

Research Article

Distribution and cover of a recently introduced alien sedge species, *Carex pilulifera* L., in the subalpine vegetation of Reunion Island

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Abstract

Carex pilulifera L., a perennial herb native to Europe, was recently introduced and found in subalpine vegetation of Reunion Island. In this study, we assessed the current distribution and cover of *C. pilulifera* within the subalpine vegetation (Piton des Neiges and Piton de la Fournaise) of the National Park of Reunion. We used GLM models to analyse relationships between *C. pilulifera* and habitat, disturbance type, and proximity to fodder and grazing areas. We evaluated the potential distribution of *C. pilulifera* using species distribution models. Presence of *C. pilulifera* was only found on Piton de la Fournaise with a mean cover of 16.6% (where present). *Carex pilulifera* was the fourth most observed alien species (27% of all observations). According to the SDM, it could also occur in Piton des Neiges but was not found. *Carex pilulifera* was significantly more present in subalpine grasslands and close to grazing and fodder areas. We believed fodder and grazing areas to be the introduction pathways of this species. This study confirmed the status of *C. pilulifera* as an invasive species in the subalpine vegetation of Reunion Island which comprises a high level of plant endemism. We suggest that management should primarily focus on surveying potentially suitable areas in Piton des Neiges to eradicate new introduction and to control the species within high biodiversity areas in Piton de la Fournaise.

Key words: plant invasion, habitat preferences, mountain ecosystems, Mascarene archipelago, tropical oceanic islands

Introduction

Introductions of alien species outside their native range are rapidly increasing and are one of the most significant factors contributing to the reduction of native biodiversity (Johnson et al. 2017). Invasive alien plants (IAS) have direct and indirect impacts on ecosystem diversity and functioning, economics and human health (Blackburn et al. 2014; Pyšek et al. 2020). To limit the ongoing spread of IAS beyond their native range and to direct control actions, it is essential to identify alien species early, and to evaluate and predict their spread and their effects on biodiversity (Aikio et al. 2010).

Herbaceous species are known to possess several characteristics associated with invasiveness such as increased competition, reproduction, and survival (Grime 1973). Indeed, their vegetative reproductive system allows them to exploit resources such as water or nutrients, to the detriment of other species (Antonio and Vitousek 1992; Cabin et al. 2002). Invasive alien herbaceous species have been reported to increase soil nitrogen availability and cycling rates (Hawkes et al. 2005; Blank 2008; Wolkovich et al. 2010) due to faster N turnover (Castro-Díez et al. 2014). Many herbaceous invaders have a relatively high growth rate and can form dense monospecific stands (Wavrek et al. 2017).

The *Carex* genus belongs to the *Cyperaceae* family and contains more than 2000 herbaceous species (Starr et al. 2009). Among these, 34 species are listed as invasive (CABI 2022). For example, *Carex kobomugi* Ohwi is known to be invasive in the United States with impacts on habitats (e.g., reduction of sand dune) and biodiversity (e.g., on rare species) (Burkitt and Wootton 2011; CABI 2022). However, impacts have not been assessed for all alien *Carex* species (CABI 2022). Lack of knowledge of this genus can be partly explained by the morphological similarity between the different species of *Carex* which makes identification difficult (Starr et al. 2009).

Carex pilulifera L., 1753 is a species native to Europe, whose habitat is restricted to hills and mountains. It is found in dry grasslands, close heathlands, and woodlands (especially in forest clearings or along trails), on neutral to acidic soil (Kjellsson 1985). *Carex pilulifera* is a perennial hemicryptophyte herb, allowing it to survive during unfavourable conditions. Being cespitose, this species often forms dense tussocks. The culms are hollow and triangular and usually carry 3 or 4 female spikes and one male spike with a lower bract which is generally membranous and shorter than the stalks. Leaves have brown, reddish lower sheaths, becoming fibrous (Figure 1) (Kjellsson 1985; Leurquin 2005). *Carex pilulifera* have different ways of dispersal (Kjellsson 1985). Myrmecochory allows movement of seeds to safe sites for germination and survival and establishment of pioneer individuals. Dispersal by autochory allows to recruit individuals near the parent plants and establish local dominance of the population. *Carex pilulifera* is also capable of vegetative reproduction and has a phalanx growth form, showing radial spread where the ramet density is often lowest in the central area, forming rings rather than filled circles (Briske and Derner 1998). *Carex pilulifera* has short rhizomes included in the tussock, forming a highly aggregated network with short inter-module distances and many ramifications. This type of growth can result in local dominance (Kjellsson 1985).

Carex pilulifera is known to be present as an alien species in Australia (GBIF 2022) and was recently introduced on Reunion Island (first anecdotal record in 2006, CBNM 2022), but no detailed studies have been carried out to date here on the distribution and invasive status of this alien *Carex* species.

