Using range filling rather than prevalence of invasive plant species for management prioritisation: the case of *Spathodea campanulata* in the Society Islands (South Pacific)

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ARTICLE INFO

ABSTRACT

Biological invasion science lacks standardised measures of invasion success that would provide effective prioritisation of invasive species and invaded areas management. Prevalence (area of occupancy) of invasive species is often used as proxy of their success but this metric ignores the extent to which a species fills its potential distribution. This study aims to estimate the performance of invasive tree species by computing the ratio between the compressed canopy area (CCA), assessed through remote sensing, and their potential distribution, estimated using invasive species distribution modelling. This index of 'range filling' (RF) has applicability to a broad set of invasive plant species in any biome. A case study is provided using the invasive African tulip tree *Spathodea campanulata* (Bignoniaceae) on three small tropical oceanic islands (South Pacific) exhibiting different invasion levels to test for differences between CCA and RF. The results show that the RF of *Spathodea campanulata* varied within islands depending on elevation but not proportionally to the CCA of the species. Another key result was that the RF of the species and its CCA provided different between-island perspectives on the invasions and lead to distinct ranking among islands to prioritise for management. Therefore, managers should disregard species' prevalence as a measure of success and rather weight it with potential distribution to quantify how an invader is performing in a given environment.

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1. Introduction

Despite intensive control efforts and management strategies, invasive alien species continue to spread at an alarming rate and pose escalating threats to biodiversity (Vilà et al., 2011). Identifying the invasive species and invaded areas towards which limited financial resources should be allocated remains a key issue for managers and conservationists to design efficient strategies (Kumschick and Richardson, 2013). Unfortunately, biological invasion science suffers from a lack of standard measures of invader performance or invasion success that would provide effective comparability between invaders or invaded areas (Hulme, 2012). Factors

driving invasion success also vary highly at local scale, so attempts to conduct non-context-dependent assessment of success (e.g., based on traits) are inherently flawed (Richardson and Pyšek, 2012). A recent review of quantitative approaches that have been used to assess tree invasions has highlighted that both observed and potential spatial extents are required to quantify invasions but none of the current metrics combine both distributions (Wilson et al., 2014).

An increasing number of vegetation atlases are being available to assess species compressed canopy area (CCA), i.e., the area of occupancy, net infestation or prevalence (Wilson et al., 2014). Maps either come from field-based vegetation surveys or from a set of more cost-effective and less time-demanding tools that spatial ecologists are developing including remote sensing and virtual globes (Visser et al., 2014). Remotely sensed images taken by multispectral, hyperspectral, radar and LiDAR sensors or a combination of them can indeed provide useful information on invasive plant species distribution if a specific radiometric signal is successfully isolated (Huang and Asner, 2009 and references therein). Vegetation maps derived from field surveys may cover any taxa but remain

limited by a coarse spatial resolution making the implementation of effective management-risk policy difficult (Hulme, 2003). On the contrary, remote sensing offer a synoptic view that would be extremely time-demanding if obtained from field observations but applicability may depend on taxon abundance and biological type. The use of remotely sensed data classification to map areas where trees are dominant in the forest canopy remains the main application of remote sensing studies targeting invasive plant species (Huang and Asner, 2009).

Remote sensing methods to assess the extent of canopy-dominant invasive trees may also be appropriate to map a wider range of biological types from mono-dominant invasive grasses such as the giant cane *Arundo donax* (Poaceae) which can be distinguished through hyperspectral AVIRIS data (Ustin et al., 2002), the cogon grass *Imperata cylindrica* (Poaceae) visible on multi-spectral SPOT images (Thenkabail, 1999) and aquatic vegetation such as the floating water hyacinth *Eichhornia crassipes* (Pontederiaceae), which is also identifiable on SPOT images (Venugopal, 1998). Remote sensing can also been used to map non-dominant species in mixed canopies and even some understory species (Joshi et al., 2004 and references therein).

Although vegetation maps can determine the CCA (distribution actually observed in nature) of plant species, this approach does not fully assess invasion status since it ignores whether a species is filling its potential distribution (the projected geographical space of its realised niche), which is critical information needed to identify which species have to be prioritised for control (Wilson et al., 2014). Reflecting this, comparison of area of occupancy versus potential distribution has been widely used to assess rare plant species conservation or protection status (Pouteau et al., 2012; Marcer et al., 2013).

Several studies conducted in Europe have attempted to estimate the future range of plant invaders using logit-transformed proportion of occupied mapping units (Williamson et al., 2009; Gassó et al., 2010). Although this approach has the merit to consider the time needed for an invader to spread, it remains limited in that it ignores that part of the region interpreted as under the threat of the invader might not be suitable.

