

Interdisciplinary historical vegetation mapping for ecological restoration in Galapagos

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Abstract Improving our knowledge of pre-anthropogenic landscapes is vital for understanding landscape-scale heterogeneity and for setting goals and objectives for ecological restoration. This is especially important in highly modified landscapes that contain few remnants of pre-impact ecosystems. This study aims to develop new methodology to improve understanding of historical vegetation, using the now-degraded inhabited highlands of the Galapagos Islands as a case study. Our multidisciplinary approach innovatively combines data from interviews with residents who were familiar with the vegetation before most degradation occurred with the more traditional sources of historical aerial photography and information from early explorer and scientist reports. We

reconstruct historical vegetation across the landscape by mapping it in the year 1960 and discussing this map in the historical context of anthropogenic change. Our results confirm published vegetation types but also define some other types not previously described, and suggest much greater spatial, temporal and structural heterogeneity than commonly understood. This result can be used by Galapagos land managers to better match species assemblages with sites and plan restoration actions that will maximise resilience against the ongoing and future threats of climate change and species invasions. Our methodology can be applied in extensive areas of the world where the majority of anthropogenic disturbance to natural ecosystems has been within the past 60 years.

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Introduction

Understanding historical ecosystems at a landscape scale is of utmost importance when planning ecological restoration. The benefit of taking a landscape approach is that it embraces spatial heterogeneity (Bell et al. 1997). The significance of history is implied in the definition of ecological restoration as an “attempt to return an ecosystem to its historic trajectory” (SER 2004, p. 1). Even as the definition of ecological

restoration shifts to include the broader goals of maintaining ecological function and services, understanding historical systems remains important for many reasons (Jackson and Hobbs 2009). In landscapes that are highly altered from their original condition, such as the highlands of inhabited Galapagos islands (Restrepo et al. 2012), it is challenging to gain a good understanding of historical ecosystems across the landscape. Thus it is important to continue improving our methods to accomplish these goals.

An example from West Africa illustrates the importance of getting it right. In a forest-savanna landscape there was a persistent common understanding that forest patches were remnants of previous extensive forest (Fairhead and Leach 1996). However, research showed that inhabitants had created forest islands around their villages and that there had been a thickening of woody vegetation in the surrounding savannas (Fairhead and Leach 1996). The error in the common understanding led to an objective to recreate broad-scale closed forest—this provoked environmental problems and was detrimental to villagers' livelihoods (Fairhead and Leach 1996). On the contrary, a good understanding of historical ecology helps to define restoration goals, determine the potential of sites to be restored, evaluate the success of restoration, and determine the conditions that will allow ecosystems to be self-sustaining into the future (White and Walker 1997). In this study, we aim to use a multidisciplinary approach to improve the understanding of historical vegetation in a landscape of the Galapagos Islands that has been modified by agriculture and plant invasions.

As in many parts of the world, Galapagos landscapes have been recently altered by humans. On the four inhabited islands, the humid highland areas have been cleared for agriculture and impacted by species invasions, creating novel ecosystems that lie outside the natural range of variability (Watson et al. 2009; Restrepo et al. 2012). Local land managers and supporting agencies are working to restore historical vegetation (García and Gardener 2011; Fundación Jatun Sacha 2012; Fundar Galapagos 2012). In Galapagos, the current common understanding of historical vegetation is largely based on the vegetation zone descriptions given in the Flora of Galapagos (Wiggins and Porter 1971). These are based on the authors' and early explorers' observations, predominantly along a transect from the south coast to the summit of Santa

Cruz Island and delineated by altitudinal boundaries, and are thus spatially limited. Of course, further investigation reveals that there are other resources (e.g. Stewart 1911; van der Werff 1978; Hamann 1981; Eliasson 1982; Huttel 1995), but the information in these has never been collated, and thus it is a daunting task to gain an integrated understanding of the historical vegetation across the landscape and over time. Existing historical vegetation maps of Galapagos do not provide sufficient detail of the highland region subject to restoration; INGALA et al. (1989) shows very broad vegetation classes and reflects a landscape already extensively cleared for agriculture. We believe restoration goals for the degraded highlands can be improved if managers have an expanded awareness of the historical vegetation. We use a mapping approach to reconstruct historical vegetation in an attempt to capture some of the previously unreported landscape complexity.

There are many approaches used to reconstruct and map historical vegetation, and all have limitations (Egan and Howell 2005). Accordingly, some studies have combined multidisciplinary information to improve their results (e.g. Fensham 1989; Grossinger et al. 2007; Duncan et al. 2010). The choice of methodology is usually determined by what data and resources are available to the project. Even information from periods following significant change can be useful. Grossinger et al. (2007) found that documents that followed substantial landscape changes could still be used in conjunction with prior materials to interpret earlier conditions. Domon and Bouchard (2007) emphasised the importance of analysing all information within the relevant historical perspective. We used three data sources in our study; historical literature, aerial photography and oral history.

The published literature is a valuable source for researching the natural history of a place; it comes in many forms, from early explorer's and traveller's accounts to local histories and early scientific investigations (Edmonds 2005). As emphasised by the oral historian Ritchie (2003), written evidence cannot necessarily be considered as more reliable than other types of information, because authors could have got it wrong. Accordingly, studies using this source often combine it with other data (e.g. Fensham 1989; Butzer and Helgren 2005; Grossinger et al. 2007), though few of these use a mapping approach. The major drawback of using published written accounts of ecosystems is

that they are a human interpretation of the environment and are influenced by the societal context of the time (Edmonds 2005).

