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Rebuilding after collapse: evidence for long-term cohort dynamics in the native Hawaiian rain forest

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**REBUILDING AFTER COLLAPSE: EVIDENCE FOR LONG-TERM COHORT
DYNAMICS IN THE NATIVE HAWAIIAN RAIN FOREST**

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Abstract

Questions. Do long-term observations in permanent plots confirm the conceptual model of *Metrosideros polymorpha* cohort dynamics as postulated in 1987? Do regeneration patterns occur independently of substrate age, i.e. of direct volcanic disturbance impact?

Location. The windward mountain slopes of the younger Mauna Loa and the older Mauna Kea volcanoes (island of Hawaii, U.S.A.).

Methods. After widespread forest decline (dieback), permanent plots were established in 1976 in 13 dieback and 13 non-dieback patches to monitor the population structure of *M. polymorpha* at approximately 5-year intervals. Within each plot of 20 x 20 m, all trees with DBH >2.5 cm were individually tagged, measured, and tree vigor assessed; regeneration was quantified in 16 systematically placed subplots of 3 x 5 m. Data collected in the subplots included the total number of *M. polymorpha* seedlings and saplings (5 stem height classes). Here we analyze monitoring data from 6 time steps from 1976 – 2003 using repeated measures ANOVA to test specific predictions derived from the 1987 conceptual model.

Results. Regeneration was significantly different between dieback and non-dieback plots. In dieback plots, the collapse in the 1970s was followed by a ‘sapling wave’ that by 2003 led to new cohort stands of *M. polymorpha*. In non-dieback stands, seedling emergence did not result in sapling waves over the same period. Instead a ‘sapling gap’ (i.e. very few or no *M. polymorpha* saplings) prevailed as typical for mature stands. Canopy dieback in 1976, degree of recovery by 2003, and the number of living trees in 2003 were unrelated to substrate age.

Conclusions. Population development of *M. polymorpha* supports the cohort

dynamics model, which predicts rebuilding of the forest with the same canopy species

after dieback. The lack of association with substrate age suggests that the long-term

maintenance of cohort structure in *M. polymorpha* does not depend on volcanic

disturbance but may be related to other environmental mechanisms, such as climatic

anomalies.

Keywords

canopy dieback; climatic anomalies; cohort senescence; cyclic succession; forest decline;

Metrosideros polymorpha; mono-dominant rain forest; montane rain forest; permanent

plots; stand demography; volcanic disturbance

Abbreviations

DBH = Diameter at Breast Height

DI = Dieback Index

Introduction

Canopy dieback has been reported from many forest ecosystems around the world (Holloway 1977; Pickard 1983; Jane & Green 1983; Wardle & Allen 1983; Stewart & Veblen 1983; White 1986; Lawesson 1988; Ogden 1988; Kohyama 1988; Stewart 1989; Auclair 1993; Enright 1993; Ogden et al. 1993; Ciesla & Donaubauer 1994). The term 'dieback' has been defined as "progressive dying back from the tips of twigs, branches or tops" (Podger 1981; Manion 1981, Ciesla & Donaubauer 1994). In recent years, the potential connection between dieback phenomena and climate change has sparked new interest and scientific debate (Allen 2009; Allen et al. 2010; Aynekulu et al. 2011; Boehmer 2011; Lewis et al. 2011).

On the island of Hawaii, about 50,000 ha of rainforest experienced a decline of *Metrosideros polymorpha* trees between 1954 and the mid-1980s ('*ohia* dieback'; Burgan & Nelson 1972, Petteys et al. 1975, Mueller-Dombois et al. 1980, Jacobi 1983, Hodges et al. 1986, Mueller-Dombois 1993). Endemic *M. polymorpha* (*Myrtaceae*; o'hi'a lehu'a) is the dominant canopy tree species in Hawaii's native montane rainforests (Mueller-Dombois & Fosberg 1998, Wagner et al. 1999). The forests affected were located on the east-facing, windward side of the volcanic mountains Mauna Loa (4168 m) and Mauna Kea (4205 m) between 700 and 1500 m elevation (Jacobi 1983; see Fig. 1). In the late 1980s, the rapid expansion came to a halt (Jacobi et al. 1988).