Alternatively, on La Réunion Island (Mascarene archipelago, Indian Ocean), Baret et al. (2006) identified three alien invasive plant population growth and spread needed to be prevented: *Clidemia hirta* (Melastomataceae), *Strobilanthes hamiltonianus* (Acanthaceae) and *Ulex europaeus* (Fabaceae). Although they were less prevalent than other species, they were selected on the basis of both their CCA and their potential spread. The authors proposed to estimate the future area of colonisation using invasive species distribution models (iSDM), a technique seeking to correlate habitat variables expressed through a set of GIS layers with points where the occurrence of the invasive species is recognised (Rouget et al., 2004; Baret et al., 2006; Pouteau et al., 2011).

Later, Wilson et al. (2007) focused on 62 major plant invaders in South Africa and compared data from the Southern Africa Plant Invaders Atlas (SAPIA) with iSDM-based projections of potential habitats published in Rouget et al. (2004). Interestingly, they found that CCA was mediated by the total extent of potentially invasible habitat. This result therefore implies that cross-species and inter-locations comparisons to determine management priorities cannot neglect species' potential distribution.

This study aims to demonstrate that the CCA of invasive plant species, when used in conjunction with iSDM, has the potential to quantitatively assess how successful species are by computing a 'range filling' (RF) index (1).

$$RF = CCA/iSDM \ \ projection \ \ area \qquad (1)$$

A value close to 0 denotes a species whose observed range is much smaller than its potential range whereas a value of 1 indicates that the species had sufficient time to canopy all environmentally suitable sites.

Three small tropical oceanic islands of the Society archipelago (French Polynesia, South Pacific Ocean) has been chosen to assess how CCA and RF differ by virtue of the contrasting invasion patterns they exhibit. This study focused on the African tulip tree *Spathodea campanulata*, considered as one of the most threatening invasive alien plant species in these islands (Meyer, 2000), and asked which management strategies should be used.

2. Material and methods

2.1. Target species

Spathodea campanulata P. Beauv. (Bignoniaceae, hereafter *Spathodea*) is a fast-growing evergreen tree native to West Africa measuring up to 30 m with a dense irregular crown (Fig. 1A) (Unwin, 1920). This species has a particular reflectance or derivative-reflectance signature that has been successfully detected in Puerto Rico using *ex situ* radiospectrometer analyses (Schellekens et al., 2005), in Hawaii using data from the airborne hyperspectral sensor AVIRIS (Asner et al., 2008) and more recently in Brazil and French Polynesia using multispectral data from the WorldView-2 and Quickbird-2 satellites (Gomes and Maillard, 2013; Pouteau and Collin, 2013).

Spathodea has been reported as invasive in Australia, Brazil, Puerto Rico and many Pacific islands including Cook Islands, Fiji, French Polynesia, Guam, Hawaii, New Caledonia and Vanuatu, and it is considered one of the world's worst invasive alien species (Meyer, 2000; ISSG, 2013). It occurs in both abandoned agricultural lands and closed-canopy forest (Labrada and Díaz Medina, 2009). It has large bright red flowers that produce pods containing about 500 wind-dispersal seeds (Fig. 1A), but can also reproduce via suckers (Little and Skolmen, 1989). *Spathodea* seedlings are considered shade-tolerant and both photosynthetic rates and growth rates indicate that seedlings can maintain growth at low light levels (Larrue et al., 2014). By overtopping native forests, modifying forest structure and reducing light incidence, it is assumed to decrease native species richness (Weber, 2003).

2.2. Study site

French Polynesia is located in the South Pacific Ocean between 7–28°S and 134–155°W. It comprises about 120 islands grouped in five archipelagos, namely the Australs, the Gambier, the Marquesas, the Society and the Tuamotu Islands. *Spathodea* was introduced for ornamental purposes first on the island of Tahiti (Society Islands) in 1932, then on several high volcanic islands of the Society, Marquesas and Gambier Islands (Meyer et al., 2008 and unpub. data). *Spathodea* invades large areas of lowland mesic to moist rainforests (Fig. 1B), but can also reach high-elevation cloud forests up to 1400 m elevation on Tahiti (Meyer, 2004). It flowers all the year round with flowering peaks in the driest period of June–August and at the end of the rainy season in March–April (unpub. data).

Study sites included three high volcanic tropical islands of the Society archipelago exhibiting contrasting invasion levels: Tahiti, Moorea and Raiatea (Fig. 2). *Spathodea* is currently reported as invasive in Tahiti and Moorea and as naturalised (i.e., established and forming self-sustaining populations) in Raiatea. These islands are the three largest, most populated and economically most developed islands in the archipelago (Table 1).

