

## Introduced Alien Plant Species in the Neotropics: the Panama Case

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**Abstract:** Non-insular tropical biomes appear relatively resistant to invasive alien species (IAS). While some argue fewer IAS in continental tropical communities is the result of the complexity of species-rich communities (*e.g.*, Elton's biological resistance hypothesis), others suggest lack of IAS might reflect fewer invasion opportunities, which could change with time. In effect, deforestation may lead to the simplification of tropical habitats, thus reducing biological resistance. Little is known about the current status of alien plants species, factors contributing to their spread and IAS in non-insular tropical systems. Here I report on the status of alien plant species in relation to area, number of native and endemics species, population, forest cover and cultivated area across provinces of Panama. Alien plant species comprise nearly 4 percent of the flora and was positively correlated with the number of native plant species ( $r = 0.84$ ,  $P < 0.001$ ) and while this pattern runs counter to Elton's premise, it is consistent with other landscape-scale studies. In Panama, the number of alien plant species is explained by population density ( $r = 0.91$ ,  $P < 0.01$ ) and potentially linked to disturbance, albeit coarsely, as the proportion of aliens negatively correlates with forest cover ( $r = 0.69$ ,  $P < 0.05$ ). Thus, despite high diversity, these results portray disturbed tropical forests becoming dotted with introduced alien species. While few species seem to become invasive in the continental tropics, rapid land use change could promote the success of IAS representing serious consequences for tropical countries' economies and biodiversity.

**Keywords:** Biological resistance, disturbance, exotics, forest cover, herbarium, human population, land use change.

### 1. INTRODUCTION

Over the last five hundred years, humans have greatly altered natural landscapes by increasing disturbance regimes and facilitating species migration (Solbrig, 1994; Orians *et al.*, 1996; Lodge, 1993). In conjunction, these two factors are linked to the successful establishment and rapid spread of many alien species (Fox and Fox, 1986). While an introduction event does not warrant successful establishment, introduced species are of concern due to their potential to become invasive, or better; invasive alien species (IAS), – defined here as non-native, non-indigenous species that rapidly propagate in a new environment having negative consequences for native ecosystems, economies and human welfare. IAS are now broadly recognized as a major threat to biodiversity and ecosystem services (*e.g.*, water, food supply, air quality, public health, etc.).

At a global scale, both the number and proportion of alien species appears to be larger in temperate than tropical regions, with the exception of tropical oceanic islands (Simberloff, 1995; Rejmanek, 1998; Lonsdale, 1999; Fine, 2002; Pyšek *et al.*, 2008). While this latitudinal asymmetry is most commonly explained by Elton's biological resistance

hypothesis –the premise that diverse, complex communities better resist invasion by introduced alien species than species-poor, simpler communities (Elton, 1958), other factors might be involved. For example, history (*e.g.*, steamship routes; Mack, 2003) as well as economical factors (*e.g.*, trade; Meyerson and Mooney, 2007) might have influenced propagule pressure – the quantity and frequency at which an organism is introduced (see Lockwood *et al.*, 2005). However, simplification of tropical communities by human-driven shifts in land use, disturbance, increased propagule pressure from growing international trade, as well as natural disturbance via climatic variability *i.e.*, recurrent severe droughts and floods associated to El Niño Southern Oscillation (ENSO) may render tropical habitats more susceptible to the successful establishment and invasion by alien species in the future.

Management, conservation, and restoration of tropical ecosystems faces serious challenges. The neotropics, for example, holds one of the highest rates of conversion of species rich forests into simpler, pasture and crop land systems (Wassenaar *et al.*, 2007). In addition, the fact that a great percentage of the population in the Neotropics depends directly on services that forested ecosystems offer (*e.g.*, water, forest products extraction, hunting, fishing, etc.) poses a severe threat to biodiversity as well as human sustainability. However, the irreversible changes that IAS can cause to ecosystem properties and forest regeneration are generally overlooked in the continental tropics. IAS

