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Abstract The largest area of intact vegetation in the Mascarene's archipelago is found on Reunion Island, but the remaining natural areas are under threats. Biological invasions are one of the main threats to biodiversity loss on this island and globally worldwide. This study aimed to quantify invasion degree by alien plants species in Reunion Island. This work was possible thanks to a large partnership between researchers and managers. All existing spatial data on invasion pattern were combined and completed by expert knowledge to develop the first 250 x 250 m map of invasion degree at the island scale. To fill the gaps where no field survey data or expert knowledge was available, we used a Random Forest model using nine climatic, landscape and anthropogenic variables. This model also provides a preliminary assessment of drivers of invasion at Reunion Island. Results showed that 85% of the extant native vegetation was invaded in different proportions; 38% are slightly invaded, 26% moderately invaded and 22% very heavily invaded. Despite the high levels of invasion in some places, more than 50% of the extant vegetation is not invaded or slightly invaded. Most of the invaded areas are located in the lowland and in the leeward coast although alien plants invade all types of vegetation from the coast to the top of the island. These results highlight a clear increase in the distribution of alien species over time. This study constitutes a key first step for about the ongoing prioritisation of management interventions on Reunion Island. Abstract in Spanish is available with online material.

Key words: invasion degree, invasive alien plants, mapping, Mascarenes, Random Forest.

INTRODUCTION

Invasive alien species (IAS), species introduced outside their native range and responsible for negative impacts on the environment (ecological, economical or health consequences) (Russel & Blackburn 2017), are a major threat to global biodiversity and to the delivery of ecosystems services (Mack *et al.* 2000; Pyšek *et al.* 2020). In recent decades, the economic and environmental impacts of invasive alien species have increased significantly (McGeoch *et al.* 2010; Simberloff *et al.* 2013; Pyšek *et al.* 2020). Biological invasions are now widespread worldwide and colonise all types of environments, without any sign of saturation in the increase in numbers of alien species (Seebens *et al.* 2017). Due to the unprecedented biodiversity crisis in terms of species extinction and habitat loss (Butchart *et al.* 2010), conservation actions have become essential to protect ecosystems from the processes that negatively impact them.

Scientists and managers often used spatial data to manage and assess threats to biodiversity (Wilson *et al.* 2006). These 'threat maps' are regularly used to plan decisions about conservation management and actions to be undertaken, which can be costly (Salafsky *et al.* 2003; Tulloch *et al.* 2015). As resources are limited, they must be allocated where they are likely

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to be most cost-effective (Krug *et al.* 2009). In the specific case of management of invasive species, it is essential to have an overview of the extent of biological invasions (often so-called 'degree of invasion'). The degree of invasion refers to the extent or severity to which a community has already been invaded (Chytrý *et al.* 2008). Characterising the spatial extent, the severity or intensity of the invasion process are important tools for resource management (Byers *et al.* 2002). This information enables to identify sites of current or future invasion (Shaw 2005), to assess the effectiveness of the control actions (Roura-Pascual *et al.* 2009), or to select sites for invasion control (McGeoch *et al.* 2016). Documenting the change in extent of invasions also enables a spatio-temporal monitoring which is important for justifying funding of management programs (Mack *et al.* 2000).

Various approaches have been applied for mapping the distribution and abundance of invasive alien plants. These range from herbarium records (Crawford & Hoagland 2009), field surveys (Brundu *et al.* 2011), road surveys (Mortensen *et al.* 2009), remote sensing approaches (Huang & Asner 2009), spatial modelling (Pearce & Boyce 2006) to citizen-science programs (Roy *et al.* 2015; Groom *et al.* 2019). These approaches differ in terms of spatial and taxonomic bias, accuracy and extent. Foxcroft *et al.* (2009) showed that selecting the appropriate spatial scale is important when studying the abundance and distribution of alien plants invasions.

Knowing the current distribution of IAS is a crucial step towards managing them. Invasions are constantly increasing, it is therefore essential to assess invasion risks and to understand the drivers favouring the survival, establishment and spread of invasive alien species in the landscape (Bellard *et al.* 2016). The identification of these factors is an essential element in order to prevent and/or limit invasions. Climate similarity with the region of origin (Gallien *et al.* 2010), propagule pressure, trade and tourism (Hulme 2009), intensity of anthropogenic disturbances (Pyšek *et al.* 2010) or land use (Chytrý *et al.* 2012) are all factors recognised as playing an important role in the spread of biological invasions.

In insular ecosystems, biological invasions represent the major threat to biodiversity conservation (Simberloff 1995; Wilcove *et al.* 1998; Lenzner *et al.* 2020; Pyšek *et al.* 2020). Reunion Island, a French oceanic island, is recognised with the Malagasy region as a biodiversity hotspot (Myers *et al.* 2000) but faces many threats, including impacts due to plant invasions (Macdonald *et al.* 1991). In 2017, an IUCN report noticed a progressive deterioration of this World Heritage site because of the spread of invasive plants, the insufficient resources allocated and the real need to reinforce the governance and the coordination amongst biodiversity managers for alien plants clearing (Osipova *et al.* 2017).

Here, we present the first results of an island-wide survey on the extent of plant invasions in order to assist managers in prioritising sites for alien plant clearing and identifying preserved systems. Although several studies have been conducted on some invasive alien species on Reunion Island (e.g. Strasberg *et al.* 2005; Baret *et al.* 2006), none of them has quantified the overall level of invasion by plants at an island's scale useful for managing invasions. This paper aims at (1) mapping the invasion degree at a scale useful for managing invasions and planning for alien plants clearing; (2) understanding the climatic, landscape and anthropogenic factors that affect the level of alien plant invasion.

