

Predicting the Invasion Risk of *Miconia calvenscens* in the Marquesas Islands (South Pacific): A Modeling Approach¹

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Abstract: Predicting the distribution of alien species in areas not yet reached or where the species are still found in low abundance is crucial for implementing timely management strategies. *Miconia calvenscens* has become one of the worst plant invaders in the Pacific including in the Society Islands (French Polynesia), the Hawaiian Islands, and tropical Australia. The species has been recently introduced to the Marquesas Islands (French Polynesia) where it started to spread. In this study, we aimed at predicting the potential distribution of *Miconia* across this archipelago. MAXENT modelling based on ~3,000 occurrence records from the native and introduced ranges of the species was used to predict its equilibrium distribution. Two types of environmental variables acting at different scales were considered: (1) climate variables at a 1 km scale for predicting the invasion risk over still *Miconia*-free Marquesan islands; and (2) topographic variables at a 10 m scale for refining prospections and guiding management strategies on the islands of Nuku Hiva and Fatu Hiva where *Miconia* currently occupies ~0.01% of the surface. Results differed substantially according to the origin of inputted occurrence records but models generally indicated that *Miconia* has the potential to spread over all inhabited Marquesan islands and over half of Nuku Hiva and a third of Fatu Hiva. Our approach provides valuable information for stakeholders to prevent future outbreaks. Without strong biosecurity measures, an early warning system, and appropriate control strategies in areas where it is already naturalized, *Miconia* could become a great threat to the outstanding biodiversity of the Marquesas Islands.

Keywords: Melastomataceae, MAXENT, niche modeling, plant, Tahiti, weed

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INVASIVE ALIEN SPECIES are major drivers of biodiversity loss (Millennium Ecosystem Assessment 2005), with dramatic impacts on oceanic island endemic biota (Vitousek 1988, Kueffer et al. 2010, Tershy et al. 2015, Russell et al. 2017). Invasive species often benefit from competitive advantages and the lack of their natural predators, while many island endemic species show lower competitive capabilities and lower growth plasticity (Loope and Mueller-Dombois 1989). Moreover, inherent characteristics of island ecosystems such as low species richness and low number of species in certain taxonomic lineages or with certain functional traits in comparison with continents provide opportunity for invasive species to take advantage of vacant niches and unused resources (Denslow 2003).

Species distribution models (SDM) are empirical methods increasingly used to extrapolate species distributions based on occurrence records (e.g., herbarium or museum specimens) combined with spatially explicit environmental variables (Phillips et al. 2006). These models found application in many fields including conservation, ecology, evolution, epidemiology, and invasive species management (Guisan and Thuiller 2005). They are especially useful in poorly sampled regions (e.g., remote tropical islands) where they provide a valuable tool for studying species distribution (Anderson et al. 2002).

Several attempts to map the potential distribution of invasive alien species in new introduction areas on the basis of SDM have been made in the last decades. Some SDM were built from occurrences in the invaded range of the species (e.g., Anderson et al. 2002, Ganeshiah et al. 2003, Underwood et al. 2004, Muñoz and Real 2006, Ward 2007). However, building SDM for ongoing invasions might pose a theoretical problem as there is a postulate behind SDM assuming that the species are in equilibrium with their environment, and this assumption is likely to be violated during early invasion stages (Guisan and Thuiller 2005). Thus, only regions where this equilibrium is respected (or nearly) can provide a reliable perspective of the environmental envelope occupied by a species.

Hence, other research has been based on occurrence records from the native range of the target species (e.g., Peterson and Vieglais 2001, Peterson et al. 2003, Iguchi et al. 2004, Giovanelli et al. 2007). A major uncertainty behind this approach is how invasive species will behave in areas with different recipient communities. For instance, projecting the distribution of an invasive species on an island on the basis of its continental distribution would ignore inherent characteristics of island ecosystems and biota (e.g., low species richness, low functional redundancy, specialized habitat), which can enlarge the environmental niche naturally occupied by the invasive species.

An alternative approach is to consider all distributional information available from both the native and invaded ranges of invasive species (e.g., Kriticos and Randall 2001,

Peterson and Robins 2003, Ficetola et al. 2007, Loo et al. 2007, Elith et al. 2012, Iñiguez and Morejón 2012, Kriticos et al. 2013, Lopez et al. 2017, Renteria et al. 2017).

In this study, we focused on *Miconia calvescens* DC (hereafter *Miconia*), a small tree native to Central and South America. The bicolorous form of *Miconia* with very large leaves (up to 1 m in length) and purple undersides occurs only in Central America, from southern Mexico to Costa Rica between 8–17° N and 77–100° W, with a mean annual precipitation above 2,000 mm/year and a mean annual temperature of about 22°C (Budowski 1965, Meyer 1997, 1998) (Figure 1). According to herbarium specimens, *Miconia* is found from lowland to montane tropical forests up to 1,350 m in Guatemala. It occurs under dense shade of primary forests, in open vegetation and disturbed habitats (Meyer 1996).

Miconia was propagated in many botanical gardens in the tropics, and has subsequently become a dominant plant invader in some tropical regions (Meyer 1997). It is currently locally naturalized or invasive in 16 oceanic and continental islands of the Pacific, Atlantic, and Indian Oceans, as well as in the Queensland region of Australia, with invaded areas reaching 80,000 ha in Tahiti (Society Islands) (Meyer 2009) and 100,000 ha in Hawai'i (Tavares and Santo 2002) (Figure 1). The success of *Miconia* as an invasive plant species is due to its self-reproductive capacity, significant (50,000 seeds/m²) and persistent (at least 16 years) soil seed bank, active seed dispersal by birds and rodents, and accidental transportation by humans (Meyer 1998, 2009). By forming dense monospecific stands, *Miconia* constitutes a direct or potential threat to native and endemic island floras. For example, 40 to 50 of the 107 plant species strictly endemic to Tahiti were considered threatened by *Miconia* (Meyer and Florence 1996), many of them classified as CR (critically endangered) and EN (endangered) according to the IUCN Red List categories (IUCN France et al. 2015). The species may also affect forest ecosystem services as it promotes soil erosion and landslides on steep slopes (Nanko et al. 2015). Therefore, it has been classified among the “100 of the world’s