The early hypothesis (Burgan & Nelson 1972) that the Hawaiian rain forest decline was caused by a virulent pathogen or a combination of biotic disease and pest agents was ruled out after a decade of intensive disease research (Klijunas & Ko 1973, 1974; Papp et al. 1979; Hodges et al. 1986). Dieback stands were found on a variety of volcanic substrates ranging in age from ca. 300 to >140 K years (Mueller-Dombois

2006). Dieback patterns were significantly related to the physical environment, particularly the slope gradient, shape of terrain, the relative position on hill slope, annual rainfall, and the type of substrate (Akashi & Mueller-Dombois 1995). Thus, an alternative hypothesis proposed that “dieback is initiated by a climatic instability [i.e. climatic anomaly] which becomes effective through the soil moisture regime under certain conditions of forest stand maturity” (Mueller-Dombois 1980:159).

This hypothesis gave rise to the ‘cohort senescence theory’ (Mueller-Dombois 1987). *M. polymorpha* populations are considered to have, in many cases, a uniform age and stand structure (‘cohorts’; Vogl 1969; Atkinson 1970), broadly comparable to tree plantations or the natural disturbance-induced cohort stands of forests in other ecozones (Boehmer & Richter 1997). According to the theory, the uniform age and stand structure, primarily induced by large-scale disturbances through volcanic eruptions, results in the simultaneous ageing and finally death of the tree cohort (‘cohort senescence’). Old cohorts of canopy trees are considered predisposed to die due to their low potential for recovery from stress (Mueller-Dombois 1987). In senescent stands, climatic anomalies such as extreme rainfall events or prolonged drought may generate a physiological shock and trigger dieback symptoms (Mueller-Dombois 1987, Gerrish et al. 1988, Gerrish 1990, Auclair 1993). However, identification of cohorts by determination of tree age and stand turnover rates, or the direct relation of growth and climatic events using dendroecological methods is difficult since *M. polymorpha* does not form annual growth rings (Gerrish & Mueller-Dombois 1999). Therefore, the postulated cohort dynamics can best be evaluated from long-term observational data.

Field data collected from 1976 to 1985 showed high numbers of seedlings and small saplings of *M. polymorpha* in dieback plots, which was interpreted by Mueller-

Dombois (1987) and Jacobi et al. (1988) as indication of a new cohort of *M. polymorpha* trees. The term ‘sapling wave’ describes the expected movement of a peak in seedling emergence through various sapling size classes into the tree layer. A conceptual population dynamics model was presented, which predicted a full regeneration of the *M. polymorpha* tree layer following dieback (Mueller-Dombois 1987, Jacobi 1993; Fig. 2). However, this prediction was in stark contrast to the general belief that the remaining rainforest “will be virtually eliminated in 15-25 years” (Petteys et al. 1975).

This model has not yet been tested with empirical data. We used a long-term data set from permanent plots established in 1976 as a unique research opportunity to compare the population dynamics of *M. polymorpha* between dieback and non-dieback plots over 27 years. Specifically we assess whether dieback led to new cohorts within the *M. polymorpha* population, and whether the forming of new cohorts occurred independently of substrate age, according to the hypothesis that cohort dynamics is a recurring phenomenon during the course of succession (Mueller-Dombois 1986). We developed the following specific predictions from the conceptual cohort dynamics model proposed by Mueller-Dombois in 1987 (see Fig. 2): **(H1)** the proportion of dead or dying canopy trees (dieback index, DI) remains low and constant in time for non-dieback plots, while for dieback plots, it decreases over time to the level of non-dieback plots; **(H2)** dieback plots have higher densities of seedlings, saplings, and young trees than non-dieback plots; **(H3)** a sapling wave occurs in dieback plots, but not in non-dieback plots; **(H4)** the shape of the DBH distribution is skewed more to the left than in non-dieback plots following disturbance and shifts back over time. In addition, we tested the association of tree vigor and *M. polymorpha* population dynamics with substrate age.