MATERIAL AND METHODS

Study area

Reunion Island (2512 km^2) is a volcanic island in the Mascarene's archipelago (Fig. 1). The average annual rainfall shows an important dissymmetry between the eastern and western sides of the island due to its rugged topography and high elevation. On the leeward coast (western-side), annual precipitation ranges from 500 to 1500 mm and can reach 5000 mm on the windward coast. At intermediate elevations, precipitation approaches 12 000 mm (Jumeaux *et al.* 2011). The average annual temperature ranges from 26°C at the coast to 11°C at the top. This large gradient of temperatures and precipitations leads to very diverse ecosystems ranging from tropical lowland forest to subalpine vegetation (Cadet 1977), with an important plant endemism rate. Indeed, more than 28% of native plants are qualified as strictly endemic to Reunion, 17% are endemic to the Mascarenes and 15% are endemic to the West Indian Ocean zone (CBNM 2020). In 2007, a National Park, covering more than 42% of the island, was established to conserve and protect the native habitats and part of the island is listed as a World Heritage Site. In comparison with other islands of the Mascarenes, Reunion Island has the largest proportion of remaining tropical rainforest and other native habitats, which still cover one-third of the island (Strasberg *et al.* 2005).

Mapping the degree of invasion by alien species based on existing data and expert knowledge

Spatial distribution of the main threats to biodiversity is essential to identify spatial conservation priorities and alien plants clearing priorities. For years, alien plants records and distribution data on the island have been compiled from several different sources (herbarium records, plant surveys and managers' field records). However, these data have never been synthetised, assembled and used to assess the degree of invasion on Reunion Island. Strasberg *et al.* (2005) made a first attempt but the spatial resolution was

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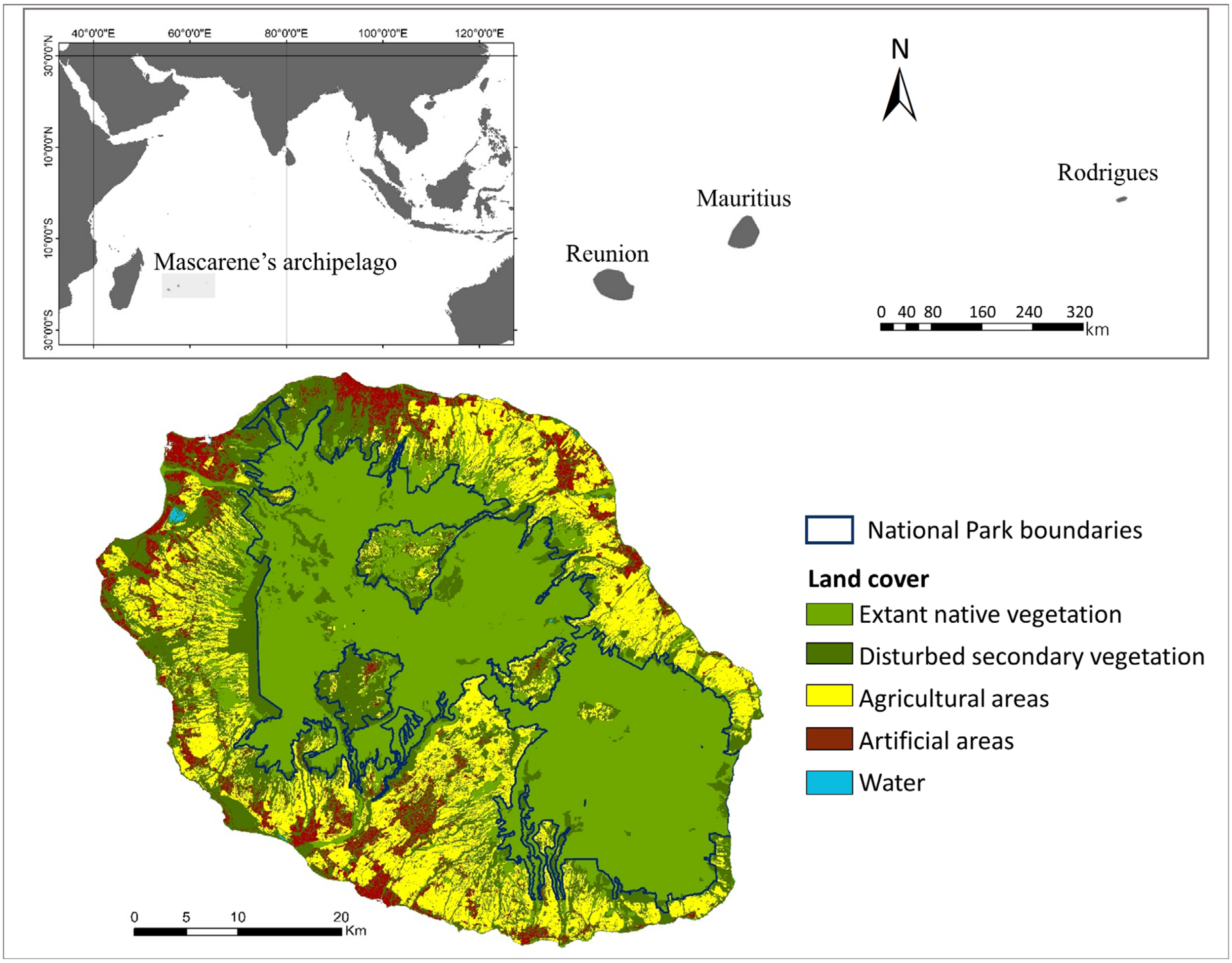

Fig. 1. Mainland cover types on Reunion Island (Modified from Dupuy & Gaetano 2019). We distinguished extant native vegetation (native vegetation comprising of indigenous species with varying degree of invasion) from disturbed secondary vegetation which included old fields, completely invaded areas or forestry plantations of alien trees.

very coarse and could not be used for management. Here, we first compiled all existing data and combined them with an expert-driven process to map the extent of plant invasion within vegetation types on the whole island.

