60 CD, 88 BCE, 92 CE, 93 CR, 95 CE, 97 BCE, 99 CE  
*Enchylaena tomentosa* R.Br. 60 BCD, 65 CD, 88 BCE, 93 BCE, 97 B, 103 E, 104 BCE  
*Rhagodia baccata* (Labill.) Moq. 18 CEF, 19 ACEF, 20 EF, 23 EF, 26 E, 27 CE, 28 EF, 29 CE, 36 F, 37 ACEF, 38 ACEF, 39 F, 60 BCD, 65 CD, 72 CD, 88 BCE, 93 BCE, 97 BCE, 103 CE, 104 BCE  
*Salsola kali* L. 60 BC, 93 B, 104 B  
*Sarcocornia blackiana* (Ulbr.) A.J. Scott 104 BCE  
*S. quinqueflora* (Bunge ex Ung.-Stern) A.J. Scott 13 CEF, 20 ACEF, 27 CE, 33 E, 35 A, 37 ACEF, 39 CEF, 43 CF, 60 CD, 121 F
- Sueda australis* (R.Br.) Moq. 39 EF  
*Threlkeldia diffusa* R.Br. 15 CEF, 18 CEF, 19 ACEF, 20 ACEF, 23 CEF, 24 CEF, 26 CEF, 27 CEF, 28 EF, 29 CE, 35 E, 36 CEF, 37 ACEF, 38 ACEF, 39 CEF, 39a EF, 40 CEF, 43 CF, 60 BCD, 65 CD, 72 CD, 87 BE, 88 BCE, 92 CE, 93 BCE, 95 BCE, 97 BCE, 98 CE, 99 BCE, 103 CE, 104 BCE, 105 CE, 109 CE, 110 CE, 111 E, 121 EF
- AIZOACEAE  
 \**Carpobrotus edulis* (L.) N.E. Br. 104 B  
*C. virescens* (Haw.) Schwantes 15 CEF, 18 CEF, 19 ACEF, 20 ACEF, 24 CEF, 26 CE, 27 CE, 28 CEF, 30 EF, 34 CEF, 35 ACEF, 36 CEF, 37 ACEF, 38 ACE, 39 CEF, 39a EF, 40 CEF, 43 CF, 47 CEF, 60 BCD, 65 CD, 72 CD, 88 BCE, 92 BCE, 93 BCE, 94 CE, 95 BCE, 96 E, 97 BCE, 99 BCE, 103 CE, 104 BCE, 105 CE, 109 CE, 110 CE, 111 CE, 114 CE, 115 CE, 118 E, 119 CE, 120 E, 121 EF  
 \**Gasoul crystallinum* (L.) Rothmaler 15 EF, 18 EF, 19 CEF, 26 EF, 27 CEF, 28 EF, 29 CEF, 39 EF, 47 E, 60 C  
*Tetragonia amplexicoma* (Miq.) Hook.f. 19 ACEF, 23 EF, 26 CE, 28 E, 36 CEF, 37 ACEF, 60 BCD, 93 BCE, 97 BE, 104 BCE  
*T. decumbens* Mill. 60 BCD, 65 CD, 88 BCE, 93 BCE, 97 B, 104 BCE
- PORTULACACEAE  
*Calandrinia calypttrata* Hook.f. 37 ACEF, 60 BCD, 65 CD, 72 CD, 88 BCE, 93 BCE, 95 BCE, 97 BCE, 98 CE, 104 BCE
- CARYOPHYLLACEAE  
 \**Cerastium glomeratum* Thuill. 60 BC, 104 BC  
 \**Polycarpon tetraphyllum* Loef. 60 CD, 104 BE  
*Sagina apetala* Ard. 15 CEF, 18 CEF, 20 CEF, 37 ACEF, 38 CEF, 39 CEF, 39a EF, 40 CEF, 41 F, 60 BCD, 65 CD, 88 C  
 \**Silene nocturna* L. 60 BCD  
*Spergularia rubra* (L.) J. & C. Presl. 93 BCE, 104 BCE  
 \**Stellaria media* (L.) Vill. 60 BCD, 65 CD, 88 C, 93 CE, 97 E, 104 BCE
- RANUNCULACEAE  
*Clematis microphylla* DC. 60 BCD, 104 BCE
- LAURACEAE  
*Cassytha racemosa* Nees 104 BCE
- FUMARIACEAE  
 \**Fumaria muralis* Sond ex Koch 104 C
- BRASSICACEAE  
 \**Brassica tournefortii* Gouan 60 BCD  
*Cakile maritima* Scop. 18 EF, 93 B, 104 BCE  
*Capsella bursa-pastoris* (L.) Medik. 60 B  
*Hymenolobus procumbens* (L.) Nutt. 37 A, 60 BC, 93 BCE, 104 CE  
*Lepidium foliosum* Desv. 19 ACEF, 60 BCD, 72 CD, 88 BCE, 93 BCE, 95 CE, 97 BCE, 99 CE, 104 CE  
 \**Raphanus raphanistrum* L. 60 C  
 \**Rapistrum rugosum* (L.) All. 60 C  
 \**Sisymbrium irio* L. 60 CD