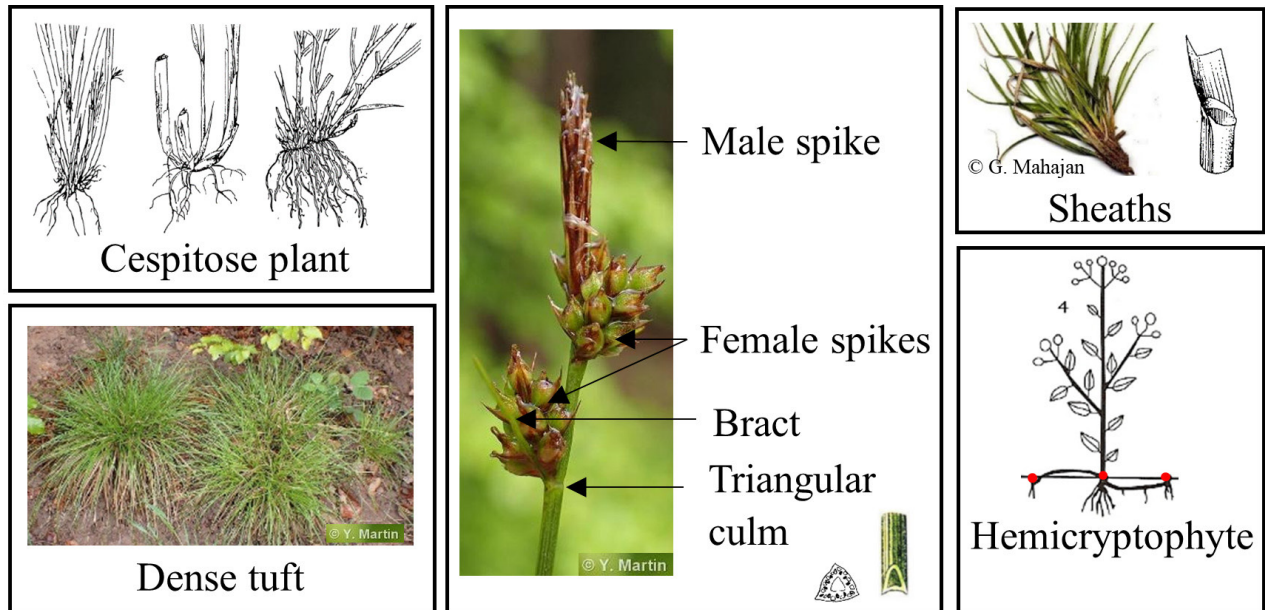


Figure 1. Species identification characteristics of *Carex pilulifera* (adapted from Leurquin 2005).

Localised in the Indian Ocean, Reunion Island is part of the Mascarene biodiversity hotspot (Myers et al. 2000). Of all the islands in the Mascarene archipelago, Reunion has the largest area of intact vegetation (Thébaud et al. 2009) but biological invasions represent the major threat to biodiversity conservation on this island (Turbelin et al. 2017). It is therefore essential to assess invasion risk and to understand the driving factors favouring the survival, establishment and spread of IAS in key biodiversity areas on the island. This paper presents the first assessment of the current and potential distribution of *Carex pilulifera* on Reunion Island and summarises the habitat preference of this species.

Materials and methods

Study site

Reunion Island has an abrupt and varied topography, reaching 3070 meters above sea level (Thébaud et al. 2009). Located near the Tropic of Capricorn, Reunion has a humid tropical climate. The average annual rainfall shows a significant dissymmetry between eastern and western sides of the island due to the topography and high elevation (Réchou et al. 2019). The humid prevailing winds blow from the southeast, with annual rainfall varying from 500 mm in the driest leeward areas to about 12 m in the wettest areas in the windward slopes of Reunion Island (Thébaud et al. 2009). The mean annual temperature ranges from 26 °C on the coast to 11 °C at the highest summit. Such climatic variability leads to very diverse ecosystems ranging from tropical lowland forest to subalpine vegetation (Cadet 1977; Thébaud et al. 2009), with important rates of plant endemism. Indeed, more than 28% of native plants are strictly endemic to Reunion Island, 17% are endemic to the Mascarenes and 15% are endemic to the West Indian Ocean zone (CBNM

2020). However, habitat loss has been severe with about 50% of natural habitats remaining (Fenouillas et al. 2021). Lowlands have been transformed more than high-altitude areas (Fenouillas et al. 2021). Nevertheless, invasive alien species spread throughout Reunion's ecosystems and altitudinal gradient (Fenouillas et al. 2021).

This study focussed on subalpine vegetation (Figure 2A) as *C. pilulifera* is principally found in this type of vegetation in its natural habitat (Kjellsson 1985). Subalpine vegetation represents around 1/5 of the area of Reunion Island and is located above 1700 m of altitude on the windward coast and from 2000 m of altitude on the leeward coast (Cadet 1977). Subalpine vegetation occurs in three main geographic areas: Piton de La Fournaise, Maïdo on Piton des Neiges massif, and the central part on Piton des Neiges (Figure 2A). This vegetation type contains a high level of plant endemism (84.4% including 32.5% strictly endemic to Reunion Island) and is one of the least invaded types by alien plant species (Lacoste and Picot 2011; Fenouillas et al. 2021). However, some woody species such as *Ulex europaeus* L., 1753 and several herbaceous species such as *Anthoxanthum odoratum* L., 1753 and *Hypochaeris radicata* L., 1753 are invasive in the subalpine vegetation (Fenouillas et al. 2021). These alien herbaceous species are much more competitive than native ones and tend to suppress the regeneration of the native species (Lacoste and Picot 2011). In addition to biological invasions, the subalpine vegetation is subject to important anthropogenic disturbances such as fires or uncontrolled grazing by feral cows. Fire and overgrazing have been shown to promote alien species in this vegetation type (*U. europaeus*, *Acacia mearnsii* De Willd, 1925, *A. odoratum*, *Holcus lanatus* L., 1753, *Prunella vulgaris* L., 1753, *H. radicata*, *Carex ovalis* Gooden, 1794) (Boulet et al. 2018).

Data collection

Current distribution

We evaluated the current distribution of *C. pilulifera* within the subalpine vegetation, on two different zones (A: Piton de la Fournaise and B: Maïdo on Piton des Neiges) (Figure 2A). These zones are the largest remaining areas of subalpine vegetation adjacent to fodder and grazing areas, and contain similar habitats (a mosaic of subalpine grasslands and shrublands, with non-perennial streams). Some of these areas were burned in the past.

