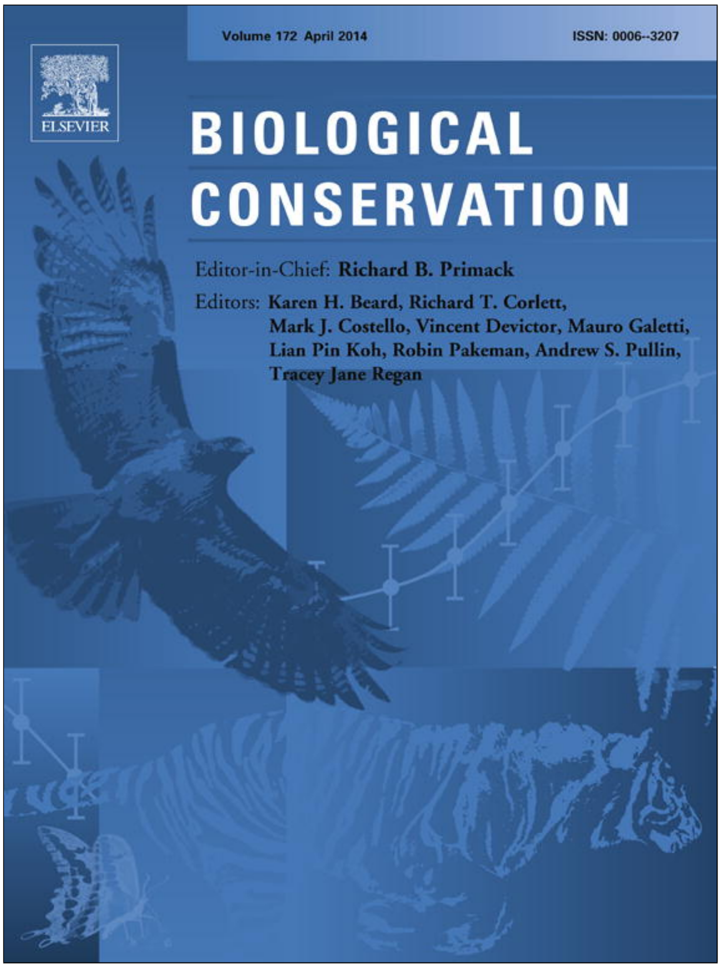
Volume 172 April 2014
ISSN: 0006-3207
ELSEVIER
BIOLOGICAL CONSERVATION
Editor-in-Chief: Richard B. Primack
Editors: Karen H. Beard, Richard T. Corlett, Mark J. Costello, Vincent Devictor, Mauro Galetti, Lian Pin Koh, Robin Pakeman, Andrew S. Pullin, Tracey Jane Regan

Biological Conservation 172 (2014) 37–48

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Identifying management options for modified vegetation: Application of the novel ecosystems framework to a case study in the Galapagos Islands

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ARTICLE INFO

Article history:
Received 31 January 2014
Accepted 4 February 2014
Available online 6 March 2014

Keywords:
Ecological restoration
Invasive species
Ecosystem management
State-and-transition models
Environmental decision-support tools
Biotic novelty

ABSTRACT

In highly modified, or 'novel', ecosystems it is often difficult to decide where limited conservation funds should be spent to reach management goals. We tested a recently-developed decision framework for novel ecosystems to help identify management options for modified native vegetation in the humid highlands of the Galapagos Islands. First, we conducted a data-based ecosystem assessment that compared contemporary vegetation to historical vegetation. This assessment characterised the biotic novelty of contemporary vegetation and resulted in a map of novelty over the landscape. Second, we considered processes affecting ecosystem change and barriers preventing the return to historical vegetation using state-and-transition models that incorporated the spatial extent of the contemporary vegetation states. Finally, we discussed options informed by our results that would address the management goals for our case study. Some of these options involve trade-offs between the goals of conserving biodiversity and maintaining ecosystem services, while other options address both goals in a win–win scenario. The novel ecosystems decision framework was a useful tool for identifying management options because it framed results that enabled a quantitative comparison of the degree of novelty of ecosystems across the landscape and also defined barriers to restoration. Tools that accounted for the spatial extent of the novel ecosystems complemented the framework, particularly for application at a landscape scale. Our approach could be broadly applied to the assessment and management of modified ecosystems, especially where historical data are available to calculate measures of biotic novelty.

1. Introduction

Human domination of the planet has resulted in highly modified ecosystems around the world (Vitousek et al., 1997; Ellis et al., 2010). There is global recognition that societies need to implement ecosystem restoration activities to curtail the loss of biodiversity and ecosystem services (Aronson and Alexander, 2013). However, any restoration project is presented with a myriad of constraints that can make conservation outcomes difficult to achieve. One major constraint is the finite resources for doing restoration. How should limited resources be used to achieve the best possible outcomes for biodiversity conservation and for people? To make effective decisions a way of conceptualising management options for human-modified landscapes is required.

There are many conceptual frameworks that could be applied to decision-making for management of modified landscapes. These include state-and-transition models (Briske et al., 2005), decision analysis (e.g. Cipollini et al., 2005), triage as in human health care (Hobbs and Kristjanson, 2003) and modelling based on end points and effort (Hyman and Leibowitz, 2000). There are also systematic approaches to conservation planning, including prioritizing restoration efforts (Wilson et al., 2011) that could be applied to modified landscapes. One framework that focuses specifically on modified landscapes is the *novel ecosystems* framework (Hobbs et al., 2009), which aims to "develop a management framework to address rapidly changing ecosystems in a way that benefits the well-being of both humans and other species" (Hobbs et al., 2013). Here, we aimed to test this new framework for its practical application using a case study in the Galapagos Islands. Specifically, we applied a novel ecosystems decision tool (Hulvey et al., 2013) to the management of the humid highlands within the National Park on Santa Cruz Island.

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http://dx.doi.org/10.1016/j.biocon.2014.02.005
0006-3207/

Like many other parts of the world, the humid highlands of the inhabited islands of Galapagos have been modified by human activity (Watson et al., 2009). Clearing for agriculture and invasions by introduced plants have transformed some of the historic ecosystems into novel ecosystems such as communities of elephant grass (*Pennisetum purpureum*), quinine trees (*Cinchona pubescens*) and blackberry (*Rubus niveus*). These transformations have resulted in reductions in the abundance of native species (Wilkinson, 2002; Jäger et al., 2009; Rentería et al., 2012a) and altered seed dispersal and pollination (Heleno et al., 2013; Traveset et al., 2013). As a National Park with World Heritage status, the biodiversity values of this landscape are important both nationally and globally. However, the native ecosystems appear to be on a downwards trajectory – plant invasions are worsening as current problem species expand their ranges (e.g. Rentería et al., 2012b). Thus, a robust framework that takes account of ongoing degradation and barriers to restoration is needed to help identify management options for these modified, dynamic ecosystems. We test the ability of the novel ecosystems framework to meet this goal for this landscape and for modified landscapes more generally.

