



The response of plant diversity to ecosystem retrogression: evidence from contrasting long-term chronosequences

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Following catastrophic disturbances, succession and vegetation development occur, but in the prolonged absence of these disturbances a decline (retrogressive) phase follows in which nutrient availability and tree biomass declines considerably. We measured plant diversity across six long-term chronosequences that each included retrogressive stages in Australia, New Zealand, Alaska, Hawaii and Sweden. In contrast to theories predicting negative or hump-shaped responses of tree diversity to biomass or soil fertility, tree species richness often peaked coincidentally with tree basal area (a surrogate of tree biomass), and declined during retrogression. Similar patterns were found regardless of whether or not species richness estimates were rarefaction-adjusted to correct for variation in stem densities across plots. The Shannon-Weiner diversity index sometimes showed the same pattern, but in two chronosequences was least when tree basal area peaked; this was driven by the domination of total basal area by single tree species in both cases. The decline in tree diversity during retrogression was often associated with reduced relative amounts of total phosphorus in soil. In contrast, total vascular plant species richness often increased during retrogression. These results demonstrate that forests with high tree diversity and biomass do not persist indefinitely in the long-term absence of catastrophic disturbance, and that similar patterns occur across the boreal, temperate and subtropical zones.

Following major disturbances in ecosystems, primary or secondary succession occurs, and this involves an initial period of ecosystem development to a maximal biomass phase. Much research has focused on this developmental period, which is generally characterized by predictable shifts in primary productivity, nutrient cycling, soil processes, and the accumulation of biomass and soil organic matter (Odum 1969, Walker and Chapin 1987). However, in the prolonged absence of catastrophic disturbance (i.e. disturbance of sufficient severity to rejuvenate the soil) and as soils age, a decline or retrogressive phase often follows during which there is a decrease in vegetation biomass and ecosystem productivity (Vitousek and Farrington 1997, Walker et al. 2001, Wardle et al. 2003). This decline is characterized by reduced availability over time of major soil nutrients, particularly phosphorus (P) (Walker and Syers 1976, Vitousek 2004), and an increase in the nitrogen (N) to P ratio of the soil (Wardle et al. 2004). This pattern is relatively consistent across a range of chronosequences (Wardle et al. 2004) and only a catastrophic disturbance will reverse these effects (Walker et al. 2001).

During the initial phases of succession, plant diversity shows a characteristic increase as species establish and accumulate on freshly exposed surfaces (Odum 1969,

Whittaker et al. 1989). However, as succession proceeds over the long-term, the response of plant diversity is less well understood (Grime 2001) and a variety of patterns have been found (Bonet and Pausas 2004, Jones and del Moral 2005, Howarth and Pendry 2006). Furthermore, little is known about how plant diversity changes along long-term chronosequences, particularly during ecosystem retrogression or as soils age (Crews et al. 1995, Richardson et al. 2004). A better understanding of this would shed light on how diversity responds to the prolonged absence of catastrophic disturbance.

There have been several studies that have considered how soil fertility, plant biomass and plant productivity affect plant diversity in herbaceous communities, using field experiments (Wilson and Tilman 2002, Suding et al. 2005) or observational studies (Grace 1999, Waide et al. 1999, Grime 2001). The majority of studies provide evidence for negative or hump-shaped responses to soil fertility or standing biomass in herbaceous communities (Grime 1973, Grace 2001, Mittelbach et al. 2001, Wilson and Tilman 2002). However, although few studies have considered tree-dominated communities, the evidence for negative or hump-shaped relationships between tree diversity and tree biomass is less clear (Wilson et al. 1996,

Mittelbach et al. 2001, 2003, Wardle et al. 2003). In this light, forested chronosequences that include long-term retrogressive phases and therefore soils of vastly differing age and fertility provide excellent opportunities for addressing the question of how tree diversity responds to shifts in soil fertility and associated changes in tree biomass.

Our study focused primarily on how tree diversity responds to ecosystem retrogression across long term chronosequences. Specifically, we hypothesized that tree diversity will increase as soils age and ecosystem retrogression proceeds, due to reductions in soil fertility and associated declines in standing tree biomass. Further, we hypothesized that tree diversity should show similar responses to long-term retrogression across contrasting locations, because different retrogressive chronosequences involve the long-term reduction of the availability of the same key resource, i.e. P (Walker and Syers 1976, Vitousek 2004, Wardle et al. 2004). To test these hypotheses, we investigated how tree diversity varied across each of six forested chronosequences located throughout the world that were each of sufficient duration for ecosystem retrogression to occur. We also assessed the extent to which shifts in tree diversity along these chronosequences were related to concurrent changes along these sequences in tree biomass, and ratios of major soil elements (C, N and P). As a secondary goal, we sought to determine how total vascular plant (including understory) diversity changed during retrogression and whether this showed the same pattern as for tree diversity. By addressing these questions across contrasting sequences, we hoped to gain insights as to whether forest vegetation diversity shows broadly consistent responses to the prolonged absence of catastrophic disturbance regardless of location.

Methods

For this investigation we focused on the same six long-term chronosequences used by Wardle et al. (2004); all sequences are of at least several thousand years (and up to 4.1 million years) in duration (Appendix 1). Two of these sequences are in the Boreal zone, i.e. the Arjeplog sequence in northern Sweden (Wardle et al. 1997, 2003, Wardle and Zackrisson 2005) and the Glacier Bay sequence of southeast Alaska (Noble et al. 1984, Chapin et al. 1994). Two are in the temperate zone, i.e. the Franz Josef sequence of Westland New Zealand (Walker and Syers 1976, Richardson et al. 2004) and the Waitutu sequence of southern New Zealand (Ward 1988, Coomes et al. 2005). The remaining two are in the sub-tropical zone, i.e. the Hawaiian island sequence (Crews et al. 1995, Vitousek and Farrington 1997, Vitousek 2004) and the Cooloola sequence of Queensland, Australia (Thompson 1981, Walker et al. 2001). These sequences are formed on vastly different substrates and have been created by different agents of disturbance (Appendix 1). In all six cases, long-term ecosystem development involving soil weathering and aging has occurred after a catastrophic disturbance event or an event that has substantially reset the successional clock. Five of these chronosequences are primary successional; the sixth sequence, Arjeplog, is a secondary succession, but we maintain that given the relatively long term duration of