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**Table 1. Pairwise Correlation Coefficients among Species, Area and Explanatory Variables for all 10 Provinces of Panama. Significant Correlations ( $P < 0.05$ ) are Shown in Boldface Type**

	Natives	Endemics	Aliens	Area <sup>1</sup>	Population	Cover <sup>2</sup>	Cultivated <sup>3</sup>	% Aliens <sup>4</sup>	P. Density <sup>5</sup>	% Cover <sup>6</sup>	% Cultivated <sup>7</sup>
Natives	—	<b>0.97</b>	<b>0.82</b>	0.61	<b>0.65</b>	0.36	0.43	0.43	<b>0.63</b>	0.16	-0.17
Endemics		—	<b>0.84</b>	0.52	<b>0.71</b>	0.26	0.42	0.41	<b>0.71</b>	0.18	-0.19
Aliens			—	0.46	<b>0.94</b>	0.23	0.25	0.39	<b>0.91</b>	0.09	-0.19
Area <sup>1</sup>				—	0.35	<b>0.86</b>	0.19	-0.20	0.19	0.33	-0.37
Population					—	0.10	0.21	0.36	<b>0.96</b>	-0.04	-0.11
Cover <sup>2</sup>						—	-0.28	-0.49	-0.05	<b>0.65</b>	<b>-0.64</b>
Cultivated <sup>3</sup>							—	<b>0.66</b>	0.22	<b>-0.64</b>	<b>0.69</b>
% Alien <sup>4</sup>								—	0.47	<b>-0.69</b>	<b>0.73</b>
P. Density <sup>5</sup>									—	-0.09	-0.03
% Cover <sup>6</sup>										—	<b>-0.94</b>
% Cultivated <sup>7</sup>											—

<sup>1</sup>Province area in km<sup>2</sup>; <sup>2</sup>Forest cover in km<sup>2</sup>; <sup>3</sup>Total cultivated area of main grains (rice, corn and beans) in km<sup>2</sup>; <sup>4</sup>Percentage of alien species in relation to native species; <sup>5</sup>Population density given by the number of habitants by km<sup>2</sup>; <sup>6</sup>Percentage of forest cover remaining in relation to total province area; <sup>7</sup>Percentage of cultivated area in relation to total province.

represents a new challenge for conservation efforts in a region where most of the world’s biodiversity and more than one third of the population of the planet resides (Cohen and Small, 1998). But, how common are IAS in the continental tropics? Our limitation to answer question arise, in part, to lack of basic information regarding introduced alien species, their natural history, potential impacts and alternative management strategies in tropical countries and their ecosystems.

This paper aims at reporting on the current status of alien plant species in Panama, Central America. Given its role as an important international trade route for over 100 years (McCullough, 1977; Ruiz et al., 2006), high biodiversity and recent appeal as a major tourist destination (Casado, 2001), Panama has potential as a model country for the study, long-term monitoring and management of introduced alien species in the tropics. I start by examining the abundance of alien species by political provinces in relation to regional scale predictors (i.e., area, total number of native and endemics species). To determine what factors are likely to influence the successful establishment of alien species in Panama, I assess how human population, forest cover, and cultivated area of primary agricultural products (e.g., rice, corn and beans) might predict the number of alien plant species.