Materials and methods

Sampling design and data collection

Study sites are located on the windward (east) side of the island of Hawaii (Fig. 3) between the Wailuku River area (north) and the Kilauea area (south) on a variety of volcanic substrates ranging from ca. 300 to 13,500 years B.P. The mean annual rainfall in this area varies (S-N) from ca. 2500 mm to 7000 mm (Juvik & Juvik 1998). Twenty-six permanent plots (20 x 20 m) were established in 1976 between ca. 900 and 1500 m of elevation throughout the study area. In a stratified sampling design, 13 dieback and 13 non-dieback forest stands were selected so as to represent the total variation in forest patterns identified from aerial photographs from 1972. An initial survey of the stands was taken in 1976, and stands were reassessed using the same protocol (see below) in 1982, 1985, 1990, 1995, and 2003. Due to its location in inaccessible terrain, one plot could not be relocated after 1985 and was dropped from the data set.

Within each plot of 20 x 20 m, every tree of at least 5m height was individually tagged, DBH measured (in cm; 1976 and 2003 only), and tree vigor quantified on a scale of 1-5, using the following classes: 1) fully foliated crowns; 2) some defoliated branches, 10-50% of the crown dead; 3) most upper crown branches defoliated, but with some foliated adventitious branches along the trunk; 4) recently dead trees with small branches and most of the bark remaining; 5) dead trees (“snags”), only major branches remaining, most of the trunk without bark.

M. polymorpha regeneration was quantified in sixteen 3 x 5 m subplots per plot, systematically placed within each 20 x 20m plot (Jacobi 1983). Data collected in the subplots include the total number of *M. polymorpha* seedlings (0.1-0.5 m tall) and the

total number of *M. polymorpha* saplings in five stem height classes (>0.5-1 m, >1-2 m, >2-3 m, >3-4 m, >4-5 m).

We determined substrate age for each plot by referring to the Digital Data Base of the Geologic Map of the Island of Hawai‘i (Trusdell et al. 2006). For each lava flow or tephra layer, we determined the median of all radiocarbon datings available from the data base. For each plot, we identified the lava flow or tephra layer on which it was situated by overlaying the GPS coordinates with the geological map in ArcGIS. Substrate age in 1976 was defined as age BP + 26 years, as BP refers to 1950. Based on information from the field, we reassigned plot 29 to an adjacent older tephra layer. No dating was available for the substrate of plot 42.

Data analysis

Dieback index (DI) was defined as the proportion of dead or dying canopy trees (vigor classes 3 - 5) per plot. Plots with DI larger than 50% in 2003 were considered outliers and classified as ‘late dieback’ plots (non-dieback in 1976, $n = 2$) or ‘no-recovery’ plots (dieback plots in 1976, $n = 3$). Thus, late dieback and no-recovery plots did not conform with H1 and will be discussed separately. Further quantitative analysis was restricted to the remaining 10 dieback and 10 non-dieback plots. For the calculation of mean DI of dieback plots, missing values for Plot 13 for years 1982 – 1995 were interpolated linearly between DI values for years 1976 and 2003.

To compare regeneration between dieback and non-dieback plots (H2), and to test for the occurrence of a sapling wave (H3), we used repeated measures ANOVA to assess the effects of dieback category, size class, and year on the number of seedlings, saplings, and young trees. Abundances were log-transformed with $y' = \log(y + 1)$ so as to stabilize

the variance based on residual analysis. In the presence of a significant interaction, we used Bonferroni-type multiple comparisons to assess for which years (6 comparisons) or size classes (7 comparisons) there was a significant difference between dieback and non-dieback plots, accounting for the nature (within- or between subject) and the total number of comparisons ($k = 13$) (Howell 2010).