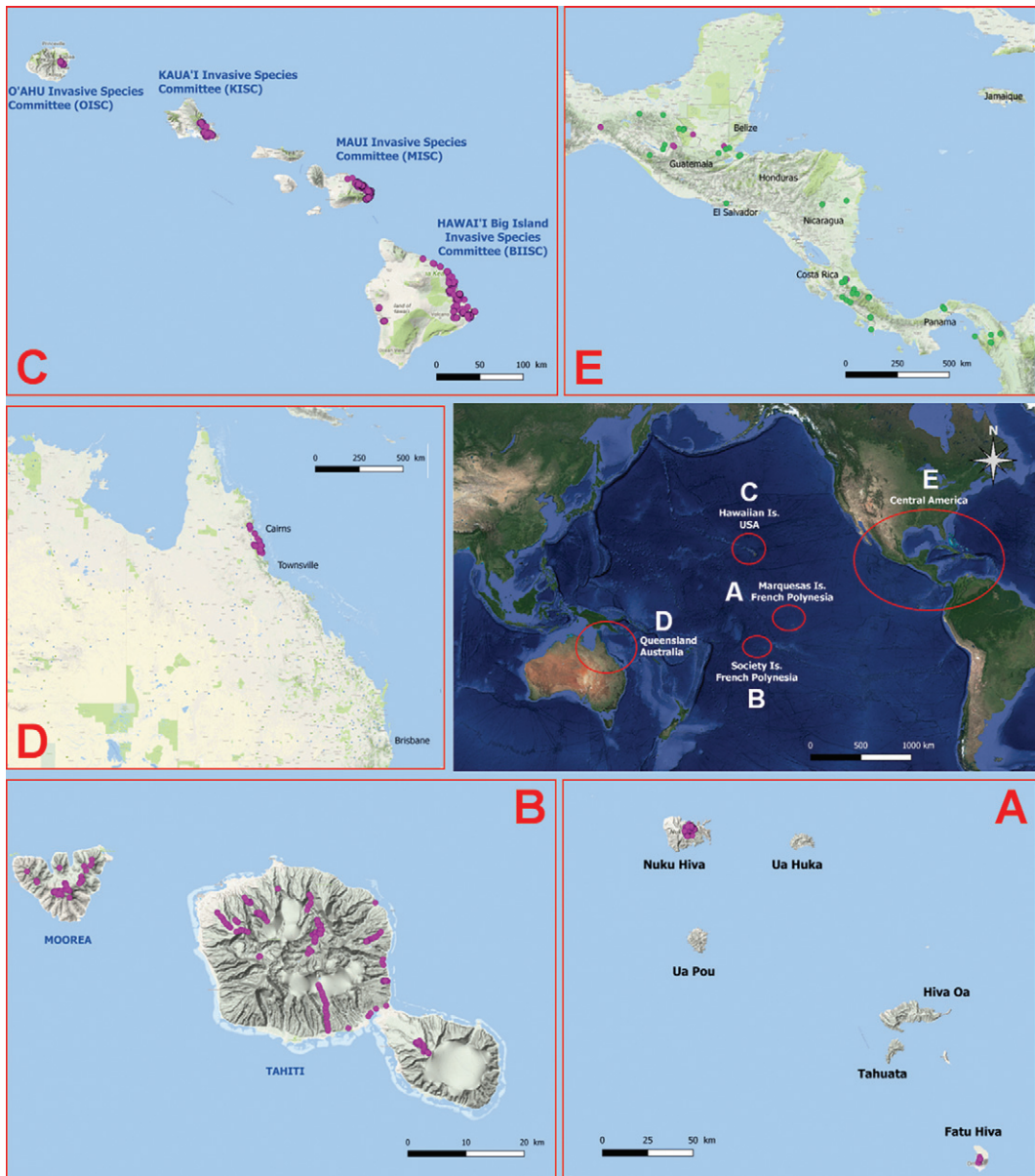


FIGURE 1. Location of the Marquesas Islands (A) and the different regions used to calibrate species distribution models (B–E) with the associated occurrence records (purple points). Green points denote herbarium specimens without bicolorous leaves not included in the models.

worst invasive alien species” (Lowe et al. 2000), a “noxious plant” in Queensland, Australia (Csurhes 2008), and a “threat to the biodiversity” in French Polynesia in 1997 (Meyer et al. 2011).

The Marquesas archipelago, located 1,400 km northeast of Tahiti and 4,000 km southeast of Hawai‘i (North Pacific), is one of the world’s most isolated island groups. Due to this remoteness, the vascular flora is unique,

with an endemism rate of 48% (Lorence et al. 2016), but also highly vulnerable as the Marquesas host the highest number of threatened endemic plant species in French Polynesia (131 species; IUCN France et al. 2015). Invasive alien plant and animal species (mainly rats, feral pigs, goats, sheep, and horses) are among the main threats to native forests (Meyer 2016). So far, *Miconia* is found in small numbers on two Marquesan islands: Nuku Hiva (387 km²) with less than 5 ha invaded and Fatu Hiva (84 km²) with less than 1 ha invaded (i.e., .01% of the surface of the islands) (Meyer et al. 2011). Management programs have been conducted in the Society and the Marquesas islands using manual (uprooting), chemical, and/or biological control methods since the early 1990s. Despite more than 25 years of control effort in the Society Islands, *Miconia* is still present, as rough terrain, steep slopes, and dense vegetation are barriers to eradication or containment, and the species continues to spread on Nuku Hiva at an alarming rate (Meyer et al. 2011).