these sequences, the ecological processes in the retrogressive phase of primary and secondary succession are comparable (Walker and del Moral 2003, Wardle et al. 2004). Previous work on these chronosequences has revealed that they all show declines in basal area following the maximal biomass phase and at relatively comparable time frames (i.e. in the order of thousands to tens of thousands of years) (Wardle et al. 2004). The mechanistic basis of the decline appears to be the same across all chronosequences (Wardle et al. 2004) and is associated with increasing limitation by nutrients, notably P, as soils age (Crews et al. 1995, Wardle et al. 2003, 2004, Richardson et al. 2004, Coomes et al. 2005). Further information on these sequences is presented by Wardle et al. (2004) and in Appendix I.

For each chronosequence, we identified several stages of ecosystem development or decline in that sequence, and then quantified plant abundances within replicate plots (circular, 10 m radius) within each stage. For all sequences except Franz Josef, the plots used are the same as those described by Wardle et al. (2004). For the Franz Josef sequence the stages were the same as those used by Richardson et al. (2004) which have all but two stages in common with those of Wardle et al. (2004); the study by Richardson et al. (2004) used plots that were established only after the study by Wardle et al. (2004) had been completed and which we believed better represented the late successional stages of the chronosequence. The number of forested stages and total numbers of plots measured were 6 and 30 for the Arjeplog sequence, 6 and 24 for Glacier Bay, 9 and 26 for Franz Josef, 7 and 17 for Waitutu, 9 and 27 for Cooloola, and 6 and 24 for Hawaii (Appendix 1). Numbers of plots per stage were not equal for the Arjeplog, Franz Josef and Waitutu sequences because of insufficient space within some stages to locate several replicate plots. In each plot, the diameter of all trees at 1.3 m height was recorded (i.e. stems with diameter > 5 cm). This was used to calculate for each plot the basal area (a surrogate for tree biomass) of each tree species, total tree species richness, and the Shannon-Weiner diversity index based on the basal area of all tree species present. This latter measure was used because measures of diversity that are based on relative abundance as well as richness can yield insights that cannot be gained by considering richness alone (Wilsey et al. 2005). Within each chronosequence, both raw and rarefaction-adjusted species richness values were considered; the latter was used to correct for varying numbers of individual stems present in different plots. This adjustment was performed because measures of species richness may vary across ecological gradients solely on the basis of variations in the density of individuals per plot across the gradient, without any biological mechanism being involved (Oksanen 1996, Gotelli and Colwell 2001). Rarefaction adjustment was performed using the programme EcoSim (Gotelli and Entsminger 2006). Restricting our analysis of diversity only to plants that exceed a predefined diameter at 1.3 m height is consistent with previous work studying drivers of forest tree diversity (Enquist and Niklas 2001, Condit et al. 2006). In addition, the total richness of all ground-rooted vascular plant species (including those in the understory) was determined for each plot in all sequences except Waitutu. This allowed us to assess whether species richness of all vegetation matches that of the trees.

Rarefaction adjustment was not possible for understory species because many understory species are clonal, preventing identification of individuals.

Response variables for each chronosequence were analysed using one-way analysis of variance (ANOVA) testing for effects of chronosequence stage. When these effects were significant at the $p=0.05$ level, the Least significant difference test was used to compare stages. In addition, regression analyses were used to assess the relationship (linear or quadratic) between measures of species diversity and tree basal area (a surrogate of tree biomass; Wardle et al. 2004) and soil nutrient ratios (carbon (C) to N, C to P and N to P), using soil nutrient data from Wardle et al. (2004). Nutrient ratio data were used because ratios are independent of soil organic matter content which also changes during retrogression, and because nutrient ratios (notably N to P) have previously been shown to serve as powerful predictors of retrogression and basal area decline across all six chronosequences (Wardle et al. 2004). For the Franz Josef sequence where some stages used in the present study differed from those used by Wardle et al. (2004), only data from those sites that were common to both studies were used for this analysis.

Results

All chronosequences showed large declines in tree basal area during the late (i.e. retrogressive) stages of succession, dropping to between approximately a quarter to a tenth of the peak in basal area (Table 1, Fig. 1). The five primary successions (i.e. all except the Arjeplog sequence) also included large initial increases in basal area (Table 1, Fig. 1). Absolute tree species richness was significantly affected by chronosequence stage for three of the sequences (Table 1, Fig. 1), and four sequences showed significant effects when species richness values were adjusted for stem density using rarefaction analyses (Table 1, Fig. 1). In all cases where tree species richness was significantly affected by chronosequence stage, richness for the oldest stages was less than for at least some of the earliest stages (Fig. 1), pointing to a decline in tree diversity during retrogression. For each of three sequences, namely Glacier Bay, Waitutu and Cooloola, tree species richness was generally maximal at the stages where basal area was maximal. Diversity increased

with a decline of basal area only for a portion of one sequence, namely the transition from stage 2 to stage 3 in the Hawaiian chronosequence (Fig. 1). The Shannon-Weiner diversity index for trees was also significantly influenced by chronosequence stage for all sequences except Glacier Bay (Table 1, Fig. 1). For the Waitutu, Cooloola and Hawaii sequences, diversity indices peaked at intermediate chronosequence stages and declined during the oldest stages (Glacier Bay also showed the same pattern but this was non-significant). In contrast, diversity indices were lowest for some intermediate stages along the Franz Josef sequence, and increased along the Arjeplog sequence. The total vascular plant species richness (i.e. trees plus understory species) responded significantly to chronosequence stage for four of the five sequences for which this was determined (Table 1, Fig. 2); in these cases richness was generally greater in the oldest stages than intermediate stages at which the basal area of the trees was maximal.