Aerial photography is a primary source of data that is not constrained by human interpretation. It is a valuable source for mapping historical vegetation because it provides landscape-scale coverage and is often available for multiple periods over the last century (Lillesand et al. 2008; Morgan et al. 2010). Interpreting landscape features in aerial photography, as in any type of remotely sensed imagery, is challenging and needs to be done in conjunction with ground-based data (Lillesand et al. 2008). This is not possible for historical photography, because we cannot go back in time to assess vegetation how it was at the time the imagery was created. Consequently, aerial photographs are primarily used to assess changes over time, where similar landscape features can be identified over a time-series of photography (e.g. Rhemtulla et al. 2002; Arce-Nazario 2007; Duncan et al. 2010; Walsh et al. 2010). Photographs from a single time in history can be analysed to identify ecological features by manually interpreting variations in tone, shape, size, pattern, texture, shadows and context (Morgan et al. 2010). Resulting polygons will have general features but cannot contain specific vegetation information without other concurrent information.

A potential source for concurrent information is oral history. Farmers and landowners are ideal people to give such history because many of them remember past land conditions and changes. Thus, a structured program of interviews can capture information about a place that might otherwise have been lost (Fogerty 2005). An important consideration is that oral descriptions of previous conditions can be limited in reliability because people tend to remember what is important to themselves, which may not coincide with what is important to the researcher (Ritchie 2003). For example, people could be expected to recall information about species that were particularly prominent or useful to them, but not so much about other species. Ecological oral history studies typically involve collating information on ecosystem changes (e.g. Fensham and Fairfax 2003; Robertson and McGee 2003; Duncan et al. 2010). Few studies have aimed to reconstruct historical vegetation at a particular point in time (e.g. Knott et al. 1998), and none have produced a vegetation map.

Our research question was: Can oral history information be combined with aerial photography and

published literature to create a historical vegetation map? We hypothesized that this multidisciplinary approach could improve understanding of historical vegetation in our Galapagos study area that is degraded by agriculture and exotic species invasions. In particular we aim to capture the spatial and temporal complexity of historical vegetation. A secondary objective of our study is to compile a centralized summary of historical vegetation information for easy accessibility for managers. From the published literature, we present a timeline that facilitates consideration of the historical context of available information. Using aerial photography and oral history, we map the vegetation at one approximate point in time and discuss this in relation to the historical context. In conservation management it has been suggested that an understanding of data uncertainties is necessary for making good decisions (Regan et al. 2005; Keith et al. 2011), yet this is an issue that is under-addressed in the field of landscape ecology (Lechner et al. 2012). Thus we also provide estimates of uncertainties in our results, thereby empowering the end-users to interpret results according to their application.

Methods

Santa Cruz Island, Galapagos

The Galapagos Islands are an isolated oceanic archipelago with a high degree of endemism that present a unique example of ecology and biogeography at work on islands (Tye et al. 2002). Ninety-seven percent of the land area has been protected as a National Park since 1959 and 97 % of the original biodiversity remains intact (Bensted-Smith et al. 2002). The higher islands have a humid highland area with greater biological productivity and higher biodiversity than the more extensive dry lowlands (Porter 1984). In these humid highlands the median annual rainfall is 813 mm (at Bellavista, 194 m.a.s.l. on Santa Cruz Island), though this is highly variable spatially and temporally (Trueman and d'Ozouville 2010). Both droughts and major rainfall events occur due to the ENSO phenomena; these are naturally occurring disturbances that dramatically affect ecosystems over time-frames of less than ten years (Snell and Rea 1999).

The archipelago remained completely free of human disturbance until discovery in 1535 and was

not inhabited until 1832; early residents were focussed on subsistence agriculture and fishing (Lundh 2006). The human population began to grow in the 1970s with the onset of commercial fishing, and this growth accelerated steeply from 1990 alongside the rapid expansion of tourism (Epler 2007).

Our study is situated in the humid highlands of Santa Cruz Island ($90^{\circ}20' W, 0^{\circ}40' S$), which is central in the archipelago (Fig. 1). The humid highlands lie across the southern slope of the island and a little north of the central ridge. An estimated 86 % of these highlands are degraded by the combined effects of agriculture and plant invasions (calculated from Watson et al. 2009). Within the agricultural area (Fig. 1) 60 % of the agricultural land is abandoned and unproductive due to the prohibitive costs of removing invasive plants (Gardener et al. 2010).

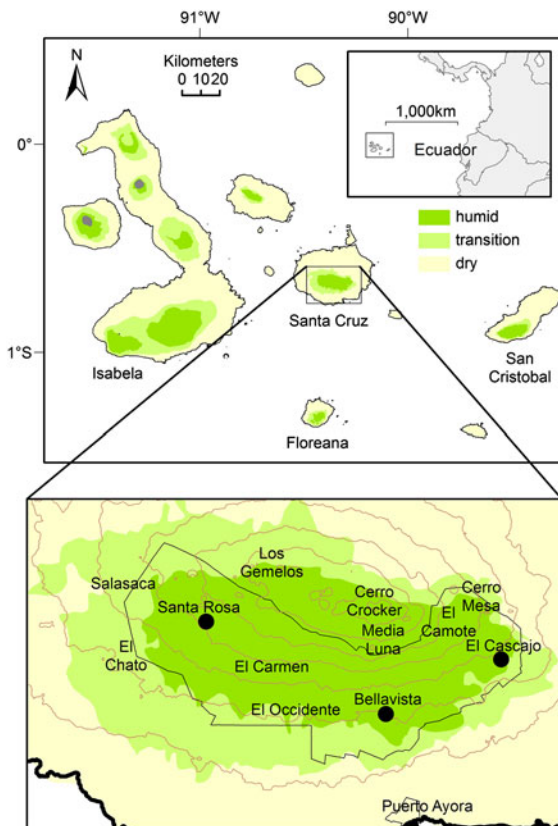


Fig. 1 Location of Galapagos showing the four inhabited islands (*labelled*) and climatic regions. The enlargement of the highlands of Santa Cruz Island shows the current agricultural zone (*outlined in black*), 100 m contours (*brown*) and village locations (*black dots*). *Labels* indicate localities mentioned in the text (including supplementary text)