## 2. MATERIAL AND METHODS

### 2.1. Study Site and Species

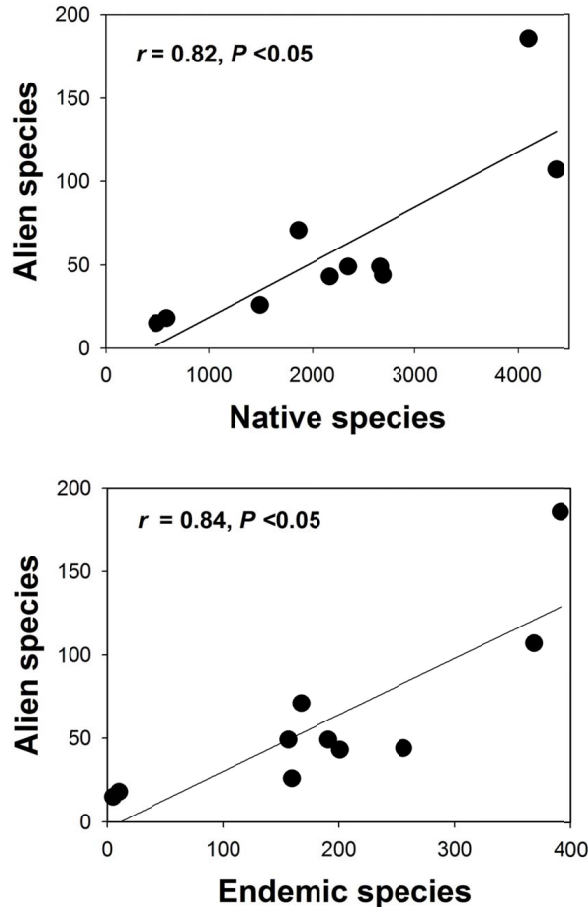
The Republic of Panama lies between 7° and 10° latitude North and 77° and 83° longitude East, comprising a total land area of 74,927 km<sup>2</sup>. Information on alien species of Panama was compiled from Correa *et al.* (2004). This report represents the most updated and official list of vascular plants in the Republic of Panama (i.e., voucher specimens at the National Herbarium, University of Panama). The information compiled in Correa *et al.* (2004) provides data on the total number of species (e.g., natives, endemics and aliens) per province. Although the political division of the country has changed recently, most information regarding plant distribution has been obtained and maintained using a system of 9 political provinces, one Indian reservation

–Guna Yala (formerly known as San Blas) – and the former Canal Zone. Because the former Canal Zone territory actually lies in the provinces of Panama and Colon, I used the fraction of alien species in these provinces represented in the Canal Zone to estimate the number of species to be included as part of the Panama and Colon provinces. It must be noted that there is considerable biases in Herbarium collections (i.e., ignoring ‘known’ exotic species in favor of native species) as personnel might have prioritize knowledge of native and endemic species over aliens. This might concomitantly promote avoidance of disturbed sites and further underestimation of alien species. While information from Correa *et al.* (2004) does not provide a direct assessment of a species’ habitat, occurrence, abundance or distribution, it is our best, albeit coarse, assessment on the status of most alien species in Panama up to 2004.

Information on human population and cultivated area per province was obtained from the Department of Censuses and Vital statistics of the General Comptroller Office of the Republic of Panama (<http://www.contraloria.gob.pa/dec/>) for the year 2002. Population per province represents the total number of inhabitants in that province. Information on province area and forest cover was obtained from a national report on forest cover and land use of the Republic of Panama (ANAM, 2003) and represents the total area of square kilometers that include some type of forest cover, which includes mature forest, secondary forest and scrubland.

### 2.2. Statistical Analysis

A multivariate Pearson’s product-moment correlation analysis was performed across variables using both; total and area-standardized data (see results Table 1). However, to test which of the explanatory variables (e.g., forest cover, cultivated land, and population) best predicts the abundance and proportion of alien species, I used Akaike’s Information Criterion (AIC) to select the best suite of explanatory variables from all possible models. AIC is an information-theoretic approach that allows selection of the most parsimonious model that adequately fits the data –the model with the lowest AIC. This approach is more robust than the traditional stepwise methods for selecting variables to

