
Hooker and islands¹

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Sir Joseph Dalton Hooker (1817–1911), friend and scientific confidant of Charles Darwin, lectured in 1866 on ‘Insular floras’ at the Annual Meeting of the British Association for the Advancement of Science. His interest and knowledge of islands had been aroused when he travelled to the Antarctic aboard the *Erebus* under Sir James Clark Ross from 1839–43. On his return, Darwin passed on to Hooker the botanical collections he had made on the *Beagle* voyage, including those from the Galapagos. Hooker’s conclusions from these and from his own material and experiences were important to Darwin as he developed the ideas that culminated in the publication of the *Origin of Species*. The 1866 lecture provided a focus for subsequent and informative studies on evolution, and islands continue to provide invaluable natural laboratories for evolutionary biology and genetics. © 2009 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2009, 96, 462–481.

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PIIONEER BIOGEOGRAPHER AND FAMOUS SCIENTIST

Joseph Hooker – the ‘younger’ Hooker – was born on 30 June 1817 at Halesworth, near Southwold in Suffolk. His time in Suffolk was short: when he was 3 years old, the family moved to Glasgow, on his father’s election to the Regius Chair of Botany in the University. Hooker Junior attended Glasgow High School and, at the age of 15 years, went to the University. Half a century later, he reminisced that he frequently accompanied his father to the Highlands, where ‘I fished a good deal, but also botanised. Well I remember on one occasion, that, after returning home, I built up by a heap of stones a representation of one of the mountains I had ascended and stuck upon it specimens of the mosses I had collected, at heights relative to those at which I had gathered them. This was the dawn of my love for geographical botany’ (Hooker, 1887).

These early expeditions were the beginning of a lifetime passion for Hooker. He wrote that ‘when still a child, I was very fond of [accounts of] Voyages and Travels; and my great delight was to sit on my grand-father’s knee and look at the pictures in Cook’s “Voyages”. The one that took my fancy most was the plate of Christmas Harbour, Kerguelen Land, with the arched rock standing out to sea and the sailors killing penguins; and I thought I should be the happiest boy alive if ever I would see that wonderful arched rock and knock penguins on the head. By a singular coincidence, Christmas Harbour, Kerguelen Land was one of the very first places of interest visited by me in the Antarctic Expedition under Sir James Ross’ (Hooker, 1887).

Hooker was particularly fortunate in being able to fulfil his childhood dreams. Through Sir John Richardson (1787–1865), Director of the Naval Hospitals at Chatham and Haslar, who had been the naturalist on Franklin’s Arctic Expeditions, his father had met James Clark Ross (1800–62), one of the most distinguished naval officers of his generation and the ‘handsomest man in the Royal Navy’ (Gurney, 1997: 186). Ross was a veteran of six Arctic expeditions, on the last of which he was involved in locating the North Magnetic

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Pole.² Because of this acquaintance, in the early autumn of 1838 the two Hookers (father and son) were invited by James Hill, a Glasgow neighbour, to breakfast with Ross. The outcome was that Ross asked the younger Hooker to accompany him on a voyage to the Antarctic, on condition that he had qualified as a surgeon. Ross wanted 'such a person as Mr Darwin' as the naturalist on the expedition, and seemed to have felt that Hooker needed to prove himself. Joseph obviously worked hard, obtaining a medical diploma from Edinburgh on 5 May 1839, less than 1 year later, although he never practised. Much later in life he wrote, 'I had to gallop through a medical degree at the last hour: Happily for the crew [on his Antarctic expedition] we had no sickness and hardly an accident to either ship throughout the voyage' (Huxley, 1918: ii: 439).

Journeying south with Ross (1839–43) was only the first of Hooker's international travels. He subsequently spent three years (1847–50) in the Himalayas, and visited Palestine, Morocco (1871), and the USA (1877). His accounts of the botany of these trips, particularly the *Flora of British India* (published in seven volumes, 1872–97), established him as a leading scientist. The citation when he received the Royal Society's Copley Medal recorded, 'As a traveller, he can perhaps only compare with Humboldt in the extent to which he has used travel as an instrument of research: to quote a remark by Professor Asa Gray, "No botanist of the present century, perhaps of any time, has seen more of the earth's vegetation under natural conditions" . . . Perhaps Sir Joseph's most important place in scientific history will be found in the rational basis upon which he placed geographical botany'. Hooker was appointed a Knight Commander of the Star of India in 1877 and advanced to Knight Grand Commander (GCSI) in 1897. He succeeded his father as Director of the Royal Botanic Gardens in 1865, retiring in 1885. He was elected to the Royal Society in 1847, receiving a Royal Medal in 1854, the Copley Medal in 1887, and a Darwin Medal in 1892, and serving as President 1873–78. He was President of the British Association in 1868. Edward VII appointed him a member of the Order of Merit in 1907. When he died in 1911, his widow rejected an offer that he should be buried near Darwin in Westminster Abbey; his grave is alongside that of his father in the churchyard of St Anne's Kew Green.³

²Ross was a career naval officer, but also an accomplished naturalist, elected to the Linnean Society in 1824 at the age of 24 years and to the Royal Society in 1828. Ross's Avens (*Geum* (*Sieversia*) *rossii*) and Ross's Gull (*Rhodostethia* (*Larus*) *rosea*) were both named in his honour.

³The fullest account of Hooker's life is the *Life and Letters of Sir J.D. Hooker*, edited by Leonard Huxley (1918). Other extensive biographies are by Turrill (1953, 1963), Allen (1967), and Desmond (1999).

The Hooker Lecture was established by the Linnean Society following a legacy from Joseph Hooker himself. It has been delivered on 18 occasions (Berry, 2007). Four of the lectures [D. H. Scott in 1912 (preceding the series proper, but a 'Hooker Lecture' in reality), H. J. Elwes in 1913, Ray Desmond in 1992 and Henry Noltie in 2005] were explicitly linked to Hooker's life and work; two were by zoologists describing their own studies (D. M. S. Watson in 1948 and Theodosius Dobzhansky in 1962); all the others were botanical in their content. Surprisingly, none dealt with Hooker's contributions to evolutionary understanding or his support for Charles Darwin. In his account of Hooker in the *Dictionary of National Biography*, Endersby (2006) judged that 'when Hooker appears in histories of nineteenth century science, it is almost invariably as a minor character in Darwin's story and his own work, attitudes and opinions have been neglected as a result'. This is certainly not true of the Hooker Lectures and it is unfair to suggest that Hooker was only a 'minor' character in Darwin's story. This nineteenth Hooker Lecture is an attempt to identify Hooker's contributions to evolutionary biology in his own studies as well as his friendship and support for Darwin.

EREBUS AND TERROR

In 1835, the recently formed British Association for the Advancement of Science petitioned the British Government to sponsor a national Antarctic expedition with the aim of locating the south Magnetic Pole. Three years later, the Royal Society, which had been given money by the Government to purchase magnetic instruments, set up a committee to consider the whole matter of magnetic stations and of a South Polar voyage. The British Association followed up their previous resolution with a call for a naval expedition to the Antarctic for magnetic investigations between the meridians of New Holland (Australia) and Cape Horn. These pleas were successful: the Prime Minister, Lord Melbourne was supportive, and Parliament voted £100 000 for the work. Clark Ross was appointed as leader, in command of HMS *Erebus* (372 tons) and HMS *Terror* (326 tons), three-masted, ice-strengthened ships built originally as 'bombs' for 'bombarding' land positions with heavy mortars.⁴

The instructions issued to Ross by the Admiralty in September 1839 were framed very broadly. Ross was

⁴*Erebus* was built in Pembroke in 1826; *Terror* was constructed at Topsham in Devon and saw service against the USA in 1812. After their return from the Antarctic in 1843, their next voyage was to the Canadian Arctic under the command of Sir John Franklin in an ill-fated attempt to sail through the North West Passage; the last sight of them was entering Baffin Bay in August 1845.

to seek the maximum coordination of simultaneous magnetic observations; to achieve this stations and observatories were to be set up at points as far apart as possible: on St Helena, the Cape of Good Hope, Hobart, and Sydney. If this could be completed by the following February, Ross was then to proceed as far as the ice permitted to the south 'to examine those places where indications of land have been noticed, and to make the requisite observations of any outlying islands . . .'

In September 1839, the *Erebus* and *Terror* left on the greatest Antarctic expedition of the nineteenth century.⁵ Since it was to be a purely naval expedition, only naval personnel were taken. However the surgeons, McCormick and Hooker on *Erebus* and Robertson and Lyall on *Terror*, were really civilians in naval guise.

Robert McCormick was the chief surgeon on the *Erebus*. He was a prickly character. Eight years previously, he had sailed on the *Beagle* with the ambition of becoming 'famous as an exploring naturalist' (McCormick, 1884: i: 218). He saw the way to achieving this was by collections and discoveries from unknown parts of the globe.⁶ He was put out by finding Charles Darwin as the *de facto* ship's naturalist on the *Beagle*. The two had no rapport with each other. Darwin considered McCormick 'an ass'. Four months into the voyage, McCormick had himself invalidated home⁷ and spent the next 4 years on half-pay. He attended lectures by Darwin's old teachers, Robert Jameson in Edinburgh and Robert Grant in London, after which 'having now fairly taken up the pursuit of natural history in addition to my ordinary professional duties and prepared and qualified myself

by a course of hard study and attendance on the lectures of the most distinguished professors, my great object was to get employed in scientific voyages of discovery' (McCormick, 1884: i: 218).

There does not seem to have been any friction between Hooker and McCormick on the *Erebus*. Six months into the voyage, Hooker wrote to his father from South Africa, 'McCormick and I are exceedingly good friends and no jealousy exists between us regarding my taking most of his department; indeed he seems to care too little about Natural History altogether to dream of anything of the kind; for my part I am rather glad to have an opportunity of doing more than is expected from my department . . . I am, *nolens volens*, the Naturalist, for which I enjoy no other advantage than the Captain's cabin, and I think myself amply repaid' (quoted in Huxley, 1918: i: 68). Hooker seems to have had complete freedom to explore his natural history interests.

One good turn that McCormick did to Hooker was to introduce him to Darwin, when they met by chance in Trafalgar Square a few days before embarking on the *Erebus* (Hooker, 1899).⁸ Darwin had returned from the *Beagle* voyage 3 years previously with an established reputation based on his collections which he had sent back to England at various times during his travels; he was elected to the Royal Society in 1839, at the age of 29 years. He was already a hero to the young Hooker. Charles Lyell (a family friend and a keen botanist; father of the geologist Sir Charles Lyell) had lent Hooker a proof copy of the *Voyage of the Beagle*, which he had 'slept with under his pillow and devoured eagerly the moment he woke in the mornings' at the time as was preparing for his medical examinations (Huxley, 1918: i: 66); the book was published just before the *Erebus* left, and Lyell gave him a bound copy which he took with him on the voyage. He was 22 years of age. Sixty years later, he wrote, 'The [book] impressed me profoundly, I may say despairingly, with the genius of the writer, the variety of his acquirements, the keenness of his powers of observation, and the lucidity of his descriptions. To follow in his footsteps, at however great a distance, seemed to be a hopeless aspiration; nevertheless they quickened my enthusiasm in the desire travel and observe' (Hooker, 1899).

Erebus and *Terror* sailed from Margate on 30 September 1839 and returned to Woolwich almost exactly 4 years later, on 4 September 1843. Their journeys

⁵The official account of the expedition was written by Ross himself (Ross, 1847); a more succinct account has been produced by Ross's great grandson (Ross, 1982).

