

**HAWAIIAN ENDEMIC FERN LINEAGE
DIELLIA (ASPLENIACEAE): DISTRIBUTION,
POPULATION STRUCTURE AND ECOLOGY**

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LIST OF ORIGINAL PUBLICATIONS

The thesis is based on the following papers:

1. Aguraiuja, R. and Wood, K. R. 2003. *Diellia mannii* (D. C. Eaton) Robins. (Aspleniaceae) rediscovered in Hawaii. *Am. Fern J.* 93: 154–156.
2. Aguraiuja, R., Moora, M. and M. Zobel. 2004. Population stage structure of Hawaiian endemic fern taxa of *Diellia* (Aspleniaceae): implications for monitoring and regional dynamics. *Can. J. Bot.* 82: 1438–1445.
3. Aguraiuja, R., Moora, M., Zobel, K. and Zobel, M. 2005. Population structure, regional dynamics and extinctions in the endemic fern lineage *Diellia* (Aspleniaceae) in Hawaii. (submitted manuscript).
4. Schneider, H., Ranker, T., Russell S. J., Cranfill, R., Geiger, J. M. O., Aguraiuja, R., Wood, K.R., Grundmann, M., Klobardanz, K. and Vogel, J. C. 2005. Origin of the endemic fern genus *Diellia* coincides with the renewal of Hawaiian terrestrial life in the Miocene. *Proc. R. Soc. B.* 272: 455–460.

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The author participated in preparing the listed co-authored publications as follows:

paper 1 – collecting data (70%), analysing data and preparing the text (50%);
paper 2 – collecting data (100%), analysing data and preparing the text (50%);
paper 3 – collecting data (80%), analysing data and preparing the text (10%);
paper 4 – collecting data (100%), analysing data and preparing the text (50%).

1. INTRODUCTION

'Conservation efforts may or may not succeed in saving any particular Hawaiian species, regardless of how intensive those efforts may be. Faced with this, our best option other than continuation of conservation efforts is to study Hawaiian species intensively. Future generations may not fault us for failure to save a species that could have been saved with reasonable, simple practical measures. They will surely fault us, however, if simple measures were available but not used and may, justifiably fault us for not gathering as much information as we can while these species are still in existence.'

Sherwin Carlquist. 1995.

There is a growing worldwide concern about biodiversity status and its trends. During recent decades serious attempts have been made to gain an understanding of the role of natural biodiversity drivers – evolutionary and biogeographic processes behind the observed pattern of diversity. Human alteration of the global environment has caused widespread changes in the global distribution of organisms and has become one of the most important drivers shaping the regional and local patterns of biodiversity and ecosystem function. Natural barriers that once prevented the movement of species have become ineffective, ending millions of years of biological isolation. Biological invasion by alien species is recognized as one of the major threats to native species and ecosystems (IUCN 2000). An understanding of biodiversity drivers would enable reasonable steps to be taken to preserve and restore biodiversity.

Two-thirds of the world's plant species are in danger of extinction in nature during the course of the 21st century (Given 2002). The most critical parts of the world are those regarded as biological 'hotspots' (Myers *et al.* 2000). Though ferns constitute only a modest percentage of all vascular plants, they are vital components of the ecosystems of biological hotspots, especially of moist tropical forests and oceanic islands. As an ancient plant group, they are of biogeographic and phylogenetic interest. There are many families and genera where the extinction of only few species not only results in permanent genomic loss but obscures the remaining evolutionary scenario (Given 2002). Ferns are often habitat specialists and presence of water is key factor determining their success (Kornaš 1985, Given 1993, Rana 1999). That makes them highly vulnerable to the change in vegetation and ecosystem processes at scales from small and local, to large and global. It also means that ferns have potential to provide useful indicators of disturbance and ecological processes especially in forests.

The life-cycle of ferns comprises two alternating generations, the small haploid nonvascular gametophyte and the diploid relatively large vascular sporophyte. Both generations consist of several developmental stages (Nayar and Kaur 1971; Cousens 1981; Cousens, Lacey and Scheller 1988). Duration of different generations and life stages seems to be specific depending of the general life strategy of the species (Cousens 1981, Dassler and Farrar 2001). Though there has been tendency to think of sporophyte generation as a dominant, the success of pteridophytes in a community is limited both by the successful establishment of free-living gametophytes and the survival of sporophytes (Werth and Cousens 1990). The ferns are characterised by good dispersal ability due to the high number of very small spores (Smith 1972; Tryon 1970, 1972, 1986), still the actual colonisation of new sites is determined by gametophyte ecology (Hill 1971; Page 1979; Dassler and Farrar 2001) and species specific breeding system (Lloyd 1974a, Lloyd 1974b, Lloyd 1988). Colonizing phases, gametophyte and sporeling (juvenile sporophyte) are most dependent on microedaphic and microclimatic conditions with mortality of individuals during these stages being the highest (Tryon 1970; Dassler and Farrar 2001; Peck *et al.* 1990). Since meiosis is a sporophyte function and fertilization is a gametophyte function, a special consideration should be paid both to the generative (gametophyte 'population') and reproductive (sporophyte 'population') phases of the life-cycle according to their different responses to the environmental stress, disturbance and competition (Grime 1985). The full life cycle (spore germination-gametophyte establishment-fertilization-sporeling establishment-sporophyte recruitment) is restricted to the domain of specific habitats where sporophytic and gametophytic tolerances overlap (Page 1979, Warne and Lloyd 1980). Also, because of their ability for long distance dispersal and colonising remote and relatively inaccessible sites, the populations with ferns only in younger stages (gametophytes, sporeling, premature) may evolve suggesting that in such circumstances the species often encounter conditions which allow establishment but are unsuitable for the sporophytic recruitment (Grime 1985). The study of the plant population ecology and dynamics, has since been concentrated mainly on seed plants. The detailed studies of structure and dynamics of natural populations of ferns are still scarce (Willmot 1985, Cousens *et al.* 1988, Peck *et al.* 1990, Bremer 1994, Waldren 1994, Hill and Silander 2001). Though often stereotyped, there seems to be a remarkable diversity of life strategies among the ferns.

The Hawaiian archipelago with eight high and 124 smaller islands, stretches ca 2580 km across the northern Pacific Ocean. It lies about 4000 km from the nearest continent and from the nearest set of high islands, the Marquesas (Juvik and Juvik 1988). The islands span a remarkable range of habitats from tropical lowlands to alpine zones, representing three moisture regimes: dry, mesic and wet (Gagne and Cuddihy 1990). Mean annual temperature decreases with increasing elevation, while precipitation is primarily controlled by exposure to the prevailing northeast trade wind. The age of the substrate in which

ecosystems have developed, varies according to the age of the island (Vitousek 2002).

The Hawaiian Islands are the most isolated island group with the highest level of endemism of any floristic region in the world and include about 40% of the endangered plant species listed in the USA (Wagner *et al.* 1990). The native flora is depauperate and consists entirely of elements derived from long-distance dispersal and evolved by adaptive radiation. It has been shown to be derived predominantly from the southwest, of the Indo-Malayan flora, but with strong Austral elements and smaller American component (Fosberg 1951). The flora of 1117 vascular species derived from about 405 colonists. Speciation within the archipelago has tripled the number of species, while approximately one-third of speciation occurs through dispersal events between islands and about two-thirds within islands (Funk and Wagner 1995).

Native vegetation on all of the main Hawaiian Islands has undergone extreme alteration because of past and present land management practices including accidental and deliberate animal and plant introductions (Wagner *et al.* 1985, Cuddihy and Stone 1990). Nine percent of the native flora are already extinct, and 52,5% are at risk (endangered, vulnerable, or rare). Of 282 listed endangered species, 133 have only 20 or fewer individuals left in the wild. Among these single-island endemic taxa, with limited habitat distributions and low historical population densities being at highest risk with rapid anthropogenic changes (Sakai *et al.* 2002). The greatest absolute numbers of taxa at risk have distributions in mesic lowland and mountain forests. Native pteridophytes to Hawaiian Islands include 145 endemic (77%) and 43 indigenous (23%) taxa (Palmer 2003). According to the IUCN criteria (2001), 34 taxa (18%) would classify as critically endangered (J. Lau, K.R. Wood 2001, pers.comm.). Primary threats to ferns include ongoing destruction and modification of habitat by introduced ungulates (goats, pigs, cattle, sheep and deer) and competition with alien plants.

The *Diellia* ferns (*D. erecta* Brack., *D. falcata* Brack., *D. pumila* Brack.) were discovered by W. D. Brackenridge, and based on their sorus position and structure described as a separate genus (Brackenridge 1845). Since taxonomic research of the genus by W. H. Wagner (1952) until present, *Diellia* ferns have been treated as a genus endemic to the Hawaiian Islands comprising of six species and one hybrid (Wagner 1999): *Diellia erecta* Brack.; *D. falcata* Brack.; *D. leucostegioides* (Baker) W.H. Wagner; *D. mannii* (D.C.Eaton) W. Robinson; *D. pallida* W.H. Wagner; *D. unisora* W.H.Wagner and *D. falcata* x *D. unisora* (*D. x lauii* W.H.Wagner). It has been treated as monophyletic genus evolved from *Asplenium* ancestry (Wagner 1952, 1953a) and radiated over the Hawaiian Islands. Comparative analyses of morphological characteristics common to *Diellia* species led W. H. Wagner to propose that *Diellia* was most closely related to the 'black stemmed' group of rock habitat species of *Asplenium*, typified by *Asplenium trichomanes* L. (Wagner 1952, 1953a,b). He identified *D. leucostegioides* as the 'prototype' of *Diellia*.

The restricted distribution of the *Diellia* species has been mentioned in most earlier published studies (Hillebrand 1888, Smith 1934, Degener 1950, Wagner 1952, Fosberg and Herbst 1975, Palmer 2003). All species have been considered to be either very rare, on the verge of extinction, or decreasing. Currently known distributions are based on the collection period followed the discovery (V. Knudsen, G. C. Munro, D. L. Topping, C. N. Forbes, F. R. Fosberg, G. W. Russ, O. Degener, A. Brodie, H. L. Lyon, C. Skottsberg *et al.*), Wagner's research (1947–1952) and recent surveys by University of Hawaii, Bishop Museum and National Tropical Botanical Garden.

Diellia erecta, and its associated forms, is the only *Diellia* species which was originally found on six of the bigger islands, now it is found only on Kauai, Oahu, Molokai, Maui and Hawaii. The five other *Diellia* species are all single island endemics. The type specimens of *D. leucostegioides*, were collected on East-Maui sometime before 1879. Since that the species has not been relocated. *D. mannii*, originally collected from Kauai, was also not found for more than 100 years. Another endemic species to Kauai, *D. pallida*, was recognized as a separate species from 1993 (Wagner). Three taxa are endemic to the island of Oahu. *Diellia falcata* is the only species showing slightly higher local abundance. It is sparsely distributed over the whole range of Waianae Mts. *Diellia unisora* was discovered in 1932 (Wagner 1951) and is localised in the southern part of Waianae Mts. The hybrid between these two local endemic species, was described recently (Wagner *et al.* 1999). All three endemic taxa occur together in the Pualii-Palawai region in the southern Waianae Mts.

The flora of Hawaiian Islands has been very well surveyed and there is a rather good information available, both about the historical occurrence of *Diellia* populations, as well as about their present distribution. Still most of this knowledge originates from the period of massive animal and plant invasions started from the middle of the 19th century. For this reason and because of the fact that these ferns are so rare today, there is no sufficient data about what could have been originally 'typical' abundance and distribution for these ferns. *Diellia* species are small to medium-sized ferns found on steep slopes in mesic lowland and mountain forests (Wagner 1951). Their specific characteristics are submarginal sori opening outward and anastomosing venation, forming areolae. They have a short decumbent or erect rhizome and brittle stipes with clathrate scales on the stipe base. *Diellia* ferns are usually terrestrial, sometimes epipetric plants, growing on old lava blocks and cliffs. They have a sexual cycle (Wagner 1952), but little is known about the life history, reproductive cycles and longevity, germination and gametophyte ecology of *Diellia* species. All *Diellia* taxa are threatened due to habitat degradation by feral ungulates and competition with alien plant species (Perlman and Wood 1995, 1996; Wood 1998, 1999). Since these negative factors continue to impact *Diellia* populations, the monitoring of the regional dynamics and understanding of the present condition of these populations, is of primary importance for the creation of a proper conservation strategy for them.

In principle, the status and trends of plant populations may be studied on four levels: population distribution, quantitative monitoring of population size/condition, monitoring of population structure, and demographic study of the population (Hutchings 1991; Menges and Gordon 1996). Long-term studies of demography give extremely useful information for conservation management, concerning critical stages and specific requirements of rare plants. Demographic studies are, however, laborious, and often take many years to complete, which prevents their wide use both in population studies and in conservation biology (Harvey 1985; Oostermeijer *et al.* 1994). Another less time-consuming way to relate the demographic performance of the populations of perennial plants to overall vegetation change is to analyse their structure in different plant communities. The structure of a population may be described by classifying the individual plants either by age, size, or their life stage (Gatsuk *et al.* 1980; Rabotnov 1985). Since it is often impossible to establish the age of individuals, and both size and reproductive capacity are poorly correlated with age (Harper 1977), the best way of describing populations of such species in a single census is by determining the relative proportions of individuals in the different ontogenetic stages of their life cycle. This approach was originally developed by T. Rabotnov in fifties (cf. Rabotnov 1983), but was long time neglected due to he published his main principles in Russian. Starting from eighties, the method has proved to be successful in a number of studies of perennial plant species, including rare and endangered species (Rabotnov 1985; Oostermeijer *et al.* 1994; Bühler and Schmid 2001; Hegland *et al.* 2001).

The current study was aimed to meet the following objectives:

1. To describe current distribution of the taxa of fern lineage *Diellia*.
2. To describe population stage structure of the taxa of *Diellia*.
3. To collect additional information about their ecology and evolution.
4. To make suggestions for conservation.

2. METHODS

2.1. Data collection

According to the USFWS Species List 1999, there are forty-two local populations of *Diellia* spp. in the Hawaiian Islands. Among them, twenty-two local populations represent *D. falcata*; the remaining twenty populations did not include *D. mannii* (rediscovered in 2002, Agurauja and Wood 2003) and populations with taxonomically unclear status. As endemic lineage of *Diellia* ferns consists of very rare and local federally listed endangered taxa, the aim was to describe as many extant *Diellia* populations as possible. The distribution data of *Diellia* species in the Hawaiian Islands were obtained from published material (Wagner 1952), collection data of several herbaria (National Tropical Botanical Garden, Bishop Museum, Botanic Garden and Botanical Museum Berlin-Dahlem, Brooklyn Botanical Garden, Harvard University, Royal Botanic Gardens Kew, New York Botanical Garden, Museum National d'Histoire Naturelle, Paris), from floristic surveys of Hawaiian Islands conducted by National Tropical Botanical Garden (Perlman and Wood 1995, 1996; Wood 1998, 1999) and Hawaii Natural Heritage Program, University of Hawaii (J. Lau, pers. comm.). In addition, on two islands (Kauai, Molokai), some areas of remnant mesic forest patches with community composition indicating for suitable habitat conditions for *Diellia* ferns, were checked also by the author.