Measures of plant diversity showed either non-significant or linear relationships with tree basal area (Table 2, Fig. 3); relationships were never quadratic. Absolute tree species richness values were significantly and positively correlated with basal area for two of the six sequences, and for three of these sequences when data were rarefaction-adjusted (Table 2). Further, across the entire data set tree species richness was positively correlated with basal area, regardless of whether richness values were rarefaction-adjusted (Fig. 3). The Shannon-Weiner index for trees was significantly and negatively correlated with basal area for one sequence (Franz Josef) and positively correlated with basal area for two others (Cooloola and Hawaii) (Table 2). Across the entire data set the diversity index was unrelated to basal area (Fig. 3). Meanwhile, total vascular plant richness was significantly negatively correlated with tree basal area for three of the five sequences for which total richness was determined (Table 2). For the entire data set vascular plant species richness was weakly positively correlated with basal area, though this was driven by a single chronosequence (Franz Josef) that contained plots with both high basal area and high understory species richness (Fig. 3).

Absolute tree species richness values showed negative linear or negative quadratic relationships with substrate C to N ratios for two sequences, with C to P ratios for two sequences, and with N to P ratios for three sequences

Table 1. Results from one-way ANOVAs (F values with p values in brackets) testing for effects of chronosequence stage on tree basal area and measures of plant diversity. F and p values in bold indicate statistical significance at $p=0.05$.

Chronosequence	F and p values					DF
	Tree basal area ($m^2 ha^{-1}$)	Tree species richness	Tree species richness (rarefied) ^a	Tree diversity (SWDI) ^b	Vascular plant species richness	
Arjeplog	12.91 (<0.001)	0.28 (0.920)	0.28 (0.921)	2.88 (0.036)	5.49 (0.002)	5, 24
Glacier Bay	6.08 (0.002)	1.09 (0.407)	7.17 (0.001)	1.09 (0.400)	70.36 (<0.001)	5, 18 ^c
Franz Josef	5.91 (0.001)	2.10 (0.095)	2.10 (0.095)	4.79 (0.003)	1.13 (0.392)	8, 17
Waitutu	15.34 (<0.001)	9.03 (0.004)	8.11 (0.005)	6.61 (0.005)	ND ^d	6, 10
Cooloola	18.21 (<0.001)	7.80 (<0.001)	4.88 (0.005)	6.25 (<0.001)	39.03 (<0.001)	8, 18
Hawaii	19.49 (<0.001)	9.27 (<0.001)	6.46 (0.002)	8.68 (<0.001)	11.26 (<0.001)	5, 18

^aDetermined by rarefaction analysis.

^bShannon-Weiner diversity index.

^cDF for vascular plant richness = 7, 24.

^dND = not determined.

