Biological Invasions (2006) 8: 201–215
DOI 10.1007/s10530-004-3574-2

Can we infer island introduction and naturalization rates from inventory data? Evidence from introduced plants in Galapagos

Alan Tye
Department of Botany, Charles Darwin Research Station, Isla Santa Cruz, Galapagos; Postal Address: CDRS, AP 17-01-3891, Quito, Ecuador (e-mail: atye@fcdarwin.org.ec)

Received 20 April 2004; accepted in revised form 21 September 2004

Key words: Galapagos, introduced plants, introduction rate, islands, naturalization

Abstract

Studies of human-mediated rates of introduction of organisms to islands are few, results fall into two models (linear and exponential), and relationships with human population and activities are obscure. Owing to their late settlement and good scientific record, data from Galapagos may be exceptionally informative. The rate of introduction of vascular plant species to Galapagos has been suggested to be exponential, paralleling the rise in human population. However, detailed reconstruction of growth in numbers of introduced plant species, based on historical and recent records, reveals changes in study criteria over the last two centuries, which obscure the true introduction rate. At first, cultivated species were deliberately excluded from most studies. From the 1960s, naturalized cultivated species were included more consistently, but non-naturalized species were still excluded. From the mid-1980s, the latter were deliberately included. Accidental introductions increased linearly from 1807 (the first records) to the present. Escapes from cultivation show increases in rate around 1906 and in the period 1970–1990, the latter coinciding with the first studies directed at areas affected by human activities. Non-naturalized cultivated species rose abruptly from the late 1980s, as they became deliberately studied. There seems to be no direct link with human population size. Data represent rate of discovery rather than true introduction rate, and the changing overall rate reflects changing botanical interests and research effort. Data from other islands also suggest that linear increases in naturalized plants are the norm. Galapagos data do not permit confident statements about the introduction rate of cultivated species, but suggest that this may depend more on human activities than human population size.

Resumen

Los estudios de la tasa de introducción de los organismos a islas causada por los seres humanos son pocos; sus resultados caben dentro de dos modelos (linear y exponencial), y la relación con la población humana y sus actividades es oscura. Los datos de Galápagos pueden ser excepcionalmente informativos, debido a su colonización tardía y registro científico bueno. Se ha sugerido que la tasa de introducción de las plantas vasculares a Galápagos es exponencial, en paralelo al crecimiento de su población humana. Sin embargo, una reconstrucción detallada del incremento en número de especies de plantas introducidas, basada en los datos históricos y recientes, revela cambios en los criterios de estudio durante los últimos dos siglos, lo que oscurece la verdadera tasa de introducción. Al principio, se excluían de la mayoría de los estudios las especies cultivadas. Desde los 1960, se incluyeron con más regularidad las especies cultivadas naturalizadas, mientras las no-naturalizadas quedaban excluidas. Desde los 1980, estas últimas fueron intencionadamente incluidas. Las especies de introducción accidental demuestran un aumento linear en su número desde 1807 (los primeros registros) hasta la presente. Las especies cultivadas naturalizadas demostraron aumentos más rápidos alrededor de 1906 y también durante el período 1970–1990, cuando se realizaron los primeros estudios dirigidos a las áreas afectadas por actividades humanas. El número de especies cultivadas no-naturalizadas empezó a aumentar abruptamente en los últimos años de los 1980, en cuanto fueron incluidas sistemáticamente en los inventarios. No parece existir ningún vínculo directo con el tamaño de la población humana. Los datos representan más bien la tasa de reportes de presencia que la tasa verdadera de introducción, y la tasa cambiante refleja los cambios en los intereses botánicos y los esfuerzos de investigación. Los datos de otras islas también sugieren que un aumento linear de plantas naturalizadas es la norma. Los datos de Galápagos no permiten conclusiones fuertes sobre la tasa de introducción de las especies cultivadas, pero sugieren que ésta depende más de las actividades humanas que del tamaño de su población.

Introduction

The principal threat to the terrestrial biodiversity of most oceanic islands, including the Galapagos, is introduced species (Loope et al. 1988). An understanding of the process of introduction of alien species by humans is therefore important for conservation planning, but there is little information on this process, and for most oceanic islands it is obscured by their long prehistory of human habitation and species translocations. Further, most tropical and temperate islands, even if uninhabited when they were discovered by European explorers during the major voyages of the 15th and 16th centuries, were quickly settled by their European discoverers, with consequent introductions of alien species and rapid extinctions of endemics during a period, up to the early 19th century, when little scientific study was carried out. Galapagos is exceptional among tropical–temperate islands in this respect (Hooker 1847b). The archipelago was uninhabited when discovered by Europeans in 1535, and there is no convincing evidence for earlier visits from South America or elsewhere (Slevin 1959; Hickman 1985). More importantly, apart from isolated castaways in the early 1800s, Galapagos was not settled until about 1830, near the beginning of the modern era of scientific investigation. Late discovery and, especially, late settlement by humans, and a relatively good history of scientific investigation, mean that we potentially have more evidence about the progress of introductions of alien species to Galapagos than for any other tropical or temperate island group. Galapagos data could thus be exceptionally informative about the influence of the arrival, expansion and activities of humans on the process of introduction of alien species to islands, and the resultant influence of the introduced species on the native flora and fauna. Many Antarctic and Subantarctic islands have a similar history of late settlement (or even none to date) but the factors operating at high latitudes differ owing to the small resident human populations, different patterns of island use, and a great difference in the size of the global fauna and flora adapted to such climates (Chown et al. 1998). Further, scientific investigation during the period of human occupation has not been as thorough on any Subantarctic group (cf. Gaston et al. 2003) as it has on Galapagos.