In Piton de la Fournaise, previous surveys of invasive plants reported *C. pilulifera* in two separate locations: it was found with moderate abundance by Fenouillas et al. (2021) in a natural subalpine habitat surrounded by fodder and grazing areas (location 1 in Figure 2B), and in another isolated patch with few individuals (location 2 in Figure 2B) in subalpine vegetation. We hypothesised that planted rangelands to be the introduction pathway of *C. pilulifera* (J. Dupont *pers. comm.*) and therefore subdivided Zone A

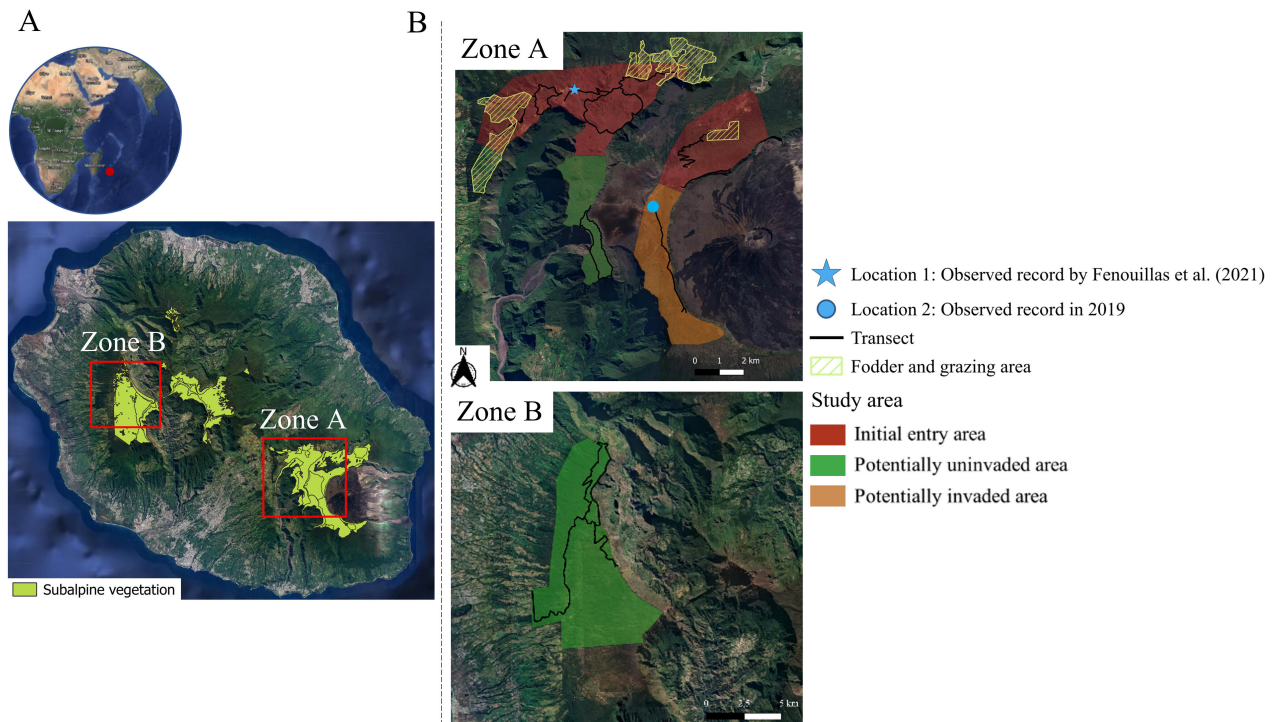


Figure 2. Localisation of Reunion Island (A) and the two study zones (B). Initial entry area: this represents the area where *C. pilulifera* has been first observed in 2019 with high cover (Fenouillas et al. 2021); potentially uninvaded area: this represent the area where *C. pilulifera* has never been observed and is supposedly absent; potentially invaded area: this represent the area where *C. pilulifera* has been seldomly observed in 2019 (map data 2015 Google).

into three distinct areas: (i) a mosaic of natural area and fodder and grazing areas, around location 1, referred to as “initial entry area”; (ii) an “area potentially invaded” around location 2 where no fodder or grazing areas occur and (iii) an “area potentially uninvaded”, where *C. pilulifera* was not recorded in previous surveys and where no fodder or grazing areas occur. *Carex pilulifera* has never been observed in the second zone – Maïdo on Piton des Neiges (B) (Figure 2B).

In both zones, several transects were set up to detect the presence of *C. pilulifera*. As alien species often establish first at ruderal and highly disturbed sites, an effective approach is to record populations along roadsides (Pauchard and Alaback 2004). Transects were chosen according to the different known and suspected populations. Eight transects ranged between 2 and 8 km were set up in zone A. Two transects of 17 and 20 km were set up along major forestry roads and hiking trails in zone B. A total of 81 km of transects was surveyed on foot from January to March 2022.

Two observers walked along each transect and recorded the presence of *C. pilulifera* within a 2 m distance of the road/path. Along the transects, whenever a *C. pilulifera* individual/tuft was found, its location (GPS coordinates and altitude) was recorded. In subalpine grassland patches (a localised vegetation sub-type) greater than 100 m², an exhaustive list of indigenous and alien species was realized in order to record presence and absence data of *C. pilulifera*.