The aim of this study is twofold: (1) to examine whether *Miconia* has the potential to invade inhabited islands of the Marquesas where it is still thought to be absent; and (2) to determine the fine-scale potential distribution of *Miconia* on islands where it is now present in order to refine prospection areas and guide management strategies. To address the first question, a range of SDM based on large-scale climate variables and occurrence records from Society Islands, Hawaiian Islands, Queensland in Australia (invaded range), and Central America (native range) were built. For the second question SDM based on fine-scale topographic variables and the distribution of *Miconia* on the closely related archipelagoes of the Society and Hawai'i were built. On these islands, *Miconia* is present and has been reproducing for a long time: e.g., Tahiti (ca. 80 years), Hawai'i (ca. 60 years), Moorea (ca. 50 years) (Meyer 2009). The Marquesas, Society, and Hawaiian Islands are regions with many common features: a volcanic origin of approximately the same age (between 1 and 5 myrs old for the high islands), a high endemism rate, and many endemic and native genera in common (Wagner et al. 1990,

Florence 1993), comparable climates due to their similar distance to the Equator, and a shared human colonization history between 1,000 and 500 years ago (Armstrong 1983, Dupon et al. 1993).

From a more theoretical point of view, this study represents a unique opportunity to test how a set of circumstances with regard to climate range, residency time, and control effort will affect SDM projections. We hypothesize that SDM will produce more accurate predictions when calibrated (a) on wider climate ranges or over higher geographical extents, as they will offer a more comprehensive perspective of the environmental conditions favored by the species and thus a better fit of its ecological niche; (b) over areas where the species is present for a longer time so that the species have had more time to reach its equilibrium; and (c) over areas with less intense control effort so that the distribution of the species is more likely to reflect environmental preferences rather than the distribution of control efforts.

MATERIALS AND METHODS

Occurrence Records

A total of 2,996 occurrences were compiled in the Marquesas (401), the Society Islands (220), the Hawaiian Islands (2,040), Queensland in Australia (282), and Central America (53) (Table 1 and Figure 1; see Appendix 1 for a detailed description of study sites). Occurrences in French Polynesia (Marquesas and the Society) were sampled opportunistically by the authors and by contractors of the "Direction de l'Environnement" (Environmental Department, DIREN) during many field surveys conducted between 2008 and 2018. Additional data were provided by the Invasive Species Committee (ISC) in the Hawaiian Islands, and by the National Four Tropical Weeds Eradication Program (4TWP) in Australia. Herbarium specimens listed in the Global Biodiversity Information Facility (<https://www.gbif.org/>, GBIF) were used to determine the native range of *Miconia* from Central to South America. All specimens identified as *Miconia calvescens* in this database

TABLE 1
Summary of the Occurrence Dataset Compiled for This Study

Region	Island	# of Occurrences before “Cleaning”	# of Occurrences after “Cleaning”	Source
Marquesas	Nuku Hiva	370	370	DIREN
	Fatu Hiva	31	31	DIREN
Society Islands	Tahiti	2,213	172	The authors
	Mo’orea	102	48	The authors
Hawaiian Islands	Hawai’i	3,924	1,087	BIISC
	Maui	24,534	650	MISC
	O’ahu	2,265	142	OISC
	Kaua’i	1,842	161	KISC
Queensland, Australia		2,665	282	4TWP
Central America		146	53	GBIF
Total		38,092	2,996	—

(1,485) have been checked and their labels or associated information consulted. Among these records, only 18 annotations of purple leaf undersides (bicolor form) were referenced and they were all found in Central America. As a result, only occurrences from Central America where most of bicolor populations are found were considered. The resulting GBIF dataset was then cleaned by converting different units of measure (foot versus meters), and removing duplicate points or data with no latitude and/or longitude (Table 1). In the Hawaiian islands and Queensland, all points in which *Miconia* might have been cultivated—i.e., located at less than 50 m from dwellings or in botanical gardens—were ignored. Only mature plants were considered in the invaded range but the reproductive status in the native range remained unknown for most specimens.

Occurrence records were derived from opportunistic sampling prone to spatial bias associated with clustered points that can induce an overrepresentation of a specific environment in SDM (e.g., ca. 2,000 occurrences from Pouteau et al. [2011a] in the Papenoo valley of Tahiti). As a result, we removed the fewest records necessary to substantially reduce the effects of sampling bias, while simultaneously retaining the greatest amount of useful information. This step was performed with the R package “spThin”

using a distance of 100 m (Aiello-Lammens et al. 2014). This distance chosen empirically was assumed to mirror the important environmental changes occurring over relatively short distances on topographically complex high-elevation volcanic islands.

Environmental Variables

Climate Data for Predicting Invasion Risk in the Marquesas Islands — Climate is one of the most important factors determining the suitability of a site for a plant to grow (Miller 2010). Thus, identifying the climatic limits and envelope of *Miconia* might help to better understand its invasion process (Jiménez-Valverde et al. 2011). Climate variables were used to determine the environmental envelope of *Miconia*, i.e., the conjunction of climatic conditions within which a species is able to persist and maintain stable population (Grinnell 1917).

Climate variables were downloaded from the WorldClim version 2 database, a free climate dataset based on records from 1971 to 2000 with a spatial resolution of ca. 1 km (<http://www.worldclim.org/>; Fick and Hijmans 2017). Five climate variables were retained according to our knowledge of the physiological needs of *Miconia* and variable collinearity ($|r| < .70$, as recommended by Dormann et al. [2013], after which collinearity begins to severely distort

model estimations and subsequent predictions): average annual temperature (°C), annual rainfall (mm/year), precipitation of the driest month (mm), precipitation seasonality (%), and annual wind speed (m/s).