Among other aspects of the introduction process about which little is known, is the rate of introduction to oceanic islands and its relationship to changes in human population and activity. Introduction rates have an obvious bearing on the influence of alien species on native biodiversity, so it is important to understand the effects of discovery date, settlement date, human population growth and changing human activities on introduction rates, in order to manage potential adverse effects better. Relationships between human population and alien species numbers (e.g. Mauchamp 1997; Chown et al. 1998; McKinney 2001) might help to explain the link between human population density and threats to native biodiversity (McKee et al. 2003).

Given the scarcity of reliable data, it is not surprising that previous analyses of introduction rate to islands are few. Linear increases have been shown in the number of introduced plants known in New Zealand (Owen 1998) and the number of introduced insects in Hawaii

(Beardsley 1991). In Galapagos, the rise in the reported number of introduced vascular plant species appeared to be exponential (Mauchamp 1997), and Peck et al. (1998) reported an exponential increase in introduced insects. What is termed here 'introduction rate' takes no account of species that were introduced but died out before they could be registered by science. It would be more accurate to use a term such as 'persisting-introduction rate' but for simplicity 'introduction rate' is used throughout this paper.

Groves and Hosking (1998) examined introduced plant naturalization rate in Australia, by reviewing plant inventories. They considered naturalization rather than introduction because data on introduction rate and the relationship between introduction and naturalization were not available. They showed that the increase in number of naturalized species in five Australian states was linear up to 1980, and that the naturalization rate of introduced plants in Australia as a whole was near-linear up to 1971. Esler and Astridge (1987) similarly demonstrated a linear increase in number of naturalized species in the Auckland region of New Zealand, from 1840 to 1985. Wu et al. (2003) also found a near-linear overall rate of increase in number of naturalized Fabaceae species in Taiwan, from 1890 to 2000. The data of Esler and Astridge (1987) suggest a declining rate for accidentals but a higher rate for deliberate introductions from 1940 to 1970 than over the rest of their study period. Groves and Hosking (1998) reported a much steeper increase in Victoria, Australia, since 1971 than before, and speculated that this might be due to increased collection effort.

Apart from these, studies of introduction and naturalization rates on islands, based on cumulative species records or otherwise, seem to be lacking. The cited studies fall into two models: linear (naturalized plants, New Zealand plants and Hawaiian insects) and exponential (supposed introduction rates of Galapagos plants and insects).

Numbers of introduced plants registered in Galapagos have continued to rise since the data published by Mauchamp (1997). However, there is continuing uncertainty about the real human-mediated introduction rate of plants to the archipelago, which is of conservation concern. The uncertainty relates to the real meaning of the figures quoted by Mauchamp and earlier authors: to what degree do the numbers of introduced species registered reflect true introduction rates over the years? Mauchamp (1997) described the data as representing an exponentially increasing rate of introduction, with more than 10 species introduced per year in the 1990s, and closely paralleling growth in the human population. Mauchamp's supposition of exponential growth (no formal analysis was carried out) was based upon this close parallel (Figure 1 of Mauchamp 1997), but these data, assumptions and conclusions merit further examination. Three suppositions are involved, which may be tested as hypotheses:

1. What form does the growth take: exponential or otherwise?
2. Whether exponential or not, do the data truly represent introduction rate (i.e. what causes the changing rate of increase in numbers registered)?
3. Is the introduction rate really linked to human population growth?

The last question is perhaps the most interesting from a conservation point of view. One might expect exponential human population growth in a newly-settled area like Galapagos, even in a non-migrational population, and since much of the growth in Galapagos has been due to immigration (c. 5% annually 1982–1998, with a birth rate of <2% per annum 1985–1995: Fundación Natura 1999), growth has been faster than expected for a non-migratory population. However, there is no *a priori* reason for numbers of introduced species to follow the same curve: any correlation may not be causal.

In this paper, I attempt to reconstruct the pattern of introduction of vascular plant species to Galapagos by humans. I review species lists in key publications and include updated figures on species known to be present in the archipelago up to the end of 2003. I attempt to clarify the meaning of the totals quoted by different authors for different years and discover the causes behind the apparently changing rate of increase. I investigate what the relatively good Galapagos plant inventory data really tell us about the two models (linear and exponential), and whether these data are sufficient to draw meaningful conclusions about introduction and naturalization rates and the influence of human activity upon them. I attempt to determine what we can actually deduce about island introduction and naturalization rates from available data.

Methods: sources and treatment of introduced plant records

I reviewed all references cited by Mauchamp (1997), which include all attempts to produce a complete Galapagos flora and some others that provided interim first records of introduced plant species, plus additional key sources of introduced plant records, which were not reviewed by Mauchamp. Table 1 presents the data and their sources. Apart from Porter (1822), Fitzroy (1839), Petit-Thouars (1841) and Wolf (1879), which are included because of their first records of introduced plants, these sources are attempts at complete floras or plant lists or numerical floral summaries for the archipelago.

To enable reliable comparison between references spanning almost two centuries, I referred all records of introduced vascular plant species in each reference, including those considered doubtfully native, to a consistent taxonomic classification, based on Jørgensen and León-Yánez (1999). Records of introduced species that have subsequently proved to be misidentifications, or about which there remains reasonable doubt regarding their identity, were excluded.