⁶Janet Browne (1995: 206) comments, 'In the entrepreneurial world of the early-nineteenth-century natural history, the possession of a substantial collection from faraway places, full of rarities and undescribed species, the enviable harvest of inland expeditions or of long periods dredging in foreign seas, frequently made the collector a scientific celebrity . . . If all else failed, the specimens possessed commercial value . . . When Francis Beaufort (the Admiralty Hydrographer) proposed putting Darwin on the Admiralty's books for victuals, Darwin's immediate response was not gratitude but anxiety that he would forfeit absolute control over his cargo'.

⁷McCormick wrote about his time in the *Beagle*, 'having found myself in a false position on board a small and very uncomfortable vessel and very much disappointed in my expectations of carrying out my natural history pursuits, every obstacle having been placed in the way of my getting on shore and making collections, I got permission from the admiral in command of the station [at Rio] to be superseded and allowed a passage home' (McCormick, 1884: i: 217). He distinguished himself in later life on one of the expeditions in search of Franklin, but fell out with the Admiralty because they failed to promote him for what he considered his exceptional service in the Antarctic.

⁸Asa Gray records an earlier meeting on 22 January 1839, when he and the two Hookers went to the Royal College of Surgeons and 'there met Mr Darwin, the naturalist who accompanied Captain King [who had preceded Fitzroy as commander of the *Beagle* on her previous voyage South] in the *Beagle*' (Gray, 1893: i: 117). Neither Darwin nor Hooker remembered this.

involved visits to a range of islands and three voyages towards the Antarctic Continent (Fig. 1):

- From London to Tasmania, stopping at Madeira (20–31 October), the Cape Verde Islands (13–20 November), the barren St Paul's Rocks in mid-Atlantic (2 December), Trinidad (or South Trinidad, a Brazilian island 1000 km east of the South American continent) (17 December), and St Helena (31 January to 9 February) on the way to the Cape of Good Hope (17 March to 6 April); thence to Tasmania via Marion (21 April) and the Prince Edward Islands (where they failed to land), Crozet (26 April) and Kerguelen (12 May to 20 July), arriving in Hobart on 16 August, 11 months after leaving England. After 3 months in Tasmania, they sailed again (12 November) to make a sweep south to the Antarctic Continent (Fig. 2) via the Auckland Islands (20 November to 12 December) and Campbell Island (12–17 December), the ice-covered Possession (11 January) and Franklin Islands (27 January), and thence back to Tasmania, arriving on 6 April 1841.
- Three months in Tasmania, leaving on 7 July for a brief visit to Sydney (14 July–5 August), 3 months in New Zealand (17 August to 23 November) and another trip south to the Antarctic (failing to land on Chatham Island); then across the Southern Ocean.
- Six months in the Falkland Islands (arriving 6 April 1842), with visits to Hermite Island off Cape Horn ('The place reminded me very much of the Trossachs or the head of Loch Long contracted': Huxley, 1918: i: 135) (Fig. 3) (8 September to 11 November), finally leaving the Falklands on 17 November for the South Shetlands and Cockburn Island⁹ (6 January) (followed by a failure to locate Bouvet Island), and a 4 month return northwards via the Cape of Good Hope, St Helena, Ascension and Rio de Janeiro.

Over this period, the expedition reached the southernmost latitude so far attained by mankind (70°14',

⁹Hooker's collections on Cockburn Island provided the first botanical specimens ever from the Antarctic proper. His survey was repeated and extended by Ron Lewis Smith of the British Antarctic Survey almost 150 years later (Lewis Smith, 1993). Cockburn Island has later proved to be of considerable geological and palaeontological significance (Stilwell, 2002). Intriguingly, Hooker, in a letter to his father in August 1869 describing his visit to the Donkia Pass between Sikkim and the Tibetan Plateau commented 'I was greatly pleased with finding my most Antarctic plant, *Lecanora miniata*, at the top of the Pass, and today I saw stony hills at 19 000 feet stained wholly orange-red with it, exactly as the rocks of Cockburn Island were in 64° South; is not this most curious and interesting? To find the identical plant forming the only vegetation at the two extreme limits of vegetable life is always interesting; but to find it absolutely in both cases painting a landscape is wonderful' (Huxley, 1918: i: 305).

seven degrees nearer the Pole than Cook on his second voyage), disproved a French belief that there was a 'La France Australe suitable for settlement which would yield timber, mines, diamonds, rubies, semiprecious stones and marble' (the claim of Kerguelen-Trémaroc, discoverer of the islands named after him, in a report to Louis XV);¹⁰ they landed on many of the islands visited by Joseph Banks on Cook's first voyage and later by Darwin on the *Beagle*.¹¹ Darwin found the formal account of the expedition by Ross disappointing, apart from Hooker's 'botanical summaries'. Hooker kept a journal, which had to be surrendered to the Admiralty at the end of the voyage, but he wrote detailed letters home, and these were distilled and published by his father (Hooker, 1843) following a summons to Buckingham Palace by Prince Albert. However, the main scientific fruits and the work which established the reputation of Hooker as a taxonomist and geographer were his three substantial publications on *The Botany of the Antarctic Cruise of H.M. Discovery Ships Erebus and Terror in the Years 1839–43, under the command of Captain Sir James Clark Ross*:

- *Flora Antarctica*, in two parts (1844–47);
- *Flora Novae-Zelandiae*, Part 1 (1853–55), Part 2 (1855);
- *Flora Tasmaniae*, Volume 1 (1855–60), Volume 2 (1860).

HOOKER AND ISLANDS

Good scientist that he was, Hooker was influenced by his observations. His notes quickly expanded from the minutiae of collecting to questions of geographical

¹⁰He declared, 'The lands which I have discovered appear to form the central mass of the Antarctic Continent . . . and the land which I have called South France is so situated to command the route to India, the Moluccas, China and the South Seas . . . South France can henceforth give new life to the Île de France and Bourbon, tripling their sea-trade and enriching them' (cited by Kirwan, 1962: 80). A determined British advocate of the existence of a massive Southern Continent was Alexander Dalrymple, first Admiralty Hydrographer. Writing following the return of James Cook from his first voyage, he demanded why the Government should bother with the North American colonies when all the wealth of the Southern Continent lay to hand; a land more 'spacious than the whole civilized part of Asia from Turkey to the eastern extremity of China . . . The scraps from this table would be sufficient to maintain the power, dominion and sovereignty of Britain' (*Historical Collection of the Several Voyages and Discoveries into the South Pacific Ocean*, 1771).

¹¹HMS *Challenger*, the next – and final – great scientific voyage of the century (1872–76) also visited many of the same islands, although its raison d'être and success was in pioneering oceanography rather than in biology. Its scientific leader, Charles Wyville Thomson wrote that the general structure of Kerguelen 'very much resembles that of the volcanic district of Antrim or part of the west coast of Scotland'.

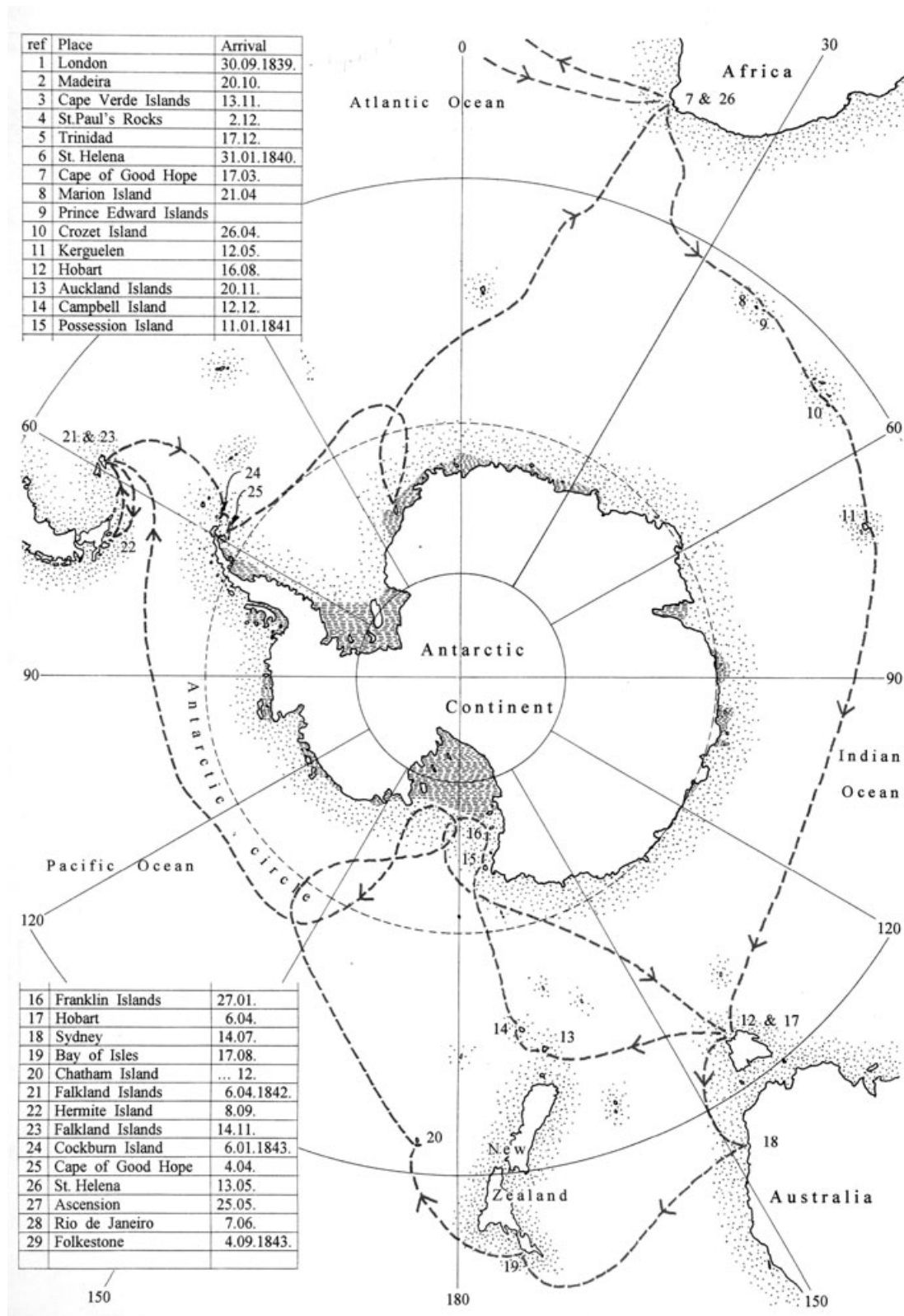


Figure 1. Hooker's voyage aboard the *Erebus* and *Terror*, 1839–43.

distribution. Madeira, his first island, ‘strongly reminded me of some of the islands on the West of Argyllshire . . . The ravines are quite like Scotch ones, but more sparingly wooded . . .’ (Huxley, 1918: i: 87). In a letter to his father written during the journey through the South Atlantic, he clearly thought that the island biotas he would find would be determined by temperature (Huxley, 1918: i: 82). By the time the *Erebus* reached Kerguelen Island, he had begun to ask deeper questions about the relationship between the floras of islands and continents.

