

Mapping the extent and spread of multiple plant invasions can help prioritise management in Galapagos National Park

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Abstract

Mapping is an important tool for the management of plant invasions. If landscapes are mapped in an appropriate way, results can help managers decide when and where to prioritize their efforts. We mapped vegetation with the aim of providing key information for managers on the extent, density and rates of spread of multiple invasive species across the landscape. Our case study focused on an area of Galapagos National Park that is faced with the challenge of managing multiple plant invasions. We used satellite imagery to produce a spatially-explicit database of plant species densities in the canopy, finding that 92% of the humid highlands had some degree of invasion and 41% of the canopy was comprised of invasive plants. We also calculated the rate of spread of eight invasive species using known introduction dates, finding that species with the most limited dispersal ability had the slowest spread rates while those able to disperse long distances had a range of spread rates. Our results on spread rate fall at the lower end of the range of published spread rates of invasive plants. This is probably because most studies are based on the entire geographic extent, whereas our estimates took plant density into account. A spatial database of plant species densities, such as the one developed in our case study, can be used by managers to decide where to apply management actions and thereby help curtail the spread of current plant invasions. For example, it can be used to identify sites containing several invasive plant species, to find the density of a particular species across the landscape or to locate where native species make up the majority of the canopy. Similar databases could be developed elsewhere to help inform the management of multiple plant invasions over the landscape.

Keywords

Invasion extent, invasion lag phase, invasive species, protected area, rate of spread, remote sensing data, satellite images, vegetation map

Introduction

Globally, plant invasions are growing in frequency and areal extent (Mack 2000). These invasions need to be managed because they have serious consequences for biodiversity and the economy (Vilà et al. 2011). Mapping is an important tool for managing plant invasions because it can identify where they are and how long they have been there. Knowing the spatial distribution of invaders can help managers identify sites of invasion (Shaw 2005), monitor the outcomes of management actions (Roura-Pascual et al. 2009) and understand processes that operate at a landscape scale (Richardson 2011). Also, quantitatively documenting the change in areal extent of invasions is important for justifying and sustaining public support of management programs (Mack 2000).

However, not all maps are useful for all purposes. The way the landscape is classified in mapping projects affects the types of management decisions that can be made (Lindenmayer and Hobbs 2007). A traditional vegetation map classifies the landscape into discrete classes that each represent distinct vegetation communities (Küchler 1967). The mapping product may identify the presence of invasive plants as a major or minor element in one or more of the vegetation communities. For example, Garzón-Machado (2011) noted the presence of invasive species in two of the communities in their vegetation map of an island National Park, which could direct the attention of managers of invasive plants to the broad areas of the landscape occupied by those communities. Landscapes can also be classified such that a particular invasive species is a specific focus of the mapping; these can give managers detailed information on the location and dynamics of the species (e.g. Müllerová et al. 2005; Pengra et al. 2007). As plant invasions continue to become more pervasive and all ecosystem researchers/managers are forced to consider invasive species (Richardson 2011), there is an increasing need to map landscapes in a way that takes account of all invasive species that may present.

The methods used to map vegetation, including plant invasions, have evolved over time. The availability of remotely sensed data, especially from satellites, has revolutionised the ability to map vegetation over large areas (Xie et al. 2008). Recently, advanced technology has been used to model invaded and non-invaded forest, giving very specific details on the location, structure and species composition of vegetation containing multiple invasive species (Asner et al. 2008). Whilst this approach provides a plethora of useful information to managers, the application of it is limited due to the expense of obtaining data. In under-resourced parts of the world, most managers have access to a limited range of data. As our study was based in the developing country of Ecuador, we aimed to use readily available

satellite data to map vegetation in a way that would give managers useful information for managing a landscape containing multiple invasive species.

One of the factors that is important for prioritising the management of plant invasions is the rate of spread of individual invaders (Pyšek and Hulme 2005). Empirical evidence suggests spread is driven primarily by dispersal ability (Coutts et al. 2011). Specifically, the ability to disperse long distances is the main reason for rapid spread of invasive plants (Richardson and Pyšek 2006). Therefore, plants dispersed by wind (e.g. *Pinus radiata*) or animals (e.g. *Acacia cyclops*, *Opuntia stricta*) exhibit the fastest rates of spread, whereas clonal plants tend to have comparatively slower rates of spread (Pyšek and Hulme 2005). Knowing this, managers may choose to delay the management of slow spreaders in favour of managing fast invaders either via attempts to eradicate the species quickly; or adopting a longer term management strategy such as biological control. Information on the rate of spread of invaders can be obtained from the known locations of invasive species at more than one point in time (Gilbert and Liebhold 2010).

Our study focuses on the humid highlands of Galapagos National Park where invasive plants have spread from areas of human habitation (Itow 2003; Rentería and Buddenhagen 2006). Known ecosystem impacts include reduced abundance and diversity of native species (Jäger et al. 2007), which aligns with global concern for the threat of plant invasions on island plant diversity (Caujapé-Castells et al. 2010). The first objective of our study was to map the location, extent and density of invasive canopy species (ecosystem transformers, sensu Gardener et al. 2013; Richardson et al. 2000) in the highlands of Santa Cruz Island, Galapagos. Our second objective was to calculate the rate of spread of individual invasive species. Results from both objectives can help managers decide which species and which parts of the landscape require intervention, and to provide a baseline for monitoring future vegetation change.