Population stage structure was studied for five taxa – *D. erecta*, *D. pallida*, *D. falcata*, *D. unisora*, and *D. erecta* f. *alexandri*. *Diellia mannii* was represented by one individual only (Agurauja and Wood 2003) and the population-level analysis was not possible. Because of uncertain taxonomy the local populations of *D. falcata*, *D. unisora* and *D. falcata* x *unisora*, found in the so-called ‘hybrid zone’ in Pualii – Palawai area on Oahu, were also omitted from analysis. In the case of *D. unisora*, three different locations were checked, but for further analysis were used only one morphologically almost ‘pure’ population patch of S-Ekahanui. *D. erecta* is the most variable species of the lineage. Wagner (1952) described the forms *D. erecta* f. *alexandri* (Hillebr.), *D. erecta* f. *erecta* and *D. erecta* f. *pumila* (Brack.) W.H. Wagner. Single intermediate individuals between f. *erecta* and f. *alexandri* or individuals with morphologically different fronds on the same plant can still be found (Wagner 1952; K. R. Wood and M. Query 1997; K. R. Wood, R. Agurauja, M. Query 1998, R. Agurauja 2003, 2004 pers. comm.). The recently discovered (2001) and currently only known population (K. R. Wood, S. Perlman, pers. comm.) of *D. erecta* f. *alexandri* on Kauai, is also morphologically highly variable, consisting of types what W. M. D. Hillebrand (1888) recognized as separate species *D. alexandri* (Hillebr.) Diels, *D. centifolia* (Hillebr.) Diels, *D. knudsenii* (Hillebr.) Diels and *D. laciniata* (Hillebr.) Diels – taxa that were not found later

by Wagner (1952). As a unique remnant of once more widely distributed taxon (there are several specimens collected earlier in the area of Waimea Canyon and Halemanu), the population of *D. erecta* f. *alexandri* was included into the current survey. In the case of relatively more abundant *D. falcata* on Oahu, only eight local populations in different valleys of Waianae Mts. were surveyed.

Three extant populations of critically endangered *Diellia pallida* were selected for detailed investigation, the population observations were made once per month. The experimental stage transition estimation was made for *D. pallida* population in W-Mahanaloa. The rare communities of Kauai Diverse Lowland Mesic Forest and Mixed Mountain Mesic Forest consist predominantly of native plant species, but are severely impacted by alien animals. In order to reduce the negative effects of alien ungulates (Stone and Loope 1987), and study their impact (Weller et al. 1988 pers comm.), several exclosures were built into Mahanaloa Valley during 1997–1998. Single mature individuals of *D. pallida* outside the fenced area were protected with net cages from 2002 onwards. As a result, the appearance of sporelings increased dramatically – 28 sporelings were recorded in May 1999 and 314 sporelings in May 2005. Since animals cause strong soil erosion, practically none of the sporelings survive on the steep slope outside the fence. As uprooted and eroded individuals of different life stages were found during every population survey, it was tested if these individuals could be revived when immediately planted back into the soil within fenced area. Altogether, 10 individuals in 2002, 8 individuals in 2003 and 46 individuals in 2004 were rescued. These individuals were monitored until June 2005 and all transitions between life stages (sporeling, premature, mature, extinct) were registered. On the basis of a total of 102 transitions, the average yearly transition probabilities between stages were calculated. It was expected that the fenced area in W-Mahanaloa represents more or less benign conditions for *Diellia* ferns, since it is a mesic forest stand with native plant species only, where the impact of alien ungulates has been eliminated.

Field surveys were conducted over the period of February 2002 – June 2005. Population data obtained during the studies in 1999 (Aguraiuja 2001) were also used for analysis. All populations were censused at least twice. The whole population was defined as the sum of all individuals of the taxon. The local populations were defined according to Hanski and Simberloff (1997) as a set of individuals that live in the same habitat patch and share a common environment. Assessments of population size were derived via direct counting of individuals, except for the relatively larger population of *D. falcata* on Oahu, where two local populations (Kahanahaiki, Huliwai) with a size of approximately 30x30 m were described with the help of ten randomly located 1x1 m sample plots, in which all individuals and their life stages were recorded. In order to describe the stage structure of the population, the following stages were differentiated: gametophyte; sporeling (young sporophyte with simple fronds); premature (pre-reproductive sporophyte with pinnate fronds); mature (reproductive sporophyte), dormant/dead. Since gametophytes are extremely difficult to observe in

field conditions, and in the case of dry looking plants it was not clear if they were dead or dormant, only three stages of sporophyte generation (sporeling, premature, mature) were used in population structure analyses.

For better understanding of the germination timing and regeneration of *Diellia* species, gametophyte populations were recorded and counted by search within and around sporophyte populations. To identify the spore release period, the frond phases were described as follows: vegetative; sori developing; sori opened; sporangia dechisced. For each individual, the number of vegetative and reproductive fronds was counted.

The general descriptions of plant communities were made for all sites. To describe the habitat conditions, elevation (altitudinal range) aspect, slope, substrate, volumetric soil moisture content, litter, groundcover and canopy closure were recorded. The species composition of plant communities in study sites were described in 25 x 25m plots. The occurrence of alien plant species, as well as soil disturbance by alien animal species were characterised. For further analyses, the following robust scales were used to characterise habitat quality. The occurrence of alien plant species was characterised by the three-level scale: scarce – single individuals of alien plant species are found occasionally; intermediate – community represents a mixture of alien and native plant species; abundant – community is predominated by alien species. The soil disturbance by alien animals (feral pig, goat and deer) was also characterised by a three-level scale: weak – animal disturbances are absent or there were few localised disturbed spots; intermediate – animal disturbances were visible, but the trampled and dug soil surface did not exceed 10% of the area; severe – disturbances were evident, trampled and dug areas sometimes exceeded 50% of the soil surface.

For better understanding of the origin and evolution of *Diellia* ferns molecular study was conducted in collaboration with the researchers from several institutions: H. Schneider, George-August-University of Göttingen; T. A. Rancker and J. M. O. Geiger, University of Colorado; S. J. Russell, M. Grundmann and J. C. Vogel, Natural History Museum, London; K. R. Wood, National Tropical Botanical Garden; K. Klobardanz; Colorado State University. The aim was to identify the nearest living relatives of *Diellia* and clarify the origin of the group, also to provide age divergence estimates and evaluate the radiation in the Hawaiian Islands. *Diellia* ferns were sampled across asplenoid ferns with particular emphasis on species of the ‘black-stemmed’ rock habitat *Asplenium* clade. Methods for DNA extraction, amplification and sequencing followed those of the Schneider et al. 2004. Phylogenetic analyses was conducted and divergence times was estimated (Schneider et al. 2005).

2.2. Data analyses

Loglinear analysis and the Freeman-Tukey deviation test (Legende & Legendre 1998) were used to search for discrepancies between field data and null model conditions. It was tested whether the frequencies of plants in particular life stages differed significantly from those predicted from null hypotheses stating a random distribution of individuals among stage classes. Also, between-population differences (within a species) and interspecific differences in life stage distribution patterns were tested, by studying the interaction terms local population*life stage and species*life stage, respectively (StatSoft, Inc. 2001). Loglinear analysis and Freeman-Tukey deviation test (Legende & Legendre 1998) were used to test the empirical life stage frequencies against null model predictions, achieved from an imitation model mimicking the empirical life stage transition dynamics recorded during the experiment with *D. pallida* in W-Mahanaloa (the 'ideal population'). This was done for different species as well as for different local populations within species. The null model was designed to imitate a population with constant annual input of sporelings and annual transitions between four life stages – sporeling, premature, mature and extinct – for 1000 seasonal cycles, using empirically estimated transition probabilities. The resulting equilibrium representation of different life stages was the following: sporelings 56.0% prematures 22.8% and matures 21.2%. This distribution was used as an alternative null model in the analysis. The data may be insufficient due to low number of observations, made with one species only. So far, it has not been possible to grow *Diellia* species through all their life-cycle in artificial conditions, thus it was possible to use only those individuals for experimental estimation, which would otherwise die. The model showed that the overall mean life span of an individual plant was only 2.6 years, mainly due to high sporeling mortality. Out of the 11% of individuals that reached the mature stage about 1% lived more than 35 years, average life span for mature plants being 23.2 years. This is in good accordance with the observations by Wagner (1952). Two alternative null models were called as 'the random null model' and 'the ideal null model'.

The comparisons of the representation of different life stages were performed in four taxa (three species and one form). More detailed comparisons of local populations within a species were possible in four cases (Table 1). *Diella mannii* was excluded, since it is represented by only one mature individual. *Diellia falcata* x *unisora* hybrid populations were not included in the classification of population conditions. A manipulated population of *D. pallida* in W-Mahanaloa also was not included.

Three types of populations were distinguished. The population was classified as 'dynamic' when the sporeling stage was represented to a significantly greater extent or mature stage to a significantly lower extent than predicted from null model conditions. The population was classified as 'regressive' when the

mature stage was represented significantly more frequently or sporeling and premature stage less frequently than predicted from null model conditions. The population was classified as 'normal' when the representation of all stages corresponded to that assumed from null model conditions. In addition, population's were classified as 'normal' when the sporeling stage was represented less frequently and premature stage more frequently than stated from null model conditions, since such a pattern may refer to between-year variation in population recruitment. Populations with less than ten individuals were considered as regressive without any statistical analysis, although they may represent not only decreasing populations, but also the result of recent colonisation events, still being prone to extinction due to their small size.

Log-linear analyses were conducted to study if the cumulative impact of alien species differed among sites where extinction events of *Diellia* species have taken place, compared to sites where *Diellia* individuals are still present.

Spearman rank correlations (StatSoft, Inc. 2001) were calculated to study: 1) the relationships between population condition estimated by using random and ideal null model conditions; 2) the relationships between the estimated population condition during the first and the second census, 3) the relationships between the population size at the first census and absolute population size, the numbers of individuals belonging to the different developmental stages, and population condition at the second census.

A repeated measures main effect GLM (StatSoft, Inc. 2001) was applied on log-transformed numbers of plant individuals, while species (except *D. mannii*, which is represented by only one individual), developmental stage, estimated occurrence of alien plants, and estimated rate of soil disturbance by alien animals were used as fixed factors, and time as a repeated measures factor.

3. RESULTS

3.1. The phytogeographical distributions

Over the period of February 2002 – June 2005, field surveys were conducted in 51 currently known and historical locations on five islands: Kauai, Oahu, Molokai, Maui and Hawaii (Fig. 1, Table 1). The ferns were found on 33 locations, on four of those the extinctions were documented during the research period. Single individuals were documented on 5 locations.

A single individual of *D. mannii* was rediscovered in Halemanu (*leg.* L. Arnold, *det.* R. Agurauja) after not being documented on Kauai for over one hundred years. It was first collected by H. Mann and W. T. Brigham as *Microlepia mannii* D. C. Eaton sometime during 1864–1865. Last known collections were probably made by V. Knudsen during the period 1871–1886. The status of the species has been assessed as probably extinct (Fosberg and Herbst 1975; Wagner et al. 1999), not seen after 1900 (Wagner et al. 1999; USFWS 1999), but considered as a species of concern as “further field research may reveal that *D. mannii* still exists somewhere in western Kauai” (Wagner et al. 1995). On April 23, 2002, a single individual of *D. mannii* was found by resource conservation technician Laura Arnold (Koke’e Resource Conservation Program) during the forest weeding work in Halemanu, and identified by the author as *D. mannii*. The original vegetation of the site, *Acacia-Metrosideros* montane mesic forest has been degraded and was dominated now by *Corynocarpus laevigatus* J. R. Forster & G. Forster. This rediscovery stimulated to pay more attention to very fragmented mesic forest communities of the area as several *Diellia* taxa have been recorded there historically (*D. mannii*, *D. erecta*, *D. erecta* f. *alexandri*). Unfortunately, no more new sites were found during this research period.

The habitat of Puu Ka Pele on Kauai (*D. pallida*) was significantly degraded. The site at Makaha on Kauai (*D. pallida*) was completely overgrown by *Erigeron karvinskianus* DC and *Blechnum appendiculatum* Willd. The area of suitable habitat for *D. erecta* at Puu Kolehaha on Molokai was reduced due to trampling and browsing by goats. Hybrid individuals of *Diellia falcata* x *unisora* were growing in four gulches in Waianae Mts. On Oahu. In S-Palawaii and S-Pualii the hybrid population was steadily increasing, while in N-Pualii and S-Ekahanui few occasional hybrid individuals were found.

Current research includes the data about 51 local populations, though the taxonomic status of 5 populations remained unclear. Among the remaining 46 populations, 28 local extinction were recorded across the six taxa studied. Among studied populations eight were known ‘historically’ (before 1950) and ten were first recorded after 1950, six of them after 1998. During the research period of 2002–2005 *Diellia* species were represented as follows: on Oahu four

taxa (*D. erecta*, *D. falcata*, *D. unisora*, *D. falcata* x *unisora*) of which 22 populations in 9 locations were studied; on Kauai three taxa (*D. mannii*, *D. erecta* f. *alexandri*, *D. pallida*) in five locations; on Molokai two taxa (*D. erecta*, *D. erecta* f. *alexandri*) in four locations; on Maui two taxa (*D. erecta*, *D. erecta* f. *alexandri*) in two locations; on Hawaii one taxon (*D. erecta*) in one location.

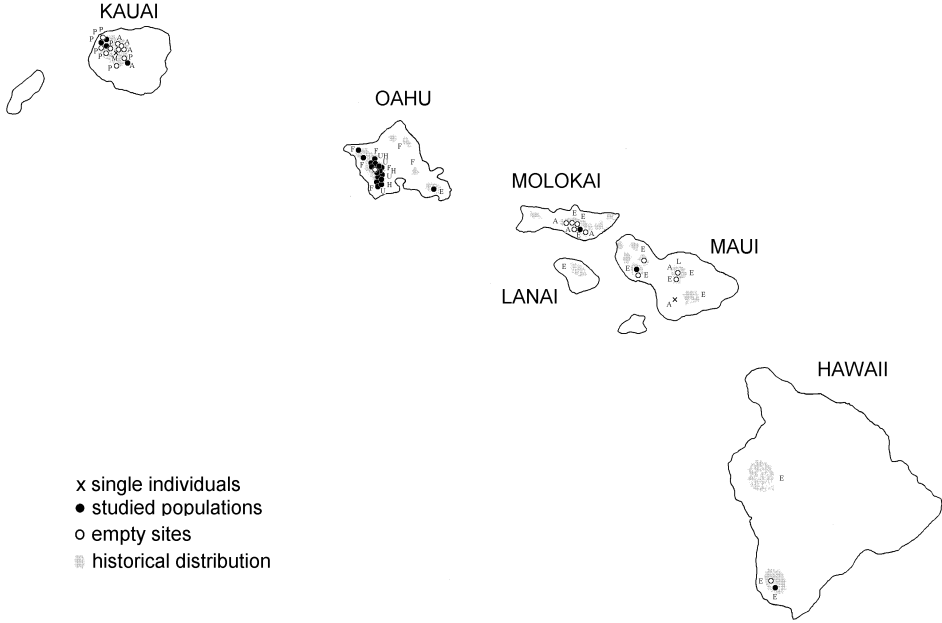


Figure1. The distribution of the fern genus *Diellia* in the Hawaiian Islands: A, *D. erecta* f. *alexandri*; E, *D. erecta*; F, *D. falcata*; L, *D. leucostegioides*; M, *D. mannii*; P, *D. pallida*; U, *D. unisora*; H, *D. falcata* x *D. unisora*.