2. Methods

2.1. Theoretical foundation

The novel ecosystems conceptual framework is based on the idea that some human-modified ecosystems fall outside their historical range of variability in terms of their biotic and abiotic components (Hobbs et al., 2009). Ecosystems can be classified into one of three categories: historical – within historical range of variability, hybrid – dissimilar to historical ecosystem but with the potential for restoration, and novel – more dissimilar to historical and restoration prevented by the presence of potentially irreversible thresholds (Hobbs et al., 2009; Hallett et al., 2013). This classification requires an ecosystem assessment and consideration of ecological and social barriers to recovery, which then allows the identification of restoration options according to management goals (Fig. 1; Hulvey et al., 2013). Thus, the novel ecosystems framework can assist management decisions about potential interventions to achieve restoration goals.

The ecosystem assessment requires a comparison of contemporary, potentially novel, ecosystems with a historical reference (Hulvey et al., 2013). The historical reference can be characterised by survey of either unmodified vegetation at the same time but in a different place, or in the same place at an earlier time (Harris et al., 2013). We used the latter to characterise the historical references because historical data were available and because human modification to vegetation in our study site extends well beyond the known range of the historical vegetation types (Watson et al., 2009).

Another essential part of the framework is the identification of ecological and social barriers that prevent ecosystem restoration (Hulvey et al., 2013). The idea of ecological barriers is usually understood in terms of non-reversible thresholds that prevent an ecosystem from persisting within its historical range of variability (Suding and Hobbs, 2009). Thresholds can be caused by a global change, such as climate, a local change such as salinity or soil nutrients, a biological change such as the local extinction of a keystone species (Hallett et al., 2013), plant invasions (Richardson and Gaertner, 2013), or combinations of these. Social factors (such as limited budgets, conflicting values or knowledge gaps) can present significant barriers to ecosystem restoration too and therefore are just as important to ecosystem management as ecological barriers (Hulvey et al., 2013).

In Galapagos there are a number of factors associated with plant invasions that may be considered barriers to restoration (Gardener et al., 2013). However, the reversibility of barriers associated with plant invasions is difficult to determine (Richardson and Gaertner, 2013). Regardless of putative ecological barriers, in Galapagos social barriers, and particularly limited budgets, inhibit the possibility of eradication of widespread invasive species (see further discussion in Section 4.1). Thus for vegetation states dominated by one or more introduced species, we considered transformation to their respective historical vegetation states to be prevented by (currently) irreversible barriers, as discussed in Section 4.1.

2.2. Methodological outline

We followed the decision process (Fig. 1) for our case study in the Galapagos Islands, focusing on the biotic ecosystem components. The first step was to conduct an ecosystem assessment to characterise the contemporary vegetation of the study area (Fig. 1 part A), which we have done using data in Section 3. We compared the species composition and structure of the contemporary vegetation states (CVSs) with that of their historical vegetation types (HVTs). We evaluated the biotic novelty of the CVSs using the metrics detailed in Section 2.4.2. To assist management decisions we extrapolated one of these metrics to map the degree

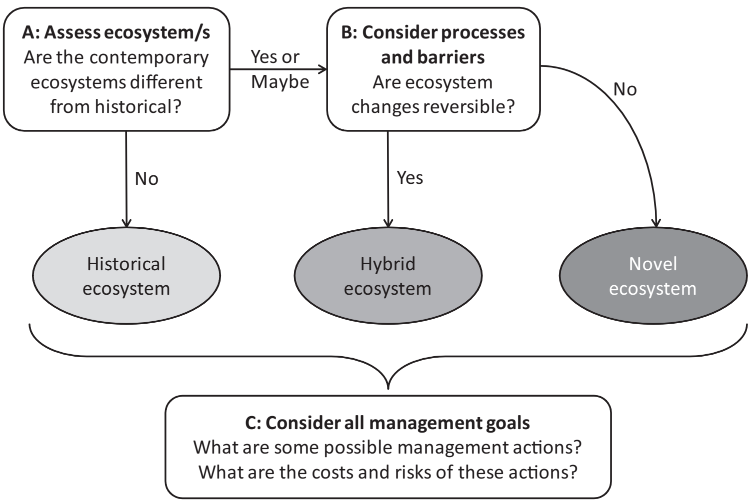

Fig. 1. Steps to identify management options under the novel ecosystems framework. Modified from Hobbs et al. (2013).

of biotic novelty over the whole study area. Next, we constructed state-and-transition models using available information to help conceptualise the vegetation dynamics and barriers to restoration; vegetation states were drawn in proportion to their spatial extent to further assist decision making (Fig. 1 part B, addressed in Section 3). Finally, in Section 4 we outline some management options to address the management goals for the study area, informed by our results and other available information (Fig. 1 part C).

2.3. Study area

Our study focused on the humid highlands area within the Galapagos National Park on Santa Cruz Island, Galapagos (approximately 8000 ha, Fig 2). Historical vegetation has been described (van der Werff, 1978; Hamann, 1981) and mapped for the study area (Trueman et al., 2013). Vegetation in the study area surrounds an extensively modified agricultural zone. It was first modified by tortoise hunters and other visitors prior to 1900 (Hamann, 1984) and later damaged by fires, grazing and feral herbivores (Kastdalen, 1982; De Vries, 2003). Introduced plant infestations began to be problematic since about 1970 (Itow, 2003); these invasions are now widespread (Trueman, unpubl. data, 2013). There are five species classified as Critically Endangered known to have populations in the study area. The study area is currently utilized by people for tourism, timber extraction, fruit harvesting, hunting of feral pigs and goats, and recreation (Trueman, pers. obs., 2011).

The overarching restoration goal is to protect native species and biodiversity – specifically, the Directorate of the Galapagos National Park (DGNP) is responsible for "the conservation of ecological integrity and biodiversity" (DGNP, 2012). A secondary goal is to ensure the "rational use of goods and services [the ecosystems] generate for the community" (DGNP, 2012), i.e. to maintain ecosystem services, which are ecosystem aspects or processes that result in benefits for human welfare (Daily, 1997). This secondary goal is particularly relevant for our study area because Santa Cruz Island has the highest human population and receives the most tourist visitors of all the inhabited islands in Galapagos.

2.4. Ecosystem assessment

2.4.1. Data

To characterise the main historical vegetation types (HVTs) within our study area, we used published historical data. Throughout, plant taxonomy follows Jaramillo and Guézou (2012); species classified in that database as doubtfully native are treated here as native. The main set of data (Hamann, 1981) was collected during field surveys completed in March to May 1972 (approximate locations on Fig. 2); we used data from seven locations (hereafter referred to as plots). Five plots consisted of five quadrats of 25 m^2; one plot (in the HVT Fernland) consisted of ten quadrats of 1 m^2, and one plot (of four in the HVT Mixed Forest) consisted of ten quadrats of 25 m^2 (Hamann, 1981). These data were published as percentage cover for some species, and an "importance value" or category of importance for most species. We used accompanying vegetation descriptions (including the total percentage cover of each stratum) to estimate the percentage cover of all species for which percentage cover was not explicitly stated.