Kerguelen is 700 miles (1100 km) east of Crozet and in the same latitude in the southern hemisphere as Jersey in the north. It is a fairly substantial land mass [Kerguelen is an archipelago with one large island 150 × 120 km (6675 km²; more than the area of Shetland, Orkney and the Hebrides combined) and around 300 small ones]. It was visited by Cook in 1776 on his third voyage. The expedition’s naturalist William Anderson wrote, ‘Perhaps no place hitherto discovered in either hemisphere, under the same parallel of latitude, affords so scanty a field for the naturalist as this barren spot’. He recorded a mere 16 species of plants, mainly cryptograms. Hooker and the *Erebus* stayed there for 68 days. Hooker found all Anderson’s species and ended up listing 18 species of flowering plants, 35 mosses and liverworts, 25 lichens, and 51 algae. His formal description of his work on Kerguelen, together with that on the Falklands and Tierra del Fuego is set out in the second part of his *Flora Antarctica*. Nearly 40 years later, he reviewed knowledge of the flora in the perspective of later collections on Kerguelen and other places in the sub-Antarctic (Hooker, 1879). He affirmed his original conclusion that the most marked influence on the Kerguelen flora was ‘Fuegian’ (i.e. related to the flora of Tierra del Fuego, which he had encountered at Hermite Island in the later stages of his *Erebus* voyage). In a paper introducing studies carried out by the Challenger expedition of 1874–75, he noted that ‘more recent collections have confirmed and even strengthened this Fuegian affinity . . . The elements of the Phænogamic flora of Kerguelen Island may be classified:

- one endemic genus which has no near ally – *Pringlea antiscorbutica* (Crucifereae)
- one endemic genus allied to an Andean one – *Lyallia kerguelensis* (Portulaceae)
- six endemic species allied to American congeners – *Ranunculus crassipes*, *R. moseleyi* (Ranunculaceae), *Colobanthus kerguelensis* (Caryophyllaceae), *Acæna affinis* (Rosaceae), and two grasses: *Poa cookii*, *Festuca kerguelensis*
- five species common to Fuegia but not found elsewhere: *Ranunculus trullifolius* (Ranunculaceae), *Azorella selago* (Araliaceae), *Galium antarcticum* (Rubiaceae), and two more grasses: *Festuca erecta*, *Deschampsia antarctica*
- six species common to America, New Zealand and the islands south of it: *Tillæa moschata* (Crassulaceae), *Montia fontana* (Portulaceae), *Callitriche obtusangula* (Plantaginaceae), *Limosella aquatica* (Scophulariaceae), and a rush and a grass: *Juncus scheuzerioides*, *Agrostis magellanica*
- two species found elsewhere but not in Fuegia: *Cotula plumosa* (Asteraceae) (common to the Auckland and Campbell Islands) and *Uncinia compacta* (Cyperaceae) (native to the mountains of Tasmania and New Zealand).’

The Fuegian flora was ‘the great botanical centre of the Antarctic Ocean’; all the islands south of New Zealand, the Falkland Islands, South Georgia, Tristan da Cunha and Kerguelen seemed to have borrowed plants’ from there. He found this astonishing; Kerguelen, for example, was 5000 miles (8000 km) from Tierra del Fuego. Not only that: Fuegia possessed a great number of English plants. His mind was drawn to ‘that interesting subject – the diffusion of species over the surface of the world’.

HOOKER AND DARWIN

Hooker was unemployed when he got back from the *Erebus* voyage. In the autumn of 1843, he worked at Kew on his *Flora Antarctica* with his father’s support. He then moved to Edinburgh to lecture in botany, with the hope of succeeding the incumbent Professor of Botany, Robert Graham who was dying. However, John Henry Balfour, a local man and William Hooker’s successor as Professor of Botany in Glasgow, was appointed. Hooker was offered the Glasgow Chair, but declined and returned to London. Apart from his travels (most notably to India and the Himalaya), his subsequent life revolved entirely around Kew.

Meanwhile, Darwin, who returned from the *Beagle* voyage in 1836, had been searching for collaborators to work on the collections he had made. His old teacher and the person responsible for his invitation to join the *Beagle*, John Stevens Henslow, had acted as a receiving officer for the material sent back during the *Beagle* years and Darwin had assumed that he would deal with the plants. However Henslow does not appear to have been interested; all he produced was a note on two Galapagos species and an account of the Keeling Island flora (Henslow, 1837, 1838). Darwin seems to have become increasingly frustrated. He wrote to Henslow (November 1839), ‘I believe you have received a message I sent you saying that Humboldt in a letter to Me expresses at great length his vivid regret that M. Henslow has not been

able to describe the species, or even characterize the genera of the very curious collection of plants from the Galapagos. Do think again of making one paper on the Flora of these islands'. Then on 12 March 1843 he wrote to William Hooker: 'I am very glad to hear you talk of inducing your son to publish an Antarctic Flora – I have long felt much curiosity for some discussion on the general character of the Flora of Tierra del Fuego, that part of the globe furthest removed in latitude from us. How interesting will be a strict comparison between the plants of those regions & of Scotland or Shetland. I am sure I may speak on part of Professor Henslow that all my collection (which gives fair representation of alpine flora of T. del. Fuego & of Southern Patagonia) will be joyfully laid at his disposal'.

Hooker disembarked from the *Erebus* on 9 September 1843. In November, Darwin wrote to him: 'I had hoped before this time to have had the pleasure of seeing you & congratulating you on your safe return from your long & glorious voyage. I am anxious to know what you intend doing with all your materials – I had so much pleasure in reading parts of some of your letters, that I shall be very sorry if I, as one of the Public, have no opportunity of reading a good deal more . . . Henslow (as he informed me a few days since by letter) has sent to you my small collection of plants – you cannot think how much pleased I am, as I feared they wd have been all lost. I paid particular attention to the Alpine flowers of Tierra Del. & I am sure I got every plant which was in flower in Patagonia at the seasons when we were there – I have long thought that some general sketch of the Flora of that point of land, stretching so far into the southern seas, would be very curious'.

Hooker responded quickly (28 November): 'I am exceedingly glad to think you attach so much importance to the comparison of the Arctic plants with the Antarctic as it was my aim throughout to establish an Analogy between the two hemispheres, & to draw up tables upon several plans, shewing for instance the proportion of plants in each of the predominant Nat. Ords. common to both . . . In my Antarctic flora I intend (following my fathers advice) to include Ld Aucklands & Campbells Islds as they contain the most southern plants of those longitudes, & as they have all the nameless peculiarities of plants of high latitudes, quite as much so as those of Fuegia (however luxuriant the vegetation may be compared with analogous Northern latitudes) . . . The Vegetation of Kerguelens Land is entirely that of Southernmost America, almost all its plants being common to the two, few in proportion common to it & Ld Aucklands & none peculiar to the two latter. (perhaps one is). The Falkland Isld. flora seems to combine the Patagonian with the Fuegian, I think of including it with the latter'.

Darwin was delighted – and very impressed with the young Hooker. At the time his mind was filled with evolutionary ideas. He had first written them down as a 'pencil sketch' in 1842; he revised and extended them into a 189 page 'essay',¹² parts of which formed the paper presented on his behalf at the Linnean Society in 1858. On 11 January 1844, he wrote to Hooker, mainly about the southern flora, but he concluded with a paragraph which has become famous:

'Besides a general interest about the Southern lands, I have been now ever since my return engaged in a very presumptuous work & which I know no one individual who wd not say a very foolish one – I was so struck with distribution of Galapagos organisms &c &c & with the character of the American fossil mammifers, &c &c that I determined to collect blindly every sort of fact, which cd bear any way on what are species – I have read heaps of agricultural & horticultural books, & have never ceased collecting facts. At last gleams of light have come, & I am almost convinced (quite contrary to opinion I started with) that species are not (it is like confessing a murder) immutable. Heaven forfend me from Lamarck nonsense of a 'tendency to progression' 'adaptations from the slow willing of animals' &c, but the conclusions I am led to are not widely different from his though the means of change are wholly so. I think I have found out (here's presumption!) the simple way by which species become exquisitely adapted to various ends. You will now groan, & think to yourself "on what a man have I been wasting my time in writing to." I shd, five years ago, have thought so. I fear you will also groan at the length of this letter. Excuse me, I did not begin with malice prepense'.

Hooker replied cautiously. He wrote about his Antarctic work at some length, and then continued, 'that there was a beginning to the creation of plants on our globe is very true. We can hardly suppose that we have now only the remains of that original stock or why should not the said cabbage grow on lands we suppose older than Kerg Land, or the Seychelle double cocoa nut on older formations than they are. There may in my opinion have been a series of productions on different spots, & also a gradual change of species. I shall be delighted to hear how you think that this change may have taken place, as no presently conceived opinions satisfy me on the subject'. Darwin was both relieved and grateful for this response. Hooker became his closest scientific friend and confidant. When Wallace's bombshell letter came to Down House in 1858, it was Hooker and Lyell to

¹²It is sometimes recorded as being 200 or more pages long. When a fair copy was made (by Mr Fletcher, the Downe schoolmaster), it occupied 231 pages.

Table 1. Hooker's analysis of the Galapagos flora (from *Voyage of the Beagle*, 1845)

Name of island	Total no. of species	No. of species found in other parts of the world	No. of species confined to the Galapagos Archipelago	No. confined to the one island	No. of species confined to the Galapagos Archipelago, but found on more than the one island
James Island	71	33	38	30	8
Albemarle Island	46	18	26	22	4
Chatham Island	32	16	16	12	4
Charles Island	68	39 (or 29, if the probably imported plants be subtracted)	29	21	8

whom he turned. Both knew the 1844 Essay and it was they who counselled Darwin and arranged for the papers to be presented jointly at the Linnean Society. It was Hooker who carried the day after the inaudible Huxley had spoken at the infamous Oxford meeting of the British Association in 1860 (Desmond & Moore, 1991: 496); and Hooker was one of the pall bearers at Darwin's funeral in Westminster Abbey.

THE BIOGEOGRAPHY OF ISLAND BIOTAS

Islands excited Hooker. As the Earth's biology became better known, the peculiarity of many island biotas became increasingly apparent (Cain, 1984). In earlier generations, islands had meant the biblical Eden and the colonization of the globe from there (Browne, 1983; Grove, 1995). Probably the first major contributor to island biology in the modern era was Thomas Vernon Wollaston who described a very large number of endemic species on the Canaries, the Madeira group and the Azores, beginning in the late 1840s. He was so intrigued by the invertebrates of St Helena that he spent 6 months there and described three quarters of the more than 150 endemic species of beetles on the island (Cook, 1995). Alfred Russel Wallace had begun to speculate about the implication of local forms of butterflies and birds during his time in Amazonia in the early 1850s (Wallace, 1853, 1855), giving him clues that eventually led to his disconcerting Darwin by independently promulgating natural selection.

It was islands that brought Hooker and Darwin together. Islands were highly influential to Darwin in developing his own ideas about evolution – even if he did not have a Damascus Road experience when he visited the Galapagos Islands as was once believed (Sulloway, 1982). His initial understanding of the possible importance of the Galapagos was expressed in his notes after leaving the islands. Puzzling over the differences in the bird and tortoise populations on

different islands, he wrote in his notebook: 'the Zoology of Archipelagoes will be well worth examining; for such facts would undermine the stability of species' (Sulloway, 1982). In his species notebooks written from 1836, Darwin tried to work out the significance of differences between islands and adjacent continents, using his own data as well as information from Humboldt and von Buch (Browne, 1983: 64). Hooker's results from the Galapagos flora (published in three papers by the Linnean Society: Hooker, 1846, 1847a, b) were very helpful. Data on the amount of endemism (approximately 50% of sub-generic taxa) were seized upon by Darwin and used in his revised edition of the *Voyage of the Beagle*, which appeared in 1845 (Table 1).¹³ However, it was only when Darwin read the third of Hooker's Galapagos papers (1847b) that he realized that the diversity of the flora could not be explained entirely by differentiation in isolation but that sundry colonists must also have been involved (Sulloway, 1984: 51).