Data sources

We conducted a literature search in the library of the Charles Darwin Foundation (CDF) in Puerto Ayora, Galapagos. Much of the relevant information was contained here in unpublished grey literature or in very old published documents that are not readily available online. We found some additional information using the Web of Science and Google Scholar. Taxonomy throughout this manuscript follows Jaramillo and Guézou (2012). Old plant names cited in the literature have been updated to their modern synonyms.

We used black and white aerial photography taken in the 1960s (2nd April 1960 and 26th May 1963) and the 1980s (1st & 2nd April 1981 and 16th April 1985) obtained from the Charles Darwin Foundation library, Galapagos, and Instituto Geográfico Militar, Quito. We scanned each photograph and used visible features to georeference each to match the location of modern SPOT satellite imagery. We chose these photographs because they are the earliest source of landscape-scale primary data available for our study site. Other parts of the world have earlier sources of data that are useful for assessing landscape changes over much longer time periods (e.g. Skaloš et al. 2011, using military maps from 1785).

We conducted oral history interviews with 38 current or former residents of Santa Cruz who were familiar with the highlands of the island prior to the 1980s. We selected participants by asking long-term residents to recommend people who might have knowledge of the historical vegetation. We requested meetings with all of those for whom we could make contact, and conducted interviews with all who were willing and able to participate. We also asked each participant to recommend others. The average age of participants was 69 years (range 42–94) and the average experience in Galapagos was 50 years (range 38–77). Author MT conducted the interviews between 2nd September and 7th December 2011 using a semi-structured process, asking people to recall what they remembered about the vegetation of the highlands prior to agricultural clearing and as early as they could remember.

Most interviews were conducted in Spanish and the remainder were in English. Information was documented in the form of written notes and where appropriate and possible, the interview was also

recorded for later reference. Some participants annotated printed maps with information about the vegetation. All were encouraged to give a dominance rating to the plant species they mentioned (using the DAFOR classification (Tucker et al. 2005)), and most indicated which species were dominant in at least one part of the highlands. Common names used by participants were translated to scientific names (*sensu* Jaramillo and Guézou 2012).

Synthesis of data

Using information from our literature search, we describe the development of the understanding of Galapagos highland vegetation and anthropogenic changes. To summarize this information, we plotted a timeline of the information sources alongside historical events that influenced vegetation.

Using the aerial photography, we first digitized the extent of the area developed for agriculture in the 1960s (7 sq km) and 1980s (80 sq km) for comparison with the size of the present-day agricultural zone (114 sq km), confirming that the majority of clearing occurred between 1960 and 1980. We identified the boundaries of this area developed for agriculture by observing pattern and shape (*sensu* Morgan et al. 2010); where straight lines and geometric patterns were assumed to represent agricultural development.

Outside of this agricultural area we digitized polygons representing types of vegetation using the 1960s photography in ArcGIS 10.0 and interpreting differences in tone and texture as variations in vegetation (*sensu* Morgan et al. 2010). In the zone not covered by 1960s photography and still not converted to agriculture by the 1980s, we followed the same process using the 1980s photography. We restricted this process to the humid and transition climatic zones (Fig. 1). Hard boundaries were digitized at a zoom range of 1:5,000–1:10,000 and soft boundaries were digitized at a zoom of approximately 1:30,000. Polygons were assigned a preliminary vegetation structure class based on author MT's interpretation of texture and tone (e.g. open vegetation, sparse forest, dense forest).

All vegetation data from oral history interviews were transferred to map format by drawing polygons that matched participants' descriptions (e.g. “the top third of our family farm”, or “between El Puntudo, Media Luna, and Los Picachos”, or an area drawn on a

printed map). For vague descriptions (e.g. “the area behind Cerro Crocker”), patterns on aerial photography were broadly used to delineate the polygons. Resulting polygons were assigned preliminary floristic vegetation classes based on participants' descriptions of dominant and other species. For the farm boundaries we used a version from the Charles Darwin Foundation GIS database that had been updated in 2008 as part of an introduced plant inventory study (Guézou et al. 2010).

We used the results of our aerial photography digitization as a base for assigning vegetation information from the oral history. Where aerial photography polygons of similar texture, tone and pattern spatially overlapped consistent oral history descriptions, those polygons were assigned a vegetation class. This was a manual process that required several iterations of reading oral histories, classifying vegetation descriptions, and spatially matching them to the aerial photography polygons. The final vegetation classes were Fern/Herbland and Miconia (combined), Mixed Shrubland, Scalesia Forest, Mixed Forest, Native Herb Meadows, Mora Nativa Shrubland, Spiny Shrubland and Dry Forest. For polygons missing aerial photography information, we used residents' descriptions of vegetation extent to estimate boundaries. Finally, the vegetation class of each polygon was re-assessed and re-assigned to best fit with both the oral history and aerial photography.