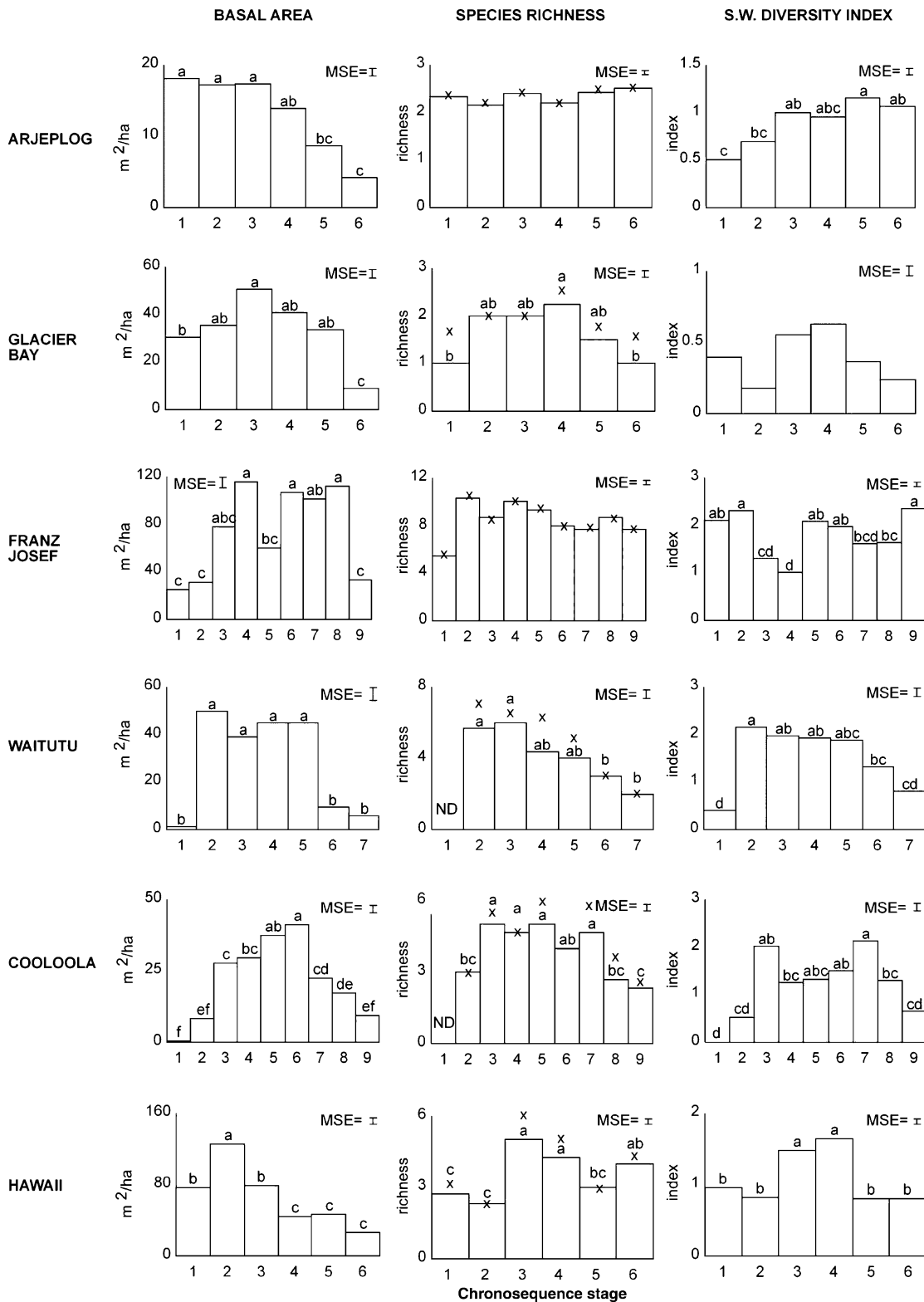


Fig. 1. Changes in tree basal area, species richness, and Shannon-Weiner (S.W.) diversity indices (mean of all plots for each stage) across all stages of ecosystem development (1 = youngest) for each of six long term chronosequences. Details of all chronosequence stages for each of the chronosequences are given in Appendix 1. For the species richness measures at each chronosequence stage, values represented by histogram bars have been corrected for varying total stem density using rarefaction analyses (Methods), while the values represented by crosses are the raw species richness values not adjusted using rarefaction. Basal area values for all sequences except Franz Josef have been derived from Fig. 1 of Wardle et al. (2004). Within each panel, histogram bars topped by the same letter do not differ significantly at $p = 0.05$ according to the Least significant difference test; this test has not been applied to panels for which chronosequence stage effects are not significant according to ANOVA (Table 1). ND = not determined. MSE = mean standard error. Stages 1 and 2 for the Glacier Bay chronosequence lack trees and are therefore not presented here.

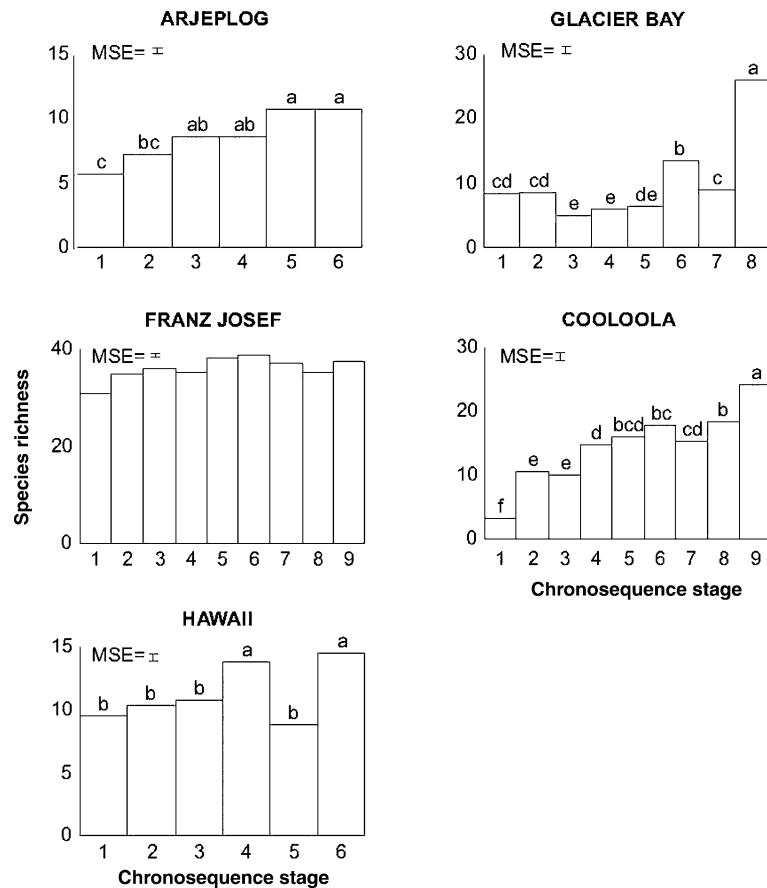


Fig. 2. Changes in total vascular plant species richness in 10 m radius plots (mean of all plots for each stage) across all stages of ecosystem development (1 = youngest) for each of six long term chronosequences. Details of all chronosequence stages for each of the chronosequences are given in Appendix 1. Within each panel, histogram bars topped by the same letter do not differ significantly at $p = 0.05$ according to the Least significant difference test; this test has not been applied to panels for which chronosequence stage effects are not significant according to ANOVA (Table 1). MSE = mean standard error.

(Table 3); when the data was rarefaction-adjusted all but two of these relationships remained significant. Meanwhile, the Shannon-Weiner diversity index for trees showed a significant relationship with C to P and with C to N ratios for all six sequences (Table 3); for all sequences except Franz Josef these relationships were either negative linear or negative quadratic. Only one sequence, namely Cooloola, showed a significant relationship between total vascular plant species richness and nutrient ratios. Here, all relationships were negative quadratic (Table 3) with species richness

increasing monotonically with increasing values of all three ratios.

Discussion

Tree species richness declined sharply during the retrogressive phase for four of the six chronosequences, and this decline broadly matched declines in tree basal area for three of them (Fig. 1). There was no evidence of increases in

Table 2. Pearson's correlation coefficients between tree basal area ($m^2 ha^{-1}$) and measures of vegetation diversity. F and p values in bold indicate statistical significance at $p = 0.5$.

Diversity measure	Chronosequence					
	Arjeplog	Glacier Bay	Franz Josef	Waitutu	Cooloola	Hawaii
Tree species richness	0.113	0.133	0.107	0.776***	0.742***	-0.279
Tree species richness (rarefied)	0.164	0.419*	0.073	0.697**	0.577**	-0.377
Tree diversity (SWDI) ^a	-0.320	0.175	-0.537**	0.853***	0.498*	-0.032
Vascular plant species richness	-0.490***	-0.606**	0.295	ND ^b	-0.123	-0.475*

*, **, *** means that r is significantly different to 0 at $p = 0.05$, 0.01 and 0.001 respectively.

^aShannon-Weiner diversity index.

^bND = not determined.