Hooker's Galapagos work was 'not only a pioneering study in the geographical relationships of island floras, it was also the first to speculate on how such a flora might be derived' (Porter, 1984). However it led to a disagreement with Darwin. In 1846, Edward Forbes had proposed that species were derived from a limited number of 'centres of creation', and that the biota of the British Isles contained many relicts left

¹³Darwin greatly modified and expanded the section on the Galapagos Islands in the second edition of the *Voyage of the Beagle* (1845) from the original version of 1839, in particular adding, 'one might really fancy that from an original paucity of birds in this archipelago, one species [of finch] had been taken and modified for different ends'. Such revisiting earlier interpretations were common practice for him. Gillian Beer (1998: 125) writes 'Darwin came to and passed the brink of his key formulations by means of the processes of writing and rewriting. Crucial also were the shifts and juxtapositions of place in which the work was written; first diaries, journals, letters, and field notes day by day or in bunches around the world, producing a set of cross-hatched images as he wrote of one site while at another; then back at home at a desk'.

after the submergence of previously continuous tracts of land, most extensively and controversially a lost Atlantis between Britain, Ireland and Iberia (Forbes, 1846). It was an idea that appealed to Hooker.¹⁴ Seeking to explain the floras of the sub-Antarctic islands, Hooker speculated that ‘the three archipelagoes, Kerguelen, the Crozets and Marion [may] all have been peopled with land plants from South America by means of intermediate tracts of land that have now disappeared; in other words, that these islands constitute the wrecks of either an ancient continent or an archipelago that formerly extended westwards and that their present vegetation consists of waifs and strays of a mainly Fuegian flora’ (Hooker, 1879).¹⁵

At the time, many geological processes were largely unknown (it was only in 1837 that Louis Agassiz had propounded the notion of a ‘Great Ice Age’); indeed, the Yale zoologist George Baur went as far as arguing that the Galapagos Islands, almost 1000 km from the coast of South America were ‘continental islands’, isolated by the subsidence of a land bridge (Larson, 2001: 112).¹⁶ By contrast, Darwin believed that long distance dispersal over the sea was more important; he carried out a series of experiments to test the survival of various seeds and fruits in water. Hooker set out the scheme he preferred in a Linnean Society paper, read in 1860 (Hooker, 1862).

The question resolves into whether the species on an island are relicts of a previously continuous distribution or whether they had colonized at a later stage. This leads to ecological-type enquiries as to their persistence and subsequent differentiation. Hooker and Darwin debated their difference in many exchanges, albeit amicably. Indeed, Darwin wrote to Hooker (29 January 1859), ‘I quite agree that we only

differ in *degree* about means of dispersal, and that I think a satisfactory amount of concordance’.

Hooker’s willingness to listen to Darwin’s ideas was important to the latter. He wrote that Hooker was ‘the one living soul from whom I have constantly received sympathy’.¹⁷ Hooker formally ‘came out’ as an evolutionist after the 1858 Linnean Society meeting. In the Foreword to *Flora Tasmaniae* (1860) (which he had begun to write at the end of 1857) he wrote: ‘In the present essay I shall advance the hypothesis that species are derivative and mutable; and this chiefly because, whatever opinions a naturalist may have adopted to the origin and variation of species, every candid mind must admit that the facts and arguments upon which he has grounded his conviction require revision since the recent publication by the Linnean Society of the ingenious and original reasonings and theories of Mr Darwin and Mr Wallace’.

Hooker’s definitive conclusions about the factors determining island floras were set out during the 1866 meeting of the British Association in Nottingham. He did not like lecturing and it took a lot out of him. In 16 January of that year, he wrote to Darwin, ‘I have in cold blood accepted an invitation to deliver an evening address on the Darwinian theory at Nottingham. I am utterly disgusted at my bravado . . . [but] the difficulty of the subject and impossibility of doing it justice had charms for me’. Later (31 July), he opined, ‘You must not suppose me to be a champion of Continental Connection, because I am not agreeable to trans-oceanic migration. I have no fixed opinion on the subject . . . Either hypothesis appears to me to well cover the facts of Oceanic Floras, but there are grave objections to both. Botanical to yours, Geological to Forbes’.¹⁸ He agonized over his preparation: ‘I am worked and worried to death with this Lecture and curse myself as a soft headed and hearted imbecile to have accepted it’ (Huxley, 1918: ii: 100).

He need not have worried. An estimated 2000 people attended the lecture on 27 August. Hooker argued that the facts regarding oceanic floras strongly supported ‘Mr Darwin’s derivative theory of species’. He accepted that both his preference of ‘continental expansion’ and Darwin’s of ‘occasional transport’ faced

¹⁴Notwithstanding Forbes was criticized from many quarters. H.C. Watson considered that Forbes’s theory, ‘absolutely teems with errors in its botany – inconclusive arguments, inconsequent logic, inept illustrations, and the guesswork of imagination put forward ostensibly as the ascertained facts of science’. However Watson was notoriously cantankerous and his opposition failed to convince many.

¹⁵In a footnote, Hooker wrote: ‘These ideas suggested themselves to me during my visit to Kerguelen Island in 1840.’ Hooker did not accept Forbes’s ideas uncritically. He wrote to Darwin in 1846, ‘I have been more coolly analysing the bearings of the Forbes Botanical question lately . . . My faith is weakened from an independent examination of the Flora of the N. Atlantic Isles and W.U. Kingdom’.

¹⁶Baur’s claim was based on his false conclusion that ‘the distribution of the animals was harmonic and that the theory of oceanic origin was therefore not correct’ (Baur, 1897: 662). He was not alone in proposing that there must have been land connections to explain the distribution of land organisms. Henry Pilsbry (1900) dreamt of a grand mid-Pacific continent, two-thirds the size of Australia, extending from the Cook Islands to the Marquesas. Kay (1994) has identified three such hypothesized Pacific continents prior to the *Origin*, and ten more in the 50 years after publication.

¹⁷Ronald Clark (1984: 144) quotes Hooker as concluding his intervention at the 1860 British Association meeting: ‘I knew of this theory fifteen years ago. I was then entirely opposed to it; I argued against it again and again; but since then I have devoted myself unremittingly to natural history; in its pursuit I have travelled the world. Facts in this science which before were inexplicable to me became one by one explained by this theory, and conviction has been thus gradually forced upon an unwilling convert’.

¹⁸Hooker to Darwin, 24 July: ‘I have been groaning over my lecture . . . I have been reading Ed Forbes again and with admiration, despite its faults – how near he was to being a very great man’.

'insuperable obstacles', although the latter offered 'a rational solution of many of the most puzzling phenomena' presented by oceanic floras. The *Nottingham Daily Express* reported that Hooker had 'succeeded in making a not very attractive subject highly interesting' (Burkhardt & Porter, 2004: 305).

The Nottingham Lecture originally appeared in parts in the *Gardener's Chronicle*; the complete version was published in the *Biological Journal of the Linnean Society* with an introduction by Mark Williamson (1984). It was a landmark in scientific support for the *Origin*, but has continuing relevance as a penetrating analysis of an important evolutionary situation. Moreover, it was the first systematic statement of the importance of islands for evolutionary studies. Hooker's identification of the main characteristics of island biotas still stands:

- They contain a high proportion of forms found nowhere else (endemics), although these endemics are usually similar to those found on the nearest continental mass;
- They are impoverished in comparison with comparable continental areas (i.e. there are fewer species on islands than on mainlands);
- Dispersal must play a part in the colonization and establishment of islands, unless the island has been cut off from a neighbouring area and therefore carries a relict of a former continuous fauna and flora; and
- The relative proportions of different taxonomic groups on islands tends to be different from non-island biota (i.e. there is taxonomic 'disharmony').¹⁹

What evidence is there of refugia where some temperate species might have survived the last glaciation? A century after Forbes, Jack Matthews (1955) argued that 'botanists most conversant with the flora of Ireland, among whom must be mentioned Lloyd Praeger, have given unqualified support to the thesis'. For animals, belief in refugia probably reached an extreme with the Irish entomologist Bryan Beirne (1952). A test case for Beirne's thesis is the small mammals on the islands to the north and west of Britain, which were long accepted to be relict

¹⁹Hooker does not use the word 'disharmony', but it is implicit in his analysis. He described the 'unequal dispersion' of species to be 'the most singular feature' of the flora. Asa Gray (1849) called this 'Hooker's Rule'; he quoted the distribution of the Hawaiian silverswords (*Argyroxiphium* and *Wilkesia*) as another example. The first section of Hooker's paper concludes with a family-by-family discussion of geographical relationships. In his analysis of the Galapagos flora, he spells out the result, 'the more an island is indebted to a neighbouring continent for its vegetation, the more fragmentary does its flora appear, migration being effected by the transport of isolated individuals, generally in no way related' (Hooker, 1847b) (i.e. the flora is comprised of a skewed sample of all the taxa in adjacent continental areas) (Porter, 1984).



Figure 2. *Erebus* and *Terror* in pack ice at 66°S, 20 January 1842: 'Our ships are involved in an ocean of rolling fragments of ice, hard as rocks of granite . . . The destruction of the ships seems inevitable from the tremendous shocks they received . . . The awful grandeur of such a scene can neither be imagined nor described, far less can the feelings of those who witnessed it be understood. Each of us secured our hold, waiting with resignation to the will of Him who alone could preserve us and bring us safely through this extreme danger' (Ross, 1847: ii: facing page 169). Courtesy of the Linnean Society.

populations. However, Corbet (1961) showed the geographical, taxonomic and geological unlikelihood of this. For example, the British island races of the Field Mouse (*Apodemus sylvaticus*) are more closely related to Scandinavian animals, suggesting that they were introduced from there, perhaps by the Vikings (Berry, 1969; Michaux *et al.*, 2003); the Orkney Vole (*Microtus (orcdensis) arvalis*) is more like southern European conspecifics than ones from northern Europe (Berry & Rose, 1975; Haynes, Jaarola & Searle, 2003). The occurrence of Pygmy Shrews as the only native small mammals in Ireland and the Isle of Man has occasioned much speculation about refugia and land-bridges, but the molecular finding that the Irish shrews are genetically very different to those on mainland Britain indicates that they must have had separate origins (Mascheretti *et al.*, 2003). This should not be taken as evidence that survival through the Ice Ages in refugia never took place, but implies that the evidence for such survival needs careful and critical evaluation (Hewitt, 1999, 2004; Willis & Whittaker, 2000).

Although the evidence for land-bridges is meagre and disputed, we cannot exclude the possibility of some such 'refugia' where temperate organisms may have survived (Stewart & Lister, 2001). Molecular studies on Scots Pine (*Pinus sylvestris*) on Arran show that it is genetically different from other north European stands; it seems possible that it is derived from

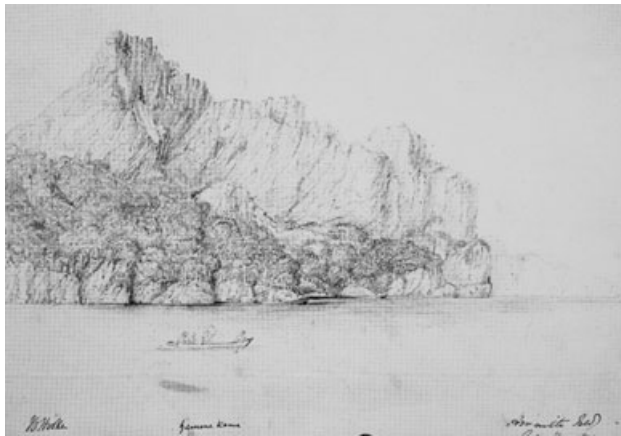


Figure 3. Hermite Island, Tierra del Fuego (Ross, 1847: ii: 287). Courtesy of the Linnean Society.

a comparatively northern refuge, perhaps in Ireland (Sinclair, Morman & Ennos, 1999). Such island refuges may account for the existence of Red Deer remains in the hilly site of Kent's Cavern 25 000 years BP, even though they are absent from other, non-wooded sites during the same glacial period (Stewart & Lister, 2001). Such unexpected survivals could have provided colonizers for post-glacial spread. This would remove the need to assume the otherwise surprisingly rapid spread of some tree species from their traditional restriction to southern Europe (Iberia, Italy, and the Balkans) at the end of the Pleistocene. They could also have provided a haven for a number of animal species.