Table 1. Characterisation of the *Diellia* spp. populations and their sites in Hawaiian archipelago: the estimates of population conditions are based on the log-linear analysis ('ideal equilibrium population' versus observed population): the proportion of sporeling stage has significantly higher representation in case of dynamic (D) populations, and mature stage significantly higher representation in case of regressive (R) populations than predicted by the null model conditions (Freeman Tukey deviation test, $p < 0.05$). In normal (N) population the representation of all stages corresponds to that assumed from null model conditions. Populations with less than ten individuals were considered as regressive without any statistical analysis. *D. falcata* x *unisora* hybrids populations are not included to the classification of population conditions. The year of extinction is indicated only when exactly known, otherwise 'not found' is mentioned.

Species	Population		First described/re-invented	Extinct	Census		Condition		Size		Habitat quality		
	Island	Site			1	2	1	2	1	2	Impact of invasive animals	Presence of invasive plants	Other
<i>D. erecta</i>	Oahu	Hawaii Loa	1840/1986		1999	2005	N	N	171	55	Severe	Abundant	Erosion
	Molokai	Puu Kolekole	1912/1949/2002		2002	2005	R	R	14	25	Intermediate	Scarce	
		E – Puu Kolekole	1912/2003	2004	2003	2004	R	R	1	0	Intermediate	Intermediate	
		E – Kawela	1993/2003	2004	2003	2004	R	R	1	0	Severe	Abundant	Erosion
		W – Kawela	1912	Not found	2003						Severe	Abundant	Erosion
	Maui	Makolelau	1987/1997	1999	1999						Severe	Abundant	Erosion
		Hanaulaiki	2000		2002	2005	R	R	7	6	Intermediate	Intermediate	
		Iao Valley	1990	Not found	2003						Intermediate	Intermediate	Erosion
		Mana Wai Nui	1997	Not found	2004						Severe	Abundant	
		Makawao	1949	Not found	2003						Intermediate	Abundant	Erosion
Hawaii	Manuka Honomalino	Manuka	1927/1992		1999	2005	R	N	149	155	Weak	Intermediate	
		Honomalino	1991	Not found	1999						Weak	Abundant	

Table 1. (Continuation)

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Species	Population		First described/re-invented	Extinct	Census		Condition		Size		Habitat quality		
	Island	Site			1	2	1	2	1	2	Impact of invasive animals	Presence of invasive plants	Other
<i>D. unisora</i>	Oahu	S – Ekahanui	2000		2002	2005	R	R	76	16	Weak	Abundant	
		Pohakea Pass	1932	Not found	2004						Severe	Abundant	Erosion
		S – Pualii	1991		1999						Severe	Abundant	Erosion
		N – Pualii 1	2000		2005		D		93		Intermediate	Abundant	Erosion
		N – Pualii 2	2000		2005		D		186		Intermediate	Abundant	Erosion
		N – Pualii 3	2000		2004	2005	D	N	285	308	Intermediate	Abundant	Erosion
		N – Pualii 4	2000		2005		N		198		Intermediate	Abundant	Erosion
		S – Palawai	1991		1999						Intermediate	Abundant	Erosion
<i>D. falcata</i> <i>x unisora</i>	Oahu	S – Ekahanui	2000		2002						Weak	Intermediate	Erosion
		S – Pualii	1991		1999						Intermediate	Abundant	Erosion
		S – Palawai	1991		1999						Intermediate	Abundant	Erosion

3.2. Habitat

The natural community where *Diellia* species grow was usually *Diospyros/Metrosideros* Mesic Forest, thereby on the island of Kauai this included rare communities of Kauai Diverse Lowland Mesic Forest and Mixed Mountain Mesic Forest and on the island of Hawaii *Nestegis* Lowland Forest. In drier and more open sites of the steep slopes *Diellia* species were growing in *Styphelia/Dodonea* Mesic Shrubland. In less disturbed conditions, the ground vegetation of such forests included several other relatively abundant fern species like *Microlepia strigosa* (Thunb.) C. Presl, *Doodia kunthiana* Gaudich., *Doryopteris decipiens* (Hook.) J. Sm., *Dryopteris sandwicensis* (Hook. & Arn.) C. Chr., *Nephrolepis exaltata* (L.) ssp. *hawaiiensis* W. H. Wagner, *Asplenium macraei* Hook. & Grev., etc. Several sites suffered due to expansion of alien plant species like *Blechnum appendiculatum* Willd, *Christella parasitica* (L.) H. Lev., *Adiantum hispidulum* Sw., *Phlebodium aureum* (L.) J. Sm., *Erigeron karvinskianus* DC, *Ehrharta stipoides* Labill., *Melinis minutiflora* P. Beauv., *Oplismenus hirtellus* (L.) P. Beauv., *Kalanchoe pinnata* (Lam.) Pers., *Passiflora suberosa* L., *Clidemia hirta* (L.) D. Don, *Psidium cattleianum* Sabine and *Schinus terebinthifolius* Raddi, as well as due to the trampling, digging and browsing by ungulates (pigs, goats and deer). Most of *Diellia* populations on Oahu were growing in remnants of native forest, usually dominated by naturalised species *Psidium cattleianum* Sabine and *Schinus terebinthifolius* Raddi, on *D. unisora* sites in N-Pualii also by *Casuarina equisetifolia* L.

Diellia species were restricted to a spatially-fragmented habitat type on the steep sides of gulches. Usually, they occurred on northern slopes at altitude of 360–1010 m a.s.l. with slope varying from gentle to steep (30°–75°), to nearly vertical cliff faces. *Diellia pallida*, *D. falcata*, *D. erecta* f. *alexandri*, *D. mannii* and *D. unisora* and the hybrids were terrestrial ferns, while *D. erecta* f. *erecta* occurred on old lava blocks and cliffs as well as on soil. Soil moisture content on *D. pallida* sites in Mahanaloa-Kuia (Kauai) reduced about 50% from February to June. Most of the severely disturbed sites had very sparse ground cover, 10–25%. In less disturbed sites it varied from 20–50% and was somewhat exceptional, varying from 10–100% on *D. erecta* f. *alexandri* site in Kawai’iki (Kauai). Typically, plants were found growing on soil that was rocky, granular and usually dry, with some leaf litter and mosses. All *Diellia* species preferred the shade of canopy and understory shrubs (canopy coverage 70–90%). Though general habitat type was similar for all taxa, there seem to be some differences in habitat preferences between different taxa. Present distributions showed that *D. mannii* and *D. erecta* f. *alexandri* grow on higher elevations than other *Diellia* taxa. *Diellia pallida* and *D. falcata* seem to prefer the dark shade of the mesic forest in the middle part of the steep slopes of the gulches (elevation 300–600 m). *D. erecta* and *D. unisora* are able to inhabit much more drier and open areas than the remaining *Diellia* species. While *D.*

falcata occurs mainly in the forest of middle part of the gulches and *D. uniosra* in more open shrubby areas in the upper part of the gulches, the hybrid of these two seems to favour the intermediate secondary community dominated by alien species. The differences of specific habitat requirements of different *Diellia* species need further analyse.

3.3 Life history and ecology

Diellia species have a short creeping (up to 0,5 cm for smaller plants and 2,5–4,5 cm for bigger plants) non-branching rhizoms and usually a clump of 2–5 fronds (6–7 fronds for *D. erecta* f. *alexandri*). Though during normal weather conditions *Diellia* species may produce new fronds all year around and sporoproducing fronds with sori in all developmental stages can be found simultaneously, the active growth takes place during the rainy season, from November to May. For the drier summer period, the growth decelerates and in case of droughts continues only during the next wet season. The age of the fronds is up to 18 months. The reduced life span of the fronds were observed when the ferns were attacked by introduced alien insects (*Heliothrips haemorrhoidalis* (Bouche)).

For all *Diellia* taxa, there was a significant difference between the frond size of the plants at different life stages (Aguraiuja 2001). The number of fronds of *Diellia* species was not correlated with the life stage and this is probably indicative of the soil and moisture conditions of the habitat. The proportion of spore producing mature individuals varied between years. Reverting of reproductive mature plants to a vegetative phase of only one or two short vegetative fronds was observed for *D. erecta*, *D. falcata* and *D. pallida*. In some cases, it was clearly a result of ageing, but seemed to be more common as the expression of the stress condition related to erosion (the rhizomes were washed out and hardly attached to the soil), drought or changed moisture condition of the substrate. Delayed stage transformation up to five years, probably caused by unfavorable microsite conditions, was observed on *D. pallida*. Since *Diellia* species are inhabitants of mesic forest communities with rather arid conditions during summer, they have been supposed to have a certain ability to survive regular or exceptional dry periods in dormant stage. Current research did not confirm the ability of *Diellia* ferns for real dormancy in mature life stage, rather was it the reduced vegetative growth during stress conditions, what ended with the death if lasted for several years. Repeated observations of dry looking sporeling individuals showed that they did not revive as well. However the timing of spore germination and establishment of gametophyte populations allow to presume that there may be some adaptations for gametophytes to survive the dry summer. Gametophyte ecology of *Diellia* species needs further study.

During the normal weather conditions, the ferns with spore-producing fronds could be found all year around. The maximum spore release was still seasonal, following the wet season. The seasonal dynamics seemed to be population specific and island specific, depending on local differences of the duration and timing of wet season. More detailed observations of *D. pallida* populations showed two peaks for germination, resulting in mixed populations of gametophytes of different age. In general the germination and establishment of gametophytes and sporelings was observed to occur from December to April. In Mahanaloa careful search was made around the locations of extinct individuals from 2000 and 2001, to check the possible germination and re-establishment. In three cases, few gametophytes and sporelings appeared two or three years after the extinction of mature plants, but did not persist because of changed microhabitat conditions and erosion. The limiting factors for sporeling survival were erosion, blanketing effect of litter or rain wash during the wet season and reduced soil moisture during the dry season.

3.4. Evolution

Diellia is a monophyletic lineage and nests within a large derived clade of *Asplenium* that includes members of the ‘black-stemmed’ rock spleenworts. The *Diellia* subclade consist solely of species of *Diellia* and is sister to the *A. normale* subclade. Nucleotide variation was insufficient to resolve the phylogenetic relationships within *Diellia* clade. Further research is needed to clarify the speciation within the lineage. Estimates of divergence times indicated that the *Diellia* lineage is old and has long been separated from other groups of ‘black-stemmed’ rock spleenworts. The divergence of the *Diellia* lineage from its nearest relatives occurred at ca. 24,3 MYR ago what matches well with an independant estimate for the renewal of Hawaiian terrestrial life (ca. 23 Myr ago). Thus, the ancestor of the *Diellia* lineage may have been among the first successful colonists of the newly emerging islands in the archipelago. Estimated time of the *Diellia* radiation (ca. 2 Myr ago) is younger than the oldest island of Kauai (ca. 5,1 Myr ago) but older than the younger major islands of Maui (ca. 1,3 Myr ago), Lanai (ca. 1,3 Myr ago) and Hawaii (ca. 0,43 Myr ago).

3.5. The population structure

Populations were classified as dynamic, normal or regressive, depending on the distribution of individuals among life stage classes. Null model conditions assumed either random distribution among stage classes, or distribution pattern corresponding to experimental ‘ideal population’ of *D. pallida*.

There was a significant Spearman rank correlation between the condition of populations estimated by 'random model' and 'ideal model' ($R=0.88$, $p<0.001$ in the first census, $R=0.71$, $p>0.05$ in the second census). In seven of the 11 cases from the first census, and in eight of the 14 cases from the second census, the estimations of the condition were similar. In the remaining cases, the random model gave one step more positive estimation of the status than ideal model, except one case (*D. unisora* in N-Pualii 4). One may decide that 'ideal model' gives more realistic estimate of the condition since it assumes larger number of sporelings and prematures in equilibrium conditions than random model.

The analysis of the last census data across all local populations within a taxon showed that the general condition of analysed *Diellia* taxa were different (Chi sq = 635.67; $p<0.001$, $df = 14$). The overall condition of populations of *D. erecta* f. *alexandri* was classified as regressive, the condition of *D. unisora* as dynamic, and the condition of *D. falcata*, *D. pallida* and *D. erecta* as normal. If compared with the estimates of the first census, the general condition of three species (*D. erecta*, *D. falcata*, *D. unisora*) slightly improved during the research period.

The total size of population during the first census was significantly correlated with total size ($R=0.92$, $p<0.001$), with the number of sporelings ($R=0.91$, $p<0.001$), premature individuals ($R=0.95$, $p<0.001$) and mature individuals ($R=0.83$, $p<0.001$) during the second census, as well as with the estimated population condition during the second census ($R=0.77$, $p<0.001$).

There was a nonsignificant Spearman rank correlation between population condition during the first census and the total size of population during the last census ($R=0.44$, $p<0.054$), as well as with the number of sporelings ($R=0.45$, $p<0.054$).

Repeated measures GLM showed that the number of individuals in local populations was significantly dependent on the particular *Diellia* species ($F=3.38$, $df=4,46$, $p=0.022$), as well as on the impact of alien animals ($F=4.26$, $df=2,46$, $p=0.020$). The disturbance of the soil surface by alien ungulates resulted in a smaller number of *Diellia* individuals in local populations. Numbers of individuals did not significantly differ between life stages, years, and with different alien plant presence ($p>0.05$).

The analysis was conducted also on the level of local populations. The Spearman rank correlation between the population status in the first and second census was nonsignificant ($R=0.40$, $p=0.0875$). In nine cases out of nineteen comparisons, the condition of the local population did not change. The condition of four local populations deteriorated, and four other local populations, earlier classified as regressive, had become extinct. These were all very small populations, consisting of one individual in two cases, three individuals in one case and of seven individuals in another. In two cases, the condition of the regressive population had improved.

