

# How to go extinct: lessons from the lost plants of Krakatau

Robert J. Whittaker<sup>1</sup>, Richard Field<sup>1\*</sup> and Tukirin Partomihardjo<sup>2</sup> <sup>1</sup>*School of Geography and the Environment, University of Oxford, Mansfield Rd, Oxford, OX1 3TB, UK, and* <sup>2</sup>*Herbarium Bogoriense, Research and Development Centre for Biology (LIPI), Jalan Ir. Juanda 22, Bogor 16122, Indonesia, e-mail: herbogor@server.indo.net.id*

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## Abstract

**Aim** Few data sets exist that allow measurement of long-term extinction and turnover rates for islands of the size of the three main islands of the Krakatau group. We test the reliability of previous estimates of plant species extinction and examine structure within the extinction data.

**Location** The data analysed are for the three older Krakatau islands: Rakata, Sertung and Panjang in the Sunda Strait, Indonesia.

**Methods** Our analysis is based on a comprehensive database incorporating all species records for each island since recolonization began after the 1883 sterilization, plus attributes such as distribution, phylogeny, population status and dispersal mechanism for each species. We employ a combination of univariate and multi-term analyses in analysing structure, and derive Minimal Adequate Models using binary logistic analyses of variance and covariance. We compare the 1883–1934 data set with the contemporary flora as represented by (1) 1979–83 records (as used in previous analyses) and (2) 1979–94 data (original).

**Results** The improved data for the contemporary flora reduces the number of missing species by one-third. We show that a variety of estimates of extinction rate can be produced depending on what assumptions are made concerning the status of particular species groups. Structural features in the extinction data persist despite the reduction in overall numbers of losses. Losses relate to: (1) the number of islands on which a species originally occurred, (2) the primary dispersal mode, and (3) the original abundance of a species (e.g. whether it was known to have established a successful resident population, and whether it was in decline or increasing in *c.* 1930). The ‘best’ descriptive model employs the variables denoted under (3). A high proportion of losses comprised species introduced by people and rare or ephemeral species. Losses of ‘residents’ that had colonized naturally could largely be accounted for by reference to (1) successional loss of habitat and, to a lesser degree, (2) other habitat disturbance or loss.

**Main conclusions** Previous analyses, based on a more limited data set, have significantly over-estimated extinction from the Krakatau flora. Few naturally colonizing and established species have become extinct. The findings indicate that caution is necessary in interpreting ‘headline’ island ecological rates, and in analysing and modelling such data. Examination of structural features of the data appear to be valuable both in providing ecological insights in their own right, and in enabling refinements to estimates of extinction and thus turnover.

## Keywords

Extinction estimates, island biogeography, Krakatau islands, plant dispersal, sampling problems, species abundance, species turnover rates, succession.

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Correspondence: Robert J. Whittaker, School of Geography and the Environment, University of Oxford, Mansfield Rd, Oxford, OX1 3TB, UK. E-mail: robert.whittaker@geog.ox.ac.uk

\* Present address: School of Geography, University of Nottingham, University Park, Nottingham, NG7 2RD, UK. E-mail: richard.field@nottingham.ac.uk

## INTRODUCTION

In his call for a new theory of Island Biogeography, Lomolino (2000) describes extinction as one of the three fundamental biogeographical processes, the other two being immigration and evolution. In the context of the dominant island theory of the last three decades, MacArthur & Wilson's (1963, 1967) Equilibrium Theory of Island Biogeography (ETIB), extinction takes the form of the local extirpation of a population of a species from an isolate. It is in this sense that the term extinction is used herein. This local-scale process is important for two closely related reasons. First, extinction is one half of the dynamic of turnover and thus of the ETIB. Indeed, the occurrence of turnover at equilibrium is arguably the critical test of this important theory (Gilbert, 1980; Whittaker, 1998, 2000; Brown & Lomolino, 2000). Second, in an applied context, the fragmentation and reduction in area of natural habitats is currently causing increased insularity of many mainland ecosystems. The ability of species' populations to persist in such landscapes is thus of central importance to conservation biology (e.g. Shafer, 1990). Yet despite the importance of extinction and turnover we still know relatively little of the distribution of probabilities of going extinct and how these vary within a species pool; whether turnover is heterogeneous (structured) or homogeneous (random); and to what extent extinction patterns are determined by competition, predation, habitat availability or system instability (Whittaker, 2000).

The most tractable systems for evaluating extinction and turnover are 'small and fast' experimental microcosms (e.g. Simberloff & Wilson, 1969; Dickerson & Robinson, 1985). Whilst findings from microcosm studies are useful, it may be dangerous to assume that findings from such systems can be scaled up to larger, slower-responding systems in which lag or buffering effects (e.g. Grandin & Rydin, 1998) are part of increasingly complex temporal responses. The key problem in evaluating turnover in island floras involving long-lived species is that a simple test of turnover requires a data series commensurate with the longevity of the majority of the species: several decades at least. Few such data sets are available. Almost inevitably, those that do exist have involved different teams of researchers, so that problems of survey efficiency and standardization (Nilsson & Nilsson, 1985) are particularly acute. This paper is concerned with extinction patterns and extinction rates from one of these rare long-duration data sets, for a tropical island flora which includes long-lived perennial species (herbs, shrubs and trees). There are four islands in this system, Rakata, Sertung, Panjang and Anak Krakatau, together constituting the Krakatau archipelago, in the Sunda Strait, Indonesia. Data from Anak Krakatau, the island which arose in 1930 and which has had a much disrupted history of colonization (Partomihardjo *et al.*, 1992; Thornton *et al.*, 1994), are excluded from statistical analysis.

Within the system, a broad-scale successional dynamic is in progress that was initiated in 1883 as a result of sterilizing eruptions of the Krakatau volcano (Whittaker *et al.*, 1989; Thornton, 1996). In their original analyses of turnover data

for Krakatau for the period 1883–1934, MacArthur & Wilson (1963, 1967) reported apparently equilibrium turnover in bird species (since shown to be a premature conclusion, e.g. see Thornton *et al.*, 1990, 1993), but a failure to equilibrate within the flora (i.e. contra their model). Although the survey data are imperfect, they are sufficient to confirm that the flora is continuing to increase in size, i.e. it is not yet an equilibrium system (Bush & Whittaker, 1991, 1993; Whittaker *et al.*, 1992, 1997), and therefore such turnover as is occurring cannot be described as 'equilibrium turnover' (*sensu* MacArthur & Wilson, 1967). It should be noted that the ETIB postulates that extinction rate rises monotonically and gradually to meet a declining immigration rate; thus turnover is predicted to occur well in advance of the attainment of equilibrium. It is with this circumstance that this paper is concerned.

In most plant and animal communities, there are few species with many individuals and many more species with few individuals. Fisher *et al.* (1943) suggested that the largest class of species is of those that are individually rarest, giving rise to the logarithmic series of abundance. Preston (1948, 1962a, b) argued that in reality species more typically fit a log-normal series of abundance, i.e. that the most numerous species were really those of middling abundance. The fit of many data sets to the logarithmic series he explained as due to insufficient sampling, which meant that the sparsest species were rarely sampled. Both models recognize that there are many relatively rare species in typical plant or animal data sets. As small populations are particularly susceptible to chance fluctuations of environment, it is to be expected that much real turnover in communities will involve these rarer species (Preston, 1962a,b; MacArthur & Wilson, 1963, 1967). Moreover, Preston's analyses point to the problem of pseudoturnover, whereby incompleteness of surveys of flora or fauna will inevitably generate some artificial extinction/re-immigration of species that are present throughout but which occur at low frequency/density and thus are missed by some surveys.

It is difficult to assess what proportion of a flora is actually recorded in each survey. Nilsson & Nilsson (1985) conducted a test of pseudoturnover on islands in Lake Möklen, southern Sweden, using standardized search techniques by two teams. The best they attained in a single survey was 79% of the flora. Their study provides no basis for estimating survey efficiency in other studies, but does point to the potential importance of survey inefficiency. Varying survey interval can also be problematic, as real turnover might be underestimated by surveys separated by many years due to species coming and going (or vice versa) between surveys, a phenomenon termed cryptoturnover (Simberloff, 1976; see Diamond & May, 1977). If it is not possible to separate real turnover from measurement error, then our ability to discriminate between competing island biogeographical hypotheses (including the ETIB) is seriously undermined.

The basic ETIB model of MacArthur & Wilson (1963, 1967) provides an essentially stochastic model of biological processes on islands, in which the properties of individual species get little attention, and turnover is regarded as homogeneous (*sensu* Rey, 1985). However, both the originators of

the ETIB and others have recognized structure in extinction and turnover (e.g. reviews in Whittaker, 1998; Brown & Lomolino, 2000). In their analysis of the Krakatau flora 1883–1983, Whittaker *et al.* (1989), although stressing limitations of their data, attributed much of the extinction in the species lists to: (1) successional processes, (2) habitat disturbance or loss additional to those driven by succession, and (3) the loss of ephemeral populations. In addition, rudimentary analysis of the patterns of persistence and loss demonstrated that extinction probability varied in relation to the primary dispersal mechanism of the species, and whether the species was originally found on one, two or three islands. New survey data, collected from Krakatau between 1989 and 1994 allow us to re-examine extinction rates and patterns, and thus to 'test' whether the conclusions drawn by Whittaker *et al.* (1989) still appear reasonable. It should be noted that ecological and especially successional structure can also be identified in the immigration/colonization data (see e.g. Whittaker *et al.*, 1989, 1997; Whittaker & Jones, 1994a, b), but this need not be considered further here.