For the HVT Scalesia Forest, we used additional data from two other sources. We used data from 18 plots of 100 m^2, surveyed between December 1980 and February 1981, by Eliasson (1984, p. 108). These data were published as cover classes for each species in each plot, which we converted to percentage cover by assigning the average percent cover for each degree of cover class (i.e., class 5: 75%, class 4: 38%, class 3: 19%, class 2: 9.5%, class 1: 3%). For the same HVT, we also added data from Wilkinson (2002, p. 127) collected in 1999; these were cover percentages averaged by the author from three 100 m^2 plots. These data were collected before the effects of human modification of the native vegetation became apparent (Trueman et al., 2013) and the authors considered them to be representative of the historical vegetation.

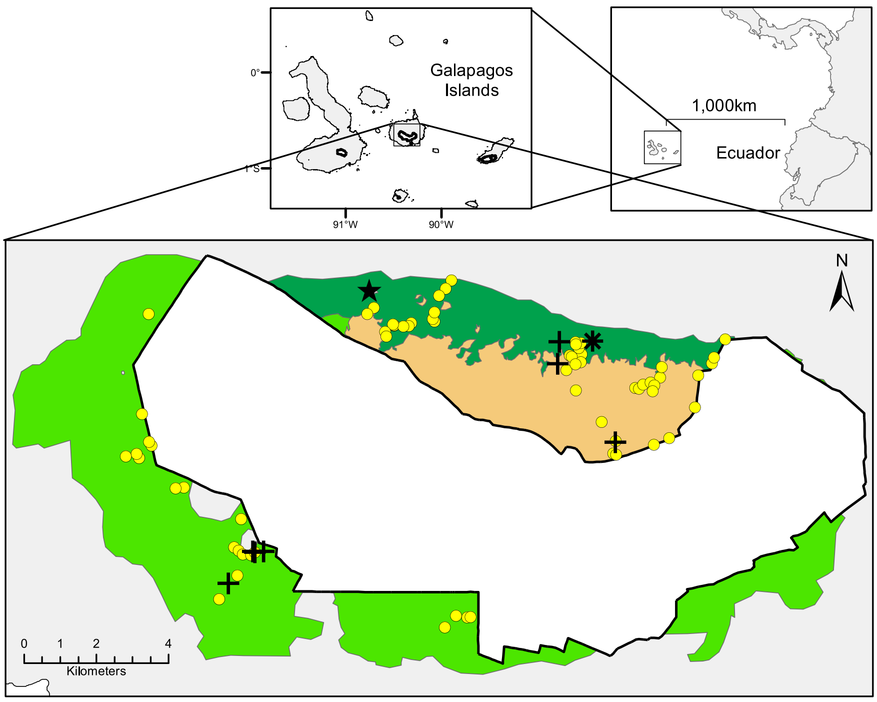

Fig. 2. Map of study area in Santa Cruz highlands showing extent of historical vegetation types (HVTs: dark green – Scalesia Forest; light green – Mixed Forest; pink – Fernland and Miconia Shrubland) and the locations of historical plots (black, source: crosses – Hamann; asterisk – Wilkinson; star – Eliasson) and contemporary plots (yellow). The white area central in the map is an agricultural zone of private lands. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

To define and describe the contemporary vegetation states (CVSs), we surveyed vegetation in 55 plots across the highlands between August and November 2011 (Fig. 2). Plots were selected to represent the different types of vegetation apparent in the highlands on a satellite image (SPOT image © CNES (2007), distribution Spot Image S.A.) and from our observations. Each plot was located at random distances and directions from the walking trails. Plots were 10 m × 2 m; we chose this size (smaller than plots used to collect most of the historical data) to enable data collection that encompassed the range of vegetation types throughout our study area. We recorded all plant species present in each plot. To estimate the percentage cover of each species, we recorded each species that touched a 3 m vertical pole placed at 0.25 m intervals along the central length of the plot. For each plant taller than the pole we visually estimated its intersection with the imagined vertical line of the pole. Thus, the maximum percentage cover for any particular species was 100% (40 points) and the minimum was 2.5% (1 point). Any species that were present in the plot but did not touch the pole at any of the points were given a minimum percentage cover of 1%. We also recorded the height of each plant touching the pole, rounded down to the nearest 0.5 m, or estimated to the nearest metre for those above the height of the pole.

2.4.2. Characterising the contemporary vegetation states

We first identified the historical vegetation type (HVT) associated with each of the contemporary plot locations by overlaying the locations on the map of historical vegetation prepared by Trueman et al. (2013). The plots intersected with the three main HVTs: Scalesia Forest, Fernland and Miconia Shrubland (combined), and Mixed Forest.

We used the percentage cover of all plant species to compare the vegetation assemblages among contemporary plots and with their associated HVT plots using PRIMER 6. We used Bray–Curtis similarity because this distance measure is recommended for species abundance data (Clarke and Warwick, 2001). Prior to analysis we standardised the cover data by total cover in plots and applied a $\log(x + 1)$ transformation to downweight species with high percentage cover so that species with lower coverage also contributed to the similarity measure (Clarke and Warwick, 2001). We visualized these comparisons using 2-dimensional MDS ordinations. We then defined and described the contemporary vegetation states (CVSs) based on the clustering of contemporary plots in the MDS ordinations and our field observations of vegetation height and the dominant canopy species (n = 1–9 plots per CVS). We described the associated HVTs based on the historical data and literature. We tested for differences between CVSs and HVTs using ANOSIM in PRIMER 6.

We calculated five measures of biotic novelty of the CVSs relative to their associated HVT. First, we calculated two types of a *degree of novelty* using metrics of dissimilarity based on vegetation assemblages: Bray–Curtis and Sorenson. Bray–Curtis dissimilarity represents the simplest measure of species turnover based on abundance data (Clarke and Warwick, 2001; Anderson et al., 2011), and is the inverse of Bray–Curtis similarity mentioned above. Sorenson dissimilarity provides a comparative measure of species turnover based on presence/absence of all species (Clarke and Warwick, 2001; Baselga, 2010; Anderson et al., 2011). Within each HVT, we calculated the average (pairwise) dissimilarity between plots representing each CVS and plots representing the HVT. We subtracted from this the average dissimilarity of all historical plots to one another, to represent the natural variability of historical vegetation (sensu Anderson et al., 2011) (Eq. (1)). Ideally we would have represented this natural variability with the average dissimilarity of only historical plots representing the relevant HVT. However we felt our historical plots did not adequately represent the spatial and temporal variation in vegetation, so we opted to use the overall average dissimilarity of all pairwise combinations of plots in each HVT. We gave equal weighting to the three sources of data for HVT Scalesia Forest. For the CVS Modified Fernland we used only the plot representing the relevant part of the HVT (Fernland), and similarly for the CVS Modified Miconia Shrubland we used only the plot representing the Miconia Shrubland.

$$\text{degree of novelty} = \frac{\sum_{i=1}^{n_c}\sum_{j=1}^{n_h}\delta_{ij}}{n_c n_h} - \frac{2\sum_{j=1}^{n_h-1}\sum_{k=j+1}^{n_h}\delta_{ik}}{n_h(n_h-1)} \tag{1}$$

where n_c is the number of CVS plots, n_h is the number of HVT plots, $i = 1\ldots n_c$, $j = 1\ldots n_h$, and δ_{ij} is the dissimilarity of CVS plot i to HVT plot j.