The approach for mapping the degree of invasion consisted of five main steps (see Fig. 2). 1) gathering all existing data; 2) generating a unified scale for categorising invasion degree and summarising it into 250 × 250 m cells; 3) using expert knowledge to review and complete the mapping; 4) modelling the degree of invasion to fill the gaps where no data or expert knowledge was available and 5) compiling all the field survey, expert knowledge and modelled data to obtain the final map. Although invasive species information was available for most records, it was beyond the scope of this study to report on spatial patterns of each invasive species on the whole island.

First, we gathered all existing spatial data on alien plants to map the extent of plant invasions on the whole island. We used four main data sources (datasets 1 to 4, see Table 1). Dataset 1 consisted of alien plant records and plot invasion level from the National Park (PNRun). These data reflect years of field surveys carried out by Park field rangers. During their surveys, the field rangers recorded the occurrence of key alien species and the overall invasion level of the area using a rating system made of six invasion categories ranging from intact areas to fully invaded areas (see Baret *et al.* 2006). Dataset 2 consisted of botanical surveys from the *Conservatoire Botanique National de Mascarin* (CBNM). The CBNM dataset was the most complete at the island's scale because it centralised all the botanical surveys from various sources. All alien species were recorded based on the ordinal scale of Braun-Blanquet *et al.* (1952). Dataset 3 were plant communities dominated by alien species, as well as plantations of alien trees. This information was extracted from the vegetation map developed by the *Office National des Forêts* (ONF). This map delimits all of the island's vegetation, both extant native and disturbed secondary formations (see section 3 in the methods). Dataset 4 was a detailed vegetation map for coastal habitats and lowland dry forests from the local government (*Direction de l'Environnement, de l'Aménagement et du Logement de La Réunion*, DEAL). DEAL used a basic scale of invasion

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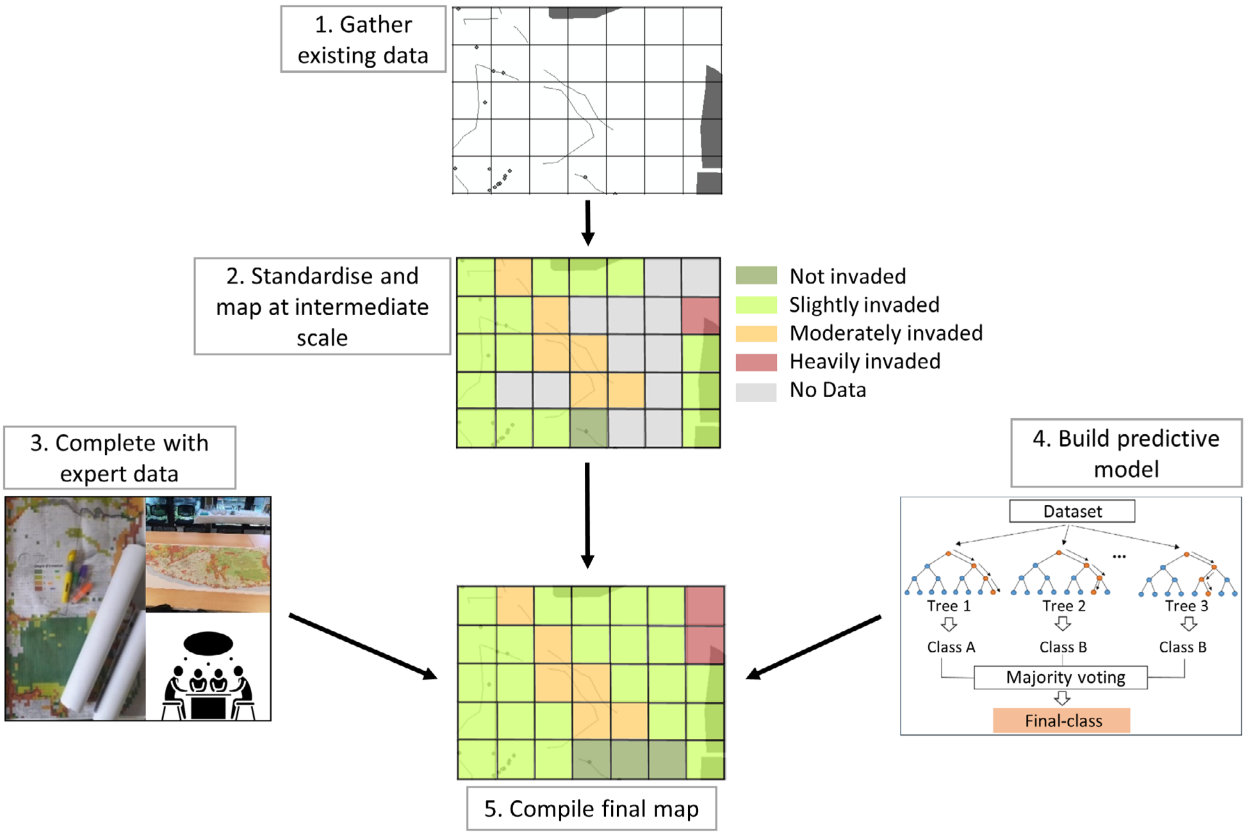

Fig. 2. Methodological approach for mapping the degree of invasion.

