Multi-decadal declines in tree density and species richness as alien plants invade a tropical island’s protected wet forests

F. B. Vincent FLORENS\textsuperscript{1,3}, Claudia BAIDER\textsuperscript{2}, Genevieve MARTIN\textsuperscript{1}, Nooshruth B. SEEGOOLAM\textsuperscript{1}, Zeyn ZMANAY\textsuperscript{1} & Dominique STRASBERG\textsuperscript{3}

\textsuperscript{1} University of Mauritius
\textsuperscript{2} The Mauritius Herbarium
\textsuperscript{3} Université de La Réunion
Invasive alien species (IAS) cause major environmental damage and represent a main threat to biodiversity.
Invasive species are a leading cause of animal extinctions

Miguel Clavero and Emili García-Berthou

Institute of Aquatic Ecology, University of Girona, E-17071 Girona, Spain

Potential for causing species extinction is most obvious and rapid in inter-trophic interactions like predation compared to con-trophic interactions like competition.

Screwpine (Pandanus vandermeeschii)

Alien mammal eradication from an offshore Mauritius islet: ‘spectacular’ population recovery
There exists a relative lack of cases demonstrating alien plants’ ability to cause plant extinction (Davis 2003, Sax and Gaines 2008, Caujapé-Castells et al. 2010, Powell et al. 2013).
Difficulties to incriminate alien plants as drivers of the observed concurrent population decline and extinction of native plants: the coincidence of plant invasion with other threats like predation (Gurevitch and Padilla 2004).
Another difficulty: competition-driven extinctions possibly take longer to occur than those caused by predation (Davis 2003).

Situation exacerbated by the longevity of many tropical trees (e.g. Fichtler et al. 2003)

A situation of extinction debt (Kuussaari et al. 2009) rather than of extinction per se may thus be favoured.
Long term studies on the effect of invasive species are rare despite the strong need for ecologists to adopt such a long-term perspective (Strayer et al. 2006).
Aims

1. Measure current invasion by woody alien plants in the best preserved and protected native forests of a tropical oceanic island (Mauritius).

2. Compare tree community changes at some of the most intact native habitats that were studied 20 and 70 years earlier (with Vaughan and Wiehe 1941; Lorence and Sussman 1986).

3. Relate results to more recent experimental approach studies (comparisons between weeded and non-weeded forests).
Methods

Quantifying current invasion level by alien plants
- 75 random quadrats of 4 x 25 m distributed in 5 best preserved wet forest sites

Quantifying tree community changes through time
- Compare tree community with data from 1980’s and 1930’s

Experimental approach: weeded v/s non-weeded
- Compare community changes between weeded and non-weeded (at 2 sites)

Investigating fitness of native plants between weeded and non-weeded forests
- Compare survival, growth and reproductive rates between weeded and non-weeded adjacent areas

**Biodiversity hotspots for conservation priorities**

-Norman Myers*, Russell A. Mittermeier†, Cristina G. Mittermeier*, Gustavo A. B. da Fonseca, & Jennifer Kent†

* Green College, Oxford University, Upper Wadham, Old Road, Headington, Oxford OX3 8QZ, UK
† Conservation International, 250 M Street NW, Washington, DC 20037, USA
‡ Center for Applied Biodiversity Science, Conservation International, 250 M Street NW, Washington, DC 20037, USA
§ 55 Dutchers Close, Headington, Oxford OX3 8SH, UK
Mauritius – basic facts

Volcanic oceanic island 7.6 MY old

890 km to the east of Madagascar

1,865 km²; highest peak 828 m

First human colonisation: 1638. Uninterrupted since 1722
Native biodiversity

Angiosperms: 691 species
39% endemic;
9% extinct;
70% threatened

Vertebrates: 50 species
72% endemic;
46% extinct;
85% threatened

Molluscs: 125 species
65% endemic;
34% extinct;
80% threatened
Confetti of habitats left

Habitat fragmentation

Minimum viable populations?
‘Ghost of past deforestation’

(Source: Vaughan and Wiehe 1937; Page and D’Argent 1997)
Study sites: National Park and Mountain reserve

The largest area of contiguous native vegetation
Invasion

Understorey heavily dominated by alien plants

(75 plots of 100 m² from 5 sites with ‘best preserved’ forests)
A perfect nightmare
Native biomass lower when invasion more severe