As further measures of biotic novelty, we calculated the average relative introduced species richness and the relative introduced plant abundance for each CVS (after Catford et al., 2012). Relative introduced species richness is calculated as the percentage of all species in a plot that are non-native. Relative introduced species abundance is the percentage of total cover that is comprised of non-native species. As a final inverse measure of biotic novelty, we calculated average native plant species richness of each CVS. For a more in-depth analysis of species turnover between HVTs and their associated CVs, we constructed a maximally ordered matrix (following Louzada et al., 2010) of plant species for each HVT.

2.4.3. Biotic novelty at the landscape scale

We reclassified the most recent vegetation map of our study area (Trueman, unpubl. data) to match our defined CVSs. We extrapolated the data on biotic novelty (Bray–Curtis) of each CVS to estimate the degree of biotic novelty across the landscape. We included on this map the known locations of critically endangered species (Charles Darwin Foundation, 2012).

2.5. Using state-and-transition models to conceptualise vegetation dynamics and potential barriers to restoration

We constructed state-and-transition models to help conceptualise the likely transitions among CVSs and barriers to their restoration to a state resembling the associated HVT. We used proportionally-sized boxes to represent the spatial extent of each vegetation state (i.e., the HVT and ascribed CVSs). We defined transitions between states based on literature and our understanding of the system, differentiating between transitions that (a) occurred in the past (i.e., unlikely to be repeated), (b) are continuing, and (c) are required for ecosystem recovery (i.e., a transition to states of lesser novelty or the historical state). Past transitions were indicated by arrows proportional in length to the degree of novelty (Bray–Curtis) of each CVS. We proposed the presence of some potentially irreversible barriers inhibiting transitions required for ecosystem recovery, indicated by a black line on the models and explained in Section 4.1.

3. Results

Thirteen contemporary vegetation states (CVSs) were identified. Within each historical vegetation type (HVT), there was at least one CVS that had a similar structure and species composition (in the canopy) to the historical vegetation. Other states were different both structurally and in species composition (Table 1). In most cases, the species composition of the CVSs and their associated HVT were significantly different (Table 2 and Fig. 3). The species composition of CVSs was significantly different from that of most other CVSs within each HVT supporting their designation as definitive vegetation states (Table 2 and Fig. 3). For some comparisons

Table 1
Description of historical vegetation types (HVTs) and their ascribed contemporary vegetation states (CVSs). Introduced species are indicated with a *, and all of these are considered ecosystem transformers in Galapagos (Richardson et al., 2000; Gardener et al., 2013).

HVT	CVS	Strata (including height of canopy)	Dominant canopy species for HVTs (van der Werff, 1978; Hamann, 1981; Trueman et al., 2013) and CVSs (as determined from contemporary field data).
Scalesia Forest		Upper (5 m), mid, lower	Forest dominated by *Scalesia pedunculata* at 60–100% cover
	Modified Scalesia Forest	Upper (5 m), mid, lower	At least 75% cover of *S. pedunculata*
	Mixed Introduced Forest	Upper (5 m), mid, lower	At least 75% combined cover of any two or more of **Cestrum auriculatum*, **Passiflora edulis*, **Psidium guajava* and **Rubus niveus*.
	Avocado Forest	Upper (10 m), lower	At least 75% cover of **Persea americana* (except one plot which had 57% cover but also contained 27% cover of another tree **Cinchona pubescens*)
	Grassland	Lower (2 m)	100% cover of **Pennisetum purpureum*
Fernland		Lower (1 m)	Open fernland of 75% plant cover, dominated by *Pteridium arachnoideum*, with abundant *Jaegeria gracilis*
Miconia Shrubland		Mid (3 m), lower	Shrubland dominated by *Miconia robinsoniana* with approximately 85% cover
	Modified Fernland	Lower (1 m)	At least 75% cover of *P. arachnoideum*
	Modified Miconia Shrubland	Mid (3 m), lower	At least 75% cover of *M. robinsoniana* (except one plot which had 70% cover)
	Cinchona Forest	Upper (6 m), lower	At least 75% cover of **C. pubescens*
	Guava Forest	Mid (5 m), lower	At least 50% cover of **P. guajava*
	Grassland	Lower (1 m)	At least 95% cover of either **Melinis minutiflora* or **Urochloa mutica*
Mixed Forest		Upper (3–6 m), mid, lower	Forest dominated by at least one of *S. pedunculata*, *Psidium galapageium* and *Zanthoxylum fagara* with a tree cover of 75–100%
	Modified Mixed Forest	Upper (3–6 m), mid, lower	Combined cover of *S. pedunculata*, *P. galapageium*, *Z. fagara*, and *Clerodendrum molle* of at least 75% (except one plot which had 70% cover).
	Cedrela Forest	Upper (10 m), mid, lower	At least 75% cover of **Cedrela odorata* (except one plot which had 58% cover of **C. odorata* plus 63% cover of **Cestrum auriculatum*)
	Grassland	Lower (2 m)	100% cover of **P. purpureum*
	Guava Forest	Upper (5 m), mid, lower	At least 50% cover of **P. guajava*

Table 2
Similarity of species composition between CVSs and their associated HVT and among CVSs within HVTs, as indicated by ANOSIM tests of Bray–Curtis similarity of (log-transformed) species abundances. R varies from 0 (similar) to 1 (different); only R values significantly different to zero are indicated ($p < 0.05$).

HVT	CVSs compared with HVT	CVSs compared with one another
Scalesia Forest	All different ($R = 0.97–1$)	All different ($R = 0.84–1$) except Modified Scalesia Forest cf. Mixed Introduced Forest
Fernland and Miconia Shrubland	Not different [a]	All different ($R = 0.45–0.99$) except Grassland cf. Guava Forest
Mixed Forest	All different ($R = 0.70–1$), except Grassland [b]	All different ($R = 0.37–0.90$), except Grassland cf. all others [b]

[a] Due to insufficient historical plots.
[b] Due to insufficient contemporary plots.

that appear different (Fig. 3) we had insufficient data to detect significant differences (Table 2).

There was a Grassland CVS associated with each of the HVTs (Table 1). Compared with other CVSs, the species composition of Grassland was the most dissimilar to the reference vegetation for all HVTs and it had the lowest native species richness and proportion of total cover comprised of native species (Figs. 3 and 4). The species composition of the avocado-dominated CVS was also very dissimilar to that of its HVT Scalesia Forest and it had very low native species richness compared with the other CVSs in that HVT (Figs. 3 and 4). Of the biotic novelty metrics, the degree of novelty (Bray–Curtis) provided the greatest distinction between CVSs, closely followed by native species richness and relative introduced species cover (Fig. 4).

Turnover of plant species was evident in the comparisons of the CVSs to their reference HVTs (Appendix A). Visualizing the landscape of our study area as a whole, it is apparent that most of the landscape has a medium degree of biotic novelty (Fig. 5). The most novel parts of the landscape are where the CVSs of highest biotic novelty occur (Grassland and Avocado Forest in the areas mapped as HVT Scalesia Forest). The least novel parts of the landscape are in the areas mapped as the combined HVT of Fernland and Miconia Shrubland, coinciding with the occurrence of critically endangered species (Fig. 5).