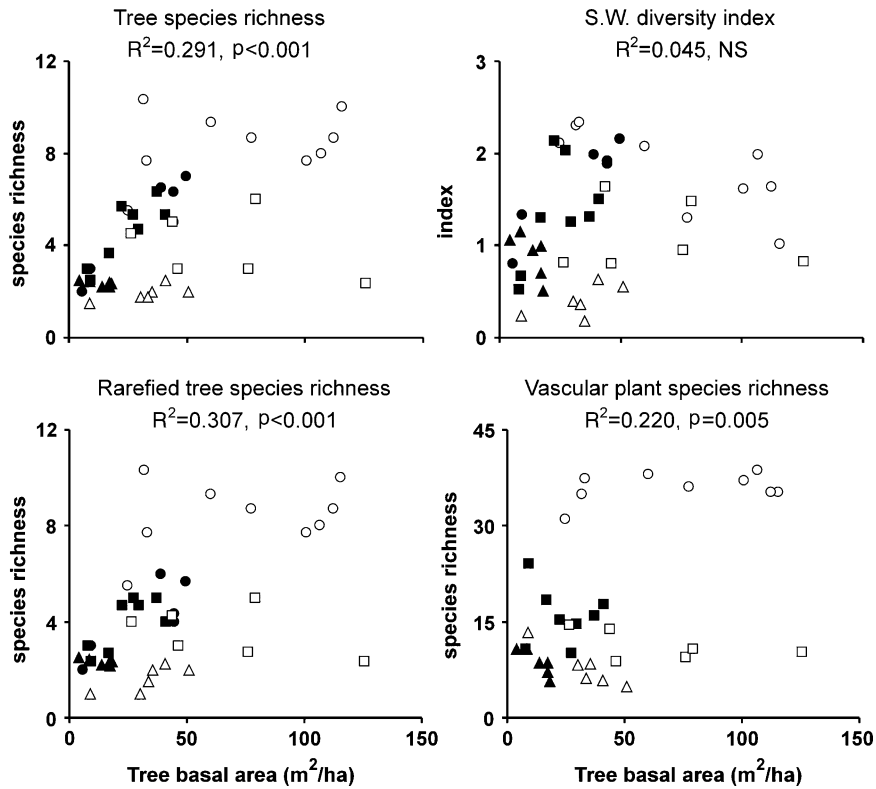


Fig. 3. Measures of plant diversity across all stages for all chronosequences. Each points represents the mean value of all plots for one chronosequence stage. Symbols are: ▲ = Arjeplog; △ = Glacier Bay; ○ = Franz Josef; ● = Waitutu; ■ = Cooloola; □ = Hawaii.

tree species richness during retrogression for any of the chronosequences, except for a portion of the Hawaiian chronosequence; therefore, this finding does not support our first hypothesis. Confirming these trends, tree species richness was either positively or not correlated with basal area, and there was no evidence of negative associations between the two (Table 2). Similar trends were identified regardless of whether or not the data was rarefaction-adjusted, meaning that the patterns that we identified are not explicable simply in terms of differences in density of stems in plots located along these sequences (Oksanen 1996, Gotelli and Colwell 2001). Collectively, our results provide partial support for the second hypothesis in that diversity of trees shows relatively similar responses to long term retrogression in geographically distinct locations.

Our failure to find strong evidence for increasing tree species richness during retrogression, and the occurrence of only neutral or positive correlations between species richness and basal area, is in contrast to patterns commonly reported for herbaceous communities where negative or hump-shaped relationships between plant diversity and biomass are commonly found (Grime 1973, Grace 1999, Waide et al. 1999, Mittelbach et al. 2001, Cornwell and Grubb 2003). Although there have been fewer attempts to characterize these relationships in forested systems, our results are in line with prior studies in forests that do not provide consistent support for such relationships (Wilson et al. 1996, Mittelbach et al. 2001, 2003, Whittaker and Heegaard 2003).

Our findings are mostly inconsistent with theory that predicts greater coexistence of plant species with increasing nutrient limitation and decreasing plant biomass, for

example through reduced competitive exclusion of subordinate tree species (Grime 2001) or through greater spatial heterogeneity of limiting soil nutrients promoting niche partitioning (Tilman 1988, Silvertown 2004). The only instance in which such mechanisms may have been operating was for a portion of the Hawaiian sequence, during the transition from stage 2 to stage 3 (Fig. 1). For three of the other chronosequences, declines in soil fertility associated with soil aging were associated with both reduced tree biomass and fewer tree species being able to persist. Those results are more consistent with competition theory pointing to the plausibility of positive relationships between plant coexistence and biomass productivity (Abrams 1995, Stevens and Carson 2002). Our results show that there are more tree species adapted for establishing and persisting in nutrient-rich (productive and high biomass) sites than nutrient-poor sites along those three chronosequences, at least at the spatial scale of our study. Greater tree diversity in fertile and productive stands is consistent with earlier suggestions that such stands support large number of slow growing shade tolerant tree species that are competitive in a deep shade environment (Cornwell and Grubb 2003). Given that our results contrast with several studies on herbaceous plant dominated systems, in which high numbers of species may be adapted for nutrient poor conditions (Grace 1999, Grime 2001), it appears that trees as a life form are generally less successful than smaller statured (e.g. herbaceous) life forms in nutrient poor conditions.

Species richness and Shannon-Weiner diversity indices for tree species showed similar responses to chronose-

Table 3. Relationships between measures of vegetation diversity and humus C to N, C to P and N to P ratios, shown as R² values from regression analyses testing for first and second order polynomial terms, the nature of the relationship, and whether the relationship is positive (+) or negative (-). F and p values in bold indicate statistical significance at p=0.05.

