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Resilience against exotic species invasion in a tropical montane forest

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Keywords

Canopy disturbance; Exotic species; Hawaii;
Invasion; Resilience; Soils; Species
composition; Tropical montane forest;
Vascular plants; Volcanic substrate

Nomenclature

Wagner et al. (1990) = for flowering plants;
Palmer (2003) = for ferns and fern allies, except
where updated by Wagner et al. (2012)

Abbreviations

NMS = non-metric multidimensional scaling;
GAM = generalized additive models;
glmm = generalized linear mixed models;
m = meters; HETF = Hawaii Experimental
Tropical Forest; LiDAR = light detection and
ranging; VE = variance explained;
DE = deviance explained

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Abstract

Question: How do canopy disturbance and soil properties structure vascular plant community species composition and resilience to encroachment by exotic species in a tropical montane wet forest?

Location: Hawai'i Experimental Tropical Forest (HETF), a tropical montane wet forest, on Mauna Kea, Hawai'i Island, Hawai'i, USA.

Methods: Previous studies employing airborne LiDAR were used to define three zones across an elevation gradient from 900 to 1500 m. Within each zone, a ~1000-m block transect was selected to cross two different volcanic substrates: one derived from surface lava and one derived from thick ash deposits. Non-metric multidimensional scaling (NMS) scores of vegetation data were related to independently-derived environmental NMS scores and spatial location with generalized additive models (GAM).

Results: Vascular plant species composition in all elevation zones consists of three NMS axes, which are best modelled by one of three possible environmental NMS axes or by location. The first NMS axis of species composition in the lowest elevation zone (40% variance explained (VE)) is a function of location on volcanic substrates (61% deviance explained (DE)). The second lowest elevation axis (27% VE) is a function of unexplained spatial heterogeneity (31% DE). The third lowest elevation NMS axis (24% VE) is a function of the spatial mosaic of canopy disturbance (16% DE). In the middle elevation zone, species composition most strongly relates to the interaction between volcanic substrate and the condition of the soil surface for all three NMS axes (41%, 27%, 24% VE; 70%, 16%, 24% DE). The primary axis of species composition in the highest elevation zone (41% VE) corresponds with substrate and soil condition (55% DE) but the second and third axes of species composition (27% and 25% VE) relate to canopy dieback disturbance (36%, 14% DE). Counts of exotic species and 0–2 m height class native tree species respond to the type of volcanic substrate and soil surface condition in all three elevation zones. Lava-derived substrates have a higher incidence of exotic species and less native tree regeneration; whereas ash-derived substrates have higher numbers of native tree species regenerating and many fewer exotic species.

Discussion: The tropical montane forests on Mauna Kea reflect a native-dominated plant community response to disturbance on both lava- and ash-derived volcanic substrates, and a higher propensity for exotic species to occur on the lava-derived substrate. Native plant communities on ash-derived soils may have higher resilience to exotic invasion than communities on lava-derived substrates. Our results indicate resource managers should explicitly account for variation in soils and substrate type when prioritizing, implementing and monitoring management interventions to foster native plant assemblages and control the spread of exotic and invasive species.

Introduction

Forest managers seek to increase the resilience of forest ecosystems to preserve ecosystem functioning and conservation value despite increasing stresses and pressures (Bengtsson et al. 2003; Drever et al. 2006; Innes & Hickey 2006; Millar et al. 2007; Guariguata et al. 2008; Littell et al. 2012). Resilience is the ability of a forest community to change in response to perturbations and yet persist in maintaining the core functions considered desirable by managers (Holling 1973; Petersen et al. 1998; Folke et al. 2010). Plant communities have long been viewed as persistently changing in species composition on multiple time scales in response to both external and internal drivers (Clements 1916; Pickett 1982; Delcourt et al. 1983; Davis 1986). Plant communities also can vary in their response to perturbations depending on their history and environmental context; some change composition rapidly in the face of novel perturbations (i.e. McWethy et al. 2010) while others resist substantial damage and still provide a viable habitat for their component species (i.e. Davies et al. 2009). The consideration of resilience adds to successional theory the sense that plant communities may be pushed by the unprecedented combination of stressors in contemporary landscapes into alternative trajectories that are undesirable to human managers. The resilience framework provides an impetus to classify the desirability of vegetation states in the forest and to identify the factors responsible for different levels of resilience to undesirable change (Gunderson & Holling 2002).

The Hawaiian Islands are home to over 965 endemic vascular plant species (Wagner et al. 1990; Palmer 2003) and 30% of all federally listed endangered plant species in the United States (Conry & Cannarella 2010). Two major sources of change to the species composition of Hawaiian montane forests are chronic predation and damage from feral animals like pigs, cattle and introduced fowl, and displacement by introduced plant species (Vitousek et al. 1987, 1997; Cuddihy & Stone 1990). Most land managers in Hawai'i consider maintaining assemblages of native plant species and controlling the spread of exotic introduced species to be management priorities (Conry & Cannarella 2010). Thus, in Hawai'i, desirable and undesirable trajectories of change are straightforwardly defined in plant communities that still support native plant populations.

The extent to which different plant communities in Hawai'i are differentially affected by exotic species may indicate differences in their resilience to exotic encroachment. Some Hawaiian forest communities change composition rapidly following the removal of native plant biomass by disturbance (Ainsworth & Kauffman 2010), and fencing and weeding efforts reveal the large difficulties

inherent in regaining native forest composition after exotic species or feral animals are controlled (Cordell et al. 2009; Nogueira-Filho et al. 2009; Kellner et al. 2011a). When exotic plant species proliferate in Hawaiian forests they have the potential – in some cases – to facilitate the invasion of other species (Boelman et al. 2007), alter ecosystem function (Vitousek & Walker 1989; Asner & Vitousek 2005) or alter disturbance regimes (Hughes & Vitousek 1993; Mack & D'Antonio 1998) so that species composition continues to develop toward increased dominance by exotic species. However not all sites and areas are equally susceptible to invasion (Penuelas et al. 2010). Variability in the level of encroachment by exotic species may indicate which local and landscape context factors are important for fostering the maintenance of native plant species composition.

Disturbance is a major force shaping the structure, function and successional trajectories of forests (Attiwill 1994) and is a key consideration when assessing the resilience of forest plant communities. Disturbance in plant communities is the removal of biomass from the living species assemblage, usually by wind, water, fire, harvesting or animal activity (Grime 1979). In the montane forests of Hawai'i the temporal and spatial properties of disturbance regimes can vary with substrate age, soil properties and the degree of ecosystem development (Kellner et al. 2011b). For example, the proportion of the landscape affected by tree canopy disturbance is higher on high-fertility, intermediate-aged substrates than on younger or older substrates (Kellner et al. 2011b). Disturbance in forests is ubiquitous and native species can persist by making use of recurring disturbance events (Attiwill 1994). Areas of higher resilience to exotic encroachment should not only have low populations of exotics but should also show evidence that the native plant community is responding positively to disturbance through native-dominated pathways and continuing to establish canopy and subcanopy native tree species (i.e. Holmes & Cowling 1993; Schumann et al. 2003). Simultaneously, it is important to know if exotic species are increasing in abundance because of canopy disturbance (Alston & Richardson 2006).

Here we describe a quantitative survey of the vascular plant community in the Hawai'i Experimental Tropical Forest (HETF) on the windward slopes of Mauna Kea on the island of Hawai'i. Specifically, we asked:

1. How do tree canopy disturbance and soil properties structure plant community composition?
2. What factors make the forest community most susceptible to encroachment by exotic species?

Previous work that used airborne LiDAR to characterize forest structure and distributions of canopy height defined three elevation zones spanning an elevation range from

900 to 1500 m (Kellner & Asner 2009). Within each of the previously defined zones, sampling transects were chosen to cross two volcanically-derived substrates of differing soil properties but similar soil quality in terms of nitrogen and phosphorus (Vitousek et al. 1995). The sampling transects record the co-occurrence of species in a spatially explicit manner that also relates species composition to three disturbance factors: canopy openings, evidence of recent or historical upper canopy dieback (Mueller-Dombois 1986), and soil excavation by feral animals. We show how canopy disturbance and soil properties shape species composition, how disturbance serves to renew native species composition and that the geophysical soil template can constrain the spread of exotic species and contribute to the resilience of the native montane wet forest community to non-native encroachment.