To test for change in stand structure (H4) in terms of the mean number of living trees (vigor classes 1 – 3) between observation periods, a repeated measures ANOVA was used to assess the effect of dieback category and year on the density of living trees per hectare (square-root transformed). The same ANOVA was repeated for the mean number of vigorous trees (vigor class 1). Temporal trend within each dieback category was tested in the manner of a polynomial contrast, performing a 2nd order polynomial regression of density of living trees against the year (standardized). If both linear and quadratic terms are significant, this indicates a general increase or decrease that levels off after some time, whereas a linear effect only indicates continuing linear trend, a quadratic effect only an increase followed by decrease or vice versa. In the presence of a significant interaction, we used Bonferroni-type pairwise comparisons to assess for which years there was a significant difference in mean density of living trees between dieback and non-dieback plots, accounting for the total number of comparisons ($k = 6$).

To assess the shape of the DBH distribution, a two-parameter Weibull distribution was fitted to the DBH (in cm) of living *M. polymorpha* trees with DBH > 2.5 cm, both for 1976 and 2003, using the function ‘fitdistr’ of the R package ‘MASS’. Difference in the skewness of the DBH distribution between dieback categories and years was tested with a repeated measures ANOVA of the Weibull shape parameter, where lower values of the shape parameter indicate more right-skewed distributions. In the presence of a

significant interaction, we used Bonferroni-type multiple comparisons to assess which of the four group means were significantly different from each other, accounting for the nature (within- or between subjects) and total number of comparisons ($k = 4$). While most data sets contained at least 9 trees, four dieback plots had only 3 – 5 trees in 1976. The estimated shape parameters for the plots with few trees were comparable to those of the other six dieback plots with at least 9 trees. Therefore, all parameters were retained and a repeated measures ANOVA model could be fitted. A separate ANOVA without these four values, ignoring the repeated measures in the error structure, resulted in the same significant effects and pairwise comparisons (results not shown).

The effect of substrate age on dieback and subsequent regeneration was assessed with separate simple linear regressions of substrate age and dieback index in 1976 (all dieback categories), dieback index in 2003 (dieback plots only), the number of new trees > 5m observed 1976 – 2003 (log-transformed, dieback plots only) and the number of living trees in 2003 (vigor classes 1 – 3, dieback plots only) on substrate age (log-transformed). All regression models were tested with and without no-recovery plots.

Results

Dieback index

We hypothesized that the DI (dieback index) remains low and constant in time for non-dieback plots, while for dieback plots, the DI is high initially and decreases over time to the level of non-dieback plots (**H1**). On the ten non-dieback plots, the DI fluctuated perpetually around 25 - 30% (Fig. 4). The DI for the ten dieback plots remained high until 1985 and then decreased rapidly, reaching the level of non-dieback plots by 2003

(Fig. 4). In three plots (“no recovery”), the dieback index remained high at an average of ca. 80 %. In two other plots, canopy decline occurred in the 1980’s (“late dieback”).

Abundance of seedlings, saplings, and young trees

We expected dieback plots to have higher densities of seedlings, saplings, and young trees than non-dieback plots (**H2**). While numbers generally decreased with size class, dieback plots showed higher mean abundances than non-dieback plots for almost all combinations of size class and year (Fig. 5).

After a period of massive seedling emergence in the mid-1970s, the number of seedlings strongly decreased. Seedling development on dieback plots was significantly different from that on non-dieback plots (Fig. 5a); the number of seedlings was significantly greater on dieback plots at all times. Here, the massive seedling emergence resulted in a sapling wave (Fig. 5b-5f) that peaked in the early 1980s (1982-1985). The number of tall saplings decreased since 1990 due to the recruitment of young, healthy individuals into the tree layer.

On non-dieback plots, seedling number was highest in 1976 as well. Since then, the numbers were fluctuating at a low level. Nevertheless, these fluctuations seemed to reflect the high oscillations in dieback plots at a lower level. Only very few saplings grew up into the new tree (NT) class in the non-dieback plots (Fig. 5g).

Sapling wave

Based on the conceptual model by Mueller-Dombois (1987), we predicted a sapling wave to occur in dieback plots, but not in non-dieback plots (**H3**). Repeated measures ANOVA of log-transformed abundance showed significant main effects for

dieback category, size class, and year (Table 1). All two-way interactions were significant, but not the three-way interaction. Dieback plots thus had consistently higher abundances of seedlings, saplings and young trees than non-dieback plots. While the magnitude of this positive difference varied between size classes or between years, it was statistically significant for all size classes (Fig. 6a, left) and for all years (Fig. 6b, centre).