As a result of this process, each mapped polygon has several attributes aimed at assisting interpretation by the end users of the map (Table 1). Five fields give information on the source of the polygon and its attributes. Three fields give subjective measures of certainty assigned by author MT based on interpretation of the aerial photography and oral history combined with knowledge of the topography and current vegetation of the highlands.

For validation, we describe our mapped vegetation classes and compare them to the well-known and often-cited vegetation zones of Wiggins and Porter (1971), and to the more formal structural vegetation classifications of Van der Werff (1978) and the detailed descriptions of plant communities by Hamann (1981). For more detailed validation, we summarise oral history information on each vegetation class (including quotes from participants), and discuss these in relation to the broader published literature (Supplement 1B).

Table 1 Attributes of mapped polygons that give information to the end user on the data source and the certainty of the mapping

| Type | Field name | Attribute | Possible values |
|-------------------------|------------|---|--|
| Result | Class | Final assigned vegetation class | See Table 2 |
| Data source | PolygSrc | Source of polygon boundary digitisation | Aerial photo, oral history |
| | Source | Year of aerial photography (only if PolygSrc = “aerial photo”) | 1960, 1981, 1985 |
| | Type | Interpretation of aerial photography | Sparse forest, textured forest, dense shrubs, open veg, etc. |
| Assessment of certainty | NumPeople | The number of people who described vegetation coinciding with the polygon | Integers (0 ^a –12) |
| | Spatial | Certainty of the location and boundaries of the polygon | Good, ok, poor |
| | Descript | Certainty in the description of the vegetation class | Good, ok, poor |
| | Classific | Certainty of the polygon containing that vegetation | Good, ok, poor |

^a For polygons in which NumPeople = 0, the vegetation class was assigned based on adjacent or nearby polygons and the interpretation of aerial photography

Results

Key historical information on the highland vegetation of Santa Cruz Island was published during the 20th century (Fig. 2; Supplement 1A). Early explorers (e.g. Stewart 1911; Howell 1942) described vegetation zones along the altitudinal gradient. Later scientists gave more detailed accounts of the vegetation zones, including the altitudinal boundaries between them (e.g. Bowman 1961; Wiggins and Porter 1971). Quantitative vegetation descriptions (van der Werff 1978; Hamann 1981) are based on remnant vegetation outside of agricultural development but pre-date major plant invasions (Fig. 2). Two sets of historical aerial photography cover the highlands (1960 and 1980s; Fig. 2), and these have been previously used with other data by INGALA et al. (1989) to produce a vegetation map that represents agriculture and broad climatic vegetation types.

Even before the first published descriptions of the vegetation, ecosystems had already experienced anthropogenic change due to tortoise hunting, fires and introduced plants and vertebrates (Fig. 2; Supplement 1A). Human settlement of the highlands began in the early 1900s and was focused on subsistence agriculture around present-day Bellavista (Lundh 2006). Several fires burned highland areas in the 1930s and 1940s, particularly impacting the *Miconia*

vegetation (Kastdalen 1982). From Bellavista agricultural development occurred towards the west from the 1960s and towards the east from the 1970s (Supplement 1A). Most clearing of agricultural land occurred during these two decades, associated with the cattle industry (Lundh 2006). Aside from these anthropogenic changes, climatic variation (including ENSO) and other natural factors caused shifts in vegetation assemblages and species distributions over relatively short time periods (Kastdalen 1982).

As described in the methods, we were able to match oral history descriptions of vegetation to patterns observed in aerial photography and produce a model of the historical vegetation in approximately 1960 (Fig. 3; Supplement 1B; Supplement 2). This map pre-dates large-scale agricultural clearing. It shows heterogeneity across the landscape that does not conform to simple altitudinal boundaries, with patches of different vegetation classes in areas that are commonly understood to be the Scalesia Zone. Most of the mapped vegetation classes correspond to previous vegetation descriptions (Table 2), though Spiny Shrubland has not been described in the past. Mora Nativa Scrub and Native Herb Meadows have been minimally mentioned in the past. Of all vegetation classes, Mixed Forest occupies the largest area (Table 3) and features *Scalesia pedunculata* as one of three dominant tree species (Table 2).

Fig. 2 Timeline of key historical information (*top*) in relation to anthropogenic effects on the vegetation (*bottom*) in the highlands of Santa Cruz Island. Decadal climatic trends are indicated (where data available)

