

Primary succession in Mount Pinatubo

Habitat availability and ordination analysis

Thomas E Marler^{1,*} and Roger del Moral²

¹Western Pacific Tropical Research Center; University of Guam; UOG Station; Mangilao, Guam USA; ²Department of Biology; University of Washington; Seattle, WA USA

Keywords: canonical correspondence analysis, detrended correspondence analysis, Mount Pinatubo, primary succession

Vegetation structure on the east flank of Mount Pinatubo was investigated to determine the inventory of species at 15 y post-eruption, then to ascertain environmental variables that have influenced the early patterns of primary succession. Unconstrained and constrained ordination methods were used to determine the influence of spatial, elevation, and substrate patterns on vegetation. Vegetation was assigned to one of 3 habitat types. Scours were eroded flat surfaces, terraces were perched flat surfaces, and talus piles were created along the canyon edges as mass waste events. The influence of habitat type on vegetation was multifaceted because they represent different conditions and different histories. The talus piles have preferential access to colonists from the vegetation on the canyon walls above and a more benign microclimate than the exposed terrace and scour sites. Scoured sites on the valley floor exhibited the least vegetation cover, as these substrates had the least mature surfaces and the most restricted capacity for root exploration. Perched terraces exhibited greater plant dominance than did the other habitats in the early stages of succession because of the ubiquitous appearance of *Parasponia rugosa* as initial colonists on these relatively flat surfaces. Polynomial canonical correspondence analysis was more closely aligned with the pattern of vegetation than linear canonical correspondence analysis, and therefore more closely approximated accurate descriptions of correlations among site ordination positions and measured variables. These results confirm that a variety of statistical approaches can clarify applications for restoration ecology following landslide and volcanic disturbances or agriculture and forestry anthropogenic disturbances in the lowland tropics.

Introduction

Mount Pinatubo erupted on June 15, 1991, when 5 to 6 km³ of ejecta were deposited on the upper slopes.¹ Pyroclastic flows covered more than 30% of the watershed for the river systems on the east flanks.² Sedimentation and scouring alternated for several years resulting in chronic changes in elevation of the canyon beds.³

These drainages have been utilized by the Aeta ethnic minority since pre-Hispanic times. Until recently, their way of life depended on extensive use of native vegetation and river resources.⁴ The eruption and subsequent lahars have threatened their culture in many ways.⁵⁻⁷ This motivated us to describe patterns of vegetation and growth form structure along 2 river systems on the east flanks of Mount Pinatubo 15 y after the eruption.⁸ We elected to focus on the river canyons for this study because ecological recovery in the riparian zones was critical for sustaining traditional knowledge in this people group.

Our earlier work enumerated the flora and used a traditional statistical approach to reveal factors that may have shaped it.⁸ However, ecologists have been trying for many years to reach consensus on a comprehensive description of species distribution

patterns and the mechanisms explaining these patterns.^{9,10} Understanding relationships between species and environmental factors is crucial when pursuing this goal. A greater understanding of all factors that have shaped the Mount Pinatubo flora may be more fully realized by use of contemporary statistical approaches. Detrended correspondence analysis (DCA) is highly reliable for data exploration in community ecology.¹¹ This statistical technique may illuminate the main factors or gradients in large data matrices. Canonical correspondence analysis (CCA) takes advantage of the fact that species abundance or probability of occurrence is often a unimodal function of the environmental variables, and can help ecologists unravel how a many species simultaneously respond to external factors.¹² The relationship between individual species and external factors is rarely linear, so the polynomial of CCA (pCCA) is often employed for improving interpretations.^{13,14}

Here we explore patterns of species and growth form composition using these ordination methods. Understanding vegetation recovery on these new substrates may provide insights for the restoration of other damaged tropical ecosystems, where agriculture, landslides, and forestry¹⁵ have taken a huge toll. The

Correspondence to: Thomas Marler; Email: tmarler@uguam.uog.edu

Submitted: 07/19/2013; Accepted: 07/27/2013

Citation: Marler TE, del Moral R. Primary succession in Mount Pinatubo: Habitat availability and ordination analysis. *Communicative & Integrative Biology* 2013; 6:e25924; <http://dx.doi.org/10.4161/cib.25924>

focus of this paper is to: 1) characterize the sites that support succession in the recovering Mount Pinatubo landscape; and 2) determine the plant and environmental variables correlated with vegetation patterns using DCA, CCA, and pCCA. Our outcomes will determine which questions can be tested in subsequent studies of primary succession in tropical volcano systems.