Diellia pallida

In 1999, the population in W-Mahanaloa was predominated by mature individuals (45% of those were spore-producing) and classified as regressive. For 2002, the condition of the population was much worsen. From 15 mature individuals recorded in 1999 (Aguraiuja 2001), seven were extinct, four uprooted by pigs and drying, the remaining browsed and without a single fertile frond. The uprooted rhizomes were immediatly planted into the neighbouring exclosure and the rest of mature individuals were protected from direct ungulate disturbance with net cages. The result of these activities and favourable weather conditions in 2003–2004, was increased spore rain and predomination of sporeling stages in 2003–2005. The population structure was classified as normal in May 2002, and further on as dynamic. The number of sporelings was highest in March 2005, with total of 605 recorded sporelings. Though because of severe angulate disturbance and erosion, most of these did not survive on the steep slope outside the fence. The number of mature individuals did not change much during 2002–2005, except one extinction through rockfall. The transition to the premature stage was very slow, resulting with 5 premature individuals in June 2005. The dynamic condition of manipulated population of *D. pallida* in W-Mahanaloa demonstrated the biological potential for self-recovery of the species if supported by conservation management – the protection of remaining habitat patches and creation of safe-sites for establishment.

The population in Kuia was predominated by sporelings through 2003–2005 and classified as dynamic. The highest number of sporelings, of 205 individuals, was reached in May 2004. As this population was in natural conditions without any protection against ungulate disturbance, the proportion of sporelings was much smaller than in W-Mahanaloa. There were two transitions into mature stage during the research period.

From two mature and one premature individuals in E-Mahanaloa recorded in 1999 (Aguraiuja 2001), only one mature survived the period 1999–2002. No changes were recorded until April 2005, when two natural sporelings were recorded.

Diellia erecta* f. *alexandri

All local populations of *D. erecta* f. *alexandri* classified as regressive. The single individual in Polipoli (Maui) was healthy and produced the spores every year, but the whole habitat patch of native vegetation was very small and isolated, and thereby would classify as ‘extinction site’. The single individual (1999) in Onini Gulch (Molokai) had two sporelings in 2002, but all three were extinct in 2003. In Kawai’iki (Kauai) the sporeling and premature stages were under-represented and the mature stage over-represented. In general the population structure did not change during the research period, though the numbers of premature and sporeling stages varied between years. This population was highly reproductive through all research period. The paucity of

gametophytes and sporelings may be the result of higher competition with other species such as *Microlepia strigosa* (Thunb.) C. Presl, *Dryopteris fusco-atra* (Hillebr.) W. J. Rob, *D. wallichiana* (Spreng.) Hyl., *D. unidentata* (Hook. & Arn.) C. Chr. and the disturbance caused by feral pigs.

Diellia erecta

Diellia erecta occurred on four islands and the stage structure of populations on these was significantly different (Pearson Chi sq = 90.77; $p < 0.001$, $df = 6$).

The population in Manuka (Hawaii) classified as a normal. It grows in the historical distribution area, known since 1927 (G. W. Russ 36, 37, *Herbarium Pacificum* Bishop Museum (BISH)), but is experiencing frequent long droughts resulting in fluctuations in spore production and new establishments. The proportion of mature individuals gradually decreased (42% in 2002; 30% in 2005) and the proportion of premature and sporeling individuals increased during 2002–2005, probably because of more favourable climate conditions during those years.

The population in Hawaii Loa (Oahu) classified as dynamic, though the numbers of individuals in each life stage class decreased steadily. It probably represented a recently colonised patch (J. Lau 1998 pers. comm.) in the historical distribution area, situated on a lava cliff and thus protected from ungulate disturbance. The number of mature individuals decreased from 30 in 1999 to seven in 2005, and was followed by smaller numbers in younger life stages. This population seemed to represent the case, where species encounter the conditions which allow the establishment, but are unsuitable for established plants for long-term persistence. Based on current data, it seems to be the ‘extinction site’ in close future.

One of the largest populations, ca 1000 individuals plus several smaller patches, were documented historically in Puu Kolekole area on Molokai (Wagner 1952). Due to the cattle, and disturbance by feral pigs and goats, the size of the population has been remarkably reduced and suitable habitat may be found only in small patches of native forest on steep slopes in the upper part of the gulches. Several of those patches were searched for *D. erecta*.

A new location with small population of *D. erecta* was found below Puu Kolekole in 2002 (R. Aguraiuja, S. Perlman pers.comm.). It consisted of only mature individuals and thus was classified as regressive. The condition of this population slightly improved during the period of 2003–2005, probably because more favorable weather conditions for germination and sporeling establishment. It became more structured, and in 2004 and 2005 all three life-stages were represented. Two single individuals were found in 2003 (R. Aguraiuja, J. Lau pers. comm.): one sporeling in E-Kawela and one mature individual in E-Puu Kolekole. Both were extinct in 2004. Occasional occurrence of new colonisations/recolonisations showed that there may be the potential for the establishment of new local populations and reecover of the species.

On the island of Maui, there was only one small population of *D. erecta* in Hanalei. This population classified as regressive since it consisted of only a few mature individuals. Any premature or sporeling individuals were recorded in this site during the whole research period.

Diellia unisora

The population of *D. unisora* at S-Ekahanui, chosen for the study from the beginning of the research, classified as regressive. It was endangered by overgrowing invasive grass, *Melinis minutiflora* P. Beauv., and the hybrid individuals of *D. falcata* x *unisora* were also found in the distance of 60 m. In 2002 and 2003, the mature individuals predominated, though premature individuals were also represented. In 2004 only mature individuals were recorded and all life stages were represented again in 2005. The population size was decreasing steadily during the whole research period and by its very unstable condition this population was distinguished as 'extinction prone'.

The population patches in N-Pualii what were described later, proved to be dynamic. These local population patches, predominated by premature and sporeling individuals may represent more recent recolonization within historical distribution area.

Diellia falcata

Diellia falcata, currently the most successful *Diellia* species, is known from almost the entire length of the Waianae Mountains on Oahu, with 14 larger local populations (40–2000) and 8 local populations smaller than 10 individuals (USFWS 1999). Though the whole population of *D. falcata* in general classified as normal, the structure of all studied populations was different (Pearson Chi sq = 124.70, $p < 0.001$, $df = 6$) and varied from dynamic to regressive.

The population in Kahanahāiki was predominated by mature individuals in 1999, and classified as regressive. The number of mature individuals on the study plot decreased over 70% during the drier period between 1999 and 2002. One possible reason may have been the reduced canopy, followed the treatment of invasive tree species and the attack of invasive *Heliothrips haemorrhoidalis* (Bouché). The population was classified as dynamic during 2002–2004 and attained the normal condition in 2005.

The population condition in Huliwai classified as dynamic and did not change during the research period. However, the numbers of individuals in all life stages decreased slowly.

The population in Waianae Kai classified as a normal in general, but was highly disturbed by ungulates. The population in the gulch bottom of N-Pualii, was predominated by sporeling and premature stages and classified as dynamic. It may represent a new recolonisation within historical distribution area. The small dynamic population on the rocks in the gulch bottom of Pohakea, consisting only of premature and sporeling individuals may represent an attempt

for recolonisation as well. One small regressive population in very degraded gulch bottom of S-Ekahanui gradually decreased and finally went extinct during 2004–2005. All studied smaller populations of *D. falcata* grew in impoverished communities and degraded habitats of gulch bottoms.

4. DISCUSSION

4.1. The phytogeographical distribution

The populations of *Diellia* species are very local and small, with plants usually growing in groups, or solitary and scattered. The younger stages are inconspicuous and their relative abundance can vary between years. In unfavourable years, or during long-lasting dry periods, *Diellia* ferns may be shriveled and wilted. Search for these species may require more than one season to locate populations. The areas where *Diellia* species could be found are mostly remote and difficult to access with native communities highly fragmented. This, together with historical distribution data and probable metapopulation type of dynamics give theoretical possibility that there could exist small local populations or single individuals that have not been discovered yet. The rediscovery of *D. mannii* over more than 100 years provides the basis for further ideas over temporal and spatial factors of fern dispersal. We do not know if this individual originates from spore rain (more individuals could be around) or from spore pool in the soil.

More research is needed on Maui, where *Diellia* ferns are in worse condition at present and on Molokai, where new attempts of recolonisation have been documented. By historical data the biggest populations of *D. erecta* were growing on these two islands (Wagner 1952). Further study is also necessary to determine the distribution of hybrids and the occurrence of *D. erecta* f. *alexandri*. The populations of *D. erecta* f. *alexandri* (Kawai'iki, Kauai) and *D. erecta* (Manuka, Hawaii) were highly reproductive and could be the spore sources for new local populations, though actual new establishments depend of how much of suitable habitat is still available. In some areas, the habitat of historical locations seems to be irreversibly degraded and recolonisation of *Diellia* ferns is hardly probable. From 10 locations studied by W. H. Wagner 58 years ago, *Diellia* species were found only in three. More attention should be paid on the fragments of mesic forest communities within their historical distribution area where the habitat conditions indicate the possible presence of *Diellia* species. As *Diellia* ferns are habitat specialists, their historical and current data of occurrence may also indicate the historical distribution of certain mesic forest communities.

4.2. The habitat

Species rich mesic forests of Hawaiian Islands, the original communities where *Diellia* species belong, are decreasing and occurring as bigger or smaller fragments only. Over most of their original range they have been replaced by

alien trees and shrubs (Cuddihy and Stone 1990). Though there are, insufficient data about species composition of mesic forest ground vegetation before massive animal and plant invasions started in the middle of 19th century, it has been estimated that native mesic forests in Hawaiian Islands were probably predominated by native ferns (Cuddihy and Stone 1990, Jacobi and Scott 1985). Abundance of ferns in fenced areas leads to assume that *Diellia* species, among other ferns, were more frequent in earlier times than they are now. Though drastically reduced in numbers, *Diellia* species have survived, in some areas even within very disturbed habitat and secondary community. This, and rediscovery of *D. mannii* in *Corynocarpus laevigatus* dominated secondary community, allow presume that *Diellia* species may persist for some time in invaded communities, probably as long as the required physical conditions of the habitat (light, moisture, soil reaction and composition) are not critically altered and as long as active inter-specific competition is not involved. Still, the reduced size of individuals, delayed stage transformations and relatively big number of sterile mature plants, refer to the stress condition of these ferns.

Millions of years of evolution in the absence of large mammalian herbivores, which consume large quantities of vegetation and cause perpetual disturbance through trampling and digging, has resulted in high vulnerability to damage by introduced ungulates (Loope and Mueller-Dombois 1989). It has been shown that biological invasions by exotic species can alter the population dynamics, whereby most alien animals have a larger effect than do most alien plants (Vitousek 1986). Pteridophytes in general, fail to exploit habitats subject to high intensity and frequency of disturbance and are relatively unsuccessful in herbaceous vegetation experiencing moderate intensities of regular disturbance (Grime 1985). The fact that most of earlier information about *Diellia* results from the study of survivors in more or less changed or degraded native communities, has probably been misleading for some earlier conclusions that ungulate disturbance might favour non-competitive *Diellia* species by creating open gaps for new colonisations/establishments. In normal conditions, *Diellia* species grow on steep slopes where a range of natural disturbances occur: rare localized hurricane damage, rainfall extremes or drought extremes, and more common small scale disturbances as landslides, treefalls and rockfalls.

The occurrence of sterile mature plants and eroded and uprooted *D. pallida* individuals in Mahanaloa (Kauai) was documented already by W. H. Wagner (1952). Since then the total population size of *D. pallida* is reduced from 250 in 1949 to 12 mature individuals in 2005. Current data confirm that the number of individuals of *Diellia* species is negatively influenced by the level of ungulate disturbances. The number of deaths of mature individuals, caused by erosion and direct uprooting, was higher than by normal senescence. In particular, the number of recent extinctions was found to be concentrated in sites where the cumulative effect of alien plant and animal species was estimated to be high. Exotic animals have frequently larger effect on native ecosystems than do most exotic plants, partly because that invading plants occupy already disturbed

habitats, but animals cause direct disturbance by themselves (Ramakrishnan and Vitousek 1989; Wester 1994). The impact of invasive plants usually becomes evident in longer time scale. If invaded by fast growing alien plant species as *Erigeron karvinskianus*, the extinction of *Diellia* ferns may happen also rather fast. It took five years from discovery to extinction of *D. pallida* in Makaha (Kauai). If arranged by species composition and abundance of alien plants species together with ungulate disturbance, the habitat descriptions of *Diellia* sites give a very clear and warning picture of gradual impoverishment and degradation of the habitat. Though their role is still underestimated the management efforts for recovery of native ground vegetation, what could reduce the erosion and surface water run-off, seem to be very important not only for ferns but for general recovery process of the whole native forest community.

4.3. Life history and ecology

Water deficiency is the key limiting factor for pteridophytes in general, but particularly in seasonally dry tropical areas (Kornaš 1985, Rana 1999). As *Diellia* species grow in the mesic forest on leeward slopes, they exhibit certain seasonality in their growth. The active growth of new fronds takes place during the rainier period, from October to April. During the dryer period, from May to September, the growth decelerates and ferns must cope with water deficiency.

Usually plant growth responses to the long-term means of climatic parameters, provided the plants are adapted to cope with the normal seasonality at their site of growth. From year to year, however, climatic parameters can deviate from their mean values. The Hawaiian climate, at times results in climatic disturbances, such as the rainfall extremes or drought extremes, what may cause setbacks in plants growing in Hawaiian forests (Mueller-Dombois and Fosberg 1998). By incident, current research fell into climate transition period of extremely dry (1999–2002) to extremely wet (2003–2004) and finally to normal weather pattern (2005 and onwards). The regeneration of *Diellia* populations during this period allows to assume that it may follow the so-called ‘window of opportunity’ (Jelinski and Cheliak 1992) model, where recruitment is a scarce event and possible in particularly favourable years. The success of mating, as well as persistence of established individuals may therefore be low due to the lack of moisture in dry years. Though the area of spore dispersal may be greater than the area in which sporophytes are recorded (Page, 1979), the small number of spores (small number of spore-producing mature individuals) is also limiting for establishment of new individuals and new populations of *Diellia* species.

The type of breeding system may have substantial influence on the colonization rate of new habitat patches by ferns. Intragametophytic selfing allows establishment from a single spore, several spores originating from the same individual are required in the case of intergametophytic selfing, while

intergametophytic crossing requires gametophyte populations originating from different mature sporophytes (Lloyd 1974 a, b). Though additional research of the breeding system is needed, it has been supposed that *Diellia* species may represent intergametophytic crossing (Wagner 1952). This may be one possible intrinsic factor for the slow colonization rate of empty suitable habitat patches and rarity of the species.

The mixed populations of gametophytes of different age, observed from April to May and experimental propagation efforts (Lyon Arboretum, N. Sugii pers. comm.) allow to presume that gametophytes of *Diellia* species may perenniate. More research is needed, both in experimental and natural conditions. As the fast growth of the roots seems to be critical for the sporelings, it may be presumed that those established during the rainy winter months have more chance for survival through the dry summer. The second germination peak might lead to further ideas of certain adaptation of gametophytes to survive drier summer conditions.