Methods

Study area

Our study concerns the humid highlands within the Galapagos National Park on Santa Cruz Island, which form a doughnut shape surrounding an agricultural zone and are surrounded by dry lowlands (Figure 1). Non-native plants have been introduced to the island since the first human visitors arrived in the early 1800s, though the majority of the current non-native flora have arrived in the last 30–50 years (Tye 2006). Major plant invasions began in the National Park with the spread of *Cinchona pubescens* in the 1970s (Eliasson 1982), followed by other invasions from the 1980s onwards (Gardener et al. 2013). To give historical context to the recent plant invasions, we refer to the four most widespread historical vegetation types (HVTs) described and mapped by Trueman et al. (2013): Scalesia Forest, Fern/Herbland & Miconia Shrubland, Mixed Forest and Dry Forest. The extent of these HVTs in the map we produce here differs slightly to

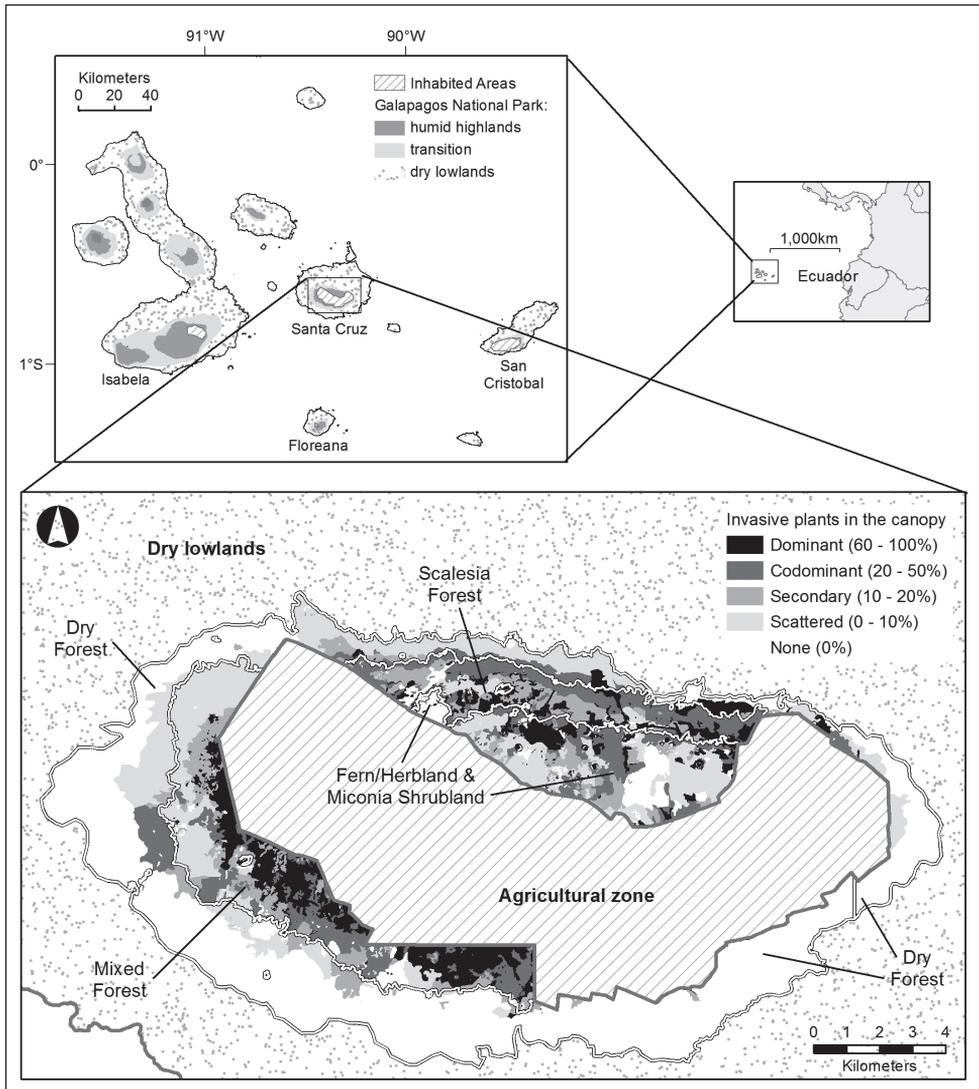


Figure 1. Location of the study area and density of invasive plants in the canopy. The upper map shows the location of the study area, spanning the humid highlands of Galapagos National Park, Santa Cruz Island. Climatic zones are indicated and the four islands inhabited by people are labelled; each of these is inhabited only in an agricultural zone in the highlands and a small coastal town in the lowlands. The lower map shows the density of invasive plants in the canopy of the study area, as indicated by shading. Co-dominant invasive species may be present with either invasive or native plants. Historical vegetation types are outlined and labelled. Of these the Dry Forest occurs on the periphery of the humid highlands that is transitional to the dry lowlands.

that of Trueman et al. (2013) due to the finer scale of data used in this study. Our core area of interest is the humid highlands because they are the most invaded (Guézou et al. 2010) but our study area also includes the transitional periphery between the

humid highlands and the dry lowlands (sensu Trueman and d'Ozouville 2010; Figure 1), coinciding with the HVT Dry Forest.