Methods

Study site and site selection

The Hawai'i Experimental Tropical Forest (HETF) is located on the windward slope of the volcano Mauna Kea between 600 and 1800 m a.s.l. (Fig. 1). The section of forest examined in this study spans two volcanically-derived substrates of differing ages: lava-derived substrates from 4000 to 14 000 yr before present (y BP), ash-derived substrates from 14 000 to 65 000 yr BP. The 'lava-derived' substrate is composed of a mixture of surface flows and has shallow

tephra deposits on its surface. The forest is managed by a partnership among the USDA Forest Service, the State of Hawai'i Department of Land and Natural Resources and the State of Hawai'i Natural Area Reserve System, which maintains an unpaved access road that traverses the lava-derived substrate (Fig. 1). The forest is fenced against cattle on the edge of the reserve but has no other systematic ungulate management besides public hunting and a 10-acre fenced pig enclosure installed in 2009 by the State of Hawai'i. The forest reserve is surrounded on the southwestern, northwestern and northeastern flanks by semi-pasture areas managed for cattle production or *Eucalyptus* plantations (Fig. 1).

Kellner & Asner (2009) used LiDAR measurements of canopy height distributions to define three zones across the elevation gradient in the HETF (Asner et al. 2007). They are the lower elevation zone from 925 to 1225 m a.s.l. with very tall koa (*Acacia koa* A. Gray) and 'ōhi'a lehua (*Metrosideros polymorpha* Gaudich.) ('Mauna Kea' in Kellner & Asner 2009); the middle elevation zone from 1225 to 1400 m ('Laupahoehoe'); and the higher elevation zone from 1400 to 1525 m, an area that is currently experiencing extensive upper canopy mortality ('Montane'). All three zones have a mixture of *A. koa* and *M. polymorpha* in the upper canopy. There is no obvious sign of current or historical dieback in the low elevation zone. In the middle elevation zone, the abundance of large-diameter fallen tree boles suggests that the forest is in recovery from a historical

Fig. 1. The Hawai'i Experimental Tropical Forest (HETF) is located on the windward slope of Mauna Kea volcano on the Island of Hawai'i. Three elevation zones in the northern section of the reserve between 900 m and 1500 m a.s.l. were defined based on patterns of canopy height distribution (Kellner & Asner 2009). Within each zone a ~1000-m block transect (short dashed lines, parallel to slope) was cyclically sampled (lower inset) to efficiently sample plot heterogeneity on multiple spatial scales. Each transect consisted of ten series, each series had plots in three cycles, each cycle consisted of six 4-m² plots for a total of 180 sample plots per transect. The longer dashed line perpendicular to the slope shows the dirt access road. Areas adjacent to the reserve extensively modified by ranching or forestry operations are indicated by hashed areas. Map data source: USGS and State of Hawaii GIS.

dieback event (Vitousek et al. 2009). The three elevation zones span a precipitation gradient ranging from ~4000 mm to ~2800 mm annual rainfall. Within each zone, sampling transect locations are similar in terms of precipitation, ranging from 3908 to 4013 mm in the lower elevation zone, 3129–3178 mm in the middle elevation zone and 2864–2984 mm in the upper elevation zone (Giambelluca et al. 2011).

Sampling design

A spatially extensive and spatially explicit plant community survey was undertaken in each of the three HETF elevation zones. We deployed a 980-m long block transect with 180 cyclically arranged 4-m² quadrats in each of the three elevation zones (inset Fig. 1; Burrows et al. 2002). The cyclical sampling design achieved the large number of observations required for a spatially explicit analysis and maximized the number of different spatial lag distances between plots needed for spatial error estimation in a generalized linear mixed model (GLMM; Venables & Ripley 2002). Within each elevation zone a starting point was arbitrarily chosen so that the sampling transect would traverse the transition between ash-derived and lava-derived substrates. Transect direction was chosen to traverse the overall slope at a consistent elevation. The locations of our 180 quadrats were determined by laying out a series of rigid poles from the starting point to the transect end. Transect orientation was maintained by compass sightings. Each pole was kept horizontal with a spirit level, using upright poles to mark beginning or ending locations on slopes. Distances between widely spaced quadrats were measured explicitly with rigid poles to maintain strict plot geo-referencing. We employed a 3/7 sampling rhythm; for every seven potential consecutive sampling quadrats along the continuous transect we sampled the first, second and fourth quadrats (Burrows et al. 2002). Each plot location was sampled with two contiguous plots, upslope and downslope, creating a block design of two parallel transects (inset Fig. 1). Each set of seven quadrats is called a cycle and each set of seven cycles is called a series. The 3/7 sampling rhythm was also employed in a fractal manner in which the first, second and fourth cycles were sampled in each series. Each transect consisted of ten sampling series with three cycles of 18 quadrats each for a total of 180 4-m² quadrats in each elevation zone. Data from a single quadrat in the upper elevation zone were lost, leaving 179 quadrats in the highest elevation zone.

Within each plot the presence of all vascular plant species was recorded separately within height classes of 0–2, 2–5, 5–15, and >15 m. We noted individuals of a species that were growing epiphytically or were rooted in nurse

logs. Nomenclature follows Wagner et al. (1990) for flowering plants and Palmer (2003) for ferns and fern allies, except where updated by Wagner et al. (2012). The presence of upper canopy trees within the sampling plot was determined with a canopy densiometer. Within each plot the environment was characterized by an assessment of the volcanic substrate within the plot (ash vs. lava); slope and aspect of the plot; the presence of canopy disturbance indicators including woody debris, fallen tree boles, standing dead snags, the lack of a > 15-m height class tree ('canopy openings'), and aerially suspended woody debris; the condition of the soil surface including the presence of exposed roots, exposed subsoil, the presence of intact litter layers, soil excavation by animals, the presence of exposed rocks, the presence of moss growing on the soil surface, pools of water and the occurrence of living or dead tree fern stems. Each plot was also classified based on the apparent amount of surface water flow at times of heavy rainfall.

Data analysis

We used non-metric multidimensional scaling (NMS) and generalized additive models (GAM) to characterize the relationships between species composition and environmental heterogeneity (Bio et al. 1998; Thuiller et al. 2003). This approach allows for the characterization of non-linear responses to spatially structured environmental heterogeneity (Austin 2002; MjM Software Design, Gleneden Beach, OR, US). Analysis was conducted with the R statistical environment (R Foundation for Statistical Computing, Vienna, AT, US) utilizing the *vegan*, *cluster*, *MASS* (Venables & Ripley 2002) and *mgcv* (Wood 2008) packages. To minimize the impact of co-linearity between observed factors and account for differently scaled variables, environmental variables were first synthesized into environmental NMS axes using the Gower distance metric (Gower 1971). The number of NMS axes was determined by the trade-off between increased dimensions and reduced stress of the solution. A reduction of <5 stress points with additional added dimensions is considered an insufficient improvement in fit for the added ordination complexity (MjM Software Design). Species composition was also synthesized into vegetation NMS axes in a similar manner using the Jaccard distance metric. Individual species in different height classes were analysed as separate taxa in the analysis, to account for differences in response between different demographic stages of tree species. Apparent variance explained by each NMS axis was determined in two steps. First, the overall correlation between the original distance matrix and the entire NMS solution was determined with the relationship: $R^2 = 1 - S^2$, where S is the stress of the ordination solution. Then the overall

variance explained (R^2) was partitioned among NMS axes according to the eigenvalue decomposition of the three-dimensional NMS solution. The significance of the correlation between individual taxa or environmental factors and NMS axis scores was determined with 1000-iteration permutation tests.