Pooled over all plots, the change in abundance through time depended on the size class. The interaction plot between size class and year (Fig. 6c, right) showed a systematic change in the skewness of the abundance distribution with size class. While seedlings were most abundant in 1976 (L-shaped distribution), saplings of $>0.5 - 2$ m showed a right-skewed distribution with maximum average abundances in 1982, saplings of $>2 - 5$ m were left-skewed with highest abundances in 1995, and young trees were most abundant in 2003 (J-shaped distribution). This suggests the occurrence of a sapling wave that affected numerous plots at the same time.

Stand structure

We predicted that density of vigorous *M. polymorpha* trees will return to the level of non-dieback plots, and the shape of the DBH distribution is skewed more to the left following disturbance than in non-dieback plots, and shifts back over time (H4).

Repeated measures ANOVA indicated a significant interaction effect between year and dieback category on the density of living trees (vigor classes 1 – 3, Table 2). In non-dieback plots, the density of living trees remained constant over time with an average of 820 trees per ha (Fig. 7a, left, no significant trend over time based on polynomial regression). In dieback plots, the density of living trees increased markedly over time, eventually levelling off (polynomial regression showed a significant positive linear trend

with p-value = 0.008 and significant quadratic term with p-value < 0.001). Density of living trees was significantly lower in dieback plots than in non-dieback plots for 1976 – 1990. By 2003, mean density had returned to 815 trees per ha (Fig. 7b, right).

Vigorous trees (vigor class 1) showed the same statistically significant effect and interaction as living trees (results not shown), but in this case there was also significant fluctuation in non-dieback plots (Fig. 7a, left).

Repeated measures ANOVA of the Weibull shape parameter indicated no overall dieback effect on the shape of the DBH distribution, but a significant difference between the two years, 1976 and 2003, and a significant interaction between dieback category and time. A Weibull shape parameter value of $c = 3.6$ corresponds to a symmetric distribution, whereas values of $1 < c < 3.6$ indicate a right-skewed distribution (Rennolls et al. 1985). Non-dieback plots showed no significant change in the shape of the DBH distribution over time, with generally right-skewed distributions (Fig. 8). Dieback plots showed a significant shift from roughly symmetrical towards a right-skewed distribution. Repeating the analysis without the shape parameter estimates that were based on less than 9 trees did not change the nature of the ANOVA results.

Stand structure and substrate age

Regression analysis indicated that the DI in 1976 was unrelated to substrate age. This was true for the full data set ($n = 24$, $R^2 = 0.007$, p-value = 0.691), for all plots with $DI > 50\%$ (dieback and no-recovery plots, $n = 12$, $R^2 = 0.009$, p-value = 0.691) and for dieback plots only ($n = 9$, $R^2 = 0.009$, p-value = 0.769). In the following, statistical results are reported for dieback plots only. The degree of recovery by 2003 ($n = 9$, $R^2 = 0.000$, p-value = 0.988) and the number of living trees in 2003 ($n = 9$, $R^2 = 0.042$, p-value =

0.599) were unrelated to substrate age, both for dieback plots ($n = 9$) and for dieback and no-recovery plots ($n = 12$). The only marginally significant association was found between substrate age (log-transformed) and the number of new trees recruited in dieback plots between 1976 – 2003 (log-transformed, without no-recovery plots, $n = 9$, $R^2 = 0.359$, p -value = 0.088), where unusually low values were only observed on the youngest substrates.

Discussion

Dieback Index over time

As predicted, the dieback index (DI) was constant over the observation period for most non-dieback plots, whereas for most dieback plots, DI returned to the non-dieback level by 2003. Due to growth of a new *M. polymorpha* cohort, the DI for dieback plots decreased rapidly after 1985.