Topographical Variables for Refining Projections and Guiding Management Strategies on Nuku Hiva and Fatu Hiva — Five topographical variables derived from a set of digital elevation models (DEM) were selected: (a) elevation (m), which is linearly correlated with air temperature according to a lapse rate of $-0.6^{\circ}\text{C}/100\text{ m}$ (Baruch and Goldstein 1999). Yet, temperature is one of the major factors that control vegetation zonation and key processes such as evapotranspiration, carbon fixation, plant productivity, and mortality in mountain ecosystems (Chen et al. 1999); (b) slope steepness (radians) driving water flux and potentially influencing seed dispersion (Wilson and Gallant 2000); (c) potential solar radiation (kWh/m^2) quantifying the energy received by the soil, which appears to have an influence on photosynthesis and evapotranspiration necessary for plants to grow (Fu and Rich 2000); (d) a topographic wetness index (*TWI*, dimensionless) describing the hydrological flow with low *TWI* values corresponding to convex areas, like mountain crests and high values concave areas like hillslope bases (Gessler et al. 2000): $TWI = \ln(A_s/\tan(\beta))$, where A_s refers to the specific catchment area (expressed in m^2) and β to the slope (in radians); and (e) windwardness (%), a windward/leeward unidimensional index that takes a value above 1 for areas exposed to wind and below 1 for wind-shadowed areas (Böhner and Antoni 2009). These topographic variables have been successfully used to model the distribution of *Miconia* in the Hawaiian Islands (LaRosa et al. 2007) and some of the Society Islands (Pouteau et al. 2011a, b). They were extracted from DEM using the software SAGA (System for Automated Geoscientific Analyses; Conrad et al. 2015).

The 5 m resolution DEM of the Marquesas (Nuku Hiva and Fatu Hiva) and the Society Islands (Tahiti and Moorea) were provided by the Service de l'Urbanisme (Urbanism Department) of the Government of French Polynesia. They were upscaled to a 10 m

resolution by averaging 2×2 adjacent pixels. The 10 m resolution DEM of Hawaiian islands were downloaded from the website of the University of Hawai'i (<http://www.soest.hawaii.edu/>). A jack-knife approach was used to evaluate the difference in accuracy between a full SDM and one with each environmental variable omitted in turns, and this difference was used to assess the relative importance of environmental variables.

Species Distribution Modeling

The MAXENT approach was chosen as it is easy to use and it performs well (Merow et al. 2013). This statistical model is based on presences and pseudo-absences (randomly selected points where the absence of the target species is assumed), which was useful in our study in which absence data were lacking (Phillips et al. 2006). MAXENT is a machine learning method based on the maximum entropy approach (i.e., it minimizes the relative entropy between the probability density estimated for the presence records and that for the landscape), which estimates a distribution probability for each pixel in the study area satisfying the given constraints (Phillips et al. 2006).

SDM built to predict the risk of invasion in the Marquesas archipelago (based on climate data) were calibrated on all regions (Society and Hawaiian Islands, Queensland in Australia, and Central America) first taken separately then taken together. Five potential distribution maps were thus obtained in the Marquesas Islands. SDM built to refine field surveys and guide management strategies on Nuku Hiva and Fatu Hiva (based on topographic data) were calibrated on the island of Hawai'i ("Big Island") ($10,458\text{ km}^2$), taken individually due to limited computational resources; other Hawaiian Islands (O'ahu, Maui, and Kaua'i); and the Society Islands (Tahiti and Moorea). Three local-scale maps of the potential distribution of *Miconia* on Nuku Hiva and Fatu Hiva were thus obtained.

SDM were trained on 10,000 pseudo-absence points drawn at random from background pixels. The convergence threshold was set at .00001, and the maximum number of iterations at 500 and suitable regularization

values, β , included to reduce overfitting were selected automatically by the program (Phillips et al. 2006). To assess the predictive capacity of the SDM, we randomly split the data at each run so that SDM were calibrated using 70% of species occurrences and evaluated for predictive accuracy using the remaining 30% of the dataset.

Model Assessment

The area under the receiver operating characteristics (ROC) curves (AUC) was used to evaluate SDM performance (Phillips et al. 2006). The ROC curve is a plot of sensitivity (i.e., the proportion of presences correctly predicted as presences) on the y -axis and 1-specificity (i.e., the proportion of absences correctly predicted as absences) on the x -axis. Sensitivity measures the proportion of positives that are correctly identified as such (observed present correctly predicted). Specificity measures the proportion of negatives that are correctly identified as such (observed absent correctly predicted). A random model is expected to have an AUC of 0.5 and a model with an AUC of 1.0 considered as perfect. The AUC is a useful indicator to estimate the accuracy of an SDM but it should be used with caution as (a) it is calculated from occurrences used to calibrate the SDM and not from occurrences in the invaded area (the Marquesas Islands in our case), and (b) a higher geographical extent will give a higher AUC, so that values of SDM calibrated on different regions cannot actually be compared (Lobo et al. 2007).

RESULTS

The SDM based on the Australian distribution of *Miconia* yielded the highest AUC (0.99) followed by the SDM based on Central America, which had a slightly lower AUC (0.96). Both SDM described suitable areas for *Miconia* mainly on the windward coast of the islands, where there is greater precipitation (Figure 2). This pattern was reflected by variable contributions, as precipitation of the driest month was the most important variable in the Australian SDM (Figure 3C) and annual

rainfall the most contributing variable in the Central American SDM (Figure 3D). In contrast, the SDM calibrated on the Society Islands produced the lowest AUC (0.89). This SDM was mainly based on precipitation seasonality and predicted low invasion risk in all the Marquesas Islands (Figures 2 and 3A). According to the SDM used to fit the distribution of *Miconia* in the Hawaiian Islands and all regions taken together, which performed reasonably well ($0.95 < \text{AUC} < 0.98$), the islands of Hiva Oa, Ua Huka, Ua Pou, and Tahuata, where *Miconia* is still absent, appeared to be potentially suitable (Figure 2). These SDM gave special significance to mean climate variables (annual rainfall and temperature) and their degree of variation (precipitation of the driest month) (Figure 3B and 3E).

The SDM based on topographic variables and the distribution of *Miconia* in the Society Islands had an AUC of 0.77. Mainly based on the slope variable (Figure 4A), this SDM estimated that 46% of the island of Nuku Hiva and 33% of Fatu Hiva present suitable environmental conditions for *Miconia* (habitat suitability > 0.5). Other SDM calibrated on Hawai'i had a higher AUC ($0.87 < \text{AUC} < 0.92$). They were mainly based on the elevation variable (Figure 4B and 4C) and predicted potentially invaded areas at much lower elevations, only located on coastal sites (Figure 5).