Carex pilulifera was identified based on the different characteristics described by Leurquin (2005) (Figure 1) which allowed it to be distinguished from native *Carex* such as *Carex brunnea* Thunb., 1784, *Carex borbonica* Lam., 1792 or *Carex boryana* Schkuhr, 1806 and from other alien *Carex* as *Carex ovalis* (Autrey et al. 2018). Specimens were collected and sent to the botanical herbarium to confirm identification. *Carex pilulifera* is a perennial, caespitose herb. The culms are trigonous, flexible, and arching after flowering. The leaves are papillose, scabrous on the upper surface, with a short trigonous tip, 1.5–3 mm wide, becoming fibrous; the sheaths are reddish-brown or wine-red, becoming fibrous, usually exceeding the inflorescence. The lower bracts are non-sheathing, leaf-like, awl-shaped, and generally exceeding the inflorescence; the inflorescence is 1.5–3 cm long; one small upper male spike, lanceolate, tawny brown and 2–4 closely spaced female spikes, sessile. The utricles are generally less than 3.5 mm long, bearing hairs and papillae, and are closely applied to the nutlets. The utricles are pubescent, trigonous and wider in the upper half (Kjellsson 1985; Leurquin 2005).

The diagnostic features of *C. pilulifera* is the presence of a single male spike, and several female spikes, and the reddish-brown (or wine-red) colour or the presence of the sheath. The endemic species *C. boryana* does not have sheath, and other *Carex* species (*C. brunnea*, *C. borbonica* and *C. ovalis*) have brown or black sheaths. The three native species (*C. boryana*, *C. brunnea* and *C. borbonica*) have basal female spikes, whereas the two exotic species, *C. pilulifera* and *C. ovalis* have female spikes at the top of the inflorescence. The shape and composition of the spikes can differentiate *C. pilulifera* from *C. ovalis*: *C. ovalis* have between 4–10 ovoid spikes that are agglomerate at the top (Leurquin 2005; ul Haq et al. 2013; Bosser et al. 2018).

Cover, species richness and habitat preference of *C. pilulifera*

In order to measure the cover of *C. pilulifera*, we selected areas where *C. pilulifera* was present (selection based on the resulting distribution map from surveys). *Carex pilulifera* presence areas were subdivided into grid cells of 250 m by 250 m (called sample areas). Sample areas were then selected to estimate plant cover (Figure 3). Four plots of 1 m by 1 m were randomly placed within each selected grid cell. For each plot, we quantified plant cover of all native and alien herbaceous species (Figure 3). In total 244 plots were surveyed. In addition, we also used 909 vegetation plots from Fenouillas (2021), where the cover of *C. pilulifera* was also recorded in 1 m², to complete our dataset.

Carex pilulifera and several other herbaceous plant species are capable of vegetative reproduction and therefore form patches. As it is difficult to estimate the number of individuals in a patch, we decided to use the canopy cover by visual evaluation (vertical projection of the outermost perimeter of the natural spread of foliage of plants expressed as a percentage within the plot) instead of the abundance (number of individuals).

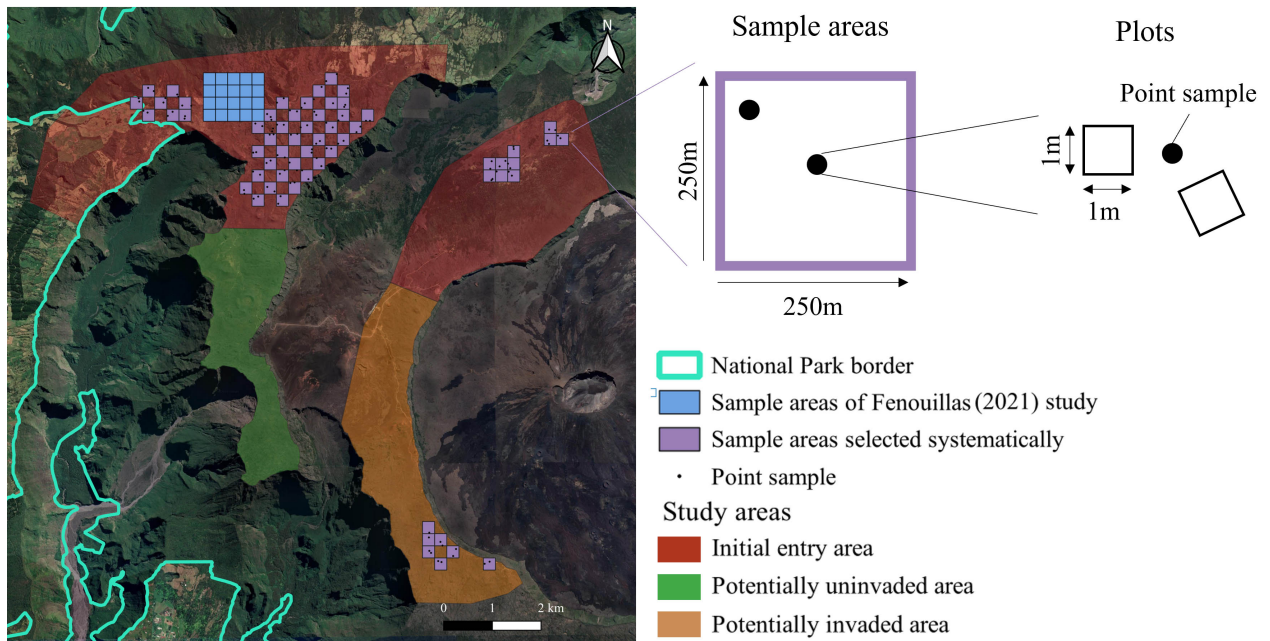


Figure 3. Survey design for measuring species cover and richness of herbaceous species. In blue and purple are areas where a systematic survey was done. The blue area refers to a previous study (Fenouillas et al. 2021) and the purple area refers to this study. Four plots of 1 m by 1 m were randomly placed within each selected grid cell (sample areas of 250 m by 250 m) to quantify the plant cover of all native and alien herbaceous species. (See figure 2 legends) (map data 2015 Google).

