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Pattern and process of vegetation change (succession) in recent volcanic landscapes of New Zealand and Hawaii

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Introduction

Volcanic activity (including lava flows, debris flows and tephra eruptions) is a regular feature of many landscapes of the North Island of New Zealand and the Hawaiian archipelago. Over the last 35 years, we have been using a combination of the chronosequence and direct monitoring methodologies (Clarkson 1998; Walker et al. 2010) to research the pattern and process of vegetation change (succession) in these landscapes. The following account summarizes pattern and process from our main study sites (Fig. 1): Whakaari (White Island), Rangitoto Island, Mt Tarawera, Mt Ngauruhoe, Mt Ruapehu, and Mt Taranaki in New Zealand and Mauna Loa in Hawaii. Most of this information is taken from our previous publications (see References) and the references contained therein. New information on Rangitoto Island *Metrosideros excelsa* patch dynamics and updated (2005) species statistics for White Island have been included. The main focus of this account is forest development following significant eruptions.

White Island (Whakaari)

White Island (Whakaari) is a 238 ha island volcano (highest point 321 m a.s.l.) located 50 km north of North Island mainland in the Bay of Plenty. It has been in the state of continuous solfataric activity, with intermittent small steam and tephra eruptions since 1826. In recent times major damage to the vegetation on the island has resulted from a complex sequence of eruptions between 1976 and 1981. Significant eruptions have also occurred periodically between January 1984 and 1994 with a decline in activity since then. Eruptions have included ejections of ash and gas, with acid rain causing death and dieback of *Metrosideros excelsa* forest and *Disphyma-Einadia* herbfields.

Metrosideros excelsa dominates a floristically depauperate community which, in places, comprised only two or three vascular species, namely *M. excelsa, Histiopteris incisa*, and *Phormium tenax.* Changes in the vascular flora on the island documented between 1912 and 2005 show between seven and thirteen species present before 1990, and 33 species in 2005, which reflects the reduction in volcanic activity (Table 1). The post-1990 arrivals, however, are mainly exotic dicotyledonous herbs, and *M. excelsa* remains the only tree species present on the island. *Metrosideros excelsa* (Fig. 3) is a mass seeder with wind dispersed seed and the ability to recover from canopy damage by epicormic resprouting. Direct succession of *M. excelsa* results from recovery of an existing population or colonization of a newly emplaced surface by *M. excelsa* seed.

Rangitoto Island

Rangitoto Island, a basalt shield volcano covering 2311 ha and rising to 260 m a.s.l. is located in the Hauraki Gulf, 8 km north east of Auckland City. It appears to have been active between 850 AD and 1800 AD, with a maximum lava activity around 1300 AD. The primary surface is mainly crusty aa basaltic lava but the summit consists of scoria cones. The last lava flows were followed by an emission of ash which filled most of the crevices and shallow hollows. *Metrosideros excelsa* is the prime lava colonizer and has coalesced to form continuous forest over large areas of the island. We have been monitoring *M. excelsa* patch establishment and development (Fig. 4) between 1980 and the present day in permanent plots established by our colleague, James O Juvik (University of Hawaii at Hilo). These represent the most extreme sites of largely unvegetated aa lava. The number of vascular species is strongly positively correlated with the size of the *M. excelsa* patch ($r^2 = 0.742$; $n = 80$) with 1–4 species recorded in patches of 0.1 m^2 and 16–19 species in patches of 100 m^2. Using patch size in six size classes (midpoints = 1 m^2, 3 m^2, 6 m^2, 12 m^2, 24 m^2, 48 m^2) and frequency of occurrence as a surrogate for age, it is possible to determine the orderly sequential establishment of species. Early establishers include *Coprosma robusta, Myrsine australis* and *Astelia banksii*. Middle and late establishers include *Pseudopanax arboreus, Collospermum hastatum,* and *Asplenium oblongifolium.* The fern, *Asplenium flaccidum*, which is mostly epiphytic on *M. excelsa*, is one of the last to arrive. Some species fluctuate in their frequency in relation to patch size, for example, *Brachyglottis kirkii, Ctenopteris heterophylla,* and *Asplenium flabellifolium.* These are usually patch edge dwellers and are sometimes lost as the *M. excelsa* canopy expands and may subsequently recolonise the edge of the patch. *Metrosideros excelsa* facilitates this deterministic establishment pattern by influencing the microclimate of the site. Surface temperature on open lava may exceed 50°C whereas in the interior of a large patch or extensive forest, it is less than 25°C. Relative humidity on open lava is less than 40% while in large patches it exceeds 45% and in the forest interior is over 55%.

