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Current distribution and potential extent of the most invasive alien plant species on La Réunion (Indian Ocean, Mascarene islands)

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Abstract La Réunion Island has the largest area of intact vegetation of the islands in the Mascarene archipelago. Biological invasions are the primary threat to biodiversity in the intact habitats of the island (those not already transformed by agriculture and urbanization). Our study aimed to identify areas to prioritize in managing invasive alien plants for biodiversity conservation. We used extensive surveys of 238 distinct untransformed areas on La Réunion to define the current distribution patterns of all invasive species. Using expert knowledge, we compiled maps of the current distribution of the 46 most widespread/important invasive plants at the habitat scale (identified according to vegetation structure). Data from 440 botanical relevés for the 20 most threatening invasive alien plant species across the island and climatic envelope models were used to derive climatic suitability surfaces; these were used to map potential distributions for these species. More than 10 species invade 16.7% of the remaining habitat. Five habitat types are invaded by 25 or more species, and eight have fewer than 10 invasive alien plant species. Cluster analysis based on presence/absence of species in the 18 habitat types produced eight groups of species that invade particular habitats. Potential distribution models show that some species have invaded large parts of their potential range (e.g. *Fuchsia magellanica*, *Furcraea foetida*, *Hiptage benghalensis*), whereas others have the potential to increase their range substantially (e.g. *Clidemia hirta*, *Strobilanthes hamiltonianus*, *Ulex europaeus*). Management implications are identified for both groups. Three broad groups of habitats were identified: (i) intact habitats with a low level of invasion (e.g. subalpine shrubland); (ii) moderately invaded habitats with varying levels of intactness (ranging from windward submountain rainforest to the *Acacia heterophylla* forest); and (iii) habitats with little remaining intact area and high levels of invasion (e.g. lowland rainforest). Different management interventions are appropriate for these three groups.

Key words: bioclimatic modelling, biodiversity hotspot, biological invasion, conservation planning, predictive model, spatial distribution.

INTRODUCTION

Invasive alien organisms are one of the most pressing threats to the conservation of native species, communities and ecosystems (Lodge 1993a,b; Simberloff 1996; Wilcove *et al*. 1998; Sala *et al*. 2000), and require urgent attention in many parts of the world. However, because of increasing threats to biodiversity and limited financial resources, conservation authorities and governments require accurate guidelines for prioritizing conservation actions. This can be addressed using conservation planning strategies that include the assessment of potential threats posed by invasive alien plants (see e.g. Foxcroft & Richardson 2003; Rouget *et al*. 2004).

The Malagasy region, including the Mascarene Islands (La Réunion, Mauritius and Rodrigues), is recognized as a biodiversity hotspot (Myers *et al*. 2000). Despite its small size, La Réunion (2512 km^2) conserves by far the largest area of relatively intact habitats in this archipelago. Around 30% of the original vegetation of La Réunion is intact (Strasberg *et al*. 2005), compared with less than 5% for Mauritius and none for Rodrigues (Lorence & Sussman 1986, 1988). However, La Réunion faces many threats, including

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severe and rapidly escalating impacts due to invasive alien species, especially plants (Macdonald *et al.* 1991; Lavergne *et al.* 1999; Baret *et al.* 2004). Since human settlement in the 17th century, more than 2000 plant species have been introduced to the island. Of these, some 628 species are naturalized, and 62 are highly invasive (Macdonald *et al.* 1991; alien status defined according to Richardson *et al.* 2000 and Pyšek *et al.* 2004).

Invasive alien plants are a major threat to the indigenous flora of La Réunion (675 species, 70% of them endemic to the Mascarene Islands) (Macdonald *et al.* 1991; Lavergne *et al.* 1999). To address threats to biodiversity, planning is underway for the creation of a national park which is scheduled for proclamation in 2006. Conservation authorities have called for advice on the boundaries of this park and for criteria on which to base spatial priorities for conservation, including requirements for the effective management of alien plant invasions. No spatial analyses have been performed for invasive alien plants across the island, and the current priority setting is simply based on checklists that are available for some areas.

As a first step, an objective assessment of habitat diversity and transformation on La Réunion Island was undertaken (Strasberg *et al.* 2005). This study derived a system of 19 different habitat types (identified according to vegetation structure variation – height, horizontal structure and density), representing suitable biodiversity surrogates for identifying broad-scale conservation priorities. Our study builds on that work and research on the spatial ecology of invasive alien plants in other parts of the world (e.g. Richardson *et al.* 1996; Higgins *et al.* 2000; Rouget *et al.* 2003, 2004) to improve our understanding of the threats posed by invasive alien plants in the 18 natural habitat types present on La Réunion (wetland habitats were excluded due to their high level of habitat transformation). Specific aims of our study were: (i) to determine the spatial distribution of the main invasive alien plants; (ii) to predict the potential extent of invasive alien plants; and (iii) to assist decision-makers and nature reserve managers in controlling the spread of invasive alien plants on La Réunion.