Materials and Methods

Field sampling

Vegetation was sampled in March and April 2006 along the Pasig-Potrero River (PR) and Sacobia River (SR) systems using a variant of the method described by del Moral and Lacher.¹⁶ Methods of positioning our plots, measuring vegetation cover, and identifying taxa were described by Marler and del Moral.⁸ The location of each plot was determined by GPS, from which elevation and distances from the caldera were ascertained. We also measured the lateral distance between the center of each plot and the edge of the canyon or the channel, to the nearest human habitation and to the alluvial fan. Aspect was determined by compass and, for the purposes of direct ordination values were converted to a 5-point scale reflecting insolation.¹⁷ Slope was determined by clinometer and converted to a 5 interval scale: 1 = 0–5°; 2 = 6–10°; 3 = 11–15°; 4 = 16–25° and 5 = > 25°. The percentage of the soil surface covered by rocks, gravel, and sand was estimated visually and converted into 5 categories. Only rocks and sand characteristics were used because also using gravel would lead to strong colinearity. For rocks, 1 = 0 to 9%; 2 = 10 to 19%; 3 = 20 to 29%; 4 = 30 to 39%; and 5 = 40% or more. For sand, 1 = 1 to 25%; 2 = 26 to 40%; 3 = 41 to 50%; 4 = 51 to 80%; and 5 = 81% or more.

For each plot, we calculated the number of species (richness species), total percent cover, Simpson's diversity index ($D = [1 - \sum P_i^2]$), and the Shannon-Weiner index ($H' = [-\sum (P_i \ln P_i)]$). For both D and H' , P_i is the proportion of total plot cover of a species.¹⁸

Site characteristics

At the time of our field work, soil surfaces remained unstable in this ecosystem. However, vegetation very rapidly colonized any soil surface that became stable. Our plots were assigned to one of 3 habitat types: 1) perched terraces, formed when torrential rains created lahar or deep aggradation deposits, then subsequent channel incision isolated the new surfaces above the elevation of the channel; terrace surfaces were typically 1–4 m above the adjacent canyon surface; 2) scoured surfaces occurred within the canyons when sheet erosion exposed large rocky surfaces and allowed vegetation to develop after the disturbance ceased; there was little soil remaining to support root development; and 3) the pyroclastic flow substrates on this volcano are vulnerable to mass waste events that ultimately form talus piles. These processes are discussed by Gran.¹⁹ We assessed the influence of habitats on vegetation traits using one-way ANOVA.

Ordination

We used detrended correspondence analysis (DCA) to analyze the full set of data,¹⁸ in particular species spatial patterns. Species found in fewer than 5 plots were excluded, and those found in

fewer than 22 plots were reduced in influence to emphasize larger scale patterns. DCA is robust with low β diversity and is scored in a measure of species turnover. DCA axes were analyzed using stepwise multiple regressions to the measured variables. Sites were treated as a multistate variable.

We used 2 approaches to conduct constrained ordinations of the relationships between vegetation patterns and environmental variables. Canonical correspondence analysis (CCA)¹² was conducted using PC-ORD.¹⁸ Once a canonical analysis of species composition was achieved, the best fit of environmental variables to each ordination axis was calculated. Monte Carlo simulations ($n = 1000$ trials) were used to assess the validity of each of the first 3 axes. Sites were treated as 3 binary variables; latitude was excluded because it is strongly correlated with elevation. The relationship between environmental factors and plots was visualized in bi-plots. The position of a plot was determined from the linear or polynomial combination of environmental factors determined by the analysis, assessed by the Pearson correlations between the vegetation data and the environmental data.

The relationship between species and environmental variables is rarely linear, which is an assumption of CCA. Therefore, we also used polynomial CCA (pCCA), described by Makarenkov and Legendre,²⁰ to improve interpretations.^{13,14} Sites were treated as binary variables while the remaining variables were spatial: coordinates based on GPS position (east–west and north–south); elevation; and distances of the plot from the incised stream channel, the edge of the canyon and the caldera rim. Other distances, e.g., to human habitation or the alluvial fan, were strongly correlated with one or more of the 7 variables used, so these were excluded from pCCA analysis.

Statistical analyses were conducted using Statistix8.²¹ Graphs were produced using Axum 7.²²

Results

Habitats

Percent vegetation cover varied greatly among sites. Cover in terraces and talus piles exceeded cover in scours (Table 1). There were no significant differences in species richness or diversity among types.

Species composition—taxonomic and growth form subsets

We found 58 identifiable taxa of vascular plants within our plots.⁸ In vegetation with such a large species pool, early patterns are often more clear when growth forms are explored. Therefore, we compared changes in the percent cover of common species arrayed by growth forms in each plot (Table 2).