2.3. Ground truth surveys

A total of 105 invaded sites were located during extensive field surveys from 2008 to 2014 on the three islands (Table 2). Here, the
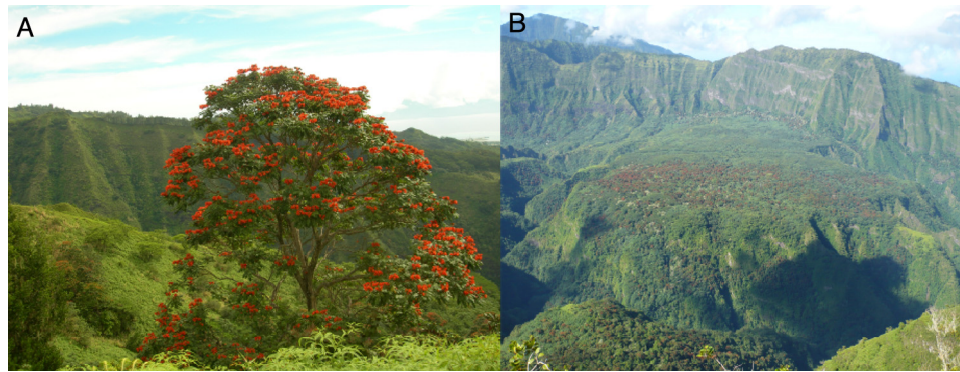
Fig. 1. (A) Flowering individual of *Spathodea* located at 600 m in Col Hamuta, Mont Aorai, Pirae (Tahiti) in April 2008 and (B) invasion of the Tetamanu Plateau, Punaruu Valley, Punaauia (Tahiti) culminating at 600 m in April 2009.
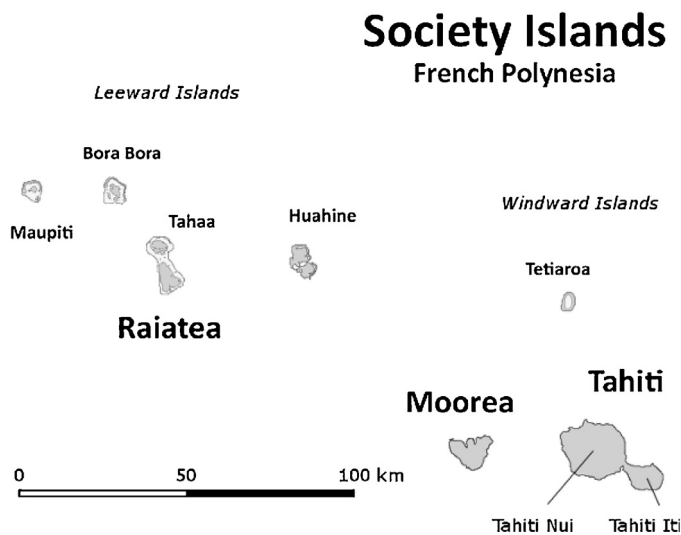

Fig. 2. Location of Tahiti, Moorea and Raiatea in the Society Islands.

term 'invaded sites' designated plots measuring at least 8 m × 8 m where *Spathodea* dominated the canopy. An invaded site can therefore describe either a large individual or a group of smaller trees. Sampling was not systematic and was therefore more representative of herbarium or museum 'opportunistic' sampling schemes. Each location was geo-referenced with a handheld GPS (either a Trimble® GeoXH™ or a Garmin GPSMAP® 62 series).

2.4. Compressed canopy area maps

On each island, the CCA of *Spathodea* was calculated using very high resolution remote sensing. The spatial scale investigated was individual canopies, which contrasts sharply with the coarse resolution of data used in previous comparable studies (Table 3). Remotely sensed images were provided by the multispectral satellite sensors Quickbird-2 (0.60 m resolution) and WorldView-2 (0.50 m), depending on the focal island (Table 2). Image pre-processing including geometric and radiometric

correction was carried out by the image provider. GPS points recorded in the field were used to test whether invaded sites had a particular spectral response on remotely sensed data and, if so, to map all pixels displaying a similar signal. Invaded sites located under clouds or in relief shadow on imagery were removed to prevent all sites under clouds or in shadow from being classified as invaded sites. Analyses were based on the three visible colour channels (red, green and blue) as well as on eight texture metrics of the grey-level co-occurrence matrix (GLCM) extracted from the panchromatic band. Mean, variance, homogeneity, contrast, dissimilarity, entropy, angular second moment and correlation were calculated in a moving window measuring 8 m × 8 m at the ground (e.g., 16 × 16 pixels on WorldView-2 panchromatic images) then up-scaled to the colour band resolution using the nearest neighbour method (Haralick et al., 1973). This GLCM window size was chosen as it was the average tree crown diameter giving the most apparent grain texture.