DISCUSSION

The threat of *Miconia* invasion across the Marquesas Islands was assessed through an array of SDM using two types of environmental variables acting at different scales and a set of occurrence records of different origins. Results based on climate variables differed substantially according to the origin of inputted occurrence records but SDM generally agreed that *Miconia* has the potential to spread over most inhabited Marquesan islands where the species is still absent. Models based on topographic variables also gave very contrasting results and the most accurate map indicated that almost half of Nuku Hiva (46%) and a third of Fatu Hiva (33%) offer suitable environmental conditions for *Miconia* to become invasive.

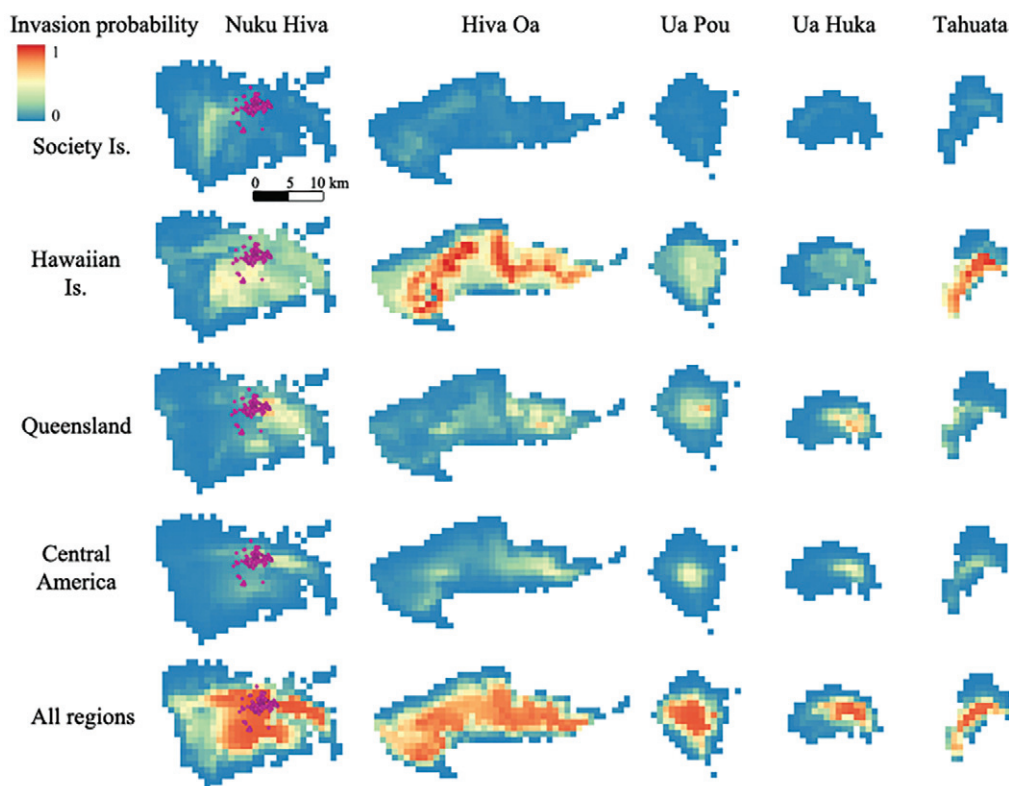


FIGURE 2. Equilibrium distribution of *Miconia* in the Marquesas Islands based on climate variables. The different Marquesas Islands are given in columns (no WorldClim data are available on Fatu Hiva) and the origin of occurrence records used to calibrate species distribution models is given in lines. Purple points indicate available occurrence records.

Between-SDM discrepancies demonstrate the importance of considering different origins for occurrences to be used to calibrate SDM, including both the native and invaded range of the species. Despite uncertainties on how *Miconia* will behave in areas with different recipient communities, our approach provides valuable information for stakeholders on what could be expected in the future.

Effects of Climate Range, Residency Time, and Control Effort on SDM Predictions

Not surprisingly, SDM accuracy was found to be positively influenced by the spatial extent of the region used for calibration with Australia, Central America, and the four regions taken together leading to the highest

AUC values. However, residency time and control effort did not appear to affect SDM success at the regional scale, where climate seems to predominate. In contrast, they were both found to affect SDM success at smaller scale as the SDM based on the Society Islands, where the species have had more time to spread (80 years) under little control, outperformed the SDM based on the Hawaiian Islands, where the species is present for a shorter length of time (60 years) and with an intense control program.

Invasion Risk of Miconia in the Marquesas Islands

A relatively low number of occurrences were found in the native region of Central America