Mauna Loa, Hawaii

The Hawaiian Islands and Hawaii Island in particular, provide a unique opportunity to study succession on volcanic surfaces ranging from 1 year to >4000 years old across a wide range of elevations, spatial scales, and climates. Studies of chronosequences can thus be designed to meet various assumptions, variation can be quantified through replication within categories, and multivariate approaches can correct for incomplete designs where chronosequence assumptions are not met. We have studied lava flows ranging from 5–300 years old on Mauna Loa, Hawaii Island, using a combination of chronosequence and direct monitoring. We have also attempted to collect data that are directly comparable to those collected on Rangitoto Island. On Mauna Loa at sites between 1035 and 1280 m a.s.l. on basalt lavas, canopy cover (Fig. 5) is dominated at first by the lichen *Stereocaulon vulcani* and the moss *Racomitrium lanuginosum.* By 50 years, *Lycopodium cernuum* and *Dicranopteris linearis* dominate. *Metrosideros polymorpha* can establish within 10 years and by 150 years completely dominates what has become continuous forest. The tree fern *Cibotium glaucum,* which can establish before 50 years, is abundant by 200 years. A well-developed *Metrosideros-Cibotium* forest is in place by 300 years (Fig. 6). As with Rangitoto Island, the number of vascular species increases with patch size expansion ($r^2 = 0.721$; $n = 40$). Patches of 1 m^2 may have 1–4 species, while those of 100 m^2 exceed 16, with Mauna Loa patches being slightly richer than those on Rangitoto Island. The high rainfall (*c.* 4000 mm yr^{-1}) here compared to the lower rainfall (*c.*1300 mm yr^{-1}) on Rangitoto Island means that species are less constrained to establishing within patches but nevertheless patch formation is still the dominant mode of forest development. Very early establishers on Mauna Loa include *Vaccinium reticulatum, Polypodium pellucidum* and *Hedyotus centranthoides*. A little later come *Vaccinium calycinum* and *Saddleria pallida.* Mid establishers include *Coprosma ochracea*, *Myrsine lessertiana,* and *Dubautia scabra*. Late establishers include *Astelia menziesiana, Cheirodendron trigynum* and *Ilex anomala*. *Xiphopteris saffordii* is the ecological equivalent of *Asplenium flaccidum*, being mainly epiphytic on *Metrosideros polymorpha* trunks. There are strong taxonomic similarities between Rangitoto and Mauna Loa, with many genera and at least one species (*Uncinia uncinata*) in common. Species richness of patches increases more rapidly on Mauna Loa than Rangitoto and this may suggest the Hawaiian flora has a greater proportion of species adapted to volcanic disturbance.