Mapping the vegetation

We mapped the native and invasive canopy vegetation across the study area using data derived from satellite images and validated with field observations. Canopy vegetation refers to the tallest layer of vegetation, which ranged in height from approximately one metre (e.g., *Melinis minutiflora* grassland) to over ten metres (e.g., *Persea americana* forest). Invasive canopy species are ecologically significant because they can modify the structure of vegetation communities and reduce the amount of light penetrating the ecosystem, negatively affecting the abundance of native understorey species and the recruitment of native canopy species (Reinhart et al. 2006).

Mapping involved the creation of a spatially-explicit database. Essentially, we drew polygons over the study region and assigned to each polygon a measure of density of each vegetation cover class using visual assessment of satellite data (Figure 2 and detailed below). We used three separate satellite datasets. Two were Worldview-2 multispectral datasets (2 m resolution, 8-band) as provided by DigitalGlobe. Scene 1 (19th October 2011, catalog ID: 103001000E276500) covered the western part of the study area and scene 2 (23rd March 2011, catalog ID: 10300100091E2400) covered the central/eastern part of the study area. The third dataset was a SPOT 5 pan-sharpened scene (30th March 2007, 2.5 m resolution, 3-band, level 2A product, image 615/351) which we georectified using 160 ground observation points and a spline transformation in ArcMap 10.0. The SPOT dataset spanned our study area, including small areas in the east that were not covered or were obscured by clouds in the Worldview-2 datasets.

We visually assessed both a true-colour image derived from each satellite dataset and multispectral classifications of each satellite dataset (Figure 2). Visual analysis of imagery, as traditionally applied to aerial photographs, results in a high degree of map accuracy (Coppin et al. 2004). We used satellite images of sufficiently high resolution (2–2.5 m) to be visually assessed in the way of aerial photographs using features such as colour and texture (Morgan et al. 2010). The added benefit of satellite datasets over aerial photography is that they include reflectance values in the infra-red (non-visible) parts of the light spectrum that are particularly useful for distinguishing different types of vegetation using classification tools (Xie et al. 2008). To take advantage of this, we performed supervised classifications using the maximum likelihood algorithm in ArcMap 10.0 which require human input to select training areas that define *a priori* classes (Xie et al. 2008). We selected training areas representative of all 26 vegetation cover classes (described below) by visually assessing the true-colour images. We computed several classifications of each dataset because the spectral signatures of the vegetation classes varied over the spatial extent of each dataset. We drew polygons based on the congruence between visual inspection of the true-colour images and the multiple

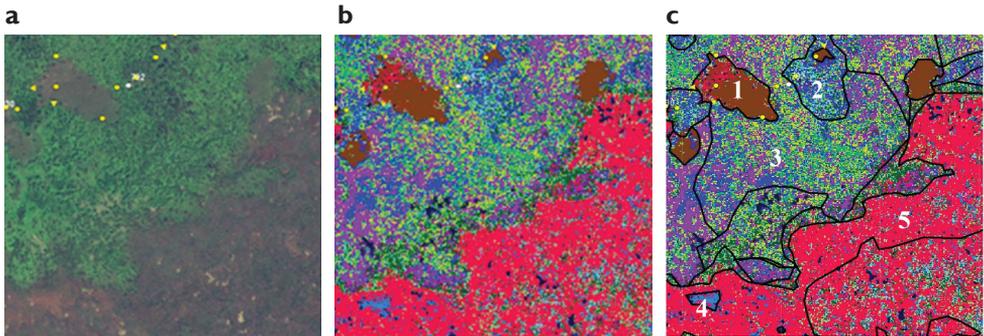


Figure 2. Polygons were manually delineated using a visual interpretation of satellite imagery (**a**: extract of Worldview-2 19th October 2011) and a classification of the imagery (**b**: Blue – *Persea americana*, Mid green – *Scalesia pedunculata*, Yellow – *Cestrum auriculatum*, Light Blue – *Psidium guajava*, Brown – *Penisetum purpureum*, Red – *Pteridium arachnoideum*, Purple – *Rubus niveus*, Dark green – *Cinchona pubescens*, Dark blue – wet depressions of mixed species). Each polygon (**c**) was assigned attributes for the level of density of each class/species present. For example, polygon 1 had *P. purpureum* dominant; polygon 2 had *P. americana* and *P. guajava* co-dominant with *C. pubescens* scattered; polygon 3 had *S. pedunculata* dominant, with *R. niveus* secondary and *C. auriculatum* and *P. americana* scattered; polygon 4 had *P. guajava* dominant; polygon 5 had *P. arachnoideum* dominant and *P. guajava* scattered.

classifications using ArcMap 10.0 at a display scale of 1:5 000 employing the Auto Complete Polygon Tool (Figure 2). Our final database consisted of 1 624 polygons.

In each polygon, we recorded the presence of any of the 26 vegetation cover classes we identified in the images. Twelve of the cover classes represented individual invasive plant species, one class was a mixture of invasive grass species, eight classes represented individual native plant species, three classes represented native plant assemblages, and two classes were non-vegetated (Suppl. material Table 1). The density of each cover classes present in each polygon was scored using the following categories: *dominant* (60–100% cover), *co-dominant* (20–50% cover, shared with other species of roughly equal cover summing to a total of 60–100%), *secondary* (10–20% cover), and *scattered* (isolated individuals or clusters of individuals with 0–10% cover).