'THE THEORY OF ISLAND BIOGEOGRAPHY'

A major advance in the understanding of island biotas has been 'the theory of island biogeography' put forward by Robert MacArthur and Ed Wilson in 1963 and expanded into a book in 1967. It was the consolidation of ideas that had been around for a long time. Alfred Russel Wallace set out the principle in 1880 in his *Island Life*: 'The distribution of the various species and groups of living things over the earth's surface and their aggregation in definite assemblages in certain areas is the direct result and outcome of... firstly the constant tendency of all organisms to increase in numbers and to occupy a wider area, and their various powers of dispersion and migration through which, when unchecked, they are enabled to spread widely over the globe; and secondly, those laws of evolution and extinction which determine the manner in which groups of organisms arise and grow, reach their maximum, and then dwindle away...'. (Wallace, 1880: 532). H. C. Watson (1835) noted that one square mile of Surrey

holds half the plant species found in Surrey as a whole; Henry Gleason generalized this in a paper in 1922, 'On the relation between species and area'. Philip Darlington (1957) anchored it for islands by pointing out that in a range of islands a ten-fold increase in area leads to a mere doubling in the number of species. But it was left to MacArthur and Wilson to give formal expression to the concept.

The core of MacArthur and Wilson's thesis was that there is a balance between immigration to an island determined by its distance from the mainland and extinction thereon of local populations, which will vary with the island area. In other words, the number of species on an island will be the difference between those continually reaching it and those which are being lost (Fig. 4). The insight of MacArthur and Wilson was that this is a present dynamic rather than a simple historical hangover: species are *continually* going extinct locally; species are *continually* appearing and establishing themselves. They suggested that recurrent colonizations and extinctions create an equilibrium in which the number of species remains relatively constant although the species concerned will vary over time. They used data from the recolonization of Krakatau to support their thesis. Wilson and Dan Simberloff went on to test the theory by fumigating four small mangrove islands off the coast of Florida so as to kill all the resident animals and then monitoring their recolonization over a period of years (Simberloff, 1969, 1976; Simberloff & Wilson, 1969, 1970).

Ornithological data have been particularly important in examining island biotas. The presence (and absence) and breeding of birds is much easier to record than for most other groups. A pioneer in the study of island birds was David Lack. In the Second World War, he became a 'civilian technical adviser' on the radio equipment used for gun-laying. He volunteered for service in Orkney, where he spent March to August 1941 (and, a mild-mannered teacher at an independent school, 'found the beer-drinking Manchester territorials excellent company') (Thorpe, 1974). Whilst there, he collected a mass of information on the birds of Orkney, and this inspired him to develop more general ideas, first set out in a paper 'Ecological features of the bird faunas of British small islands', published in 1942 (Lack, 1942). In this, he compared the breeding birds of Caithness, Orkney, Shetland, and Faroe with previously published lists. He noted that at the time of his survey, 26 species had established themselves on Orkney since 1800, whereas at least another eight species (and perhaps as many as twenty) bred occasionally. Thirteen of the 26 'new' species could be attributed to the planting of woods, gardens, trees, and bushes in the 19th Century, assisted by an increase in the land under

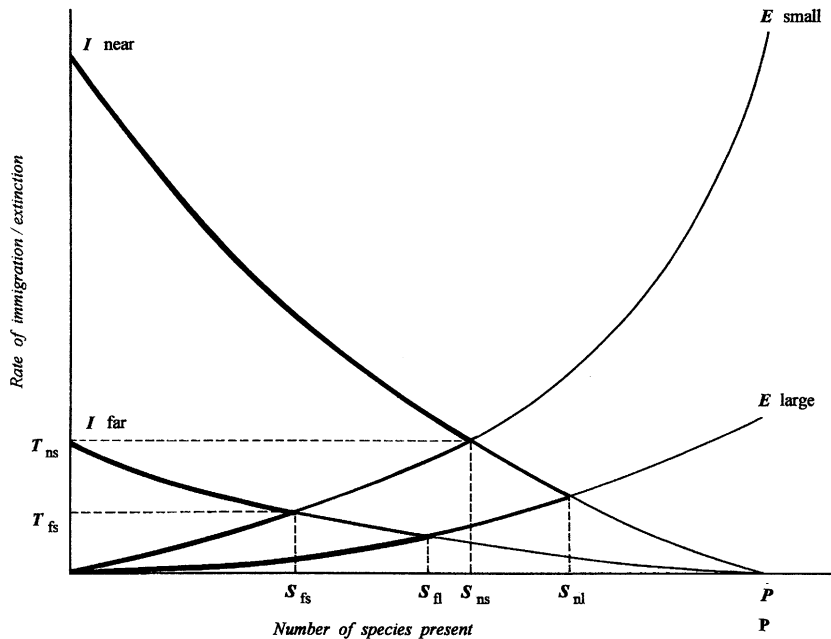


Figure 4. MacArthur and Wilson's theory of island biogeography. The number of species on any island (S) is the point at which immigration (I) matches extinction (E). I is greater on islands near to a source of migrants (ns) than on islands far from such a source (fs); E is greater on small islands than large ones.

cultivation. A further eight species resident in Orkney in 1800 had extended their range to other islands; in contrast, six species no longer bred on Orkney. Local extinction is, of course, the result of a fluctuation in numbers to zero: Lack found that 61 (84%) of the inland breeders and 15 (60%) of the sea and shore birds changed significantly in density over his study period. This turnover in the avifauna was one of the most striking features of his survey.

Tim Reed (1980, 1981) extended enormously Lack's work with data for 73 of the British islands, which he collected from a range of sources – local societies, bird observatory reports, etc. He found that the best predictor of species number on any island was the number of habitats on the island, which usually (but not inevitably) increased with the land area of the island (hilly islands will have more area for colonization than 'flat' ones). Stuart Pimm and his colleagues have further expanded these findings, showing from data collected on 67 species at 16 Observatories on islands around the British and Irish coasts that the likelihood of extinction is linked to population size (and therefore island area), but also to body size: large birds (which have a longer life-span than small ones) are less susceptible to extinction at low numbers, but are at greater risk at high ones (above seven pairs) – presumably because of their greater need for resources (Pimm, Jones & Diamond, 1988).

Area is also important in another and more indirect way: larger islands are likely to have a greater area of habitat available for any particular species. A species may reach an island but, if there is too little suitable habitat, it will be unable to breed successfully. In practice, there must be enough habitat to support a population greater than a threshold size which will differ for each species.

MacArthur and Wilson described the balance between immigration and extinction as an 'equilibrium', although, as Mark Williamson (1981) has pointed out, it is really nothing more than a logical necessity: the number of species on an island can only be increased by two processes – immigration, which in turn will depend on the distance of the island from the source of potential colonizers and the availability of ecological space for them; and be decreased only by those which fail to survive, i.e. by extinction. For David Lack, 'most species turnover is ecologically trivial'. Certainly, the theory needs supplementing with ecological information. For birds, Russell *et al.* (2006) found that ideas of optimal foraging improved its predictions because organisms will stay longer in an area if the distance to a neighbouring island is large.

Notwithstanding, the MacArthur and Wilson theory has proved useful: there is a turnover of species on any island over a period of years but the total number of species tends to remain fairly constant.

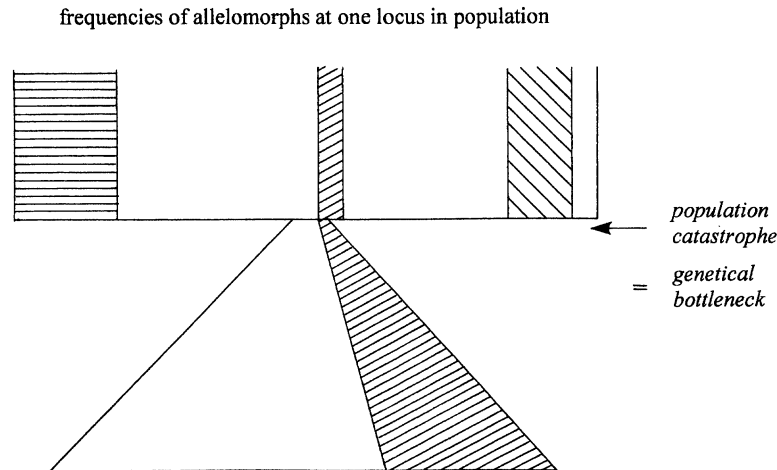


Figure 5. The effect of sampling when major reductions in numbers occur (as in colonization or population catastrophes) will almost certainly lead to a loss of alleles and a change in allele frequencies at most (if not all) loci. A newly-founded population will be immediately different from the source population.

ENDEMICITY

A major problem with the MacArthur and Wilson theory is that it implies nothing about the evolution of endemic island forms. Indeed, the *Theory of Island Biogeography* is misleading in its discussion of the origins of island endemicity. Chapter 7 of the book is entitled 'Evolutionary Changes Following Colonization', but the authors omit any mention of genetic changes that may occur as a result of a colonizing event. At least part of the reason for this is historical. MacArthur and Wilson's book was published in 1967. In the previous year, Harry Harris working in London on human material and Jack Hubby and Dick Lewontin in Chicago on *Drosophila pseudoobscura* had reported that heterozygosity in any individual (i.e. different alleles inherited from the two parents) occurs in 10% or more of gene loci (Harris, 1966; Lewontin & Hubby, 1966). This discovery produced a radical rethinking of population biology.

Traditionally, biologists thought of individual animals or plants as genetically rather uniform. Clearly, inherited variation occurs (such as bridled Guillemots, black Rabbits, pin versus thrum Primroses, mammalian blood groups, etc.) but the proportion of variable gene loci was thought to be very small. Indeed, there was a simple calculation showing too much genetic variation could not be tolerated: it produced a 'genetic load', which reduced fitness and hence the survival of the population (Müller, 1950; Haldane, 1957). The heterozygosity data showed this was too simplistic. The assumption of genetical homogeneity was wrong; virtually all species have an enormous amount of hidden genetic variation.

Two consequences of this are crucial to understanding the differentiation of island forms: a small group of individuals drawn from a large population will almost certainly differ from its parental group in the frequency of alleles at a large number of loci; and some alleles will be absent or relatively over-represented in the smaller group. If the small group is isolated (i.e. is a colonizing propagule), the daughter group will be immediately different from the source population (Fig. 5). This only became evident after the time that MacArthur and Wilson were developing their ideas.

Wilson and MacArthur were not particularly interested in the processes of speciation (for a discussion of these as they occur on islands, see Grant, 1998). However, they have a chapter in their book on evolutionary changes. They begin that, as 'we believe that evolution through natural selection has produced the biotic differences which characterize islands, it is appropriate for us to study how natural selection works on islands'. They go on, 'We can think of the evolution of the new population as passing through three overlapping phases. First the population is liable to respond to the effects of its initial small size. This change, if it occurs at all, will take place quickly, perhaps only in a few generations. The second phase, which can begin immediately and must continue indefinitely, is an adjustment to the novel features of the invaded environment. The third phase, an occasional outgrowth of the first two, consists of speciation, secondary emigration and radiation' (MacArthur & Wilson, 1967: 154).