The two ‘late-dieback’ plots (22 and 23), where canopy decline did not occur until the 1980s, suggest that there were different phases of dieback initiation. The progression of dieback in the period from 1982 to 1985 (Akashi & Mueller-Dombois 1995) may be related to the extreme El Niño-event in 1982/1983, which caused a serious drought in Hawaii’s montane rain forests (Boehmer & Niemand 2009). This interpretation is supported by the marked reduction in tree vigor observed in non-dieback plots in 1982 and 1985 (Fig. 7a, left).

There were three ‘no-recovery’ plots (24, 37 and 43) in which the DI remained high. Additional field data (Braun-Blanquet vegetation relevés) for 1976, 1990, and 2003 showed high cover of *Cibotium* tree ferns in all three plots, though equally high subcanopy cover did not prevent recovery in four of the dieback plots. On the one hand,

tree fern trunks and decaying logs provide safe sites for germination of *M. polymorpha*; such microhabitats typically provide for “seedling banks” in developed rain forests (Mueller-Dombois et al. 1980, Medeiros et al. 1993). On the other hand, a special form of competitive stress to *M. polymorpha* seedlings is exerted by *Cibotium glaucum* and the less abundant *Cibotium menziesii*. Drake & Pratt (2001) reported 60.3 % damaged seedlings due to physical disturbance by senescing fern fronds. Plant community data collected in 1976, 1990 and 2003 will need to be analysed in detail to clarify whether the lack of recovery observed in the three ‘non-recovery’ plots can be attributed to competitive interference from tree ferns (‘displacement dieback’; Mueller-Dombois et al. 1980), or to effects of invasive alien species (Minden et al. 2010 a, b).

Population dynamics of M. polymorpha

The time series analysis showed consistently higher numbers of seedlings, saplings of all five height classes, and new trees, for dieback plots as compared to non-dieback plots. This effect occurred in almost all combinations of size classes and years. Dieback plots exhibited a nearly synchronous massive seedling emergence during the mid 1970s. As the mass occurrence of seedlings and the development of saplings were largely restricted to dieback plots, they represent the dieback phenomenon that Mueller-Dombois et al. (1980) and Jacobi et al. (1988) described as ‘replacement dieback’ (i.e. replacement of an old *M. polymorpha* canopy by a new generation of the same species after dieback).

From a high number of seedlings, a sapling cohort developed. At the same time, the number of seedlings decreased constantly. Although non-dieback plots showed a considerable number of seedlings, these seedlings did not develop into saplings and young trees, indicating that regeneration success was low in the absence of canopy

disturbance. Some regeneration was apparent in non-dieback plots located on very moist substrates (plot 25 with 54 and plot 19 with 11 new trees). Plot 25 is located on shallow, discontinuous soil over poorly drained pahoe-hoe lava, and plot 19 on a low-lying ridge on oligotrophic ash in the bog-formation terrain on Mauna Kea (Balakrishnan & Mueller-Dombois 1983). The remaining non-dieback plots produced 0 - 3 young trees over the entire period of 1976 - 2003.

After ca. 30 years, the sapling wave resulted in a new cohort of *M. polymorpha* trees. These trees show great vigor and are expected to continue to grow up to full height, with growth rates depending on the specific site conditions. By 2003, average tree density in dieback plots had reached the original level of non-dieback plots estimated at 820 living trees per ha. In non-dieback plots, the number of living trees (vigor classes 1-3) was relatively constant over time, whereas the number of vigorous trees (vigor class 1) showed considerable fluctuations. A low percentage of dead or partly defoliated canopy trees (vigor classes 3 – 5) appears to be a normal characteristic of the undisturbed montane *M. polymorpha* rain forest. Since 1976, this proportion has been fluctuating around 25 - 30% on non-dieback plots.