Past and ongoing transitions have been responsible for the departure of all of the CVSs from their historical references (Fig. 6). Plant invasions are most commonly associated with these departures (Fig. 6 T5). The Modified Fernland and Modified Miconia Shrubland appear to be undergoing a counter-process of unassisted recovery towards less novel states. Overall in our state-and-transition models (Fig. 6) we suggested that there are potentially immovable barriers inhibiting the return of all CVSs to their historical species assemblages in all HVTs (see explanation in Section 4.1). As such, according to the decision framework (Fig. 1), we classified all of the CVSs as novel ecosystems.

4. Discussion

We conducted a quantitative ecosystem assessment that provides measures of ecosystem novelty across the landscape. We also proposed ecological transitions between our defined vegetation states and suggested potential barriers to recovery. We acknowledge that similar to most other state-and-transition models, our models are descriptive, consisting of working hypotheses regarding the transitions and barriers that need further investigation. We incorporated the area occupied by vegetation states to emphasize the spatial component of ecosystem changes due to the lateral spread of some vegetation states, which is likely to be a feature of

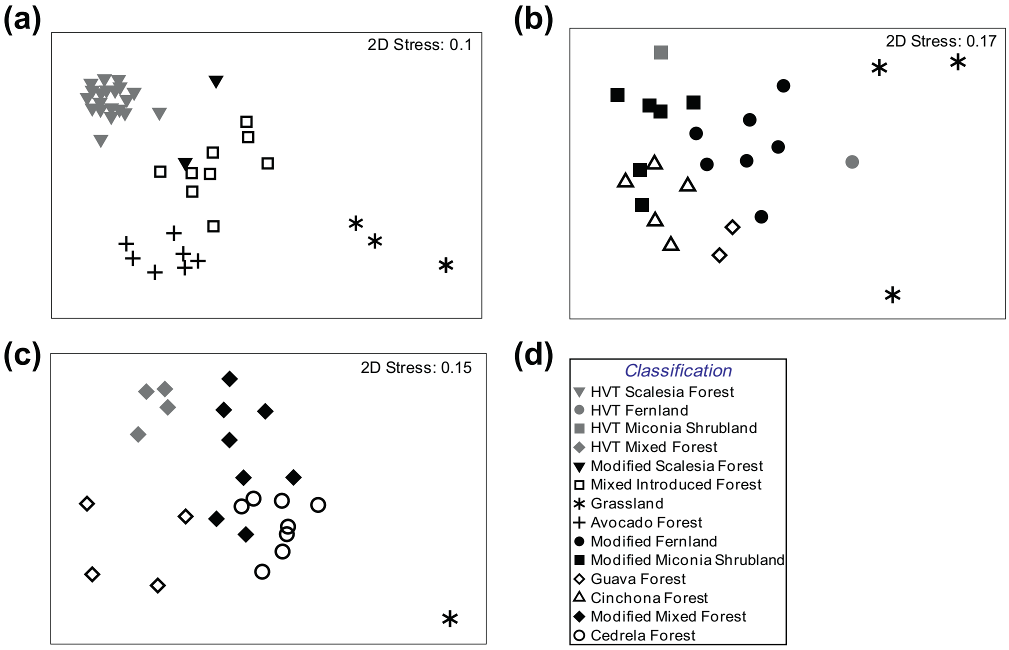

Fig. 3. MDS-plots of historical and contemporary vegetation plots in each historical vegetation type (HVT: (a) Scalesia Forest, (b) Fernland and Miconia Shrubland, (c) Mixed Forest), based on Bray–Curtis similarity of relative abundance (percentage cover) of all plant species using log transformed data (symbol key in panel d).

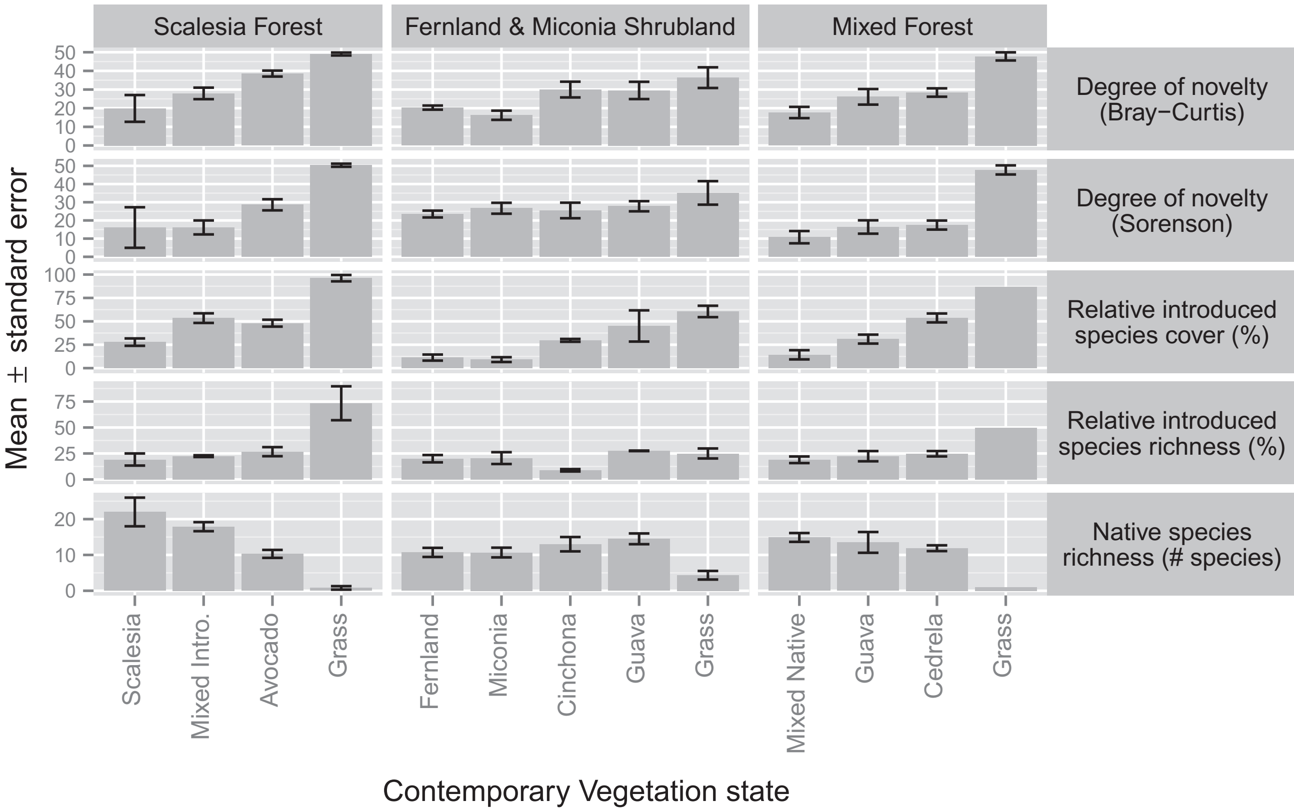

Fig. 4. Comparisons of biotic novelty measures and native species richness of contemporary vegetation states associated with each historical vegetation type.

plant invasions around the world. Our quantitative and descriptive results will facilitate the consideration of management options because they enable a comparison of ecosystems across the landscape. The decision framework specifically requests consideration of all management goals, without this, we may have focussed entirely on biodiversity conservation as a goal, without considering ecosystem services. Using examples, we elaborate on some options for management below.