In order to identify the habitat preference of *C. pilulifera*, we recorded habitat type (shrubland, subalpine grassland, or non-perennial stream) and the disturbance (evidence of fire or lack thereof) in each plot. Based on the spatial distribution of fodder and grazing areas, we calculated the nearest distance to a grazing/fodder area for each plot in GIS.

Analyses

Analyses were performed using R version 4.1.2 software (RCoreTeam 2021) and all spatial analyses were conducted using QGIS version 3.18 (QGIS. org 2022).

Species distribution modelling

To identify the potential spread of *C. pilulifera*, species distribution models (SDM) were built based on climatic conditions (Guisan et al. 2013; Barbet-Massin et al. 2018).

The models were built with the presence data from the results of the distribution analysis of *C. pilulifera* on Reunion Island. Pseudo-absences were simulated: determining true absences is limited because the species could be absent for reasons other than climatic conditions (for example, not having been detected, not having reached the locality, etc.) (Senay et al. 2013). Pseudo-absences were randomly generated with a minimum distance of 1 km and a maximum distance of 20 km of known records. A total of 386 presence points and 386 pseudo-absence points were used.

Native species on La Reunion are distributed according to annual mean precipitation, varying between east and west coasts, and temperature, varying with elevation (Cadet 1977). Like Baret et al. (2006), we assumed that invasive species are also distributed according to the precipitation and temperature. Temperature variables are commonly used in species distribution modelling and precipitation is important to take into account for marked changes in topography, as dramatic changes in precipitation happens over short distances in La Reunion (Gardner et al. 2019; Booth 2022). Climatic variables (temperature and rainfall) were obtained from the database MétéoFrance (<https://portail-api.meteofrance.fr/devportal/apis>) with a resolution of 150 m. Four variables were selected after testing for autocorrelation: Temperature seasonality (BIO4), rainfall seasonality (BIO15), mean temperature of warmest months (January–February–March) (BIO10) and precipitation of driest quarter months (August–September–October) (BIO17).

To build the SDMs, six different modelling techniques were used, implemented within the *biomod2* package (Thuiller et al. 2021) including two regression methods: Generalized Linear Model (GLM) and Multiple Adaptive Regression Splines (MARS), two classification methods: Classification Tree Analysis (CTA) and Flexible Discriminant Analysis (FDA), one machine learning methods: Random Forest (RF) and an envelope-style method: Surface Range Envelope (SRE). To test the accuracy of the models, we used the true skill statistics (TSS) (Hirzel et al. 2006). We generated an ensemble model by averaging all models with TSS value above 0.8.

Habitat preference of *C. pilulifera*

In order to identify the habitat preference (habitat type, disturbance, and distance to the fodder and grazing areas) of *C. pilulifera*, two generalized linear models (GLMs) were built. We used two explanatory variables: habitat type (habitat burned or not) and distance to fodder and grazing areas. Firstly, we used a GLM from the binomial family to relate the probability of presence of *C. pilulifera* (response variables) to two explanatory variables (Zuur et al. 2009a). We set the intercept to 0. As the data contain considerably more zeros than ones (902 and 216 respectively), a clog-log link function was used (Zuur et al. 2009b). Secondly, we calibrated a GLM with Gaussian family and a logit-link function to assess the relationship between the cover of *C. pilulifera* and the explanatory variables. The response variable, cover of *C. pilulifera*, was log-transformed for normalized residuals (Zuur et al. 2007). We only used data where *C. pilulifera* was present. Selections of the appropriate model to run were done following recommended preliminary graphical exploration, analyses and testing of model assumption. Residuals were used to validate models by checking for outliers and violation of homogeneity (Zuur et al. 2007). We used a backward approach for simplification of the GLM by eliminating the most non-significant predictors