METHODS

Data sources

Distribution pattern of invasive alien species

Broad-scale species distribution – presence and abundance for all introduced plant species. An extensive survey was conducted between 1985 and 2000 in all untransformed areas of La Réunion to identify zones of ecological interest (Dupont 1985–2001). These zones are called 'Type-1 ZNIEFF' (*Zones Naturelles d'Intérêt Ecologique Floristiques et Faunistiques*). The surveys were undertaken as part of a national (French) initiative initiated in the 1980s under the control of the Environmental Ministry. The boundaries of the 238 Type-1 ZNIEFF were based on expert knowledge and were mapped on 1:25 000 topographical sheets (Dupont 2000). They follow topographical features and defined zones of land management. Habitat type descriptions and a species inventory were made for each of these units. A detailed description of the approximate extent of habitat degradation (mostly by invasive plant species), and possible future threats (such as spread of recently introduced alien plant species) were also included. According to the field knowledge of Dupont (1985–2001), these ZNIEFF descriptions distinguished five levels of alien plant invasion:

- Areas not invaded: canopy and understorey not invaded
- Areas where alien plants are present: lightly invaded understorey (alien species <10%) and presence of some alien plant individuals in an intact canopy
- Areas having a low-level invasion: understorey invaded (10–50%) but canopy largely intact (native species cover >90%)
- Invaded areas: understorey heavily invaded (50–90%) but canopy largely intact (native species cover >90%)
- Heavily invaded areas: understorey heavily invaded (10–90%) and canopy lightly invaded (alien species cover >10%)

These levels were coded from 0 (not invaded) to 4 (heavily invaded).

In this study, we focused on the current and potential future extent of alien plant invasions in untransformed native habitats. Data for the ZNIEFF facilitated the mapping of the presence of the 46 most invasive alien plants on La Réunion which are able to invade untransformed habitats. The list of invasive alien plant species includes: (i) 31 species of the 33 listed by Macdonald *et al.* (1991) as being the most widespread invaders (only *Stachytarpheta indica* and *Tibouchina viminea* were excluded from this list, since both species invade mainly along roads or forestry trails and do not penetrate natural or semi-natural vegetation); and (ii) 15 other species recognized by ourselves and other field botanists as highly invasive within untransformed habitats (Appendix I). Such data allowed us broadly to quantify the extent to which each ZNIEFF has been invaded.

Habitat-level species distribution and presence for the 46 most important invaders. We used the map of habitats for La Réunion (Strasberg *et al.* 2005). This map defines four broad natural communities that are separated on the basis of moisture availability and elevation. Each of these is subdivided into habitat types on the basis of vegetation structure (Table 1). These habitats were used as biodiversity surrogates for identifying conservation priorities (Strasberg *et al.* 2005). Using only untransformed Type-1 ZNIEFF, 18 habitat types were studied (Table 1). Wetlands and coastal habitats are not adequately dealt with in our study since most are transformed. The situation regarding invasions in these habitats requires further attention.

Data on presence and average extent of invasion for all alien plant species were only available for each ZNIEFF and not for each habitat type. We therefore intersected the ZNIEFF with the 18 habitat types in geographical information system using Arc View software (ESRI, Redlands, CA, USA) to determine which vegetation types occur in each ZNIEFF. Based on information contained in the written description for each ZNIEFF and the expert knowledge of field botanists, the occurrence of each species listed in the ZNIEFF was assigned to a specific habitat type. This was used to generate a map of the current distribution of the 46 most important invasive plant species on La Réunion at the habitat level.

Fine-scale distribution for 20 invasive alien plant species. A list of 20 most widespread and threatening invasive species was compiled in consultation with the forestry service and other local experts. Unpublished field data from 440 relevés along 44 transects on 130 km of trails and 220 km of roads collected in 1998 throughout the island by Roger Lavergne were collated to map the distribution (presence records only) of the 20 species at a finer scale. The relevés listed all alien plant species present in 100-m^2 quadrats.

Environmental data and climatic surface

Environmental data, comprising topography (slope and elevation) and geology, were available from the Atlas of La Réunion (DIREN 2001). Climatic surfaces were available at a scale too coarse for the analysis. Therefore, we used a detailed map of elevation as a surrogate for temperature. We also compiled a precipitation surface by modelling mean annual precipitation based on data from 57 weather stations. We used a local regression model to predict mean annual precipitation at a 500-m resolution. The best model (hereafter called 'precipitation') was obtained using a Gaussian model with a 0.75-span in S-Plus. The final model included elevation, latitude and longitude as independent variables. The eastern and western parts of the island were modelled separately since rainfall patterns are markedly different in these two zones.

Table 1. The 18 habitats (among those described by Strasberg *et al.* 2005) used in this study are classified according to broad-scale categories

Habitats	Abbreviation	% Area	% Remaining
Lowlands		51.2	12.7
Coastal habitats	CH	0.6	20.0
Lava flows	LF	3.9	83.3
Lowland open woodland	LOW	7.7	0.0
Lowland rainforest	LR	20.2	15.2
Semi-dry forest	SDF	18.8	0.5
Submountain		18.1	42.0
Windward submountain rainforest	WSR	6.8	68.3
Pandanus humid thicket	PHT	1.1	71.5
Leeward submountain rainforest	LSR	7.1	10.0
Submountain mesic forest	SMF	3.0	47.2
Mountain		24.2	66.6
Windward mountain rainforest	WMR	11.5	86.0
Pandanus mountain humid thicket	PMHT	1.6	100.0
Leeward mountain rainforest	LMR	6.2	54.2
Philippia mountain thicket	PMT	0.9	41.6
Acacia heterophylla forest	AH	4.0	22.1
Subalpine		6.5	57.7
Subalpine *sophora* thicket	SST	0.5	0.6
Subalpine grassland	SG	1.1	52.2
Subalpine shrubland	SH	4.6	62.1
Subalpine shrubland on lapilli	SSL	0.3	100.0

Percentage area indicates the original extent over the whole island. Percentage of original area remaining indicates the non-transformed area.