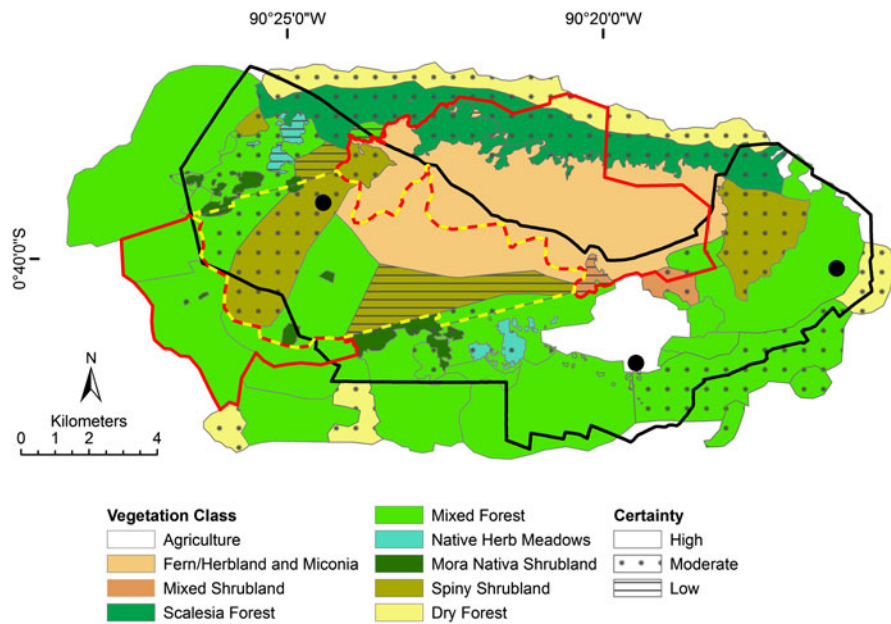
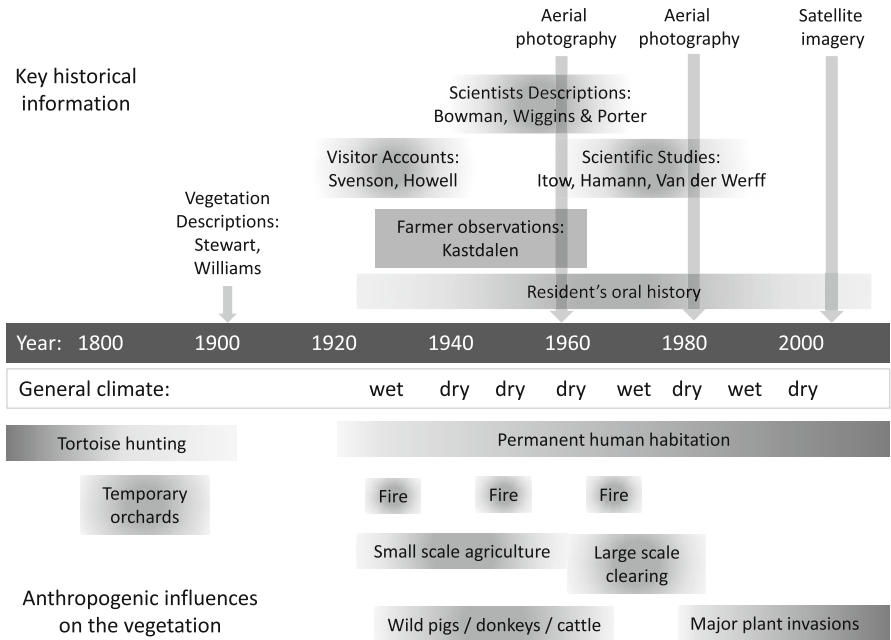


Fig. 3 Historical vegetation map of Santa Cruz highlands, approximately 1960. For spatial reference, the outline of the current agricultural zone is shown in black, and the present-day villages of Santa Rosa (in the west), Bellavista (central) and El Cascajo (east) are shown as black dots. The certainty of the mapping is indicated as follows (using attribute “Classific” described in Table 1): *high certainty* (absence of hatching) indicates that multiple sources of information are in agreement

on the vegetation at the given location, *low certainty* indicates that there is a lack of detail or few information-sources about the vegetation, and *moderate certainty* is in between. Where 1960s aerial photography was incomplete, polygon boundaries are derived from 1980s aerial photography (outlined in red) or oral history (outlined in yellow). Vegetation classes are further explained in Table 1 and Supplement 1B. The ESRI shapefile of this map is available for download in Supplement 2

Table 2 Vegetation classes of our vegetation map (Fig. 3) in relation to the vegetation zones of Wiggins and Porter (1971), and the structural vegetation classifications of Van der Werff (1978) (dominant species included here) and plant communities of Hamann (1981)

| Our mapped class | Detail (our description)* | Wiggins & Porter | Van der Werff | Hamann |
|-------------------------------------|--|---|--|---|
| Agriculture | Cleared or significantly altered by humans prior to 1960 | Not applicable | Not applicable | Not applicable |
| Fern/ Herbland and Miconia | Two vegetation types: Open fern/herbland dominated by <i>Pteridium arachnoideum</i> , AND Shrubland dominated by <i>Miconia robinsoniana</i> | Fern/sedge zone AND Miconia zone | Evergreen broad-leafed weedy vegetation: <i>P. arachnoideum</i> , <i>Jaegeria gracilis</i> , <i>Trisetum howellii</i> AND Mossy evergreen orthophyll scrub: <i>M. robinsoniana</i> | Moderately mesophytic, microphyllous ± seasonal fern meadow. <i>P. arachnoideum</i> - <i>J. gracilis</i> community AND Mesophytic, mesophyllous evergreen scrub. <i>M. robinsoniana</i> community |
| Mixed Shrubland | Shrubland of <i>Zanthoxylum fagara</i> , <i>Psidium galapageium</i> and <i>M. robinsoniana</i> with hanging brown epiphytic liverworts | Not mentioned, but Bowman (1961) named this the Brown Zone | Open gnarled evergreen mossy forest: <i>Z. fagara</i> , <i>Tournefortia pubescens</i> | Mentioned remnant vegetation in a crater that might have been similar to Bowman's brown zone: small <i>Scalesia pedunculata</i> , <i>Z. fagara</i> , <i>Ioichroma ellipticum</i> and <i>Urera caracasana</i> |
| Scalesia Forest | Forest dominated by <i>S. pedunculata</i> | Scalesia zone | Evergreen soft-wood orthophyll forest: <i>S. pedunculata</i> | Mesophytic, mesophyllous evergreen forest: <i>S. pedunculata</i> community |
| Mixed Forest | Dominant trees from at least one of three species: <i>S. pedunculata</i> , <i>P. galapageium</i> and <i>Z. Fagara</i> . Variable throughout the mapped class | Scalesia zone/Transition zone | Evergreen soft-wood orthophyll forest: <i>S. pedunculata</i> ; noting that most had been cleared for agriculture | Mesophytic, microphyllous evergreen forest: <i>P. galapageium</i> - <i>Z. fagara</i> community (with <i>S. pedunculata</i>) AND Mesophytic, microphyllous evergreen forest: <i>P. galapageium</i> - <i>S. pedunculata</i> community AND Mesophytic, mesophyllous evergreen forest: <i>S. pedunculata</i> - <i>Z. fagara</i> community |
| Native Herb Meadows | Patches of native herbs and grasses that were interspersed with Mixed Forest | Mentioned "heavy masses of intertangled vegetation" on the margins of cleared areas and trails in the Scalesia zone | Not mentioned | Mesophytic, microphyllous ± seasonal herb-grass meadow: <i>Paspalum conjugatum</i> - <i>Blechnum pyramidatum</i> community |
| Mora Nativa Shrubland | Patches of vegetation in which <i>Caesalpinia bonduc</i> is dominant | Not mentioned | Not mentioned | Mentioned in the south-west as spreading from lower elevations into Scalesia forest |