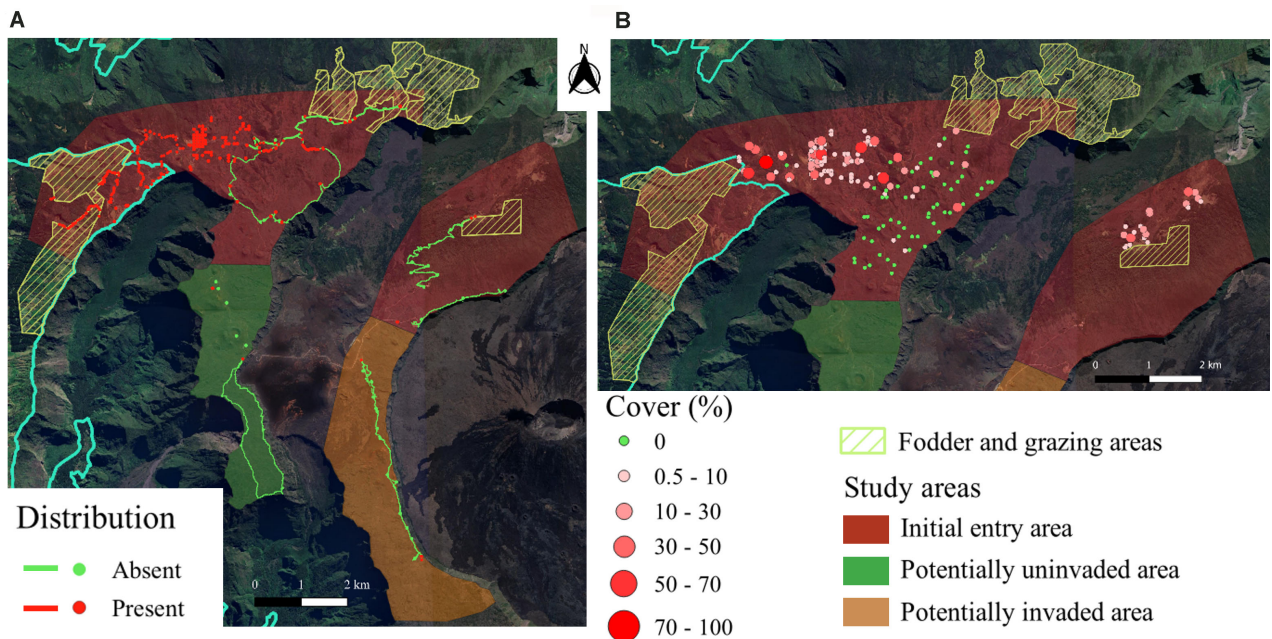


Figure 4. Distribution (A) and cover (B) of *C. pilulifera* in the area of Piton de la Fournaise (map data 2015 Google).

one at a time (Zuur et al. 2009c). Each iteration was compared using Akaike Information Criterion (AIC) to select the most parsimonious model (Zuur et al. 2009c). We calculated the amount of variance explained by the final models (explained deviance) as: $((\text{null deviance} - \text{residual deviance}) / \text{null deviance}) \times 100$ (Zuur et al. 2009c).

Results

Distribution and cover of Carex pilulifera

Current distribution and cover

In total, 36 alien herbaceous species have been observed across the whole study area (Supplementary material Appendix 1). Among them, 29 species have been observed in less than 5% of the samples. *Carex pilulifera* (as well as *P. vulgaris* and *Erigeron karvinskianus* DC., 1836) have been observed in 27% of the 1×1 m invaded plots. *Hypochaeris radicata* and *A. odoratum* have been observed in more than 70% of the invaded plots (respectively, 75 and 72%).

Carex pilulifera has been recorded from 1748 to 2422 m above sea level, with a mean of 2076 m above sea level. Despite a considerable survey effort (37 km of trails and forestry paths), it was not found in non-perennial streams, subalpine grasslands and shrublands in zone B. It was found in zone A but not observed everywhere (Figure 4A). The most frequent observation occurred in the mosaic of natural and fodder and grazing patches, referred as “initial entry area” (Figure 4A). In the “area potentially invaded”, *C. pilulifera* was only observed once, in a subalpine grassland patch, and only twice in the “area potentially uninvasion”, along the major footpath (Figure 4A).

Table 1. Results of the multivariate GLM analyses. Significance of model parameters are denoted with a “*” for $P < 0.05$ and with “***” for $P < 0.001$.

Question	Variables selected from the best model		Results			
			Estimate	SE	z-value	P-value
In which type of habitat and disturbance is <i>C. pilulifera</i> present most often?	Subalpine grassland	Unburned	2,5128	0,3590	6,9985	2,59E-12 ***
		Burned	3,7016	0,4592	8,0616	7,53E-16 ***
	Non-perennial stream	Unburned	0,4650	0,5644	0,8239	0,4100
		Burned	6,1663	68,5503	0,0900	0,9283
And how the distance to fodder and grazing areas affects the present of <i>C. pilulifera</i> ?	Shrubland	Unburned	0,4699	0,2795	1,6814	0,0927 .
		Burned	2,1280	0,4225	5,0361	4,75E-07 ***
	Distance to fodder and grazing area		-1,20E-03	1,39E-04	-8,6550	4,93E-18 ***
	Variables selected from the best model		Estimate	SE	t-value	P-value
When <i>C. pilulifera</i> is present:	Intercept (unburned subalpine grassland)		1,4631	0,1397	10,4725	7,54E-21 ***
In which type of habitat and disturbance level <i>C. pilulifera</i> is the most abundant (cover)?	Subalpine grassland	Burned	-0,1174	0,1645	-0,7139	0,4761
		Unburned	-0,2837	0,2742	-1,0345	0,3021
	Non-perennial stream	Burned	-0,2432	0,2414	-1,0074	0,3149
		Unburned	-0,2347	0,1063	-2,2078	0,0284 *
And how the distance to fodder and grazing area affects the cover of <i>C. pilulifera</i> ?	Shrubland	Burned	-0,2755	0,1349	-2,0430	0,0423 *
		Unburned	-0,2347	0,1063	-2,2078	0,0284 *
	Distance to fodder and grazing area		-1,44E-04	6,56E-05	-2,2032	0,0287 *

In zone A, when *C. pilulifera* was present, its average cover was 16.6% (s.d. of 18.4%). Cover ranges from 0.5% and 90%. The cover of *C. pilulifera* was highest near fodder and grazing areas (Table 1). We could not estimate its cover in the “area potentially invaded” (see Figure 2) as only one *C. pilulifera* tuft was observed.

Potential distribution

Each SDM model displayed a good performance (TSS: from 0.896 to 0.948) (Appendix 2). In the average model (ensemble model), *C. pilulifera* was expected to occur in both study zones (A: Piton de la Fournaise and B: Maïdo on Piton des Neiges massif) which correspond to subalpine vegetation (Figure 5). The area of high likelihood of *Carex pilulifera* presence (> 0.8) represented 91 km² and occurred principally in zone A, part of zone B and in some places in Piton des Neiges (Roche-Ecrite). Medium likelihood of presence (0.4–0.6) was observed around Piton de la Fournaise and in zone B (Maïdo) and represented 33 km² (Figure 5).