Analysis

Clustering species based on co-occurrence

Since our goal was to provide information useful for shaping future management of invasive alien plants, we decided to regroup the most threatening invasive alien plants according to the habitats that they colonize. We used cluster analysis (K-means; MathSoft, Inc. 2000) to group species according to their presence/absence in the 18 habitat types. The most meaningful clustering of species according to expert knowledge was obtained for six, seven and eight groups.

Modelling species distribution

Environmental modelling. Modelling the distribution of species is always complex. For instance, the role of climate in controlling distribution is not the same for all species, and other factors such as disturbance regimes and biotic interactions may override climatic factors. These factors are especially challenging for invading alien species (Richardson & Bond 1991; Hulme 2003; Rouget *et al.* 2004). Cadet (1977) remarked that indigenous plants on La Réunion are distributed according to annual average precipitation and temperature (varying with elevation) and also light availability (species growing in the understorey or among the canopy). This led Cadet to classify all the indigenous plants in La Réunion using these environmental parameters. An important assumption of our study is that invasive plant species are also mainly distributed according to precipitation (with important variation between east and west coasts) and temperature (correlated with elevation).

We used these two climatic factors to model the potential range of invasive alien plants. To refine our determination of the potential range of invasive alien plants, we also included slope, a factor with an important role in plant distribution (e.g. Pabst & Spies 1998). Preliminary analyses showed that geology was not a significant predictor and this variable was not considered in subsequent analyses.

Species envelopes. Predictive models based on presence/absence data could not be used as information on the absence of a species was not systematically recorded. Although the field relevés listed all alien plant species present in 100-m^2 plots, the absence of a given plant species in a relevé is not really representative of the absence of the plant in a larger area (>100-m^2). Therefore, we used a variant of climatic envelope models (CEMs) based on the Mahalanobis distance to derive environmental suitability surfaces for each species (see Farber & Kadmon 2003; Rouget *et al.* 2004). This approach generates predictive maps of species distribution using data on the environmental (in our case because we included the slope variable) characteristics of the sites where the species were recorded. Farber and Kadmon (2003) showed that CEMs applying the Mahalanobis distance, perform better (i.e. produce more accurate predictive maps) than models using rectilinear envelopes. Two principal advantages over rectilinear modelling led us to adopt this approach: the ability to take account of the central tendency in species responses to environmental gradients; and the ability to take account of the environmental characteristics of all observations in determining the boundaries of the environmental envelope.

Using this variant CEM, 20 of the most threatening invasive alien plant species in La Réunion Island were analysed. For each species, the following procedure was followed. We extracted the relevé records where the species occurs, and determined the climate characteristics of each relevé based on the three factors (slope, 'precipitation' and altitude). We calculated the mean vector (m) of the three factors, which represents the 'optimum' climatic condition. We also calculated the covariance matrix (C) from a matrix whose rows represent the relevés where the species was recorded and whose columns represent the corresponding values of the three factors. Next, we assigned a Mahalanobis distance using m and $\mathbf{C}$, defined as:

$$d^2 = (x - m)^T \mathrm{C}^{-1} (x - m)$$

where x represents the set of climatic conditions in each 500 × 500 m cell, and d is the Mahalanobis distance from which we derived a climatic suitability index.

Mapping potential range. The Mahalanobis distance (d) ranges from 0 to infinity, where 0 represents the optimum condition (in our case, the optimum climatic condition). Relevés with a Mahalanobis distance of less than 3 were considered climatically suitable. This arbitrary cut-off was supported by expert assessment, which found that envelopes including d-values greater than 3 were unrealistic for species whose climatic envelopes were well understood. We rescaled the d-values to obtain a climatic suitability index ranging from 0 to 100, where 0 represents any value of d greater than 6, 50 represents $d = 3$ and 100, $d = 0$. We assumed that alien plant species would have the potential of spreading in areas identified as the most climatically suitable (i.e. greater than 50).

Model accuracy. Unfortunately, no other independent dataset was available for testing model predictions of the invasive species. For each species, we used the absence data from the relevés and presence records to

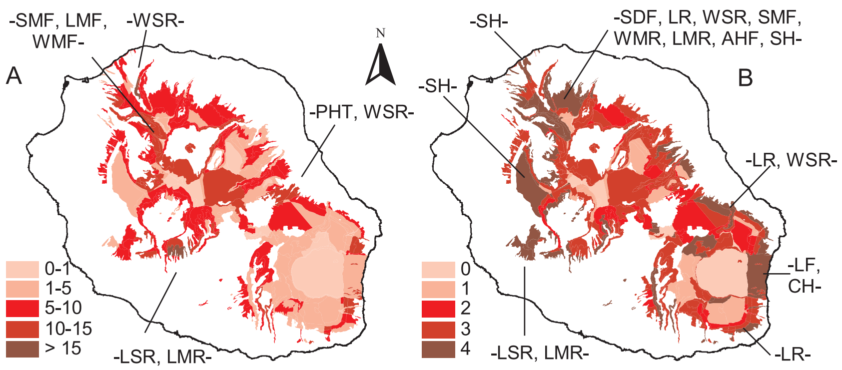

Fig. 1. (a) Alien plant species richness per ZNIEFF for each habitat type (based on the 46 most invasive plants on La Réunion); and (b) average invasion extent for each ZNIEFF land management unit. Invasion extent was scored as following: 0: canopy and understorey not invaded, 1: presence of some alien plant individuals in an intact canopy and lightly invaded understorey (alien species <10%), 2: canopy intact (native species cover >90%) but understorey invaded (10–50%), 3: canopy intact (native species cover >90%) but understorey invaded (50–90%), 4: canopy lightly invaded (alien species cover >10%) and understorey invaded (10–90%). Lines indicate the most invaded ZNIEFF or where the number of alien plants is very important (>12 species present within each area). The habitat types (see Table 1 for the abbreviations used) present in the most invaded ZNIEFF are specified.