MacArthur and Wilson explicitly equate their first phase with 'the founder effect', a concept put forward by Ernst Mayr (1942) in *Systematics and the Origin of*

Species and described more fully in a 1954 essay 'Change of genetic environment and evolution'. The two biogeographers regarded the founder effect as 'an omnipresent possibility but one easily reduced to insignificance by small increases in propagule size, immigration rate, or selection pressure... The founder principle is actually no more than the observation that a [founding] propagule should contain fewer genes [alleles] than the entire mother population'.

This is wrong. It would have been a reasonable when they wrote it, but the post-1966 realization of the enormous genetic variability in any group of organisms means that the founder effect will almost certainly change allele frequencies as well as reducing variability to some extent. The geneticist Sewall Wright, one of the founders of modern population genetics, pointed out the error in a letter to Victor McKusick in May 1977. He referred to Mayr's emphasis on the founder effect as leading to gene (or allele) loss and a reduction in variability, but for Wright, 'I attribute most significance to the wide random variability of gene frequencies (not fixation or loss) expected to occur simultaneously in tens of thousands of loci at which the leading alleles are nearly neutral, leading to unique combinations of gene frequencies in each of innumerable different local populations... The effects attributed to the "founder effect" by Mayr [and also by MacArthur and Wilson] are the most obvious but the least important of the three' (Provine, 1989: 57).

In other words, the main effect of the colonization of an island by a small number of individuals will be a population differing from its parent at a large number of loci, producing instant differentiation. Every colonizing event will be unique and a new experiment, exposing to the environment a novel set of reaction systems determined by the alleles carried by the founding group. It is the outcome of these environment-gene interactions that represent an individual's ability to respond (or not: most colonizations result in rapid extinction because of the failure of the animals or plants to cope in their new situation) to natural selection. This response is phase 2 in the MacArthur and Wilson scheme; it will necessarily be conditioned by the chance collection of alleles present in the founders.

This 'instant' effect of a founding event is evident once the consequence of taking a small number of individuals from a genetically heterogeneous source is realized. Peter Grant has described it as 'perhaps the most novel and influential contribution of the [20th] century to ideas about how evolution of all organisms, and not just birds, occurs on islands' (Grant, 2001: 389). Notwithstanding, some theoreticians regard it having only a minor role in speciation (Barton &

Charlesworth, 1984; Barton, 1989, 1996) because they find no obvious reason why it should lead to reproductive isolation. Others have countered this objection by using models that involve epistasis between loci (Wagner, Wagner & Similioni, 1994; Hollocher, 1998). Certainly, there are many examples where founder effects can clearly be seen, perhaps most notably in human populations (e.g. retinitis pigmentosa on Tristan da Cunha, porphyria variegata in South Africa, Huntington's disease in the USA, DNA variants on Adriatic islands, etc.), but its longer-term importance has proved difficult to demonstrate in practice (Clegg *et al.*, 2002); although see critical commentary by Grant (2002) and Abdelkrim, Pascal & Samadi (2005). Goodacre (2001) argues that there is a 'significant historical dimension' in the distribution of variation in the well-studied snail *Partula taeniata* on Moorea.

A problem in obtaining critical data in natural situations is that it is usually extremely difficult to know whether immigration subsequent to the original arrivals has taken place. The impact of immigration is well shown by the insect fauna of Gough Island, where Gaston *et al.* (2003) regard 71 of the 99 species to be human introductions; they list 233 human landings subsequent to the first recorded one in 1675. However, they do not include any data on genetics. One situation where there has certainly been no immigration is with the Mouflon (*Ovis aries*) population on one of the Kerguelen islands, which was founded by a single pair of animals in 1957. Here, the heterozygosity has significantly and surprisingly increased over a 50-year period (Kaeuffer *et al.*, 2007). The most likely explanation is that there must have been selection for the increase.

Island species are certainly less variable than their conspecifics on the mainland. Fifty-six island populations reviewed by Frankham (1997) had an average of 29% less heterozygosity than their mainland relatives. However, this heterozygosity is not as low as expected. In experimental situations, it has been shown that genetic variability remains low only if the bottleneck in numbers following its founding persists for a long period or is repeated (Bryant, Meffert & McCommas, 1990). Kaneshiro (1995) has suggested that the disruption of a few individuals entering a new habitat may lead to the breakdown of sexual selection and thus involve a higher proportion of males breeding than usual, so increasing the effective gene pool.

Island populations are likely to suffer from a range of stresses as they adjust to environmental hazards (Lande, 1988; Pimm, 1991). The importance of genetic factors (notably inbreeding depression and the need to adapt) in affecting survival is uncertain in such situations, although they may be presumed to play a

part (Frankham, 1998). Captive breeding management (as employed with endangered species maintained in zoos) properly makes great efforts to avoid inbreeding and the potential loss of inherited variation, but it is possible that this risk may be over-emphasized in field (i.e. non-managed) situations, particularly on islands where competitive pressures may be less than on mainlands (Bowen & Van Vuren, 1997; Torchin *et al.*, 2003). Woolfit & Bromham (2005) have collated data that show a significantly greater rate of nonsynonymous to synonymous substitutions in DNA in island endemics than in their mainland relatives, which they attribute as probably due to purifying selection in the generally small effective breeding populations (which will be lower than the total population size) on islands. It is not yet clear what the effect of this has on fitness. Saccheri *et al.* (1998) record the extinction of an inbred population of the Glanville Fritillary (*Melitaea cinxia*) on Åland Island but Gage *et al.* (2006) found no effect at the population densities in island Rabbits, despite an increased proportion of abnormal sperm in inbred populations, including animals from the Uists, the Isle of May, and Inner Farne.

The operation of the founder effect does not, of course, reveal anything about the operation of natural selection in newly established populations. Intuitively, it is probably operating particularly strongly in most such situations (Berry, 1986, 1996). There are a number of situations where selection has been detected in island populations (Carlquist, 1974), including House Mice on sub-Antarctic islands (Berry, Bonner & Peters, 1979) and experimental populations of Spittle-bugs (*Philaenus spumarius*) in the Baltic (Halkka, Halkka & Raatikainen, 1975). The commonness of flight loss in island animals is well-known. For example, Tristan da Cunha has twenty endemic species of beetles, eighteen with reduced wings; on Hawaii, 184 of the 200 endemic species of carabids are flightless, as are representatives of another six arthropod orders. Darwin wrote excitedly to Hooker (7 March 1855) after reading a book by Thomas Wollaston on the insects of Madeira: 'It is an *admirable* work. There is a very curious point in the astounding proportion of Coleoptera that are Apterous & I think I have grasped the reason, viz that powers of flight wd be injurious to insects inhabiting a confined locality & expose them to be blown to the sea; to test this, I find that the insects inhabiting the Dezerta Grande, a quite small islet, would be still more exposed to this danger, & here the proportion of apterous insects is even considerably greater than on Madeira proper'. Selection on islands would probably be even better appreciated if populations were more commonly sampled at successive times, rather than on single occasions as tends to be usual, especially on remote islands.

FOUNDER EFFECT: IS THERE A GENETIC REVOLUTION?

At the same time that Robert MacArthur and Ed Wilson were exploring island biogeography, a group of evolutionary geneticists was speculating in Asilomar, California about the genetics of colonizing species (Baker & Stebbins, 1965). The discussions were summed up by Ernst Mayr, who emphasized the need of ecologists to know something about the genetics of the organisms they studied, and for geneticists to become familiar with the ecology of their organisms – as he had attempted to do in describing the 'founder effect'. Although his original proposal about the origin of differentiation was similar to that of Wilson and MacArthur – on changes *following* colonization – in his 1954 paper, Mayr extended his idea by proposing that animals and plants are faced with a new 'genetic environment' when they are isolated and as a consequence undergo a 'genetic revolution'.

As a young man, Mayr had worked on the birds on the islands north of Australia. Time and time again, he found that species that differentiated little on larger land masses were represented on the smaller islands by very different forms – and by forms that differed from those on other islands. He wrote 'that mutation, recombination, selection and isolation are the four cornerstones of evolution is now generally acknowledged... [However] the role of a sudden change in the genetic environment seems never to have been properly considered'. He did not believe the sufficiency of the two factors usually cited for 'the striking dissimilarity' of peripherally isolated populations: differences of physical and biotic environment (MacArthur and Wilson's explanation) or genetic drift (random changes in a small population); he focused on the importance of 'gene-flow or immigration'. He pointed out that genetical experiments in laboratories go to great length to avoid immigrants; they are regarded as 'genetic contaminants' (Mayr, 1954).

Mayr argued that in a widely distributed population continually exposed to individuals moving in from elsewhere, there will be selection for genes that will tolerate combination with 'alien' genes. He cited populations of plants subjected to powerful stresses due to high salinity or desiccation that may develop locally adapted races (or 'ecotypes') but which tend to be very variable due to the inflow of genes from nearby populations. If we think of single genes, we can measure their effects on physiology and reproductive success, but all the genes carried by an individual work together to produce a functioning whole; it is wrong to think of them behaving as discrete entities like beans in a bean bag. All species have their own genetic architecture so that the loss or gain of a particular allele may affect other genes than the one

at its locus. Such genetic architecture is often referred to as a 'coadapted' system. The effect of this is seen when two varieties (or sub-species) breed together. Usually, the two forms remain distinct, despite the occurrence of obvious hybrids between them.

Importantly, as Brakefield (1991) has commented, 'the existence of coadaptation between genes and of forms of non-additive genetic contributions to quantitative variation are likely to make variability within populations more resistant to loss than would be expected on the basis of theory developed largely from the perspectives of genes acting independently from each other and in a purely additive manner'.

All this led Mayr to suggest that a group isolated on an island will undergo a 'genetic revolution' in the sense that they will not have to cope with a constant influx of new alleles and can therefore adapt to the circumstances on the island without the need to compromise due to the disrupting effect of immigrants. A difficulty is that the power of genetic cohesion or coadaptation remains unknown, although evidences of its occurrence are common (e.g. epistasis and other specific gene interactions; complex traits being controlled by many loci; selection favouring the formation of 'balanced' chromosomes with positive and negative traits intermingled, etc.) (Berry, 1977). As noted above, coadaptation may increase the likelihood of reproductive isolation. Recent findings from gene-mapping show that higher organisms have fewer genes than previously supposed. This implies that many genes act together in development and behaviour and strengthens the idea of the importance of genetic architecture. Studies of hybrid zones have revealed the complexity of interactions and what may be termed the 'viscosity' of genomes (Teeter *et al.*, 2008). However, for the time being, the effect of Mayr's 'genetic revolution' remains unproven.