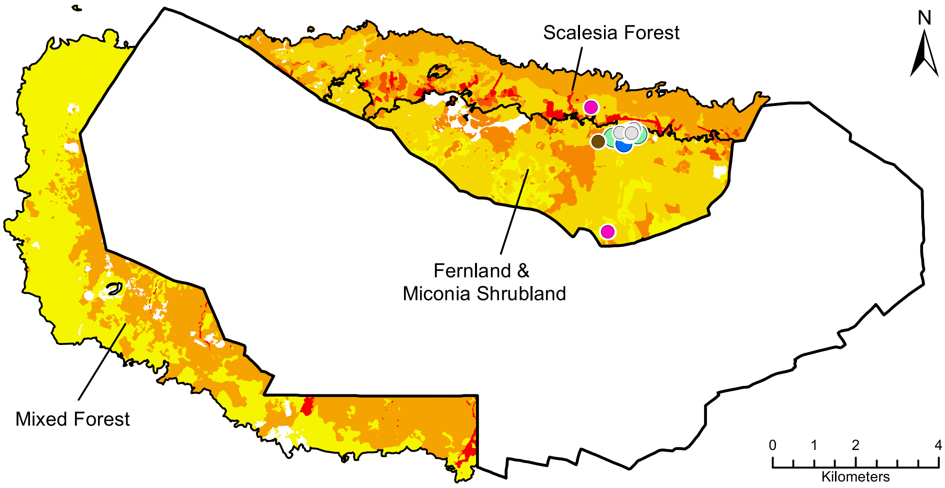

Fig. 5. Degree of biotic novelty (Bray–Curtis) over the study area, graded from yellow (lowest novelty) to red (highest novelty) based on extrapolated data for each contemporary vegetation state. The extent of each historical vegetation type is outlined in black and labelled. Known locations of critically endangered species are indicated with dots: Green – *Acalypha wigginsii*, blue – *Cyperus grandifolius*, grey – *Drymaria monticola*, pink – *Pterodroma phaeopygia*, brown – *Sticta damicornis*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.1. Barriers preventing the return to historical conditions

We argue that plant invasions cannot be stopped while people continue to live in Galapagos and the resources for management are limited. Invasions are ultimately caused by regional development by humans that has led to ecosystem disturbance and the introduction of many introduced plant species. Thus invasion is driven by social factors at a regional (arguably global) scale that are beyond the scope of management (following Hulvey et al., 2013). This thesis acknowledges that multiple introduced plant species are socially and biologically integrated into contemporary ecosystems. For example, many introduced plants are dispersed by native species (Blake et al., 2012; Heleno et al., 2013), and others are valued from a social perspective (e.g. *C. odorata* for timber). Management attempts to eradicate invasive plants have been unsuccessful for both social and biological reasons (Gardener et al., 2010). Also, control of invasive plants has been limited to particular areas (García and Gardener, 2012). Invasion would not be prevented by the removal (eradication) of all invasive plants, even if that were possible, because future invasions are expected to occur from the pool of introduced plants in gardens and farms (Trueman et al., 2010). Further, monitoring and removal of new invaders, which would require the unwavering support of all the local residents, has not been possible in the past (Gardener et al., 2013).

4.2. Options for management in our study area

4.2.1. Goal: protect native species and biodiversity

The primary management goal for our study area is to protect native species and biological diversity (Section 2.3). Our analysis highlighted the degrees of biotic novelty across the landscape and where biotic novelty intersects with the locations of endangered species. This analysis can help to guide research and management. If endangered species of conservation concern requires native-dominated habitat then management could focus on reducing biotic novelty in areas where the species occurs. For example, the critically endangered Galapagos Petrel (*Pterodroma phaeopygia*) nests in an area of the HVT Miconia Shrubland. Its conservation is the focus of a targeted restoration program that controls invasive plants and rats in this HVT (Cruz and Cruz, 1987). Alternatively, if an endangered species appears to be persisting in areas of high biotic novelty then managers might focus on establishing the habitat quality of the novel communities before investing in potentially unnecessary weed-control programs. For example, the vulnerable Galapagos tortoise (*Chelonoidis nigra*) eats many introduced plants (Blake et al., 2012) and thrives in areas of high biotic novelty in the HVT Mixed Forest. More research on the feeding preferences of tortoises can help to guide future management of this habitat. Our study has only considered biotic changes, and further work is needed to understand changes to abiotic ecosystem processes that may be caused by invaders associated with novel CVSs. For example, *Cinchona pubescens* may cause altered hydrological regimes or soil nutrient processes in Galapagos (Jäger et al., 2009, 2013), which may, in turn, have consequences for other species.

Maximising biodiversity conservation requires the minimisation of biotic novelty at the landscape scale. We showed that novelty is not restricted to one region so interventions would have to occur at multiple sites across the landscape to achieve this goal. Our state-and-transition models identified the transitions that would likely result in a lowering of biotic novelty and thus provided a focus for management efforts. For example, in the historical vegetation type (HVT) Scalesia Forest, native species richness is comparatively low in the contemporary vegetation state (CVS) Avocado Forest and significantly lowest in the CVS Grassland, yet these two CVSs are spreading (Trueman, unpubl. data). Ongoing invasion leading to the enactment of these transitions at multiple sites would see an increase in biotic novelty across the landscape and localised extinctions could potentially result. Thus efforts to either stop the spread of these vegetation CVSs or eliminate them might be deemed worth a significant financial investment. More generally, the continuation of a rigorous quarantine program and enactment of the Galapagos weed-risk assessment program will help slow the introduction and invasion process and hinder transitions to more novel states (Gardener et al., 2013).

4.2.2. Goal: maintain ecosystem services

The second management goal for our study area is to maintain ecosystem services (Section 2.3). Arguably the most important ecosystem services in Galapagos are those deliver benefits for the nature-tourism industry, which is the main economic activity in Galapagos (Epler, 2007). Often, the location of tourism activities determines where restoration efforts are delivered. Sometimes these restoration efforts help to achieve biodiversity conservation as well as tourism benefits. For example, at the Los Gemelos tourist site introduced plants are kept under control to showcase the native