calculate presence accuracy (% of records, where the species occurs, correctly classified by the CEM), absence accuracy (% of records, where the species is supposed absent, correctly classified by the CEM), and the Kappa statistic. The Kappa statistic evaluates the predictive model accuracy relative to the accuracy that might have resulted by chance (Cohen 1960; Fielding & Bell 1997). It ranges from −1 (complete disagreement) to 1 (perfect agreement) with 0 indicating random agreement. Model accuracy (i.e. high Kappa value) should be greater for species at equilibrium with the environment. We assumed that species introduced long time ago would have reached pseudo-equilibrium.

RESULTS

Spatial distribution of invasive alien plant species

Two hundred and sixty-four alien plant species were recorded in untransformed habitats of La Réunion Island. Figure 1 shows the distribution and abundance of the 46 most invasive alien plant species present in land management units in natural habitats (ZNIEFF). More than 13% of the natural habitat defined by ZNIEFFs has 0 or 1 invasive species; 16.7% has more than 10 species (Fig. 1a). More than 21% of the natural habitat is lightly invaded (density classes 0–1); 60% is heavily invaded (density classes 3–4) (Fig. 1b). Some of the most heavily invaded land management units have few alien plant species. Inversely, some lightly invaded land management units have many alien plant species. Based on 18 habitat types, the average extent of invasion decreased significantly from the lowlands to the highlands (Fig. 2).

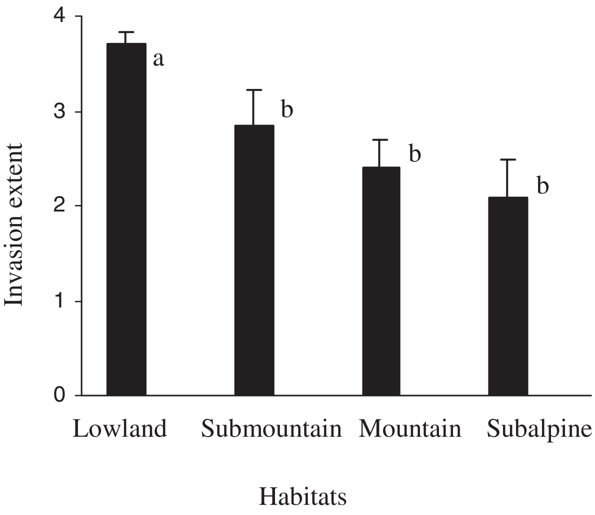

Fig. 2. Average extent of invasion (±SE) in the broad-scale habitat categories on La Réunion (see Table 1 for information on habitats). See Figure 1 for details of the extent of invasion. Different letters above column indicate that extent of invasion values are significantly different ($P < 0.05$, Mann–Whitney test, Statistix 1998).

Species clusters

Based on species distribution (presence/absence) in the 18 habitat types, a cluster analysis separated the 46 most invasive alien plant species into eight groups (Fig. 3): species which are widely present in mountain and subalpine habitats (Group 1 – G1) or lowlands and submountains (G2), localized species present in mountains only (G3), generally present on the eastern lowland (G4), present on submountains and mountains (G5), from lowlands to mountains (G6), present

Fig. 3. Homogenous groups of the invasive alien plants on La Réunion defined in a cluster analysis based on species presence in relation to the 18 habitats (Table 1). Circles with solid lines show groups defined when six groups are separated. The groups of species encircled by broken lines are additional groups that are separated when eight groups are defined in the cluster analysis.

from lowland rainforest to leeward mountain rainforest (G7) and the widespread species occurring in all habitats from lowlands to mountains (G8). Groups 7 and 8 are not strongly separated (Fig. 4).

Figure 4 shows the distribution of the top 20 species in the 18 habitat types and the number of species (of the 46 most important invaders) in each habitat type. Five habitat types are invaded by 25 or more species: leeward mountain rainforest (33), windward mountain rainforest (30), windward submountain rainforest (29), leeward submountain rainforest (25) and submountain mesic forest (25). Eight habitat types have fewer than 10 invasive alien plant species (Fig. 4).

Potential distribution of invasive alien plant species

The observed and modelled distributions of six species (representative of each major cluster) over the whole island are shown in Figure 5. The predictive model indicates that *Clidemia hirta* (Melastomataceae) is mainly suited to lowland habitats such as coastal habitat, lowland rainforest or lava flows (see Table 2). Although *Furcraea foetida* (Agavaceae) and *Hiptage benghalensis* (Malpighiaceae) belong to different groups (G6 and G2; Fig. 3), the two species seem to invade similar habitats such as lowland open woodland, semi-dry forest and leeward submountain rainforest (Table 2). *Fuchsia magellanica* (Onagraceae) preferentially invades mountain habitats, notably *Philippia* mountain thicket, leeward mountain rainforest, *Acacia heterophylla* and windward mountain rainforest habitats (Table 2). *Strobilanthes hamiltonianus* (Acanthaceae) colonizes submountain and mountain habitats such as *Pandanus* humid thicket, leeward and windward submountain rainforest, windward mountain rainforest (Table 2; Meyer & Lavergne 2004). *Ulex europaeus* (Fabaceae) mainly invades mountain and subalpine habitats such as *Pandanus* mountain thicket, *A. heterophylla*, Leeward and windward