(excellent conservation status, good conservation status, partially invaded, heavily invaded). The combined alien plant distribution data set includes 100,717 species localities, 444 kilometres of transects and 31,160 hectares of vegetation surveys (Table 1).

Secondly, it was necessary to standardise and generate a single scale as all four data sources used different protocols and rating systems for quantifying invasion degree. We created a scale of invasion made of four ordinal classes: (1) Not invaded – where no alien plant was recorded; (2) Slightly invaded area – where a maximum alien plant cover of 25% was recorded; (3) Moderately invaded – where a maximum alien plant cover of 75% was recorded; (4) Very heavily invaded or anthropised area – where more than 75% of alien plant cover was recorded.

Thirdly, all these data were summarised into grid cells of 250 × 250 m. In cases where a grid cell contained several records of invasion degree (different values of invasion), the highest value was attributed to the cell. Foxcroft *et al.* (2009) studied the patterns of alien plant distribution at multiple spatial scales and their implications for ecology, management and monitoring. They showed that 100 × 100 m and 250 × 250 m scales are the most useful in ecological studies. These scales are appropriate for planning management intervention and monitoring programmes. They also suggested that finer scales were most useful for specific aspects of research like plant distribution patterns or distribution modelling. A 250m mapping scale was considered to be suitable for taking management decisions on alien plant clearing.

Due to the change of spatial resolution between the original records of invasion and the resulting map, it was difficult to categorise alien cover in the final map (250m cells). For moderately invaded areas, while alien cover could be up to 75% in the original data, field observation of these areas suggested that the cell was seldomly 75% invaded. Indeed, in these cells, invasive species tend to occur in few dense patches within a matrix of native vegetation. Moderately invaded areas were, by large, areas of native vegetation, with few dense patches of invasive species, which can be restored by removing alien plants. Heavily invaded areas represent densely invaded areas, dominated by invasive species, which would require intensive clearing and active planting of native plants for restoration.

Finally, the resulting map of invasion degree was taken through a process of expert review in order to validate and complete the map; several workshops (one per geographic sector of the island) have been set up involving more than 30 managers, field agents and researchers from various organisations. All the people involved in these workshops have an extensive knowledge of the field.

Expert knowledge was used in two different ways. First, in cells with insufficient or out-of-date data, the experts were able to modify the invasion-degree class. Secondly, the experts were asked to complete, when possible, the

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Table 1. Data used for mapping the degree of invasion. Date indicate the duration of data collection

Dataset	Source	Date	Data format
(1) Alien plant records and plot invasion level	National Park	2007-2018	10,331 localities
(2) Botanical surveys	Conservatoire Botanique National de Mascarin	1972-2018	90,386 localities 102,527 transects (443 km) 5,427 polygons (5,729 ha)
(3) Areas invaded by alien plants	Office National des Forêts	2018	261 polygons (14,160 ha)
(4) Detailed vegetation map for coastal habitats and lowland dry forest	Direction de l'Environnement, de l'Aménagement et du Logement	2012-2017	11,164 polygons (11,573 ha)

areas where no data were listed. We either modified or defined the invasion-degree class by expert knowledge only when experts had a good knowledge of an area and when there was consensus between them; no extrapolation has been made for areas where no knowledge (survey or expert) was available.

Mapping habitat diversity and transformation

Broad land cover types were identified from remote sensing based on 2017 spot imagery (Dupuy & Gaetano 2019, see Fig. 1). The most up-to-date vegetation map of the Forestry Service (ONF 2018) was used to distinguish extant native vegetation (vegetation comprising of indigenous species with varying degree of invasion) from disturbed secondary vegetation which included old fields, completely invaded areas or forestry plantations of alien trees. The Forestry Service vegetation map was also used to further classify extant native vegetation into various vegetation types. This map was originally based on Strasberg *et al.* (2005) with significant updates on vegetation boundary and classification. The resulting extant native vegetation map was made up of a two-level hierarchical classification. The first level was composed of seven units of extant vegetation and the second level, 35 vegetation units.

Table 2. Major vegetation types in Reunion (level-1 classification). Number of level-2 units indicates for each level-1 classification habitat, the number of sub-habitats included in level-2 units

Vegetation code	Vegetation type	Surface (ha)	Number of level-2 units
COAST	Coastal vegetation	161	4
DRY	Seasonally dry thickets and forests	6687	6
LOW	Lowland thickets and rainforests	8723	2
SUB	Submountain thickets and rainforests	18 775	3
MOUNT	Mountain thickets and rainforests	50 542	9
ALPI	Subalpine vegetation	17 701	4
WET	Wetlands	2431	4
ROCK	Rocks and lava flows	8886	3

Here we present results based on the first level of classification of extant native vegetation (see Table 2 for the list of these different types of vegetation).

Modelling the degree of invasion and identifying key drivers of invasion

We explored the role of climatic, landscape and anthropogenic factors in explaining the spatial pattern of invasion and in predicting the degree of invasion for areas with missing data.

Data acquisition

We used nine variables at a 100×100 m spatial resolution, grouped into three major types: climatic, anthropogenic and landscape (Table 3). Climatic data (mean annual temperature and mean annual rainfall for the last 30 years) were obtained from the French weather institute (source Météo France). The anthropogenic variables 'distance to urban areas' was derived from a 2017 land cover map (Dupuy & Gaetano 2019) and 'distance to roads' from available topographic data.