Mt Tarawera

Mt Tarawera (Fig. 7), a series of coalescing rhyolite domes and an associated crater lake (Lake Rotomahana) 25 km south-east of Rotorua, erupted in 1886, initiating primary successions over *c.* 10 km^2 and secondary successions over a further *c.* 20 km^2. The highest domes (summit 1111 m a.s.l.), were formed by the 1314 AD Kaharoa eruption, and are mantled with the 1886 eruptive material, basaltic ash and lapilli. We have been monitoring vegetation change on the dome tops since 1978 with recourse to previous studies, in particular research by Burke (1964). The major primary successional pathway on the dome tops involves colonization of bare surfaces by grass-herb-lichen patches, occasionally with heath shrubs such as *Dracophyllum* and *Gaultheria,* lasting approximately 70 years. Subsequently, shrubs of *Coriaria arborea* (Fig. 8), which fixes nitrogen through symbiosis with an actinomycete endophyte, *Frankia*, enter these aggregations and coaslesce to form continuous scrub. Seedlings and saplings of forest trees, especially *Griselinia littoralis,* established in this type before 1979. The likely forest dominants of this developing forest are, depending on browsing impacts, *G. littoralis, Weinmannia racemosa*, and *Podocarpus hallii.* Unusually severe frosts periodically cause dieback of the *Coriaria,* enabling colonization of non-forest species such as *Cortaderia fulvida*, or releasing saplings of forest trees such as *Griselinia*. Forest on the edge of the dome tops within 1.5 km of the nearest crater mostly survived the eruption. Emergent trees such as *Podocarpus hallii* were killed and their dead spars remained for more than a century after the 1886 eruption. The main canopy species represented include *Weinmannia, Phyllocladus glaucus* and *Knightia excelsa. Coriaria arborea* is the keystone species in facilitating development of forest as it has a disproportionate effect on ecosystem change both floristically and structurally. The nitrogen produced by *Coriaria* has such an imprint on the forest ecosystem long after the plant's demise that *Coriaria* could be more correctly considered a nexus species as defined by Temperton et al. (2004).

Mt Ngauruhoe

Lava (aa) and pyroclastic flows from Mt Ngauruhoe, an andesite central North Island cone reaching 2291 m a.s.l., have impacted up to 10 km^2 of vegetation between 1550 AD and the present day. At 1675 m a.s.l., Ngauruhoe lava flows erupted in 1870, support a sparse cover (25–39%) of mainly *Rytidosperma setifolium, Gaultheria colensoi,* and *Dracophyllum recurvum.* The grasses, herbs and shrubs grow mainly in ash or gravel which has accumulated on the lava with mosses and lichens only present on the lava boulders. There have been no detectable changes in the cover or composition of the vegetation here since Uhe (1971) measured them in 1966, largely result of the harsh subalpine conditions. The flows erupted in 1949 and 1954, extending in a westerly and north-westerly direction from 2070 to 1324 m a.s.l., have even less-developed vegetation. Boulder-sized lava blocks support *Stereocaulon vesuvianum* and *Racomitrium lanuginosum* as they did in 1966 when measured by Uhe (1971). The pyroclastic flows of 1975 comprised a greater mixture of different sized particles and subsequent debris flows have continued to add to this. They support *Raoulia albosericea* and 6–10 other vascular species, depending on the proportion of gravel or boulders. None of these examples shows true succession as there is a continuing gradual accumulation of species but no group of species has been replaced.

Mt Ruapehu

Mt Ruapehu (2797 m a.s.l.), an andesitic volcano and the highest peak in the North Island, has erupted *c.* 50 times since 1861. Most eruptions have been phreatic, involving steam explosions caused by the contact of lava and water, from the Crater Lake. Until 1995, the largest recorded eruptions had occurred in 1945 when ash fell across much of the North Island, and in 1953 when a lahar destroyed the rail bridge across the Wangaehu River. In September 1995 Mt Ruapehu entered a new phase of eruptions, following months of increased seismic activity, rising lake temperatures and increases in the magnesium and chloride concentrations of Crater Lake. Volcanic activity continued at heightened levels through until late October 1995. Throughout the eruptions, ash plumes were produced, with some reaching as high as 19 km into the atmosphere. Most of the erupted volcanic material was deposited to the north and east of the crater, a consequence of prevailing wind and the breached crater topography. We measured plots in the Tukino sector of Mt Ruapehu to determine the effects of the ash deposition. The plots were positioned along an altitudinal (1500–1760 m a.s.l.) and impact gradient (*c.* 3–6.5 km from the crater). For background information on the vegetation structure and composition prior to the eruptions we relied on Leslie (1984) and Atkinson (1981). Our February 1996 measurements showed that foliage death range from 50% of total cover at 1760 m a.s.l. to 34% at 1500 m a.s.l. Mean ash depths range from 65 to 25 mm along this gradient. The ash was characterized by high sulfur content and the potential to increase soil acidity. Below 1500 m a.s.l. foliage death was largely insignificant. Species that suffered the greatest damage tended to be those of small stature, for example, *Luzula colensoi,* a diminutive woodrush, was completely wiped out between 1520 and 1760 m a.s.l. Similarly, the cushion forming mosses, *Racomitrium* and *Andreaea*, were severely damaged in the same zone. Ash depth per se was less important than the length of time ash persisted before being washed off by rain. Of the two dominant species in this zone, the small shrub *Gaultheria colensoi* (Fig. 10), was most affected (40–60% foliage death) as ash tended to accumulate on its horizontally oriented leaves more than on the erect needle leaves of the bristle tussock, *Rytidosperma setifolia* (11–30% foliage death). However, in February 1996, *Gaultheria colensoi* was already recovering well by resprouts. The composite herb, *Anaphalioides alpina*, showed similar levels of defoliation to *G. colensoi* but did not resprout. New growth of *Anisotome aromatica*, a soft-leaved perennial herb, was noted emerging through the ash. A further eruption in June 1996 killed off many of the *G. colensoi* resprouts at altitudes between 1600 m and 1760 m a.s.l. The overall picture that emerged was of a community dominated by a long-lived (possibly >200 years) shrub capable of resprouting after damage caused by eruptions of this scale and impact.