We collected field observations to validate the spatially-explicit database. Data collection points were selected to representatively sample the different patterns visible on the SPOT true-colour image. Field observations were recorded between September–December 2010 and July–November 2011. We recorded the canopy species present within an area of 400 m² centred on 591 points within the study area; in total pertaining to approximately 2 000 ha of the full 14 214 ha study area. For validation we intersected the spatially-explicit database with our field observations. The confusion matrix is commonly used for this purpose (Xie et al. 2008) but was not suited to our accuracy assessment because our database contained the density of not one but multiple vegetation classes in each polygon.

The spatial intersection confirmed that our database accurately represented field observations as follows: Classes recorded as dominant in our database were observed at 81% of intersecting observation points, and at least one of the two or more species comprising the co-dominant classes was observed at 82% of intersecting points. These scores were consistent with the average estimated total cover represented by these two density categories (60–100%). Classes recorded as secondary in our database were observed at 45% of intersecting points, while classes recorded as scattered in our database were observed in 37% of intersecting points. This is higher than the average estimated cover represented by these density categories (10–20% cover and 0–10% cover respectively), but is consistent with the fact that each of these classes are dispersed within the vegetation cover, and that observation points relate to cover within a small area rather than a single point.

Invasion extent

We mapped the presence of invasive plants in the canopy using the highest density category for any invasive species recorded in each polygon of our spatially-explicit database. For each HVT, we summed the areas of polygons containing invasive plants in these categories. We also calculated the total area invaded by summing the areas of all polygons in which at least one invasive species was recorded. We calculated the approximate total coverage in 2011 of individual invasive species by summing the area of all polygons in which each occurred in each HVT, weighted by the average percentage cover of its density category (i.e., dominant 80%, co-dominant 35%, secondary 15%, scattered 5%). We did this for seven of the invasive species we had mapped as a single class (we excluded *Syzygium jambos* because it had very low presence) and for the invasive grass species combined. We then calculated the percentage of the canopy vegetation that was comprised of invasive plants by summing the area of total coverage of all invasive species in each HVT and dividing by the total area of each HVT.

Rates of spread

We calculated the mean annual rate of spread of each of invasive species to allow comparison of our results with spread rates reported in the literature (Pyšek and Hulme 2005). Rate of spread is commonly measured in terms of distance per year and can be calculated using a variety of methods (Gilbert and Liebhold 2010; Higgins and Richardson 1999). According to the popular Skellam (1951) model, the square root of the area occupied by an invading organism increases linearly with time (Shigesada et al. 1995). This regression approach is suited to cases such as ours where the introduction location of the invading organism is unknown (Gilbert and Liebhold 2010; Pyšek and Hulme 2005). In our case, the areal extent is only known from a single date, and so we calculated the mean linear rate of spread as the square root of the area occupied at that

date divided by the number of years since introduction into the study area (National Park area of Santa Cruz Island). We derived the first record of each species from the literature, herbarium records, and personal communications with past Galapagos plant researchers and residents. Finally, we reviewed literature to compile information on dispersal mechanisms of each canopy invader.

Data resources

The spatial database underpinning the analysis reported are deposited at PANGAEA Data Publisher for Earth & Environmental Science: <http://dx.doi.org/10.1594/PANGAEA.833752>

Results

Our spatially-explicit database covered a total area of 14 214 ha, representing the full extent of the highlands of Santa Cruz Island that fall within the Galapagos National Park, including the transitional periphery between the humid highlands and the dry lowlands (Figure 1). Of this area 7 782 ha (55% of the total area mapped) contained invasive plants in the canopy (Figure 1). Invaders were dominant in 1 527 ha (11%), co-dominant in 1 945 ha (14%), secondary to native species in 1 395 ha (10%), and scattered among native species in 2 916 ha (21%) (Figure 1). Of the invaders present in the canopy as co-dominants, some were co-dominant with native species (especially *Cinchona pubescens*) while others were co-dominant with both native and invasive species (especially *Psidium guajava* and *Cestrum auriculatum*). Overall, 21% of the canopy of the study area was comprised of invasive species.

The Scalesia Forest and Mixed Forest were the most invaded of the HVTs, both with 96% of their area containing invasive plants in the canopy (Figures 1, 3). The HVT Scalesia forest had the highest proportion of the canopy vegetation comprised of invasive plants (52%), followed by the HVT Mixed Forest (46%). Twenty six percent of the canopy of the HVT Fern/Herbland & Miconia Shrubland was comprised of invasive plants. Most of the invasion-free areas occurred in the HVT Dry Forest (Figures 1, 3), of which only 5% of the canopy was comprised of invasive plants. Excluding this drier periphery from our calculations, 92% of the humid highlands contained some degree of invasive plants in the canopy, while approximately 41% of the canopy was comprised of invasive plants.

Of all the invasive plants featured in our database, the first to arrive into the study area was *Cinchona pubescens* in 1966, and the others arrived later (Table 1). In the 50 year record, *Cedrela odorata* was the fastest canopy invader and had the largest area of canopy cover (Table 1), predominantly in the HVT Mixed Forest (Suppl. material Table 2). In both speed and extent, this invader was closely followed by *Psidium guajava* (Table 1)

Table 1. List of invasive species and their approximate total canopy coverage and rate of spread. Results are for our 14 214 ha study area spanning the highlands of Galapagos National Park on Santa Cruz Island. Details on the distribution of these species within the historical vegetation types and in four categories of density are provided in the Suppl. material Table 2.