Box and whiskers plots of basal area of native woody plants against relative degree of invasion by alien plants. Each relative category of invasion (low, medium, high) comprises the respective five plots from each site for a total of 25 plots per category. All differences between pairs of categories are significant at $P < 0.05$ (Post Hoc Tukey Test).
"it is now impossible to find even a small area free from exotics"

(Vaughan & Wiehe 1941, J. Ecol. 29: 127-160)
### Comparison over 70 years

<table>
<thead>
<tr>
<th></th>
<th>Macchabé (per 1000 m²)</th>
<th>Vaughan &amp; Wiehe 1941</th>
<th>Florens et al. unpubl.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Aliens</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&gt; 1 cm dbh</td>
<td>2 (0.002 m⁻²)</td>
<td>4,303 (4.3 m⁻²)</td>
<td></td>
</tr>
<tr>
<td><strong>Natives</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>&gt; 10 cm dbh</td>
<td>171 ± 24.6*</td>
<td>85 (P &lt; 0.05)</td>
<td></td>
</tr>
<tr>
<td><strong>Native spp richness</strong></td>
<td>32.5 ± 5</td>
<td>30 (NS)</td>
<td></td>
</tr>
</tbody>
</table>

*Note: DBH represents Diameter at Breast Height.*
## Alien plant invasion progress over 20 years

<table>
<thead>
<tr>
<th>&gt; 2.5 cm, &lt; 10 cm dbh</th>
<th>Sites</th>
<th>Lorence &amp; Sussman 1980’s</th>
<th>This study</th>
<th>P &lt; 0.01</th>
</tr>
</thead>
<tbody>
<tr>
<td>% alien plants</td>
<td>Brise Fer</td>
<td>34.8</td>
<td>60.7</td>
<td>↑</td>
</tr>
<tr>
<td></td>
<td>Bel Ombre</td>
<td>20.8</td>
<td>25.7</td>
<td>↑</td>
</tr>
<tr>
<td>Native species richness</td>
<td>Brise Fer</td>
<td>54</td>
<td>47.6 ± 16.2</td>
<td>n.s.</td>
</tr>
<tr>
<td></td>
<td>Bel Ombre</td>
<td>46</td>
<td>37.9 ± 7.4</td>
<td>↓</td>
</tr>
<tr>
<td>Native density (100 m⁻²)</td>
<td>Brise Fer</td>
<td>76.2</td>
<td>58 ± 9.1</td>
<td>↓</td>
</tr>
<tr>
<td></td>
<td>Bel Ombre</td>
<td>71.5</td>
<td>63 ± 11.2</td>
<td>n.s.</td>
</tr>
</tbody>
</table>
### Mortality

**Sideroxylon grandiflorum** (Sapotaceae)* ‘Dodo-tree’

<table>
<thead>
<tr>
<th>Site</th>
<th>Forest regime</th>
<th>N</th>
<th>Deaths *</th>
<th>Mortality rate (over 3 ¾ years)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Brise Fer</td>
<td>Non-weeded</td>
<td>71</td>
<td>2</td>
<td>2.82%</td>
</tr>
<tr>
<td>Mare Longue</td>
<td>Non-weeded</td>
<td>31</td>
<td>8</td>
<td>25.81%</td>
</tr>
<tr>
<td>Macchabé</td>
<td>Non-weeded</td>
<td>38</td>
<td>3</td>
<td>7.89%</td>
</tr>
<tr>
<td>Brise Fer</td>
<td>Weeded</td>
<td>133</td>
<td>1</td>
<td>0.75%</td>
</tr>
<tr>
<td>Mare Longue</td>
<td>Weeded</td>
<td>23</td>
<td>0</td>
<td>0%</td>
</tr>
<tr>
<td>Macchabé</td>
<td>Weeded</td>
<td>4</td>
<td>0</td>
<td>0%</td>
</tr>
</tbody>
</table>

*Cyclone snapped trees not included

**Total tree mortality compared**

**Non-weeded forest:** 9.3% (N = 140)

**Weeded forest:** 0.6% (N= 160)
Reproductive output

Canopy tree *Sideroxylon grandiflorum* – ‘Dodo tree’

Invasion strongly reduces reproductive output

Flowering is more abundant in areas without alien plants*

\[ U_{122,78} = 3520.5; P = 0.002 \]

Fruiting is on average 37 times higher in weeded areas*

\[ U_{140,135} = 6662.5; P < 0.001 \]

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Another canopy tree *Canarium paniculatum* (Burseraceae)

*C. paniculatum* produced significantly more seeds in weeded areas at both sites studied.