In the light of the above, we have two aims herein. First, we examine the reliability of estimates of turnover, more specifically of its extinction component, from general floristic surveys of these moderate-to-large islands. Second, we examine in closer detail than hitherto attempted the structural features in the extinction data, with reference both to previous empirical analyses and to the theoretical expectations outlined above.

## STUDY AREA

In 1883, Krakatau (6°06' S, 105°25' E) consisted of three islands arranged in a caldera, located in the Sunda Strait between Java and Sumatra. Two-thirds of the main island (now named Rakata) was destroyed (totally) in the eruptions that culminated on 27th August of that year. Each island was entirely stripped of all vegetation and greatly re-shaped. All three islands gained extensive areas of new land resulting from the emplacement of pyroclastic deposits, which were typically of the order of 60–80 m depth in the lowlands (Docters van Leeuwen, 1936). No evidence for any surviving plant or animal life was found shortly after the eruptions, and the first signs of plant life, a 'few blades of grass', were detected in September 1884 (Whittaker *et al.*, 1989). While it is conceivable that some viable propagules were later uncovered by erosion of the ash mantle (Whittaker *et al.*, 1995), there is no evidence of survival, and indeed the densest populations of early plant colonists were located on *terra nova*. The islands can be said to have been as near completely sterilized as makes no practical difference (accounts in: Docters van Leeuwen, 1936; Simkin & Fiske, 1983; Whittaker *et al.*, 1989; Thornton, 1996). For the next half century, the group consisted of Rakata (now *c.* 17 km<sup>2</sup> in area, maximum elevation *c.* 730 m a.s.l.), Sertung (13 km<sup>2</sup>, 182 m a.s.l.) and Panjang (3 km<sup>2</sup>, 142 m a.s.l.).

These dramatic events initiated a primary successional sequence across the whole caldera, from open habitat, through pioneering fern, herb and grassland communities, which in

turn were gradually replaced by shrub and tree communities (Ernst, 1908; Docters van Leeuwen, 1936; Whittaker *et al.*, 1989). By the end of the 1920s, forest closure had occurred throughout most of each island, with corresponding reductions in area available to the pioneering assemblages. The succession to forest appears to have been simplest and most rapidly attained on the coastal fringe, involving mainly sea-dispersed species. Colonists are assumed to have been drawn preferentially from Java and Sumatra, *c.* 40 km away, and also from nearby islands in the Sunda Straits (see Whittaker & Jones, 1994a, table 1), many of which were, however, also badly impacted by the 1883 Krakatau eruptions.

Volcanic activity recommenced at the end of the 1920s and a new island, Anak Krakatau, established in the caldera centre in 1930. It has remained intermittently active ever since, periodically disturbing the forests of Panjang and Sertung islands, but not directly impacting on Rakata (Whittaker *et al.*, 1992; Schmitt & Whittaker, 1998). These events have complicated the successional sequence and, it has been suggested, might have served to depress the colonization curve for Panjang and Sertung (Whittaker *et al.*, 1989).

It is of some relevance to the present analyses that the geomorphology of the islands has been subject to continuous, rapid change. The first months and years after the 1883 eruptions saw extremely rapid dissection of the tephra covering the island interiors, forming steep-sided gully systems. None now contain permanent watercourses but they remain dynamic features, subject to temporary flows, landslips and other erosional/depositional processes. Coastal erosion has been dramatic, especially in the early decades, as the unconsolidated pyroclastic deposits forming the majority of the coastline provided little resistance to wave action (Bird & Rosengren, 1984). The combination of sediment transport from the gully system and coastal cliff erosion provided large sediment volumes, contributing to dynamic depositional features in sheltered locations, most notably a lengthy spit at one end of Sertung. This feature was a focus of early plant collecting on Sertung (account in Docters van Leeuwen, 1936) and it has evolved constantly in form and size. In the early 20th century it contained two small lagoons of brackish water, which subsequently disappeared along with a small number of localized plant species (Whittaker *et al.*, 1989). Between 1992 and 1997 we witnessed the breaching and destruction of the Sertung spit.

## MATERIALS AND METHODS

### Surveys

Surveys of the flora have been carried out intermittently throughout the post-1883 period by numerous individuals and teams. None can be considered complete, and there has been no standardization of survey efforts. The islands are large, deeply dissected, and each contain some extremely difficult terrain, such that some substantial areas, especially in the centre of Sertung island, have tended to be neglected by researchers, and particular pockets doubtless exist that have never been crossed by a collector. Rakata, with a maximum

elevation over 730 m, is also particularly steep in much of its interior, adding considerably to the effort needed to survey it. Unsurprisingly, some species recorded from Krakatau have been observed to have very small, localized populations (e.g. see Docters van Leeuwen, 1936) increasing their likelihood of being overlooked. Fortunately, the relative poverty of the flora, especially early on, means that botanists have been able to hone their search towards any rare species occurring within stands dominated by a few common species.

Over the past century, voucher specimens have been deposited at Herbarium Bogoriense, Kew, Leiden, and elsewhere; but by no means can all records in our database be traced to vouchers. Fortunately, the botanical expertise built up by the principal collectors means that taxonomic problems are limited. Moreover, previous accounts have paid considerable attention to the validity of each species' record (e.g. Ernst, 1908; Docters van Leeuwen, 1936; van Borssum Waalkes, 1960; Flenley & Richards, 1982; Bush *et al.*, 1986).

Collecting effort over the first 50 years was greatest on the largest island and least on the smallest (Table 1). Collections were made in 1886, 1896/97, 1905/06 and 1908 by various collectors, but foremost among the early botanists was W. M. Docters van Leeuwen, who spent some 54 days collecting within the period 1919 to 1932. His records were supplemented by a few additional species collected by K. B. Boedijn in 1933/34. Docters van Leeuwen's (1936) detailed synthesis of the survey data for the first 50 years conveniently allows us to subdivide the data series into 1883–1934 and post-1934 periods. Between 1934 and 1979 only one survey was conducted, by van Borssum Waalkes (1960) in 1951/52. His data are both temporally isolated and far from complete (Whittaker *et al.*, 1989) and are therefore disregarded from the present analysis. The 1979–83 data were previously collated by Whittaker *et al.* (1989) to provide the contemporary state of the flora for comparative purposes. Our subsequent surveys, between 1989 and 1994, add to those data, but were not designed as full stand-alone surveys. The search for addi-

tions to our previous species lists was undertaken as a low-key activity alongside other ecological studies, and generally focused on species either new to the islands or not recently recorded. Hence, we lump all data for the 16-year period 1979–94 as the contemporary flora with which to compare the 1883–1934 flora. We continued working on the islands in 1995–97, but with the exception of some revisions to data for the genus *Ficus* (N. A. Mawdsley, S. G. Compton & R. J. Whittaker, unpublished data) have not attempted to work up data for this period.

### Attributes used in analyses

In analysing the structural features of the floristic data, each species has been assigned to a category for each of: phylogenetic group, dispersal type, growth form, island combination, abundance, population status and habitat exclusivity. Species were allocated to phylogenetic groups to test for any effects of taxonomic selectivity and/or non-independence in the data (see e.g. Harvey *et al.*, 1996). For angiosperms ( $n = 262$  species), this was done using the latest ordinal classification published by the Angiosperm Phylogeny Group (APG, 1998). For the rest of the flora ( $n = 63$  species), the Tree of Life (<http://phylogeny.arizona.edu/tree/>; D. R. Maddison) was used. Three different grouping levels were assessed in the analyses, varying from six categories (pteridophytes, monocots, rosids, asterids, other eudicots, and other spermatophytes) to 41 categories (order-level classification). This form of quantification of taxonomic relatedness was considered a reasonable way to investigate the importance of phylogenetic effects given that the analysis involves several multi-state categorical predictors and a binary response variable (presence/absence).

The other variables used were based primarily on information from the 1884–1934 period, supplemented by subsequent revisions to the species lists (Flenley & Richards, 1982; Bush *et al.*, 1986; Whittaker *et al.*, 1989; see the latter for nomenclatural authorities). The key data source was Docters van Leeuwen's (1936) monograph, which provides descriptions of the vegetation from all expeditions up to 1934. He also provides separate accounts for each species, typically describing dispersal agent, habitat, where and when a species was first found, and if and where it subsequently spread.

The following primary dispersal categories were used: human-dispersed, sea-dispersed, animal-dispersed and wind-dispersed seed plants, and ferns and their allies (wind-dispersed spores) (as used in Whittaker *et al.*, 1989, 1997). These reflect the most probable means of long-distance dispersal to the islands, based on both direct observation and literature review (e.g. Ridley, 1930; Docters van Leeuwen, 1936; van der Pijl, 1982). Diplochores (Whittaker & Jones, 1994a) were assigned to just their primary mode of dispersal. Growth form categories used were: tree, shrub, climber/liana, nonepiphytic herb and epiphytic herb.