Trees were dominated by *Parasponia rugosa*, were abundant throughout the study area, and exhibited greater cover in terraces and talus piles than in scours. Shrubs were rare, although shrub cover in talus piles greatly exceeded that in terraces or scours, while vine cover was less. Large, spreading grasses were abundant. *Saccharum spontaneum* was the dominant large grass, and was most abundant on terraces. In contrast, *Miscanthus floridulus* was more common in talus piles. Total large grass cover was greatest in terraces. Small graminoids were also common, and their cover was greatest in talus piles. Forbs were common

Table 1. Species richness (number of species per plot), percent cover, Shannon-Wiener Diversity (H'), and Simpson's Diversity (D)

Trait	Scour	Terrace	Talus pile
Richness	12.2	10.5	11.7
Cover (%)	107.5b	139.4a	143.2a
H'	1.587	1.402	1.615
D	0.686	0.664	0.700

Note: Differences among habitat types were determined separately by ANOVA, followed by Bonferroni comparisons when significant.

in aggregate, but no single species dominated. *Pityrogramma calomelanos* was the most common fern, and was more common in talus piles.

Unconstrained ordination

The general pattern of vegetation, visualized with DCA, employed 33 species after omitting rare ones; of these, 21 were down-weighted. The analysis spread plots well in floristic space. The total variance of the data was 1.384, of which 21.2% was found on the first axis, and 8.7% was on the second. Although there was some overlap between the 2 rivers, plots tended to segregate by their river (Fig. 1). Terrace vegetation of the 2 rivers was similar, and found in the center of the ordination. Talus pile vegetation was more distinct, and found with lower DCA-1 scores. Scoured sites tended to occur with higher DCA-1 scores. The SR scours were extreme on DCA-1, with only one PR scour plot near them in this space.

Individual species patterns did not produce readily interpretable results. The low end of DCA-1 was dominated by species common in talus piles (e.g., *Parasponia rugosa*, *Mikania scandens*, *Miscanthus floridulus*, *Pogonatherum crinitum* and *Pityrogramma calomelanos*, while the higher end was dominated by species common on scours (e.g., *Calopogonium mucunoides*, *Saccharum spontaneum*, and *Mimosa pudica*). *Parasponia rugosa* and *Melinis repens* dominated the low end of DCA-2, while *Phragmites karka*, *Centrosema molle* and *Miscanthus floridulus* characterized the higher end. This weaker gradient suggested a shift from PR plots to SR plots.

The environmental interpretation of the first 2 axes was improved by a multiple regression of the DCA scores vs. the environmental variables. DCA-1 was related to east–west position ($t = 7.37$) and to surface type ($t = -6.55$), indicating a strong gradient from talus piles to scours ($r^2 = 0.682$) that is consistent with the visual analysis. Elevation declines from west to east. DCA-2 was weak ($r^2 = 0.228$) and related to the north–south coordinates ($t = 3.12$) and to rock surface ($t = 2.85$). These provisional interpretations required examination by direct methods.

Constrained ordination

CCA clarified the pattern of species distributions found in the DCA. We excluded highly correlated variables (i.e., longitude is related to elevation on these east-trending valleys) and those with low predictive value in preliminary analyses (aspect, surface composition and distance to the channel). Habitat types again were binary variables. The total variance in this linear analysis (i.e., the eigenvalue) was 1.684 (Table 3). The Pearson correlation between the floristic ordination and the constrained ordination was 0.893 on Axis 1 and 0.786 on Axis 2; both the correlations and the size of the eigenvalues were highly significant ($p < 0.0001$ by Monte Carlo permutation tests).

The strong concentration of variation on Axis 1 was evident when the sites were plotted as linear combinations of the predictive variables with the environmental vectors overlain (Fig. 2A). Distance to the caldera (Cald) and elevation (Elev) were nearly mirror images. Elevation was a good surrogate for distances to the alluvial fan (Fan). The degree of slope was inversely correlated with the distance to the caldera, because sites became steeper closer to the caldera. Latitude (N–S) represented a third direction of variation. Terraces and talus pile sites were at opposite sides of the ordination, while scours (not shown) were intermediate. Floristic differences among sites appeared greater than differences among habitat types within a site.

Polynomial CCA (pCCA) was applied to these data (Table 3) and appeared to be more closely aligned with the pattern of vegetation than was CCA. In pCCA, the relationship between site positions and the predicted values was substantially larger, more of the floristic variance was explained, and the eigenvalues were larger. The quadratic variables combined to account for 39.4% of the canonical variation in the first 2 axes. The result was highly significant.