ISLANDS: EXCITING AND WORTHWHILE LABORATORIES FOR EVOLUTION

Evolutionary change is largely driven by adaptation produced by environmental stress, although it is not impossible that evolutionary novelties arising on islands or through the lottery of colonization may have contributed to the survival and subsequent spread of a 'hopeful monster' or two (Orr, 2005). We shall probably never know if that has ever happened or how significant it may have been. What is incontestable is the role that islands have had in challenging and extending our understanding of evolutionary processes in general (Giddings, Kaneshiro & Anderson, 1989). Whatever their motives for their expeditions, island explorers throughout the modern era have unveiled a scientific cornucopia. George Low of

Orkney provided, together with Gilbert White, a significant part of the biological information used by pioneering travel writer Thomas Pennant, who was a correspondent of both Joseph Banks and Linnaeus [Pennant dedicated his *Tour in Scotland and Voyage to the Hebrides* (1774–76) to Banks and published Banks's description of Staffa, which excited much interest in islands²⁰]; Banks had travelled with James Cook and visited many islands; Georg Forster, who followed Banks as naturalist on Cook's second voyage inspired Alexander Humboldt, who in turn Darwin treated as a model; Thomas Wollaston and his insect studies on Madeira excited Darwin; Hooker wanted to emulate Darwin as a naturalist; Alfred Russel Wallace stumbled on a range of biogeographical goodies during his time on the Indonesian islands; Julian Huxley introduced Charles Elton to Spitzbergen and the usefulness of island simplicity for unravelling ecological complexity. Sherwin Carlquist (1974) has reviewed knowledge of islands generally and Hawaii in particular; Ian Thornton (1966, 2007) and Sturla Fridriksson (1975, 2005) have exploited the volcanic eruptions on respectively Krakatau and Surtsey to study colonization; Tim Clutton Brock and Josephine Peters have used genetic isolation as a tool to investigate Red Deer on Rum and Soay Sheep on St Kilda (Clutton-Brock, Guinness & Albon, 1982; Clutton-Brock & Pemberton, 2004); genetic tracers are increasingly being employed to study colonization patterns (Carlson, 1983; Giddings *et al.*, 1989; Bilton *et al.*, 1998; Jaarola *et al.*, 2004; Martinková, McDonald & Searle, 2007); the saga continues.

Ten years ago, Peter Grant, who through his careful and long-continued studies on 'Darwin's Finches' (Weiner, 1994; Grant & Grant, 2007) has probably done more than anyone else to elucidate evolution on islands, wrote: 'An outstanding feature of islands is their strangeness; many of them are downright weird. Naturalists of the last three centuries brought back to civilization accounts of strange and unimagined creatures found only on remote islands. Dodos. Sphenodon. The Komodo dragon. Daisies as tall as trees. What is it about islands that promotes such strangeness?' (Grant, 1998: 5). Hooker did not know the answer to this, but he was a pioneer in beginning the search and his work inspired – and continues to inspire – his successors. Through his start, we can now start to answer reasonably Grant's question.

²⁰Banks's original account was published in the *Scots Magazine*. Pennant was 'essentially an intellectual entrepreneur, a popularizer and compiler of other people's observations and ideas' (Mabey, 1986: 106). Although his reliance on second-hand information came close to plagiarism, his success in raising interest in islands qualifies him to be included in this historical pantheon.

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REFERENCES

- Abdelkrim J, Pascal M, Samadi S. 2005.** Island colonization and founder effects: the invasion of the Guadeloupe islands by ship rats (*Rattus Rattus*). *Molecular Ecology* **14**: 2923–2931.
- Allen M. 1967.** *The Hookers of Kew*. London: Michael Joseph, 1785–1911.
- Baker HG, Stebbins GL. 1965.** *The genetics of colonizing species*. New York, NY: Academic Press.
- Barton N. 1989.** Founder effect speciation. In: Otte D, Endler JA, ed. *Speciation and its consequences*. Sunderland, MA: Sinauer, 229–256.
- Barton N. 1996.** Natural selection and random genetic drift as causes of evolution on islands. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **351**: 785–795.
- Barton N, Charlesworth B. 1984.** Genetic revolutions, founder effects and speciation. *Annual Review of Ecology and Systematics* **15**: 133–164.
- Baur G. 1897.** New observations on the origin of the Galápagos Islands, with remarks on the geological age of the Pacific Ocean. *American Naturalist* **31**: 661–680.
- Beer G. 1998.** Writing Darwin's islands: England and the insular condition. In: Lenoir T, ed. *Inscribing science: scientific texts and the materiality of communication*. Stanford, CA: Stanford University Press, 119–139.
- Beirne BP. 1952.** *The origin and history of the British fauna*. London: Methuen.
- Berry RJ. 1969.** History in the evolution of *Apodemus sylvaticus* (Mammalia) at one edge of its range. *Journal of Zoology* **159**: 311–328.
- Berry RJ. 1977.** *Inheritance and natural history*. London: Collins New Naturalist.
- Berry RJ. 1986.** Genetics of insular populations of small mammals, with particular reference to differentiation and founder effects in British small mammals. *Biological Journal of the Linnean Society* **28**: 205–230.
- Berry RJ. 1996.** Small mammal differentiation on islands. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **351**: 753–764.
- Berry RJ. 2007.** The Hooker Lectures. *The Linnean* **23**: 22–25.
- Berry RJ, Bonner WN, Peters J. 1979.** Natural selection in mice from South Georgia (South Atlantic Ocean). *Journal of Zoology* **189**: 385–398.
- Berry RJ, Rose FEN. 1975.** Islands and the evolution of *Microtus arvalis* (Microtinae). *Journal of Zoology* **177**: 395–407.
- Bilton DT, Mirol PM, Mascheretti S, Fredga K, Zima J, Searle JB. 1998.** Mediterranean Europe as an area of endemism for small mammals rather than a source for northwards postglacial colonization. *Proceedings of the Royal Society of London Series B, Biological Sciences* **265**: 1219–1226.
- Bowen L, Van Vuren D. 1997.** Insular endemic plants lack defenses against herbivores. *Conservation Biology* **11**: 1249–1254.
- Brakefield PM. 1991.** Genetics and the conservation of invertebrates. In: Spellerberg IF, Goldsmith FB, Morris MG, eds. *The scientific management of temperate communities for conservation*. Oxford: Blackwell Scientific, 45–79.
- Browne J. 1983.** *The secular ark*. New Haven, CT: Yale University Press.
- Browne J. 1995.** *Charles Darwin voyaging*. London: Jonathan Cape.
- Bryant EH, Meffert LM, McCommas SA. 1990.** Fitness rebound in serially bottlenecked populations of the house fly. *American Naturalist* **136**: 542–549.
- Burkhardt F, Porter DM. 2004.** *The correspondence of Charles Darwin*, Volume 14, 1866. Cambridge: Cambridge University Press.
- Cain AJ. 1984.** Islands and evolution: theory and opinion in Darwin's earlier years. *Biological Journal of the Linnean Society* **21**: 5–27.
- Carlquist S. 1974.** *Island biology*. New York, NY: Columbia University Press.
- Carlson HL. 1983.** Chromosomal sequences and interisland colonizations in Hawaiian *Drosophila*. *Genetics* **103**: 465–482.
- Clark RW. 1984.** *The survival of Charles Darwin*. London: Weidenfeld & Nicolson.
- Clegg SM, Degnan SM, Kikkawa J, Moritz C, Estoup A, Owens IAP. 2002.** Genetic consequences of sequential founder events by an island-colonizing bird. *Proceedings of the National Academy of Sciences of the United States of America* **99**: 8127–8132.
- Clutton-Brock TH, Guinness FE, Albon SD. 1982.** *Red deer. Behavior and ecology of two sexes*. Edinburgh: Edinburgh University Press.
- Clutton-Brock TH, Pemberton J, eds. 2004.** *Soay sheep. Dynamics and selection in an island population*. Cambridge: Cambridge University Press.
- Cook LM. 1995.** T. Vernon Wollaston and the 'monstrous doctrine'. *Archives of Natural History* **22**: 33–48.
- Corbet GB. 1961.** Origin of the British insular races of small mammals and of the 'Lusitanian' fauna. *Nature* **191**: 1037–1040.
- Darlington PJ. 1957.** *Zoogeography*. New York, NY: Wiley.
- Desmond A, Moore JR. 1991.** *Darwin*. London: Michael Joseph.
- Desmond R. 1999.** *Sir Joseph Dalton Hooker. Traveller and plant collector*. Woodbridge: Antique Collectors' Club.

- Endersby J. 2006.** Sir Joseph Dalton Hooker (1817–1911). *Dictionary of National Biography*, on line edition. Oxford: Oxford University Press.
- Forbes E. 1846.** On the connexion between the distribution of the existing fauna and flora of the British Isles, and the geological changes which have affected their area, especially during the epoch of northern drift. *Memoirs of the Geological Survey of Great Britain* **1**: 336–432.
- Frankham R. 1997.** Do island populations have less genetic variation than mainland populations? *Heredity* **78**: 311–327.
- Frankham R. 1998.** Inbreeding and extinction. *Conservation Biology* **12**: 665–675.
- Fridriksson S. 1975.** *Surtsey. Evolution of life on a volcanic island*. London: Butterworths.
- Fridriksson S. 2005.** *Surtsey. Ecosystems formed*. Reykjavik: University of Iceland Press.
- Gage MJG, Surridge AK, Tomkins JL, Green E, Wiskin L, Bell DJ, Hewitt GM. 2006.** Reduced heterozygosity depresses sperm quality in wild rabbits, *Oryctolagus cuniculus*. *Current Biology* **16**: 612–617.
- Gaston KJ, Jones AG, Hänel C, Chown SL. 2003.** Rates of species introduction to a remote oceanic island. *Proceedings of the Royal Society of London Series B, Biological Sciences* **270**: 1091–1098.
- Giddings LV, Kaneshiro KY, Anderson WW, eds. 1989.** *Genetics, speciation and the founder principle*. New York, NY: Oxford University Press.
- Gleason HA. 1922.** On the relation between species and area. *Ecology* **3**: 158–162.
- Goodacre S. 2001.** Genetic variation in a Pacific island land snail: population history versus current drift and selection. *Proceedings of the Royal Society of London Series B, Biological Sciences*, **268**: 121–126.
- Grant PR, ed. 1998.** *Evolution on islands*. Oxford: Oxford University Press.
- Grant PR. 2001.** Reconstructing the evolution of birds on islands: 100 years of research. *Oikos* **92**: 385–403.
- Grant PR. 2002.** Founder effects and silvereyes. *Proceedings of the National Academy of Sciences of the United States of America* **99**: 7818–7820.
- Grant PR, Grant BR. 2007.** *How and why species multiply. The radiation of Darwin's finches*. Princeton, PA: Princeton University Press.
- Gray A. 1849.** On some plants of Order Compositae from the Sandwich Islands. *American Association for the Advancement of Science* **2**: 397–398.
- Gray A. 1893.** *Letters of Asa Gray*, 2 volumes. Boston, MA: Houghton Mifflin.
- Grove RH. 1995.** *Green imperialism*. Cambridge: Cambridge University Press.
- Gurney A. 1997.** *Below the convergence. Voyages towards Antarctica 1699–1839*. New York, NY: WW Norton.
- Haldane JBS. 1957.** The cost of natural selection. *Journal of Genetics* **55**: 511–524.
- Halkka O, Halkka L, Raatikainen M. 1975.** Transfer of individuals as a means of investigating natural selection in operation. *Hereditas* **80**: 27–34.
- Harris H. 1966.** Enzyme polymorphisms in man. *Proceedings of the Royal Society of London Series B, Biological Sciences* **164**: 298–310.
- Haynes S, Jaarola M, Searle JB. 2003.** Phylogeography of the common vole (*Microtus arvalis*) with particular emphasis on the colonisation of the Orkney archipelago. *Molecular Ecology* **12**: 951–956.
- Henslow JS. 1837.** Description of two new species of *Puntia*. *Magazine of Zoology and Botany* **1**: 466–469.
- Henslow JS. 1838.** Florula Keelingensis: an account of the native plants of the Keeling Islands. *Annals of Natural History* **1**: 337–347.
- Hewitt GM. 1999.** Post-glacial recolonization of European biota. *Biological Journal of the Linnean Society* **68**: 87–112.
- Hewitt GM. 2004.** Genetic consequences of climatic oscillations in the Quaternary. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences* **359**: 183–195.
- Hollocher H. 1998.** Island hopping in *Drosophila*: genetic patterns and speciation mechanisms. In: Grant PR, ed. *Evolution on islands*. Oxford: Oxford University Press, 124–141.
- Hooker JD. 1844–1860.** *The botany of the Antarctic voyage of H.M. Discovery Ships Erebus and Terror in the years 1839–1843. Part 1. Flora Antarctica, in two parts (1844–47); Part 2. Flora Novae-Zelandiae, volume 1 (1853–55), volume 2 (1855); Part 3. Flora Tasmaniae, volume 1 (1855–60), volume 2 (1860)*. London: Reeve Brothers.
- Hooker JD. 1846.** An enumeration of the plants of the Galapagos Islands, with descriptions of the new species. *Proceedings of the Linnean Society* **1**: 276–279.
- Hooker JD. 1847a.** An enumeration of the plants of the Galapagos Archipelago; with descriptions of those which are new. *Transactions of the Linnean Society* **20**: 163–233.
- Hooker JD. 1847b.** On the vegetation of the Galapagos Archipelago as compared with that of some other tropical islands and of the continent of America. *Transactions of the Linnean Society* **20**: 235–262.
- Hooker JD. 1862.** Outlines of the distribution of Arctic plants. *Transactions of the Linnean Society* **23**: 251–348.
- Hooker JD, ed. 1872–1897.** *Flora of British India*, 7 volumes. London: Reeve Brothers.
- Hooker JD. 1879.** Observations on the botany of Kerguelen Island. *Philosophical Transactions of the Royal Society of London* **168**: 9–16.
- Hooker JD. 1887.** Address at the Anniversary Dinner of the Royal Society. 30 November 1887.
- Hooker JD. 1899.** A Darwin statue at Oxford. *The Times*, 15 June (reprinted as Reminiscences of Darwin. *Nature* **56**: 187–188).
- Hooker WJ. 1843.** Notes on the botany of the Antarctic Voyage conducted by Captain James Clark Ross in Her Majesty's Discovery Ships Erebus and Terror; with observations on the tussac grass of the Falkland Islands. *London Journal of Botany* **2**: 247–329.
- Huxley L. 1918.** *Life and letters of Sir Joseph Dalton Hooker, OM, GCSI*, 2 volumes. London: John Murray.