- \**S. orientale* L. 39a E, 60 BCD, 65 CD, 72 CD, 88 BCE, 93 BCE, 95 CE, 97 BCE, 104 BCE
- CRASSULACEAE  
*Crassula colorata* (Nees) Ostenf. 60 BCD, 65 CD, 88 BCE, 93 BCE, 104 BCE  
*C. glomerata* L. 60 BCD, 104 BCE  
*C. pedicellosa* (F. Muell.) Ostenf. 60 C, 88 C, 93 CE, 104 BCE
- PITTOSPORACEAE  
*Pittosporum phylliraeoides* DC. 19 C, 93 B, 104 BCE
- MIMOSACEAE  
*Acacia cyclops* A. Cunn. ex G. Don 60 BCD, 104 B  
*A. rostellifera* Benth. 60 BCD, 88 B, 104 BCE
- FABACEAE  
*Hardenbergia comptoniana* (Andr.) Benth. 104 BCE  
*\*Medicago polymorpha* L. 60 BCD, 88 B, 93 B, 104 BCE  
*\*Melilotus indica* (L.) All. 19 ACEF, 36 CEF, 37 ACEF, 38 CEF, 43 CF, 60 BCD, 65 CD, 72 CD, 88 BCE, 93 BCE, 95 C, 97 BCE, 98 E, 104 BCE  
*\*Trifolium campestre* Schreb. in Sturm 60 BCD  
*\*T. scabrum* L. 60 C  
*\*T. tomentosum* L. 60 BCD
- GERANIACEAE  
*\*Erodium botrys* (Cav.) Bertol. 19 A  
*\*E. cicutarium* (L.) L'Hérit. ex Ait. 60 BCD, 88 BCE, 93 BC, 97 BCE  
*\*Geranium molle* L. 60 BCD, 104 C  
*Pelargonium capitatum* (L.) Ait. 60 BCD, 104 C
- OXALIDACEAE  
*Oxalis corniculatus* L. 88 C, 104 BC
- ZYGOPHYLLACEAE  
*Nitraria schoberi* L. 19 CEF, 26 CEF, 27 CEF, 29 CEF, 34 CEF, 36 CEF, 37 ACEF, 60 BCD, 72 CD, 87 BCE, 88 BCE, 92 BCE, 93 BCE, 94 CE, 95 CE, 96 CE, 97 BCE, 99 BCE, 104 BCE, 105 CE, 144 CE, 115 CE, 120 CE  
*Zygophyllum billardieri* DC. 88 BC, 93 B
- POLYGALACEAE  
*Comesperma integerrimum* Endl. 60 C
- EUPHORBIACEAE  
*\*Euphorbia peplus* L. 19 C, 38 ACF, 60 BCD, 65 CD, 104 CE  
*\*E. terracina* L. 104 CE
- RHAMNACEAE  
*Spyridium globulosum* (Labill.) Benth. 38 ACEF, 60 BCD, 104 BCE
- MALVACEAE  
*\*Lavatera arborea* L. 19 CEF, 60 BCD, 88 BCE, 93 CE, 95 E, 97 CE, 104 CE  
*L. plebeia* Sims 19 ACEF, 37 ACEF, 60 BCD, 72 CD, 88 BCE, 92 CE, 93 BCE, 95 BCE, 97 BCE, 98 E, 99 BCE  
*\*Malva parviflora* L. 60 BCD, 88 BCE, 93 BCE, 97 BCE, 104 CE
- FRANKENIACEAE  
*Frankenia pauciflora* DC. 19 ACEF, 20 ACEF, 36 CEF, 37 ACEF, 38 ACEF, 60 BCD, 65 CD, 72 CD, 93 BCE, 104 BCE, 121 EF
- APIACEAE  
*Apium prostratum* Vent. 60 BCD, 65 CD, 88 BCE, 93 BCE, 97 BCE, 103 CE, 104 BCE  
*Daucus glochidiatus* (Labill.) Fisch. et al. 60 BCD  
*Hydrocotyle diantha* DC. 60 CD
- EPACRIDACEAE  
*Acrotriche cordata* (Labill.) R.Br. 38 ACEF  
*Leucopogon parviflorus* (Andr.) Lindl. 38 ACEF
- PRIMULACEAE  
*\*Anagallis arvensis* L. 19 C, 60 BCD, 104 BCE
- GENTIANACEAE  
*Centaurium spicatum* (L.) Fritsch 60 B
- APOCYNACEAE  
*Alyxia buxifolia* R.Br. 38 CEF, 104 BCE
- CONVOLVULACEAE  
*Dichondra repens* Forst. & Forst. f. 104 BC  
*Wilsonia backhousei* Hook. f. 104 BCE
- SOLANACEAE  
*Anthocercis littorea* R.Br. 104 B  
*\*Solanum nigrum* L. 60 BCD, 88 B, 93 B, 97 B, 104 BC  
*S. symonii* Eichler 38 F, 60 BC
- SCROPHULARIACEAE  
*\*Bellardia trixago* (L.) All. 60 CD, 104 C  
*\*Dischisma arenarium* E. Mey. 60 BCD, 104 BCE  
*\*Parentucellia latifolia* (L.) Caruel 60 B
- MYOPORACEAE  
*Eremophila glabra* (R.Br.) Ostenf. 104 CE  
*Myoporum adscendens* R.Br. 88 BC, 93 BCE, 97 BCE, 104 BCE
- RUBIACEAE  
*\*Galium murale* (L.) All. 38 E, 60 BCD, 65 C, 104 CE
- GOODENIACEAE  
*Scaevola crassifolia* Labill. 19 ACEF, 20 ACEF, 38 ACEF, 60 BCD, 104 BCE
- ASTERACEAE  
*\*Actites megalocarpa* (Hook. f.) N.S. Lander 60 BCD, 93 B  
*Angianthus cunninghamii* (DC.) Benth. 104 B  
*\*Arctotheca calendula* (L.) M. Levyns 60 BCD, 88 BC, 93 B, 97 C, 104 BCE  
*\*A. populifolia* (Berg.) T. Norl. 93 B  
*Calocephalus brownii* (Cass.) F. Muell. 39a EF, 60 BCD, 104 CE, 121 EF  
*\*Carduus pycnocephalus* L. 60 BCD, 104 B  
*\*Centaurea melitensis* L. 60 CD  
*\*Conyza canadensis* (L.) Cronquist 104 B  
*Cotula australis* (Sieb. ex Spreng.) Hook. f. 60 B  
*C. coronopifolia* L. 60 BCD  
*\*Crepis foetida* L. 60 CD  
*Helichrysum cordatum* DC. 104 BCE  
*\*Hypochoeris glabra* L. 60 BCD, 104 B  
*\*Inula graveolens* Desf. 39a E  
*\*Lactuca saligna* L. 104 CE  
*\*L. serriola* L. 60 C  
*Olearia axillaris* (DC.) F. Muell. 20 ACEF, 38 ACEF, 39a EF, 60 BCD, 88 B, 93 B, 104 BCE  
*Podosperma angustifolium* (Labill.) 60 BCD