Sites were plotted using linear combinations of the predictive variables and overlain with the environmental vectors (Fig. 2B). The polynomial result demonstrated significant patterns in each of the first 3 axes. Axis 1 was associated with habitat and to a lesser degree with slope. Elevation, distance to the alluvial fan, distance to the caldera, and latitude all combine the first 2 axes. Plots formed reasonable clusters within a sample site. Pasig-Potrero River sites were well separated from the Sacobia River sites.

While pCCA provided greater confidence in providing provisional explanations for what was controlling vegetation, the pattern of species distribution in the 2 methods was similar. Mann-Whitney U-tests of species order Axis 1 and Axis 2 of the 2 constrained ordinations were similar (0.90 in Axis 1 and 0.60 in Axis 2). Thus, only pCCA will be described.

Centroids are the weighted mean position of each species, such that species concentrated in sites with negative scores occur near the negative end of an axis, while those that tend to occur primarily in sites at the positive extreme have a high value. Widespread species and those found in sites near the middle of an ordination axis have values near zero in this representation. Species such as *Pennisetum setaceum*, *Chromolaena odorata*, and *Muntingia calabura* were more abundant in the PR drainage, while *Chloris barbata*, *Phragmites karka*, and *Centrosema molle* represent species more common on SR. *Pityrogramma calomelanos*, *Pogonatherum crinitum*, *Mikania scandens*, and *Miscanthus floridulus* were common in talus piles, while *Phragmites karka*, and *Crotalaria pallida* represent those absent from talus piles and more common in the other habitats.

Table 2. Distribution of common species and growth forms across habitat types. Differences were determined by ANOVA, followed by Bonferroni comparisons ($p < 0.05$). Only common species are listed; growth form totals are for all species in group

Species	Scour	Terrace	Talus pile
<i>Leucaena leucocephala</i>	1.15	0.36	1.05
<i>Parasponia rugosa</i>	29.9b	45.7ab	55.4a
Trees	31.7b	46.2ab	58.4a
<i>Buddleja asiatica</i>	0.37	0.11	1.7
Shrubs	0.39b	0.19b	2.87a
<i>Calopogonium mucunoides</i>	4.86a	1.99ab	0.20b
<i>Centrosema molle</i>	2.56ab	4.04a	0.83b
<i>Macroptilium atropurpureum</i>	0.33	0.3	0.54
<i>Mikania scandens</i>	0.76b	0.45b	5.51a
Vines	16.3	15.3	9.3
<i>Miscanthus floridulus</i>	0.25b	0.80b	8.50a
<i>Phragmites karka</i>	1	0.8	0
<i>Saccharum spontaneum</i>	44.9ab	57.3a	34.2b
Large Grasses	46.4b	58.9a	43.8b
<i>Eragrostis tenella</i>	0.17b	2.68a	0.12b
<i>Imperata cylindrica</i>	0.67	0.94	0.58
<i>Melinis repens</i>	2.91	5.28	6.86
<i>Pennisetum setaceum</i>	2.47	1.19	2.03
<i>Pogonatherum crinitum</i>	0.19b	0.05b	4.91a
Small graminoids	4.72b	8.94ab	12.5a
<i>Chromolaena odorata</i>	1.96	4.76	5.68
<i>Conyza albida</i>	0.80ab	0.31b	1.84a
<i>Crotalaria pallida</i>	1.33a	0.76ab	0b
<i>Desmodium tortuosum</i>	0.88a	0.64ab	0b
<i>Lindenbergia philippensis</i>	0.9	0	1.01
<i>Mimosa diplotricha</i>	1.93a	1.64a	0b
<i>Tridax procumbens</i>	0.45	1.2	1.3
Forb	6.47	9.51	10.5
<i>Nephrolepis hirsutula</i>	0.64	0.01	1.16
<i>Pityrogramma calomelanos</i>	0.32b	0.34b	5.72a
Ferns	0.96b	0.44b	6.87a

However, these are merely trends, and no species mentioned was confined to one habitat type (see Table 2). Several do, however, fail to occur on talus piles and are found with negative Axis 1 scores.