Records were also assigned to the following status categories:

- Doubtfully native (NaQ): 51 species classed as 'introduced' (accidental) by Porter (1983), which were classed as 'native' by Lawesson et al. (1987) and most other authors, plus a few others of similarly doubtful status (naturalized, mainly non-useful species known to be easily spread accidentally by people, which were registered by early collectors but first on an inhabited island).
- Accidental (Ac): species introduced accidentally to Galapagos by people; all are naturalized.
- Escaped (Es): species introduced deliberately to Galapagos (useful species) that have subsequently naturalized.
- Cultivated (Cu): non-naturalized deliberately introduced species.
- Endemic: species restricted to Galapagos.
- Native: species that are generally agreed (in authoritative Galapagos publications, especially Wiggins and Porter 1971; Porter 1984 and Lawesson et al. 1987) to have arrived naturally or evolved in Galapagos (includes endemics).

Early authors often made no distinctions between accidental introductions, cultivated escapes or natives. Later authors, including Porter (1983), Lawesson et al. (1987) and Mauchamp (1997), made varying attempts to distinguish between accidentals and cultivated escapes or between naturalized and non-naturalized cultivated species. Their categories and classifications were, however, not consistent. In view of this, all records have been given consistent classifications for Table 1, rather than simply accepting each author's view of whether a species was native or introduced. Most cases where the classification used here disagrees with the original author's assessment refer to non-endemic native vs introduced accidental, or cultivated escape vs accidental. Classifications of some species, especially useful ones, changed during the 200 years of records, as cultivated species became naturalized; changes of status accepted in Table 1 are usually based on the original author's comment.

Data from Mauchamp (1997) for 1990 and 1995 cannot be used for analyses other than of total introduced species, since he did not list species and no contemporary list exists that can be evaluated according to the classifications listed above. However, revised figures for those years, as well as data for 1999, 2000 and 2003, have been generated for Table 1 from the Charles Darwin Research Station's Database of the Galapagos Flora, by extracting taxa whose first record dates fall up to the year in question. In many cases, the numbers of species given for a reference do not agree with those cited by Mauchamp (1997), who missed some species in some references (see footnotes to Table 1). In part, this may have been caused by differing views on the status (native or introduced) of certain species.

Cumulative totals, calculated by comparing the species listed in each publication, are also given

Table 1. Reports of introduced plant species from Galapagos.

Year of latest record included	NaQ	Ac	Es	Cu	Ac + Es + Cu	Ac + Es + Cu + NaQ	Native taxa listed (including NaQ)	Sources and comments on introduced species
1535	0	0	0	0	0	0	0	Discovery of Galapagos.
1807				2	2	2	9	Porter 1822. First introduced plants recorded.
1837	11	6	0	17	23	34	236	Fitzroy 1839: 10 cultivated. Petit-Thouars 1841: 10 cultivated. Hooker 1847a, b: "17 cultivated".
1853	19(20)	13	2	11(20)	26[a](35)	45(55)	353	Andersson 1858. Naturalized and some cultivated species.
1875	1(21)	0(13)	0(2)	19(29)	19(44)	20(65)		Wolf 1879. Not complete flora, so excluded from analyses. Includes several first records.
1899	35(37)	27	8	10(30)	45[a](65)	80(102)	570	Robinson 1902. Mostly naturalized, some cultivated.
1906	42(44)	34	20	17(31)	71[a](85)	113(129)	580	Stewart 1911,1915. Mostly naturalized, some cultivated.
1970	50(55)	63	54	39(49)	156[a](166)	206(221)	625	Wiggins and Porter 1971. 117 naturalized.
1976			57		130	181	582	Porter 1976. Most of the non-Es were probably Ac, due to attempted exclusion of Cu and NaQ. Species not listed. Excluded from analyses.[b]
1982	53(57)	79	64	2(49)	145(192)	198(249)	603	Porter 1983, 1984. Only naturalized species. Excluded from analyses[b] except those of naturalized species, doubtful natives and cumulative totals, due to exclusion of Cu spp.
1986	52(57)	89	76	93(106)	258(271)	310(328)	603	Lawesson et al. 1987. Includes cultivated spp. and results of new surveys for introduced, especially cultivated, plants.
1987					260	311		Stone et al. 1988. Excluded from analyses.[b]
1989	8(57)	79(89)	71(76)	87(106)	237(271)	245(328)		Lawesson 1990. Excluded from analyses.[b]
1990	57	95	103	166	"310"[c] 364	421		Mauchamp 1997 & in litt. (in quotes); CDRS Galapagos Flora Database, first records up to 1990. Includes new surveys for introduced plants, and cultivated species.
1995	57	96	107	201	"438"[c] 404	461		Mauchamp 1997 (in quotes); CDRS Galapagos Flora Database, first records up to 1995. Includes new surveys for introduced plants, and cultivated species.

Table 1. Continued.

Year of latest record included	NaQ	Ac	Es	Cu	Ac + Es + Cu	Ac + Es + Cu + NaQ	Native taxa listed (including NaQ)	Sources and comments on introduced species
1999	58	99	110	228	437	495	609	CDRS Galapagos Flora Database, first records up to 1999.
2000	58	103	112	238	453	511	610	CDRS Galapagos Flora Database, first records up to 2000. Includes complete survey of Santa Cruz Agricultural Zone.
2003	58	106	117	263	486	544	610	CDRS Galapagos Flor Database, records up to December 2003. Includes complete survey of Floreana and partial survey of Puerto Ayora.