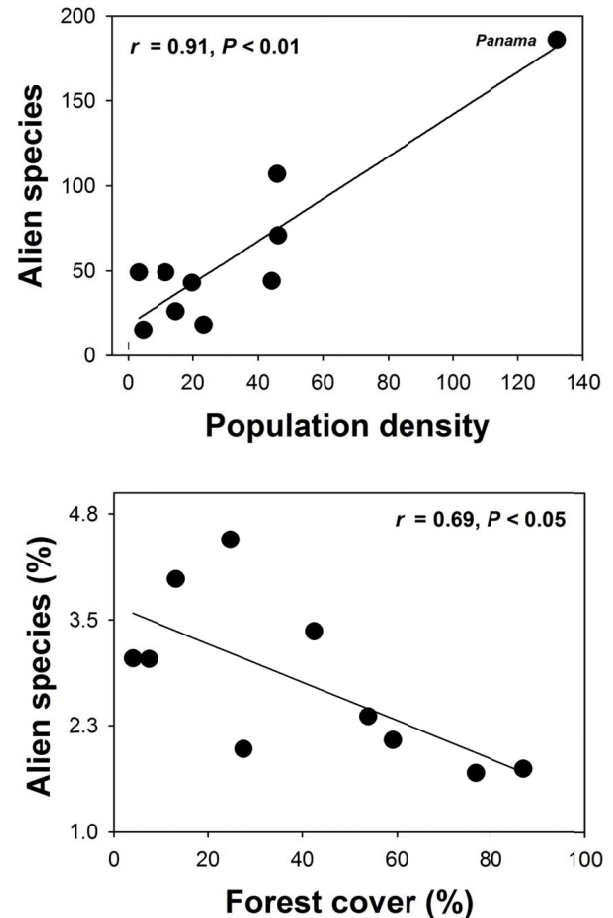


**Fig. (1).** Pearson product-moment correlation between the total number of alien species and native (A) and endemic species (B), across 10 political provinces of Panama. Each point represent the total number of plant species of each category reported for each province at the National Herbaria summarized by Correa *et al.*, 2004 (see methods section).

include in a model, therefore avoiding the problem of overfitting — and indirectly, collinearity — as it places a penalty on the number of parameters used in the model (see Rushton *et al.* 2004). AIC was applied to a set of *a priori* models where the effect of area is removed. Therefore, explanatory variables are standardized by area across provinces expressing the proportion of alien species [alien species/native species] per province in relation to; the proportion of forest cover [forest cover area/province area in  $\text{km}^2$ ], the proportion of agricultural land [cultivated area/province area in  $\text{km}^2$ ] and population density [habitants/province area in  $\text{km}^2$ ]. I further applied a correction to the AIC for small sample sizes, termed  $\text{AIC}_c$  and compared the models using the estimated delta AIC on the corrected scores termed  $\Delta_i$  (Burnham and Anderson 2004). A total of 4 models were used, among which comparison of  $\text{AIC}_c$ 's and  $\Delta_i$ 's is reported. All statistical analysis were conducted using R v 2.4.0 (2008).

### 3. RESULTS

In Panama there are a total of 9,520 species of vascular plants of which 373 are known alien species (*i.e.*, 4%; Correa *et al.* 2004). Alien species was significantly



**Fig. (2).** Pearson product-moment correlation between the total number of alien species vs. population density (A) and the proportion of alien species in relation to the remaining forest cover (B), across 10 political provinces in Panama. The percentage of aliens represents the total number of alien plant species divided by the total of native species in each province.

correlated with the total number of native and endemic species reported for each political province (Table 1; Fig. 1A and B). Pairwise correlation analysis among explanatory variables also reveals that the number of alien species was significantly correlated with population and population density, while the percentage of aliens showed a negative correlation with the proportion of forest cover (Table 1; Fig. 2A and B,  $r = 0.91$ ,  $P < 0.001$  and  $r = -0.69$ ,  $P < 0.05$ , for population density and the proportion of forest cover, respectively). Although, the relationship between aliens and population density appears to be driven by Panama, a province with nearly 50% of the country's population, once removed from the analysis the relationship remains significant.

The use of the Akaike's Information Criterion reveals that the percentage of forest cover in conjunction with population density generates the most parsimonious (*i.e.*, simplest) model for predicting the proportion of alien plant species across provinces of Panama. That is evidenced by the lowest  $\Delta_i$  value among all competing models (Model<sub>1</sub>  $\text{AIC}_c = 29.18$ ; see Table 2). However, the AIC approach

**Table 2. Corrected Akaike's Information Criterion (AIC<sub>c</sub>) and Delta AIC<sub>c</sub> ( $\Delta_i$ ) Scores for Selected Models. Models 1-4, Represent those where all Explanatory Variables have been Standardized by Province Area to Predict the Proportion of Alien Plant Species Per Province (see Methods)**