Empirical evidence for conceptual model

Our four predictions (H1-H4) focused on transition of *M. polymorpha* individuals through different size classes over time relative to Mueller-Dombois' (1987) conceptual model of ohi'a dieback. The bar graphs in Fig. 9, representing our permanent plot data from 1976 and 2003, allow for a direct comparison of observed size-class distributions to those predicted by the model for non-dieback plots (Fig. 2A) and dieback plots (Fig. 2B). The empirical data largely confirm the conceptual model. The wide-spread death of the

established *M. polymorpha* cohort triggered large-scale synchronous regeneration, during which a large number of seedlings resulted in a “sapling wave” (Fig. 9, top right). From this sapling wave, a new tree cohort was recruited (Fig. 9, bottom right). Non-dieback plots showed a mature cohort stand with a ‘sapling gap’, especially in 2003 (Fig. 9, lower left).

Long-term cohort dynamics

Dieback seems to be a recurring natural phenomenon in the dynamics of Hawaii's montane rainforests. A similar loss of *M. polymorpha* canopy was reported from the lowland rainforest on the windward side of the neighbouring island of Maui in the early 1900's (“Maui Forest Trouble”; c.f. Lewton-Brain 1909, Lyon 1909, 1919; Holt 1983, Mueller-Dombois 2006), another one even earlier from Kauai (Clarke 1875).

Our results show that following dieback of canopy trees in the 1970's, a new cohort of *Metrosideros* trees was established on a wide range of substrate ages from ca. 300 to 13,500 years. About thirty years after dieback, we found no correlation between substrate age and the reduction of dieback index by 2003, the number of new trees recruited 1976 - 2003, or tree density in 2003. The lack of correlation between regeneration success and substrate age (see also Jacobi et al. 1988, Akashi & Mueller-Dombois 1995) suggests that volcanic disturbance is not the main driver of present-day cohort dynamics. We conclude that large-scale dieback causes a wide-spread regeneration of *M. polymorpha*, leading to the maintenance of cohort dynamics even thousands of years after the initial volcanic disturbance.

Recently, Hart (2010) presented very detailed structural data combined with novel age data for a similar forest on Mauna Kea. In this forest, he found three different cohorts

of *M. polymorpha* separated by 200-250 years. Although gap dynamics is, as far as we know today, not a relevant process in our study area, forest regeneration between episodes of dieback may be driven by canopy gap dynamics in places (Kellner et al. 2011). More research is needed applying novel tree dating methods to our non-dieback permanent plots to determine whether the co-occurrence of multiple cohorts within stands is a general phenomenon or linked to the specific history of the stand studied by Hart (2010).

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- 582 Appendix S1: Substrate age and stand composition of permanent plots in 1976
583 and 2003.

584 Table 1: Repeated measures ANOVA of the effect of dieback category, size
 585 class, and year on log-transformed sapling abundance. The final model
 586 includes main effects and two-way interactions only, as the three-way
 587 interaction was not statistically significant.

Error component	Term	Df	Sum Sq	Mean Sq	F value	p-value
Plot	Dieback	1	293.6	293.62	25.50	< 0.001
	Residuals	18	207.3	11.51		
Within	Stage	6	545.9	90.99	111.30	< 0.001
	Time	5	41.5	8.31	10.16	< 0.001
	Dieback:Stage	6	60.1	10.02	12.25	< 0.001
	Dieback:Time	5	10.3	2.06	2.51	0.029
	Stage:Time	30	127.1	4.24	5.18	< 0.001
	Residuals	768	627.8	0.82		

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Table 2: Repeated measures ANOVA of the effect of year and dieback

category on the density of living trees (square-root transformed).

Error component	Term	Df	Sum Sq	Mean Sq	F value	p-value
Plot	Dieback	1	122.6	122.62	15.72	0.0009
	Residuals	18	140.4	7.80		
Within	Year	5	36.0	7.21	5.59	0.0002
	Year:Dieback	5	31.5	6.29	4.88	0.0005
	Residuals	90	116.0	1.29		

Table 3: Repeated measures ANOVA of the effect of year and dieback category on Weibull shape parameter as an indicator for the skewness of DBH distribution.