Species	Family	Canopy cover (ha)	First record in National Park (Santa Cruz)	Mean rate of spread (m yr ⁻¹)	Dispersal vector
<i>Cedrela odorata</i>	Meliaceae	870	1986 Lawesson and Ortiz (1990)	118	Wind Itow (2003)
<i>Cestrum auriculatum</i>	Solanaceae	545	1985 Charles Darwin Foundation (2012)	90	Birds Buddenhagen and Jewell (2006)
<i>Cinchona pubescens</i>	Rubiaceae	312	1966 Eliasson (1982)	39	Wind Itow (2003)
<i>Cordia alliodora</i>	Boraginaceae	13	1995 Alan Tye & Mark Gardener, pers. comm. 2013	22	Wind Mark Gardener, pers comm. 2013
<i>Persea americana</i>	Lauraceae	61	Pre-1967 Wiggins and Porter (1971)	11	Gravity Itow (2003)
<i>Psidium guajava</i>	Myrtaceae	777	1984 Lawesson and Ortiz (1990), Steve Devine & Carlos Carvajal, pers. comm. 2011	103	Birds, tortoises, mammals Heleno et al. (2013), Blake et al. (2012), Itow (2003)
<i>Rubus niveus</i>	Rosaceae	191	1990 Moll (1998), Itow (2003), Alan Tye pers. comm. 2013	66	Birds, tortoises Heleno et al. (2013), Blake et al. (2012)
Grasses ‡	Poaceae	157	Pre-1974 § Charles Darwin Foundation (2012)	2.3	Vegetative (mainly) §, birds, tortoises Itow (2003), Heleno et al. (2013), Blake et al. (2012)

† Expansion of 5 patches between 1981 (as traced on aerial photography) and 2011

‡ Grasses include *Melinis minutiflora* and *Urochloa decumbens* (in the HVT Fern/Herbland & Miconia), and *Pennisetum purpureum* (in other HVTs)

§ *P. purpureum* only; expansion of 8 patches between 1981 (as traced on aerial photography) and 2011.

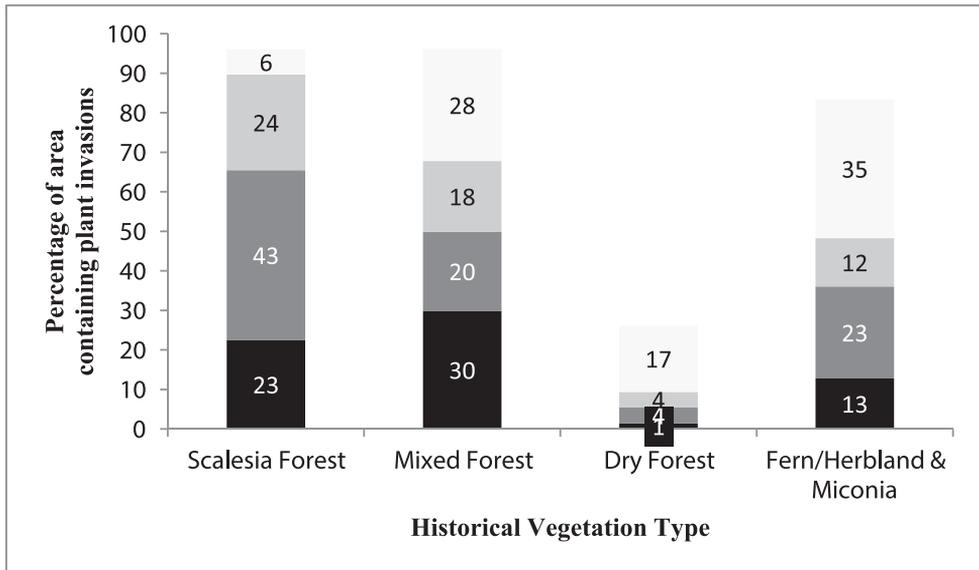


Figure 3. Percentage of the canopy of each historical vegetation type (HVT) containing invasive plants. Four levels of density are indicated by shading: Black – dominant; Dark grey – co-dominant; Mid grey – secondary; Light grey – scattered.

which has spread extensively within all of the HVTs (Suppl. material Table 2). *Cestrum auriculatum* also had a large area of canopy cover (Table 1), mainly in the HVTs Scalesia Forest and Mixed Forest (Suppl. material Table 2). These three species are the most rapid spreaders of all the invasive species we recorded and are dispersed by wind or birds. However, not all species with these dispersal mechanisms invaded so quickly (Table 1). *Persea americana* and the grass *Pennisetum purpureum* had the slowest invasion rates and were the only species purposefully introduced to the National Park and also the only invasive species with vegetative and gravity-assisted means of dispersal (Table 1).

Discussion

Our map of invasions highlights the fact that invasive canopy plants have an extensive distribution in the humid highlands of the Galapagos National Park on Santa Cruz Island. The drier periphery of our study area (the HVT Dry Forest) was less invaded, probably because most invasive plants in Galapagos are suited to wet climates and consequently thrive in the more humid areas (Guézou et al. 2010). We applied a robust, repeatable method of mapping that allows for the comparison of our data with other data that are obtained using similar methods elsewhere or at the same place in the future.