Habitat preference of *Carex pilulifera*

There was an effect of habitat/disturbance on the presence and the cover of *C. pilulifera*. The presence of *C. pilulifera* was significantly more likely in burned habitats, and near fodder and grazing areas (Table 1). The presence of *C. pilulifera* was also more likely in subalpine grassland than in the other tested habitats. There was no significant difference in non-perennial streams and unburned shrublands (Table 1). Few variables had a significant effect on *C. pilulifera* cover and the explanatory power of the cover model was lower

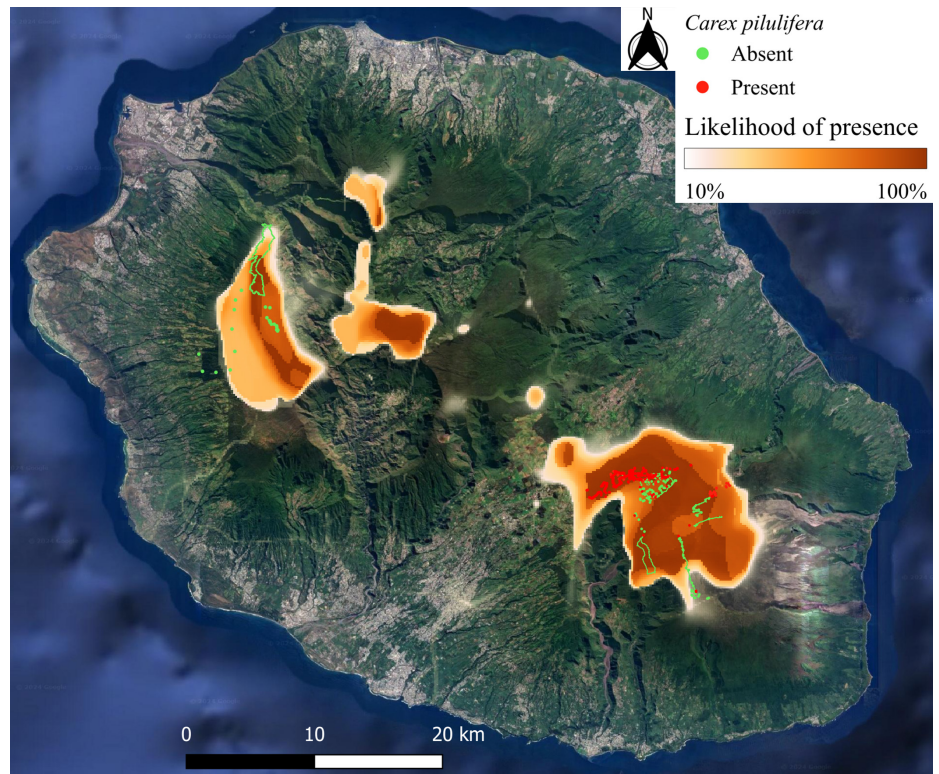


Figure 5. Potential distribution of *C. pilulifera* based on ensemble model. Presence and absence of *C. pilulifera* from surveys are indicated. Likelihoods of presence between 0 and 10% have been removed for the map (map data 2015 Google).

than the one of the presence model. The cover of *C. pilulifera* was significantly lower in shrublands than in unburned subalpine grasslands but higher near fodder and grazing areas (Table 1).

Discussion

This study revealed a widespread distribution of *Carex pilulifera* in the area of Piton de la Fournaise (zone A) and a potential absence in Maïdo on the Piton des Neiges massif. In piton de la Fournaise *C. pilulifera* was mostly distributed near fodder and grazing areas (Table 1). Isolated individual patches were also found near parking areas and along footpaths (see Figure 4A). Mountains are often considered to be at low risk from alien plants, however several studies suggest that mountain ecosystems are not inherently more resistant to invasion than other types of ecosystems (Pauchard et al. 2009; McDougall et al. 2011). Even if our survey revealed no presence of *C. pilulifera* in Maïdo (Zone B, Piton des Neiges), our SDM results indicated that the species could potentially occur in the subalpine vegetation of the Piton des Neiges (including Maïdo). More surveys are necessary to confirm the presence or the absence in the subalpine vegetation areas on the Piton des Neiges massif. The species might have not been introduced yet and its absence might be due to the lack of dispersal in the early phase of the invasion process. The topography of Reunion Island might be a natural barrier for the spread of *C. pilulifera*. *Carex pilulifera* might have not yet reached this

locality. Spread into areas away from sites of introduction is limited by geographic barriers and often needs humans to access the new environment (Richardson et al. 2000). Considering its high cover and widespread distribution, this species can be considered as locally invasive in the area of Piton de la Fournaise. We suspect that the presence of *C. pilulifera* may have been underestimated in previous botanical surveys in Reunion Island. In *Carex* species, reliable morphological identification is complicated due to closely related species (Standley et al 2002). Identification mostly requires reproductivity mature material that is not available all the time and a good understanding of the morphology of the genus (Naczi and Bryson 2002).

Carex pilulifera was probably introduced for foraging purposes or by unvolunteered ways (e.g., *C. pilulifera* seeds contamination in pasture seeds mix). Pastures can be a major source of invasions because they are dominated by alien plant species that out-compete native species, which do not tolerate grazing by cattle (Clout et al. 2009; Driscoll et al. 2014; Boulet et al. 2018). *Anthoxanthum odoratum*, *Holcus lanatus*, *Prunella vulgaris*, *Hypochaeris radicata*, *Carex ovalis* are examples of alien species introduced through pastures, most of them being well-established now in the subalpine vegetation of Reunion Island (Fenouillas et al. 2021). *Carex pilulifera* probably spreads into the protected area via footpaths and roads. Both are suitable habitats and represents one of the most important pathways for the dispersal of alien species into new territories (Godefroid and Koedam 2004; Truscott et al. 2005).