Allocation to an island combination was on the basis that any record for an island within the 1883–1934 period indicates presence for that period. Two variables were derived from these island combinations: (1) the number of islands occupied

**Table 1** Approximate number of days or weeks involving plant collection from Rakata, Sertung and Panjang islands. Fuller details up to 1983 are given by Whittaker *et al.* (1989). Quantification of sampling effort in the 1989–94 period is problematic as members of our team have visited the islands for at least a few weeks each year and for varied purposes. Partomihardjo, in particular, has undertaken general floristic survey and/or purposeful survey of previously poorly explored areas on numerous occasions, amounting to many weeks on the archipelago. However, much of our time on the islands has been devoted to other tasks. This practice continued in 1995–97, more than doubling the post-1983 survey time, but as the plant records used here pre-date 1995, our estimate of recent survey effort is for 1989–94 only.

Dates	Rakata	Sertung	Panjang
1883–1934	42 days	17 days	11 days
1951	9 days	< 1 day	< 1 day
1979–83	29 days	20 days	10 days
1989–94	20 weeks	5 weeks	9 weeks

by each species, and (2) presence or absence on the island of Rakata. To provide an alternative measure of distribution for that period, species were also assigned to one of the following abundance categories: widespread and abundant, widespread and rare, localized and abundant, localized and rare, and singleton record. An additional population status categorization was devised, based on the trajectory of the species' populations for the end of Docters van Leeuwen's survey period, i.e. the end of the 1920s/beginning of the 1930s. The categories were: considered extinct by 1934; declining; no trend/no information; and increasing. Each species was also categorized according to the habitat(s) in which it was found in 1883–1934. This classification was necessarily crude in nature, being restricted to strand-line habitats (beach to just behind the strand-bank), *Cyrtandra* wilderness (an early successional high-altitude vegetation type on Rakata), anthropogenic habitats and 'none/other'. Most species were placed in the final category. To ensure objectivity, attribution to these newly created abundance, population status and habitat classes was undertaken by R. Field, who had not then undertaken any analysis of turnover in the Krakatau flora.

For the subset of species classified extinct as of 1979–94, two further categorizations were made. First, species were classed as either resident (i.e. evidence of an established or widespread breeding population) or ephemeral (evidence pointing against establishment of a breeding population) within the 1883–1934 period. Second, species were classed according to the likely driving force of the extinction: (1) succession, (2) disturbance or loss of habitats other than successional, and (3) uncertain cause. These classifications were based once again on the descriptive accounts provided by Docters van Leeuwen (1936).

### Statistical analyses

All data were added to a database of the Krakatau flora maintained by the first author (following Whittaker *et al.*, 1989, 1997). The analyses presented here are based on a (minimal) number of assumptions. The most important of these are that: (1) the survey data accurately reflect the distribution of the species in the archipelago, and that (2) turnover (and especially extinction) *within* each collation period can be disregarded. The latter assumption we know to be flawed for 1883–1934, and hence we also examine evidence for extinctions within that period.

The structural features of the data are analysed for both univariate and multivariate effects. To address the possibility that some of the univariate effects are consequences of the influences of other factors, and to investigate interactions between explanatory variables, a number of multiple analyses of variance and covariance were performed, using binary logistic analysis (see Crawley, 1993). All analyses were performed on each of two binary response variables: presence or absence of each species recorded in 1883–1934, in (1) 1979–83 and (2) 1979–94. These analyses were performed in S-Plus version 4.5, using the binomial distribution as the error distribution, and the logit link function.  $\chi^2$  tests were performed to determine significance.

Modelling was performed by stepwise model simplification from maximal models, which included both the main effects and interactions between the explanatory variables (Crawley, 1993). Different maximal models were examined, incorporating alternative measures for some of the variables. For example, only one of the three phylogeny variables was allowed into any one model. Other substitutions explored included: (1) fitting some variables that were rankable (such as number of islands occupied, population status and abundance) as covariates instead of factors; (2) replacing island combination (a 7-level factor) with number of islands (a 3-level factor) and presence/absence on Rakata; and (3) replacing the 5-level factor of abundance with a 3-level one (single, localized and widespread). In each case, the validity of the substitution was tested using the change in explained deviance and the change in degrees of freedom, in a  $\chi^2$  test. For each maximal model tried, both a 5% minimal adequate model (MAM) and, if different, a 1% MAM were obtained. A MAM is a model in which all remaining terms are significant at the given probability level, when tested by deletion from the model (Crawley, 1993).

The aim of this approach was to gain as robust a picture as possible of the factors potentially influencing the probability of extinction in the Krakatau plants. A number of models resulted, and all were considered when evaluating the influences on extinction. In addition, all models generated for the 1979–83 data were fitted to the 1979–94 data, and vice versa, to examine further the similarities and differences between the two data sets. To supplement these analyses, stepwise model building techniques were also attempted, and the resulting models compared with those obtained via model simplification. In practice, no increase in explanatory power or insight resulted from model building, thus the results presented are all derived from the preferred model simplification procedure (Crawley, 1993).

## RESULTS

### Estimates of turnover rate

Our first aim was to examine the reliability of extinction rate estimates when sampling effort was extended from a 4-year period encompassing three discrete surveys, to a 15-year period. In calculating extinction rates, convention dictates that a species should have established a population on an island in the first place (Lynch & Johnson, 1974). In practice, this is often unknown, and in such cases researchers have sometimes used the criterion of a species being recorded on two or more separate occasions as a guide to likely breeding status, and residency by, that species (see Thornton *et al.*, 1990, for an evaluation for Krakatau birds). Accordingly, in this section of the results we present analyses both for the full set of 1883–1934 records (ALL1883–1934), and for a subset from which singleton records (species found once, typically as one individual, or a small group of juveniles) are excluded (MULT1883–1934, i.e. multiple records). The range of extinction rates resulting is from 0.873% per annum using ALL1883–1934 records and the 1979–83 sample, down

**Table 2** Estimates of extinction for the Krakatau island group excluding Anak Krakatau. ALL1883–1934 = all higher plant species recorded at least once on any combination of Rakata, Sertung and Panjang islands. MULT1883–1934 = multiple records, being the subset of ALL1883–1934 species excluding those species only recorded once (as a single of a few individuals) between 1883 and 1934 (as documented by Docters van Leeuwen, 1936). Figures for percentage extinction per year calculated using 1934–83 (i.e. 49 years) as the interval.

Datum for flora	1979–83	1979–94
ALL1883–1934, <i>n</i> = 325 species		
Number present	186	231
Number extinct	139	94
Per cent extinct	42.8%	28.9%
Per cent extinct per year	0.873%	0.590%
MULT1883–1934, <i>n</i> = 264 species		
Number present	167	202
Number extinct	97	62
Per cent extinct	36.7%	23.5%
Per cent extinct per year	0.749%	0.480%

to 0.480% per annum using MULT1883–1934 records and the 1979–94 sample (Table 2). Our choice of 1934 as time 1 and 1983 as time 2 for these calculations of extinction rate is arbitrary, and carries with it the assumption that all species present within each period were also present on those particular dates. This is particularly unrealistic with respect to the 1934 datum, although it is the obvious date to use for time 1. For time 2, a case could be made for any date between 1979 and 1994, providing scope for a range in extinction rates for the data in Table 2 from 0.951% per annum down to 0.391% per annum depending on choice of survey, survey interval for rate calculations, and between the full 1883–1934 data set and the subset for multiple records.

Of the 1883–1934 species, 61 were denoted as singleton records. Of these, 32 have not been recorded since, and half of these were considered by Docters van Leeuwen (1936) to be extinct by 1934. This might be taken to indicate that singleton records should be screened out from the calculations altogether, but it should also be noted that 29 of the singletons *have* been recorded in 1979–94. Indeed, these records include the first observations of some species which had recently colonized and which are now quite common (e.g. *Antidesma montanum*).

In simple terms, the addition of the post-1983 records to the analysis has resulted in about one third of the species previously categorized as extinct being accounted for as present (Table 2). This applies whether all or only multiple 1883–1934 records are used in analysis. Nonetheless, using our (thus far) most conservative value for extinction, some 24% of the 1883–1934 flora remains categorized as extinct. However, the reduction in ‘false’ extinctions (i.e. pseudoturnover) in these revised extinction estimates, does involve an increased risk of cryptoturnover, i.e. the error of failing to recognize real turnover when it has occurred. This begs the question as

to what the real rates of extinction may be and shows that simple analyses of ‘headline’ rates in an unreplicated system are of limited power. The next step in analysis is therefore to examine structural features within the extinction data, for which we revert to using ALL1883–1934 data.

### Analysis of structural features in extinction

Unless otherwise indicated, each of the main univariate effects described in the results (e.g. abundance and number of islands) is highly significant:  $\text{pr}(\chi^2) < 0.0005$ .