Diversity measure	Nutrient ratio	Chronosequence					
		Arjeplog	Glacier Bay	Franz Josef	Waitutu	Cooloola	Hawaii
Tree species richness	C to N	NS ^b	NS	0.288 quadratic (-)	NS	NS	0.428 quadratic (-)
	C to P	0.201 quadratic (-)	NS	NS	0.697*** linear (-)	NS	NS
	N to P	NS	NS	NS	0.712*** linear (-)	0.256* quadratic (-)	0.303 quadratic (-)
Tree species richness (rarefied)	C to N	NS	NS	0.301* quadratic (-)	0.290* linear (-)	NS	NS
	C to P	0.243* quadratic (-)	NS	NS	0.714*** linear (-)	NS	NS
	N to P	NS	NS	NS	0.598*** linear (-)	0.250* quadratic (-)	NS
Tree diversity (SWDI) ^a	C to N	0.175* linear (+)	NS	NS	0.532** quadratic (-)	0.388** quadratic (-)	NS
	C to P	0.280* quadratic (-)	0.213** linear (-)	0.355* quadratic (+)	0.791*** quadratic (-)	0.412** quadratic (-)	0.170* linear (-)
	N to P	0.283** linear (-)	0.285** quadratic (-)	0.324* quadratic (+)	0.698*** quadratic (-)	0.330** quadratic (-)	0.251* quadratic (-)
Vascular plant species richness	C to N	NS	NS	NS	ND ^c	0.606*** quadratic (-)	NS
	C to P	NS	NS	NS	ND	0.588*** quadratic (-)	NS
	N to P	NS	NS	NS	ND	0.400** quadratic (-)	NS

*, **, *** means that R² is significantly different to 0 at p=0.05, 0.01 and 0.001 respectively.

^aShannon-Weiner diversity index.

^bNS = no significant relationship.

^cND = not determined.

quence stage along four of the sequences, but not along the Arjeplog or Franz Josef sequences. In these cases, stands with high values for basal area (and therefore biomass) sometimes had the lowest diversity indices. This is due to domination of these stands by a single tree species; for stage 1 of the Arjeplog sequence *Pinus sylvestris* comprised 78% of the total basal area while for stage 4 of the Franz Josef sequence *Metrosideros umbellata* comprised 66% of the total basal area. Thus, although species richness did not respond to chronosequence stage for either sequence, there was a distinct decline in evenness at the maximal biomass phase that was driven by dominance by a single species. Although this result is consistent with studies from herbaceous systems showing dominance by a small number of species when plant biomass is maximal (Grime 1973, Grace 1999), subordinate tree species were still able to persist and there was no obvious evidence of reduction of total tree species richness (e.g. through competitive exclusion) by these dominants. While we recognize the need for caution in interpreting derived diversity indices (Magurran 1988), our results nevertheless support the view that indices that incorporate evenness can yield insights about patterns of diversity that species richness data on its own cannot (Stirling and Wilsey 2001, Wilsey et al. 2005).

While our primary focus was on drivers of forest tree diversity, which is consistent with many other studies (Enquist and Niklas 2001, Wright 2002, Condit et al. 2006), we also took the opportunity to assess total vascular plant species richness across five of the chronosequences. Vascular plant richness increased during retrogression in four of the five sequences where we measured total richness (Fig. 2), and this pattern was driven by an increased richness of understory plant species in the oldest stages. This increase was driven by increasing numbers of inherently smaller statured species, such as shrubs and herbaceous plants, rather than by tree species present at the maximal biomass phase reverting to non-tree forms during retrogression. We note that the six chronosequences are dominated by evergreen tree species, and that evergreen forests support few spring ephemeral herbs, which is in contrast to productive and fertile sites in temperate deciduous forests. As such, the sites that we considered need not necessarily support a species rich understory at the maximal tree biomass phase, in the same way that might be expected for high biomass deciduous forests (Loucks 1962).

There are three plausible reasons for this increase in understory (and hence total) vascular plant diversity during ecosystem retrogression. First, competition by trees for belowground resources may decline during retrogression, leading to reduced competitive exclusion of non-tree growth forms (Grime 2001); in this light, there is experimental evidence of reduced plant competition intensity during retrogression in the Arjeplog sequence (Wardle and Zackrisson 2005). Second, it has been proposed that as soil fertility declines, such as happens during retrogression, there is a greater spatial heterogeneity of limiting soil nutrients and that this heterogeneity promotes niche partitioning and therefore vegetation diversity (Tilman 1988, Silvertown 2004; but see Stevens and Carson 2002). Third, as tree basal area declines during retrogression, there is likely to be greater amounts of light

reaching the understory (Wardle et al. 2003, Coomes et al. 2005) and a greater heterogeneity of light regime as a result of increased openings in the tree canopy (Pacala et al. 1996, Uriarte et al. 2005). This might increase the likelihood of species coexistence in the understory through increased partitioning of light (Kohyama 1993, Gough et al. 2000, but see Lusk et al. 2006). Regardless of the mechanisms involved, our results provide evidence that there are a high range of plant species with smaller statured life forms, but not tree life forms, adapted for low fertility retrogressive stages of ecosystem succession.

Tree species richness showed negative linear or quadratic relationships with at least one of the three soil nutrient ratios tested (i.e. C to N, C to P and N to P) for five of the six sequences (or for four sequences when data was rarefaction-adjusted) (Table 3). Meanwhile, the Shannon-Weiner index for tree diversity showed negative relationships with C to P and N to P for five of the sequences (the sixth relationship was positive). For all the chronosequences except Arjeplog, there was an initial period of increasing tree species richness or diversity as increasing numbers of species established over time (Walker and del Moral 2003); during this build-up phase it is plausible for increased diversity to coincide with increased soil C and N and decreased soil P, and thereby with increased soil C to P and N to P ratios. Meanwhile, during retrogression, reduced relative availability of P (and continued increases in C to P and N to P ratios) (Walker and Syers 1976, Vitousek 2004, Wardle et al. 2004) is associated with reduced tree diversity for most chronosequences. This latter finding is inconsistent with studies in grasslands pointing to plant diversity being promoted by decreasing soil concentrations of P (Crawley et al. 2005, Wassen et al. 2005) and increasing soil age (Pärtel 2002), but is consistent with predictions that plant diversity can be regulated by the most limiting resource in a community (Stevens and Carson 2002). When total (tree plus understory) plant species richness is considered, there were significant relationships with nutrient ratios only for the Cooloola sequence. In that case, the increase in total plant diversity with increasing ratios of C to N, C to P and N to P are all consistent with the results of grassland studies which show increasing plant diversity with increasing nutrient limitation (Grime 2001, Crawley et al. 2005).