Table 2 continued

| Our mapped class | Detail (our description)* | Wiggins & Porter | Van der Werff | Hamann |
|------------------|--|------------------|--|---|
| Spiny shrubland | Shrubland dominated by <i>Psychotria rufipes</i> , <i>C. bonduc</i> (in the west, not in the east) and <i>Z. fagara</i> | Not mentioned | Not mentioned | Not mentioned |
| Dry forest | Similar in composition to Mixed Forest, but at lower elevations and added prominence of <i>Clerodendrum molle</i> and <i>Croton scouleri</i> | Transition zone | Dry-season semi-deciduous forest: <i>Pisonia floribunda</i> , <i>P. galapageium</i> , <i>Piscidia carthagenensis</i> . | Moderately mesophytic, microphyllous evergreen forest: <i>P. galapageium</i> - <i>Z. fagara</i> community (with <i>S. pedunculata</i>) |

*Full class descriptions are given in Supplement 1B

Table 3 Total area of each mapped vegetation class

| Vegetation class | Area (ha) |
|---------------------------|-----------|
| Agriculture | 662 |
| Fern/herbland and Miconia | 3,575 |
| Mixed shrubland | 183 |
| Scalesia forest | 1,841 |
| Mixed forest | 10,386 |
| Native herb meadows | 216 |
| Mora nativa shrubland | 339 |
| Spiny shrubland | 2,290 |
| Dry forest | 1,402 |
| Total area mapped | 20,894 |

We also provide an assessment of the certainty of our map based on the data used to create it (Fig. 3). Certainty is generally high where 1960s aerial photography coincides with historical reports and oral history. However certainty is also high in some areas not covered by 1960s photography either because there were multiple oral history reports that agreed on the vegetation present, and/or because we believed the 1980s aerial photography was a reasonable approximation of vegetation boundaries in 1960. Certainty is lowest where only few oral history reports applied. The resultant model covers the greatest spatial extent possible with the data, albeit at varying levels of certainty (Fig. 4).

Discussion

In this paper, we have presented an approach that uses multidisciplinary information to develop an

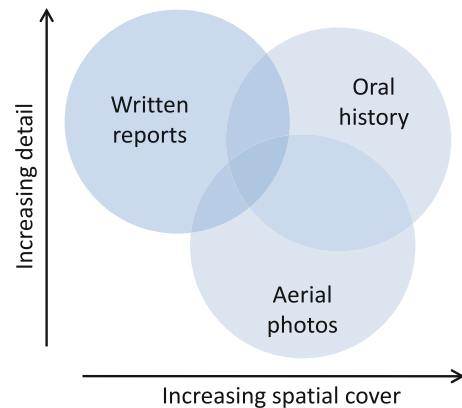


Fig. 4 Representation of certainty of each data source (*circle*) and their combinations; darker shades have higher certainty. Each data source is positioned according to the estimated degree of floristic and structural detail and the approximate extent of spatial cover. Written reports have been assigned a higher degree of certainty than other sources because they are published (some peer-reviewed) and generally cover a greater temporal period

understanding of historical vegetation patterns in a landscape that has undergone rapid change in the past few decades. Our results have relevance both to Galapagos and in a broader context. In our case study, we confirm the commonly understood historical vegetation types but suggest below that there was greater spatial and temporal heterogeneity in species compositions. Below we discuss the validity of our map as a model of the pre-disturbance vegetation in the local context. We also explain the uncertainty across our map, the management implications of our model, and the potential for broader application of our method.

Increased heterogeneity

Our approach revealed greater vegetation heterogeneity across the landscape than commonly understood. Native Herb Meadows, Mora Nativa Shrubland, and Spiny Shrubland have not previously been recognised as distinct vegetation types on Santa Cruz Island. Mapping these patches separately adds a whole lot of complexity to the area commonly understood as the Scalesia Zone. Furthermore, the residents' oral history together with a thorough reading of the historical literature, reveals that the forests of this zone were composed of at least three tree species (*P. galapageium*, *S. pedunculata*, *Z. fagara*) with variable dominance over the landscape, rather than being purely dominated by *S. pedunculata*. This agrees with Hamann's (1981) plant communities but is more heterogenous than the Scalesia Zone described in more commonly cited publications (e.g. Wiggins and porter 1971).