It has been demonstrated that, at least in culture, several genera of ferns complete their life cycle within 2 to 3 years (Klekowski, 1969). In a natural habitat they may have greatly different life spans related to the seasonality of environmental conditions and the stability of the habitat (Farrar and Gooch, 1975). Wagner's experiments on *Diellia* species showed that it took nine to ten months from spore germination to sporeling formation and the maturity was reached on 3rd year (Wagner 1952). Current observations of natural populations of *D. pallida* showed that transformation from sporeling stage into premature stage may take place within 6–12 months depending on microhabitat and local weather conditions. The observations of *D. pallida* showed that if protected and in favourable microhabitat conditions, this species may reach maturity within 5 years. Based on current experimental stage transformation estimates, the average life span for mature plants could be 23,2 years and 1% of mature individuals could live more than 35 years. In present conditions however, the whole life span is probably much shorter, mainly because of severe ungulate disturbance and increased erosion. The healthy spore-producing mature individuals were found only in places well protected either by rocks and tree roots or by fences.

4.4. The population structure

It has been suggested that the study of population stage structure may be a vital technique in monitoring population condition (Hutchings 1991, Oostermeijer et al. 1994, Hegland et al. 2001, Eckstein et al. 2004), as well as the condition of the whole plant community (Bühler and Schmid 2001). For the ferns with short non-branching rhizome and morphologically well differentiated developmental stages of the sporophyte, the population stage structure seems to be the best

indicator of its condition. The current data made it possible to analyse the short-term dynamics of 20 local populations of *Diellia* ferns during 2–6 years. In general there was a good accordance between the estimated population condition during the first census and its future dynamics during following years. Dynamic populations increased in size, mainly on the expense of sporelings and premature individuals, and regressive populations were stable or decreased. Four smallest regressive populations went extinct during the research period, consisting of one individual in two cases, three individuals in one case and seven individuals in other. The monitoring and analysing of population stage structure proved to be a useful tool to make difference between relatively stable well structured populations, and more vulnerable small dynamic and small mature dominated populations in short-term.

In addition to the age/stage structure, the fate of local populations depends critically on their size (Eriksson and Ehrlén 2001; Matthies et al. 2004; Honnay et al. 2005). If the concern is the future trends of the populations of critically endangered species, most of which have very small population size, special attention should be paid on small dynamic or small mature dominated populations. The very small dynamic populations with few spore-producing mature and many sporeling individuals (*Diellia pallida*, Kauai) are probably most unstable. These populations have potential for recovery, but their actual future trend depends of the habitat quality and any stochastic environmental event. For the survival of these populations the active conservation management is needed. The small mature dominated unstructured (*D. erecta*, Hanaulaiki, W-Maui) or poorly structured (*D. erecta* f. *alexandri*, Kawai’iki, Kauai) populations have high reproductive potential, though for some environmental reason there is no establishment of young sporophytes. If such individual/ population inhabits just in single small habitat remnant (*D. erecta* f. *alexandri*, Polipoli, E-Maui), it seems to be extinction site in the future. If such population inhabits in the area where more suitable habitat community is still available (*D. erecta*, Hanaulaiki, W-Maui), the improvement of habitat quality through conservation management could restore the population structure and reverse to its normal dynamics. Also, in case of documenting new locations with single mature individuals, it stays problematic if these represent remnants or new attempts to establish (re-establish). By the population size (single individual, few individuals) and structure (no structure), they would classify as regressive. Current data of *Diellia* distribution on Molokai could be the example. The single sporeling of *Diellia* from E-Kawela was clear case of the re-establishment. At the same time there was no information about the history of single individuals in E-Puu Kolehale and Onini Gulch. The whole area is historical distribution area and more single individual sites could be found within it. The last is a good indicator of habitat availability and reproductive potential of the species, helpful for setting the priorities for conservation management activities. Consequently, the estimation of the condition of a local population on the basis of their stage structure has to be combined with information about the size of the population –

single individuals, small dynamic and small mature dominated populations, are all extinction prone.

The fern life-cycle consists of two alternative but anatomically, physiologically and ecologically distinct generations (gametophytes and sporophytes). For most fern species both generations share similar habitat conditions, although in some cases, like seasonal habitats, the limiting habitat requirements can be somewhat different as a result of the different anatomical structure of gametophytes and sporophytes. Populations that consist mainly of mature individuals and are deficient in a balanced gametophyte/sporophyte population-dynamic indicate that the local habitat conditions are somewhat changed and no longer support the gametophyte and sporeling establishment. This could be the result of temporary fluctuations of climate conditions, successional change of the community, or varied disturbance levels of intensity and frequency. Populations dominated by sporeling stages indicate the conditions are still suitable for the survival of the population yet may be very unstable and critically influenced by changes in local environmental conditions and disturbance (*Diellia pallida*, Kauai). One may conclude that the proportion of individuals in the premature life stage reflects the suitability of the habitat for establishment of a healthy population-dynamic and is the most reliable indicator for assessment of population conditions and predicting possible future trends.

The regional dynamics of plant populations has frequently been discussed, and recent reviews claim that many plants appear not to be arranged as metapopulations (Bullock et al. 2002; Freckleton and Watkinson 2003; Murphy and Lovett-Doust 2004), though local processes alone are clearly not sufficient for understanding regional dynamics for most plant populations (Ehrlén and Eriksson 2003). In the case of perennial plants, the extended life span of plant individuals and the limited dispersal ability of many species often make it difficult to observe particular colonization and extinction events (Ouborg and Eriksson 2004; Honnay et al. 2005) and to collect good data for understanding the regional dynamics of plant species.

The historical and current distribution data, stage structure of local populations, the emergence of new local populations and the extinction of old ones indicate that *Diellia* species in Hawaiian Islands may exhibit metapopulation dynamics. Since ferns are characterised by good dispersal ability due to their high number of very small spores, metapopulation dynamics may partly occur for biological reasons. At the same time, the number of recorded extinction events clearly exceeds the number of recorded appearance events, and the localities of previous extinctions were characterised by the highest cumulative impact of alien animals and plants. Mesic forest fragmentation and habitat destruction, which has taken place already long time and accelerated since the middle of the 19th century (Loope and Mueller-Dombois 1989; Pimm 1996), has certainly amplified regional dynamics and made local populations more unstable than they may have been historically. If the local extinctions are the result of local habitat destruction or deterioration, regional dynamics may more

likely follow the colonisation-extinction dynamics of ‘slow environmental tracking’ rather than the extinction-colonization dynamics of classical meta-population (Jäkäläniemi et al. 2005). The more comprehensive data of the emergence of new local populations and the extinction of old ones shows that current regional dynamics of *Diellia* species may rather corresponds to ‘slow environmental tracking’. Further experimental research on recovery of *Diellia* populations and distribution of mesic forest communities may help to clear the problem.

4.5. Suggestions for conservation

Removal of feral ungulates from areas managed for their values as native ecosystems in Hawaii is a key step in reducing disturbance of native ecosystems and preserving their many endangered endemic species (Stone et al. 1992, Cabin et al. 2000). It is well known that for conservation of any endangered species, the primary task is to stabilize existing populations through protecting their natural habitat and increasing the number of reproductive individuals. Though some aspects of species biology and ecology of *Diellia* species need further study, the exclusion of ungulate disturbance (as shown in case of *D. pallida*) would improve the condition of their populations immediately. As mentioned already in recovery plans for the Hawaiian plants (USFW 1995, USFW 1996, USFW 1998), the exclusion of ungulates and removal of aggressive plant invaders, is emergent for the survival and recovery of all *Diellia* taxa. Based on the results of current research, the author is convinced that well planned, scientifically based efforts of active conservation management, involving propagation, rescue of eroded individuals and outplanting, are highly worthwhile and feasible.

More detailed suggestions for different species and local populations would be as follows.

Diellia mannii

In order to protect the single individual of the species and potentially suitable habitat for regeneration, the author would suggest to fence at least the area of 30 x 200 m along the slope on this site. Carefully planned and gradually conducted alien plant control and the recovery of the native community could be started within the fence. Though the canopy is dominated by non-native *Corynocarpus laevigatus* J. R. Forster & G. Forster, it is important to consider that any bigger changes of canopy coverage could critically change the moisture conditions for *D. mannii*. Thus the hand-weeding of the seedlings and saplings of alien species and gradual replacement of *C. laevigatus* canopy with *Charpentiera elliptica* (Hillebr.) A. Heller, *Cryptocarya mannii* Hillebr., *Hedyotis terminalis* (Hook & Arnott) W. L. Wagner & Herbst, *Nestegis sandwicensis* (A. Gray) Degener,

I. Degener & L. Johnson, *Psychotria mariniana* (Cham. & Schlechtend.) Fosb., *Pelea anisata* H. Mann and *Pouteria sandwicensis* (A. Gray) Baehni & Degener dark-leaved shade-giving canopy could be started. The natural spore and seed pool of the most common species of the original vegetations is available in the site.

Diellia pallida

Very small but highly dynamic local populations of *Diellia pallida* (Kuia, W-Mahanaloa) have potential for self-recovery if protected with fences, and would serve as source populations for the recovery of the species within its historical distribution area. In case of finding eroded or uprooted by animals premature/mature individuals, they should be directly re-planted into the fenced areas without removing them from the site. Uprooted-eroded sporelings should not be wasted, but rescued and boosted to revival, and thereafter used to increase the number of individuals of the site. The site in Kuia needs immediate control over alien *Kalanchoe pinnata* (Lam.) Pers., at least within a distance of 10 m around the group of mature reproductive individuals.

Diellia erecta* f. *alexandri

The single individual of *Diellia erecta* f. *alexandri*, Polipoli (Maui) is critically endangered by any stochastic disturbance. This site could be classified as a potential “extinction site” due to small size of suitable habitat remnant and successional changes in the small patch of native community. One possible way to prolongate the persistence of the taxon in this site and to enhance recruitment could be careful site management by creating small gaps of open soil in the vicinity of the single reproductive individual. The most of efforts should be focused on the *ex situ* propagation by spores.

The population in Kawai’iki (Kauai) serves a special attention as the only extant population representing the morphological variability of the group of ferns recognized by W. M. D. Hillebrand as *Diellia alexandri* (Hillebr.) Diels, *D. centifolia* (Hillebr.) Diels, *D. knudsenii* (Hillebr.) Diels and *D. laciniata* (Hillebr.) Diels. This only population of *D. erecta* f. *alexandri* is extremely important for further studies of speciation within the lineage. It needs to be fenced against increasing ungulate disturbance. The coverage of non-native plant species has also increased during the research period of 2002–2005.

Diellia erecta

The largest population of *Diellia erecta* in Manuka (Hawaii) is at present in good condition, but fluctuating during longer droughts. As a source population for the whole species, it needs to be continuously monitored and controlled against invasive plant species, particularly against *Oplismenus hirtellus* (L.) P. Beauv. and *Nephrolepis multiflora* (Rxb.) F. M. Jarrett ex C. V. Morton.

The only population of island Oahu (Hawaii Loa) is clearly dynamic by its structure. However, the population size has been continuously decreasing. It differs from all other *Diellia* populations by a high proportion of two life cycle stages – sporelings and dead individuals. It seems to represent the case, where species encounters conditions, which allow establishment, but are unsuitable for the established plants (Grime 1985). Though protected from ungulate disturbance due to growing on the steep cliff, the abruptly changing moisture conditions of porous lava (very wet in wet season and very dry in dry season) do not support the long-term persistence of the population on this site. The author would suggest to focus on *ex situ* propagation efforts and use the reproductive potential of the population as a source for artificial establishment of new populations within protected areas.

The populations of *D. erecta* at Puu Kolekole (Molokai) and in Hanalei (Maui) are the only source populations of the species for these islands. For improvement of the population condition, the potential suitable habitat area around these populations needs to be fenced, with following gradual removal of invasive plant species. The earlier known sites in Iao Valley and at Kanaha stream (Maui) need further search for *D. erecta*. Though not recorded recently, the small population patches or scattered single individuals could probably be found in these areas.

Diellia unisora

Diellia unisora, needs a special concern due to the two ongoing processes: habitat degradation and hybridization. The population in S-Ekahanui needs immediate weed control. The smallest of *Diellia* species is almost overgrown by *Melinis minutiflora* P. Beauv. If direct inter-specific competition in herb layer is involved, only careful weeding by the hand is feasible. The small, almost ‘pure’ dynamic population patches of *D. unisora* in N-Pualii should be the conservation priority as a source population of the species. The ferns are growing on steep eroding slope where community is dominated by alien plants. The weed control in this area should be gradual and very carefully planned, preventing additional erosion and extreme changes in the habitat conditions. Eroded sporelings should be rescued for establishing new local populations in protected (fenced) areas.

Diellia falcata

For *Diellia falcata* it is important to continue the monitoring of population condition, as only one of the biggest populations is currently fenced and protected from ungulate disturbance. Most of smaller populations, consisting of ten to twenty individuals, are extinction prone due to growing in disturbed and degraded habitats where community is dominated by non native plant species. The author would suggest to check all currently known populations of *D. falcata* and choose the core areas for fencing.

CONCLUSIONS

The population life stage structure is a useful tool for the rough assessment of population condition and understanding of regional dynamics of ferns with non-branching short creeping or erect rhizome and morphologically easily distinguishable life-cycle stages. It gives vital information for making conservation management decisions how to improve the condition of very small populations of rare ferns, but is not informative enough for predicting their long-term future trends. For *Diellia* species particularly, the proportion of individuals in the premature life stage seems to reflect the suitability of the habitat for normal population dynamics and could be used as the most reliable indicator for predicting possible future trends in short-term.

The stage structure of local populations of *Diellia* species, together with historical and current distribution data, indicate that *Diellia* species may exhibit metapopulation dynamics when growing in undisturbed conditions. At the same time, the habitat destruction, what has taken place from the middle of 19th century, has certainly amplified regional dynamics of the species and made local populations more unstable as they may have been historically. The current regional dynamics of *Diellia* ferns rather corresponds to ‘slow environmental tracking’ (*sensu* Jäkäläniemi *et al.* 2005), where the equilibrium conditions are violated by habitat destruction. Since the number of local extinctions in disturbed localities clearly exceeds that of appearances, the whole lineage is critically endangered.

Introduced ungulates represent the greatest immediate threat to the native ferns of Hawaii by browsing the fronds, destroying the ground vegetation, changing the soil moisture condition, increasing the erosion and opening gaps for plant invasions. Ungulate disturbance and invasion of alien plant species have cumulative effect on the number of individuals in *Diellia* populations.

Three taxa are close to extinction: *D. mannii*, *D. pallida*, and *D. erecta* f. *alexandri*. The next by vulnerability are *D. erecta* and *D. unisora*. Though critically endangered, *Diellia* species have biological potential for survival and recovery if active conservation and habitat improvement methods will be immediately applied.