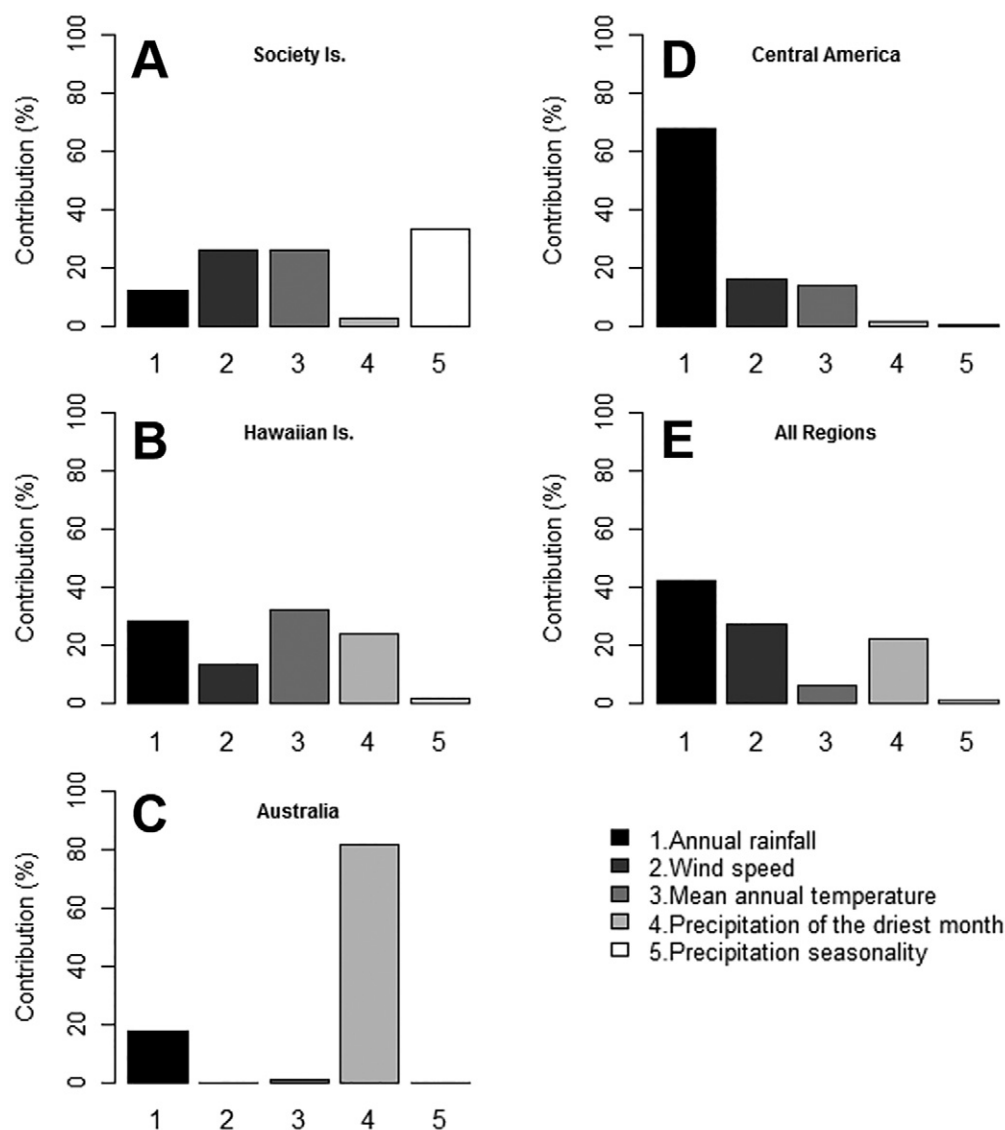


FIGURE 3. Relative importance of the five climate variables used to project the distribution of *Miconia* in the Marquesas Islands according to the origin of occurrence records used to calibrate species distribution models.

(Figure 1E), which could have led to an underestimation of the potential distribution of *Miconia* in the Marquesas (Figure 2). The relative early stage of invasion in Australia and the Hawaiian Islands could also have affected the resulting maps. For these reasons, the SDM calibrated with all regions taken together may have produced the most reliable

potential distribution of *Miconia* in the Marquesas.

The SDM built from occurrences of *Miconia* in the Hawaiian Islands and all regions taken together converged and predicted a much wider potential distribution than the best performing SDM based on occurrences in Australia or Central America

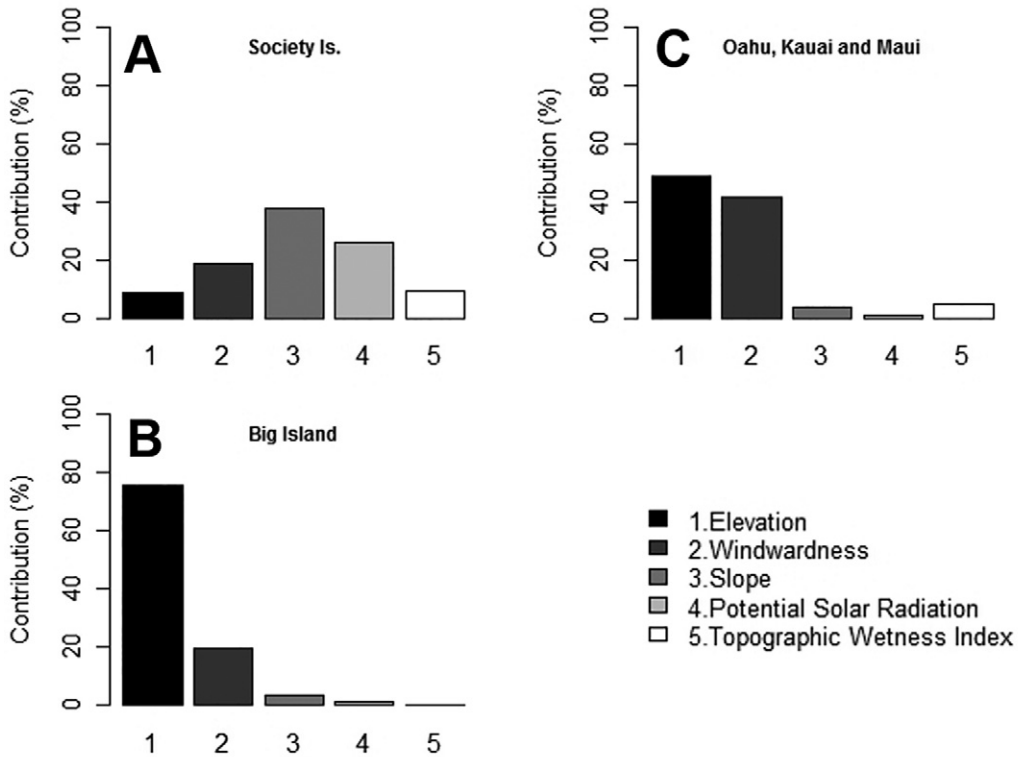


FIGURE 4. Relative importance of the five topographic variables used to project the distribution of *Miconia* in Nuku Hiva and Fatu Hiva according to the origin of occurrence records used to calibrate species distribution models.

(Figure 2). However, these pessimistic scenarios should focus the attention of stakeholders because they reflect the nature of invasive species and predict the worst situation to be considered (Jiménez-Valverde et al. 2011).