Status: NaQ doubtfully native; Ac accidental introduction (naturalized); Es escaped from cultivation (deliberate introduction, naturalized); Cu cultivated (deliberate introduction, not yet naturalized). Data in parentheses are cumulative totals (see text).
[a]Several of these species were missed in the analysis of Mauchamp (1997).
[b]These data were included by Mauchamp (1997) but are excluded from analyses herein because they include fewer introduced species than an earlier reference and either do not give species lists or do not add any new species with respect to earlier publications.
[c]Mauchamp's (1997) figure for 1995, in quotes, has been reduced to that out of quotes, since his total included a large group of misidentifications from surveys carried out by non-experts, which have subsequently been removed from the Galapagos list. Mauchamp's 1990 data may suffer from a similar problem, but the reduction is more than compensated by earlier first records not included by Mauchamp, especially those in Lundh, in press.

in Table 1. These are greater than the sum of an author's own list when the author omitted species mentioned by a previous author. All species recorded by early authors (other than those for which there is good reason to suspect a misidentification) are known or suspected to occur currently in the islands. For analyses using cumulative totals (but not for analyses using non-cumulative) I therefore assumed that a species recorded by an early author was still present in Galapagos, even though later authors may have missed it. This carries a risk of considering a species continuously present even though it was introduced several times and disappeared between surveys. However, this would have been most common with cultivated (non-naturalized) species, which form a small proportion of early records (see below) and, since the proportion of species with 'gaps' in their record is small, this does not affect the conclusions.

Data on the native flora from the same references, when available, are included in Table 1 for comparison. The data on native taxa are simply the totals of taxa listed in each source without regard to subsequent taxonomic revisions.

Results

Growth in knowledge of the native and introduced flora of Galapagos

Table 1 represents the most detailed reconstruction to date of the growth in numbers of introduced vascular plant species in Galapagos.

Early visitors had mentioned some plants recognisable to species, but the first record of introduced plants was by Porter (1822), who was in the islands in 1813. He was a naval captain, not a botanist, but described elements of the vegetation amounting to at least nine native species, plus the introduced 'pumpkins and potatoes', which were being cultivated by the exile Patrick Watkins on Floreana island about 1807.

The first botanical collections in Galapagos to be documented (by Hooker 1847a) were made by David Douglas and John Scouler in 1825 (Robinson 1902) and our knowledge of the native flora appears to have been nearly complete by 1900, within 75 years (Figure 1). This is not an entirely true picture, because many of the early-described taxa were later synonymised. However, less than

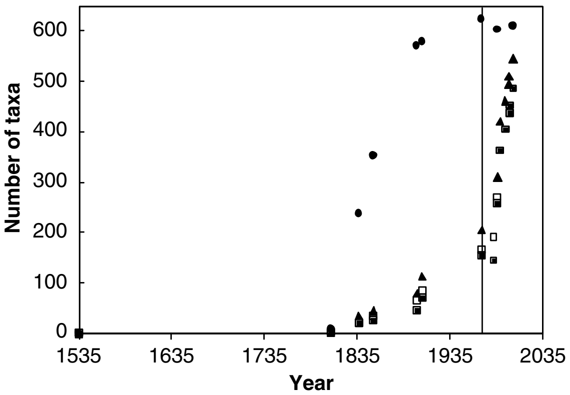

Figure 1. Rates of increase in numbers of introduced and native plants recorded in Galapagos since discovery in 1535. Circles, native taxa; squares, universally accepted introduced species (open symbols, cumulative data where different); triangles, introduced species including doubtful natives. Vertical line, 1970.

30% of native taxa have been discovered since 1900, and almost all of them before the publication of Wiggins and Porter (1971). In contrast, records of introduced species initially grew more slowly, with 70% of species added since the publication of Wiggins and Porter (1971).

What form does the curve of total introduced species registered take?

Since the data in Table 1 differ slightly from those that Mauchamp (1997) used to construct his Figure 1, the form of the introduced species curve (Figure 1) also differs slightly. Analyses here use the non-cumulative 'total introduced species' data, excluding doubtful natives, of Table 1 (Ac + Es + Cu data not in parentheses; Figure 1 solid squares). Using Mauchamp's (1997) original data (supplied by A. Mauchamp in litt.) makes no difference to the conclusions, while using the cumulative data strengthens them.

The data fit an exponential distribution fairly well (all data $\log_e y = 0.014x - 23.023, r^2 = 0.885$); even better using only data from 1807 onward ($\log_e y = 0.021x - 36.253$, $r^2 = 0.936$). However, the fit to an exponential model is no better than that for two linear stages (Figure 2 solid squares), 1807–1982 ($y = 0.896x - 1630$, $r^2 = 0.937$) and 1982 onward ($y = 15.073x - 29686, r^2 = 0.934$).

In fact, examination of Figures 1 and 2 suggests that the process might have comprised three periods of differing but approximately linear rate. Up to 1899, the rate was slower than 1900–1982, and finally it was much faster from 1986 onwards.

Do the data truly represent introduction rate? Evidence from comments and species recorded by different authors

The first two introduced species mentioned (Porter 1822) were both cultivated, and Hooker (1847b), Andersson (1858), Robinson (1902) and Stewart (1911) each listed a few cultivated species. Hooker and Robinson both worked from collections made by others (Macrae, Darwin, Edmondston, Baur, Snodgrass and Heller, among others), and did not state directly whether the non-native species they included were naturalized or not. The comments and omissions of Hooker (1847b), Robinson (1902) and Stewart (1911, 1915) illustrate well the dismissive attitude of the early botanists to cultivated and other introduced species, an attitude that, to some degree, persisted up to the 1980s (Wiggins and Porter 1971; Porter 1976, 1983, 1984).

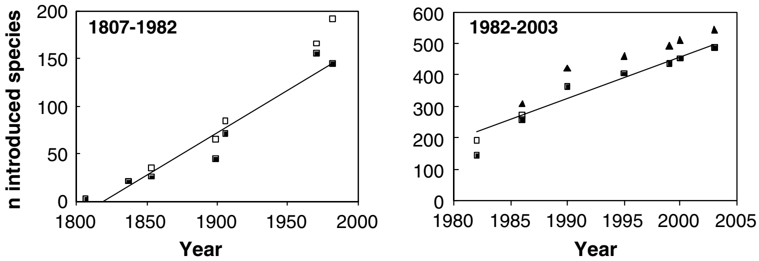

Figure 2. Multi-stage linear growth in introduced plant numbers? Symbols as in Figure 1. Regression line based on non-cumulative data (solid squares).