Our database details the extent and density of multiple invasive species at a landscape scale and thus provides a benchmark for monitoring future vegetation change. Our

map of invasions shows that some areas in the HVT Fern/Herbland and Miconia Shrubland are free of canopy invaders, which is likely a result of management action to control *Cinchona pubescens* (García and Gardener 2012). Further, our database allows for the identification of areas of high densities of multiple invasive species, where managers might apply control measures for several species, and also areas where careful intervention may be required to conserve the native canopy species that coexist with non-native species. Most of the vegetation classes featured in our database relate to single species, and the density of each is modelled over the landscape. As such, if managers choose to focus on a single species, the percentage cover of that species can be mapped over the landscape. Also, the data can be further classified to match other studies or meet needs for consistency in vegetation classification (De Cáceres and Wiser 2012). The database has already been reclassified to map the distribution of vegetation states of varying degrees of novelty across the study area, to identify options for management (Trueman et al. 2014).

Decisions on management interventions may depend on the rate of spread of individual invasive species. The range of spread rates exhibited by the species in our study can be only partially explained by their dispersal vectors. The two species in our study with the lowest dispersal ability; *Persea americana* and the grass *Pennisetum purpureum* – dispersed either by gravity or vegetatively (noting that birds and tortoises also disperse seeds of *P. purpureum* but seeds tend not to establish (Itow 2003)) were among three of the slowest spreaders (0.003–0.008 km² yr⁻¹). This result is consistent with research illustrating that spread is driven by dispersal ability (Courtts et al. 2011). However, the remaining species we studied, which are distributed by either wind or animals over long distances, had variable spread rates (0.008–0.35 km² yr⁻¹). This variability supports the idea that species traits alone do not determine rates of spread (Pyšek and Hulme 2005). Our results fall within the lower end of the range of areal spread rates reported elsewhere, probably because such results are often inflated due to inclusion of the entire geographic extent of species and without density estimates (Pyšek and Hulme 2005). Our study has taken density into account by using the actual area of canopy coverage, and therefore our results are deflated compared with other published rates of spread.

All of the invasions reported in our study have occurred since 1966 or more recently. In less than 50 years 41% of the native canopy vegetation in the humid highlands of Santa Cruz Island in Galapagos National Park has been replaced by invasive species. We have assumed a constant rate of spread, though in reality there is likely to be temporal variability in the spread of invasions (Pyšek and Hulme 2005). In general, plant invasions spread slowly initially (lag-phase), then rapidly (exponential phase), and finally, spread slowly or not at all (Pyšek and Hulme 2005). These phases were apparent for species in our study. For example, *Cestrum auriculatum* exhibited a lag time of 15–20 years following the first record of its occurrence (1985); it was not recognized as invasive until sometime between 2001 and 2005 (Rentería and Buddenhagen 2006; Tye 2001). Conversely, *Cinchona pubescens* was an earlier invader (first observed in the study area in 1966) that

expanded in range quickly and may have reached its peak distribution in the early 2000s (Buddenhagen et al. 2004). It is important for managers to account for potential variability in the timing of invasion among species. For example, non-native species covering small areas could rapidly expand (i.e., become invasive) after a lag phase. Thus, assuming constant spread rates could lead to management decisions to ignore potential future invasions.

Another important management consideration is that some invasive species requiring management do not feature in the vegetation canopy and are thus not detected in satellite images or data derived from them, such as ours. For example, in our study area *Tradescantia fluminensis* is a ground-cover plant that has invaded rapidly since its introduction to the study area after 2001 (Fausto Llerena, pers. comm.). By 2011 we observed it widespread in all HVTs except for Fern/Herbland and Miconia, with abundances of up to 100% cover, forming a thick mat that is thought to inhibit the growth of native plants (Gardener et al. 2013). Other species that do feature in the canopy may also require management elsewhere where they only occur in the understorey. Our database featured mono-dominant stands of *Rubus niveus* that form a canopy, but our methods could not detect where it occurs under other vegetation. During field work in 2011 we observed it as widespread at low to moderate abundance in all HVTs except for Dry Forest, though its extent and density have since grown during years that have been wetter than the long term average (Wilson Cabrera, personal observation 2013). New methods have been used to map the structure of vegetation canopies, producing promising results that will help managers identify invasive species in the understorey and sites of early invasion (Asner et al. 2008).

Future plant invasions are likely in Galapagos. New invasions are predicted to occur from within the existing non-native flora due to the short residence time of many ornamental species and increasing human-mediated propagule pressure (Trueman et al. 2010a). Invasion by current or new non-native species may also be facilitated by the projected increased precipitation in Galapagos (Trueman et al. 2010b). Such a trajectory of ongoing invasions is a huge challenge for management. We reiterate the suggestion of others to apply prevention strategies (e.g. quarantine) and early intervention strategies (e.g. eradicating or containing species that have small distributions) to lower the risk of future invasions (Gardener et al. 2013). Additionally, engagement with private landholders and relevant government agencies is necessary for managing non-native plants in inhabited areas that are the source of invasions to the surrounding National Park.

In summary, invasive plants have been spreading in the last 50 years and now make up a substantial proportion of the canopy vegetation in the humid highlands of Galapagos National Park on Santa Cruz Island. The invasion process is continuing, and early intervention is the strategy most guaranteed to prevent invasion by new arrivals. Local managers can use our spatially-explicit database to identify areas requiring management by targeting sites with multiple invasive species (i.e., site-led management) or particular invasive species (weed-led; Timmins and Owen 2001) and to assess the efficacy of efforts to control canopy invaders, thereby helping to curtail the

expansion of current canopy invaders. Our methods could be applied elsewhere to help managers deal with plant invasions across landscapes under their care.