#### Phylogenetic relatedness

The most striking finding concerning the ‘effects’ of the phylogenetic groupings on the probability of extinction is that the limited significance attributable to them in relation to the 1979–83 data set was lost when the more complete 1979–94 data set was analysed. Table 3 shows the numbers and proportions going extinct in both data sets, in each group of the 6-level categorization (the broadest of the groupings). When fitted on its own to the 1979–83 data, this 6-level phylogeny variable is marginally significant ( $\text{pr}(\chi^2) = 0.033$ ). This effect is attributable to the two ‘other’ categories (i.e. other eudicots and other spermatophytes): when these were combined into one category, the effect became insignificant ( $\text{pr}(\chi^2) = 0.765$ ). For the 1979–83 data, the 9-level phylogeny variable was not significant ( $\text{pr}(\chi^2) = 0.100$ ), but the 41-level (order-level) variable was ( $\text{pr}(\chi^2) = 0.0057$ ). Some of the multiple-term minimal adequate models (considered more fully below) obtained from binary logistic analysis included the 6-level phylogeny factor; in each case its significance can be attributed to the ‘other’ categories. When the more complete 1979–94 data set was used, none of the phylogeny variables were significant, whether fitted on their own or in multiple-term models. When fitted singly,  $\text{pr}(\chi^2)$  values for the 6-, 9- and 41-level variables were 0.264 (or 0.872 if the ‘other’ categories are combined), 0.500 and 0.145, respectively. This indicates that structural features identified below for the 1979–94 data set can reasonably be considered to be independent of taxonomic artefacts.

#### Dispersal categories

Figure 1 shows how the proportion of the ALL1883–1934 data set categorized as extinct diminished with the addition of the post-1983 records. In respect of primary dispersal mode, the proportion of species missing in the 1979–83 collation diminished from human-dispersed, to wind-dispersed (flowering plants), to ferns, to sea-dispersed to animal-dispersal categories. The reduction in extinctions when using the 1979–94 data was roughly proportional across these categories, and the same ordering was preserved, except that fern losses were reduced to marginally lower than those of the sea-dispersal category. The species introduced by people up to 1934 were concentrated in two locations (Docters van Leeuwen, 1936; Whittaker *et al.*, 1989). First, c. 1916–22, in an area of south-east Rakata subsequently lost to coastal erosion, several species were found in association with a jetty and temporary dwelling established as a base for a pumice collecting operation. Second, a small vulcanological survey team was stationed on

**Table 3** Persistence of species in relation to phylogenetic grouping. If the two 'other' groups are combined, the proportions lost for the resulting group are 43.5% for 1979–83 and 26.1% for 1979–94.

Phylogenetic group	1979–83 data			1979–94 data		
	Lost ( <i>n</i> )	Present ( <i>n</i> )	Lost (%)	Lost ( <i>n</i> )	Present ( <i>n</i> )	Lost (%)
Pteridophytes	26	35	42.6	16	45	26.2
Monocots	38	43	46.9	27	54	33.3
Rosids	36	60	37.5	26	70	27.1
Asterids	29	35	45.3	19	45	29.7
Other eudicots	10	6	62.5	6	10	37.5
Other spermatophytes	0	7	0	0	7	0

'Other eudicots' group:

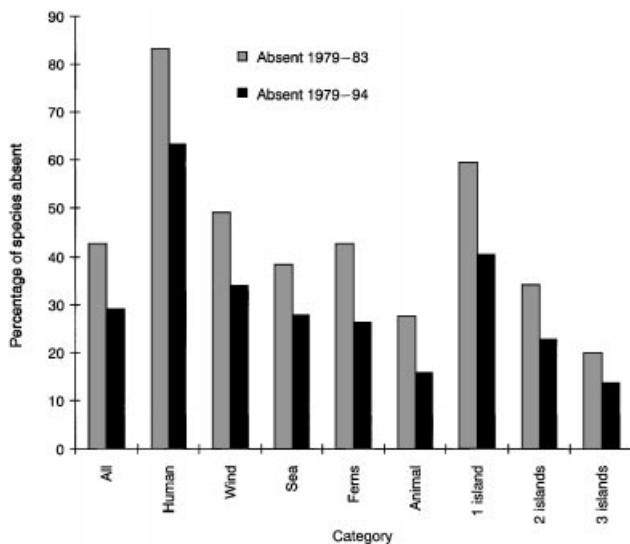
Lost: *Boerhavia erecta*, *Opuntia elatior*, *Cyathula prostrata*, *Kalanchoe pinnata*, *Nepenthes* sp., *Leea aequata*.

Rediscovered during 1984–94: *Portulaca oleracea*, *Pericampylus glaucus*, *Ximenia americana*, *Sesuvium portulacastrum*.

Persisting: *Antigonon leptopus*, *Tetrastigma lanceolarium*, *Leea sambucina*, *Cyclea barbata*, *Tinospora glabra*, *Cayratia trifolia*.

'Other Spermatophyte' group (all persisting):

*Piper blumei*, *Gnetum gnemon*, *Pothomorphe subpeltata*, *Aristolochia tagala*, *Cycas rumphii*, *Hernandia peltata*, *Cassytha filiformis*.



**Figure 1** Proportion of extinctions from the 1883–1934 Krakatau flora as calculated using the 1979–83 collation and the 1979–94 collation to represent the contemporary flora. The 1883–1934 flora includes all species originally occurring on one or more of Rakata, Sertung and Panjang Islands. Extinction is from the group as a whole. The subsets represent (1) primary dispersal categories human-, wind-, sea- and animal-dispersed spermatophytes, and ferns (all wind-dispersed), and (2) island combinations on which the species were recorded between 1883 and 1934.

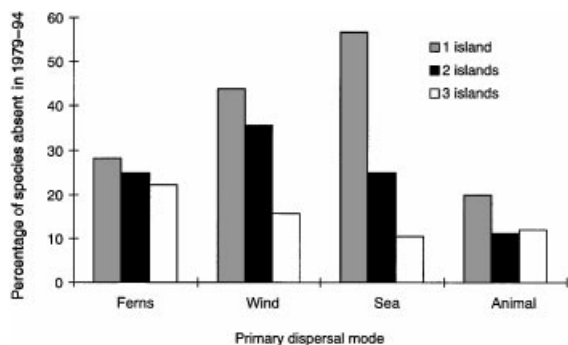
Panjang between 1928 and 1931, and a number of weed species were found associated with their camp. Most introduced species in both locations were shaded out soon after abandonment of the dwellings.

#### Island combinations

Given three islands, there are seven combinations of islands on which species were recorded in 1883–1934, allowing a number of approaches to modelling. Substituting number of islands (3 levels) and presence/absence on Rakata (2 levels) for island combination (7 levels) resulted in an insignificant reduction in deviance explained ( $\text{pr}(\chi^2) > 0.05$ ), regardless of model complexity. The further simplification of substituting number of islands (3 levels) for island combination was also generally justifiable. Thus, the simplest means of assessing the distribution of a species for 1883–1934 is the number of islands on which it was recorded. [Which islands species persist on is not examined in these analyses]. As expected, the proportion of species lost from the 1883–1934 flora diminishes from those found originally on one island (using 1979–94 data, 40% extinct), to two islands (23% extinct), to three islands (14%) (Fig. 1). Consistent with this finding, the simplification of the 3-level factor of number of islands to a covariate was found to be statistically acceptable. This suggests that the statistical effect of island combination on extinction probability is largely reducible to the influence of how widespread each species was in the initial time period. Analysing the data instead in relation to presence/absence on Rakata in 1883–1934, we found that those present on Rakata were more likely to persist, using the 1979–94 data, than those not found on Rakata, but that this effect ( $\text{pr}(\chi^2) = 0.0057$ ) was weaker than that for number of islands.

#### Dispersal/island interactions

A pattern clearly exists of varying proportions of losses for different dispersal groups and for different island combinations, and the interrelation of these categories is illustrated using the 1979–94 data in Fig. 2. First, using ALL1883–1934 data, the ferns show almost exactly the same proportion of losses (26.2%) to those of the flowering plants (28.9%, Table 2), but unlike the flowering plants, ferns have been



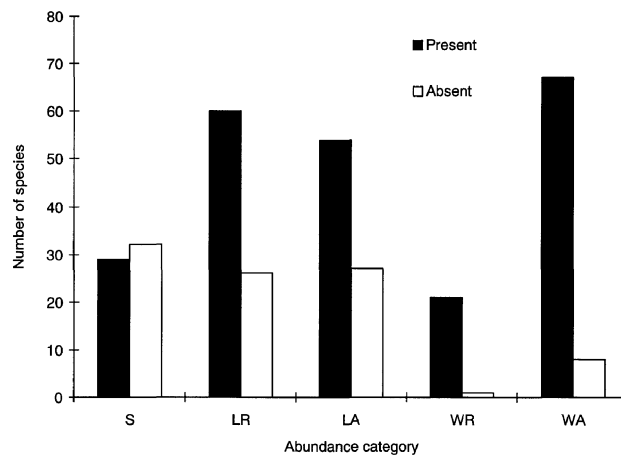
**Figure 2** Losses from the 1883–1934 Krakatau flora (Rakata, Sertung and Panjang) by island and dispersal category combinations using the 1979–94 collation to represent the contemporary flora. The human-introduced species group is not illustrated here as all species occurred on one island only. See Figure 1 for overall rates for this and other categories.

lost in similar proportions irrespective of how many islands they were originally recorded from. Second, the tendency for greater losses amongst species found on only one island is found for each dispersal category of flowering plants. Third, this trend is strongest for sea-dispersed species: of those originally found on only one island, 56.7% have been lost; while of those known from all three islands, just 10.4% have been lost, which is marginally the lowest figure of any category. The interaction between these two variables was significant for the 1979–83 data set ( $\text{pr}(\chi^2) = 0.0145$  with only these variables fitted), but not for the more complete 1979–94 data set. The main effects are both significant when fitted together and for either data set ( $\text{pr}(\chi^2) < 0.01$  in each case).