Accessibility was modelled based on Frakes *et al.* (2015) (Appendix S1). Finally, the island's slope and elevation was

Table 3. Variables used to explain the spatial pattern of invasion

Variable	Type	Source
Mean annual temperature (°C)	Climatic	Météo France
Mean annual rainfall (mm)	Climatic	Météo France
Distance to roads (m)	Anthropogenic	IGN
Distance to urban areas (m)	Anthropogenic	Dupuy & Gaetano 2019
Area accessibility (s)	Anthropogenic	Modelling
Vegetation (7 types)	Landscape	ONF 2018
Geomorphology (9 types)	Landscape	Modelling
Elevation	Landscape	DEM
Slope	Landscape	Derived from DEM

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taken from a 5 m Digital Elevation Model (DEM) (BD Alti ® 2017, available at www.ign.fr). The vegetation map comes from the Forestry office (see above). We used the first level of vegetation in this analysis because the scale used (100 × 100 m) was not sufficiently fine to properly discriminate some very rare habitats. We excluded wetlands, as aquatic invasive species were not documented and mapped. Geomorphology of the island was modelled based on Dikau (1989) and Hammond (1964) (Appendix S2) into nine major types of reliefs.

Statistical methods

Model construction using random Forest

We developed a Random Forest model (Breiman 2001) relating nine variables (two climatic, four landscape and three anthropogenic variables) to invasion degree in order to predict the invasion degree and to quantify the relative importance of each driver. We decided to use a *Random Forest* model as it is commonly used and has been found to perform well in ecological applications (Cutler *et al.* 2007; Oliveira *et al.* 2012). Other models were tested (regression, classification trees) but the results are not be presented here.

Random Forest is an ensemble learning method based on a large number of individual decision trees that operate as an ensemble to produce accurate predictions (Breiman 2001). In this study, the response variable, namely the invasion degree, had four categories: not invaded area, slightly invaded area, moderately invaded area and very heavily invaded or anthropised area. Each tree in the *Random Forest* model leads to a prediction amongst the four invasion categories and the corresponding misclassification rate.

The 250m grid dataset was split into two datasets: the training dataset and test dataset. In our case, the training dataset also called the In-Bag (IB) data represented 75% of observations (n = 17 237) and the test dataset, which is named as Out Of Bag (OOB) samples are used for model validation (Cutler *et al.* 2007) and represent the remaining 25% of observations (n = 5746). The number of trees (Ntree) and the number of features (Mtry) randomly selected at each node were fixed in order to optimise the Random Forest's performances. To identify the optimal Ntree and Mtry, we used the OOB error rates. To achieve minimum misclassification error, we used 1000 trees and an Mtry of 3.

Five Random Forest models were constructed. The first three models were constructed according to the three types of explanatory variables: a climatic model, a landscape model and an anthropogenic one. Then a full model was constructed, using all the nine variables. Finally, a more parsimonious model was created. To identify the appropriate number of variables to use for this parsimonious model, the misclassification rate was investigated at varying numbers of independent variables.

All model calculation and validation were implemented in the open-source R software 3.6.2 (R Core Team 2019) using 'randomForest' (Liaw & Wiener 2002) and 'caret' (Kuhn 2020) packages.

Model validation and variable importance analysis

In order to validate all models, we used the test dataset (OOB). The model error was evaluated by an error distribution provided by the OOB data in each Bootstrap replicate. Even if the robustness of this approach has been validated, some authors recommended the addition of other validation techniques (Evans *et al.* 2010). Here, we used the *Kappa* statistic in addition to the basic validation technique of *Random Forest* (Cohen 1960).

Random Forest is commonly used to assess variables importance. Here, the *Gini* index was used to measure the importance of each predictor: a large *Gini* index indicates a high importance (Strobl *et al.* 2007).

Filling the gap with modelled data

We used the predicted categories of invasion degree from the parsimonious model to fill the gaps where no field survey data or expert knowledge was available in extant native and disturbed secondary vegetation. This enabled us to complete the map of the degree of invasion for all extant native and disturbed secondary vegetation areas.

At the end, three different sources of data were used to compile the invasion-degree map: data from field survey, expert knowledge and modelled data. Then we assessed the relative contribution of each source of data.

To conclude, we assessed the degree of invasion within extant native vegetation for each vegetation type (level-1 classification). We also listed the major invasive species per vegetation type based on the CBNM dataset, by selecting the five most frequent species occurring in each vegetation type. As species-level data is incomplete on the island, we could not report on the identity of species within each 250 × 250 m cell.

RESULTS

We first present the spatial patterns of the invasion degree and then its modelling with associated environmental factors.

Degree of invasion

We mapped the degree of invasion for all extant native and disturbed secondary vegetation areas, covering 183,012 ha. The relative contribution (in terms of area) of field survey, expert knowledge and modelled data was 41%, 31% and 28%, respectively.

Looking at extant native vegetation only (113,910 ha), the relative contribution of field survey, expert knowledge and modelled data were 38%, 45% and 17%, respectively (see Fig. 3). Concerning the contribution of expert knowledge, 42% dealt with modifying the invasion-degree class from field survey while 58% dealt with completing the map with new data. More than 85% of the extant native vegetation was invaded in different proportions (Table 4). We