Images were segmented in two classes, 'invaded' and 'non-invaded', using support vector machines (SVM), a machine learning algorithm that overcomes most of the practical difficulties and data limitations that face conventional classification algorithms (Mountrakis et al., 2011). SVM work in a hyperspace where each dimension corresponds to an image band and aim to circumscribe a hypervolume by maximising the distance of presence and absence points. The shape of this hypervolume depends on a kernel function and a regularisation parameter. The kernel function was used to discriminate pixels where *Spathodea* was present from those where it was absent as both were not linearly separable (Boser et al., 1992). The Gaussian radial basis function (RBF) was chosen as kernel because it relies on tuning only one kernel-specific hyperparameter γ and it yields numerically accurate maps (Hsu et al., 2010). The regularisation parameter *C* controls the trade-off between generalisation of the hypervolume and minimisation of misclassification errors.

As non-invaded sites were not reported in the field, pseudo-absences (i.e., points not verified in the field where *Spathodea* was assumed to be absent) were randomly selected. The number of pseudo-absence pixels was taken as equal to the total number of pixels within invaded sites to prevent classifications from problems associated with unbalanced training sets (Batuwita and

Table 1
Characteristics of the three high volcanic islands of the Society archipelago where *Spathodea campanulata* is considered invasive.

Island	Surface (km²)	Max. elevation (m)	# of inhabitants[a]	Pop. density (inhab./km²)
Tahiti	1045	2241 (Mont Orohena)	178,173	170
Moorea	142	1207 (Mont Tohiea)	16,208	120
Raiatea	171	1017 (Mont Tefatoaiti)	12,008	70

[a] *Source*: ISPF (2007).

Table 2
Summary of remotely sensed data, computational procedures and accuracy assessment on the three islands.

Island	Remotely sensed data classification										Invasive species distribution modelling				
	Satellite sensor	Shooting date	Pixel size (Panchro) (m)	Pixel size (Colour) (m)	# of sampled invaded sites	Best γ 2^X	Best C 2^X	AUC	OA	Kappa	Best γ 2^X	Best C 2^X	AUC	OA	Kappa
Tahiti	WorldView-2	2013	0.50	1.80	60	−3	1	0.989	0.976	0.950	1	1	0.901	0.874	0.870
Moorea	Quickbird-2	2006	0.61	2.40	15	2	1	0.993	0.988	0.953	6	1	0.883	0.887	0.869
Raiatea	WorldView-2	2011	0.50	1.80	30	−4	3	0.977	0.866	0.791	0	1	0.854	0.880	0.879

Palade, 2014). Hyperparameters (γ and C) were selected through the "tune.svm()" function of the R package "e1071" (Meyer et al., 2014) to find the combination of γ and C in the range $[2^{-10}, 2^{-9}, \ldots, 2^{10}]$ that outputs the best accuracy after 10-fold cross-validation to prevent overfitting (Table 2). As SVM yielded continuous maps where pixel values was related to habitat suitability, these maps were converted to presence/absence maps by selecting thresholds where sensitivity was equal to specificity (Liu et al., 2005). Remotely sensed images were captured by different sensors and at different dates potentially corresponding to different stages of *Spathodea*'s phenology such that a new SVM was built on each of the three islands (Fig. 3).

2.5. Potential distribution maps

On each island, the CCA map was inputted as a set of presence points in an iSDM to predict the potential extent of *Spathodea*. Again, SVM was chosen as iSDM algorithm (Drake et al., 2006). A one-class SVM (i.e., without pseudo-absences) found in the "e1071" implementation was used and the procedure to find the optimal γ and C was the same as for CCA map generation.

Instead of describing pixels with regard to their colour or texture, the hyperspace was described here with a set of GIS oro-topographic layers derived from a 5 m-resolution digital elevation model (DEM) of Tahiti and Moorea and a 10 m-resolution DEM of Raiatea. Table 4 presents the five oro-topographic variables selected on the basis of past works on the vegetation of the Society Islands (Papy, 1951–54; Florence, 1993; Mueller-Dombois and Fosberg, 1998) and more recent attempts to model the potential distribution of other highly invasive trees and native plant species of conservation concern (Pouteau et al., 2011, 2012). One could argue that range structure rather than climatic suitability could prevail in shaping *Spathodea*'s distribution at such a fine scale (Veldtman et al., 2010). However, this is unlikely to be the case on high volcanic islands of French Polynesia where strong topographic gradients cause dramatic environmental changes over very short distances. Prior to iSDM training, the current distribution of *Spathodea* was upscaled using the nearest neighbour method to match the spatial resolution of the DEM.

Although *Spathodea* is likely to occupy similar habitats on the three islands, the distribution of habitats along topographic gradients can differ greatly from an island to another, e.g., depending on their land surface and elevation (the "Massenerhebung effect" or "telescoping effect"; Grubb, 1971). For instance, the lowest limit of mountain cloud forests is around 800–900 m on the north-west of Tahiti Nui but 300 m on the south-east of Tahiti Iti, 700–800 m on Moorea and 400–500 m on Raiatea (Meyer, 2010 and pers. obs.). The three islands may also harbour slightly distinct recipient plant assemblages, and have different human occupation and land use histories, thereby precluding the use of the same oro-topographic correlates to map *Spathodea* on the three islands. A different SVM model was therefore used for each island.