#### Abundance

Considering the abundance categories shown in Fig. 3, singleton records show 53% losses, those present as localized populations show losses of 32% (or 38% including the singletons), and those classed as widespread exhibit losses of only 9%. This result is consistent with the pattern shown for the number of islands occupied, but differs in that it represents a finer spatial scale of analysis. As with island combinations, simplification of the abundance variable to a covariate with values from 1 (singleton) to 5 (widespread abundant), in the order shown in Fig. 3, was statistically justified. Simplification from 5 to 3 levels (1 = singleton, 2 = localized, 3 = widespread), was also statistically justified, and interestingly increased the deviance explained (with no change in degrees of freedom, thus  $\text{pr}(\chi^2) = 0$ ). This may have been because of the low extinction rate of the small sample of 'widespread rare' species (Fig. 3).

Of the 32 species known only from singleton records and not found in 1979–94, 10 were sea-dispersed taxa: *Opuntia elatior*, *Intsia amboinensis*, *Tristellateia australasiae*, *Cyperus odoratus*, *Spondias novoguineensis*, *Ochrosia oppositifolia*, *Crotalaria mucronata*, *Mucuna pruriens*, *Xylocarpus moluccensis* and *Centella asiatica*. Three were ferns and 10 were wind-dispersed spermatophytes, eight of which were orchids. Five of these orchids were not fully determined to species in



**Figure 3** Fate, c. 1979–94, of the 1883–1934 Krakatau flora (Rakata, Sertung and Panjang) according to initial abundance as determined from descriptive accounts in Docters van Leeuwen (1936). Categories are as follows: S, singleton record (one or a few individuals); LR, localized and rare; LA, localized but abundant; WR, widespread but rare (i.e. low density); WA, widespread and abundant.

the 1883–1934 data, but were included in the tabulation of the flora for completeness and in the analysis of extinction because they were, for instance, known to genus where no member of that genus now occurs. Similarly, one of the other two records of this wind-dispersed group, *Nepenthes* sp., was also a poorly supported record for which no voucher was collected. Six were introduced by people, including a lone specimen of *Citrus* sp. observed once only on the path towards the summit and considered to have been the product of a seed discarded by a previous expedition group. The other five were *Cyperus cylindrostachys* (syn. *C. cyperoides*), *C. kyllingia*, *Stemodia verticillata*, *Kalanchoe pinnata*, *Ricinus communis* and *Boesenbergia pandurata*. Only three singletons now considered extinct were classed as animal-dispersed: *Antidesma bunius*, *Digitaria rhopalotricha* (a rather dubious dispersal attribution; Docters van Leeuwen, 1936) and *Ficus asperiuscula*. Of these, *F. asperiuscula* was in fact re-discovered on both Rakata and Panjang in 1995 by N. A. Mawdsley (N. A. Mawdsley, S. G. Compton & R. J. Whittaker, unpublished data). Arguably, all of the records that were not determined to species might properly have been excluded from the analysis. In total, this would reduce the number of species in the 1883–1934 data by eight, from 325 to 317, and the number of extinctions by the same number.

Of the species originally known from singleton records that persist on the islands, some are now common, for example, *Antidesma montanum*, a small animal-dispersed tree which is now extremely abundant on each island, and *Gnetum gnemon*, which although dispersed within the islands by birds is considered to have been originally introduced by people. Several of these species had probably only recently colonized at the end of the 1883–1934 period, e.g. *A. montanum*, *Sterculia foetida*, *Solanum torvum*, and *Aeschynanthus radicans*, all of

**Table 4** Persistence of species in relation to population status as described by Docters van Leeuwen (1936) for the end of the 1920s/ beginning of the 1930s for both data sets. Those classed as 'no change/no data' consist primarily of species showing relatively little change in abundance, although some with no data may have to some extent been declining or increasing in population size.

Status	1979–83 data			1979–94 data		
	Lost ( <i>n</i> )	Present ( <i>n</i> )	Lost (%)	Lost ( <i>n</i> )	Present ( <i>n</i> )	Lost (%)
Lost	45	15	75.0	36	24	60.0
Declining	14	18	43.8	8	24	25.0
No change/no data	65	113	36.5	42	136	23.6
Increasing	15	40	27.3	8	47	14.5

**Table 5** Persistence of species in relation to (a) habitat exclusivity grouping for the period 1883–1934, and (b) growth form. In (a), the 'none/other' category consists mainly of species that were not specific to any one habitat, but also contains one or two species that were specific to other habitats (such as *Saccharum* wilderness (tall grassland) found on Rakata during that time); and it may contain species that were specific to certain habitats, but which were not recorded as such by Docters van Leeuwen (1936). In (b), the two herb categories include pteridophytes (ferns and their allies).

(a)	1979–83 data			1979–94 data		
	Lost ( <i>n</i> )	Present ( <i>n</i> )	Lost (%)	Lost ( <i>n</i> )	Present ( <i>n</i> )	Lost (%)
Exclusivity group						
Beach/strandbank	16	32	33.3	10	38	20.8
<i>Cyrtandra</i> wilderness	11	14	44.0	10	15	40.0
Anthropogenic habitat	24	6	80.0	19	11	63.3
None/other	88	134	39.6	55	167	24.8
(b)	1979–83 data			1979–94 data		
	Lost ( <i>n</i> )	Present ( <i>n</i> )	Lost (%)	Lost ( <i>n</i> )	Present ( <i>n</i> )	Lost (%)
Growth form						
Tree	22	49	31.0	15	56	21.1
Shrub	13	24	35.1	9	28	24.3
Climber	13	35	27.1	9	39	18.8
Non-epiphytic herb	72	53	57.6	52	73	41.6
Epiphytic herb	19	25	43.2	9	35	20.4

which were first recorded on Panjang between 1929 and 1934 (Docters van Leeuwen, 1936).

#### Population status 1929–34

Although it should be noted that we were unable to classify the majority of the species with certainty to the classes for population status *c.* 1929–34, the data show a highly significant trend of increasing likelihood of persistence in the order: species considered already lost, those classed as declining, those with little change or no information, and those described as increasing (Table 4). It is likely that species whose population statuses were not referred to by Docters van Leeuwen (1936) were mostly stable or gradually increasing in population size. This suggestion is supported by the fact that if population status is fitted as a linear covariate predicting extinction probability, there is a non-significant ( $\text{pr}(\chi^2) > 0.05$ ) reduction in deviance explained, whether this variable is fitted singly, or in combination with other terms. Of those classed as extinct by 1934, only one (*Blumea balsamifera*) was ever widespread in distribution. Indeed, 29 were singleton records, a category highly likely to have included several species that never established breeding populations at the time. However, of these 29 species, 13 were found again between 1979 and 1994. In such cases it is difficult to distinguish between the persistence of species at low density and their failure and subsequent re-immigration.

#### Habitat exclusivity and growth form

Table 5a shows that species confined in 1883–1934 to anthropogenic habitats, and to a lesser extent those confined to the *Cyrtandra* wilderness, were more likely to go extinct than other species. Many of the species confined to these habitats, especially the anthropogenic habitats, were non-epiphytic herbs, which were also disproportionately lost from the archipelago (Table 5b). For this reason, these two variables are to some extent picking up the same signal. The dispersal categorization also reflects this effect, with a disproportionately high percentage of human-introduced species going extinct (Fig. 1). The habitat exclusivity variable, although significant when fitted on its own ( $\text{pr}(\chi^2) = 0.00016$  for both data sets), explains very little of the deviance. When other variables were fitted with it, the effect was no longer significant—indicating that other variables better account for the trends seen in Table 5. It is a similar story for growth form, which is weakly significant as a univariate model ( $\text{pr}(\chi^2) = 0.0030$ ), except that some of the multi-term models contain this variable as a (usually marginally) significant term. Dispersal type appears to account for most of the pattern picked up by both habitat exclusivity and growth form, as well as accounting for variation not picked up by these two variables. Table 5 also indicates that herbs, especially epiphytic species, were under-sampled in the 1979–83 data, in comparison with the rest of the flora.

**Table 6** The preferred models of factors affecting the probability of extinction of plant species on Krakatau, selected on the grounds of simplicity and explanatory power from the many alternative minimal adequate models (MAMs) obtained by stepwise model simplification. '1983 preferred' & '1994 preferred' are the preferred MAMs for the 1979–83 and 1979–94 data, respectively. '1983 main preferred' is the preferred MAM for the 1979–1983 data when only main effects (and not interactions between variables) are considered. In each case, all terms within the models are significant at the 1% level for the data set for which they were originally generated. The terms in the models are: number of islands fitted as a covariate, dispersal type (i.e. sea, human, animal, wind, ferns), population status fitted as a covariate, and abundance fitted as a covariate (using 1 = single occurrence, 2 = localized, 3 = widespread). A colon between terms indicates that the interaction between these terms is fitted, as well as their main effects. 'Df' is the degrees of freedom used by the model; null d.f. in each case is 324. Note that the model '1983 preferred' has only 9 d.f. instead of 10 because the human dispersal: number of islands interaction parameter was intrinsically aliased (each human dispersed species occurred on only one island). The last two columns show the amount of deviance explained by the models in relation to the 1979–83 data and the 1979–94 data, respectively. Null deviance for the 1979–83 data set is 443.72, and that for the 1979–94 data set is 390.95.