Mt Taranaki

On Mt Taranaki, a west coast North Island, andesite stratovolcano (2518 m a.s.l.), tephra eruptions and associated debris flows and fires over the last 450 years have destroyed *c.* 6700 ha and damaged an equivalent area. Pollen analysis suggests that areas of upper montane forest completely destroyed or badly damaged by the Burrell eruption of 1655 AD have shown a succession from shrubs, including *Coriaria arborea,* to *Kunzea ericoides* and *Fuchsia excorticata*, and then to *Weinmannia* forest (Fig. 11). However, *Libocedrus bidwillii* has not, as yet, regained lost ground, being found as scattered survivors over a low canopy of broadleaved shrubs such as *Brachyglottis elaeagnifolia*. The treeline and upper altitudinal limits of tree species are generally lower on Mt Taranaki than on the adjacent less-affected Pouakai Range. Forest composition at the treeline varies in relation to the direction and depth of recent ash showers, especially the Burrell eruption of 1655 AD. A suite of tree species, *Weinmannia racemosa, Libocedrus bidwillii, Griselinia littoralis and Podocarpus hallii*, is found in various different combinations at different treeline sites depending on past eruption effects. Above Dawson Falls and at Stratford Plateau, where the effects of the Burrell eruption were most devastating, *Libocedrus* is scarce and *P. hallii* and *G. littoralis* more abundant. *Libocedrus* numbers increase gradually to the north and south until at North Egmont and Lake Dive respectively, there are extensive stands. *Weinmannia* has its lowest altitudinal limit on the eastern side of the mountain (1000 m a.s.l.) below Stratford Plateau, again reflecting the main axis of the Burrell eruption. The patterns and processes evident in the upper altitude forests of Mt Tarawera give insights into the earlier development of the similar *Podocarpus*–*Weinmannia* forests of Mt Taranaki. Again, in primary forest successions the facilitation role of *Coriaria arborea* is likely to have been very important. The overwhelming dominance of *Weinmannia* (Fig. 12) on Mt Tarawera and Mt Taranaki probably results from its ability to resprout from epicormic buds after its canopy has been damaged, and from its characteristics as a mass seeder, and ability to establish epiphytically, especially on trees damaged or killed by the impacts of eruptions.

Conclusion

Our results show a range of pattern and process relating to the frequency, intensity and scale of the volcanic disturbance and biogeographic setting. At one extreme are deterministic direct successions characterized by low to medium species richness and strong facilitation and aggregation mechanisms. At the other are probabilistic multiple pathway successions, characterized by medium to high species richness, and tolerance and inhibition as well as facilitation mechanisms. Full understanding of vegetation pattern and change on recent volcanic landscapes requires long-term (several human generations) experimental and observational studies using both direct monitoring of permanent plots as well as careful use of chronosequences.