Carex pilulifera was more present in subalpine grassland vegetation than in other habitats (Table 1). In its native range, *C. pilulifera* was generally found in grassland and in closed heathland (INPN 2022). Subalpine vegetation on the Piton de la Fournaise massif is a low and open heathland comprising mainly native species as *Stoebe passerinoïdes* (Lam.) Willd., 1803, *Phyllis nitida* Lam., 1797, *Erica reunionnensis* E.G.H. Oliv., 1993, *Hypericum lanceolatum* subsp. *angustifolium* (Lam.) N. Robson, 1979, *Hubertia tomentosa* var. *conyzoides* (Bory) C. Jeffrey, 1992 and *Faujasia squamosa* (Bory) C. Jeffrey, 1992 with high level of plant endemism (Strasberg et al. 2005; Ah-Peng et al. 2014). The subalpine vegetation contains patches of subalpine grasslands (Strasberg et al. 2005; Ah-Peng et al. 2014) which were more invaded by *C. pilulifera* than other habitats (Baret et al. 2006), probably due to uncontrolled grazing by feral cows (Boulet et al. 2018). Disturbances increase resource availabilities which promote the colonisation of invasive alien species (Davis et al. 2000; Lake and Leishman 2004). Disturbance also reduces the cover of competitors of alien plants by destroying native plant populations. Therefore, alien plants can colonize disturbed area easily using less energy for competition than in undisturbed areas (Davis et al. 2000). In particular, alien herbaceous species often occur in degraded or disturbed grassland areas such as fallow agricultural areas, pasture, mowed areas and roadsides. This is the case for *A. odoratum*, *Holcus lanatus*, *Prunella vulgaris*, *H. radicata*, *Carex ovalis* in Reunion Island (Boulet et al. 2018; Gentili and Citterio 2021).

Several management strategies could be considered for *C. pilulifera*. Given that the species is already widespread over a large area, eradicating the species throughout its entire range is no longer possible. However, one could contain its spread and avoid new infestations in Piton de la Fournaise. For example, in the area initially labelled “potentially invaded” (see Figure 2), one could locally eradicate the species as few individuals have been found. In Piton des Neiges, where the species has not yet been found, eradication might be possible if control is done early. It is important to carry on monitoring in Piton des Neiges and to remove any individual to keep this area free from *C. pilulifera*. We also recommend investigating clearing techniques and restoration protocols as it is not known how to restore densely-invaded areas by *C. pilulifera*.

Studying the impact of *C. pilulifera* would be important to determine how the species exploits the environment and facilitate effective control and restoration programs (van Kleunen et al. 2014). However, it is challenging to estimate impact at early stage of the invasion process. Although some invasive species can be associated with specific trait (Mathakutha et al. 2019; Milbau et al. 2003), no studies has been conducted on *Carex* species. Dense tussocks formed by *C. pilulifera* might reduce the cover of other species and influence the local environment characteristics and the community structure (Leurquin 2005). *Carex pilulifera* exhibits different ways of reproduction (phalanx-type vegetative reproduction and auto-gamy reproduction), rapid and early germination, and a capacity to survive during unfavourable conditions (Harper 1977; Kjellsson 1985). These traits suggest a strong colonisation capacity and a local dominance (Baker 1965; Kjellsson 1985). Therefore, *C. pilulifera* have a long-lived seed bank (viable for 30–40 years) (Mallik et al. 1984), which can ensure its colonisation potential over time. Long-term monitoring could be carried out to analyse the effect of the invasion on the species composition and the environmental structure (Hejda and Pyšek 2006). Analysing the different associations between the presence of *C. pilulifera* and alien herbaceous species would also allow a better understanding of its biological invasion.

Conclusions

Our study shows that *C. pilulifera* is well established in the subalpine vegetation of Piton de la Fournaise as *A. odoratum* and *H. radicata* (Fenouillas et al. 2021) and is principally distributed near areas of higher human activity. Effective management of invasive alien plants on La Reunion Island is crucially important for preserving natural habitats. Therefore, we suggest that management in Piton des Neiges should primarily focus on surveying potentially suitable areas to eradicate newly established patches of *C. pilulifera*. Within the current range of *C. pilulifera*, we suggest preventing spatial spread in order to prevent escalating impact.

Author's contribution

OBG, CAS and MR equally contributed to research conceptualisation, sampling design and methodology. All authors contributed to investigation and data collection. OBG conducted all data analysis and wrote the original draft. All the other co-authors contributed to reviewing and editing the manuscript.

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Ethics and permits

A research permit was obtained from the National Park of Reunion Island to conduct this study (DIR-I-2022-163).

Availability of data

The datasets used and/or analysed during the current study are available at <https://dataverse.cirad.fr/dataset.xhtml?persistentId=doi:10.18167/DVN1/85EKDH>.

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Supplementary material

The following supplementary material is available for this article:

Appendix 1. List of the 36 alien species.

Appendix 2. Result of the evaluations (TSS and ROC) and potential distribution of the six different methods used for the SDMs of *C. pilulifera*.

This material is available as part of online article from:

http://www.reabic.net/journals/bir/2024/Supplements/BIR_2024_Boulesnane-Guengant_etal_SupplementaryMaterial.pdf