Although nutrient ratios were often a good predictor of tree and total plant species richness, historical biogeographic influences and therefore regional species pool sizes might also help explain results for some of the chronosequences, especially for Hawaii (Price 2004). The Hawaiian chronosequence is spread across an island chain in which islands differ in both area and age, and several species across this chain have strong dispersal barriers. These factors, and especially the age of the island, are powerful determinants of the total available island species pool (Price 2004), which might help explain some of our results. For example, the highest vascular plant diversity occurs on plots on the oldest island for which speciation would have had the greatest amount of time to occur.

These results have several implications. First, they provide evidence that as soils age in the prolonged absence of catastrophic disturbance, and the amounts of available nutrients (notably P) declines, there is often a decline in

the diversity of trees and a corresponding increase in understory plant diversity. Forests with relatively high standing biomass and high diversity of trees are transient, and do not persist indefinitely in the long-term absence of catastrophic disturbance (i.e. disturbance of sufficient severity to rejuvenate soils). Second, these results point to some similarity of responses of plant diversity to ecosystem retrogression in boreal, temperate and subtropical systems; in most cases tree diversity showed a neutral or negative response to retrogression and soil aging. Whether or not such patterns are also characteristic of other ecosystem types such as hyperdiverse tropical rain forests (Ashton 1989) or ancient soils dominated by non-forest vegetation, merits investigation. In this light, our finding that species richness varied in relation across gradients of soil age and fertility, and therefore that several species can occur only along portions of these gradients, is in sharp contrast to recent studies of hyperdiverse tropical rainforest where species occurrence is largely independent of soil fertility (Hubbell 2005). Finally, these results point to the value of well characterized natural experiments for understanding long-term community and ecosystem processes in systems dominated by long lived organisms (e.g. trees) in a manner that cannot be achieved in any other way (Pickett 1989, Fukami and Wardle 2005).

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Appendix 1. Ages and dominant plant species for each stage of each of the 6 chronosequences, and key references.

n = number of plots sampled at each stage. For further information see Wardle et al. (2004).

COOLOOLA chronosequence, Australia (27°30'S, 153°30'E). Chronosequence is caused by sand dunes of varying age caused by aeolian sand deposition. For more information see Thompson (1981), Walker et al. (2001).

Stage 1: 10 years. Sand dunes with sparse individuals of *Banksia integrifolia*. (n = 3)

Stage 2: 50–100 years. Establishing low forest. *Banksia integrifolia*, *B. serrata*, *Casuarina littoralis*. (n = 3)

Stage 3: 500–1000 years. Mid-high open forest. *Banksia integrifolia*, *B. serrata*, *Callitris columnararis*, *Casuarina littoralis*, *Eucalyptus intermedia*, *Monotoca* sp. (n = 3)

Stage 4: 2500–3500 years. Mid-high open forest. *Banksia serrata*, *Casuarina littoralis*, *C. torulosa*, *Eucalyptus intermedia*, *E. racemosa*, *Lophostemon confertus*, *Monotoca* sp. (n = 3)

Stage 5: 6500–9000 years. Tall open forest. *Banksia serrata*, *Casuarina torulosa*, *Cinnamomum baileyianum*, *Eucalyptus pilularis*, *Monotoca* sp. (n = 3)

Stage 6: 100 000–140 000 years. Extremely tall closed forest. *Banksia aemula*, *B. integrifolia*, *Casuarina torulosa*, *Eucalyptus intermedia*, *E. pilularis*, *Monotoca* sp. (n = 3)

Stage 7: 230 000–300 000 years. Mid-high open shrubby forest. *Banksia aemula*, *Casuarina littoralis*, *Eucalyptus signata*, *Leptospermum attenuatum*, *Monotoca* spp. (n = 3)

Stage 8: 450 000–550 000 years. Low shrubby woodland. *Angophora woodsiana*, *Banksia aemula*, *Eucalyptus intermedia*, *E. signata*, *Leptospermum semibaccatum*. (n = 3)

Stage 9: >600 000 years. Dwarf shrubby open woodland. *Banksia aemula*, *Eucalyptus signata*, *E. intermedia*. (n = 3)

ARJEPLOG chronosequence, Sweden (65°02'N, 17°49'E). This sequence is based on islands of varying sizes, in which large islands have burned as a result of lightning strike more often than have small islands; the retrogression is caused by increasing time since last major fire. The stages are determined on the basis of island size (with stage inversely related to island size) and the age given for each stage is the mean time since fire for all the islands in that stage. For more information see Wardle et al. (1997, 2003).

Stage 1. 160 years. Forest dominated by *Pinus sylvestris* and ground layer dominated by *Vaccinium myrtillus*. (n = 3)

Stage 2. 767 years. Forest dominated by *Pinus sylvestris* and ground layer dominated by *Vaccinium myrtillus*. (n = 7)

Stage 3. 1571 years. Forest dominated by *Betula pubescens* and conifers, and ground layer dominated by *Vaccinium vitis-idaea*. (n = 5)

Stage 4. 2457 years. Forest dominated by *Betula pubescens* and conifers, and ground layer dominated by *Vaccinium vitis-idaea*. (n = 5)

Stage 5. 2869 years. Forest dominated by *Picea abies* and *Betula pubescens* and conifers, and ground layer dominated by *Empetrum hermaphroditum*. (n = 7)

Stage 6. 4278 years. Forest dominated by *Picea abies* and *Betula pubescens* and conifers, and ground layer dominated by *Empetrum hermaphroditum*. (n = 3)

GLACIER BAY chronosequence, Alaska (59°N, 136°W). Chronosequence involves surfaces of varying ages caused by glacial retreat. For more information see Noble et al. (1984) and Chapin et al. (1994).