Our results also indicated that vegetation composition fluctuated temporally over the landscape due to natural factors. Kastdalen (1982) observed rapid changes in the composition of species in the Mixed Forest community. Stand-level dieback and regeneration of *S. pedunculata* has been observed in response to climatic events (Lawesson 1988; Itow 1995; Hamann 2001). Additionally, the Miconia vegetation also was apparently negatively affected by drought in the lower parts of its range, and by intense drizzle and cold in the upper parts of its range (Kastdalen 1982), implying that the extent of this vegetation fluctuated up and down the altitudinal gradient with natural climatic variations. These observations are supported by paleoecological studies showing that natural climatic variability results in wet and dry periods that have been influencing the Galapagos vegetation for millennia (Colinvaux and Schofield 1976; Steinitz-Kannan et al. 1999). The most recent of these studies suggests that pre-human vegetation responded to climatic changes in the short term (decadal) but was generally stable over the past >2000 years (Restrepo et al. 2012). Thus, the vegetation at any one point in time can be considered to be a variation of longer term stability. Our map represents vegetation already influenced by humans (as discussed above) and subject to natural climate variations.

We were unable to map the boundary between the Fern/Herbland and Miconia vegetation, thus our map poorly illustrates the heterogeneity across this zone.

Pre-disturbance vegetation

Our map of vegetation in approximately 1960 reflects the landscape prior to extensive agricultural clearing, but already influenced by fire, introduced herbivores, and small-scale agriculture (including plant introductions). The map broadly represents the pre-disturbance vegetation, with some constraints as discussed below.

Some parts of the highlands had been affected by introduced animals prior to 1960, though other parts persisted in their natural state (Hamann 1981). The oral history confirmed that wild donkeys and cattle lived in the drier parts of the island and had created obvious trails through the native vegetation in the area that became developed for agriculture. It is possible that their trampling disturbance contributed to the openness of the Native Herb Meadows or altered the understorey of Scalesia Forest, Mixed Forest and/or Dry Forest. However, descriptions of these forests are fairly consistent from the early 1900s through to the more scientific studies of the 1960s–1980s, and generally match the oral history (Supplement 1B). Thus any impact of feral animals on the vegetation prior to 1960 is probably not reflected in our mapping.

Our map shows that *C. bonduc* was widespread in 1960, both as the dominant species in the Mora Nativa Shrubland and as a major component in the Spiny Shrubland. However this species is classified as “doubtfully native” in Galapagos (Jaramillo and Guézou 2012), so it is questionable whether this species naturally existed on the island. Lundh (2006) asserts that it was introduced to the highlands by farmers, though oral history participants emphasised that it was widespread before 1960 in areas that were not farmed until after 1960. Hamann (1981) reported that it was invading the native forest from lower elevations. It is known as a pan tropical coastal species (Mabberley 1997), so Galapagos seeds could have been naturally transported inland by grazing tortoises, although tortoises have not been observed eating it (Stephen Blake, personal communication). Unless it can be clarified that this species is naturally occurring in Galapagos, the presence of a Mora Nativa community and the composition of the Spiny Shrubland vegetation in the highlands prior to anthropogenic disturbance cannot be confirmed.

With or without *C. bonduc*, the Spiny Shrubland is dissimilar to other vegetation types described by previous authors (Supplement 1B). In our study it was only described by three residents and thus has low

certainty. However, it is possible that it simply missed out on being described earlier. The area mapped with this vegetation is distant from the general transect visited by early explorers and was cleared for agriculture prior to more detailed vegetation studies (e.g. van der Werff 1978; Hamann 1981). Conversely, there should be little debate about the occurrence of Native Herb Meadows within the commonly understood Scalesia Zone prior to disturbance—they were clearly observed by Stewart (1911) and later described by Hamann (1981) (Supplement 1B).

The combined Fern/Herbland and Miconia vegetation class on our map represents the area covered by two main vegetation types: Low vegetation dominated by ferns, especially *P. arachnoideum* (Bracken), and a mixture of herbs; and a shrub community dominated by *M. robinsoniana* (Miconia). We could not spatially separate these classes because the boundary between them was not apparent in the aerial photography or oral history. In any case, the 1960 boundary between these vegetation types did not reflect pre-disturbance conditions. The majority of this area was altered by fires between 1934 and 1980 (Supplement 1A), which drastically reduced the extent of the Miconia vegetation (Itow 1971; Hamann 1975; Kastdalen 1982) to a small area south of Media Luna (as mapped by INGALA et al. 1989). There is only one report of the upper altitudinal boundary of the Miconia zone that pre-dates fires; Howell (1942) visited in 1932 and documented that Miconia vegetation was entirely replaced by ferns at about 630 m a.s.l. Thus, we estimate that approximately the southern half of our mapped Fern/Herbland and Miconia area was Miconia shrubland, and that most of the remainder was Fern/Herbland prior to the damaging fires. While the Fern/Herbland was dominated by *P. arachnoideum*, it was also interspersed with various herb, sedge and sphagnum bog communities (Howell 1942; Itow 1971; Wiggins and Porter 1971; Mueller-Dombois and Fosberg 1998), making it heterogeneous across the landscape. It is possible that the species composition of both the Fern/Herbland and the Miconia vegetation were also significantly altered by the fires (further discussed in Supplement 1B).