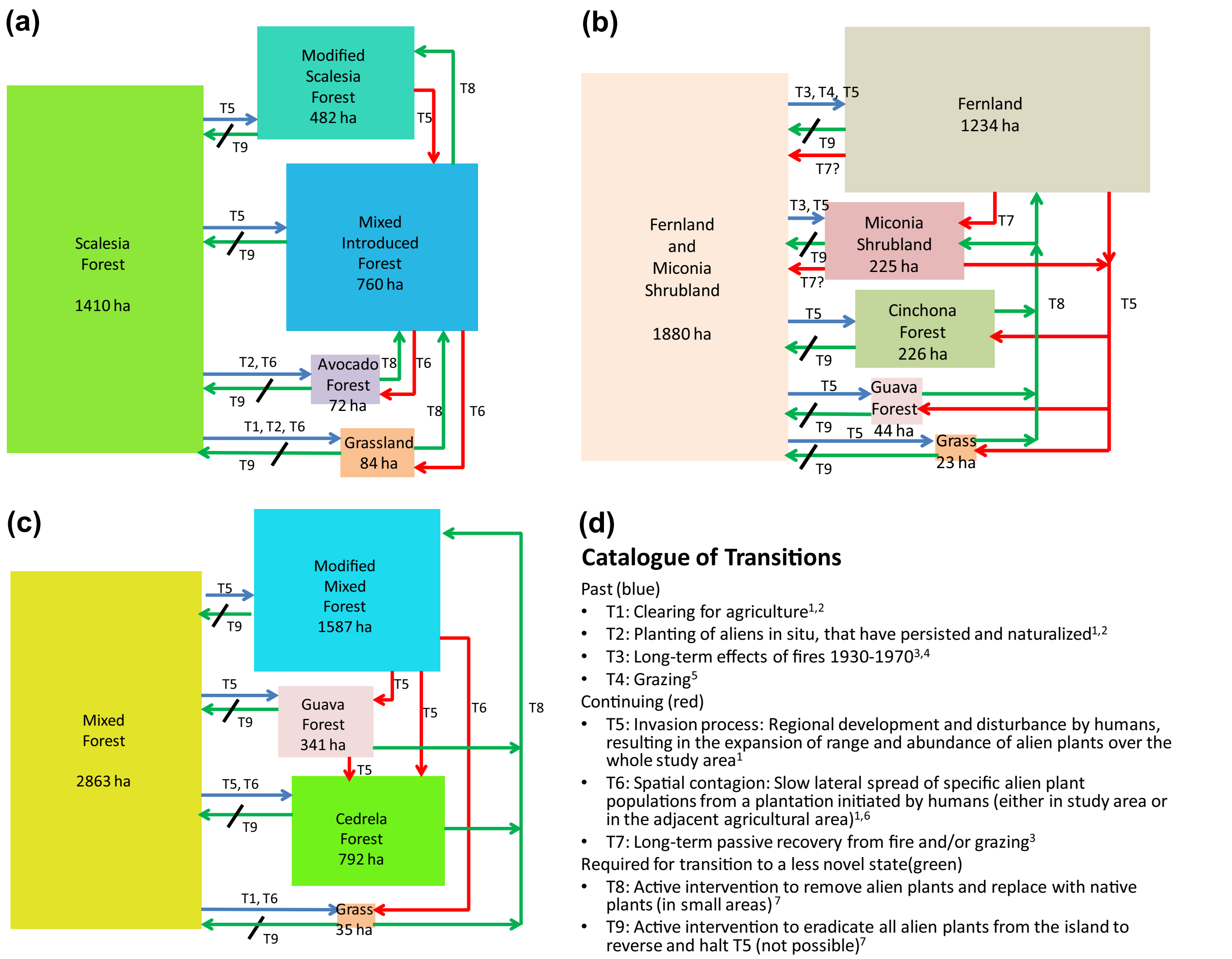

Fig. 6. State and transition models for each historical vegetation type (HVT) (a–c); the catalogue of transitions (d) are generally applicable. HVTs and their associated contemporary vegetation states (CVSs) are represented by boxes that are proportional to the area they occupy. Blue arrows indicate transitions that have occurred from the HVTs, with the length of the line proportional to the degree of novelty (Bray–Curtis) of the CVS. Red arrows represent likely ongoing transitions (observed as recently as 2011) and green arrows represent transitions to a less biotically-novel state. Black lines represent immovable barriers (transition not possible). (1) Trueman, unpubl. data, (2) Hamann (1984), (3) De Vries (2003), (4) Kastdalen (1982), (5) Hamann (1975), (6) following Bestelmeyer et al. (2011), (7) see Section 4.2.1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ecosystems at the site (García and Gardener, 2012). This is a win–win situation that simultaneously addresses goals based on both ecosystem services and biodiversity conservation. However, in other situations, values associated with tourism can directly conflict with biodiversity conservation. For example, *T. fluminensis* is a widespread plant invader that inhibits regeneration of native plants (Gardener et al., 2013), however is valued by some tourism operators because it contributes to an open understorey that is easy and picturesque to walk through (M. Trueman, pers. obs. 2011). Thus, in this example, maintaining the tourism value in a given area would necessarily trade-off with biodiversity conservation.

Other human values can also conflict with biodiversity conservation. For example, introduced plant species can provide direct benefits to humans (e.g. *Cedrela odorata* and *C. pubescens* for timber, and *Passiflora edulis* and *Citrus spp.* for fruit), yet the harvesting of these resources introduces local disturbance that accelerates plant invasions (Trueman, pers. obs. 2011). One way to satisfy such conflicting values could be to use a zoning scheme that manages some areas for biodiversity conservation and others for specific human use. Win–win solutions are also possible. For example, a project that promotes the planting of native species as ornamentals on private land helps to slow the spread of introduced ornamental plants while also meeting the human need for attractive gardens (Atkinson et al., 2011).

4.3. Applying the novel ecosystems framework elsewhere

4.3.1. Ecosystem assessment using reference data

We used historical data, collected prior to major human disturbance, to characterise the reference ecosystem states. In places where historical data are not available or where there is a long history of modification by indigenous people (Hulvey et al., 2013), an alternative is to use contemporary reference sites as a proxy for historical conditions (Harris et al., 2013). However, if degradation is widespread then suitable reference sites may not exist. In such a case, the generic measures of biological invasion suggested by Catford et al. (2012), which do not require reference data, might be useful. In our study, the measure of relative introduced species abundance gave a reasonable level of distinction between our CVSs while relative introduced species richness did not. In cases like ours, where maintaining native species diversity is a specific goal of management, native species richness is also an important and distinguishing metric.

One consideration when comparing historical and contemporary data is that the methodology used to collect or store two sets of data may be different. In our case, the historical data were mostly obtained from larger plots than we used to obtain the contemporary data. Due to the species-area relationship (Williams, 1943), we may have missed some species present at low abundances in the contemporary vegetation states (CVSs), whereas this error is less likely for the species list compiled for the historical vegetation types (HVTs) (Hamann, 1981). However, this is unlikely to have a strong effect on the degree of biotic novelty because community similarity measures such as Bray–Curtis are not strongly influenced by species at low abundances (cf. Sorenson; Clarke and Warwick, 2001). Another factor that would influence any comparison between historical and contemporary communities is the spatial spread of the sampling. In our case, the plots representing the HVT Mixed Forest were constrained to a small geographic area. These may not have adequately represented ecosystem heterogeneity or species richness, causing us to underestimate the novelty of associated CVSs. In general, mismatched methodologies are limitations of using historical data, whereas mismatched conditions are limitations of using contemporary data to characterise HVTs.

The *degree of novelty* measure based on Bray–Curtis dissimilarity of modified ecosystems compared with reference ecosystems provided the greatest distinction between CVSs. This metric would represent biotic novelty most effectively if reference data represented the spatial and temporal heterogeneity of historical ecosystems (see Section 2.4.2). Such a metric allows for comparisons of novelty across different landscapes and vegetation types and could also be used to define cut-offs for management intervention. For example, managers might decide that areas where the degree of novelty is less than 25 should be managed for conservation, including the removal of introduced plants.