The relationship between each vegetation NMS axis and the environment was modelled in two ways: as a function of the tensor product of each environmental NMS axis and spatial location and as a function of location alone. Tensor product models allow characterization of the interaction between spatial location and environment and accounts for the spatial structure of the underlying environmental heterogeneity (Wood 2006). Each vegetation–environment model was compared to the location-alone model using gcv-ubre scores (Wood 2006). When comparing two models, the model with lower gcv-ubre scores has a better likelihood given the additional number of parameters (analogous to the AIC criterion). Thus each vegetation NMS axis was provided an opportunity to be explained by each environmental NMS axis but still allowed to not be explained by the measured environmental factors at all. The lowest gcv score models for each vegetation NMS axis were visualized as bird's-eye view plots of spatial location on the x -axis and environmental NMS axis score on the y -axis with the size of individual sample icons scaled to the fitted predictor values of the model.

We then contrasted the influence of important environmental factors on perpetuating native species composition by modelling the number of exotic species and the number of native tree and tree fern species seedling/saplings in the 0–2 m height class ('regeneration') in each plot. The additional analysis was added to clarify the apparent patterns of exotic species encroachment and native tree species establishment observed in the NMS analysis and to confirm that the observed patterns remained when spatial autocorrelation between quadrats is taken into account. The number of exotic species and native sapling/seedling species in each quadrat were modelled separately with a GLMM quasi-likelihood model (Venables & Ripley 2002) following the procedure detailed in Dormann et al. (2007). We used a log-link function and an exponential spatial error term to account for spatial auto-correlation between quadrats. Presence on the ash- or lava-derived substrates and the environmental NMS 1 score of each quadrat were used as explanatory variables in the spatial GLMM model.

Results

Environmental factors

Across the three elevation zones, four major sources of environmental heterogeneity appear as suites of co-occurring environmental factors (Table 1). In NMS of the

environmental factors, comparisons of total stress against the number of dimensions indicate a three-dimensional solution as the best trade-off in all three elevation zones (Table A1). The most important group of factors in all three elevation zones is soil surface features, explaining 47.2%, 45.8%, and 47.1% of the overall variance in the environmental factors in the lower, middle and higher elevation zones, respectively. Positive plot scores on environmental NMS axis 1 are associated with exposed rocks, exposed subsoil, exposed primary tree roots and excavations made by feral pigs. In the middle and higher elevation zones these exposed subsurface features are also associated with areas of increased surface water flow. Negative plot scores on environmental NMS axis 1 are associated with intact litter layers, prone tree boles, tip-up mounds, and in the highest and lowest elevation zones with more southerly aspects. In the lower elevation zone exposed sub surface features tend to be associated with ash-derived lava substrates, while in the other two zones exposed subsurface features tend to be associated with lava-derived substrates (Table 1).

The second most important suite of environmental factors in all three zones describe tree canopy disturbance, with environmental NMS axis 2 explaining 24.5%, 26.8% and 26.0% of overall observed environmental variability (Table 1). In the lower and middle elevation zones negative environmental NMS axis 2 scores are associated with woody debris and aerially suspended woody debris derived from gap-generating and branch-fall disturbances. Positive scores are associated with signs of lack of disturbance such as erect tree fern stems, litter layers permeated by fine rootlets, and moss mats growing on the soil surface. The higher elevation zone canopy disturbance is manifested by dieback, shown by standing dead snags and prone fallen tree boles. The dieback patches are negatively associated with stream bed and gully topography indicated by the presence of persistent pools of water, steep slopes, collected woody debris and prone tree fern boles. In the lower and middle elevation zones streambed features are the third environmental NMS axis (explaining 21.5% and 20.4%, respectively), and they are contraposed to groves of tree ferns, indicated by both prostrate and erect tree fern stems. In the higher elevation zone tree fern groves occur independently of other features and explain 23.6% of the variability in environmental factors.

Species composition

Major growth forms – trees, tree ferns, vines, shrubs, herbs and ferns – vary between elevation zones and between height classes within each elevation zone (Table 2). The lower and middle elevation zones have high percentage occurrence of tree ferns in the 2–5 and 5–

Table 1. Individual observed environmental factors that compose three environmental NMS axes in each of the three elevation zones. Individual factors are related to the axis scores by permutation tests ($i = 1000$) which provide correlation scores listed by each factor and significance values. Significance based on 1000 permutations is indicated by: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ' $P < 0.1$. All factors with a correlation higher than ± 0.63 (equivalent to an $r^2 > 0.4$) are included in the table. The lists of factors are used to interpret the underlying process generating the assemblage of environmental factors which gives each NMS axis its name.

Environmental factor associations with environmental NMS axes

Lower elevation

Environ. NMS axis 1: Soil surface (47.2%)	<i>r</i>	<i>P</i>	Environ. NMS axis 2: Canopy Disturbance (24.5%)	<i>r</i>	<i>P</i>	Environ. NMS axis 3: Stream bed vs. Tree fern groves (21.5%)	<i>r</i>	<i>P</i>
Tip-up Mound	−0.97	*	Pig Sign	−0.92	***	Increased Surface Water Flow	−0.97	**
Intact Litter Layer	−0.95	***	Woody Debris	−0.87	***	Pools of Water	−0.95	**
Prone Tree Bole	−0.79	***	Suspended Woody Debris	−0.79	***	Exposed Roots: Bole-shaped	−0.68	***
Southerly Aspect	−0.76	***	Multi-stem Composite	−0.69	*			
Multi-stem Composite	−0.72	*						
Exposed Roots: Bole-shaped	0.73	***	Erect Tree Fern Bole	0.73	***	Erect Tree Fern Bole	0.68	***
Exposed Mineral Soil	0.90	***	Moss on Soil Surface	0.75	***	Prone Tree Fern Bole	0.95	***
Pig Digging	0.95	***	Intact Litter Layer with Rootlets	0.95	***			
Ash Soil	0.95	***						
Rocks	0.97	***						

Middle elevation

Environ. NMS axis 1: Soil surface (45.8%)	<i>r</i>	<i>P</i>	Environ. NMS axis 2: Canopy Disturbance (26.8%)	<i>r</i>	<i>P</i>	Environ. NMS axis 3: Stream bed vs. Tree fern groves (20.4%)	<i>r</i>	<i>P</i>
Intact Litter Layer	−0.96	***	Woody Debris	−0.72	***	Erect Tree Fern Bole	−0.70	***
Ash Soil	−0.92	***	Suspended Woody Debris	−0.67	***	Prone Tree Fern Bole	−0.68	***
Tip-up Mound	−0.86	*						
Prone Tree Bole	−0.81	***						
Exposed Roots	0.74	***	Prone Tree Fern Bole	0.70	***	Exposed Bedrock	0.85	***
Exposed Roots: Bole shaped	0.90	***	Erect Tree Fern Bole	0.71	***	Pools of Water	0.94	***
Rocks	0.91	***	Moss on Soil Surface	0.76	***			
Exposed Mineral Soil	0.91	***	Intact Litter Layer with Rootlets	0.82	***			
Pig Digging	0.96	***	Slope	0.88	***			
Increased Surface Water Flow	0.97	***	Southerly Aspect	0.96	**			

Higher elevation

Environ. NMS axis 1: Soil surface (47.1%)	<i>r</i>	<i>P</i>	Environ. NMS axis 2: Stream bed vs. Canopy Dieback (26.0%)	<i>r</i>	<i>P</i>	Environ. NMS axis 3: Tree fern groves (23.6%)	<i>r</i>	<i>P</i>
Intact Litter Layer	−0.95	***	Pools of Water	−0.90	***			
Ash Soil	−0.81	***	Woody debris	−0.85	***			
Southerly Aspect	−0.81	**	Slope	−0.66	***			
Intact Litter Layer with Rootlets	−0.79	***	Prone Tree Fern Bole	−0.65	***			
Exposed Mineral Soil	0.76	***	Snag	0.72	***	Prone Tree Fern Bole	0.63	***
Increased Surface Water Flow	0.85	***	Prone Tree Bole	0.88	***	Erect Tree Fern Bole	0.97	***
Pig Digging	0.98	***						
Rocks	0.98	***						
Prone Tree Bole	0.99	**						

Significance (based on 1000 permutations): *** <0.001 , ** <0.01 , * <0.05 , ' <0.1 .