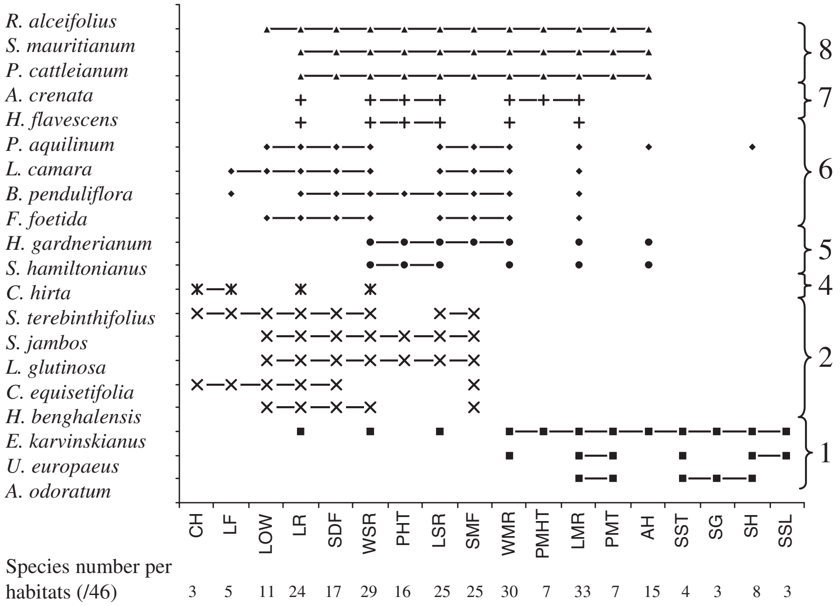

Fig. 4. Presence of the 20 most widespread and threatening invasive plant species within the 18 different habitat types. The number of alien plant species among the 46 most invasive on La Réunion is indicated below the figure. Abbreviated habitat names are explained in Table 1. Mean altitude for habitat types increases from left (lowlands) to right (subalpine). Group membership from Figure 3 (cluster analysis) is shown by symbol and the number specified on the right of the figure.

Table 2. Percentage of the natural area in each habitat group potentially suitable for six invasive alien plant species (one each from clusters 1–6 in Fig. 3)

	Clidemia hirta	*Furcraea foetida*	*Fuchsia magellanica*	*Hiptage benghalensis*	*Strobilanthes hamiltonianus*	*Ulex europaeus*	Remaining habitat (ha)
Lowlands	34.6	12.9	0.0	14.9	4.2	0.2	21 275
Submountain	2.2	17.0	3.3	6.2	35.2	4.6	21 650
Mountain	0.0	1.4	31.7	0.1	25.2	40.4	41 850
Subalpine	0.0	0.0	2.0	0.0	0.0	37.8	13 575
Potential area (ha)	7840	7010	14 250	4570	19 090	23 070	
% Accuracy	0.87	0.76	0.73	0.85	0.52	0.70	
Kappa statistics	0.43	0.27	0.33	0.39	0.08	0.14	

Percentage accuracy (>0.6 indicates a good model) and Kappa statistics test (degree of concordance: 0.21–0.40, 'Fair'; 0.41–0.60, 'Moderate'; 0.61–0.80, 'Substantial'; 0.81–1.00 'Almost perfect'; Landis & Koch 1977).

mountain rainforest, and all subalpine habitats. Species like *U. europaeus*, *S. hamiltonianus* and *F. magellanica* have a large potential range and could invade 27.2%, 22.5% and 16.8% of the currently remaining natural habitat, respectively. Less than 10% of natural habitat could be invaded by *C. hirta* (9.2%), *F. foetida* (8.3%) and *H. benghalensis* (5.4%).

Kappa values confirmed that our models are acceptable for all plant species studied except for *S. hamiltonianus* (Table 2).

DISCUSSION

Our study focused on the major plant invaders identified by Macdonald *et al.* (1991) and expert botanists, because these are the invasive species most likely to be the most problematic, demanding most management intervention, over the next few decades. Clearly, species other than these will also become important invaders in the future, and will require attention.

Spatial distribution of invasive alien plant

Our results provide information on the current distribution of invasive alien plants at two spatial scales. From information derived from Type-1 ZNIEFF (land management units) we produced broad-scale maps for all alien plant species (264 species) and their average extent of invasion in the remaining untransformed habitats on La Réunion (Fig. 1). At this scale, we show that the extent of invasion is generally higher in the lowlands than in the highlands.