2.6. Map accuracy evaluation

CCA and potential distribution maps were assessed from a randomly selected 25% hold-out dataset using three metrics (Fielding and Bell, 1997): (i) the area under the curve (AUC) of the receiver operating characteristics (ROC) plot that expresses the combination of sensitivity (true positive rate) and specificity (true negative rate). A model that perfectly discriminates between presence and absence records has an AUC of 1 while a model predicting presence and absences no better than by chance has an AUC of 0.5 (ii) the overall accuracy that denotes the proportion of successfully classified pixels; and (iii) the Kappa coefficient that expresses whether or not correctly assigned pixels have been assigned by chance based

Table 3
Difference of spatial scale investigated between this study and previous related studies.

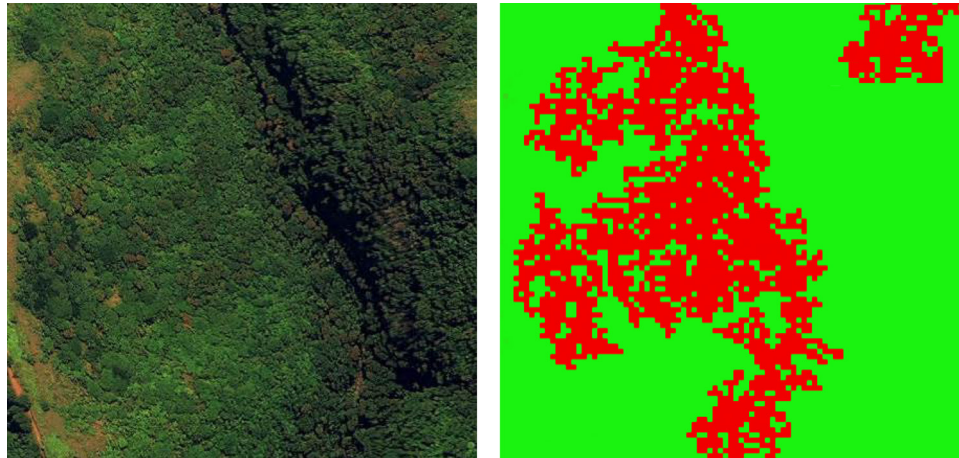| Reference	Location	Area of occupancy	iSDM projections
This study	Society Islands (French Polynesia)	0.25–0.36 m^2	25–100 m^2
Baret et al. (2006)	La Réunion Island	100 m^2	2.5 km^2
Gassó et al. (2010)	Spain	100 km^2	100 km^2
Williamson et al. (2009)	Ireland, Britain, Germany, Czech Republic	100–130 km^2	100–130 km^2
Wilson et al. (2007)	South Africa	15 min^2	1 min^2

Fig. 3. Zoom on a 400 m × 400 m window on Tahiti displaying the result of the remote sensing data classification (red: presence of *Spathodea*; green: absence) (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

on the classification decision rule. A Kappa value of 1 indicates perfect agreement while 0 indicates a pattern arising by chance.

2.7. Quantifying management priority

Management priority should be given to the area where a management plan is the most likely to be successful and where the potential severity of ecological effects is the highest (Baret et al., 2006; Wilson et al., 2007, 2014). Here, the three islands were classified in terms of management priority using two criteria: (i) the chance of eradication success (i.e., complete removal from the island) computed as the inverse of invasion success (through either the CCA or the RF, both expressed in % of the island area); and (ii) the potential extent of the species (also expressed in % of the island). In order to balance the weight of both criteria, individual island scores were transformed into a proportion (such that the sum of the scores for each criterion equalled 1). Finally, the overall priority of islands was calculated as the product of both criteria subsequently transformed into a proportion that expressed the relative weight of each island in the final decision.

3. Results and discussion

All accuracy assessment metrics indicated that CCA maps were reliable on the three islands. The current area where *Spathodea* forms monotypic stands is larger on Tahiti, where the species was first introduced, than on Moorea and Raiatea, both in absolute surface area and in terms of the proportion of the island area (Table 5). On Tahiti, the invasion is for now mainly concentrated on the northwestern side of both Tahiti Nui and Tahiti Iti and represents 1.1% of the total island area. On Tahiti Nui, *Spathodea* is present below 1100–1200 m elevation with a pronounced CCA at 600 m elevation where it seems to find optimal environmental conditions. On Tahiti Iti, where the climate is moister, *Spathodea* is found below 500 m (Figs. 4 and 5). This pattern is clearly distinct from what occurs on Moorea where the species is much more scattered across the island but in the form of sparsely distributed patches of relatively small size located below 900 m elevation and representing 0.42% of the whole island. On Raiatea, only isolated individuals or small groups of adult trees were found at low elevation (<200 m) on the leeward coast and they cover less than 0.01% of the whole island. The absence of large monotypic stands on Raiatea can explain the slightly lower accuracy of CCA maps on this island.