10 m height classes while tree ferns in the upper elevation zone are more restricted to the 2–5 m height classes. The middle and upper elevation zone show higher percentage occurrence of vines, especially in the 5–10 and 10–15 m height classes. The middle and upper zones also show a

higher percentage of shrubs in the 2–5 m height class. The percentage of species initiating on nurse logs or occurring as epiphytes also varies between elevation zones and among height classes (Table 2). The representation of epiphytic and nurse-log rooted species is especially high in

the middle elevation zone. Among the dominant >15 m trees in the middle elevation zone, 24.6% are rooted in nurse logs. Species richness of both natives and exotic species declines with taller height classes and with increasing elevation (Table 2).

Species composition differs in each elevation zone; however, there are some commonalities across zones (Tables 3, 4). Like the environmental data, NMS of the species–height class composition data also indicates a three-dimensional solution as the best trade-off in all three elevation zones (Table A1). The most important trend is a compositional gradient, characterized on one extreme by increased occurrence of the sub-canopy tree *Coprosma rhynchocarpa* A. Gray, the shrub *Rubus hawaiiensis* A. Gray or the fern *Dryopteris wallichiana* (Spreng.) Hyl. On the other extreme, the gradient is characterized by vine *Alyxia stellata* (J. R. Forst. & G. Forst.) Roem. & Schult, seedling and sapling *Metrosideros polymorpha* Gaudich. or *Melicope clusiifolia* (A. Gray) T. G. Hartley & B. C. Stone (Table 3). In all three elevation zones the *Coprosma*–*Alyxia* compositional gradient is characterized by vegetation NMS axis 1, which explains 40.3%, 41.2% and 40.7% of compositional variability, respectively (Table 3, 4). The *Coprosma* end of the compositional gradient (negative scores) also is characterized by increased presence of exotic species, while the *Alyxia* end of the axis (positive scores) does not have significant loadings of exotic species. The other two vegetation NMS axes have less compositional similarity between elevation zones than the first axis but exhibit two themes: (1) compositional contrasts of understorey tree species, like *Ilex anomala* Hook. & Arn and *Cheirodendron trigynum* (Gaudich.) A. Heller subsp. *trigynum*; and (2) opposing sets of species associated with the major canopy dominants *M. polymorpha* and *A. koa* (Tables 3, 4).

Predictors of species composition

Not all sources of environmental heterogeneity explain variation in species composition. The GAM compare models combining each environmental NMS axis with spatial location against models using spatial location alone; models with the lowest gcv score are considered the best fit, penalized by the number of model parameters. In the lower elevation zone spatial location alone is the best model for vegetation NMS axes 1 and 2 (61% and 31% deviance explained (DE)), while the third vegetation NMS axis is best explained by the spatial mosaic of canopy disturbance (16% DE; Table A2). Visualization of the predicted values for the first vegetation NMS axis shows that there is a marked increase in vegetation NMS axis 1 scores near the transition from lava-derived to ash-derived soils (Fig. 2). The *Alyxia* end of the compositional gradient is associated with ash-derived soils while the *Coprosma* end

and exotic species are associated with the lava-derived substrate. The second lower elevation zone vegetation NMS axis does not show the same transition at the change in volcanic substrate and remains as unexplained spatial pattern (Fig. 2). The third vegetation NMS axis shows a heterogeneous pattern where >15 m *A. koa* canopies and associated understorey species are associated with woody debris and canopy disturbance.

In the middle elevation zone all three vegetation NMS axes are best modelled by the spatial mosaic of volcanic substrate and soil surface condition (70%, 16%, 24% DE; Table A2). Just as in the lower elevation zone the *Alyxia* end (positive scores) of the first vegetation NMS axis is associated with ash-derived soils while the *Coprosma* end (negative scores) and exotic species are associated with the lava-derived substrates (Fig. 2). Soils with more intact organic horizons and nurse logs tend to have more positive scores and soils with exposed subsurface layers tend to have decreased vegetation NMS axis 1 scores. The second vegetation NMS axis, with positive scores indicating 0–5 m *I. anomala*, *R. hawaiiensis* and associated ferns (Tables 3, 4), is highest on nurse tree and organic substrates or on the ash-derived volcanic substrate. Negative scores indicate larger 2–5 m *C. trigynum* and occur with exposed subsoil features on the lava-derived substrate or on the ash-derived substrate. The third vegetation NMS axis of the middle elevation zone shows negative values (associated with >15 m *A. koa*) on the ash soils, giving way to positive values at the extreme lava-derived end (associated with higher abundance of *M. polymorpha* in the >15, 5–15 and 2–5 m height classes).

The higher elevation zone vegetation NMS axes are predicted either by soil surface features and volcanic substrate or by upper tree canopy dieback disturbance (Table A2). The first vegetation NMS axis, like the middle elevation zone, is best predicted as a combination of volcanic substrate and soil surface composition (55% DE). The *Alyxia* end of the compositional gradient (positive scores) is high on ash-derived substrates but also high on fallen tree boles and intact organic litter layers on the lava-derived substrate (Fig. 2). Higher elevation vegetation NMS axes 2 and 3 both are best explained by dieback canopy disturbance (36% and 14% DE; Table A2). The second vegetation NMS axis shows negative scores, increased *A. koa* in the 5–15 m height class and associated species that tend to occur with dieback disturbance (Fig. 2). In contrast, 2–5 m height class *M. polymorpha* and associated species (negative vegetation NMS axis 3 scores) show a bi-modal pattern of an association with dieback disturbance on the lava-derived substrate but not on the ash-derived substrate. Woody debris is associated with >15 m *M. polymorpha* on ash soils in the higher elevation transect.

Table 2. The relative percentage occurrence of major growth forms within each height class varies between elevation zones. The percentage of species initiating on nurse logs or occurring as epiphytes also varies between elevation zones and among height classes. Species richness of both natives and exotic species declines with taller height classes and with increasing elevation.

	0–2 m	2–5 m	5–10 m	10–15 m	>15 m
Lower elevation					
Tree	15.7	46	79.9	100	100
Tree fern	3.4	35.6	14.6	0	0
Vine	6.5	4.2	0.7	0	0
Shrub	12.6	7.4	1.4	0	0
Herb	11.8	2.4	2.8	0	0
Fern	49.9	4.4	0.7	0	0
% Nurselogs	17.5	15.6	16	33.3	6.7
% Epiphytic	12.1	15.4	18.8	8.3	0
# Native species	59	31	14	3	2
# Exotic species	10	5	2	0	0
Middle Elevation					
Tree	14	24.2	77.2	83.3	100
Tree fern	6.7	59.5	10.2	3.3	0
Vine	4.8	1.5	7.1	13.3	0
Shrub	7.3	14.1	5.1	0	0
Herb	16.4	0.3	0.5	0	0
Fern	50.8	0.3	0	0	0
% Nurselogs	15.5	14.7	27.4	26.7	24.6
% Epiphytic	11	7.4	38.5	23.3	3.3
# Native species	38	16	12	6	2
# Exotic species	6	1	1	1	0
Upper elevation					
Tree	9.5	29.8	78	95.7	99.2
Tree fern	6.4	42.6	2.8	0	0
Vine	3.6	7	16.3	3.4	0.8
Shrub	5.9	18	2.1	0	0
Herb	14.2	0.5	0	0	0
Fern	60.4	2.1	0.7	0	0
% Nurselogs	20.7	25.2	35.5	28.4	10.9
% Epiphytic	5.7	5.9	7.1	4.3	0
# Native species	32	16	9	5	2
# Exotic species	10	2	1	2	1