<i>Senecio lautus</i> Forst.f. ex Willd. 15 EF, 19 ACEF, 37 E, 38 ACEF, 39a E, 60 BCD, 65 CD, 72 C, 88 BC, 93 BCE, 95 BCE, 97 BCE, 104 BCE	39 EF, 39a F, 60 BCD, 65 CD, 72 CD, 88 BCE, 93 BCE, 95 CE, 97 BCE, 103 E, 104 BCE, 121 EF
* <i>Sonchus oleraceus</i> L. 19 ACEF, 37 ACEF,	* <i>Urospermum picroides</i> (L.) F.W. Schmidt 60 BCD

Appendix 2

Planar area and maximum elevation of islets visited. Each set of three numbers denotes the code number of the island (Abbott, 1977, Fig. 1), island area (m<sup>2</sup>) and elevation (m), respectively.

9, 20, 2	10, 220, 3	11, 20, 3	12, 20, 2.5	13, 40, 3
14, 3, 1, 3	15, 70, 6	16, 50, 3	17, 10, 1	18, 70, 5
19, 1200, 6	20, 80, 3	21, 10, 2	22, 60, 3	23, 40, 3
24, 40, 4	25, 1300, 6	26, 1500, 6	27, 840, 6	28, 20, 5
29, 120, 4	30, 20, 3	31, 10, 2.5	32, 10, 2	33, 190, 2.5
34, 280, 10	35, 500, 6	36, 140, 10	37, 330, 10	37a, 20, 4
38, 140, 4	39, 170, 6	39a, 70, 3	40, 40, 5	41, 60, 5
42, 20, 1.8	43, 90, 13	47, 30, 2.5	60, 160900, 17	65, 20, 2.5
72, 2150, 12	84, 40, 5	87, 220, 3	88, 8900, 10	89, 20, 5
90, 150, 4	91, 15, 4	92, 400, 4.2	93, 12100, 9	94, 230, 6
95, 1600, 10	96, 70, 5	97, 4450, 10	98, 20, 2.5	99, 400, 5
100, 230, 4	101, 30, 3	102, 2, 1.3	103, 140, 5	104, 119000, 20
105, 450, 6	106, 20, 4	107, 4, 2.5	108, 4, 2	109, 560, 5
110, 10, 10	111, 220, 6	112, 3, 2	113, 3, 1	114, 220, 6
115, 160, 5	116, 40, 3	117, 70, 5	118, 110, 5	119, 110, 5
120, 220, 5	121, 900, 5	121a, 15, 2		