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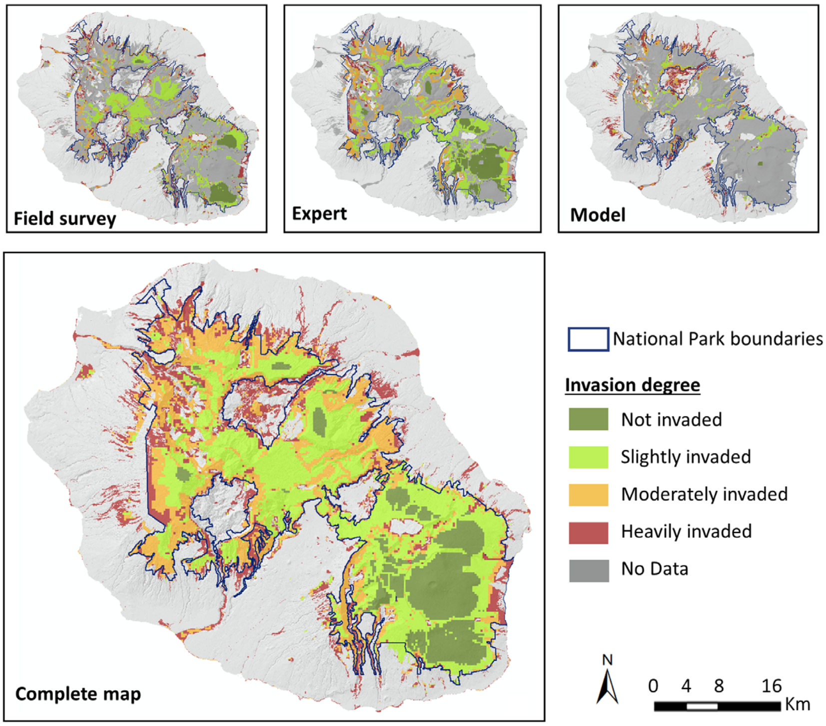

Fig. 3. Invasion degree by alien plants species in extant native vegetation of Reunion Island. The three maps at the top of the figure respectively represent the data source: field survey, expert knowledge and modelled data.

Table 4. Change in invasion degree by alien plants species on Reunion Island between Strasberg *et al.* (2005) and this study. Strasberg *et al.* (2005) estimated the invasion degree across the all island using similar categories

	Invasion-degree class (ha)			
Study	Not invaded	Slightly invaded	Moderately invaded	Heavily invaded
This study	16,187	42,963	29,934	24,826
Strasberg *et al.* (2005)	64,307	20,849	17,584	27,632

found that only 15% were mapped as not invaded, 38% slightly invaded, 26% moderately invaded and 22% very heavily invaded. Globally, a pattern in relation to elevation was observed; most invaded areas were located in the lowlands whereas the less invaded ones were mostly located in montane and isolated areas. However, some high-elevation areas were invaded too. Habitats on the windward coast have been less heavily transformed than those on the leeward coast.

Degree of invasion within vegetation types

Here, we report on the extent of invasion within extant native vegetation only. The origin of the data varies from one habitat to another; some habitats have been subject to numerous surveys and thus present many field data (subalpine vegetation) while other habitats have been mostly completed thanks to expert knowledge and modelling (Rocks and lava flows). Major differences were found in the degree of invasion within vegetation types (Fig. 4). In general, the highest levels of invasion were concentrated in lowland vegetation types whereas montane vegetation types had the lowest rates of invasion. Amongst the most invaded vegetation types, coastal vegetation was the only vegetation type to be completely invaded. Nearly 75% of coastal vegetation was very heavily invaded, while the remaining 25% moderately invaded. For example at a finer scale (level 2 vegetation classification), 96% of coastal grassland vegetation on rocky shores and 90% of coastal dry vegetation on rocky shores were very heavily invaded

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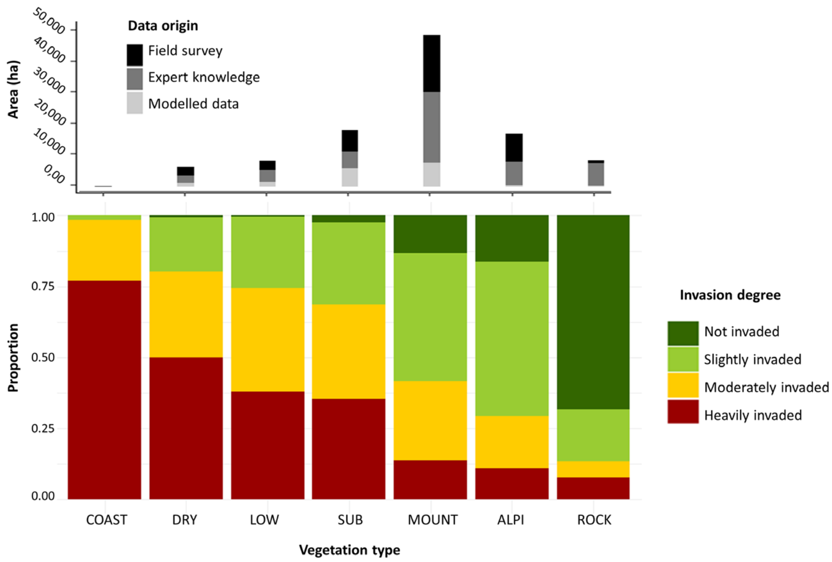

Fig. 4. Invasion degree according to the level-1 habitat classification. COAST: Coastal vegetation; DRY: Seasonally dry thickets and forests; LOW: Lowland and thickets rainforests; SUB: Submountain and thickets rainforests; MOUNT: Thickets and mountain forest; ALPI: Subalpine vegetation; ROCK: Interior rocks and lava flows. The top figure represents the area of each vegetation type according to the origin of data.