Predictors of resilience

Native tree and tree fern species regeneration (<2 m height class) and exotic species vary in numbers in opposing ways across all three elevation zones. The number of exotic species in each plot increased on lava-derived volcanic substrates in all three elevation zones (Fig. 3, top row). In contrast the count intensity of < 2 m native tree and tree fern species is higher on ash-derived substrates in the middle elevation and higher elevation zones (Fig. 3, bottom row). For exotic species the effect of both the substrate and soil factors is significant in the lower elevation zone ($P < 0.0203$, $P < 0.0063$), just the soil factor is significant in the middle elevation zone ($P < 0.0111$) and just substrate type is significant in the higher elevation zone ($P < 0.0575$; Table A3). For native tree species regenera-

tion, neither substrate nor soil factors are significant in the lower elevation zone, but substrate is significant in the middle elevation zone ($P < 0.015$) and both substrate type and soil surface are significant in the higher elevation zone ($P < 0.00001$, $P < 0.0175$). The range term for exponential spatial autocorrelation ranges from 1.5 to 1.7 m for exotic species counts and between 0.8 and 2.2 m for native species regeneration (Table A3). The transition in counts for both variables occurs at distances of ~1550, 650 and 500 m (lower, middle and higher, respectively) from the access road and does not show a consistent relationship with the distance to the access road or to the pasture margin (Fig. 3). Together, lava-derived substrates have a higher incidence of exotic species and less native tree regeneration; whereas ash-derived substrates have larger numbers of native tree species regenerating and many fewer exotic species.

Discussion

Disturbance and plant community structure

Montane rain forest vegetation composition on the slopes of windward Mauna Kea is structured by differences in elevation, canopy disturbance and volcanic substrate. Each of the three elevation zones was defined by remote sensing data based on patterns of tree height distribution (Kellner & Asner 2009). On the ground, the three elevation zones also show different species assemblages (Tables 3, 4), differences in the importance of particular exotic species (Tables 3, 4), differences in the relative abundance of tree ferns, shrubs and vines (Table 2) and decreasing overall species richness as elevation increased (Table 2).

While the elevation zones differ botanically, within all three elevation zones environmental factors co-vary in four similar ways: (1) soil surface and volcanic substrate; (2) legacies of canopy disturbance; (3) erosional features due to the beginning of gully formation; and (4) groves of erect and fallen tree fern stems (Table 1). Not all environmental heterogeneity on the landscape explains variability in plant species composition. While erosion features and tree fern stems are important to the establishment of plants in many Hawaiian environments (Drake & Mueller-Dombois 1993; Porder et al. 2005), they do not have a strong effect on overall plant community composition in these three elevation zones.

The impact of canopy disturbance on plant community composition in the HETF depends on the spatial and temporal scale of the disturbance. Each elevation zone appears to have a differently scaled canopy disturbance process (Kellner & Asner 2009; Vitousek et al. 2009). In the lower elevation zone gap formation disturbance is associated with >15 m *A. koa* trees and a few understorey species and is a minor part of the overall variability (vegetation NMS

Table 3. The occurrence of tree species (regular text), tree ferns (bold) and vines (bold italics) on three primary vegetation NMS axes varies within each of the three elevation zones. Individual taxa are related to the axis scores by permutation tests ($i = 1000$) which provide correlation scores listed by each factor and significance values. Significance based on 1000 permutations is indicated by: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ' ' $P < 0.1$. All taxa with a correlation higher than ± 0.63 (equivalent to an $r^2 > 0.4$) are included in the table. Non-native species are indicated by a # symbol.

Trees, Tree ferns and Vines								
Lower elevation zone								
Vegetation NMS axis 1 (40.3%)	<i>r</i>	<i>P</i>	Vegetation NMS axis 2 (26.5%)	<i>r</i>	<i>P</i>	Vegetation NMS axis 3 (23.6%)	<i>r</i>	<i>P</i>
Coprosma rhynchocharpa 5-15M	−0.99	**	Cheirodendron trigynum 5-15M	−0.94	***	Acacia koa >15M	−0.83	***
Psidium cattelianum 2-5M #	−0.98	**	Psidium cattelianum <2M #	−0.86	.	Cibotium menziesii 2-5M	−0.82	***
Perrotetia sandwicensis 5-15M	−0.89	**	Ilex anomala 2-5M	−0.86	.			
Coprosma rhynchocharpa <2M	−0.87	***	Ilex anomala 5-15M	−0.83	**			
Coprosma rhynchocharpa 2-5M	−0.82	***	Cibotium chamissoi	−0.74	***			
			Freyinetia arborea	−0.69	***			
Metrosideros polymorpha 2-5M	0.76	***						
Melicope clusiifolia 2-5M	0.76	***	Sadleria pallida	0.73	.	Cibotium glaucum 2-5M	0.67	***
Dicranopteris linearis	0.79	***	Cibotium glaucum 2-5M	0.73	***	Cibotium menziesii <2M	0.75	**
Cheirodendron trigynum <2M	0.86	**	Metrosideros polymorpha 5-15M	0.88	***	Metrosideros polymorpha >15M	0.77	***
Ilex anomala <2M	0.90	.	Perrotetia sandwicensis 2-5M	0.92	***	Smilax melastomatifolia	0.79	***
Myrsine lessertiana	0.96	***				Cibotium glaucum <2M	0.88	.
Melicope clusiifolia <2M	0.96	***						
Alyxia stellata	0.97	***						
Middle elevation zone								
Vegetation NMS axis 1 (41.2%)	<i>r</i>	<i>P</i>	Vegetation NMS axis 2 (26.5%)	<i>r</i>	<i>P</i>	Vegetation NMS axis 3 (23.9%)	<i>r</i>	<i>P</i>
Coprosma rhynchocharpa <2M	−0.92	**	Cheirodendron trigynum 2-5M	−0.65	***	Acacia koa >15M	−0.75	**
Coprosma rhynchocharpa 2-5M	−0.86	*				Cibotium glaucum 2-5M	−0.69	***
Passiflora tarminiana <2M #	−0.76	**						
Melicope clusiifolia 5-15M	0.71	***	Ilex anomala <2M	0.67	.	Metrosideros polymorpha >15M	0.84	***
Metrosideros polymorpha <2M	0.78	**	Passiflora tarminiana >2M #	0.73	***	Metrosideros polymorpha 5-15M	0.89	
Melicope clusiifolia 2-5M	0.80	***	Ilex anomala 2-5M	0.83	***	Metrosideros polymorpha 2-5M	0.91	
Cheirodendron trigynum <2M	0.86	***				Cibotium glaucum <2M	0.94	
Acacia koa <2M	0.92	***						
Cibotium menziesii 2-5M	0.92	***						
Alyxia stellata	0.94	***						
Cibotium menziesii <2M	0.95	***						
Melicope clusiifolia <2M	0.96	***						
Ilex anomala 5-15M	0.98	.						
Higher elevation zone								
Vegetation NMS axis 1 (40.7%)	<i>r</i>	<i>P</i>	Vegetation NMS axis 2 (26.5%)	<i>r</i>	<i>P</i>	Vegetation NMS axis 3 (24.9%)	<i>r</i>	<i>P</i>
Passiflora tarminiana >2M #	−0.94	***	Acacia koa 5-15M	−0.90	***	Metrosideros polymorpha 2-5M	−0.84	**
			Passiflora tarminiana <2M #	−0.78	*	Coprosma rhynchocharpa <2M	−0.83	**
Ilex anomala 5-15M	0.71	**						
Ilex anomala 2-5M	0.72	***	Acacia koa >15M	0.83	***	Metrosideros polymorpha >15M	0.82	**
Metrosideros polymorpha 2-5M	0.74	**	Cheirodendron trigynum 2-5M	0.87	**	Fraxinus uhdei #	0.90	*
Ilex anomala <2M	0.77	*				Cibotium glaucum 2-5M	0.97	***
Acacia koa <2M	0.80	*						
Metrosideros polymorpha <2M	0.83	***						
Cibotium menziesii <2M	0.90	***						
Cheirodendron trigynum 5-15M	0.91	***						
Myrsine lessertiana	0.93	*						
Cibotium menziesii 2-5M	0.96	***						
Alyxia stellata	0.96	***						

Significance (based on 1000 permutations): *** <0.001 , ** <0.01 , * <0.05 , ' ' <0.1 .