Minimum adequate model (MAM)	Terms in model	d.f.	Deviance explained	
			1979–83 data set	1979–94 data set
1983 preferred	No. islands (cov.), dispersal, population status (cov.), no. islands (cov.): dispersal	9	86.10	58.82
1983 main effects preferred	No. islands (cov.), population status (cov.)	2	63.69	44.85
1994 preferred	Abundance (cov.), population status (cov.)	2	52.12	49.46

#### Multi-term models

Thus far we have mostly considered each variable individually. The development of multi-term models using binary logistic analyses of variance and covariance allowed interactions between variables to be explored and the key explanatory variables to be identified. In extensive exploratory analyses (not illustrated), two notable differences between the results for the 1979–83 and the 1979–94 data sets emerged. First, phylogenetic variables were in many cases (but not always) significant in the minimal adequate models (MAMs) generated from the 1979–83 data, but were not significant in any of those generated from the more complete 1979–94 data set. Second, interaction effects featured at the 1% level only for the 1979–83 data. Thus, in general, much of the apparent complexity in extinction as judged *c.* 1979–83 disappeared when the more complete 1979–94 data set was used, i.e. improved sampling reduced the 'pattern' (bias) in the data.

The criteria used in generating the MAMs were purely statistical (tests of significance using the  $\chi^2$  statistic). However, in evaluating the MAMs, simple models (number of terms and degrees of freedom used) were regarded as preferable to models of greater complexity, even where the latter accounted for slightly more of the deviance. Of the alternative MAMs produced, the three best models according to these criteria, are presented in Table 6. To illustrate the degree of similarity between the two (overlapping) data sets, the preferred MAMs for each data set were also run for the alternate data set. In each case, all terms within the models are significant at the 1% level for the data set for which they were originally generated (indicated in the model name). For the 1979–83 data, the simplest model (2 d.f.) is that considering only main effects, whilst that involving interactions between variables accounts for more of the variation at the expense of increasing complexity (9 d.f.). For the 1979–94 data set, fewer alternative MAMs were produced, and at the 1% significance level

none included interaction terms, hence only one preferred model for the 1979–94 data set is given in Table 6. While each of the three models is essentially telling a similar story, there is a switch between the 1979–83 and 1979–94 preferred MAMs in the variables representing distribution within the archipelago: from number of islands (fitted as a covariate) in the former, to the three-point abundance scale (fitted as a covariate) in the latter. Considering the alternative two-term models, the explanatory power of each with respect to the data set for which they were generated is similar (compare deviance explained with null deviance), with the '1983' model explaining a slightly higher proportion of the deviance. Given that the 1979–94 data set is by definition more complete than the 1979–83 data set, the preferred model of extinction patterning in this study is that which employs the three-point abundance scale (singleton, localized and widespread) and the trend in population status at the end of the first 50 years; both fitted as covariates.

#### Proximate causes of loss within the species considered extinct

As noted above, in their analyses of extinction patterns using the 1979–83 collation, Whittaker *et al.* (1989) suggested that the extinction data might be interpreted in relation to: (1) successional processes, (2) habitat disturbance or loss additional to those driven by succession, and (3) the loss of ephemeral populations. But they did not attempt to quantify these features. To pursue these issues further, we classified those species extinct in *c.* 1979–94 as either ephemeral or resident in 1883–1994, and according to the likely driving force of their extinction. An example of a species we class as ephemeral is *Indigofera zollingeriana*, which was described by Docters van Leeuwen (1936) in these terms: 'shoots up, but does not maintain its ground', usually being found near the beach. In contrast, *Phaseolus adenanthus* was described as being quite common, mainly near the coast, and was said to

have spread greatly. This we take to indicate an established, bridgehead population. *Blumea balsamifera* is an example of a resident lost due to succession. It was described as having 'soon disappeared through shading', once having been common on all three islands. Non-successional changes in habitat are attributable to coastal erosion, especially the great changes in the location and size of the Sertung spit (cf. Bird & Rosengren, 1984; Whittaker *et al.*, 1989). Relatively few cases of this type were identified with certainty from the list of 'resident' species, but several of the sea-dispersed 'ephemerals' listed below are described from strand-line locations and failed to establish either because the habitat was fundamentally unsuitable or because of the geomorphological instability of the habitat.

Of the 94 lost species, 41 were classed by us as ephemerals and 52 as residents, while one species, *F. asperiuscula*, was rediscovered in 1995 (above). Of the 41 ephemerals, doubts exist about the identification of seven (*Ficus hirta*, *Nepenthes* sp., *Habenaria* sp., *Oberonia* sp. not *monstruosa*, *Taeniophyllum* sp., *Thrixspermum* sp. 1 not *comans*, and *Metathelypteris flaccida*), five were introduced by people but shaded out without apparently establishing a population (*Cyperus kyllingia*, *Stemodia verticillata*, *Kalanchoe pinnata*, *Ricinus communis*, and *Boesenbergia pandurata*), and one other human introduction (*Citrus* sp., above) was swept away in a landslide. Fourteen were sea-dispersed species that were singleton records or rarities, and failed to find appropriate habitat or quickly lost it (*Avicennia alba*, *Intsia amboinensis*, *Tristellateia australasiae*, *Cyperus odoratus*, *Cassia siamea*, *Messerschmidia argentea*, *Dioscorea nummularia*, *Erythrina fusca*, *Indigofera zollingeriana*, *Spondias novoguineensis*, *Ochrosia oppositifolia*, *Crotolaria mucronata*, *Mucuna pruriens* and *Xylocarpus moluccensis*). This seems to apply to one further human introduction to Rakata, *Cyperus cylindrostachys*. The ephemeral class also included a few animal-dispersed seed plants (*Antidesma bunius*, *Digitaria rhopalotricha*, *Erioglossum rubiginosum* and *Gluta reinghas*), wind-dispersed seed plants (*Acanthephippium parviflorum*, *Eulophia zollingeri*, *Galeola kuhlii* and *Nervilia punctata*) and ferns (*Blechnum orientale*, *Lygodium microphyllum*, *Christella parasitica* and *Sphaerostephanos polycarpus*).

Of the 52 lost species considered to have once attained resident status, doubts exist about the identification of three: *Operculina* sp. (possibly confused with *Merremia peltata*, a species recorded in 1979–94), *Vrydagzynea* sp. and a tree fern, designated merely as genus ignota (Cyatheaaceae). At least four species, all sea-dispersed, can be attributed to loss of habitat due to coastal erosion: *Excoecaria agallocha*, *Lumnitzera racemosa*, *Ipomoea digitata* and *Halophila ovalis*. Others might be added to the category, e.g. *Serianthes gradiflora*, a species that was found at the foot of the Sertung spit, an area subject to both coastal erosion and volcanic disturbance within the last 60 years. Twenty-eight can be attributed to successional loss of habitat, involving the conversion of open to wooded habitats. Twelve of the 28 were introduced by people (*Commelina benghalensis*, *Euphorbia hirta*, *Euphorbia thymifolia*, *Eragrostis amabilis*, *Desmodium triflorum*, *Boerhavia erecta*, *Lindernia crustacea*, *Cyathula prostrata*,

*Eleutheranthera ruderalis*, *Synedrella nodiflora*, *Acalypha indica* and *Eleusine indica*), two are sea-dispersed (*Cyperus cuspidatus* and *Centella asiatica*), six are wind-dispersed seed plants (*Erechtites valerianifolia*, *Thrixspermum merguense*, *Blumea balsamifera*, *B. tenella*, *Erigeron linifolius* and *Neyraudia madagascariensis*), and eight are ferns (*Ornithium siliculosum*, *Lindsaea repens*, *Sphenomeris chinensis*, *Belvisia callifolia*, *Psilotum complanatum*, *Acrostichum aureum*, *Macrothelypteris torresiana* and *Sphaerostephanos unitus*). We were unable to attribute the remaining 16 formerly resident species to a particular cause of loss. They were: *Cyrtococcum oxyphyllum*, *Alocasia longiloba*, *Ficus padana*, *Leea aequata*, *Lycianthes laevis*, *Mallotus multiglandulosa*, *Ipomoea glaberrima*, *Phaseolus adenanthus*, *Tylophora exilis*, *Aeschynanthus pulchrum*, *Zeuxine gracilis*, *Malaxis latifolia*, *Peristylus gracilis*, *Ceropegia curviflora*, *Vittaria zosterifolia* and *Ophioglossum reticulatum*.

#### *Species rescued by Anak Krakatau and the hard core of lost species of Krakatau*

The fourth island in the group, Anak Krakatau, has not hitherto been considered in these calculations. From collections made between 1979 and 1993 (reported in Partomihardjo *et al.*, 1992; Partomihardjo, 1995), eight of the 94 extinctions from the 1883–1934 Krakatau flora are 'rescued': *Blechnum orientale* (a fern), *Spondias novoguineensis*, *Erigeron linifolius*, *Excoecaria agallocha*, *Digitaria rhopalotricha*, *Eleusine indica*<sup>1</sup>, *Eragrostis amabilis*, and *Neyraudia madagascariensis*. Of the eight, *Erigeron linifolius* and the three grasses introduced by people (*Eleusine indica*, *Eragrostis amabilis* and *Neyraudia madagascariensis*) were considered lost from the other Krakatau islands due to successional loss of habitat. *Excoecaria agallocha*, a 'resident' known from all three older islands and considered lost from them due to habitat disturbance or loss, was found on Anak Krakatau in 1992. Given the extent of the pioneer habitats available on Anak Krakatau at this time (Partomihardjo *et al.*, 1992), it is unsurprising that some of the early successional species lost, or undetectable on the largely forested older islands, should re-appear on this young volcanic island.