In his floral analysis, Hooker (1847b, p. 259) wrote that he had 'excluded seventeen species [to leave a total of 96] from the flora of this islet [Floreana], as being almost certainly introduced with cultivation'. Hooker's systematic list (1847a) includes only 88 species recorded for 'Charles' (Floreana) but Hooker would probably have seen specimens of seven additional Floreana species (Porter 1980), while one of the specimens that Hooker lists for 'Galapagos', could also have been from Floreana, resulting in 96. Therefore, it seems that Hooker had already excluded the 17 from his (1847a) systematic list. Although he nowhere says what these 17 were, they may have been the cultivated species listed by Fitzroy (1839) and Petit-Thouars (1841), which add up to 16 or 17, depending on whether Petit-Thouars' potatoes and Fitzroy's sweet potatoes are regarded as referring to the same or different species. Alternatively, they might include some of those listed in Hooker's (1847b) footnote on p. 261–2, but most of these were not actually collected in Galapagos or were unidentified to species. Of Hooker's (1847a) systematic list, six species are now classed as accidental and 11 as doubtful natives, one of the former, *Amaranthus caraccasanus* (= *A. hybridus*) being the only species which he annotated "on cultivated ground. Probably ... introduced into the Galapagos" (p. 189). His explicit exclusion of other introduced species implies that he regarded those he did list as native, or at least possibly so. He thus excluded cultivated species and seems to have tried to exclude accidentals too. When the collections he studied were made (1825–1841), there would almost certainly have been more than 17 introduced plants in cultivation, since Floreana had already been inhabited for some years, and we know, from contemporary letters, of additional cultivated species that were not mentioned by any botanist (Latorre 1999). Similarly, Andersson (1853) and Robinson (1902) omitted cultivated species listed by previous authors (compare source and cumulative totals in Table 1), and Robinson meant to exclude others, such as *Solanum tuberosum* (p. 201), which he placed in square brackets and annotated "included by Andersson ... but only on the basis of cultivated specimens."

Stewart (1911) described Galapagos vegetation types but made no mention of habitats influenced by people. Although Hooker (1847b) had acknowledged the recent influence of man as an agent of dispersal to the islands, Stewart (1911) did not include humans among the introduction agents in his analysis of floral origins. He included some naturalized (mostly accidental) and 10 cultivated species in his systematic list, although he too excluded most of the cultivated species mentioned by earlier authors. The cultivated species included in his list were often accompanied by comments indicating that they were escaped (naturalized) or that he was unsure whether they were escaped or not. He later (Stewart 1915) mentioned by name seven additional cultivated plants (which I include in the totals for Stewart in Table 1), plus 'many... common vegetables and fruit' that he had not included in his 1911 systematic treatment, confirming that he was not especially interested in collecting or describing cultivated and other introduced plants. The first study stage was thus marked by deliberate exclusion of cultivated species, and varying attempts to exclude accidentals too.

The second stage began when, after a 60-year gap since Stewart's (1911) review, Wiggins and Porter (1971) included 140 introduced species in the systematic part of their book (twice the number reported by Stewart 1911), 85% of them apparently naturalized, judging by accompanying comments. However, in their Introduction, Wiggins and Porter (1971, p. 7) mention in passing an additional 16 cultivated species (to give a total of 39). Their cultivated-plus-escaped total of 93 species is known (see below) to be an incomplete list of plants cultivated on the islands during the 1960s, when people had been farming there for 150 years. Further, they intended that several other species that had been mentioned by previous authors should be excluded, such as various *Citrus* spp. (p. 744), *Cucurbita pepo* (p. 393) and *Tagetes erecta* (p. 366), which they suspected were not naturalized or 'not persist[ing] in the wild' or 'casual escape[s] from cultivation' (I include these in their totals in Table 1). Finally, Wiggins himself collected and identified in the 1960s several additional introduced plant species (specimens at Herbarium CDS, e.g. *Crescentia cujete*), which are not mentioned anywhere in his Flora (Wiggins and Porter 1971). Similarly, Porter (1976, 1983, 1984) included naturalized species but even more rigorously excluded species present only in cultivation; the two cultivated species for Porter (1983, 1984) in Table 1 were actually regarded by him as naturalized. During this second stage (1960s to early 1980s) therefore, cultivated (non-naturalized) species were still deliberately excluded (Wiggins and Porter 1971; Porter 1976, 1983, 1984).

The third stage begins with the sudden near-doubling in numbers reported by Lawesson et al. (1987), only 20 years after the studies of Wiggins and Porter (1971), followed by similar increases reported by Mauchamp (1997) for 1990 and 1995, and steady increases since 1995. These were due to the systematic inclusion of cultivated species, following surveys specifically for introduced plants. All major publications since Lawesson et al. (1987) have included both cultivated and naturalized species. Surveys since 2000 have to date encountered some 100 introduced plant species new for the Galapagos list (unpubl. data: not yet all definitively identified and therefore not all included in Table 1), but not all were introduced since the previous survey: evidence, including interviews with landowners and the size of individuals of newly registered species of tree, shows that many were present for decades before they were detected. Many were introduced in the 1960s or earlier, so were already present when Wiggins and Porter (1971) reported only 93 cultivated and escaped species in the archipelago.