Fig. 1. C. paniculatum produced significantly more seeds in areas weeded of alien weeds at both study sites.

Fig. 2. Reproductive output of *C. paniculatum* improves with time after removal of invasive alien weeds.

Another canopy tree *Canarium paniculatum* (Burseraceae)
Invasive alien plants elicit reduced production of flowers and fruits in various native forest species on the tropical island of Mauritius (Mascarenes, Indian Ocean).

M.L. Fabiola Monty¹*, F.B. Vincent Florens¹ and Cláudia Baider²

¹Department of Biosciences, University of Mauritius, Réduit, Mauritius
Growth rate

Growth rate of a canopy native tree (4 years monitoring)

Comparison between adjacent weeded and non-weeded forest

*Sideroxylon grandiflorum* (Sapotaceae)

Growth rate (dbh)

<table>
<thead>
<tr>
<th>Management regime</th>
<th>N</th>
<th>Mean yearly growth rate (mm ± SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Non-weeded area</td>
<td>125</td>
<td>0.47 ± 0.23</td>
</tr>
<tr>
<td>Weeded area</td>
<td>155</td>
<td>1.11 ± 0.21</td>
</tr>
</tbody>
</table>
## Mean annual growth rate of the whole woody native species community (Monitored over about 4 years)

<table>
<thead>
<tr>
<th>Species</th>
<th>Non weeded</th>
<th>Weeded</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N</td>
<td>Growth (dbh, mm)</td>
</tr>
<tr>
<td>Brise Fer</td>
<td>795</td>
<td>0.10</td>
</tr>
<tr>
<td>Mare Longue</td>
<td>1353</td>
<td>0.08</td>
</tr>
</tbody>
</table>

Mean annual growth rate of the whole woody native species community.
Whole community monitored over 4 years

Native woody plants > 1 cm dbh

<table>
<thead>
<tr>
<th></th>
<th>Invaded</th>
<th>Weeded (8 yrs earlier)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number</td>
<td>Difference (%)</td>
</tr>
<tr>
<td>Brise Fer</td>
<td>Recruitment</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>Retrogression</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>Deaths</td>
<td>52</td>
</tr>
<tr>
<td>Mare Longue</td>
<td>Recruitment</td>
<td>52</td>
</tr>
<tr>
<td></td>
<td>Retrogression</td>
<td>27</td>
</tr>
<tr>
<td></td>
<td>Deaths</td>
<td>49</td>
</tr>
</tbody>
</table>

* Per plot of 0.01 ha (100 m²)
‘Same plot changes’ over 4 years

Weeded
Not weeded

Number of individuals

DBH class (cm)
Control of invasive alien weeds averts imminent plant extinction

Cláudia Baider · F. B. Vincent Florens
Cascading impacts? Large epiphytic ferns

(Bindewald, Baider & Florens unpubl)
Population recovery within 24 years of weeding

**Asplenium nidus**

Kruskal-Wallis test:
\[ H = 154.49; \ p < 0.001 \ (0.1\text{ha plots}) \]

**Microsorum**

Kruskal-Wallis test:
\[ H = 122.73; \ p < 0.001 \ (0.1\text{ha plots}) \]
Downward expansion after weeding

Weeded in 1986 (24 years)

Weeded in 1996 (14 years)

(Invaded)
Conclusions

• Presence of alien plants in protected native forests may come about through two broad ways with different implications for conservation:

1. They may be merely filling unoccupied spaces
2. They may be displacing native species.

• Although other factors may contribute to the decline observed (e.g. habitat fragmentation, predation by alien animals etc), this study shows a strong role played by ontrophic (plant-plant) interactions in driving the decline.
Many species, including threatened ones, can recover strongly as a consequence of the sole removal of invasive alien plants.

Shows that the threat these pose can be overwhelmingly important in driving native species population declines.

Our findings also indicate that imminent plant extinctions can be averted by little more than timely control of the invading plants.
Acknowledgments

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organisers  Thank you