Table 4. The occurrence of shrubs (bold text), herbaceous species (bold italic) and ferns (regular text) on three primary vegetation NMS axes varies within each of the three elevation zones. Individual taxa are related to the axis scores by permutation tests ($i = 1000$) which provide correlation scores listed by each factor and significance values. Significance based on 1000 permutations is indicated by: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ' ' $P < 0.1$. All taxa with a correlation higher than ± 0.63 (equivalent to an $r^2 > 0.4$) are included in the table. Non-native species are indicated by a # symbol.

Shrubs, Herbs, and Ferns								
Lower elevation zone								
Vegetation NMS axis 1 (40.3%)	<i>r</i>	<i>P</i>	Vegetation NMS axis 2 (26.5%)	<i>r</i>	<i>P</i>	Vegetation NMS axis 3 (23.6%)	<i>r</i>	<i>P</i>
Diplazium sandwichianum	−0.93	***	Asplenium lobulatum	−0.83	***	Pipturus albidus	−0.70	**
Nothoperanema rubiginosa	−0.91	***	Peperomia cookiana	−0.80	***			
Vandenboschia davallioides	−0.90	***	Asplenium normale	−0.76	***			
Hedychium gardnerianum #	−0.82	**	Dryopteris glabra	−0.72	**			
Psilotum hawaiiensis	−0.77	*	Asplenium polyodon/complanatum	−0.67	***			
Clidemia hirta #	−0.76	***	Astelia menziesii	−0.66	***			
Rubus hawaiiensis	−0.70	***						
Persicaria punctata #	−0.69	***						
Ophioglossum pendulum L.	0.68	*	Persicaria punctata #	0.66	***	Deparia petersenii #	0.69	***
Athyrium microphyllum	0.75	*	Pipturus albidus	0.71	**	Diplazium amottii	0.73	**
Peperomia hypoleuca	0.77	**				Adenophorus tamariscinus	0.89	*
Mecodium recurvatum	0.82	***				Lepisorus thunbergianus	0.91	**
Vaccinium calycinum	0.86	***				Adenophorus tripinnatifidus	0.95	***
Grammatis tenellus	0.91	***						
Elaphoglossum warae	0.97	**						
Middle elevation zone								
Vegetation NMS axis 1 (41.2%)	<i>r</i>	<i>P</i>	Vegetation NMS axis 2 (26.5%)	<i>r</i>	<i>P</i>	Vegetation NMS axis 3 (23.9%)	<i>r</i>	<i>P</i>
Microlepia strigosa	−0.87	.						
Dryopteris wallichiana	−0.86	***						
Pipturus albidus	−0.79	.						
Rubus hawaiiensis	−0.68	***						
Ehrharta stipoides #	−0.65	***						
Broussatia arguta	0.66	.	Rubus hawaiiensis	0.72	***	Astelia menziesii	0.71	***
Astelia menziesii	0.70	***	Peperomia cookiana	0.75	**	Broussatia arguta	0.75	.
Erechtites valerianifolia #	0.77	*	Asplenium polyodon/complanatum	0.81	***	Marrattia douglasii	0.88	.
Vaccinium calycinum	0.78	***	Diplazium sandwichianum	0.95	***			
Athyrium microphyllum	0.82	***	Nothoperanema rubiginosa	0.97	***			
Peperomia hypoleuca	0.84	***	Vandenboschia davallioides	0.99	***			
Dryopteris glabra	0.85	***						
Asplenium normale	0.90	***						
Higher elevation zone								
Vegetation NMS axis 1 (40.7%)	<i>r</i>	<i>P</i>	Vegetation NMS axis 2 (26.5%)	<i>r</i>	<i>P</i>	Vegetation NMS axis 3 (24.9%)	<i>r</i>	<i>P</i>
Dryopteris wallichiana	−0.89	***	Drymaria cordata #	−0.95	**	Ehrharta stipoides #	−0.87	***
			Rubus rosifolius #	−0.93	*	Rubus hawaiiensis	−0.71	***
Peperomia hypoleuca	0.71	***	Nothoperanema rubiginosa	−0.80	***	Rubus arguta #	−0.67	*
Vaccinium calycinum	0.73	***	Veronica plebeia #	−0.73	***	Veronica plebeia #	−0.66	***
Asplenium polyodon/complanatum	0.76	***	Rubus arguta #	−0.71	*			
Asplenium institutum	0.88	***	Korthasella complanatum	0.85	**	Phytolacca sandwicensis	0.75	.
Asplenium normale	0.89	***				Athyrium microphyllum	0.82	***
Dryopteris glabra	0.97	***				Asplenium polyodon/complanatum	0.92	*
						Diplazium sandwichianum	0.95	***

Significance (based on 1000 permutations): *** <0.001 , ** <0.01 , * <0.05 , ' ' <0.1 .

axis 3, 23.6%). A larger portion of compositional variability (vegetation NMS axis 2, 26.5%) remains as unexplained spatial pattern, which might indicate larger disturbance patches in the past but could also be derived

from other processes (Fig. 2). In the middle elevation zone the environment associated with fallen large-diameter tree boles plays an important role in structuring all aspects of community composition (Fig. 2). The pervasive distribu-

Fig. 2. Vegetation patterns are shaped by soil substrate and disturbance. Models with the lowest gcv score have the best trade-off between model fit and number of parameters compared to alternative models. The model's fitted value (trend) for each sample is plotted against plot location and an environmental NMS axis score, either soil surface condition (environmental NMS axis 1) or canopy disturbance (environmental NMS axis 2). Data point size is scaled to the magnitude of the fitted value. Large values are associated with the species on the positive end of the vegetation NMS axis while small values are associated with the species on the negative end of the vegetation NMS axis (Tables 3, 4). Vegetation NMS axes 1 and 2 in the Mauna Kea elevation zone are best modelled with location alone as a co-variate. Transitions from lava- to ash-derived soils are indicated as vertical dashed lines.

tion of the fallen trees, the high incidence of upper canopy trees rooted in nurse logs, and the synchronized dieback phenomenon in *M. polymorpha* stands strongly suggest recovery from a large dieback event in the past in this elevation zone (Atkinson 1970; Mueller-Dombois 1986; Vito-

usek et al. 2010). Fallen trees, by providing a new growth substrate, seem to have a greater influence on community composition than does more transient canopy gap formation in Hawaiian montane rain forest (Santiago 2000). The upper elevation zone is experiencing an active period of

upper canopy dieback; here larger-sized patches of dieback canopy disturbance have the second highest impact on species composition, after soil substrate (Fig. 2). Mature individuals of either *A. koa* or *M. polymorpha* are negatively associated with smaller-stature individuals of the same species. Standing snags and fallen tree boles predict patches of young *A. koa* on ash-derived soils but predict 2–5 m *M. polymorpha* regeneration on lava-derived soils. The species potentially replacing the canopy dominant growing into the disturbance patch is contingent on the underlying soil substrate. Large *A. koa* were harvested in the higher elevation zone in the 1970s, and it is unclear how past selective logging is influencing the patterns of *A. koa* regeneration today.