According to iSDM projections, whose accuracy was also estimated as largely fair, *Spathodea* might possibly spread to half of the low- to mid-elevation areas (200–900 m) of Tahiti Nui and Tahiti Iti especially those found on the leeward coast, which represents a total of more than 30,000 ha and a third of the island's total surface area. However, the species has the potential to invade an even higher proportion of Moorea and cover over half of the island, which corresponds to *c.* 7500 ha (Table 5). On Raiatea, the potential distribution of *Spathodea* might reach about 1000 ha, namely 6% of

Table 4
Summary of the five oro-topographic variables used in this study. The last column 'Proxy' presents a non-exhaustive list of proximal biophysical variables to which our oro-topographic variables can be used as proxy.

Oro-topographic variable	Unit	Proxy
Elevation	Meter (m)	Temperature, Vegetation zonation
Slope steepness	Degree (°)	Flow velocity, Water drainage, Effect on plant rooting, Effect on seed dispersion
Slope aspect	Degree (°)	Solar insolation, Evaporation
Windwardness	Dimensionless	Trade wind exposure, Precipitation
Topographic wetness index (Moore et al., 1993)	Dimensionless	Runoff rate, Soil water content, Geomorphology

Table 5
Summary of surface results.

Island	Compressed canopy area (CCA) derived from remote sensing (% of the island area)	Potential range area derived from iSDM (% of the island area)	Range filling score (CCA/potential range) (%)
Tahiti	1141 ha (1.10%)	35,270 ha (33.75%)	3.24
Moorea	63 ha (0.42%)	7659 ha (53.94%)	0.82
Raiatea	<1 ha (<0.01%)	979 ha (5.73%)	0.10
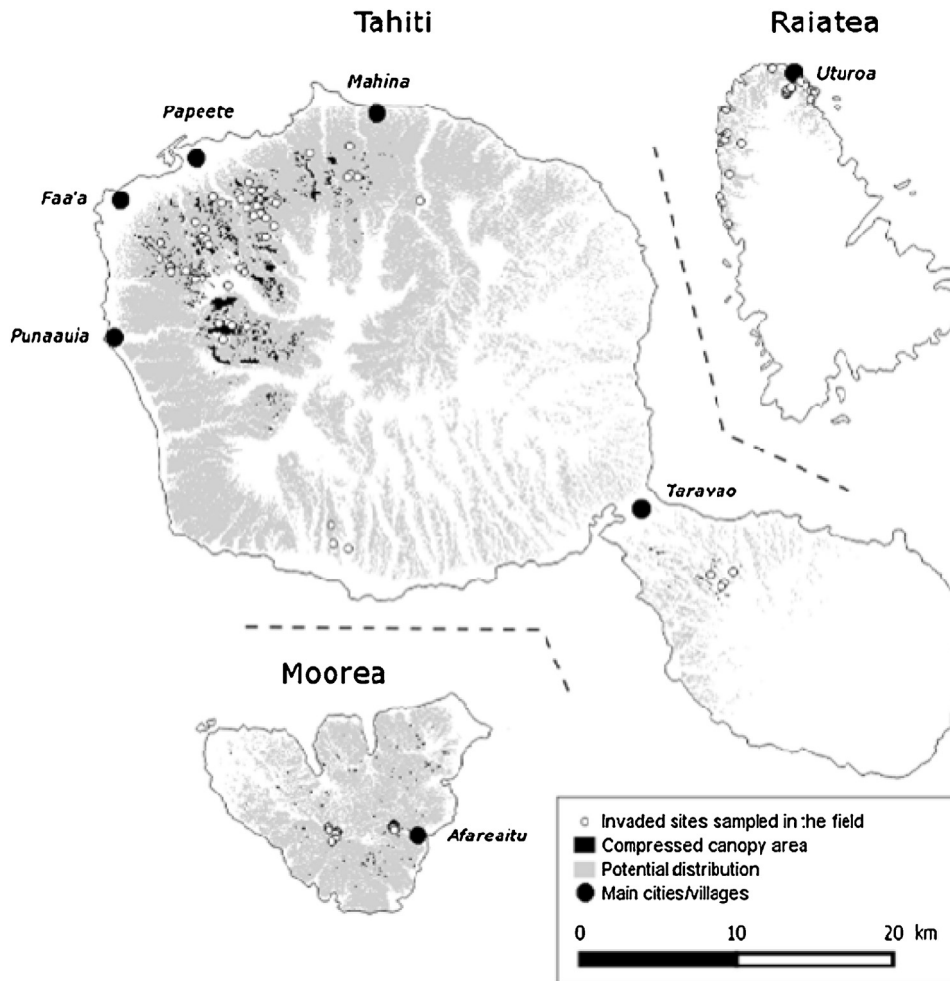
Fig. 4. Compressed canopy area and potential distribution of *Spathodea campanulata* in the three focal islands.
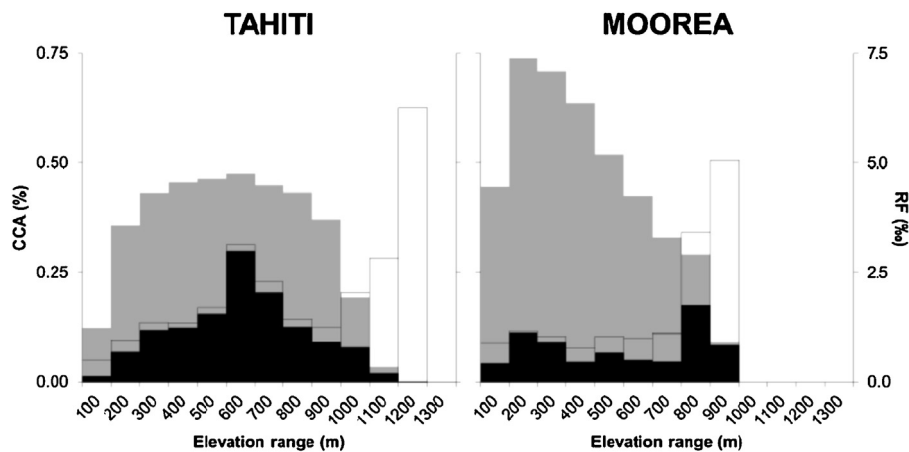