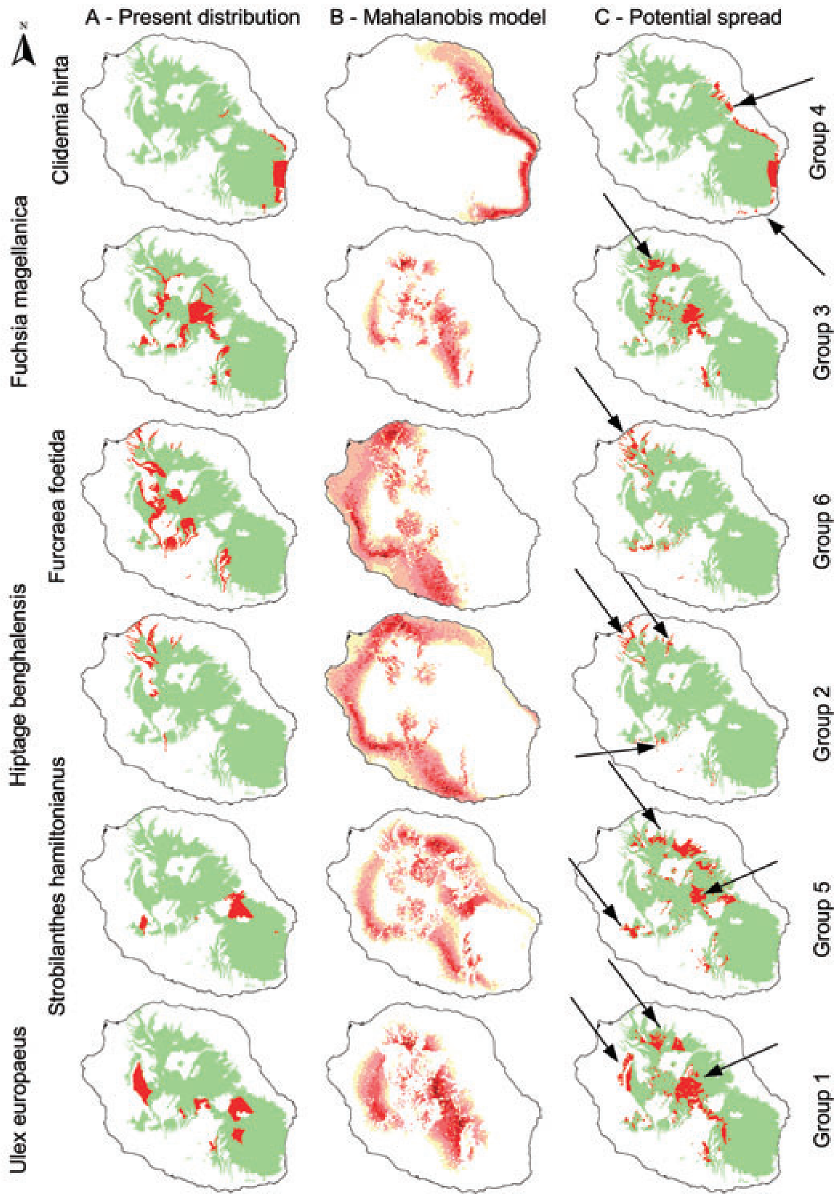

Fig. 5. Distribution of six characteristic invasive alien plants on La Réunion (one each from the six main clusters shown in Figure 3). Maps in column A show the current distribution (in red) at the habitat scale within ZNIEFF (green colour corresponding to the natural areas not invaded by the species described, the white corresponding to the transformed areas – urban, farming, secondary vegetation). Maps in column B indicate potential distribution based on the climatic envelope model (Mahalanobian model; colours indicate the probability of species occurrence – red: most probable; yellow: less probable; white: very low probability). Maps in column C are potential distribution maps for each species only within intact habitats (red areas: potential presence of the invasive alien plants within intact habitats; green areas: natural areas not invaded by the species described; white: transformed areas. Arrows indicate localities region where the species are currently absent but where conditions are potentially suitable.

This supports the findings of Strasberg *et al.* (2005). Remaining lowland habitats are also under considerable pressure from agriculture and urbanization. Our more detailed study re-emphasizes the importance of urgent management action in remaining lowland habitats. However, not only lowland habitats are threatened by invasive plants (see also Lavergne *et al.* 1999; Baret *et al.* 2004).

While a map showing the average extent of alien plant invasions (Fig. 1) might be useful for decision-makers in identifying broad conservation priority habitats (such as the lowlands), finer scale information is required by managers of alien plant clearing programmes. Current and potential species distribution maps at the scale of habitat types (Fig. 5) can inform planning for medium- and long-term management.

Extent of future invasion

The variant of climate envelope models (CEMs) used in this study allowed us to provide objective projections of the potential distribution of invasive plants on La Réunion. Rouget *et al.* (2004) showed that this kind of model was appropriate for use at the broad scale (South Africa, Lesotho and Swaziland). Our study has confirmed that this modelling approach is also suitable for use at smaller spatial scales, such as the 2512 km^2 area of La Réunion. An important assumption in this type of modelling of invasive species is that species are in equilibrium with the environment (i.e. that all species have had sufficient time to reach all potentially suitable habitats). As we selected the most abundant and widespread species in intact habitats, we limited potential bias that could be introduced by including species at early stages of invasion. Indeed, we have sufficient data on current distribution of major plant invaders within the island for us to have reasonable confidence in the generated potential distributions. The variant of CEMs based on the Mahalanobis distance to derive environmental suitability surfaces for each species used are validated by the Kappa statistic test (Cohen 1960; Fielding & Bell 1997). There is a bias in this test because some invasive alien plant species have yet to reach all potentially suitable habitats; the climatic envelop for such species will be bigger that their current distribution. This bias explains, for instance, why the Kappa test did not validate the model for *S. hamiltonianus* which has spread recently and was not abundant in our relevés dating from 1998.