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SUMMARY IN ESTONIA

Havai endeemsed sõnajalad *Diellia* Brack. (Aspleniaceae): levik, populatsiooni struktuur ja ökoloogia

Vulkaanilise tekkega Havai saarestik on kõige isoleeritum saarestik maailmas ja see määrab tema elustiku omapära – 96% looduslikest õistaimedest ja 77% looduslikest sõnajalgtaimedest on endeemid. Pikaajalise inimõju ja võõrliikide invasiooni tulemusena on 52,5% Havai saarestiku looduslikest liikidest ohustatud. Käesoleva uurimistöö eesmärgiks oli kuue kriitiliselt ohustatud Havai endeemse sõnajala – *Diellia erecta* Brack., *D. erecta* f. *alexandri* (Hillebr.) W.H.Wagner, *D. falcata* Brack., *D. mannii* (D. C. Eaton) W. J. Rob., *D. pallida* W. H. Wagner, ja *D. unisora* W. H. Wagner – populatsioonide seisundi hindamine, ning lisateave saamine nende elukäigu ja ökoloogia kohta.

Populatsioonide seisundit hinnati populatsioonide arengujärgulise struktuuri ja selle muutuste kirjeldamise põhjal. Sõnajalgtaimedele on iseloomulik põlvkondade vaheldus: haploidne gametofüüdi põlvkond ja diploidne sporofüüdi põlvkond. Kuigi sporofüüdi põlvkonda on peetud domineerivaks sõnajalgtaimede arengutsükklis, toimub kõige olulisem sõnajalaliigi populatsiooni asustumisel (idanemine ja gametofüüdi areng, viljastumine ja eosikute asustumine), just gametofüüdi põlvkonnas. Viimane on looduslikes tingimustes raskesti uuritav. *Diellia*, nagu teistegi lühikese mitteharuneva risoomiga sõnajalgade puhul on suhteliselt hästi jälgitavad järgmised sporofüüdi arengujärgud: eosikud (noored morfoloogiliselt vähe eristunud sporofüüdid), prematuursed (vegetatiivsed pre-reproduktiivsed sporofüüdid) ja matuursed (reproduktiivsed sporofüüdid) isendid.

Sporofüütide arengujärgulise struktuuri alusel klassifitseeriti populatsioonid järgnevalt: 'dünaamiline' – populatsioonis on eosikud ülekaalus; 'normaalne' – kõik arengujärgud on esindatud vastavalt häirimata looduslikes tingimustes olevale tasakaalulisele populatsioonile; 'regressiivne' – populatsioonis on reproduktiivsed isendid ülekaalus. Uurimisperioodi 2002–2005 jooksul tehtud populatsioonide kirjelduste analüüsi põhjal vastas *D. unisora* kogu populatsiooni struktuur dünaamilisele populatsioonile; *D. pallida*, *D. erecta* ja *D. falcata* populatsioonid normaalse struktuuriga populatsioonidele; *D. erecta* f. *alexandri* populatsioon regressiivsele populatsioonile. Samas varieerus eri liikide lokaalpopulatsioonide seisund regressiivsest kuni dünaamiliseni. Kuna tegemist on haruldaste liikide väga väikeste populatsioonidega, siis populatsioonide seisundi hindamisel ohustatuse seisukohast, tuleb kindlasti arvestada populatsioonide suurst: nii üksikisendid, kui ka väga väikesed regressiivsed populatsioonid ja väga väikesed dünaamilised populatsioonid on otseses hävimisohus.

Kokkuvõttes, sõnajalgade populatsioonide elujärguline struktuur aitab mõista liigi regionaalset dünaamikat, seda vähemalt lühikese harunemata risoomi ja

morfoloogiliselt selgelt eristuvate sporofüüdi arengujärkudega sõnajalgade puhul. *Diellia* liikide puhul on oluline arvestada, et 19. saj. keskpaigast intensiivistunud kasvukohtade halvenemine ja hävimine on tõenäoliselt muutnud nende liikide regionaalset dünaamikat ning populatsioonide seisund on ebastabiilsem kui kunagi varem. Üliarvukad introdutseeritud sõralised on suurimaks ohuks Havai looduslikele sõnajalaliikidele, süües lehti, vigastades ja juurides välja risoomi, kahjustades metsa looduslikku alustaimestikku ning seeläbi muutes mulla niiskustingimusi ja suurendades erosiooni. Enamus gametofüütidest ja eosikutest hävib.

Kuuest uuritud taksonist on kolm hävimisohus: *Diellia mannii*, *D. pallida* ja *D. erecta* f. *alexandri*. Ohustatuse poolest järgnevad *D. erecta* ja *D. unisora*. Kokkuvõttes, 51 varem teadaoleva leiukoha ja populatsiooni uurimine näitas, et *Diellia* sõnajalgade arvukus väheneb ning et *Diellia* sõnajalad on stressiseisundis (väiksem kasv, aeglustunud arengujärkude vahetus, suurenenud vegetatiivses seisundis püsivate matuursete isendite arv). Uurimistulemused näitavad ühtlasi, et vaatamata väikestele populatsioonidele ja stressiseisundile, omavad *Diellia* sõnajalad bioloogilist potentsiaali püsimiseks ja taastumiseks, tingimusel kui koheselt kaitsta nende kasvukohti sõraliste poolt tekitatud häiringu eest.

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POPULATION STRUCTURE, REGIONAL DYNAMICS AND EXTINCTIONS IN THE ENDEMIC FERN LINEAGE *DIELLIA* (ASPLENIACEAE) IN HAWAII

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Running headline: Population structure of endemic fern lineage

SUMMARY

1. We analysed data of the distribution and stage structure of populations of the endemic fern lineage *Diellia* in the Hawaiian Islands, using two censuses (1999–2004 and 2005). Populations were classified as ‘dynamic’ (sporelings predominate), ‘normal’ (stage structure corresponds to equilibrium population in undisturbed conditions), or ‘regressive’ (mature plants predominate). Habitat quality was characterised via the occurrence of alien plants in the vegetation and the disturbance of the soil surface by alien animals.
2. Six taxa were studied: *Diellia erecta*, *D. erecta* f. *alexandri*, *D. falcata*, *D. mannii*, *D. pallida*, and *D. unisora*.
3. The condition of 19 local populations, estimated during the first census, was marginally non-significantly correlated with their condition during the second census. In nine cases, the condition had remained the same, in four cases the condition deteriorated. Four smallest regressive local populations had become extinct. The condition of two previously regressive populations had improved as a result of a combination of favourable moisture conditions and the lack of animal disturbances.

4. The size of local populations during the first census was correlated with the number of individuals in all life stage classes, as well as with population condition, during the second census.
5. The number of individuals in existing local populations was negatively dependent on the degree of soil disturbance by alien animals. Thus, the primary mean to protect local populations is to exclude ungulates.
6. The available data on 46 local populations from the middle of the 19th century show that altogether 28 recorded populations have become extinct. The locations of those populations are currently characterised by significantly stronger cumulative impact of alien animals and plants than other sites. Eight local populations recorded before 1950 still persist. Four new populations have been recorded between 1950 and 1998, and six after 1998.
7. We conclude that the whole lineage is endangered, since the number of local extinctions in disturbed localities clearly exceeds that of appearances. Regional dynamics of *Diellia* populations are likely to follow 'slow environmental tracking', where species track the availability of the habitat, partly destroyed by the external disturbances.

Key-words: extinction, endemic fern, Hawaiian Islands, invasive species, population stage structure, regional dynamics.

INTRODUCTION

Despite huge conservation efforts, a large number of habitats and species across the globe continue to decline and the overall status of the remaining ones continues to deteriorate (Vitousek 1994; Pimm *et al.* 1995; Thomas *et al.* 2004). Understanding the ecological mechanisms for these declines is, however, hampered by a lack of information on the historical status and current demography of most species in most parts of the world. On a large scale, declines and increases can be deduced from current species distributions alone (Wilson *et al.* 2004). Increasing attention on the regional dynamics of plant populations has become, despite some doubts, a vital part of studies, aimed to improve understanding of the persistence and extinction of plant populations and species (Ouborg & Eriksson 2004).

The Hawaiian Islands comprise, one of the most striking examples of the human-induced decrease of biodiversity in the world, due to massive loss of species during their colonization by Polynesians and later by Europeans (Pimm 1996). The islands have the highest level of endemism of any floristic region in the world and include about 40% of the endangered plant species listed in the USA (Loope & Mueller-Dombois 1989; Wagner *et al.* 1990). Since the flora of the Hawaiian Islands has been very well surveyed, there is rather complete information about the historical occurrence, and the present distribution of

populations of many endangered species. Also, their specific habitat types are rather well described (Wagner 1951), and the historical human impact in the islands is known as well (Loope & Mueller-Dombois 1989; Cuddihy & Stone 1990). Thus, endemic plant species in the Hawaiian Islands represent good models for studying regional dynamics of populations of endangered species.

In order to understand the regional dynamics of endangered plant species and the forces behind the change, we used the species of the fern lineage *Diellia* as models. *Diellia* species have both very restricted regional distributions and small populations (Wagner 1952; Fosberg & Herbst 1975). *Diellia* is currently represented by six species and one hybrid (Wagner *et al.* 1999), but *D. leucostegioides* (Baker) W.H.Wagner is presumably extinct (USFWS 2000).

In conditions where the laborious demographic study of populations is not possible, an important way of describing the condition of populations of such species in a single census is by determining the relative proportions of individuals in the different ontogenetic stages of their life cycle (Gatsuk *et al.* 1980; Rabotnov 1985). This method has been successfully used in a number of studies of perennial plant species, including rare and endangered species (Rabotnov 1985; Oostermeijer *et al.* 1994; Bühler & Schmid 2001; Hegland *et al.* 2001; Brys *et al.* 2003; Eckstein *et al.* 2004; Agurauja *et al.* 2004). On the basis of population stage structure, it is possible to give a rough assessment of the condition of populations – i.e., are they ‘dynamic’, ‘normal’ or ‘regressive’ (Hegland *et al.* 2001; Brys *et al.* 2003).

In a previous paper (Agurauja *et al.* 2004), we studied the stage structure of six taxa of *Diellia* and suggested that the condition of a local population might predict its future dynamics. We also indicated that the feasibility of such predictions might be challenged by the specific features of ferns: the spores of ferns are highly mobile, but the success of spore germination, gametophyte development, the fertilization process, and the survival of the sporelings, are highly dependent on the presence of moisture (Peck *et al.* 1990) and mechanical disturbances (Cousens 1988).

The general aim of the present paper was to understand the regional dynamics of populations of *Diellia* species in conditions where the habitats are fragmented due to both natural reasons (islands) and the destruction of habitats. In particular, the first aim of the present paper was to estimate the condition of local populations on the basis of life stage structure, by using an experimental ‘ideal population’ as a template for comparisons. Second, we aimed to check whether the estimations of the population condition made on the basis of stage structure earlier (Agurauja *et al.* 2004) predicted the short-term dynamics of local populations. Third, we aimed to analyse the main threats to *Diellia* populations in the Hawaiian Islands.

MATERIAL AND METHODS

STUDY AREA

The Hawaiian archipelago, with eight high and 124 smaller islands, stretches 1600 km across the northern Pacific Ocean. The Hawaiian archipelago is nearly 4000 km from the nearest continent and from the nearest set of high islands, the Marquesas (Juvik & Juvik 1988). The islands span a remarkable range of habitats, from tropical lowlands to alpine zones, representing three moisture regimes: dry, mesic, and wet (Gagne & Cuddihy 1990). Mean annual temperature decreases with increasing elevation, while precipitation is primarily controlled by exposure to the prevailing northeast trade wind. The age of the substrate on which ecosystems have developed varies, according to the age of the island (Vitousek 2002). The flora of 1117 vascular species is derived from about 405 colonists. Speciation within the archipelago has tripled the number of species, since approximately one third of speciation occurs subsequent to dispersal events between islands and about two-thirds subsequent to those within islands (Funk & Wagner 1995).

The main climatic vegetation types in the Hawaiian Islands include dry, mesic, and wet forests, as well as subalpine and alpine vegetation (Price 2004). *Diellia* species grow in the understory of mesic forests. We studied potential habitats for *Diellia* species on five islands where they had been recorded earlier: Kauai, Oahu, Molokai, Maui, and Hawaii. The natural community was usually *Diospyros/Metrosideros* Mesic Forest (annual precipitation 1200–2500 mm), thereby on the island of Kauai this includes rare communities of Kauai Diverse Lowland Mesic Forest and Mixed Mountain Mesic Forest and on the island of Hawaii, *Nestegis* Lowland Forest. In drier and more open sites of steep slopes, *Diellia* ferns were growing in *Styphelia/Dodonea* Mesic Shrubland. In less disturbed conditions, the understory of such forests include several other relatively abundant ferns species, like *Microlepia strigosa* (Thunb.) C. Presl, *Doodia kunthiana* Gaudich., *Doryopteris decipiens* (Hook.) J. Sm., *Dryopteris sandwicensis* (Hook. & Arn.) C. Chr., *Nephrolepis exaltata* (L.) ssp. *hawaiiensis* W. H. Wagner, *Asplenium macraei* Hook. & Grev., etc. Several sites suffer due to expansion of invasive plant species like *Blechnum appendiculatum* Willd, *Christella parasitica* (L.) H. Lev., *Adiantum hispidulum* Sw., *Phlebodium aureum* (L.) J. Sm., *Erigeron karvinskianus* DC, *Ehrharta stipoides* Labill., *Melinis minutiflora* P. Beauv., *Oplismenus hirtellus* (L.)P. Beauv., *Kalanchoe pinnata* (Lam.) Pers, *Passiflora suberosa* L., *Clidemia hirta* (L.) D. Don, *Psidium cattleianum* Sabine *Schinus terebinthifolius* Raddi, and *Casuarina equisetifolia* L., as well as due to the trampling and browsing of feral pigs, goats, and deer (Aguraiuja *et al.* 2004).

STUDY SPECIES

Diellia is a monophyletic lineage that has radiated over the six Hawaiian Islands and is currently found on five. A phylogenetic analysis has shown that the ancestor of the *Diellia* lineage may have been among the first successful colonists of a newly emerging island of the archipelago approximately 24 million years ago (Schneider *et al.* 2005). We included five taxa in our study of population structure – *D. erecta*, *D. pallida*, *D. falcata*, *D. unisora*, and *D. erecta* f. *alexandri*. *Diellia mannii* was represented by one individual only (Agurauja & Wood 2003) and, thus a population-level analysis was not possible. Because of uncertain taxonomy we omitted the local populations of *D. falcata*, *D. unisora*, and *D. falcata* x *unisora* found in a so-called ‘hybrid zone’ in Pualii – Palawai area on Oahu. In the case of *D. unisora*, we checked three different locations, but for further analysis used only morphologically almost ‘pure’ population patches of N-Pualii.