Fig. 5. Compressed canopy area (black bars referring to the left axis; in ‰ of the island surface located in the corresponding elevation range) *versus* potential distribution (grey bars referring to the left axis; in %) and range filling (colourless bars with black outlines referring to the right axis) according to elevation on Tahiti and Moorea.
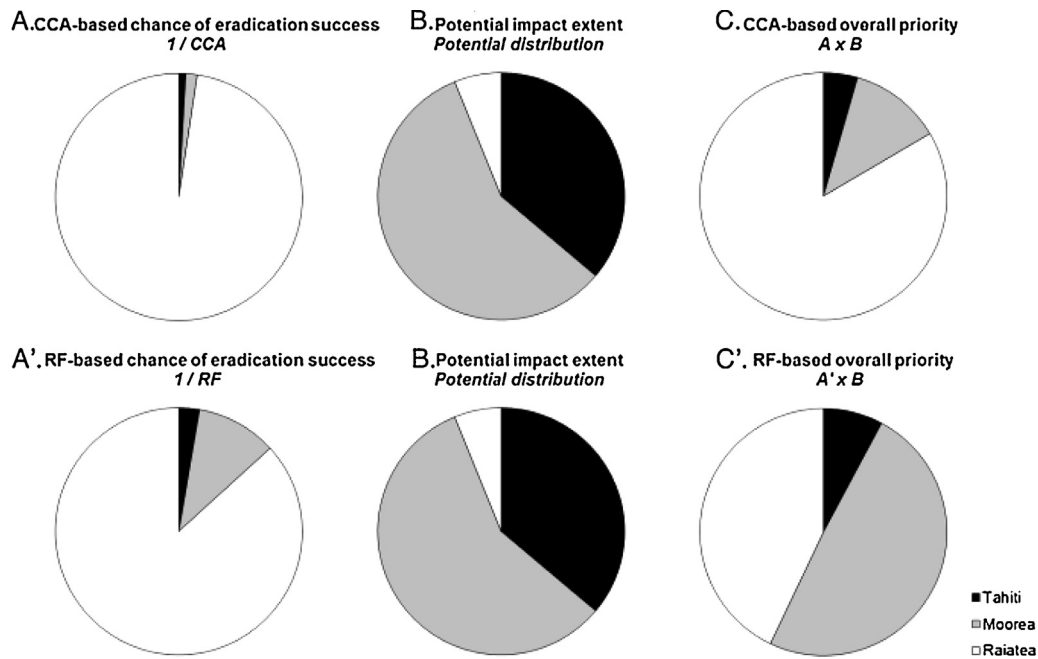
Fig. 6. Conceptual diagram representing priorities of *Spathodea campanulata* control from the compressed canopy area (CCA, first line) *versus* the range filling score of the species (RF, second line). Sectors of each pie chart represent the priority allocated to each island. (A and A') Chance of eradication success based on the CCA (A) and the RF (A'); (B) potential impact extent; and (C and C') overall priority based on the CCA (C) and the RF (C').

the island's surface, mainly on north-western downslopes located below 100 m elevation.