Volcanic substrate is a stronger influence on species composition than either elevation or legacies of canopy

disturbance. The first vegetation NMS axis in all three elevation zones is associated with volcanic substrate (Fig. 2). The ash-derived and lava-derived soils differ from each other in similar ways across all three zones (Tables 3, 4). Species that associate with the lava-derived substrate across zones are *Coprosma rhynchocarpa*, *Rubus hawaiiensis*, *Ehrharta stipoides* Labill, *Passiflora tarminiana* Coppins & Barney and *Dryopteris wallichiana*. More species consistently occur across zones on the ash-derived soils, including: *Alyxia stellata*, *Peperomia hypoleuca* Miq., *Vaccinium calycinum* Sm., *Asplenium normale* D. Don, *Athyrium microphyllum* (Sm.) Alston, *Melicope clusiifolia*, <2 m *Cheirondendron trigynum*, *Cibotium menziesii* Hook, *Myrsine lessertiana* A. DC. and <2 m *Acacia koa*. Similar results were found by Kitayama & Mueller-Dombois (1995) in the middle elevation zone between relevés on ash-

Fig. 3. Volcanic substrate type influences the occurrence of exotic species (all height classes) and regeneration of tree and tree fern species (0–2 m height class) in all three elevation zones. Circular data points indicate the counts of exotic species or the counts of 0–2 m height class native tree species in each plot. The trend line is the fitted value for the GLMM model of species counts as a function of volcanic substrate type or environmental NMS axis 1 with an exponential spatial error term to account for spatial autocorrelation. Trend line values are presented as expected value for counts in each plot. The dashed lines delineate the transition from ash-derived soils to lava-derived soils in each transect. Plot locations are represented on the ordinate as distance in meters on the contour to the access road. In the middle elevation zone the access road crosses the sampling transect where marked by a 'v.'

derived and lava-derived substrates. The exception is the abundance of *P. tarminiana*, which was higher on the ash-derived soils in their study, perhaps due to either difference in the scale of sampling or changes in the abundance of *P. tarminiana* since that time. There is a positive relationship between ash-derived soils and pig excavations in the lower elevation transect but a negative association in the other two transects. Soil surface features or pig soil excavation alone does not explain the differences in species composition across substrates, because a similar species assemblage occurs on ash-derived soils in the lower elevation zone despite soil surface features and pig activity, which resemble the lava-derived substrate in the other two transects.

The importance of volcanic substrate is reinforced by the examination of counts of native seedling/sapling tree and exotic species as well as in the correspondence of the first NMS vegetation axis with the soil substrate environmental NMS axis (Fig. 3). In all three zones there are increased counts of exotic species on the lava-derived substrate and less native tree regeneration than on the ash-derived substrate. In all three elevation zones 0–2 m native trees and exotic species load strongly on the first vegetation NMS axis (Tables 3, 4). The difference between substrates can be seen in both analyses. The pattern is more striking in that in each elevation zone different exotic species are generating the same dichotomy (Tables 3, 4).

Substrate influence on plant community resilience

Can we attribute greater resilience to exotic encroachment in the plant community on one substrate compared to the other? Several criteria need to be met in order to detect a difference in resilience between sites, including: (1) the ability to identify two or more community states which are relevant to management; (2) evidence of one or both sites switching states or beginning to alter states; and (3) evidence of a response to perturbation that could lead back to a favourable state in one site versus the other.

In this study of the HETF we satisfy these three criteria. First, maintenance of native biodiversity is an important priority for management in Hawaiian forests (Cuddihy & Stone 1990; Conry & Cannarella 2010); and we can clearly see increased exotic species presence against native Hawaiian species dominance as two alternative states from this perspective. However, it should be noted that exotic species can maintain or enhance certain ecosystem services in some contexts; thus, depending on management objectives, exotics may facilitate other dimensions of forest resilience (Zavaleta et al. 2001; Mascaro et al. 2012). To meet the second criteria, as discussed previously, lava-derived soils demonstrate higher exotic species count intensity than ash-derived soils. Inspection of the spatial pattern of

increased exotic presence in either negative scores of the first NMS axes (Fig. 2) or the counts of exotic species in plots (Fig. 3) substantiates the abrupt change in fitted scores at the lava–ash transition. For exotic species counts spatial autocorrelation ranges out to a few meters (Table A3) and does not diminish the overall pattern. Also there is no consistent change in fitted values for the second or third vegetation NMS axes that do not have strong exotic species loadings (Fig. 2). Finally, in all three elevation zones canopy disturbance influences native species composition, indicating the possibility of native-dominated response pathways after perturbations such as canopy gap disturbance or dieback. Thus, the plant community on the ash-derived substrate is more resilient to exotic encroachment than the community on the lava-derived substrate.

What might explain the difference in resilience to exotic encroachment between the two volcanic substrate types? The two most striking differences between the substrate types are (1) their proximity to roads or pastures that could lead to increased invasion rates and (2) their differences in soil properties. Road density, proximity to pasture edges and propagule pressure have all been shown to favour increased exotic species abundance and provide a plausible explanation for differences between the two substrate types (Lonsdale 1999; Rouget & Richardson 2003; Alston & Richardson 2006). In the HETF the situation is not straightforward because the lava-derived substrate is bisected by a gravel access road but the ash-derived substrate in the two higher elevation zones is bordered by a highly disturbed wooded pasture system (Fig. 1). The distance to the access road does not seem to correspond to the change in exotic species count intensities as well as does the correspondence with the transition between substrate types (Fig. 3). Likewise in the higher and middle elevation zones exotic species count intensity does not increase as the sampling transects approach the edge of a large disturbed pasture–woodland mosaic on the same volcanic substrate type. These observations favour the interpretation that there is an intrinsic difference between the two substrate types that influences their resilience to exotic encroachment.

Soil property differences between the two volcanic substrates are nuanced (Vitousek et al. 1995). Both the 4000 to 14 000-year-old lava-derived substrates and 14,000–65,000-year-old ash-derived substrates are at stages of long-term ecosystem development resulting in the highest concentrations of foliar nutrients along the Hawaiian soil development chronosequence (Crews et al. 1995; Vitousek et al. 1995). A recent phylogenetically constrained leaf morphology analysis of invasive species on the Island of O'ahu (which included many of the species we found here) posits invasive species gain competitive advantage over native species by making leaf tissues that are wasteful

of nutrients (Penuelas et al. 2010). Such an exuberant resource-use strategy ought to provide an advantage on nutrient-rich landscapes (Huenneke et al. 1990; Daehler 2003) and the litter of invasive species may also increase rates of nutrient cycling and promote further invasion by exotic species (Allison & Vitousek 2004). Previous analysis of foliar nutrients in the middle elevation zone in the HETF found foliar levels of N, P and leaf area index to be similar between the two substrate types across a wide range of native species (Vitousek et al. 1995). It is possible that lower levels of other plant nutrients, or soil properties unrelated to plant nutrition, favour the suite of native species abundant on the ash-derived soils over the suite of exotics proliferating on the lava-derived substrate.

If the underlying processes promoting resilience are amenable to manipulation, then resilience can be promoted in forest ecosystems (Spies et al. 2010). Distinguishing between the two potential explanations for the difference in resilience in the HETF is important for management to increase the resilience of Hawaiian montane forests to further proliferation of exotic species. In many forest systems worldwide exotic encroachment is driven by proximity to human land use and disturbance due to access roads and trails (i.e. Alston & Richardson 2006). However, our results indicate resource managers should explicitly account for variation in soils, parent bedrock type and substrate type, as well as human land-use patterns, when prioritizing, implementing and monitoring management interventions to foster native plant assemblages and control the spread of exotic species.

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Appendix

The appendix provides tables of statistical results that include the relationship between number of NMS dimensions and ordination stress (Table A1), the parameters of the four alternative gen-

eralized additive models (GAM, Table A2), and the parameters of the generalized linear models with a spatial error term of exotic species and native tree species regeneration species counts.

Table A1. The relationship between number of NMS dimensions and ordination stress for both environmental variables and species composition in the three HETF elevation zones. Stress decreases with increased number of dimensions. Typically a reduction of <5 stress points with additional added dimensions is considered an insufficient improvement in fit for the added ordination complexity (McCune and Grace 2002). In both the environmental and vegetation ordinations three-dimensional solutions indicate the best stress-complexity trade-off. The number of environmental features, the total number of species-by-height class types and the overall species richness all decline as the elevation zones increase in elevation.