Rates of increase in different categories of naturalized and non-naturalized species

Given these changes in recording criteria, further evidence for introduction rates may be obtained by examining the growth in the different categories of introduced plant (Figure 3). Despite some attempts to exclude obviously introduced escapes from cultivation, even the earliest botanists seem to have collected naturalized species, especially accidentals, so their numbers may most accurately reflect introduction rate. Figure 3 also includes endemic taxa as an index of study effort (endemics rather than all natives as endemics are 'indubitably native', thereby avoiding potential confusion between non-endemic natives and introduced accidentals, and also minimizing problems of taxonomic revision).

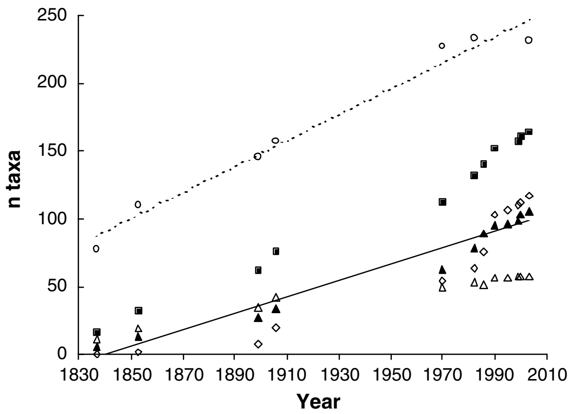

Figure 3. Numbers of naturalized species. Circles, endemic taxa (for comparison: see text); open triangles, doubtful natives; solid triangles, unquestioned accidentals; solid squares, all accidentals (including doubtful natives); open diamonds, naturalized cultivated species.

The growth in numbers of undoubted accidentals (Figure 3, filled triangles, solid trendline) appears to be linear, apart from a possible temporary increase in rate in the 1980s, and with an overall slope rather less than the growth in numbers of endemics (Figure 3, open circles, dashed line).

Growth in 'doubtful natives' was also linear up to 1906 (Figure 3, open triangles), with their numbers per study slightly greater than the undoubted accidentals; but while accidentals continued to increase, the doubtful natives levelled off from 1970 onward.

The rate for cultivated escapes appears to change more than once, with an inflection at 1906 and a higher rate between 1970 and 1990 (Figure 3, diamonds).

Finally, the rate for non-naturalized cultivated species clearly increases over the studied period, and can be compared with human population growth (Figure 4).

Discussion

Reported and real rates of increase in Galapagos introduced plants

It is impossible to distinguish statistically between an exponential increase and a multi-stage linear

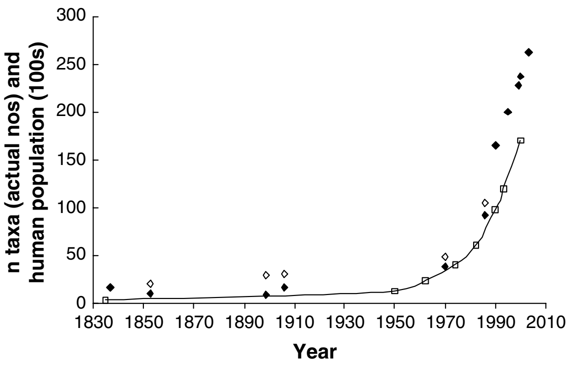

Figure 4. Numbers of non-naturalized cultivated species (diamonds; open diamonds are cumulative data) and humans.

process in the overall data for introduced plant species, and the evidence suggests that a three-stage process best describes the changing rate. Examination of the species recorded and comments made by different authors shows that collection and inclusion criteria changed over the 178-year study period, and that studies fall into three distinct phases, reflected in the composition of the species lists in the references cited in Table 1, and representing differing rates of recording native, naturalized and cultivated plants.

The early authors, such as Hooker (1847b), Andersson (1858), Robinson (1902) and Stewart (1911), each listed some cultivated species that were apparently collected or noted in passing by the collectors, but made no attempt to register the cultivated flora exhaustively. They mentioned few introduced species, partly because there surely were fewer than today, but also because their interest was focussed primarily on uninhabited areas and the unique endemic flora, and they made no special effort to collect and record introduced species, or even deliberately ignored them (especially cultivated non-naturalized species). Early floristic analyses (Hooker 1847b; Andersson 1858; Robinson 1902; Stewart 1911) were aimed at understanding the nature and origins of the indigenous flora, rather than the effects of humans upon it.

The increased rate of recording new species during the second stage appears to have been caused by a combination of increased botanical study (including the first modern flora: Wiggins and Porter 1971), increasing naturalization of species that were perhaps introduced well before their first registration, and deliberate inclusion of the naturalized introduced flora, with more interest in the inhabited areas and in naturalized introduced species that were beginning to be seen as invaders (as exemplified by the studies of Porter 1976, 1983, 1984).

The steep increase in the third stage, since 1987, mainly results from specific surveys for introduced plants and the inclusion of non-naturalized cultivated species. Recent surveys included the Agricultural Zone of Santa Cruz (the 2001 increase), the Agricultural Zone and village gardens on Floreana, and (partially completed by December 2003) the town of Puerto Ayora, the largest population centre in Galapagos. These are the most thorough introduced plant surveys carried out so far in Galapagos but, as no previous survey was complete, the many new species encountered in each survey since the early 1980s do not necessarily represent a high recent introduction rate. Indeed, we know that many species first detected only recently were present for decades beforehand.

The available data obviously represent reporting rate by botanists, rather than introduction rate, and botanists formerly ignored introduced species. Conclusions about change in introduction rate must therefore be drawn with extreme caution because of the confounding effect of changing research effort and criteria. The increasing rate of rise in overall numbers of introduced species registered, and of cultivated species in particular, reflects the increased interest in recent years in the introduction process, as well as increased botanical sampling, rather than a true change in introduction rate.