4.3.2. Management goals, options, costs and risks

The clear definition of management goals for our study area allowed us to identify management options according to our ecosystem assessment. In places where goals are poorly defined, these will first need to be clarified before applying the framework. When ecosystems are classified as novel, as in our case study, goals to restore ecosystems to their historical state become unrealistic and should be reassessed. Accepting this fact will be difficult for some people (Standish et al., 2013), but does not mean that ecosystems cannot transition to less novel states. It is helpful to balance the outcomes of a novel ecosystems approach with other opinions on management. In our case, our recommendations align with those of a group of experts who recommend balancing costs with prioritised outcomes for biodiversity and functionality in the highlands of Galapagos' inhabited islands (Gardener et al., 2013). This recommendation is similar to the approach taken in New Zealand, where sites and species are prioritized for management in recognition that it is not possible to apply unlimited weed control (Timmins and Owen, 2001).

4.3.3. Future considerations

In Galapagos and elsewhere, the goals and options for ecosystem management will need to be continually revised alongside the status of ecosystems, drivers of change, and barriers to recovery. All these factors can change over time. Indeed, our study area has been transformed by plant invasions in just 50 years (Trueman, unpubl. data) and globally, novel ecosystems currently outnumber wildlands (Ellis et al., 2010). In the future, new tools for managing introduced plants may be developed, in which case novel ecosystems could be reclassified as hybrid, thus altering the management options. Conversely, global change drivers may transform species composition and ecosystem functioning to produce more novel states in more places. A strength of the novel ecosystems framework is the acknowledgement of the dynamics of socio-ecological systems, and specifically, that defining and managing novel ecosystems as such does not imply any future obligation or necessarily constrain options that might be adopted in the future (Hulvey et al., 2013). Effective management into the future will require an understanding of the values people attach to modified ecosystems in addition to scientific evidence and frameworks for decision making.

Acknowledgements

Planet Action provided the SPOT satellite image (through their grant to Charles Darwin Foundation, titled "Vegetation change in Galapagos"). Marcelo Loyola, Paul McFarlane and others helped in the field. Patricia Jaramillo, Mark Gardener and Heinke Jäger helped with plant identification. The Charles Darwin Foundation provided logistical support. Field work was financed by postgraduate funds from the University of Western Australia and approved by the Directorate of Galapagos National Park. RJH and RJS were supported by the ARC Centre of Excellence for Environmental Decisions. Mark Gardener and three anonymous referees provided helpful comments on draft versions of the paper.

Appendix A. Plant species abundance in historical vegetation types (HVTs) and contemporary vegetation states (CVSs) in the highlands of Santa Cruz Island, Galapagos

Species turnover is apparent in the transition of the HVT Mixed Forest to its associated CVSs (Fig. A1). The three native canopy species that characterized this HVT (*Psidium galapageium*, *Scalesia pedunculata* and *Zanthoxylum fagara;* Table 1) had moderate to high cover in the HVT and lower cover in most CVSs. Other native species, such as *Justicia galapagana, Alternanthera halimifolia* and *Piscidia carthagenensis*, had high cover in the HVT but were absent from most CVSs and had low cover in others. Conversely, the natives *Passiflora colinvauxii* and *Paspalum conjugatum* had low cover in the HVT yet had high cover in all or most CVSs. Among the introduced species, only four were present and had low cover in the HVT and yet many were present in the CVSs. Five of these (*Cedrela odorata, Psidium guajava, Cestrum auriculatum, Tradescantia fluminensis* and *Pennisetum purpureum*) were frequent and/or abundant in the CVSs.

Turnover of plant species is evident in the transition of the HVT Scalesia Forest to its associated CVSs (Fig. A2). The endemic tree *Scalesia pedunculata* that characterized this HVT (Table 1 main paper) had high cover in the HVT and in the Modified Scalesia Forest. In the Mixed Introduced Forest it had moderate cover and was not present in the other CVSs. *Psychotria rufipes* and *Spermacoce remota* had moderate abundance in the HVT yet low cover in the CVSs in which it was present. Many other native species were present in the HVT and absent from all or some of the CVSs. Nine native species have higher average cover in the CVSs than in the HVT; *Commelina diffusa* is particularly notable for being abundant in the Avocado Forest. Among the introduced species, eight had low cover in the HVT yet many more were present in the CVSs, and eight had moderate to abundant cover in the CVSs (*Cestrum auriculatum*, *Psidium guajava*, *Passiflora edulis*, *Rubus niveus*, *Persea americana*, *Tradescantia fluminensis*, *Cinchona pubescens*, and *Pennisetum purpureum*.

Turnover of plant species is also evident in the transition of the HVT Fernland and Miconia Shrubland to associated CVSs (Fig. A3). A defining feature of the historical Fernland was *Pteridium*

Fig. A1. Maximally ordered matrix of plant species in the historical vegetation type (HVT) Mixed Forest and ascribed contemporary vegetation states (CVSs). The matrix lists species in the HVT first, then species are ordered by the number of CVSs in which they occurred and their average abundance in the contemporary plots. Shading indicates species abundance: black – high (>40% cover), dark grey – moderate (10–40% cover), light grey – low (<10% cover), white – absent. Introduced species are indicated by *.

Fig. A2. Maximally ordered matrix of plant species in the historical vegetation type (HVT) Scalesia Forest and ascribed contemporary vegetation states (CVSs). The matrix lists species in the HVT first, then species are ordered by the number of CVSs in which they occurred and their average abundance in the contemporary plots. Shading indicates species abundance: black – high (>40% cover), dark grey – moderate (10–40% cover), light grey – low (<10% cover), white – absent. Introduced species are indicated by *.

Fig. A3. Maximally ordered matrix of plant species in the historical vegetation type (HVT) Fernland and Miconia Shrubland and ascribed contemporary vegetation states (CVSs). The matrix lists species in the HVT first, then species are ordered by the number of CVSs in which they occurred and their average abundance in the contemporary plots. Shading indicates species abundance: black – high (>40% cover), dark grey – moderate (10–40% cover), light grey – low (<10% cover), white – absent. Introduced species are indicated by *.

arachnoideum; it had moderate cover in the historical plot, high cover in the Modified Fernland and low or moderate cover in all other CVSs. The other defining species of the historical Fernland was *Jaegeria gracilis*, which had moderate cover in the historical plot and low cover in only two of the CVSs. The historical Miconia Shrubland was dominated by *Miconia robinsoniana*, which had high cover in the historical plot and in the Modified Miconia Shrubland, and moderate cover in two other CVSs. The endemic *Psychotria rufipes* also had high cover in the historical plot, yet was only recorded at low cover in one CVS (Cinchona Forest). The native *Thelypteris balbisii* had moderate cover in the HVT but was not recorded in any of the CVSs. Seven native species had higher average abundance in the CVSs than recorded in the historical plots and many other native species that were not recorded in the historical plots were present in the CVSs. Of the introduced species, only three were present (with low cover) in the historical plots. There were 15 introduced species recorded in the CVSs, of these *Hyptis rhomboidea*, *Cinchona pubescens*, *Psidium guajava*, *Rubus niveus*, *Piper peltatum*, *Melinis minutiflora*, *Urochloa mutica* and had high or moderate cover in at least one of the CVSs.

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