Discussion

Spatial effects such as elevation and geographic position as well as habitat type were the main explanatory variables found in our analyses. Greater cover in terraces and talus piles than in scours was a function of at least 2 factors. First, terraces and talus piles were generally more mature than scours in the same location. Second, health and growth of some species were

constrained on the scoured surfaces where substrates suitable for root proliferation were limited. In one striking example, an unidentified armored scale exclusively attacked weak *P. rugosa* trees on scours, while vigorous individuals of this species in adjacent terrace and talus pile surfaces were not attacked. This Homoptera pest severely reduced canopy density of the infested trees. Dominance was stronger on terraces than talus piles or scours. This was due to the dense *P. rugosa* cover on all terraces. Rarely do the young Mount Pinatubo terrace surfaces initially support a significant number of plants other than *P. rugosa*.

Trees, shrubs, smaller graminoids, and ferns all increased in cover from scours to talus piles, indicative of the greater fertility and subsequent stability of the talus piles compared with scoured

areas. The other growth forms exhibited no significant patterns, though forbs also tended to increase on talus piles. Larger grasses and vines, adept at claiming space and holding soil in unstable surfaces, generally performed better on terraces and scours. Subsequent studies would benefit by spreading sampling along elevational gradients on the major habitat types to capture the existing variation more efficiently.

Gradient analysis

DCA separated the samples well considering the limited β diversity. Both river systems and habitat types exhibited an impact on vegetation. Variation appeared greater on the SR. DCA-1 was defined by SR talus pile and scoured plots. PR tended to occur at low scores of DCA-2, which had substantially less information than DCA-1, but plots of both drainages intermingled.

CCA separated the plots of the 2 river systems very well and a gradient from talus piles to other habitat types was revealed. The pCCA revealed more details in the vegetation pattern. Talus piles were sufficiently different from the other habitats to support distinct vegetation. The analysis preserved the floristic distinction between the river systems and emphasized the importance of spatial variables. The nature of spatial effects remains uncertain because distance could relate to local land use patterns and distance to colonists, or it could be an indicator of subsequent disturbance. While detailed investigation of this question awaits further field studies, it is clear that combined use of traditional statistics, DCA, and pCCA results in a more accurate characterization of the factors that are shaping primary succession.

Applications

As plants become established their roots help stabilize riparian surfaces.²³ Calculations from areas below the alluvial fan of these Mount Pinatubo drainages indicated that vegetation decreased flow velocities by up to 12%, added 8.21–12.31 kPa of cohesion to stream banks, decreased channel width, and created more stable stream banks.²⁴ Vegetation development has the potential to reduce the extent of rill erosion of the canyon walls

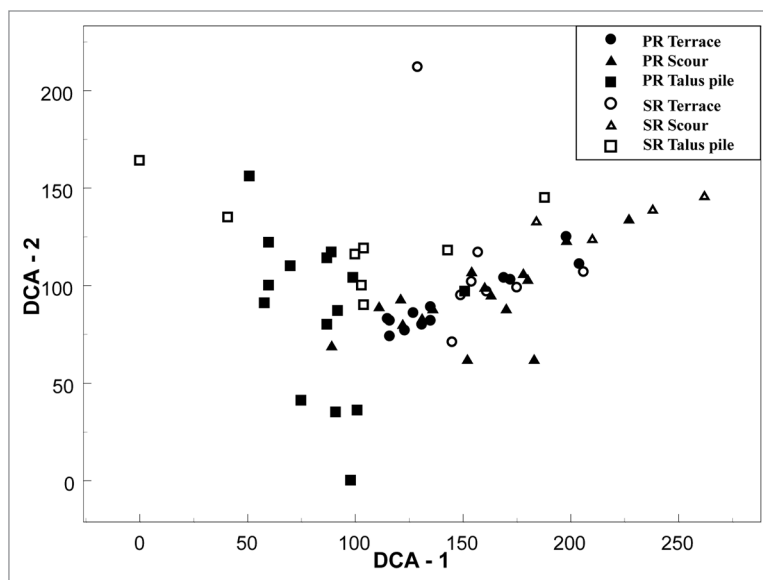


Figure 1. Detrended correspondence analysis of all 63 plots of vegetation along 2 river systems of Mount Pinatubo, arranged by site and habitat type characteristics. PR, Pasig-Potrero River; SR, Sacobia River.

and surface erosion of the canyon bottoms in Mount Pinatubo river systems.³ These habitats exhibit continuing surface scouring and sedimentation at small scale spatial scales, a phenomenon that increases α diversity without affecting β diversity.²⁵ These issues underscore the fact that our ability to understand what is influencing vegetation recovery will in turn advance our understanding of ecosystem recovery in Mount Pinatubo.