Selecting six representatives of the widespread and threatening invasive plants in intact habitats on La Réunion (one from each of the objectively defined clusters based on presence/absence in habitat types), we show that some alien plant species have the potential to invade substantial additional area (e.g. *C. hirta*, *S. hamiltonianus*, *U. europaeus*). Some other species seem to have already invaded large parts of the potentially invadable area (e.g. *F. magellanica*, *F. foetida*, *H. benghalensis*). This finding should be taken as indicative rather than defining the absolute potential distributions of all species. We have some reasons to be cautious about some predicted distributions. For instance, the model does not consider disturbance, which clearly mediates invasibility of some habitats (e.g. see Higgins & Richardson (1998) for insights on the complex role of disturbance on tree invasions in South Africa). Species such as *F. foetida* and *H. benghalensis* preferentially invade disturbed sites like gaps, landslides and river banks (S. Baret, pers. obs. 2003). The potential distribution of some species may therefore be underestimated because the model does not invoke local-scale processes or disturbance. Moreover, *F. foetida* invades mainly very steep slopes that do not cover large areas when mapped in two dimensions. Thus, even if these alien plants are mainly localized in intact habitat, they could progressively colonize forest habitats and displace indigenous pioneer species (see Baret 2002 for an example on *Rubus alceifolius*).

Prioritizing management of invasive alien plants

Effective management of invasive alien plants on La Réunion is crucially important for preserving representative samples of the region's natural habitats. Our study focused on remnants of intact native habitat on La Réunion. Unfortunately, invasive alien plant species are widespread within these native habitats. Based on current and potential distribution, we were able to distinguish two groups of species:

- Species which could potentially invade substantial new areas
- Species which have probably already invaded a large part of their potentially suitable habitat

We suggest that management of the first group should focus primarily on surveying potentially suitable areas to eradicate new invasion foci. For both groups, attention should be given to preventing population growth within their current range, thus preventing escalating impact. Grouping invasive alien species according to their ecology, colonization strategy, management requirements and other biological criteria could help to facilitate effective control and restoration programmes (see Newsome & Noble 1986; Roy 1990; Reichard & Hamilton 1997; Daehler 1998). Our grouping of invasive alien species (Fig. 3) is a first step in this direction.

Managing invasive species should be carried out at the ecosystem level (in our case at the scale of habitat types) (Zavaleta *et al.* 2001). Figure 6 illustrates how habitats can be prioritized for management intervention based on percentage remaining and extent of invasion. Three broad groups of habitats may be defined: (i) intact habitats with a low level of invasion (e.g. subalpine shrubland); (ii) moderately invaded habitats with varying levels of intactness (ranging from windward submountain rainforest to the *A. heterophylla* forest); and (iii) habitats with little remaining intact area and high levels of invasion (e.g. lowland rainforest). Different management interventions are appropriate for these three groups. Sound arguments can be made for assigning priority to either G1 or G3. Management is most cost-effective in G1, but most urgent to alleviate impacts in G3. Within this third group, it is also possible to assign priority. Some of the habitats included in this group have intact areas of less than 2000 ha in La Réunion. Such habitats include coastal habitats (58 ha), subalpine *Sophora* thicket (230 ha), and lowland open woodland

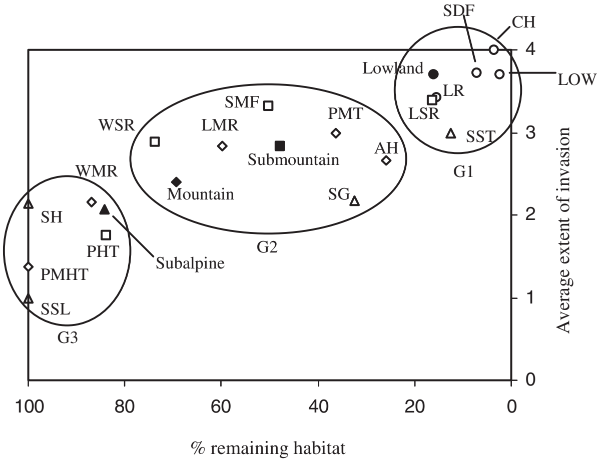

Fig. 6. Distribution of the 18 habitat types in relation to average extent of invasion and percentage of remaining habitat. Abbreviated habitat names are explained in Table 1. Black symbols represent the four broad habitat categories: lowland (circle), submountain (square), mountain (diamond) and subalpine (triangle). G1: habitats with little remaining intact area and high level of invasion, G2: moderately invaded habitats with varying level of intactness, G3: intact habitats with a low level of invasion.

(410 ha). Urgent action is required to combat alien plant invasions in these areas. Rapid action is also called in the subalpine shrubland on lapillis (belonging to G3), in the *Philippia* mountain thicket (G2) and in subalpine grassland (G2) habitats; these habitats are represented by only by 794 ha, 935 ha and 960 ha, respectively. Further information on impacts and management requirements are needed to define objective control programmes.

This study has provided information that can be used to incorporate the best available understanding of threats posed by invasive alien plants in systematic conservation planning. Because of increasing threats to biodiversity and limited financial resources, conservation authorities require accurate guidelines for prioritizing conservation actions. The results of this study are informative in this respect. Indeed, the results are already being used in discussions and planning for the proposed national park and for setting priorities for control programmes against invasive plants by the forestry service which manages most of the intact vegetation on La Réunion. The intact vegetation of 40 000 ha is currently afforded protection in reserves, mainly under control of the forest service. Unfortunately, the present reserves comprise the most widespread habitats which are generally less threatened by invasive alien plants. Thus, according to our data and in order to manage alien plant and preserve biodiversity, the actual goal of the forestry service is to include these threatened habitats rapidly in future reserves (A. Brondeau, pers. com. 2004).