Stage 1. 12 years. Mostly bare moraine. Scattered *Dryas drummondii* shrubs. (n = 4)

Stage 2. 20 years. Sparse, short shrubland. *Dryas drummondii*, *Salix alaxensis*, *S. arctica* and *S. sitchensis*. (n = 4)

Stage 3. 60 years. Dense, tall shrubland. Dominated by *Alnus sinuata*. (n = 4)

Stage 4. 107 years. Forest. *Picea sitchensis*. (n = 4)

Stage 5. 225 years. Forest. *Picea sitchensis* and *Tsuga heterophylla*. (n = 4)

Stage 6. 1300 years. Forest. *Tsuga heterophylla*. (n = 4)

Stage 7. 11 000–14 000 years. Forest. *Tsuga heterophylla* and *Oplopanax horridus*. (n = 4)

Stage 8. 14 000 years. Bog. Shrubs of *Ledum groenlandicum*, *Empetrum nigrum* and *Rubus chamaemorus*, and scattered *Tsuga heterophylla* and *Pinus contorta*. (n = 4)

HAWAII chronosequence, Hawaii, USA (19–22°N, 155–160°W). Chronosequence involves surfaces of varying ages caused by volcanic lava flow. For more information see Crews et al. (1995), Vitousek and Farrington (1997) and Vitousek (2004).

Stage 1. 300 years. Forest. *Metrosideros polymorpha* with *Cibotium glaucum* understory. (n = 4)

Stage 2. 2000 years. Forest. *Metrosideros polymorpha* with *Cibotium glaucum* understory. (n = 4)

Stage 3. 22 000 years. Forest. *Metrosideros polymorpha* with some *Acacia koa* and *Cheirodendron trigynum*; understory of *Cibotium glaucum* and *C. chamissoi*. (n = 4)

Stage 4. 150 000 years. Forest. *Metrosideros polymorpha* with some *Cheirodendron trigynum* and *Melicope clusii-folia*; understory of *Cibotium glaucum* and *C. chamissoi*. (n = 4)

Stage 5. 1 400 000 years. Forest. *Metrosideros polymorpha* and some *Cheirodendron trigynum*; understory of *Cibotium glaucum*. (n = 4)

Stage 6. 4 100 000 years. Forest. *Metrosideros polymorpha* and some *Cheirodendron trigynum*, *Melicope anisatum*, *Cyrtium* sp., *Psychotria* sp. (n = 4)

FRANZ JOSEF chronosequence, New Zealand (43°25'S, 170°10'E): Chronosequence involves surfaces of varying

ages caused by glacial retreat. For more information see Walker and Syers (1976) and Richardson et al. (2004).

Stage 1. 60 years. Short forest. Domination by several species, notably *Coriaria arborea*, *Melicactus ramiflorus* and *Schefflera digitata*. (n = 2)

Stage 2. 150 years. Short forest. *Myrsine divaricata*, *Griselinia littoralis* and *Olearia avicenniaefolia*. (n = 3)

Stage 3. 250 years. Short forest. *Schefflera digitata*, *Cyathea smithii*, *Weinmannia racemosa* and *Metrosideros umbellata*. (n = 3)

Stage 4. 500 years. Forest. *Weinmannia racemosa* and *Metrosideros umbellata*, with understory of *Cyathea smithii*, *Pseudowintera colorata* and *Myrsine divaricata*. (n = 3)

Stage 5. 1000 years. Forest. *Weinmannia racemosa* and *Metrosideros umbellata*, with understory of *Schefflera digitata*, *Dicksonia squarrosa*, *Cyathea smithii* and *Pseudowintera colorata*. (n = 3)

Stage 6. 5000 years. Forest. *Metrosideros umbellata* and *Weinmannia racemosa*, with understory of *Schefflera digitata*, *Dicksonia squarrosa* and *Cyathea smithii*. (n = 3)

Stage 7. 12 000 years. Forest. *Weinmannia racemosa*, *Dacrydium cupressinum* and *Prumnopitys ferruginea*, with understory of *Quintinia acutifolia* and *Dicksonia squarrosa*. (n = 3)

Stage 8. 60 000 years. Forest. *Weinmannia racemosa*, *Dacrydium cupressinum* and *Metrosideros umbellata*, with understory of *Quintinia acutifolia* and *Dicksonia squarrosa*. (n = 3)

Stage 9. 120 000 years. Shrubby forest. *Phyllocladus alpinus*, *Manoao colensoi*, *Leptospermum scoparium*, *Podocarpus hallii*, *Quintinia acutifolia* and *Coprosma* spp. (n = 3)

WAITUTU chronosequence, New Zealand (46°06'S, 167°30'E): Chronosequence involves terraces of varying ages caused by uplift of marine sediments. For more information see Ward (1988) and Coomes et al. (2005).

Stage 1. 3000 years. Shrubland. Domination by *Brachyglottis rotundifolius* and *Coprosma rhannoides*. (n = 3)

Stage 2. 80 000 years. Forest. *Weinmannia racemosa*, *Nothofagus solandri*, *Metrosideros umbellatum* and *Dacrydium cupressinum*. (n = 3)

Stage 3. 100 000 years. Forest. *Weinmannia racemosa*, *Nothofagus solandri*, *N. menziesii* and *Dacrydium cupressinum*. (n = 2)

Stage 4. 120 000 years. Forest. *Weinmannia racemosa*, *Nothofagus solandri*, *Dacrydium cupressinum*, and *Metrosideros umbellatum*. (n = 3)

Stage 5. 209 000 years. Forest. *Holocarpus biformis*, *Dacrydium cupressinum*, *Podocarpus hallii* and *Weinmannia racemosa*. (n = 1)

Stage 6. 291 000 years. Shrubland/short forest. *Holocarpus biformis*, *H. bidwillii*, *Nothofagus solandri* and *Leptospermum scoparium*. (n = 3)

Stage 7. 600 000 years. Shrubland. *Holocarpus biformis*, *H. bidwillii*, *Nothofagus solandri* and *Leptospermum scoparium*. (n = 2)