Samples that were at the same elevation and in the same habitat type tended to cluster in the ordinations, but the exceptions point to interesting issues. For example, one SR terrace plot was well isolated from the others, another SR scour plot was scattered, and one set of PR scour plots was not closely clustered. These plots hint that establishment from moderate distances has a distinct stochastic element.²⁶ Nakashizuka et al.,²⁷ found that dispersal rates onto a small debris avalanche slowed with distance to the edge and were dominated by wind

Table 3. Characteristics of linear (CCA) and polynomial (pCCA) canonical correspondence analyses

Characteristic	CCA	pCCA
Total CA variance	1.684	1.684
Coefficient of multiple determination	0.363	0.634
% of total variance explained	39.6	65.2
Canonical eigenvalues—Axis 1	0.236	0.280
Canonical eigenvalues—Axis 2	0.128	0.153
% explained variance of CA—Axis 1	14.0	16.6
% explained variance of CA—Axis 2	7.63	9.08
% explained canonical variance—Axis 1	35.4	25.5
% explained canonical variance—Axis 2	20.3	13.9
Sum of all canonical eigenvalues	0.667	1.097

CA = the indirect ordination (correspondence analysis)

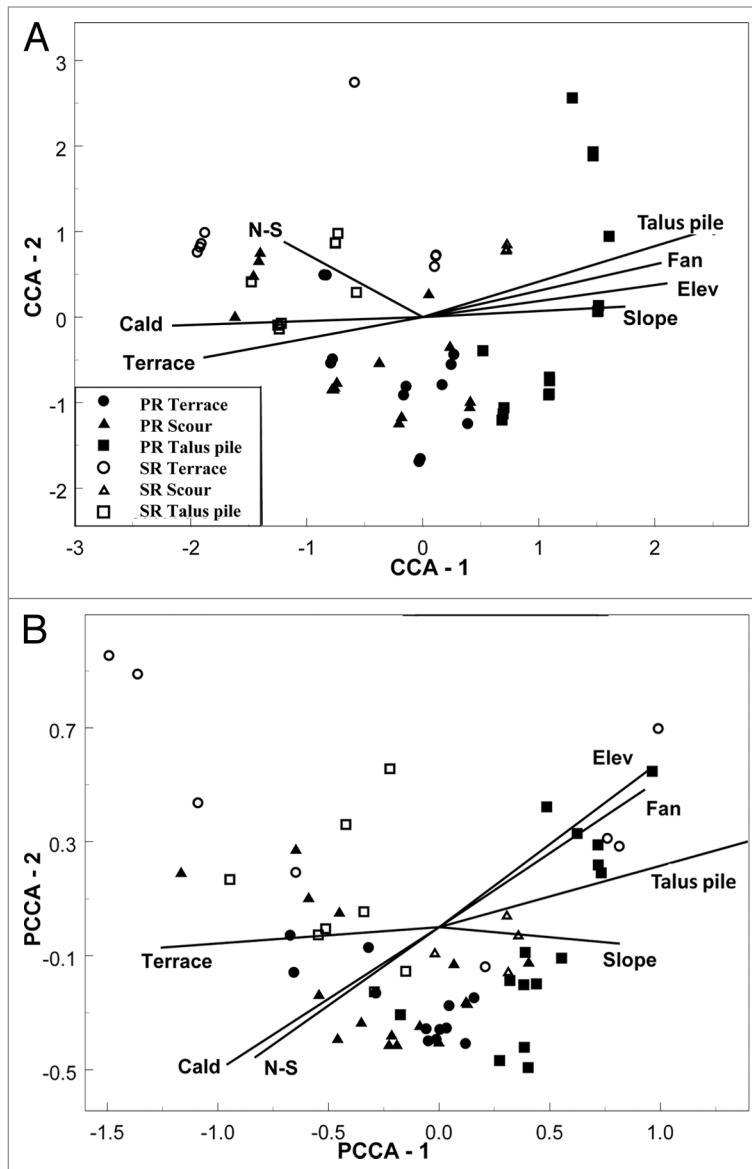


Figure 2. Direct gradient analysis using: 3 habitat types (terrace, scour, talus piles); elevation, latitude (N-S), slope, and aspect; and distance to nearest habitation, edge of river basin, alluvial fan, the caldera. Plots are located as linear combination of predictor variables. (A) Linear canonical correspondence analysis (CCA; environmental vectors multiplied by 2.5 to reduce confusion.) (B) Polynomial CCA with the same variables (pCCA; environmental vectors multiplied by 3 to reduce confusion.)

dispersed species. These factors lead to low predictability in species composition. In contrast, talus pile vegetation at any location was much less variable. This may be due to competitive effects of trees, vines, and strongly rhizomatous grasses. Further research is needed to determine if vegetation within terrace and scour habitats will become more predictable with continued vegetation development.