Uncertainty

Above we have discussed our map as a model of the pre-disturbance vegetation in the context of the historical literature as a way of validating our map

and providing an overall model/reconstruction of historical vegetation. An additional source of uncertainty is associated with the fact that we used 1980s aerial photography to delineate vegetation boundaries where the 1960s photography did not cover our complete study area. This is important given that climatic conditions can change the distribution of vegetation on a decadal time-scale. However, we believe that the 1980 boundaries are a good estimate of 1960 boundaries because in areas where both sets of aerial photography were overlapping, boundaries were coincident. This was especially obvious along the northern boundary of the Fern/Herbland and Miconia with the Scalesia Forest. Additionally, at the scale of our map we believe short-term climatic shifts in vegetation would not be apparent except for the boundary between the Fern/Herbland and Miconia vegetation which we were unable to map.

We have provided this assessment of the uncertainty of our map so that information-users will be able to avoid undesirable management outcomes due to a lack of assessment of uncertainty (Regan et al. 2005). We suggest that Keith et al.'s (2011) proposal to “embrace uncertainty” in an adaptive management approach can also be applied to restoration ecology. Various restoration targets based on uncertain historical interpretations can be tested under current conditions, and management can be adapted according to the success or failure in achieving the target.

Implications for restoration and conservation

Our mapping has identified more vegetation classes and greater spatial and temporal variability in the historical vegetation of the highlands of Santa Cruz Island than commonly understood. The main differences are within the zone commonly understood as the Scalesia Zone (sensu Wiggins and Porter 1971), which coincides with the majority of the present-day agricultural area and adjacent parts of the Galapagos National Park. Firstly, our results broaden the restoration palette available to contemporary managers. This increased understanding of heterogeneity offers some practical alternatives for long-term management than the popular target community of dominant *S. pedunculata*. For example, the Mixed Forest shown to occur across most of the agricultural zone (Fig. 3), consisted of mixtures of three dominant tree species (Table 2). *P. galapageium* and *Z. fagara* are longer-lived

trees compared with the faster growing *S. pedunculata*, which could provide a more stable habitat that requires less intensive management over the long term. A good, stable forest cover would make ecosystems less susceptible to weed invasions (Rentería 2011). Secondly, our research identified non-forest vegetation types within the extent of the Scalesia Zone (Spiny Shrubland, Mora Nativa Shrubland and Native Herb Meadows). We suggest that these areas may not support native forest and therefore Scalesia Forest would be an unsuitable restoration target. Thirdly, our oral history results highlight the prevalence of some species (*I. ellipticum*, *P. floribunda*, *P. rufipes*—see Supplement 1B) that are now significantly less common. It would be wise to incorporate these species into restoration projects before their populations are further compromised by the ongoing threats of species invasions and climate change (Sachs and Ladd 2010; Trueman et al. 2010).

Given that Galapagos plant communities were naturally somewhat dynamic over short time-periods in response to climatic fluctuations; it is challenging to identify target communities, especially in a globally changing climate. Changes to the terrestrial climate in Galapagos are not yet apparent (Trueman and d'Ozouville 2010), though predictions suggest increased rainfall and a continuation of fluctuating wet and dry periods (Sachs and Ladd 2010). As identified by Bush et al. (2010), a greater understanding of cool-season fog is needed before predictions can be made regarding ecological implications in the upper parts of the highlands. Due to these uncertainties, restoration targets should include diverse vegetation communities so that if future conditions are unfavourable for some species, others will be able to thrive. Two species that may be sensible choices for an unpredictable future climate scenario are *Z. fagara* and *C. scouleri*, which were both naturally widespread from coastal areas up to the highlands and thus have a broad environmental niche.

One final important point for management is that fire is clearly a disturbance that is destructive to native vegetation over the long term, thus the prevention of wildfire should be a priority.

Broader application

We successfully reconstructed historical vegetation that provides greater spatial, temporal and floristic/structural detail than previously commonly understood

for our study area. A few aspects of our approach are particularly useful to others with a similar goal of increasing understanding of historical ecosystems. Two of the data sources used in our study—written records and aerial photography—are readily available and commonly used in historical ecology studies. In particular, our combination of these sources in a timeline of key information alongside anthropogenic changes aids in the interpretation of historical data. Additionally, our method using local knowledge in a mapping approach can provide considerable information in places where major anthropogenic change has occurred within the past 70 years. Others wishing to use this approach must do so quickly while landholders or other people who cleared or worked in natural landscapes are still alive and remember well. We found that several of the people who were strongly suggested as participants by members of the community were no longer capable of passing on their knowledge (due to illness) or had passed away or moved away. Results of historical reconstructions will always depend on the quality and extent of the information available in the study area and must be interpreted accordingly. Our approach in estimating uncertainty throughout the process is a useful way to empower managers to interpret results according to their needs.

Conclusion

We combined information from aerial photography, oral history and written reports and accepted all levels of uncertainty in our reconstruction of historical vegetation for the highlands of Santa Cruz Island, Galapagos. The resultant historical vegetation map illustrates spatial, temporal and structural heterogeneity in the forested humid highland area, broadening the common understanding of the Scalesia Zone. The mapped extent of Fern/Herbland and *Miconia* vegetation in the higher parts of the island is imprecise, though we discuss it in the historical context and suggest the probable pre-disturbance extent of each. Our reconstruction of historical vegetation provides Galapagos land managers with a more accurate and detailed picture of pre-disturbance vegetation, thus broadening the alternatives for restoration goals. Our innovative multidisciplinary method is applicable in many other parts of the world where major ecosystem disturbance has been recent.

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