The SDM based on the Society Islands appears to be the least consistent because it failed to predict high-risk areas in Nuku Hiva, which is already experiencing an outbreak. There are several possible reasons for this result, including the accuracy of input environmental data sets. For example, WorldClim presents high uncertainties on the Pacific Islands due to a low number of weather stations and specific microclimates inherent to islands (Hijmans et al. 2005, Fick and Hijmans 2017). A high level of doubt could also exist

on climate data over the Marquesas archipelago where only 11 weather stations have been set up (five in Nuku Hiva, three in Hiva Oa, and only one each in Ua Huka, Ua Pou, and Fatu Hiva), mainly at low elevation (Laurent et al. 2004). Average temperature estimates from WorldClim and weather stations in the Society and Marquesas archipelagoes matched well ($r=0.88$; P -value < 0.01 ; $n=8$) but rainfall data differed slightly more ($r=0.39$; P -value < 0.05 ; $n=31$).

Invasion Risk of Miconia on Nuku Hiva and Fatu Hiva

The SDM obtained from topographic variables and based on the Society Islands diverged from the SDM based on the

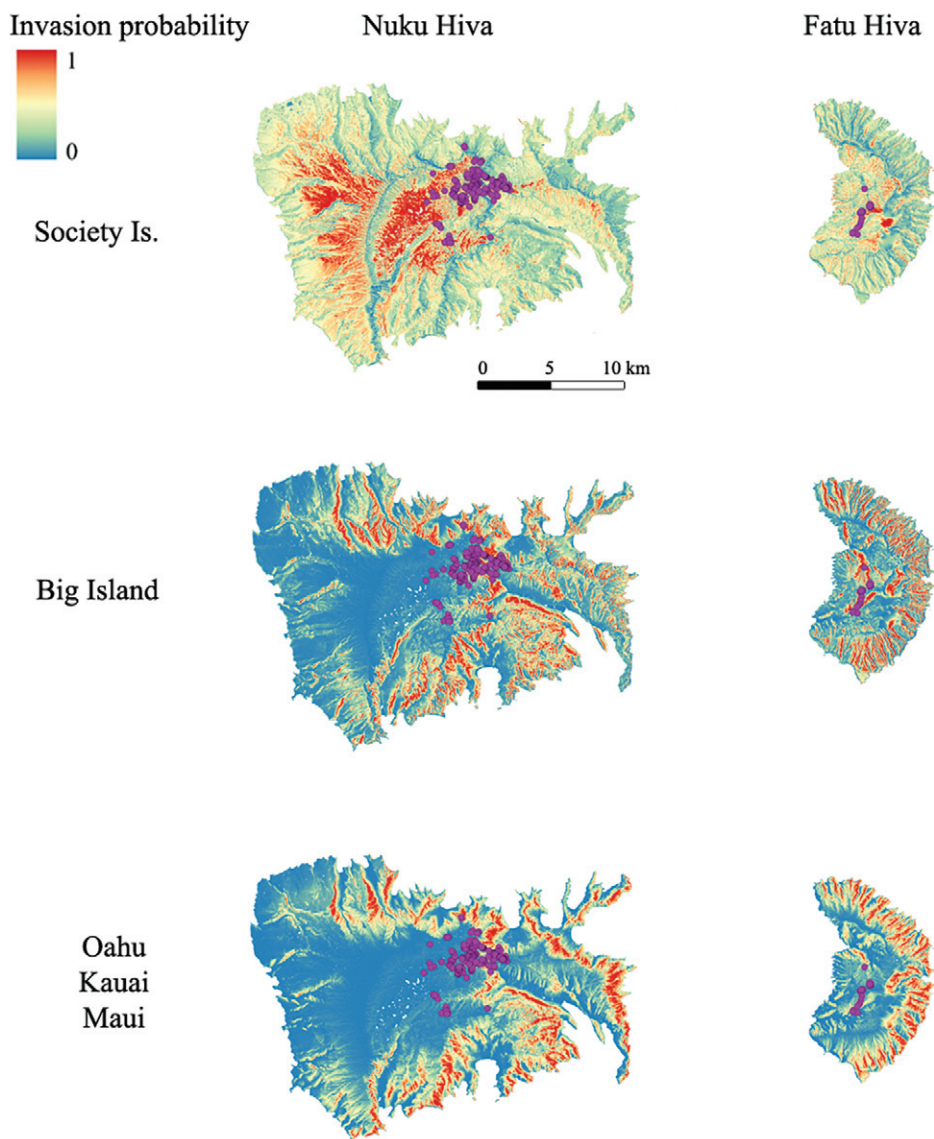


FIGURE 5. Equilibrium distribution of *Miconia* in Nuku Hiva (left column) and Fatu Hiva (right column) based on topographic variables. The origin of occurrence records used to calibrate species distribution models is given in lines. Purple points indicate available occurrence records.

Hawaiian Islands, and the former appeared to better predict the current invaded sites on Nuku Hiva and Fatu Hiva than the latter. According to results obtained from Society Islands, *Miconia* could spread over mesic to

wet areas and mountane cloud forests of Nuku Hiva and Fatu Hiva, where many narrow-range endemics and endangered plant and animal species are found (Lorence et al. 2016, Meyer 2016) (Figure 4). However, certain

areas covered by unsuitable vegetation types for *Miconia* to spread should be removed from our estimates of potential areas of invasion (Florence 1993). Such is the case, for instance, of *Dicranopteris linearis* fernlands or *Miscanthus floridulus* grasslands, as the large-leaved *Miconia* is typically a forest understory (or edge) species requiring a high hygrometry and semi-shade conditions to grow (Meyer 1996, Meyer and Florence 1996, Pouteau et al. 2011a). In Fatu Hiva and Nuku Hiva, *Miconia* is currently restricted to *Hibiscus tiliaceus*-dominated forest stands (pers. obs.).