Talus piles result from landslides, which are known to foster heterogeneous edaphic environments for plant and soil development.^{28,29} The movement of soil, vegetation, and litter varies greatly with each mass waste event, creating patches of

heterogeneous fertility. Resource patchiness within a landslide is therefore highly dynamic, both spatially and temporally.²⁹ Because of this trait, we expected the vegetation in talus piles to be less predictable than in scours and terraces, but our results did not conform to this expectation. Results indicate that the factors driving primary succession in this environment may be more influenced by differences in exposure and microclimate than by traits of the substrates.

Polynomial CCA was more closely aligned with the pattern of vegetation than the CCA, as more of the CA variance was explained and the eigenvalues were larger. These statistics confirm that the polynomial approach more closely approximated an accurate description of the correlations among site ordination positions and measured variables during Mount Pinatubo primary succession.³⁰ Our results add to previously described lessons that can be learned from Mount Pinatubo^{5,8,25} by showing how these ordinations can disentangle the complex interacting factors that will foster continued primary succession.

The scour habitats were clearly more stressful environments than the talus piles. This disparity may shape future species interactions, as positive interactions among plants are stronger in stressful areas, whereas negative interactions predominate in less stressful environments.³¹ Therefore, examples of facilitation may be more prevalent in the scour environments, and examples of competition may shape continued succession in talus piles.

This immature vegetation is developing along several alternative pathways on these 3 habitat types. Terraces and talus piles are relatively stable, permitting rapid species assembly and maturation. Scours are subject to more frequent, unpredictable disturbances that retard further development and even force retrogression. Since these disturbances differ in timing and intensity within and between the 2 river systems, scour vegetation existed in a mosaic of patches at different developmental states. The rate of development on all habitat types was affected by climatic factors that change with elevation. They are also affected by landscape factors that influence colonization in a more random way. Finally, local surface factors influence establishment of some species.

This complex example of primary succession on a tropical volcano has disclosed some surprises, and we have no doubt that many more remain to be revealed.

Disclosure of Potential Conflicts of Interest

No potential conflicts of interest were disclosed.

Acknowledgments

Funds were provided by the Western Pacific Tropical Research Center (to TEM) and the US NSF (DEB05-41972 and DEB-1118593 to RdM)