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Fig. 1 Location of volcanoes studied on North Island, New Zealand

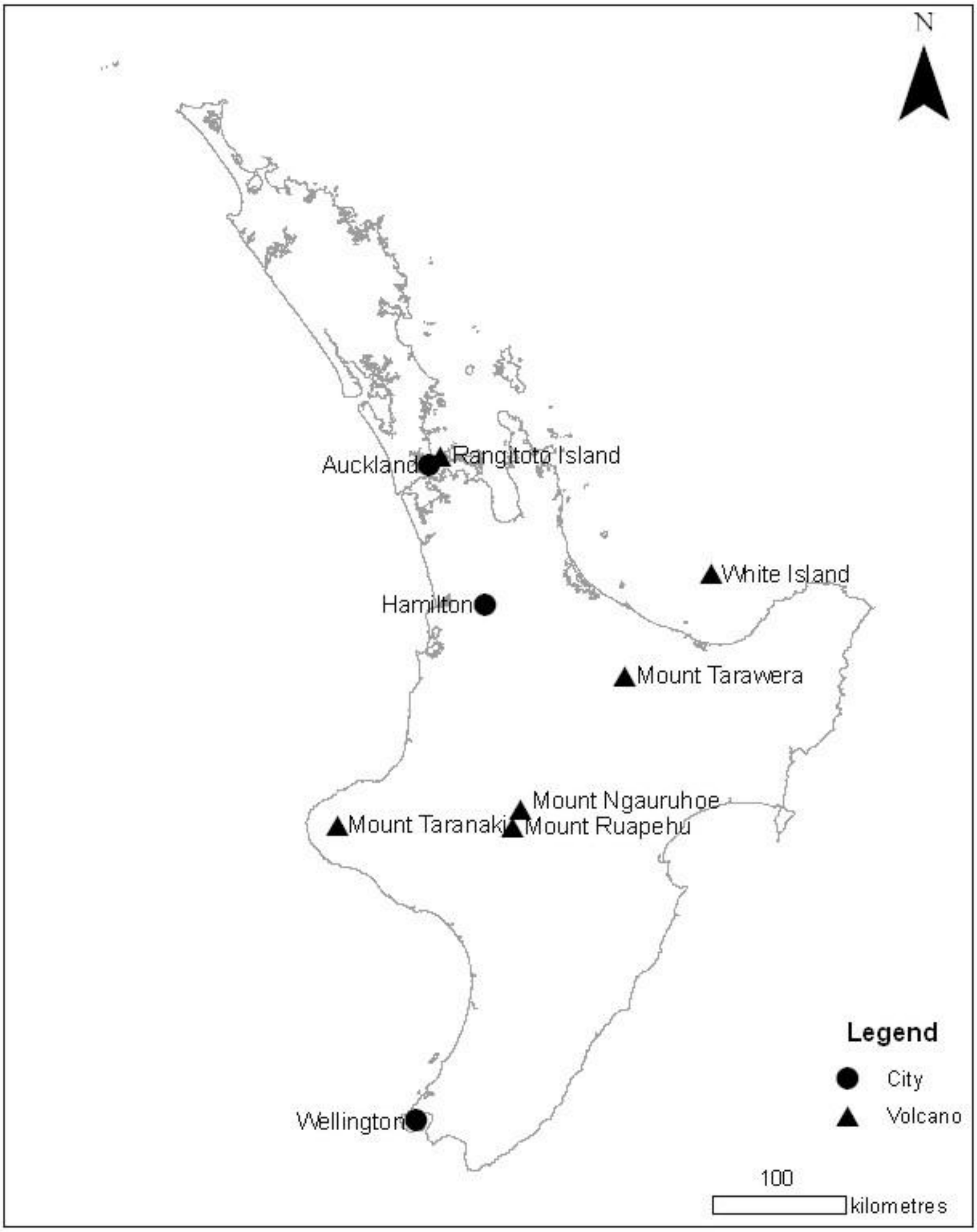

Fig. 2 *Metrosideros excelsa* recovering by epicormic resprouting, White Island May 1990