Thus, the true figure for losses of seemingly once established species of the 1883–1934 Krakatau flora, using the available 1979–94 records, could arguably be set at the figure of the 49 residents identified to species, of which just 37 species colonized naturally. The figure can be further reduced to 35, as *Erigeron linifolius* and *Excoecaria agallocha* were found on Anak Krakatau between 1979 and 1994. Within this hard core of 35 lost natural colonists, we have attributed 19 to deterministic processes, essentially loss of habitat as the result of succession or of geomorphological disturbance (principally coastal erosion), leaving just 16 to unattributed and/or 'stochastic' processes of turnover.

<sup>1</sup>Schmitt (1997) has also reported *D. rhopalotricha* and *E. indica* as germinating from seed bank germination trials from samples collected, respectively, from Rakata and Panjang, thus indicating that both in fact persist on the older Krakatau islands too.

## DISCUSSION

### Reliability of the extinction estimates

Our first aim was to examine the reliability of estimates of species extinction, as a key component in island species turnover. In simple terms, our additional surveys between 1984 and 1994 reduced the number of extinctions by a third. But our analyses also reveal the difficulty of defining an appropriate base-line of species considered present at time 1 by which to judge the subsequent extinction rate at time 2, time 3, etc. By considering the structure inherent within the revised extinction data, we can reduce the figure for extinction from the initial *c.* 1979–83 head-line value of 135 of the original 325 species records, down to fewer than 50, with perhaps as few as 16 losses of naturally colonizing resident species that cannot simply be attributed to disruption of habitat by autogenic or allogenic processes. In such circumstances, there is scope to generate widely different estimates of extinction rates from the same data set.

Before considering the implications of the structural features identified above, it is important to set out some of the assumptions involved, and to establish those features of the surveys themselves that may have produced bias in the data. First, by examining loss of species at the archipelago level, genuine losses from each island are hidden, as species persist on one of the other two islands. To explore this, we have calculated species losses for each island separately. The resulting figures, using 1883–1934 as time 1 and 1979–94 as time 2, and excluding records not determined to species are: Rakata 29.6% extinct, Sertung 32.7% and Panjang 36.8%. Ignoring those species introduced by people, the respective figures are 24.7%, 32.1% and 33.1%. The Rakata values are close to the values for the whole data set (Table 2). The slightly higher values for the other two islands are considered below.

Second, as we have only one survey (*c.* 1951) between 1934 and 1979, and have ignored it here due to its inherent deficiencies (e.g. virtually no sampling from Panjang and Sertung), the possibility of a species 'turning over', i.e. becoming extinct and re-immigrating in the intervening 45-year period, is not addressed by our analyses. This, together with the crude lumping of the data into two time periods, constitutes a serious weakness in respect of using these data in formally evaluating the ETIB. Although it is possible to address this to a degree by using more time slices and appropriate filtering of the data (see Whittaker *et al.*, 1989; Whittaker, 1998, Figure 8.9), the present analyses serve to highlight the dangers involved.

It is quite clear (e.g. see Docters van Leeuwen, 1936; van Borssum Waalkes, 1960; Partomihardjo *et al.*, 1992) that some of the species classed here as 'ephemeral' have taken root (whether from spores, seeds or planting by people) in the archipelago on more than one occasion. *Nypa fruticans* is an example of an ephemeral that has frequently taken root both in the first 50 years and since, so that it counts as a persisting species, although it has never been observed to reach maturity. It is also certain that many resident populations have been bolstered by supplementary recruits from outside the archi-

pelago, some on a large scale (cf. Partomihardjo *et al.*, 1993). It is not possible with the available data to say how many of these resident species might have been temporarily extinct, only to recolonize, but this is least likely for longer-lived tree species of large initial populations. Studies of germination from buried Krakatau seed banks and from elsewhere also establish the possibility of seed plant species that have greatly diminished, or indeed disappeared from the extant vegetation, reappearing from seed banks following disturbance to the canopy and/or subsoil (Whittaker *et al.*, 1995; Grandin & Rydin, 1998).

Pteridophytes have been shown to be disproportionately rich on Krakatau relative to seed plants and in comparison to regional source pools (Whittaker *et al.*, 1997). As they reproduce from highly dispersive, wind-borne microscopic spores, it would seem reasonable to suggest that habitat availability is more limiting than dispersal to their arrival and persistence on the islands. Yet, the survivorship of ferns and their allies in the 1979–94 data is no different from that of the spermatophytes. However, the improvement in pteridophyte persistence in the 1979–94 data (relative to 1979–83 data) is marginally better than for spermatophytes, especially so if human introductions are discounted from the latter group. The same can be said for wind-dispersed spermatophytes compared to sea-dispersed and animal-dispersed groups. These marginal improvements may be a reflection of an intensive survey by Partomihardjo (1995) of epiphytes (most of which are wind-dispersed) between 1989 and 1993, which resulted in several re-discoveries of species not sampled between 1979 and 1983. In contrast to the vast and complex interiors, the strand-line environments are fairly discrete and well-investigated, as collecting teams walk around the coastlines to find points to access the interiors. *A priori*, it is to be expected that sampling of sea-dispersed species will be more efficient than that of animal- and wind-dispersed species. Our analysis of the ephemerals category and supporting documentation in Docters van Leeuwen (1936) indeed points to a degree of over-sampling of the strand-line flora, whereby juveniles have been recorded although they clearly have never established populations (e.g. *Opuntia elatior*, *Intsia amboinensis*, *Xylocarpus moluccensis* and *Avicennia alba*). The combination of effective sampling in 1883–1934 and rapid coastal geomorphological change accounts for the high number of losses in sea-dispersed species found only on one island, whilst those found originally on all three are a species-stable set: the core members of the Krakatau strand-line vegetation.

Another general consideration with respect to rates of extinction is the quality of the records. The vast majority of identifications are undoubtedly sound, with most problems associated with the comparatively few early records identified uniquely to a particular genus, but not determined to species. However, some Krakatau plant taxa are particularly troublesome, examples including the genus *Ficus*, certain fern genera and particular genera of Euphorbiaceae. Recent revisions of the *Ficus* lists are incorporated here. Of fig species in which we are confident of presence in the 1883–1934 period, only *F. padana* has not been recorded in the contemporary period (N. A. Mawdsley, S. G. Compton & R. J. Whittaker, unpublished

data). There are a very few cases of genera in which one species was consistently recorded by the earlier botanists, and a different member of the genus has been consistently recorded in the contemporary data. These changes may indicate inconsistencies in attribution of specimens, which further herbarium work might be able to resolve. Examples include the pteridophyte genera *Acrostichum*, *Macrothelypteris* and *Vittaria*, and spermatophyte genera *Ipomoea* and *Peristylus*.

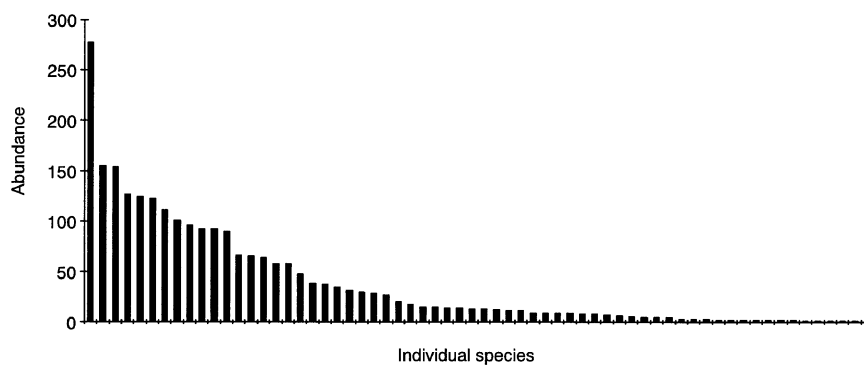
### Structural features in the extinction data

The second main aim of the present study was to examine structural features in the extinction data, with reference both to previous empirical analyses (Whittaker *et al.*, 1989) and to the theoretical expectations in respect of species-abundance patterns underpinning turnover (e.g. Preston, 1962a, b). We have shown that while some plant species found between 1883 and 1934 on Krakatau have failed to persist, many of the losses reflect sampling problems affecting the least widespread species rather than proper turnover. In essence, we are analysing extinction from lists, which may inaccurately reflect real extinction in the archipelago. Our historical analyses have been based on categorical distributional data, and although for some species rough estimates of numbers were offered in the original sources, we are unable to quantify more precisely the abundance patterns for the 1930s. However, we are able to show that the species-abundance relationship within the contemporary Krakatau flora approximates to the typical pattern alluded to in the introduction, wherein the majority of species are rare (Fig. 4). This is the case notwithstanding that the general poverty of the flora as a function of island size (unpublished data) might in theory allow for higher population sizes of the constituent species. Similarly, population estimates of *Ficus* species based on stratified sampling of plots on Panjang and Rakata indicate that contemporary population sizes of fig species vary from < 50 to > 100,000 individuals per species (these extremes are both for species that were present in the 1920s) (N. A. Mawdsley, S. G. Compton

& R. J. Whittaker, unpublished data). These real differences in population size and status today equate to our categorical treatment of species as, for example, 'singleton' records, 'local-rare' status or 'ephemeral' status in the historical record.