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References

- Asner GP, Hughes RF, Vitousek PM, Knapp DE, Kennedy-Bowdoin T, Boardman J, Martin RE, Eastwood M, Green RO (2008) Invasive plants transform the three-dimensional structure of rain forests. *Proceedings of the National Academy of Sciences* 105: 4519–4523. doi: 10.1073/pnas.0710811105
- Buddenhagen CE, Rentería JL, Gardener MR, Wilkinson SR, Soria M, Yanez P, Tye A, Valle R (2004) The control of a highly invasive tree *Cinchona pubescens* in Galapagos. *Weed Technology* 18: 1194–1202. doi: 10.1614/0890-037X(2004)018[1194:TCOAH1]2.0.CO;2
- Caujapé-Castells J, Tye A, Crawford DJ, Santos-Guerra A, Sakai A, Beaver K, Lobin W, Vincent Florens FB, Moura M, Jardim R, Gomes I, Kueffer C (2010) Conservation of oceanic island floras: Present and future global challenges. *Perspectives in Plant Ecology, Evolution and Systematics* 12: 107–129. doi: 10.1016/j.ppees.2009.10.001
- Coppin P, Jonckheere I, Nackaerts K, Muys B, Lambin E (2004) Digital change detection methods in ecosystem monitoring: a review. *International Journal of Remote Sensing* 25: 1565–1596. doi: 10.1080/0143116031000101675
- Coutts SR, Van Klinken RD, Yokomizo H, Buckley YM (2011) What are the key drivers of spread in invasive plants: dispersal, demography or landscape: and how can we use this knowledge to aid management? *Biological Invasions* 13: 1649–1661. doi: 10.1007/s10530-010-9922-5
- De Cáceres M, Wiser SK (2012) Towards consistency in vegetation classification. *Journal of Vegetation Science* 23: 387–393. doi: 10.1111/j.1654-1103.2011.01354.x
- Eliasson U (1982) Changes and constancy in the vegetation of the Galapagos Islands. *Noticias de Galapagos* 36: 7–12.
- García G, Gardener MR (2012) Evaluación de proyectos de control de plantas transformadores y reforestación de sitios de alta valor en Galápagos. Dirección del Parque Nacional Galápagos y Fundación Charles Darwin, Puerto Ayora, Galapagos, Ecuador, 24 pp.

- Gardener MR, Trueman M, Buddenhagen C, Heleno R, Jäger H, Atkinson R, Tye A (2013) A pragmatic approach to the management of plant invasions in Galapagos. In: Foxcroft LC, Pyšek P, Richardson DM, Genovesi P (Eds) *Plant Invasions in Protected Areas: Patterns, Problems and Challenges*. Springer Netherlands, Dordrecht, 349–374. doi: 10.1007/978-94-007-7750-7_16
- Garzón-Machado V, Arco Aguilar M-J, Pérez-de-Paz P-L (2011) A tool set for description and mapping vegetation on protected natural areas: an example from the Canary Islands. *Biodiversity and Conservation* 20: 3605–3625. doi: 10.1007/s10531-011-0153-6
- Gilbert M, Liebhold A (2010) Comparing methods for measuring the rate of spread of invading populations. *Ecography* 33: 809–817. doi: 10.1111/j.1600-0587.2009.06018.x
- Guézou A, Trueman M, Buddenhagen CE, Chamorro S, Guerrero AM, Pozo P, Atkinson R (2010) An extensive alien plant inventory from the inhabited areas of Galapagos. *PLoS ONE* 5: e10276. doi: 10.1371/journal.pone.0010276
- Higgins SI, Richardson DM (1999) Predicting plant migration rates in a changing world: The role of long-distance dispersal. *The American Naturalist* 153: 464–475. doi: 10.1086/303193
- Itow S (2003) Zonation pattern, succession process and invasion by aliens in species-poor insular vegetation of the Galapagos Islands. *Global Environmental Research* 7: 39–58.
- Jäger H, Tye A, Kowarik I (2007) Tree invasion in naturally treeless environments: Impacts of quinine (*Cinchona pubescens*) trees on native vegetation in Galápagos. *Biological Conservation* 140: 297–307. doi: 10.1016/j.biocon.2007.08.014
- Küchler AW (1967) *Vegetation mapping*. Ronald Press Co., New York, 472 pp.
- Lindenmayer DB, Hobbs RJ (2007) Synthesis: landscape classification. In: Lindenmayer DB, Hobbs RJ (Eds) *Managing and Designing Landscapes for Conservation: Moving from Perspectives to Principles*. Blackwell, Oxford, 46–48. doi: 10.1002/9780470692400.ch5
- Mack RN (2000) Assessing the extent, status, and dynamism of plant invasions: current and emerging approaches. In: Mooney H, Hobbs RJ (Eds) *Invasive species in a changing world*. Island Press, Washington, DC, 141–168.
- Morgan JL, Gergel SE, Coops NC (2010) Aerial photography: A rapidly evolving tool for ecological management. *Bioscience* 60: 47–59. doi: 10.1525/bio.2010.60.1.9
- Müllerová J, Pyšek P, Jarošík Vc, Pergl J (2005) Aerial photographs as a tool for assessing the regional dynamics of the invasive plant species *Heracleum mantegazzianum*. *Journal of Applied Ecology* 42: 1042–1053. doi: 10.1111/j.1365-2664.2005.01092.x
- Pengra BW, Johnston CA, Loveland TR (2007) Mapping an invasive plant, *Phragmites australis*, in coastal wetlands using the EO-1 Hyperion hyperspectral sensor. *Remote Sensing of Environment* 108: 74–81. doi: 10.1016/j.rse.2006.11.002
- Pyšek P, Hulme PE (2005) Spatio-temporal dynamics of plant invasions: Linking pattern to process. *Ecoscience* 12: 302–315. doi: 10.2980/i1195-6860-12-3-302.1
- Pyšek P, Richardson DM, Rejmánek M, Webster GL, Williamson M, Kirschner J (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *TAXON* 53: 131–143. doi: 10.2307/4135498