Rates for accidentals, escaped cultivated, and non-naturalized cultivated species

Given that they were collected by earlier botanists, numbers of naturalized species (especially accidentals) registered may closely reflect naturalization rate and, assuming a constant relationship between naturalization and introduction, may also more closely reflect true introduction rate than do overall numbers of introduced species.

It appears that the true rate of introduction–establishment–naturalization of accidentals in Galapagos has been linear, as found by Esler and Astridge (1987), Owen (1998) and Groves and Hosking (1998) for New Zealand and Australia, and Wu et al. (2003) for Taiwan. Unlike in New Zealand (Esler and Astridge 1987), the Galapagos rate for accidentals has not declined in recent years. Apart from a possible temporary increase in rate in the 1980s, which coincides with the first studies specifically directed at areas affected by human activities, effort per study for accidentals has probably been more or less constant. Linear growth in accidentals is presumably a result of both study (compare linear growth in endemics) and introduction–naturalization (introduction–establishment and naturalization being a single process for accidentals). However, the data still do not permit distinction between two hypotheses for accidental introductions: that there was a constant introduction rate with a discovery rate that paralleled it, or that many accidentals were introduced very early but increasing study has revealed them gradually.

Growth in 'doubtful natives' was also linear up to 1906, but while accidentals continued to increase, the doubtful natives levelled off from 1970 onward. This is as expected: doubtful natives were consistently collected and it is precisely because the pan-tropical weeds that comprise the majority of them were recorded so early that their status is uncertain; we do not know whether they came on the feathers of birds or the socks of pirates (see Porter 1984).

In contrast, the rate for cultivated escapes appeared to change, with an inflection at 1906 and a higher rate between 1970 and 1990. Thus, although the early botanists collected accidentals, up to about 1900 they either did not collect many escapes from cultivation (because they recognised them as non-native) or there were genuinely fewer at that time: the data cannot separate these two possibilities. The higher rate between 1970 and 1990 coincides with the first studies directed at areas affected by human activities and the sudden inclusion of non-naturalized cultivated species. Two factors probably contributed to this: cultivated escapes were probably overlooked when human-disturbed areas were avoided by earlier collectors, and they may also have been deliberately excluded because they were readily recognized as non-native. For these reasons, the higher 1970–1990 rate cannot be unequivocally taken to indicate a higher rate of introduction–naturalization of cultivated species then. Further, the latest levelling off indicates that the overall naturalization process for cultivated escapes approaches linear, as for accidentals. Groves and Hosking (1998) similarly suggested that an apparent increase in rate of naturalisation since 1971 in the Australian state of Victoria could simply be due to increased collection effort. As in the Auckland area (Esler and Astridge 1987), the proportion of naturalized species that derive from cultivated plants has increased in Galapagos over the years.

Finally, the rate of registration of non-naturalized cultivated species clearly increased over the studied period. As they now comprise over half of the introduced species total, they contribute most to the increasing rate of total introduced species in Figure 1 and Mauchamp's (1997) Figure 1. However, this clearly cannot be taken to indicate an increasing introduction rate, but rather reflects the changing interests of botanists over the years. Non-naturalized cultivated species were so inconsistently recorded up to 1987 that no meaningful conclusions can be drawn about their introduction rate. Introduction of cultivated species is not reliably revealed by botanical inventory data, due to their deliberate exclusion from many floras. Increasing interest in introduced plants, and study of non-naturalized cultivated species, generated by the realisation that introduced plants are a serious conservation problem for Galapagos, was largely responsible for the steep rise in introduced species recorded since the 1980s.

The data reveal no recent declines in Galapagos plant introduction or naturalization rates such as might be caused by the majority of possible colonisers having already arrived (aside from doubtful natives, whose declining rate is caused by increasing certainty of status among newly registered species). The data from Australia and New Zealand, where rates are also not significantly declining despite thousands of species having been introduced and naturalized, suggest that it will be long before that point is reached in Galapagos.

Links to human population growth or human activities?

Given the foregoing, one cannot simply assume that the correlation with exponential human population growth noted by Mauchamp (1997) is meaningful, but must seek evidence in underlying factors that may explain the rate of increase. A causal basis for the parallel with the human population's exponential growth would require that each new human resident (immigrant or birth) be responsible, on average, for the arrival of the same number of new plants. Changing activity patterns, aside from the evident change in botanical study criteria, could obviously interfere with such a simple relationship.

The linear arrival-establishment-discovery rate of naturalized species, despite increased interest in them in recent years, eliminates the hypothesis of an exponential rate directly linked to growth in the human population: the rate simply did not increase. Although the increase of cultivated non-naturalized species does appear to be exponential and to parallel human population growth, this may be entirely due to changing study criteria and effort. Mauchamp's (1997) apparent exponential growth in the number of alien plant species, implying exponentially increasing introduction rate linked to the growth of the human population, does not survive closer examination. The link with human population growth is not directly causal.

Since records began, four factors have probably contributed to the changing rate of rise in records of introduced species: genuine new introductions, new naturalizations, individual introduced species becoming more conspicuous as their populations and ranges grow and, perhaps most importantly, changing botanical study criteria and effort, with sudden recent interest in introduced plants, including specific surveys for them.