Diellia erecta is the most variable species of the lineage. Wagner (1952) described the forms *D. erecta* f. *alexandri* (Hillebr.) and *D. erecta* f. *pumila* (Brack.) W.H. Wagner. Single intermediate individuals between f. *erecta* and f. *alexandri* or individuals with morphologically different fronds on the same plant can still be found (Wagner 1952; K.Wood, pers. comm.). The recently discovered (2001) and currently only known population (K.Wood, S.Perlman, pers. comm.) of *D. erecta* f. *alexandri* on Kauai, is also morphologically highly variable, consisting of types that Hillebrand (1888) recognized as *Diellia alexandri* (Hillebr.) Diels, *D. centifolia* (Hillebr.) Diels, *D. knudsenii* (Hillebr.) Diels and *D. laciniata* (Hillebr.) Diels – taxa that were not found later by Wagner (1952). As a unique remnant of once more widely distributed taxon (there are several specimens collected earlier in the area of Waimea Canyon and Halemanu), the population of *D. erecta* f. *alexandri* was included into the current survey.

Diellia species are small to medium-sized terrestrial, sometimes epipetric (*D. erecta*) plants, growing on old lava blocks and cliffs. They have a short decumbent or erect non-branching rhizome and brittle stipes with clathrate scales on the stipe base. The fronds are with characteristic submarginal sori opening outwards and anastomosing veins. Little is known about the life history, reproductive cycles and longevity, germination and gametophyte ecology of *Diellia* species. They have a sexual cycle (Wagner 1952), but the breeding system needs further study.

DATA COLLECTION

We used the published material about the distribution of *Diellia* taxa in the Hawaiian Islands (Wagner 1952), and the collection data of several herbaria (National Tropical Botanical Garden, Bishop Museum, Botanic Garden and Botanical Museum Berlin-Dahlem, Brooklyn Botanical Garden, Harvard University, Royal Botanic Gardens Kew, New York Botanical Garden, and

Museum National d'Histoire Naturelle, Paris). We also obtained information about the occurrence of *Diellia* taxa from the materials of floristic surveys of the Hawaiian Islands conducted by the National Tropical Botanical Garden (Perlman & Wood 1995,1996; Wood 1998, 1999) and the Hawaii Natural Heritage Program, University of Hawaii (J. Lau, pers. comm.). During the whole study period, 1999–2005, mesic forest sites on five islands (Kauai, Oahu, Molokai, Maui, and Hawaii) were regularly visited in order to check for the presence and conditions of formerly recorded populations, and to search for new ones.

We aimed to describe in detail all local *Diellia* populations on the Hawaiian Islands (Fig. 1), except *D. falcata*, which is spread over a larger area, and also the taxa with an uncertain taxonomy. We defined a local population according to Hanski & Simberloff (1997) as a set of individuals that live in the same habitat patch and thus share a common environment. Over the period of February 1999 – June 2005, field surveys were conducted in 51 sites or areas where *Diellia* species have occurred (Wood 1999; Agurauja & Wood 2003) (Fig. 1, Table 1).

Assessments of population size were derived via direct counting of individuals, except for the relatively large population of *D. falcata* in Kahanahaiki and Huliwai, where two local populations with a size of approximately 40x40m were described with the help of ten randomly located 1x1 m sample plots, in which all individuals and their life stages were recorded. In order to describe the stage structure of the population, the following stages were distinguished: gametophyte, sporeling (young sporophyte), premature (pre-reproductive sporophyte); mature (reproductive sporophyte), dormant/dead. Since gametophytes are extremely difficult to observe in field conditions, and in the case of dry looking plants we were not able to decide whether they were dead or dormant, only three stages of sporophyte generation (sporeling, premature, and mature) were used in later population analyses.

We described the species composition of plant communities in study sites in 25x25m plots. In particular, we characterised the occurrence of alien plant species, as well as soil disturbance by alien animal species. The following scales were used to characterise habitat quality. The occurrence of alien plant species was characterised by the three-level scale: (1) scarce – single individuals of alien plant species are found occasionally; (2) intermediate – community represents a mixture of alien and native plant species; (3) abundant – community is predominated by alien species. The soil disturbance by alien animals (feral pig, goat, and deer) was also characterised by a three-level scale: (1) weak – animal disturbances are absent or there were few localised disturbed spots; (2) intermediate – animal disturbances were visible, but the trampled and dug soil surface did not exceed 10% of the area; (3) severe – disturbances were evident, trampled and dug areas sometimes exceeded 50% of the soil surface. We also estimated a ‘cumulative impact of alien species’ – as the arithmetic sum of the two above mentioned estimates, varying between 2 (minimum cumulative impact) and 6 (maximum cumulative impact).

THE EXPERIMENTAL STAGE TRANSITION ESTIMATION

In Mahanaloa Valley, the rare communities of Kauai Diverse Lowland Mesic Forest and Mixed Mountain Mesic Forest consist predominantly of native plant species, but are strongly impacted by alien animals. In order to reduce the negative effects of alien animals (Stone & Loope 1987), small parts of it were fenced in 1997–1998, and single mature individuals of *D. pallida* outside the fenced area were protected with net from 2002 onwards. As a result, the appearance of sporelings increased dramatically – 28 sporelings were recorded in May 1999 and 314 sporelings in May 2005. Since animals cause strong soil erosion, practically none of the sporelings survive on the steep slope outside the fence. As uprooted and eroded individuals of different life stages were found during every population survey, we decided to test if these individuals could be revived when immediately planted back into the soil within fenced areas. Altogether, 10 individuals in 2002, 8 individuals in 2003 and 46 individuals in 2004 were rescued. These individuals were monitored until June 2005 and all transitions between life stages (sporeling, premature, mature, extinct) were registered. On the basis of a total 102 transitions, we calculated average yearly transition probabilities between stages. We expect that the fenced area in W-Mahanaloa (Table 1) represents more or less benign conditions for *Diellia* ferns, since it is a mesic forest stand with native plant species only, where the impact of alien ungulates has been eliminated.

STATISTICAL ANALYSES

Log-linear analysis and the Freeman-Tukey deviation test (Legendre & Legendre 1998) were used to search for discrepancies between field data and null model conditions. First, we tested whether the frequencies of plants in particular life stages differed significantly from those predicted from null hypotheses stating a random distribution of individuals among stage classes. Also, between-population differences (intraspecific) and interspecific differences in life stage distribution patterns were tested, by studying the interaction terms local population*life stage and species*life stage, respectively (StatSoft, Inc. 2001). Secondly, we used log-linear analysis and Freeman-Tukey deviation test (Legendre & Legendre 1998) to test the empirical life-stage frequencies against null model predictions, achieved from an imitation model mimicking the empirical life stage transition dynamics recorded during the experiment with *D. pallida* in W-Mahanaloa (the ‘ideal population’). This was done for different species as well as for different local populations within species. The null model was designed to imitate a population with constant annual input of sporelings and annual transitions between four life stages – sporeling, premature, mature and extinct – for 1000 seasonal cycles, using empirically estimated transition probabilities (Table 2). The resulting equilibrium representation of different life stages was the following: sporelings 56.0%, prematures 22.8% and matures 21.2%. This distribution was used as an

alternative null model in the analysis. We admit that the data may be insufficient due to low number of observations, made with one species only. So far, it has not been possible to grow *Diellia* species in artificial conditions, and all destructive research methods in the field are inconceivable when studying rare and protected species, thus it was possible to use only those eroded individuals, which would otherwise die. The model showed that the overall mean life span of an individual plant was only 2.6 years, mainly due to high sporeling mortality. Out of the 11% of individuals that reached the mature stage about 1% lived more than 35 years, average lifespan for mature plants being 23.2 years. This is in good accordance with the observations by Wagner (1952). We shall later call the two alternative null models ‘the random null model’ and ‘the ideal null model’.

The comparisons of the representation of different life stages were performed in four taxa (three species and one form). *Diellia manni* was excluded, since it is represented by only one mature individual. More detailed comparisons of local populations within a species were possible in four cases (Table 1).

In the present paper, populations are classified as ‘dynamic’ when the sporeling stage is represented to a significantly greater extent or mature stage to a significantly lower extent than predicted from null model conditions. Similarly, populations are classified as ‘regressive’ when the mature stage is represented significantly more frequently or sporeling and premature stage less frequently than predicted from null model conditions. Populations are classified as ‘normal’ when the representation of all stages corresponds to that assumed from null model conditions. In addition, population are classified as a normal when the sporeling stage was represented less frequently and premature stage more frequently than stated from null model conditions, since such a pattern may refer to between-year variation in population recruitment. Populations with less than ten individuals were considered as regressive without any statistical analysis, although they may represent not only decreasing populations, but also the result of recent colonisation events, still prone to extinction due to their small size. *Diellia falcata* x *unisora* hybrid populations were not included in the classification of population conditions. A manipulated population of *D.pallida* in W-Mahanaloa also was not included.

Log-linear analyses were conducted to study if the cumulative impact of alien species differed among sites where extinction events of *Diellia* species have taken place, compared to sites where *Diellia* individuals are still present.

Spearman rank correlations (StatSoft, Inc. 2001) were calculated to study: 1) the relationships between population condition estimated by using random and ideal null model conditions; 2) the relationships between the estimated population condition during the first and the second census, 3) the relationships between the population size at the first census and absolute population size, the numbers of individuals belonging to the different developmental stages, and population condition at the second census.

A repeated measures main effect GLM (StatSoft, Inc. 2001) was applied on log-transformed numbers of plant individuals, while species (except *D. mannii*, which was represented by only one individual, and two *D. falcata* populations in Kahanahaiki and Huliwai, where the total number of individuals was not known), developmental stage, estimated occurrence of alien plants, and estimated rate of soil disturbance by alien animals were used as fixed factors, and time (first and second census) as a repeated measures factor.

RESULTS

There was a significant Spearman rank correlation between the condition of populations estimated by the ‘random model’ and the ‘ideal model’ ($R=0.88$, $p<0.001$ in the first census, $R=0.71$, $p>0.05$ in the second census). One may see from Table 3 that in seven of the 11 cases from the first census, and in eight of the 14 cases from the second census, the estimations of the status were similar. In the remaining cases, the random model gave always one step more positive estimation of the status than ideal model, except one case (*D. unisora* in N Pualii 4). We decided that ‘ideal model’ gives more realistic estimate of the condition since it assumes larger number of sporelings and prematures in equilibrium conditions than random model, and used it in the further analyses.

The analysis of the last census data across all local populations within a taxon showed that the general condition of analysed *Diellia* taxa were different (Chi sq = 635.67; $p<0.001$, $df = 14$) (Fig. 2). The overall condition of populations of *D. erecta* f. *alexandri* was classified as regressive, the condition of *D. unisora* as dynamic, and the condition of *D. falcata*, *D. pallida* and *D. erecta* as normal. When one compares these estimates with those made during the first census, one may see that the general condition of three species (*D. erecta*, *D. falcata*, *D. unisora*) has slightly improved.

The analysis was also conducted on the level of local populations (Table 1). In the second census, also the condition extinct was used. The condition of each local population during the second census was compared with its condition during the first census. The Spearman rank correlation between the population status in the first and second census was marginally non-significant ($R=0.40$, $p<0.087$). In nine cases out of nineteen comparisons, the condition of the local population did not change. The condition of four local populations deteriorated, and four other local populations, earlier classified as regressive, had become extinct. These were all very small populations, consisting of one individual in three cases and of seven individuals in one case. In two cases, the condition of regressive populations had improved.

There was a marginally non-significant Spearman rank correlation between population condition during the first census and the total size of the population during the last census ($R=0.44$, $p<0.054$), as well as with the number of sporelings ($R<0.45$, $p<0.054$). Populations in good conditions tended to increase in size, while regressive populations frequently decreased.

The total size of the population during the first census was significantly correlated with total size ($R=0.92$, $p<0.001$), with the number of sporelings ($R=0.91$, $p<0.001$), premature individuals ($R=0.95$, $p<0.001$) and mature individuals ($R=0.83$, $p<0.001$) during the second census, as well as with the estimated population condition during the second census ($R=0.81$, $p<0.001$).

Repeated measures GLM showed that the number of individuals in local populations was significantly dependent on the impact of alien animals ($F=3.77$, $df=2,37$, $p<0.032$). The disturbance of the soil surface by alien animals resulted in a smaller number of *Diellia* individuals in local populations. Numbers of individuals did not significantly differ between species, life stages, years, and with different alien plant presence ($p>0.05$).

The available data about the disappearance of old and appearance of new local populations is presented in Table 1. There are data about 51 local populations, though the taxonomic status of 5 populations remained unclear. Among remaining 46 populations, 28 local extinction events have been recorded across six taxa studied. Among studied populations eight are known 'historically' (before 1950) and ten have been first time recorded after 1950, six of them after 1998. Log-linear analysis showed that sites where the current cumulative impact of alien species was high (5) or very high (6) were characterised by significantly higher number of extinctions ($p<0.05$) than sites with lower cumulative impact of alien species.

DISCUSSION

CONDITION OF LOCAL POPULATIONS

It has been suggested that the study of population stage structure may be a vital technique in monitoring population condition (Hutchings 1991; Oostermeijer *et al.* 1994; Hegland *et al.* 2001; Eckstein *et al.* 2004), as well as the condition of the whole plant community (Bühler & Schmid 2001). We estimated earlier the condition of local populations of six *Diellia* taxa in the Hawaiian Islands (Aguraiuja *et al.* 2004). The current data made it possible to improve the estimations by taking into account the possible stage structure of the 'ideal population', and to check whether the short-term dynamics of local populations during the next 2–6 years was in accordance with the expectations.

We may conclude that, in general, there was a relatively good accordance between the estimated population condition during the first census and its future dynamics during the next 2–6 years. Dynamic populations increased in size, mainly at the expense of sporelings and premature individuals, and regressive populations were stable or decreased. In approximately half of the cases, the condition of local populations had not changed between the two censuses, while the four smallest regressive populations had become extinct during the observation period. All localities of extinct populations were either intermediately or severely disturbed by alien animals. There were two cases

(*D. erecta* in Manuka, Hawaii and *D. falcata* in Kahanahaiki, Oahu) where the condition of a population improved, which may be due to the interaction of rainy periods and negligible impact of invasive animals. In particular, the site in Kahanahaiki has been fenced since 1997 and is distinguished by the complete lack of ungulates. When the condition of species was estimated by pooling data from all local populations, in three cases (*D. erecta*, *D. falcata* and *D. unisora*) the condition had improved. This change is evidently related to an unusually moist period during the last three years, although protection of a population against invasive animals may have had an impact as well.

Thus, population stage structure may be a useful and robust tool in monitoring the condition of endangered species and their local populations. There may be, however, specific cases when population condition does not predict exactly the future dynamics of a local population, since a particular population may depend on a unique combination of external impacts, like climatic fluctuation and disturbance regime. Two cases where the condition of local populations improved serve as examples here.