(Appendix S3). Thickets and seasonally dry forests were also globally well-invaded; more than 50% of this vegetation were heavily invaded. For example, leeward mosaic of seasonally dry and moist forest and the seasonally dry forest were mostly very heavily invaded (59% and 58%, respectively). However, in the high-elevation vegetation (montane and subalpine areas), plant invasion was less frequent (less than 15% of very heavily invaded areas). These types of vegetation were also the only ones to have large areas still intact from invasion (around 15% of intact areas). Alpine shrublands did not present very heavily invaded areas and nearly 25% was intact from invasion. Finally, the moist thickets and forests have intermediate invasion value. Lava flows represented a special case of habitat because there is very few vegetation. A large proportion of this habitat is intact at higher altitudes (nearly 70%) but in the lowlands, recent lava flows were partly invaded.

A wide range of exotic species in Reunion Island have become invasive; some of the more invasive ones are presented in the Table 5 (see Appendix S4 and S5 for a more detailed description of these species). These species cover different families and have multiple sites of origin (Appendix S4). The five most widespread invasive species in native vegetation were *Psidium cattleyanum Afzel. ex Sabine*, *Litsea glutinosa (Lour.) C.B. Rob.*, *Ardisia crenata Sims*, *Rubus alceifolius Poir.* and *Syzygium jambos* (L.) Alston. While some alien species can invade several vegetation types, some were restricted to one type only (e.g. *Anthoxanthum odoratum* invading subalpine vegetation).

Drivers of invasion

We present the results of five *Random Forest* models (Table 6). Three simple models were based exclusively on one type of variable (climatic, landscape or anthropogenic type). These three models gave similar accuracy (around 60% of good classification rate) with a *Kappa* statistic of around 0.45. A full model (using all nine variables) resulted in an overall accuracy of 81.87%, and a Kappa statistic of 0.74. Finally, a parsimonious model (using the six best variables) resulted in an accuracy of 79.84% and a Kappa statistic of 0.72. Three landscape variables were not used in the parsimonious model (Table 6).

The 'moderately invaded' category was the most difficult to predict. This category had the most important misclassification rate, 40% for the parsimonious model. However, the models predicted relatively well the categories 'not invaded' and 'very heavily invaded' (the lowest misclassification rates of 12% and 11%, respectively). The 'slightly invaded' category had an intermediate misclassification rate of 22% (see Appendix S6 for all models results).

The three most important variables in the parsimonious model were 'rainfall', 'elevation' and 'distance to urban areas' (Table 6).

DISCUSSION

This study is the first spatially explicit assessment of the invasion degree within habitats in Reunion Island

Table 5. Major invasive species per vegetation types on Reunion island (species occurrence data from CBNM dataset)

Vegetation types	Major invasive species (by decreasing order of frequency)
Coastal vegetation[†]	*Schinus terebinthifolia, Casuarina equisetifolia*
Seasonally dry thickets and forests	*Litsea glutinosa, Psidium cattleyanum, Furcraea foetida, Hiptage benghalensis, Leucaena leucocephala*
Lowland thickets and rainforests	*Psidium cattleyanum, Ardisia crenata, Syzygium jambos, Rubus alceifolius, Miconia crenata*
Submountain thickets and rainforests	*Psidium cattleyanum, Ardisia crenata, Rubus alceifolius, Hedychium gardnerianum, Litsea glutinosa*
Mountain thickets and rainforests	*Psidium cattleyanum, Ageratina riparia, Rubus alceifolius, Hedychium gardnerianum, Erigeron karvinskianus*
Subalpine vegetation	*Erigeron karvinskianus, Hypochaeris radicata, Anthoxanthum odoratum, Ulex europaeus, Ageratina riparia*
Rocks and lava flows[†]	*Desmanthus virgatus, Casuarina equisetifolia, Schinus terebinthifolia*
Disturbed secondary vegetation	*Psidium cattleyanum, Litsea glutinosa, Syzygium jambos, Furcraea foetida, Schinus terebinthifolia*
All vegetation combined	*Psidium cattleyanum, Litsea glutinosa, Ardisia crenata, Rubus alceifolius, Syzygium jambos*

[†]Vegetation types for which not enough data was available to assess invasive species. See Appendix S4 for a more detailed description of the species.

Table 6. Variable importance and prediction accuracy of models. The upper sign (>) indicates the importance of the variables. The closer the value of Kappa index is to one, the more important are the concordance of results

Model	Variables	Accuracy (%)	Kappa statistic
Climatic	Rainfall > Temperature	61.31	0.45
Landscape	Elevation > Slope > Vegetation > Geomorphology	63.16	0.48
Anthropogenic	Distance to urban areas > Distance to roads > Accessibility	61.75	0.45
Full	Rainfall > Elevation > Distance to urban areas > vegetation > Accessibility > Distance to roads > Temperature > Slope > Landform	81.41	0.74
Parsimonious	Rainfall > Elevation > Distance to urban areas > Accessibility > Distance to roads > Temperature	80.39	0.72

at a scale relevant for managers. The originality of this collaborative work holds in the usage of a combination of field survey data, expert knowledge and modelled data, allowing to quantify the invasion degree by exotic plants at the island scale. A striking result is that 15% of extant native vegetation is not invaded whereas 22% is heavily invaded.

This study provided an initial monitoring over time of Reunion Island spatial situation about invasive species. Our results confirm the broad pattern of invasion found by Strasberg *et al.* (2005): Around third of the island still contains habitats where invasion is localised (represented here by the categories 'not invaded' and 'slightly invaded'). However, a clear increase in the distribution of alien species was observed. Strasberg *et al.* (2005) identified 130 372 ha of natural vegetation; today we have identified 113 910 ha, that is, a loss of 16 462 ha. That study stated that 49% of natural vegetation was in pristine status; today it concerns only 14%. However, a slight decline in heavily invaded areas should be noted. Indeed, clean-up operations against IAS and restoration work are carried out on the island every year. Strasberg *et al.* (2005) also identified two habitats as intact; the Pandanus Mountain wet thicket and the subalpine shrubland on lapilli. Our results showed that despite the harsh environmental conditions characterising these two habitats, some exotic species are beginning to establish. This is the case of *Anthoxanthum odoratum* and *Hypochaeris radicata*, two highly invasive herbaceous species gradually colonising the lapilli areas.