Despite the fact that human population may sometimes be an empirical predictor of numbers of introduced species, at least in spatial comparisons (e.g. McKinney 2001), introduction rate may be more closely linked to changing human activities (besides their changing research interests) than to simple population growth. Before human settlement, the rate of introduction of cultivated species would have been low, although the rate for accidentals might have been high, with highly mobile weeds arriving with the first visitors. Settlement would then have seen rapid introduction of the basic crop species. Although the foregoing suggests caution in drawing conclusions, the change in rate for escaped cultivated species around 1900 might reflect increased introduction–naturalization of crops and ornamentals in the early 20th century, when there was rapid development of farms on three of the four inhabited islands, especially the newly-settled island of Santa Cruz (which now has the highest human population). This preceded the major period of human population growth, which took place in the second half of the 20th century (Figure 4 and Mauchamp 1997). Introduction rate might even have fallen during this period, because immigrants in the first half of the 20th century (and earlier) had to develop subsistence agriculture, whereas later immigrants would have found most of the commonly cultivated agricultural, medicinal, timber and ornamental species already present in the islands. Further, many of the late 20th century immigrants came to work in tourism and support industries, rather than on the land (Hickman 1985). However, these predominantly urban dwellers could yet be contributing to what may currently be the highest ever introduction of ornamentals, coinciding with greater affluence and a more leisured lifestyle among some sectors of Galapagos society.

Relevance to other areas and taxa

Galapagos floral inventory data help to eliminate some hypotheses (such as exponential introduction rates linked to human population) and establish a linear model of introduction–naturalization for accidental introductions and probably other naturalized species, despite exponential human population growth but consistent with the few comparable studies from other parts of the world (Esler and Astridge 1987; Groves and Hosking 1998; Owen 1998; Wu et al. 2003). Interestingly, they also eliminate a directly proportional link to the exponentially increasing transport to the islands (Fundación Natura 1999; cf. Gaston et al. 2003; Kraus 2003). However, owing to inconsistent research effort over the last

200 years, the relatively strong Galapagos data provide limited evidence on the changing rate of deliberate introduction of useful species, which now form the majority of the introduced flora.

We still have no good method to determine true overall, and especially deliberate, introduction rates. Methods based on other data are therefore required, such as quarantine and import records (which requires a strict import control system), inventory data with respect to a well-established baseline (not yet established even for Galapagos, though the latest thorough surveys may soon provide it), and perhaps closer examination of the effects of different human activities (including whether pirates wore socks).

The changes in botanical interest over the past two centuries that have occurred in Galapagos probably apply worldwide, especially the recent growth in interest in invasive plants, so the Galapagos conclusions are relevant to all islands. The fact that comparable published studies from other areas could not be found suggests that good data on true introduction rates do not exist for any oceanic islands.

This problem might, however, be peculiar to plants, where most introductions are deliberate and species spend some time in cultivation before naturalizing, during which time they were until recently, and in most places still are, ignored by botanists. For taxa such as invertebrates, where collection is more often necessary for identification than it is for plants, and where most species are introduced by accident or, even if introduced on purpose, rapidly 'naturalize', first record date might be more closely linked to introduction date, so that detection rate would be a closer representation of introduction rate (see Cowie 1998). However, even for insects, Peck et al. (1998 p. 234) recognised that rate of detection is not the same as rate of introduction and the exponential detection rate they report for introduced insects in Galapagos need not represent an exponentially increasing introduction rate. Further, the other good island insect introduction rate study (Beardsley 1991) reported a linear rate for Hawaii. For some taxa introduced primarily by accident, the over-riding factor influencing introduction rate may be frequency of transport (cf. Gaston et al. 2003), although the present study shows that a directly proportional link may not always exist.

In summary, the evidence for exponentially increasing introduction and naturalization rates is poor, for both plants and insects, while stronger evidence exists for linear rates.

Long-term plant introduction rates in Galapagos and elsewhere

One firm conclusion that can be drawn for Galapagos is that the archipelago has, since its discovery in 1535, experienced introduction of at least 550 alien plant species in 470 years, or 1.2 species per year. This compares with a probable natural arrival rate of about one species per 10,000 years (Porter 1983). The human-mediated rate of arrival of new plant species is thus about 13,000 times the natural rate.

During this time, at least 223 introduced plant species (not including the doubtful natives) have naturalized, or about one species every two years. This compares with about 10 species naturalized per year in Australia over the past 200 years (Groves and Hosking 1998), and four per year in the Auckland area of New Zealand (Esler and Astridge 1987). The lower Galapagos rate is undoubtedly due to the vast difference in size and habitat diversity of the areas concerned, and in their degree and diversity of development. Just over 40% of the plant species introduced to Galapagos are classed as naturalized, clearly violating the 'tens rule' of Williamson and Fitter (1996) as on many other island groups (e.g. Kraus 2003) and especially with cultivated plants (Harrington et al. 2003).

The introduction of the Galapagos quarantine system, which began in 1998, combined with rapidly increasing awareness among the local population of problems caused by invasive species, should help to reduce the real introduction rate in the coming years. However, there are certainly many more introduced plant species already present in Galapagos, awaiting detection by botanists, and more survey in the inhabited islands may result in an even higher rate of discovery of 'new' introduced species in the near future. Hopefully, quarantine, combined with control and eradication of species already present in the islands (Tye et al. 2002), may eventually result in reductions, not only in the introduction rate, but also in the total number of introduced plant species present in the archipelago.

Acknowledgements

André Mauchamp kindly provided the data used in his 1997 paper, and he and Clifford Smith made valuable suggestions for additional analyses. Scott Henderson thoroughly reviewed drafts, which benefited from his profound study of Galapagos plant introductions, while Chris Buddenhagen, Heinke Jäger, Aníbal Pauchard and two referees also gave helpful comments. Damalis Azuero improved the Spanish of the Resumen. This paper is contribution number 576 of the Charles Darwin Research Station.

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