- Jaarola M, Martinková N, Gündüz I, Brunhoff C, Zima J, Nadachowski A, Amori G, Bulatova NS, Chondropoulos B, Fraguédakis-Tsolis S, González-Esteban J, López-Fuster MJ, Kandaurov AS, Kefelioglu H, da Mathias ML, Villate, I, Searle JB. 2004.** Molecular phylogeny of the speciose vole genus *Microtus* (Arvicolinae, Rodentia) inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* **33**: 647–663.
- Kaeuffer R, Coltman DW, Chapuis J-L, Pontier D, Réale D. 2007.** Unexpected heterozygosity in an island mouflon population founded by a single pair of individuals. *Proceedings of the Royal Society of London Series B, Biological Sciences* **274**: 527–533.
- Kaneshiro KY. 1995.** Evolution, speciation and the genetic structure of island populations. In: Vitousek PM, Loope LL, Adersen H, eds. *Islands: Biological Diversity and Ecosystem Function*. Berlin: Springer-Verlag, 22–33.
- Kay EA. 1994.** Darwin's biogeography and the oceanic islands of the Central Pacific. 1859–1909. In: MacLeod R, Rebbock P, eds. *Darwin's laboratory*. Honolulu: University of Hawaii Press, 49–69.
- Kirwan LP. 1962.** *A history of Polar exploration*. Harmondsworth: Pelican.
- Lack D. 1942.** Ecological features of the bird faunas of British small islands. *Journal of Animal Ecology* **11**: 9–36.
- Lande R. 1988.** Genetics and demography in biological conservation. *Science* **241**: 1455–1460.
- Larson EJ. 2001.** *Evolution's workshop*. London: Allen Lane.
- Lewis Smith RI. 1993.** The vegetation of Cockburn Island. *Polar Biology* **13**: 535–542.
- Lewontin RC, Hubby JL. 1966.** A molecular approach to the study of genic heterozygosity in natural population. II. Amount of variation and degree of heterozygosity in natural populations of *Drosophila pseudoobscura*. *Genetics* **54**: 595–609.
- Mabey R. 1986.** *Gilbert White*. London: Century.
- MacArthur RH, Wilson EO. 1963.** An equilibrium theory of island biogeography. *Evolution* **17**: 373–387.
- MacArthur RH, Wilson EO. 1967.** *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
- McCormick R. 1884.** *Voyages of discovery in the Arctic and Antarctic Seas and round the world*, 2 volumes. London: Sampson Low, Marston, Searle & Rivington.
- Martinková N, McDonald RA, Searle JB. 2007.** Stoats (*Mustela erminea*) provide evidence of natural overland colonization of Ireland. *Proceedings of the Royal Society of London Series B, Biological Sciences* **274**: 1387–1393.
- Mascheretti S, Rogatcheva MB, Guduz I, Fredga K, Searle JB. 2003.** How did pygmy shrews colonize Ireland? Clues from a phylogenetic analysis of mitochondrial cytochrome b sequences. *Proceedings of the Royal Society of London Series B, Biological Sciences* **270**: 1593–1599.
- Matthews JR. 1955.** *Origin and distribution of the British flora*. London: Hutchinson.
- Mayr E. 1942.** *Systematics and the origin of species*. New York: Columbia University Press.
- Mayr E. 1954.** Change of genetic environment and evolution. In: Huxley JS, Hardy AC, Ford EB, eds. *Evolution as a process*. London: Allen & Unwin, 157–180.
- Michaux JR, Magnanou E, Paradis E, Nieberding C, Libois R. 2003.** Mitochondrial phylogeny of the woodmouse (*Apodemus sylvaticus*) in the western Palearctic Region. *Molecular Ecology* **12**: 685–697.
- Müller HJ. 1950.** Our load of mutations. *American Journal of Human Genetics* **2**: 111–176.
- Orr HA. 2005.** The genetic basis of reproductive isolation: insights from *Drosophila*. *Proceedings of the National Academy of Sciences of the United States of America* **102** (Suppl. 1): 6522–6526.
- Pilsbry HA. 1900.** The genesis of the mid-Pacific faunas. *Proceedings of the Academy of Natural Sciences of Philadelphia* **52**: 568–575.
- Pimm SL. 1991.** *The balance of nature*. Chicago, IL: Chicago University Press.
- Pimm SL, Jones HL, Diamond J. 1988.** On the risk of extinction. *American Naturalist* **132**: 757–785.
- Porter DM. 1984.** Relationships of the Galapagos flora. *Biological Journal of the Linnean Society* **21**: 243–251.
- Provine WB. 1989.** Founder effects and genetic revolution in microevolution and speciation: an historical perspective. In: Giddings LV, Kaneshiro KY, Anderson WW, eds. *Genetics, speciation and the founder principle*. New York, NY: Oxford University Press, 43–76.
- Reed TM. 1980.** Turnover frequency in island birds. *Journal of Biogeography* **7**: 329–335.
- Reed TM. 1981.** The number of breeding landbird species on British islands. *Journal of Animal Ecology* **50**: 613–624.
- Ross JC. 1847.** *A voyage of discovery and research in the Southern and Antarctic Regions, during the years 1839–43*, 2 volumes. London: John Murray.
- Ross MJ. 1982.** *Ross in the Antarctic*. Whitby: Caedmon.
- Russell GJ, Diamond JM, Reed TM, Pimm SL. 2006.** Breeding birds on small islands: island biogeography or optimal foraging? *Journal of Animal Ecology* **75**: 324–339.
- Saccheri I, Kuussaari M, Kankare M, Vikman P, Fortelius W, Hanski I. 1998.** Inbreeding and extinction in a butterfly metapopulation. *Nature* **392**: 491–494.
- Simberloff D. 1969.** Experimental zoogeography of islands: a model for insular colonization. *Ecology* **50**: 296–314.
- Simberloff D. 1976.** Species turnover and equilibrium island biogeography. *Science* **194**: 572–578.
- Simberloff D, Wilson EO. 1969.** Experimental zoogeography of islands. The colonisation of empty islands. *Ecology* **50**: 278–296.
- Simberloff D, Wilson EO. 1970.** Experimental zoogeography of islands. A two year record of colonization. *Ecology* **51**: 934–937.
- Sinclair WT, Morman JD, Ennos RA. 1999.** The postglacial history of Scots pine (*Pinus sylvestris* L.) in western Europe: evidence from mitochondrial DNA variation. *Molecular Ecology* **8**: 83–88.
- Stewart JR, Lister AM. 2001.** Cryptic northern refugia and the origins of the modern biota. *Trends in Ecology & Evolution* **16**: 608–613.

- Stilwell JD. 2002.** Geological exploration of Cockburn Island, Antarctic Peninsula. *Polish Polar Research* **23**: 47–73.
- Sulloway FJ. 1982.** Darwin and his finches. The evolution of a legend. *Journal of the History of Biology* **15**: 1–53.
- Sulloway FJ. 1984.** Darwin and the Galapagos. *Biological Journal of the Linnean Society* **21**: 29–59.
- Teeter KC, Payseur BA, Harris LW, Bakewell LW, Thibodeau LM, O'Brien JE, Krenz JG, Sans-Fuentes MA, Nachman MW, Tucker PK. 2008.** Genome-wide patterns of gene flow across a house mouse hybrid zone. *Genome Research* **18**: 67–76.
- Thornton I. 1996.** *Krakatau. The destruction and reassembly of an island ecosystem*. Cambridge, MA: Harvard University Press.
- Thornton I. 2007.** *Island colonization. The origin and development of island communities*. Cambridge: Cambridge University Press.
- Thorpe WH. 1974.** David Lambert Lack, 1910–1973. *Biographical Memoirs of Fellows of the Royal Society* **20**: 271–293.
- Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM. 2003.** Introduced species and their missing parasites. *Nature* **421**: 628–630.
- Turrill WB. 1953.** *Pioneer plant geography. The phytogeographical researches of Sir Joseph Dalton Hooker*. Hague: Nijhoff.
- Turrill WB. 1963.** *Joseph Dalton Hooker. Botanist, explorer and administrator*. London: Thomas Nelson.
- Wagner A, Wagner GP, Simillion P. 1994.** Epistasis can facilitate the evolution of reproductive isolation by peak shifts: a two-locus two-allele model. *Genetics* **138**: 533–545.
- Wallace AR. 1853.** *A Narrative of Travels on the Amazon and Rio Negro*. London: Reeve & Co.
- Wallace AR. 1855.** On the law which has regulated the introduction of new species. *Annals and Magazine of Natural History* **18**: 184–196.
- Wallace AR. 1880.** *Island life*. London: Macmillan.
- Watson HC. 1835.** *Remarks on the geographical distribution of British plants*. London: Longman.
- Weiner J. 1994.** *The beak of the finch*. London: Jonathan Cape.
- Williamson MH. 1981.** *Island populations*. Oxford: Oxford University Press.
- Williamson MH. 1984.** Sir Joseph Hooker's lecture on insular floras. *Biological Journal of the Linnean Society* **22**: 55–77.
- Willis KJ, Whittaker RJ. 2000.** The refugial debate. *Science* **287**: 1406–1407.
- Woolfit M, Bromham L. 2005.** Population size and molecular evolution on islands. *Proceedings of the Royal Society of London Series B, Biological Sciences* **272**: 2277–2282.