Unfortunately, the data on alien plant distribution and abundance (in ZNIEFF) were collected during the 1980s and 1990s. In some cases, the situation has changed markedly in the last two decades. The distribution of some plants is thus considerably underrepresented in our analysis. This is the case for species such as *C. hirta* and *Strobilanthes hamilthonianus* which are both currently much more widespread and abundant than was the case in the 1980s. A thorough resurvey of the ZNIEFF would facilitate improved precision of the models for use in future conservation planning.

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APPENDIX I

List of the 46 most widespread invasive alien plants (*sensu* Richardson *et al.* 2000) on La Réunion

The list contains 31 of the 33 species listed by Macdonald *et al.* (1991) (only *Stachytarpheta indica* and *Tibouchina viminea* were excluded from their list of species, as they invade only roadsides and other disturbed habitats) and 15 other species considered similarly widespread/abundant according to our observations. One species in the list (*Pteridium aquilinum*) is included here, although there is some debate regarding its status as an alien; most botanists in La Réunion consider the taxa to be alien. Data are: year of first record on La Réunion (FRD); life cycle (LC); biogeographical origin (BO – AM, America; EU, Europe; AS, Asia; AF, Africa; AU, Australia; COS, Cosmopolitan) and ranked importance in the column RI according to Macdonald *et al.* (1991). Arrows in the RI column mark species which have increased substantially in abundance and distribution since Macdonald *et al.*'s (1991) ranking exercise.

Family	Species	FRD	LC	BO	RI
Fabaceae	*Acacia mearnsii*	1860	Perennial	AU	
Asteraceae	*Ageratina riparia*	1980s	Annual	AM	
Poaceae	*Anthoxanthum odouratum*	?	Annual	EU	
Myrsinaceae	*Ardisia crenata*	1856	Perennial	AS	17
Begoniaceae	*Begonia cucullata*	?	Perennial	AM	18
Urticaceae	*Boehmeria macrophylla*	1856	Perennial	AS	7
Urticaceae	*Boehmeria penduliflora*	1970	Perennial	AS	8
Casuarinaceae	*Casuarina cunninghamiana*	1840	Perennial	AU	30
Casuarinaceae	*Casuarina equisetifolia*	1768	Perennial	AS	14↑
Casuarinaceae	*Casuarina glauca*	1877	Perennial	AU	
Melastomataeceae	*Clidemia hirta*	1950	Perennial	AM	15↑
Lythraceae	*Cuphea ignea*	1967	Perennial	AM	31
Cyatheaceae	*Cyathea cooperi*	?	Perennial	AU	
Rosaceae	*Duchesnea indica*	1973	Annual	AS	
Asteraceae	*Erigeron karvinskianus*	1970	Annual	AM	10
Rosaceae	*Eriobotrya japonica*	1825	Perennial	AS	25
Onagraceae	*Fuchsia boliviana*	1962	Perennial	AM	12
Onagraceae	*Fuchsia magellanica*	1970	Perennial	AM	9
Onagraceae	*Fuchsia x exoniensis*	1970	Perennial		
Agavaceae	*Furcraea foetida*	1825	Annual/biennial	AM	16
Zingiberaceae	*Hedychium coccineum*	1930s	Perennial	AS	
Zingiberaceae	*Hedychium flavescens*	1825	Perennial	AS	21
Zingiberaceae	*Hedychium gardnerianum*	?	Perennial	AS	5
Malpighiaceae	*Hiptage benghalensis*	1967	Perennial	AS	20↑
Asteraceae	*Hypochaeris radicata*	1967	Annual/biennial	EU	
Verbenaceae	*Lantana camara*	1840	Perennial	AM	3
Fabaceae	*Leucaena leucocephala*	1825	Perennial	AM	22
Oleaceae	*Ligustrum robustum* ssp. *walkeri*	1960	Perennial	AS	4
Lauraceae	*Litsea glutinosa*	1825	Perennial	AS	13
Caprifoliaceae	*Lonicera confusa*	?	Perennial	AS	24
Caprifoliaceae	*Lonicera japonica*	1825	Perennial	AS	24
Pinaceae	*Pinus pinaster*	1825	Perennial	EU	27
Myrtaceae	*Psidium cattleianum*	1818	Perennial	AM	1
Dennstaedtiaceae	*Pteridium aquilinum*	1856	Perennial	COS	
Rosaceae	*Rubus alceifolius*	1840	Perennial	AS	2
Rosaceae	*Rubus rosifolius*	1768	Perennial	AS	19
Anacardiaceae	*Schinus terebinthifolius*	1843	Perennial	AM	26
Solanaceae	*Solanum mauritianum*	1825	Perennial	AM	6
Acanthaceae	*Strobilanthes hamiltonianus*	1956	Perennial	AS	
Myrtaceae	*Syzygium jambos*	1825	Perennial	AS	11
Bignoniaceae	*Tecoma stans*	1856	Perennial	AM	
Ulmaceae	*Trema orientalis*	1856	Perennial	AF	32
Melastomataceae	*Tristemma mauritianum*	1790	Perennial	AF	28
Fabaceae	*Ulex europaeus*	1856	Perennial	EU	
Scrophulariaceae	*Verbascum thapsus*	1825	Biannual	EU	
Araceae	*Zantedeschia aethiopica*	1825	Annual	AF	33↑