Fig. 3 *Metrosideros excelsa* flower on Tuhua (Mayor Island)

Fig. 4 *Metrosideros excelsa* patch on aa lava showing well-developed understorey association, Rangitoto Island

Fig. 5 Change in species canopy cover over 400 years on aa lava, Mauna Loa, Hawaii (STER: *Stereocaulon vulcani*; DICR: *Dicranopteris linearis*; RACO: *Racomitrium lanuginosum*; CIBO: *Cibotium glaucum*; LYCO: *Lycopodium cernuum*; METR: *Metrosideros polymorpha*)

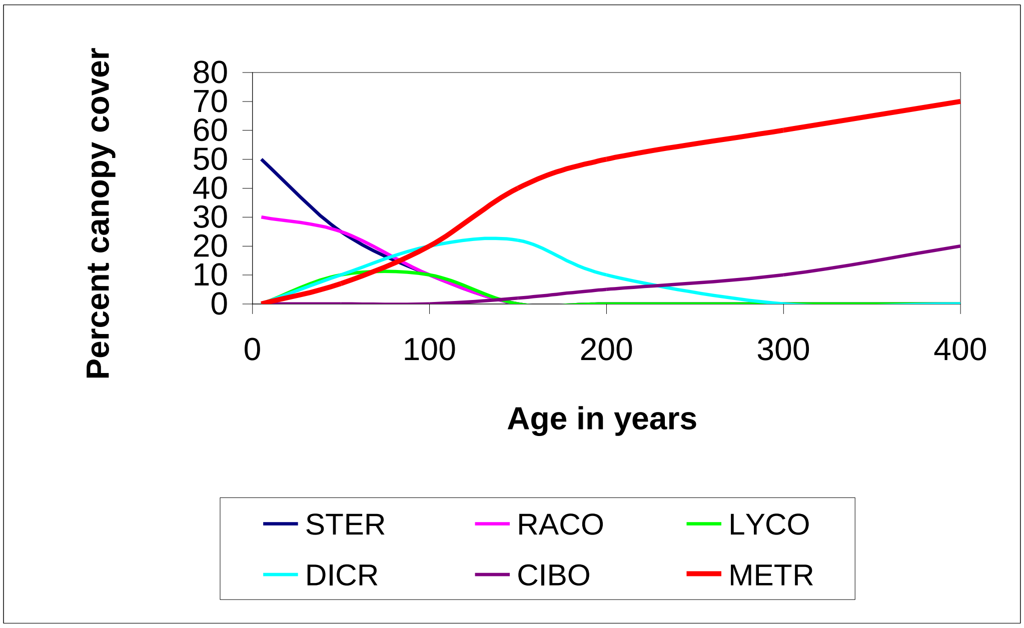

Fig. 6 *Metrosideros polymorpha* – *Cibotium glaucum* forest on 300-year-old aa lava, Mauna Loa, Hawaii

Fig. 7 View of high domes of Mt Tarawera

Fig. 8 *Coriaria arborea* invading early successional vegetation, Mt Tarawera

Fig. 9 Mt Ngauruhoe showing 1975 pyroclastic flow overlying older lava flows

Fig. 10 *Gaultheria colensoi* damaged by temporary ash burial on Mt Ruapehu (1995)

Fig. 11 *Weinmannia racemosa* dominated forest ('goblin forest') at 900 m a.s.l, Mt Taranaki

Fig. 12 *Weinmannia racemosa* flowers and seed capsules in cultivation, Hamilton

Table 1 White Island vascular species changes 1912–2005

	Year						
	1912	1949	1965	1967	1986	1990	2005
Ferns	1	1	1	1	1	1	4
Dicot herbs	5	7	4	8	3	3	21
Monocot herbs	1	1	1	1	1	1	2
Grasses	2	1	1	1	1	1	4
Dicot shrubs	1	1	1	1	0	0	1
Dicot trees	1	1	1	1	1	1	1
TOTAL	11	12	9	13	7	7	33