Despite the increase of invasion levels within extant native vegetation, Reunion Island remains the most preserved island at the scale of the Mascarene archipelago. Considering the extreme reduction of native vegetation in Mauritius and Rodrigues, the persistence of relatively intact ecosystems in the Mascarene archipelago depends on their effective conservation on Reunion Island (Strasberg *et al.* 2005). There is, therefore, a real need to conserve the well preserved and functional habitats of Reunion Island because

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they can be rapidly threatened by further invasion, as well as habitat loss and fragmentation. Within the Western Indian Ocean biodiversity hotspot, Reunion Island hosts the most important number of recorded invasive species (Rouget 2020), with 129 invasive plant species representing a considerable invasion debt.

Studying the drivers of invasion is essential to understand what promotes survival, establishment and spread of exotic species and to assess invasion risk (Bellard *et al.* 2016). We have shown in this study that climatic, landscape and anthropogenic factors partly explained invasion levels. Indeed, the three most important variables identified by the analysis were 'rainfall', 'elevation' and 'distance to urban areas'. It is widely recognised that a climate matching between native and invaded regions is an essential condition for successful invasions worldwide (Ficetola *et al.* 2007; Gallardo *et al.* 2015; Bellard *et al.* 2016). Urban areas are also recognised as hotspot for biological invasions and are key points of entry for many alien species and are also responsible for secondary dispersal (Gaertner *et al.* 2017). A more comprehensive study on the drivers of invasion is needed to identify potential pathways of invasion within the National Park.

Increasingly, a wide range of data sources is being used to monitor the distribution of species, including invasive ones. In addition to data obtained during field survey, remote sensing (Royimani *et al.* 2019), modelling (Srivastava *et al.* 2019) or expert knowledge and citizen scientists (Roy-Dufresne *et al.* 2019) can be used to monitor invasive species. Here, this survey was possible because three different sources of data have been used: field survey data, expert knowledge data and modelled data. Available data of IAS abundance and distribution are limited, but this information is essential for their management. Marvin *et al.* (2009) showed that possibly due to an emphasis on early detection and rapid response, it exists a bias towards small infestations areas rather than large ones concerning point distribution of invasive species. These incomplete or spatially biased data could result in incorrect model projections (Thuiller *et al.* 2004). Some of these missing data exist but are not compiled in a digital form but are dispersed amongst a wide range of experts (Marvin *et al.* 2009; Bradley & Marvin 2011). There is a need to further develop citizen science programs to monitor the spread of invasive species and to generate up-to-date species distribution data (Pyšek *et al.* 2020). All IAS that can affect biodiversity and ecosystems are not subject to a surveillance program or are not eligible under government-funded schemes. Engaging volunteers in surveillance and monitoring of IAS is an efficient and low-cost option (Roy *et al.* 2015; Groom *et al.* 2019).

Due to the wide distribution of IAS and the limited resources allocated to this issue, there is a real need to prioritise sites and species for intervention (McGeoch *et al.* 2016). On Reunion Island, a process is currently being implemented to prioritise areas for alien plant clearing and restoration. This will enable to identify the geographic locations for appropriate management interventions and to monitor the effectiveness of clearing efforts. The map of invaded areas produced here would help towards prioritising areas for clearing. We recommend prioritising invasion fronts (i.e. invaded areas adjacent to non-invaded ones) to limit the spread of invasive species into new habitats. Our map enables to identify such invasion fronts. A more comprehensive approach would require additional information on biodiversity value and implementation factors (such as accessibility by clearing teams) in order to prioritise clearing in high biodiversity value, invaded and accessible areas. Up-to-date data on the spread of invasive species will enable to set up management actions in time, including early detection and rapid response programmes (see Büyüktahtakın & Haight 2018 for review).

In Reunion Island, a priority objective, listed in several strategic documents on nature conservation, is the control of the spread of biological invasions. While this new map of invasion degree could help the identification of priority areas for management, important information is missing on the extent and abundance of key invasive species. Additional information (including spatial data) on major invasive species (such as richness, abundance, biological type) should guide the type of management to be carried out: early detection and rapid response, eradication, control or restoration. In Reunion Island, effective control methods are only known and implemented on few species (ONF 2016). Not all alien species are of concern and have the same impacts on environment. For example, transformer alien species that alter the character, condition, form or nature of an ecosystem over area (Richardson *et al.* 2000), deserve special attention. Managing new focal points of invasion by localised invasive species would also seem essential (Tassin *et al.* 2009; Wilson *et al.* 2013).

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CONFLICT OF INTEREST

The authors acknowledge that there is no conflict of interest.

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DATA AVAILABILITY STATEMENT

Data on the degree of invasion are available at https://www.especesinvasives.re/en-pratique/documents-et-outils/article/documents-et-outils

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SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Appendix S1. Accessibility.

Appendix S2. Geomorphology.

Appendix S3. Invasion degree according to vegetation type (level two).

Appendix S4. Major invasive plants species on Reunion Island.

Appendix S5. Spatial distribution of major invasive species on Reunion Island (based on all existing botanical surveys since 1980).

Appendix S6. Misclassification rates per invasion categories for each Random Forest models.

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