Error component	Term	Df	Sum Sq	Mean Sq	F value	p-value
Plot	Dieback	1	0.244	0.244	0.32	0.5773
	Residuals	18	13.607	0.756		
Within	Year	1	6.055	6.055	19.38	0.0003
	Year:Dieback	1	4.854	4.854	15.53	0.0010
	Residuals	18	5.625	0.313		

Fig. 1:

Fig. 1: A 1972 aerial photograph of *Metrosideros polymorpha* dieback in the montane rain forest on the eastern flanks of Mauna Kea and Mauna Loa, island of Hawaii. (Photograph by Dieter Mueller-Dombois)

Fig. 2:

Fig. 2: Conceptual model of *M. polymorpha* stand structure before and after dieback (Mueller-Dombois 1987). Reprinted with permission from BioScience 37, by American Institute of Biological Science.

Fig. 3:

Fig. 3: Study area on the island of Hawaii. Grey colour indicates *M. polymorpha*-dominated forests. Numbers indicate plot numbers of dieback (white) and non-dieback plots (black).

Fig. 4:

Fig. 4: Change of dieback index DI over time. Left: mean DI (proportion of dead or dying canopy trees per plot, vigor classes 3 - 5) for non-dieback (squares, dashed line, n = 10) and dieback plots (circles, solid line, n = 10). Right: DI for three no-recovery plots (solid lines) and two late dieback plots (dashed lines; Plot 32 with missing values for 1985 – 1995).

Fig. 5:

Fig. 5: Regeneration of *Metrosideros polymorpha* from seedlings to new trees in seven height classes. Barplots showing the mean $\pm$ SE of log-transformed counts of seedlings, saplings and new trees for each time step, separately for non-dieback (white, n = 10) and dieback plots (grey, n = 10).

Fig. 6:

Fig. 6: Interaction plots of abundance as a function of size. Abundance (log-

transformed) is plotted for each size class (0: seedlings 0.1 – 0.5 m, 1 – 5: sapling height classes 1 – 5, T: young trees > 5 m) and dieback category (a; circles: dieback plots, n = 10, squares: non-dieback plots, n = 10), time step and dieback category (b), and time step and size class, pooled over both plot types (c; 0: seedlings 0.1 – 0.5 m, 1 – 5: sapling height classes 1 – 5, T: young trees > 5 m; line types group size classes with similar changes over time). Star notation indicates significance of one-sided t-tests comparing dieback and non-dieback plots for each size class, using Bonferroni correction for the total number of tests (*: $p < 0.05 / 13$, **: $p < 0.01 / 13$, ***: $p < 0.001 / 13$).

Fig. 7:

Fig. 7: Mean density of living trees over time. Each stacked barplot shows the mean density of trees of vigor classes 1 (dark grey), 2 (medium grey) and 3 (light grey) per ha and per observation period for the ten non-dieback plots (a) and the ten dieback plots (b). Error bars denote mean + SE for the number of living trees (vigor classes 1 – 3). Asterisks indicate years with a significant difference between the mean density of living trees in non-dieback and dieback plots based on Bonferroni tests of $k = 6$ pairwise comparisons (*: $p < 0.05 / 6$, **: $p < 0.01 / 6$).

Fig. 8:

Fig. 8: Skewness of DBH distributions. Each boxplot shows the shape parameters of a 2-parameter Weibull distribution fitted to the DBH data of all living *M. polymorpha* trees (vigor classes 1 – 3) with DBH > 2.5 cm, separately for dieback (left, n = 10) and non-dieback plots (right, n = 10) and the two years 1976 and 2003. Letters indicate significance of pairwise differences (Tukey HSD, $\alpha = 0.05$).

Fig. 9:

Fig. 9: *M. polymorpha* stand structure based on empirical data. Empirical

population structure of *M. polymorpha* in non-dieback (left, A) and dieback stands (right, B) in 1976 (top) and 2003 (bottom) to be compared to the conceptual model in Fig. 2. Each bar shows the number of individuals of seedlings (K), each of five saplings height classes (S1 – S5), and different DBH classes (D0 – D9), where D0 contains trees with a DBH of 2.5 cm up to < 10 cm, D1 of 10 cm up to < 20 cm, etc. Note that the y-axis is interrupted for dieback plots in 1976 to accommodate the extremely high number of seedlings.