- Reinhart KO, Gurnee J, Tirado R, Callaway RM (2006) Invasion through quantitative effects: Intense shade drives native decline and invasive success. *Ecological Applications* 16: 1821–1831. doi: 10.1890/1051-0761(2006)016[1821:itqeis]2.0.co;2
- Rentería JL, Buddenhagen CE (2006) Invasive plants in the *Scalesia pedunculata* forest at Los Gemelos, Santa Cruz, Galapagos. *Galapagos Research* 64: 31–35
- Richardson DM (2011) Invasion science. The roads travelled and the roads ahead. In: Richardson DM (Ed) *Fifty years of invasion ecology: The legacy of Charles Elton*. Wiley, Hoboken, USA, 397–407.
- Richardson DM, Pyšek P (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography* 30: 409–431. doi: 10.1191/0309133306pp490pr
- Richardson DM, Pyšek P, Rejmanek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6: 93–107. doi: 10.1046/j.1472-4642.2000.00083.x
- Roura-Pascual N, Richardson DM, Krug RM, Brown A, Chapman RA, Forsyth GG, Le Maitre DC, Robertson MP, Stafford L, Van Wilgen BW, Wannenburgh A, Wessels N (2009) Ecology and management of alien plant invasions in South African fynbos: Accommodating key complexities in objective decision making. *Biological Conservation* 142: 1595–1604. doi: 10.1016/j.biocon.2009.02.029
- Shaw DR (2005) Translation of remote sensing data into weed management decisions. *Weed Science* 53: 264–273. doi: 10.1614/ws-04-072r1
- Shigesada N, Kawasaki K, Takeda Y (1995) Modeling stratified diffusion in biological invasions. *The American Naturalist* 146: 229–251. doi: 10.1086/285796
- Skellam JG (1951) Random dispersal in theoretical populations. *Biometrika* 38: 196–218. doi: 10.1093/biomet/38.1-2.196
- Timmins SM, Owen S-J (2001) Scary species, superlative sites: assessing weed risk in New Zealand's protected natural areas. In: Groves RH, Panetta FD, Virtue JD (Eds) *Weed risk assessment*. CSIRO Publishing, Collingwood, Australia, 217–227.
- Trueman M, Atkinson R, Guézou A, Wurm P (2010a) Residence time and human-mediated propagule pressure at work in the alien flora of Galapagos. *Biological Invasions* 12: 3949–3960. doi: 10.1007/s10530-010-9822-8
- Trueman M, d'Ozouville N (2010) Characterizing the Galapagos terrestrial climate in the face of global climate change. *Galapagos Research* 67: 26–37.
- Trueman M, Hannah L, d'Ozouville N (2010b) Terrestrial ecosystems in Galapagos: Potential responses to climate change. In: Larrea I, Di Carlo G (Eds) *Climate change vulnerability assessment of the Galapagos Islands*. WWF and Conservation International, USA, 29–46.
- Trueman M, Hobbs RJ, Standish RJ (2014) Identifying management options for modified vegetation: Application of the novel ecosystems framework to a case study in the Galapagos Islands. *Biological Conservation* 172: 37–48. doi: 10.1016/j.biocon.2014.02.005
- Trueman M, Hobbs RJ, Van Niel K (2013) Interdisciplinary historical vegetation mapping for ecological restoration in Galapagos. *Landscape Ecology* 28: 519–532. doi: 10.1007/s10980-013-9854-4

- Tye A (2001) Invasive plant problems and requirements for weed risk assessment in the Galápagos islands. In: Groves RH, Panetta FD, Virtue JD (Eds) *Weed risk assessment*. CSIRO Publishing, Collingwood, Australia, 153–175.
- Tye A (2006) Can we infer island introduction and naturalization rates from inventory data? Evidence from introduced plants in Galapagos. *Biological Invasions* 8: 201–215. doi: 10.1007/s10530-004-3574-2
- Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14: 702–708. doi: 10.1111/j.1461-0248.2011.01628.x
- Xie Y, Sha Z, Yu M (2008) Remote sensing imagery in vegetation mapping: a review. *Journal of Plant Ecology* 1: 9–23. doi: 10.1093/jpe/rtm005

Supplementary material I

Index of vegetation classes and results on the distribution of invasive plants from the spatial database of canopy plant densities over the National Park on Santa Cruz Island, Galapagos

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Data type: Tabular information

Explanation note: This document contains an index to the vegetation classes featured in the spatial database. It also has an additional table of results on the distribution of invasive plants in the canopy in each historical vegetation type, and in each density category.

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