While the increased survey effort reduced apparent extinctions of 1883–1934 species by one third, it is noteworthy that the structure apparent in relation to island combinations and primary dispersal class originally identified by reference to the 1979–83 data remained apparent in the 1979–94 data (Figs 1, 2 & 3, Appendix 1). Further, we have expanded on the earlier analysis (Whittaker *et al.*, 1989) to demonstrate the relationship to distribution/abundance at a finer scale of analysis than simply number of islands occupied. Interestingly, this measure of abundance provides a more powerful predictor of extinction than island combinations when using the 1979–94 data (see Table 6 for an example).

The multi-term analyses revealed that phylogenetic relatedness, which was significant in some MAMs derived for the 1979–83 data set, was not significant in any MAM for the more complete 1979–94 data set. The second and related conclusion is that much of the complexity (particularly interactions between variables) apparent in the less complete data set was not evident (i.e. was not significant) when the more complete data were analysed. This is consistent with a reduction in sampling bias with increased sampling effort. Bearing in mind the danger of over analysing data which remain imperfect, we choose a simple two-term model ('1994 preferred' in Table 6) as the most reasonable representation of the basic structural features in the extinction data. This model combines a measure of the abundance of a given species early on in the recolonization of the islands, with a measure of the trend in its population size towards the end of this early period. In short, as Charles Darwin pointed out in *On the Origin of Species* (Darwin 1859), rarity is often the precursor of extinction. The other variables considered in the modelling process, while showing interesting and probably important relations to extinction when analysed on their own, seem to add little to the explanatory power of the model.



**Figure 4** Species-abundance plot for Krakatau woody species (excluding climbers) of all strata. The data consist of one transect on each of Rakata, Sertung and Panjang, sampled in 1994. The transects were orientated by compass to traverse areas in the lowlands of each island. Each transect was 1000 m long and 20 m wide, and the occurrence of each species was scored in every 10 m of the length of the transect. The data were summed across transects, giving a frequency or abundance measure ranging from 0 to 300 for each species. Data with kind permission of S. F. Schmitt; for further details of the data set see Schmitt (1997), Schmitt & Partomihardjo (1997) and Schmitt & Whittaker (1998).

The formal modelling analyses do not, however, extend to the subdivision of the lost plants into causes of disappearance, and the distinction between ‘residents’ and ‘ephemerals’. The additional analyses reported above indicate that a high proportion of the apparent extinctions can be accounted for by reference to loss of habitats. Habitat loss or disturbance can be attributed to a number of forces, e.g. succession, geomorphological erosion (especially of coastal locales), extreme climatic phenomena and, in this case, volcanism. Whilst it is agreed that volcanic disruption has at times over the last 60 years interrupted the accumulation of plant species on Anak Krakatau, it is less clear what the impact of the volcano may have been on species turnover on the older, non-volcanically active islands (Whittaker *et al.*, 1989; Partomihardjo *et al.*, 1992; Thornton, 1996). To examine this, we considered the fate of species as a function of presence or absence from Rakata in 1883–1934; as unlike Panjang and Sertung, Rakata has not been directly affected by damaging ash-fall. In the main statistical analyses, lower losses were found among those species recorded from Rakata, but it was a comparatively weak pattern. The tendency to better survival of species occurring on Rakata is, however, further supported by the finding that extinction of naturally colonizing species judged on an island-by-island basis is about 7% higher for both Panjang (33%) and Sertung (32%) than for Rakata (25%). This is consistent with volcanic disturbance driving higher extinction rates on the two affected islands. Analysis of this is, however, confounded by other differences that may relate to turnover, including some not considered in our analyses, e.g. Rakata is much larger and higher than the other islands. Given which, a conservative interpretation would be that while vegetation patterns, and the diversification of both vegetation and flora likely have been affected on Sertung and Panjang (Schmitt & Whittaker, 1998), post-1930 volcanism does not appear to have caused a great extinction pulse for plants at the scale of the whole archipelago. The more obvious signal that was found in the data analysed on this scale, once the ephemera were taken out of play, was of successional loss of plants of open habitats, with a lesser role for habitat loss due to coastal erosion.

### Implications

Few ecological data sets exist that allow detailed appraisal of species turnover from moderate- to large-islands over a time span of several decades (but see e.g. Russell *et al.*, 1995). In view of the theoretical and applied interest in processes and patterns of extinction, such data sets *potentially* have great importance. In the Krakatau archipelago, species go extinct as victims of community-wide (or island-wide) successional processes, and through other processes of habitat loss. Indeed, many species fail to establish and proliferate because their habitats are lacking in the first place. These findings are consistent with the notions that turnover is structured (heterogeneous *sensu* Rey, 1985) and that with sufficient detailed data on particular islands, relatively high proportions of losses can be attributed to ‘deterministic’ rather than ‘stochastic’ causes. Moreover, there have been far fewer extinc-

tions of established species than appeared to be the case 10 years ago (cf. Whittaker *et al.*, 1989). In sum, the simple model at the core of the ETIB, if true, appears largely trivial (as Williamson, 1989) as it applies to our data set. In this specific case, the acceptance at face value of headline rates of plant species extinction has been shown to be unsound (as cautioned by Bush & Whittaker, 1993). Whilst we also caution against assuming that the findings reported here have generality, the problems detailed in respect of calculations of the headline island ecological rates—extinction, immigration and turnover—are far from unique to this study. In the absence of the sort of descriptive detail available in the Krakatau plant literature, the use of surrogate ecological indicators, such as dispersal or habitat categorizations, can provide a simple tool for analysis, and a means of understanding structural features inherent in the data. They can also provide a means of refining or framing estimates of island species turnover.

Arguably, the derivation of rates of extinction, turnover, etc., are now of less theoretical interest than analyses of the structural features embedded in such data (Whittaker, 1998, 2000; Weiher & Keddy, 1999; Brown & Lomolino, 2000). The loss of significance attributable to variables like phylogenetic relatedness and growth form, and to between-variable interactions, with improved sampling effort, are illustrative of the dangers inherent in structural analyses of general survey data. If we had only the 1979–83 data to work from, then the statistics would have pointed to a complex web of interacting variables influencing extinction probability on these islands. In the event, analyses of the more exhaustive (but still incomplete) 1979–94 data set demonstrated that much of that complexity was essentially the product of sampling bias. Despite our enthusiasm for issues relating to structural features in island assembly (or disassembly), this is an important lesson that needs to be borne in mind when analysing and modelling patterns in a large, unreplicated system such as Krakatau.

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## BIOSKETCHES

**Rob Whittaker** has been working on the Krakatau islands since 1979. His research interests include theories and patterns of community assembly and disassembly, processes of dispersal, inter-specific interactions and succession, responses of ecosystems to disturbance, and the relationship between plant diversity and climate at the macro-scale. He is the author of *Island Biogeography: Ecology, Evolution and Conservation* (Oxford University Press, 1998).

**Richard Field's** work focuses on the forces that structure ecological communities. His research interests include modelling and prediction of global patterns of plant diversity, the ecology of invasive tree species within Britain, and island biogeography and community structure in Indonesia.

**Tukirin Partomihardjo** has been working on the Krakatau Islands since 1981, completing a PhD thesis on their ecology in 1995 (see reference list). His interests include terrestrial biology, especially botany, plant ecology and animal–plant interactions, in particular of galling insects.

**Appendix I** Cross-tabulation of (a) species records from the 1883–1934 Krakatau flora and losses from this flora, as determined (b) for 1979–83 and (c) for 1979–94 collations. R, Rakata; S, Sertung; P, Panjang. The species are entered for the island combination for which they were recorded during 1883–1934. Species are classed as 'extinct' if not recorded at all within periods (b) or (c) anywhere on Rakata, Sertung or Panjang. Species originally found on one island but now found only on another would not be classed as 'extinct'. Data drawn from Docters van Leeuwen (1936), Whittaker *et al.* (1989) and a data base of the Krakatau flora held by the senior author. Strictly, ferns should be 'ferns and their allies' in the Pteridophyta.

### (a) All records 1883–1934

Islands	Ferns	Wind	Sea	Animal	Human	All
R	36	28	10	28	19	121
S	3	2	16	7	2	30
P	0	2	4	5	9	20
RS	4	8	6	11	0	29
RP	0	5	2	2	0	9
SP	0	1	0	5	0	6
RSP	18	19	48	25	0	110
All	61	65	86	83	30	325

### (b) 'Extinct' as of 1979–83

Islands	Ferns	Wind	Sea	Animal	Human	All
R	16	14	7	12	14	63
S	2	1	13	3	2	21
P	0	0	4	1	9	14
RS	1	5	3	2	0	11
RP	0	2	0	0	0	2
SP	0	1	0	1	0	2
RSP	7	5	6	4	0	22
All	26	28	33	23	25	135

### (c) 'Extinct' as of 1979–94

Islands	Ferns	Wind	Sea	Animal	Human	All
R	9	14	4	7	12	46
S	2	0	10	1	0	13
P	0	0	3	0	7	10
RS	1	2	2	1	0	6
RP	0	2	0	0	0	2
SP	0	1	0	1	0	2
RSP	4	3	5	3	0	15
All	16	22	24	13	19	94