References

1. Newhall CG, Punongbayan RS. Fire and Mud: eruptions and lahars of Mount Pinatubo, Philippines. Univ Washington Press, Seattle and London 1996.
2. Major JJ, Janda RJ, Daag AS. Watershed disturbance and lahars on the east side of Mount Pinatubo during the mid-June 1991 eruptions. In CG Newhall and RS Punongbayan [eds.], Fire and Mud: eruptions and lahars of Mount Pinatubo, Philippines. Univ Washington Press, Seattle and London 1996.
3. Gran KB, Montgomery DR. Spatial and temporal patterns in fluvial recovery following volcanic eruptions: Channel response to basin-wide sediment loading at Mount Pinatubo, Philippines. *Geol Soc Am Bull* 2005; 117:195-211; <http://dx.doi.org/10.1130/B25528.1>
4. Fox RB. The Pinatubo Negritos: their useful plants and material culture. *Philipp J Sci* 1952; 81:173-414
5. Marler TE. The aeta - pinatubo loop. *Commun Integr Biol* 2011; 4:788-90; PMID:22446557
6. Gaillard J-C, Leone F. Implications territoriales de l'éruption du Mt Pinatubo pour la minorité ethnique aeta: cas des bassins-versants des rivières Pasig et Sacobia (Provinces de Pampanga et Tarlac-Philippines). *Cahiers Savoisiens de Géographie* 2000; 1/2000:53-68
7. Seitz S. Coping strategies in an ethnic minority group: the Aeta of Mount Pinatubo. *Disasters* 1998; 22:76-90; PMID:9549174; <http://dx.doi.org/10.1111/1467-7717.00076>
8. Marler TE, del Moral R. Primary succession along an elevation gradient 15 years after the eruption of Mount Pinatubo, Luzon, Philippines. *Pac Sci* 2011; 65:157-73; <http://dx.doi.org/10.2984/65.2.157>
9. Gaston KJ. Global patterns in biodiversity. *Nature* 2000; 405:220-7; PMID:10821282; <http://dx.doi.org/10.1038/35012228>
10. Rosenzweig ML. Species diversity in space and time. Cambridge Univ Press, Cambridge UK 1995.
11. Shaw PJA. Multivariate statistics for the environmental sciences. Hodder Arnold, London 2003.
12. Ter Braak CJF. The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio* 1987; 69:69-77; <http://dx.doi.org/10.1007/BF00038688>
13. Hyvonen T, Holopainen J, Tiainen J. Detecting the spatial component of variation in the weed community at the farm scale with variation partitioning by canonical correspondence analysis. *Weed Res* 2005; 45:48-56; <http://dx.doi.org/10.1111/j.1365-3180.2004.00430.x>
14. Svenning JC, Skov F. The relative roles of environment and history as controls of tree species composition and richness in Europe. *J Biogeogr* 2005; 32:1019-33; <http://dx.doi.org/10.1111/j.1365-2699.2005.01219.x>
15. Langenberger G, Martin K, Sauerborn J. Vascular plant species inventory of a Philippine lowland rainforest and its conservation value. *Biodiv Cons* 2006; 15:1271-301; <http://dx.doi.org/10.1007/s10531-005-2576-4>
16. del Moral R, Lacher IL. Vegetation patterns 25 years after the eruption of Mount St. Helens, Washington, USA. *Am J Bot* 2005; 92:1948-56; PMID:21646112; <http://dx.doi.org/10.3732/ajb.92.12.1948>
17. Whittaker RH. Vegetation of the Great Smoky Mountains. *Ecol Monogr* 1956; 26:1-80; <http://dx.doi.org/10.2307/1943577>
18. McCune B, Mefford MJ. PC-ORD multivariate analysis of ecological data. version 4.0. Glendened Beach, OR: MjM Software Design; 2002.
19. Gran KB. Strong seasonality in sand loading and resulting feedbacks on sediment transport, bed texture, and channel planform at Mount Pinatubo, Philippines. *Earth Surf Process Landf* 2012; 37:1012-22; <http://dx.doi.org/10.1002/esp.3241>
20. Makarenkov V, Legendre P. Nonlinear redundancy analysis and canonical correspondence analysis based on polynomial regression. *Ecology* 2001; 83:1146-61; [http://dx.doi.org/10.1890/0012-9658\(2000\)83\[1146:NRAACC\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2000)83[1146:NRAACC]2.0.CO;2)
21. Analytical Software. Statistix8 for Windows. Analytical Software, Tallahassee, FL 2003.
22. Mathsoft. Axum 7 for Windows user's guide. Insightful Corporation, Seattle, WA 2001.
23. Tal M, Gran K, Murray AB, Paola C, Hicks DM. Riparian vegetation as a primary control on channel characteristics in multi-thread rivers. Riparian vegetation and fluvial geomorphology. By S.J. Bennett, A. Simon. Water Science and Application 8. American Geophysical Union. 2004. p. 43-58.
24. Dunn EO. Incipient vegetation recovery and its effect on braided channel morphology at Mount Pinatubo, Philippines. MS Thesis. Univ Minn 2011.
25. Marler TE. Recovering plant biodiversity: Mount Pinatubo lessons to learn. *Plant Signal Behav* 2011; 6:1380-2; PMID:22019638; <http://dx.doi.org/10.4161/psb.6.9.16962>
26. Fuller RN, del Moral R. The role of refugia and dispersal in primary succession on Mount St. Helens, Washington. *J Veg Sci* 2003; 14:637-44; <http://dx.doi.org/10.1111/j.1654-1103.2003.tb02195.x>
27. Nakashizuka T, Iida S, Suzuki W, Tanimoto T. Seed dispersal and vegetation development on a debris avalanche on the Ontake Volcano, Central Japan. *J Veg Sci* 1993; 4:537-42; <http://dx.doi.org/10.2307/3236081>
28. Shiels AB, West CA, Weiss L, Klawinski P, Walker R. Soil factors predict initial plant colonization on Puerto Rican landslides. *Plant Ecol* 2008; 195:165-78; <http://dx.doi.org/10.1007/s11258-007-9313-x>
29. Shiels AB, Walker LR, Thompson DB. Organic matter inputs create variable resource patches on Puerto Rican landslides. *Plant Ecol* 2006; 184:223-36; <http://dx.doi.org/10.1007/s11258-005-9067-2>
30. del Moral R, Titus JH, Cook AM. Early primary succession on Mount St. Helens, Washington, USA. *J Veg Sci* 1995; 6:107-20; <http://dx.doi.org/10.2307/3236262>
31. Bertness MD, Callaway R. Positive interactions in communities. *Trends Ecol Evol* 1994; 9:191-3; PMID:21236818; [http://dx.doi.org/10.1016/0169-5347\(94\)90088-4](http://dx.doi.org/10.1016/0169-5347(94)90088-4)