The SDM based on the Hawaiian Islands appeared less consistent because they predicted potential invaded areas mainly located on coastal areas of Nuku Hiva and Fatu Hiva. In such locations, we suspect that *Miconia* will not spread because of unfavorable ecological conditions associated with dry conditions, ocean spray, and a high level of disturbance (Figure 4). This result could be due to different stages of invasion between the Society and the Hawaiian Islands. On Tahiti, *Miconia* has been naturalized for almost 80 years, and we can reasonably assume that the species has reached its equilibrium distribution. In the Hawaiian Islands, *Miconia* may have not reached all potential areas because it has been introduced later (50 to 60 years ago), and intensive control efforts implemented by the Invasive Species Committees may have limited its expansion (including in elevation). As a result, we noticed that *Miconia* is not found above 870 m on the Hawaiian Islands, whereas it is present up to 1,315 m on Tahiti. As elevation best explains the potential distribution of *Miconia* in the Hawaiian Islands (Figure 3), the SDM based on those islands can hardly predict properly the potential distribution of *Miconia* in the Marquesas.

Management Implications

The most cost-effective method of control with invasive species is to prevent their introduction in new areas where they have a high risk of invasion, and SDM theoretically represent extraordinary tools for that purpose (Genovesi 2005). Based on our SDM projections at the scale of the archipelago, we recommend strengthening biosecurity con-

trol on islands where *Miconia* is still thought to be absent but has the potential to become invasive (Hiva Oa, Ua Pou, Ua Huka, and Tahuata). However, while our SDM approach was useful to show that large areas are suitable across the islands under the multiple SDM considered, the strong intra-island differences in predicted *Miconia* potential distribution make our results less directly actionable for within-island management.

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APPENDIX 1

History of Introduction and Distribution of *Miconia* in the Invaded Ranges

Society Islands, French Polynesia

With 14 islands located between 16 and 18° S and between 148 and 154° W, the Society Islands are the main group of high volcanic islands in French Polynesia (Figure 1B). *Miconia* is already established in four islands of this archipelago: Moorea, Raiatea, Tahaa, and Tahiti. In this study, the highly invaded islands of Tahiti and Moorea were specifically targeted because Raiatea and Tahaa are at an early stage of invasion (Meyer and Malet 1997). The climate of the Society Islands is tropical oceanic with two seasons: a humid and warm season (from October to March) and a drier and cooler season (from April to September). Annual rainfall averages 1,700 mm/year and mean annual temperature is 26° C (Laurent et al. 2004).

Tahiti is the highest (2,241 m) and largest island of the Society archipelago (1,045 km²) (Dupon et al. 1993). *Miconia* was introduced for its ornamental value in the Papeari Botanical Garden in 1937 from the Peradeniya Botanical Garden of Sri Lanka by H. W. Smith, an American botanist (Meyer 1996). Since then, *Miconia* has spread to occupy two thirds of the island (Meyer 2009). Moorea (130 km²), the nearest island from Tahiti (located 20 km northeast), has been invaded since the 1970s by *Miconia*, probably dispersed by wind, birds, or accidentally introduced by people (hikers or individuals spreading ornamental plants) coming from Tahiti (Meyer 1996). The species now covers one quarter of the island (Pouteau et al. 2011).

Marquesas Islands, French Polynesia

Located between 8 and 11° S and between 138 and 141° W, the Marquesas have a moist tropical climate with annual rainfall ranging from 900 to 2,200 mm/year and mean annual temperatures averaging 25° C (Figure 1A). Six of the dozen oceanic islands composing the archipelago are inhabited: Fatu Hiva (or Fatu

Iva), Hiva Oa, Nuku Hiva, Tahuata, Ua Huka, and Ua Pou. Two of these islands are invaded by *Miconia*: Nuku Hiva and Fatu Hiva. On Nuku Hiva, *Miconia* was first discovered in 1997 and probably introduced by vehicles carrying soil infected by seeds in two sites located in rainforests at 400 and 1,000 m a.s.l. (Meyer et al. 2011). In Fatu Hiva where it was first discovered in 1996 by pig hunters, isolated plants or small populations of *Miconia* have been observed in seven sites, probably disseminated on the island by birds or pigs. On this island, *Miconia* is found in rainforests at ca. 600 m (Taputuarai 2017). Despite active control efforts conducted on those islands for the past 20 years, new populations with mature plants have been recently observed (Butaud 2015, Taputuarai 2017).

Hawaiian Islands, USA

The Hawaiian archipelago is composed of eight major islands expanding over 2,580 km on the North Pacific Ocean between 154 and 178° W and between 18 and 28° N (Wagner et al. 1990) (Figure 1C). *Miconia* is present on four of them: Hawai'i, Kaua'i, Maui, and O'ahu. On these islands, *Miconia* occurs where rainfall reaches at least 1,500 mm/year (Medeiros et al. 1997). O'ahu is the first island where *Miconia* has been reported, introduced in the Wahiawa Botanical Garden in 1961. *Miconia* then reached Hawai'i (the largest island of the archipelago also known as Big Island) in 1964. On the island of Maui, an isolated plant was first discovered during a reconnaissance mission by helicopter in 1996 (Chimera et al. 1996), but it is actually supposed to have reached the island as early as in the 1960s. The first control effort against *Miconia* was established on Maui in 1991. Finally, Kaua'i is the last island to have been invaded, in the early 1980s (Medeiros et al. 1997).

Queensland, Australia

Miconia has first been recorded in the Townsville Botanical Garden (Northern Queensland) in 1963. The species has been declared as a noxious plant in Australia in 1997 and

an eradication program was subsequently launched (Csurhes 2008). In Queensland, *Miconia* is found close to nursery stocks and private gardens, but some plants have naturalized in neighboring forests and have produced a large quantity of seeds and seedlings. In the wet tropical rainforests of North Queensland, rainfall averages 2,600 mm/year and the temperature averages 20° C during the wet season (Congdon and Herbohn 1993). In this study, the region of Queensland is considered with an extent ranging from 140 to 153° W and from 12 to 26° S (Figure 1D).

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