Comparison of the area where *Spathodea* dominates the canopy with the extent of its suitable habitat shows that the species has invaded a higher proportion of its potential range on Tahiti (RF = 3.3%) than on Moorea (0.8%) or Raiatea (0.1%) (Table 5). The higher RF found on Tahiti indicates that CCA and RF may contain a signal of introduction history since the most invaded island is also the one where the species has had the most time to spread. *Spathodea* currently occupies portions of its potential area of colonisation that are mainly located on slopes found above the main cities or villages (Fig. 4). This pattern may arise either from shorter distances to the source of introduction or from higher disturbance regimes around inhabited areas. Considering that *Spathodea* can produce up to 300,000 seeds/kg of pod and that the winged seeds are able to be dispersed over long distances by wind (Francis and Rodriguez, 1993), the CCA of *Spathodea* seems to be a product of the human foot print on habitats rather than resulting from dispersal limitation

RF also varies highly within islands along elevational gradients but not proportionally to CCA. Interestingly, RF reaches its maximum value at the highest elevations where *Spathodea* occurs while CCA is rather low at such elevations (Fig. 5). On Tahiti, RF increases from 0.5% at sea level to 3% at 600 m elevation, decreases to 1.0% at 900 m then re-increases up to 6.5% at 1200 m. On Moorea, RF remains below 1.0% from sea level to 800 m, then reaches 5.0% in the range 800–900 m.

Both CCA and RF identify Raiatea as the island with the best chance of eradication success (Fig. 6). However, the calculation based on RF provides the island of Moorea, and to a lesser extent Tahiti, with a far better score than when calculated from the CCA. This probably arises from the fact that the potential distribution of *Spathodea* is much smaller on Raiatea than the total island area (5%) so that CCA represents a poor surrogate for the species' success. In contrast, on Moorea and Tahiti, the potential extent of the species is so large (54% and 34%, respectively) that CCA is a reasonable proxy of *Spathodea*'s success. As a result, the overall management priority based on CCA indicates that the highest priority for control should be given to Raiatea while RF designates Moorea as the first island to

prioritise for management. Although CCA and RF produced a similar ranking of island's invasional status, this study demonstrates that the CCA of an invasive plant species and its RF yield different magnitudes of the state of an invasion. Thus, considering CCA rather than RF to prioritise control of an invasive species can lead to different decisions.

A key difference explaining the contrasting values of CCA and RF on the three islands is that the latter depends on both residence time and disturbance regime while the former is also a function of the proportion of potential habitat covering the island. However, this additional information borne by CCA is independent of the notion of success.

On Tahiti and Moorea, *Spathodea* is already dominating forest canopy in 1141 ha and 63 ha, respectively. In these already extensively invaded areas ("novel habitats") it is likely that ecological thresholds ('tipping points' at which a habitat shifts to an alternative stable state) have been crossed so that it would be difficult for native vegetation to completely recover without active management (Meyer et al., 2015). The rough topography of high volcanic islands may constitute a barrier to eliminate populations found on steep slopes or some summits, which makes on-site operations (including manual, mechanical and chemical control or a combination of these methods) hardly feasible in such areas.

Since it seems unrealistic to stop the invasion process on Tahiti and Moorea, biological control should be envisaged to limit the abundance of *Spathodea* to a level which does not compromise habitat integrity and sustainable co-existence with native biota. The introduction of the fungal pathogen *Colletotrichum gloeosporioides* f. sp. *miconiae* (*C.g.m.*) to control the short-statured alien invasive tree *Miconia calvescens* (Melastomataceae) may serve as an example of a success story for biological control in French Polynesia. This host-specific fungal pathogen attacks the large leaves with purple undersides of *Miconia*, increases light incidence in the understory and subsequently enhances growth, fertility and seedling recruitment of native plants (Meyer and Fourdrigniez, 2011; Meyer et al., 2012).

The action of biological control agents can nonetheless be habitat-dependent, as for example the *C.g.m.* defoliation of *Miconia*

leaves significantly increases with elevation and remains less effective in low-elevation areas (Meyer and Fourdrigniez, 2011; Meyer et al., 2012). Thus, on-site manual and chemical control can be needed to complement the effect of biological control in selected accessible habitats where the invader is less affected by introduced natural enemies. On Raiatea, invaded sites are represented for now by only a few emerging trees located at lower elevations, and the results of this study predict that the species may invade up to 5% of the island in the near future. These findings suggest that *Spathodea* invasion is at an early stage and on-site eradication should be attempted on this island.

4. Conclusion

The location of sites still invader-free but prone to be invaded is critical for prioritising control. RF has the advantage to integrate both the prevalence and the potential extent into a single metric and remains more consistent with the concept of species performance. Managers in charge of status reports might be misled by regarding species' prevalence as a measure of success. They should rather use RF to quantify how an invader performs in their geographical area.

This study examined in which area a single invasive plant species should be prioritised for control. The same approach applies to other different invasive plant species within a single area. However, irrespective of species success, decision-makers will always need to consider the different impacts that individual invasive plant species impose on native biota.

Acknowledgements

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