Ordination	Dimensions (Stress)						Samples	Types	Species	Exotics
	1	2	3	4	5	6				
Environment										
Lower elevation	37.3	24.6	18.7	13.9	11.2	9.3	180	27	–	–
Middle elevation	36.5	24.7	18.2	14.1	11.4	9.4	180	25	–	–
Higher elevation	38.6	23.7	16.7	12.5	10.1	8	179	21	–	–
Vegetation										
Lower elevation	42.8	30	22.7	18.2	15.4	13.4	180	89	71	10
Middle elevation	41.6	27.5	20.7	16.4	13.7	11.5	180	63	48	5
Higher elevation	40.9	27.1	19.9	16.1	13.5	11.4	179	57	43	9

Table A2. Variability in each vegetation component score is modelled in each elevation zone with four alternative generalized additive models (GAM). Models are a) null model with spatial location alone as the explanatory variable, b) an interaction (modelled as a tensor product) between spatial location and soil substrate characteristics (environmental NMS axis 1), c) an interaction between spatial location and canopy disturbance (environmental NMS axis 2), and d) an interaction between spatial location and presence of fallen tree fern stems (environmental NMS axis 3). Models with the lowest gcv scores are considered the best trade-off between fit and number of parameters. The lowest gcv models for each vegetation axis are indicated by a bold value in the gcv-score column.

Generalized additive model parameters									
Lower elevation									
Vegetation NMS axis 1	<i>n</i>	<i>edf</i>	Ref. <i>df</i>	<i>F</i>	<i>P</i> -value		Adj. <i>R</i> -sq.	Dev Expl. %	GCV
~ s (Location)	180	8.32	8.87	30.6	<2e-16	***	0.6	61.1	0.02111
~ te(Location, Soil)	180	8.46	8.89	28.12	<2e-16	***	0.58	59.7	0.02217
~ te(Location, Disturbance)	180	7.53	8.38	27.5	<2e-16	***	0.56	57.7	0.02303
~ te(Location, Fern Grove)	180	11.85	14.64	17.45	<2e-16	***	0.59	61.3	0.02218
Vegetation NMS axis 2									
~ s (Location)	180	6.74	7.85	8.98	<3.81e-10	***	0.28	30.6	0.02422
~ te(Location, Soil)	180	5.19	6.06	5.56	<2.49e-5	***	0.15	17.1	0.02841
~ te(Location, Disturbance)	180	5.7	6.64	5.09	<4.05e-5	***	0.15	17.5	0.02843
~ te(Location, Fern Grove)	180	6	7	5.07	<2.98e-5	***	0.16	18.3	0.02827
Vegetation NMS axis 3									
~ s (Location)	180	4.54	5.57	1.42	0.214		0.03	5.3	0.02925
~ te(Location, Soil)	180	4.6	5.41	1.22	0.302		0.02	4.9	0.02939
~ te(Location, Disturbance)	180	13.88	16.11	1.63	0.0658		0.09	15.8	0.02904
~ te(Location, Fern Grove)	180	4.59	5.45	1.12	0.353		0.02	4.1	0.02964
Middle elevation									
Vegetation NMS axis 1									
~ s (Location)	180	7.49	8.44	46.19	<2e-16	***	0.68	69.7	0.0113
~ te(Location, Soil)	180	6.7	7.58	52.69	<2e-16	***	0.69	70	0.01107
~ te(Location, Disturbance)	180	8.59	8.94	45.02	<2e-16	***	0.69	70.4	0.0112
~ te(Location, Fern Grove)	180	10.53	12.66	28.96	<2e-16	***	0.67	69	0.012

Table A2. (Continued).

Middle elevation									
Vegetation NMS axis 2									
~ s (Location)	180	4.41	5.42	3.43	0.0044	**	0.09	10.9	0.02063
~ te(Location, Soil)	180	6.83	7.98	3.57	0.0008	***	0.12	15.7	0.02008
~ te(Location, Disturbance)	180	7.85	8.62	3.19	0.0016	**	0.12	15.7	0.02032
~ te(Location, Fern Grove)	180	4.79	5.63	2.64	0.0201	*	0.07	9.22	0.02111
Vegetation NMS axis 3									
~ s (Location)	180	7.43	8.4	5.3	<4.04e-6	***	0.18	21.4	0.01702
~ te(Location, Soil)	180	10.65	12.98	3.68	<3.89e-5	***	0.2	24.3	0.01701
~ te(Location, Disturbance)	180	8.25	8.83	4.61	<2.1e-5	***	0.17	20.4	0.0174
~ te(Location, Fern Grove)	180	8.13	8.75	4.59	<2.4e-5	***	0.16	19.9	0.01748
Higher elevation									
Vegetation NMS axis 1									
~ s (Location)	179	8.48	8.92	18.67	<2e-16	***	0.48	50	0.01244
~ te(Location, Soil)	179	13.93	15.92	12.06	<2e-16	***	0.51	54.5	0.01207
~ te(Location, Dieback)	179	16.86	19.24	8.82	<2e-16	***	0.48	52.4	0.0131
~ te(Location, Fern Grove)	179	10.72	13.01	10.44	<5.41e-16	***	0.43	46	0.01379
Vegetation NMS axis 2									
~ s (Location)	179	6.66	7.79	6.68	<1.79e-7	***	0.22	24.7	0.012
~ te(Location, Soil)	179	16.73	18.89	4.2	<2.03e-7	***	0.28	34.7	0.01174
~ te(Location, Dieback)	179	16.37	18.61	4.29	<1.43e-7	***	0.29	35.5	0.01156
~ te(Location, Fern Grove)	179	7.08	8.05	5.42	<4.07e-6	***	0.19	22	0.01249
Vegetation NMS axis 3									
~ s (Location)	179	6.94	8.03	2.98	0.0037	**	0.11	14.3	0.01278
~ te(Location, Soil)	179	14.39	17.1	1.9	0.0206	*	0.13	19.8	0.01308
~ te(Location, Dieback)	179	5.76	6.71	3.81	0.0009	***	0.11	14.3	0.01261
~ te(Location, Fern Grove)	179	4.17	5.13	1.68	0.14		0.03	5.58	0.01363

Significance: ***<0.001, **<0.01, *<0.05, '.' <0.1.

Table A3. Generalized linear models with a log-link and an exponential spatial error term of exotic species or native tree species (< 2 m height class) species counts in individual plots as a function of volcanic substrate type and each elevation zone's environmental NMS axis 1 (soil surface features).

Parameters of Generalized linear models with exponential spatial error							
	<i>n</i>	Value	SE	<i>df</i>	<i>t</i> -value	<i>P</i> -value	Range
Lower elevation							
Exotic Species							
(Intercept)	180	0.4	0.1	177	3.9	0.0002	***
Substrate	180	−0.5	0.2	177	−2.3	0.0203	*
Soils	180	−1.9	0.7	177	−2.8	0.0063	**
Native Trees <2 m							
(Intercept)	180	1.1	0.1	177	13.8	0	***
Substrate	180	−0.1	0.1	177	−0.4	0.6572	
Soils	180	0.8	0.5	177	1.6	0.106	
Middle elevation							
Exotic Species							
(Intercept)	180	−0.1	0.1	177	−0.8	0.4113	
Substrate	180	−0.5	0.4	177	−1.4	0.174	
Soils	180	−2	0.8	177	−2.6	0.0111	*

Table A3. (Continued).

Middle elevation								
Native Trees <2 m								
(Intercept)	180	0.4	0.1	177	3.4	0.0008	***	1.3 m
Substrate	180	0.5	0.2	177	2.5	0.015	*	
Soils	180	1	0.7	177	1.5	0.1386		
Higher elevation								
Exotic Species								
(Intercept)	179	0.1	0.1	176	0.9	0.3551		1.7 m
Substrate	179	−0.5	0.3	176	−1.9	0.0575	.	
Soils	179	0.8	0.7	176	1.1	0.2648		
Native Trees <2 m								
(Intercept)	179	0.2	0.1	176	2.2	0.0293	*	0.8 m
Substrate	179	0.7	0.2	176	4.3	0	***	
Soils	179	−0.9	0.4	176	−2.4	0.0175	*	

Significance: ***<0.001, **<0.01, *<0.05, '.'<0.1.