The fate of local populations also depends critically on their size (Eriksson & Ehrlén 2001; Matthies *et al.* 2004; Honnay *et al.* 2005). Our data showed that the number of individuals in a population during the first census was strongly correlated with the number of individuals in different life stage classes, as well as with population condition, during the second census. In particular, only those regressive populations that were distinguished by the smallest number of individuals had become extinct. Consequently, the estimation of the condition of local populations on the basis of their stage structure has to be combined with information about the size of populations – small regressive local populations are extinction prone.

REGIONAL DYNAMICS

Though there are, insufficient data about species composition of the mesic forest understory before massive animal and plant invasions started in the middle of the 19th century, it has been estimated that native mesic forests in Hawaiian Islands were probably predominated by ferns (Cuddihy & Stone 1990; Jacobi & Scott 1985). The abundance of ferns in fenced areas leads us to assume that *Diellia* species, among other ferns, were more frequent in earlier times than they are now. Current data show that the level of disturbances made by alien feral ungulates negatively influences the number of individuals of *Diellia* species in particular local populations. At the same time, the evidence on the impact of alien plant species was less clear. Exotic animals frequently have a larger effect on native ecosystems than do most exotic plants, partly because invading plants occupy already disturbed habitats, but animals may cause direct strong disturbance by themselves (Ramakrishnan & Vitousek 1989; Wester 1994). The impact of invasive plants may become evident over longer time scales.

The regional dynamics of plant populations has frequently been discussed, and recent reviews claim that many plants appear not to be arranged as metapopulations (Bullock *et al.* 2002; Freckleton & Watkinson 2003; Murphy & Lovett-Doust 2004), though local processes alone are clearly not sufficient for understanding regional dynamics for most plant populations (Ehrlén & Eriksson 2003). In the case of perennial plants, the extended life span of plant individuals and the limited dispersal ability of many species often make it difficult to observe particular colonization and extinction events (Ouborg & Eriksson 2004; Honnay *et al.* 2005) and to collect good data for understanding the regional dynamics of plant species.

In a previous paper (Agurauja *et al.* 2004), we suggested that stage structure of local populations of *Diellia* might indicate metapopulation dynamics, where dynamic populations represent relatively recent colonization events and a regressive population may become extinct in the near future. The more comprehensive data we have now about the emergence of new local populations and the extinction of old ones indicates that *Diellia* taxa in Hawaiian Islands rather exhibit ‘slow environmental tracking’ (sensu Jäkäläniemi *et al.* 2005), where species slowly track the availability of the habitat. Since ferns are characterised by good dispersal ability due to the production and release of high number of very small spores, metapopulation dynamics may partly occur for in undisturbed conditions. At the same time, the number of recorded extinction events of *Diellia* populations clearly exceeds the number of recorded appearance events. The localities of previous extinctions were characterised by the highest cumulative impact of alien animals and plants. Habitat destruction, which has taken place for a long time and has accelerated since the beginning of the 19th century (Loope & Mueller-Dombois 1989; Pimm 1996), has certainly amplified regional dynamics and made local populations more unstable than they may have been historically.

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Table 1. Characterisation of the *Diellia* spp. populations and their sites in Hawaiian archipelago: The estimates of population conditions are based on the Loglinear analysis ('ideal equilibrium population' versus observed population): the proportion of sporeling stage has significantly higher representation in case of dynamic (D) populations, and mature stage significantly higher representation in case of regressive (R) populations than predicted by the null model conditions (Freeman Tukey deviation test, $p < 0.05$). In normal (N) population the representation of all stages corresponds to that assumed from null model conditions. Populations with less than ten individuals were considered as regressive without any statistical analysis. E – extinct during the current study. *D. falcata* x *unisora* hybrids populations are not included to the classification of population conditions. The year of extinction is indicated only when exactly known, otherwise 'not found' is mentioned.

Species	Population		First described/re-invented	Extinct	Census		Condition		Size		Habitat quality		
	Island	Site			1	2	1	2	1	2	Impact of invasive animals	Presence of invasive plants	Other
<i>D. erecta</i>	Oahu	Hawaii Loa	1840/1986		1999	2005	N	N	171	55	Abundant	Severe	Erosion
	Molokai	Puu Kolekole	1912/1949/2002		2002	2005	R	R	14	25	Scarce		
		E – Puu Kolekole	1912/2003	2004	2003	2004	R	E	1	0	Intermediate	Intermediate	
		E – Kawela	1993/2003	2004	2003	2004	R	E	1	0	Severe	Abundant	Erosion
		W – Kawela	1912	Not found	2003						Severe	Abundant	Erosion
	Maui	Makolelau	1987/1997	1999	1999						Severe	Abundant	Erosion
		Hanaulaiki	2000		2002	2005	R	R	7	6	Intermediate	Intermediate	
		Iao Valley	1990	Not found	2003						Intermediate	Intermediate	Erosion
		Mana Wai Nui	1997	Not found	2004						Severe	Abundant	
		Makawao	1949	Not found	2003						Intermediate	Abundant	Erosion
Hawaii	Manuka	1927/1992		1999	2005	R	N	149	155	Intermediate	Intermediate		
	Honomalino	1991	Not found	1999						Weak	Weak		

Table 1. (Continuation)

Table 1. (Continuation)

Species	Population		First described/re-invented	Extinct	Census		Condition		Size		Habitat quality		
	Island	Site			1	2	1	2	1	2	Impact of invasive animals	Presence of invasive plants	Other
<i>D. mannii</i>	Kauai	Halemanu	1864–1876/2002		2002	2005	R	R	1	1	Severe	Abundant	Erosion
		Kumuwela trail	1871–1886	Not found	2005						Severe	Abundant	Erosion
		Kumuwela ridge	1871–1886	Not found	2005						Severe	Abundant	
		Halemanu-Kokee trail	1871–1886	Not found	2004	2005					Severe	Abundant	
		W – Maha-naloa	1949/1996		1999	2005	N	D	28	326	Severe	Scarce	Erosion
<i>D. pallida</i>	Kauai	E – Maha-naloa	1949/1991		1999	2005	R	R	4	2	Severe	Scarce	Erosion
		Kuia	1999		2003	2005	N	N	23	71	Severe	Intermediate	Erosion
		Puu ka Pele	1998	1990	1999	2005					Severe	Abundant	Erosion
		Paa`iki	1949	Not found	2002	2005					Severe	Abundant	Erosion
		Poopo`iki	1949	Not found	2003	2005					Severe	Intermediate	Erosion
		Makaha	1994	1999	1999	2005					Intermediate	Abundant	
		Koaie	1987	1900	2005						Intermediate	Intermediate	

Table 1. (Continuation)

Species	Population		First described/re-invented	Extinct	Census		Condition		Size		Habitat quality		
	Island	Site			1	2	1	2	1	2	Impact of invasive animals	Presence of invasive plants	Other
<i>D. unisora</i>	Oahu	S – Ekahanui	2000		2002	2005	R	R	76	16	Weak	Abundant	
		Pohakea Pass	1932	Not found	2004						Severe	Abundant	Erosion
		S – Pualii	1991		1999						Severe	Abundant	Erosion
		N – Pualii 1	2000		2005		D	D	93		Intermediate	Abundant	Erosion
		N – Pualii 2	2000		2005		D	D	186		Intermediate	Abundant	Erosion
		N – Pualii 3	2000		2004	2005	D	N	285	308	Intermediate	Abundant	Erosion
		N – Pualii 4	2000		2005		N	N	198		Intermediate	Abundant	Erosion
		S – Palawai	1991		1999						Intermediate	Abundant	Erosion
<i>D. falcata</i> <i>x unisora</i>	Oahu	S – Ekahanui	2000		2002						Weak	Intermediate	Erosion
		S – Pualii	1991		1999						Intermediate	Abundant	Erosion
		S – Palawai	1991		1999						Intermediate	Abundant	Erosion

Table 2. Annual transition probabilities between four life stages (S – sporeling, P – premature, M – mature, E – extinct) in the experimental ‘ideal population’ of *Diellia pallida* in fenced mesic forest stand without alien plants in W-Mahanaloa, Kauai. The observations were made during years 2002–2005.

S→S 51.0%
S→P 17.6%
S→E 31.4%
P→P 46.7%
P→M 13.3%
P→E 40.0%
M→M 85.7%
M→E 14.3%

Table 3. Comparison of population condition estimated with Loglinear analysis and Freeman-Tukey deviation test, using two different null models: the ‘random model’ assuming random distribution of individuals among three life stages (sporeling, premature, mature), and ‘ideal model’ assuming the same stage distribution as in an experimental equilibrium population of *Diellia pallida* in undisturbed conditions. Populations only with more than ten individuals were included.

Species	Population	First census (1999–2004)		Second census (2005)	
		Random model	Ideal model	Random model	Ideal model
<i>D. erecta</i>	Hawaii Loa	D	N	D	N
	Puu Kolehale	R	R	R	R
	Manuka	R	R	N	N
<i>D. erecta</i> f. <i>alexandri</i>	Kawai’iki	R	R	R	R
<i>D. falcata</i>	Kahanahaiki	R	R	N	R
	Huliwai	D	N	D	N
	Waianae Kai	N	N	R	R
	N – Pualii	D	N	D	N
<i>D. pallida</i>	W – Mahanaloa	R	R	manipulated	manipulated
	Kuia	D	N	D	N
<i>D. unisora</i>	S-Ekahanui	R	R	N	N
	N-Pualii 1			D	D
	N-Pualii 2			D	D
	N-Pualii 3	D	D	N	N
	N-Pualii 4			R	N

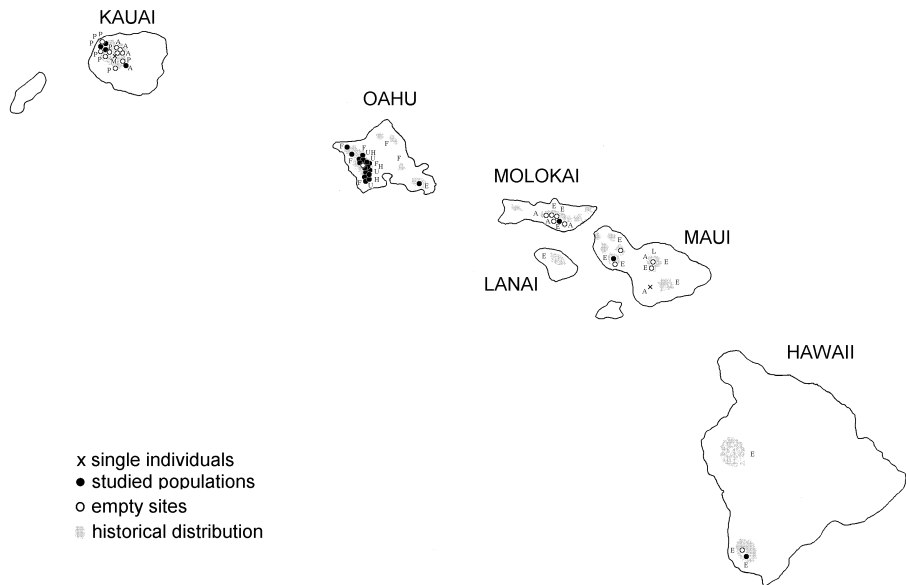


Figure 1. The distribution of the fern genus *Diellia* in the Hawaiian Islands: A *D. erecta* f. *alexandri*; E *D. erecta*; F *D. falcata*; L *D. leucostegioides*; M *D. mannii*; P *D. pallida*; U *D. unisora*; H *D. falcata* x *D. unisora*.

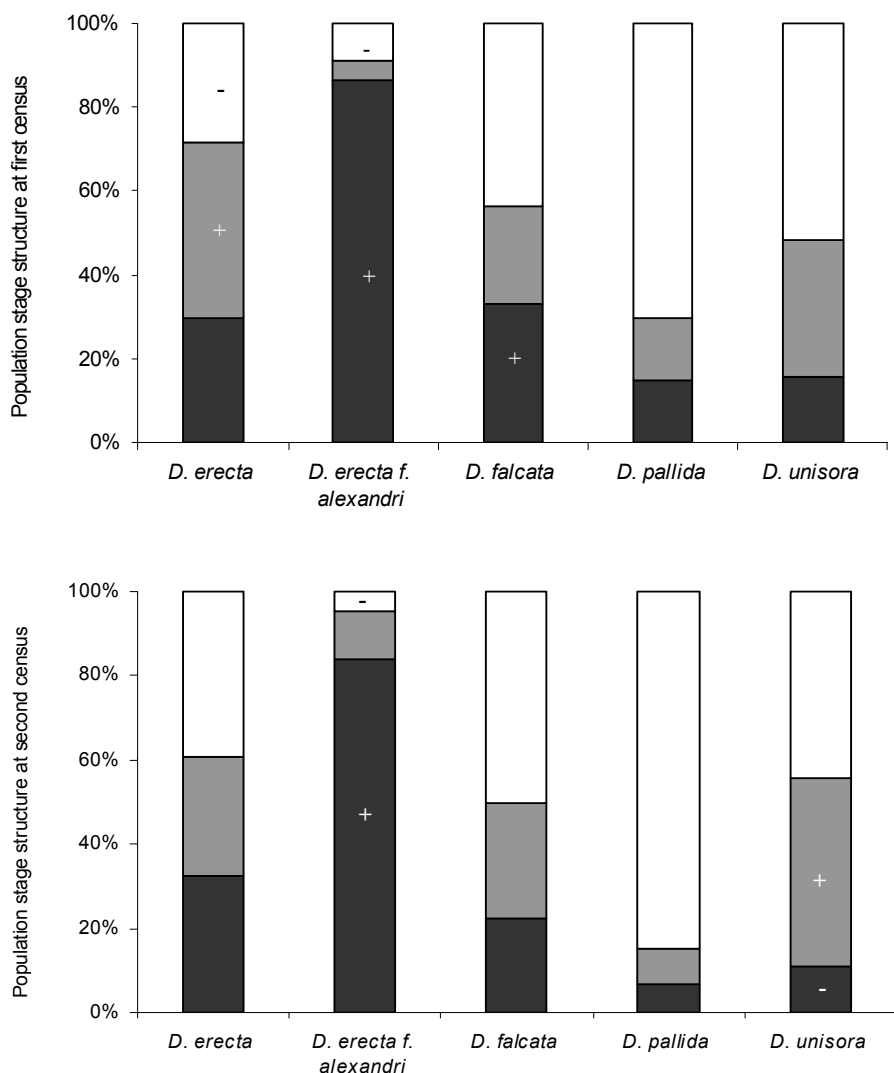


Figure 2. The population stage structure of four species and one subspecies of an endemic *Diellia* family in the Hawaiian archipelago. White parts represent a relative number of sporeling stage, light grey parts the premature stage, dark grey parts the mature stage across all local populations. Plus signs indicate significantly higher proportions and minus signs indicate significantly lower proportions than predicted by ‘ideal null model’ conditions (Loglinear analysis, Freeman-Tukey deviation test, $p < 0.05$).

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Publications

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