Model Considered	Df	AIC <sub>c</sub>	$\Delta_i$
M <sub>1</sub> % Aliens = % Cover + P. Density	4	29.18	0.00
M <sub>2</sub> % Aliens = % Cover + % Cultivated	4	32.78	3.60
M <sub>3</sub> % Aliens = P. Density + % Cultivated	4	29.47	0.29
M <sub>4</sub> % Aliens = % Cover + % Cultivated + P. Density	5	32.52	3.34

Aliens= total aliens, Area= province area in km<sup>2</sup>, Cover= forest cover in km<sup>2</sup>, Cultivated= land of main grains e.g., rice, corn, beans in km<sup>2</sup>, P. Density= number of habitants per km<sup>2</sup>

generates very little resolution between Model<sub>1</sub> and a Model<sub>3</sub> where the proportion of agricultural land and population density become the main drivers for explaining alien species across provinces (Table 2). Although the great majority of alien species (67.6%) are reported as cultivated either for agriculture, gardening, medicinal or for folkloric use, I found that nearly five percent of all aliens (~18 species) are recognized as invasive elsewhere (see Table 3 for a list of some of these species).

#### 4. DISCUSSION

Across all provinces, alien plant species represent nearly 4 percent of the flora of Panama, ranging from 1.6 to 4.5 percent. These numbers are considerably lower than the global mean value of 16 percent reported in Lonsdale (1999), and that of neighboring Costa Rica, a country with similar plant diversity, geography and demographics, where aliens make up to 10 percent of the flora (Chacón and Saborio 2006). While Costa Rica holds a 3.5 times higher deforestation rate and nearly 11% less forest cover than Panama (estimated for the period 1990-2000; Butler 2009), the discrepancy in the number of aliens may lie on Costa Rica's recent botanical sampling efforts and not in deforestation *per se*. In 1989 Costa Rica launched a national initiative to inventory and catalogue their biodiversity wealth with a particular emphasis on plants. Such efforts might have increased the number of aliens reported; as much as 20% of the flora might have been identified and described in the last two decades (Tanglely 1990, Green 2004). Without a thorough inventory it is difficult to assess what total percentage of the flora is alien and which species can be considered invasive, however many alien species occurring in Panama are reported as invasive or problematic elsewhere (Table 3). Pyšek (2008), has recently emphasized the importance of tracking ornamentals in IAS research programs in order to gain knowledge about "innocuous" species that might become invaders. Thus, our assessment not only underestimates total number of aliens, but underscores a pressing need for base-line research and long-term monitoring on introduced alien species in Panama and the region.

Across all political provinces of Panama, alien species might be better explained in relation to human population density. However, once the explanatory variables are standardized by area, the fraction of remaining forest cover together with population density becomes the most important variables in explaining alien species number. This finding,

together with newly available information on invasive species generated by regional initiatives (Inter-American Biological Information Network 2008) suggests that alien species are becoming widespread across tropical landscapes. Yet, some of the results presented here should be taken cautiously given the potential skewness nature of Herbarium data (see Methods) and the number of observations taken. Despite this, in Panama and Central America for example, many aliens are well known invasives revealing the urgent need to create proficient mechanisms to quantitatively assess, monitor and implement management policies for alien species at the country and regional level.

The scarcity of IAS in continental tropical biomes has been attributed to Elton's biological resistance hypothesis (Elton 1958). This is, high species diversity might increase invasion resistance owing to increased competition for resources *e.g.*, space, light, nutrients, etc. In this study, the number of alien species was found to be positively correlated to the total number of native species. This is congruent with other findings in which species-rich areas support more aliens (Lonsdale 1999, Eriksson *et al.* 2006, Westphal *et al.* 2008; but see Simberloff and Holle 1999). Yet, area might influence habitat heterogeneity and thus underlie this relationship (see Brose 2001), but the limitations of the data ( $n=10$ ) preclude us from detecting a clear pattern. Because population, forest cover and agricultural land may also covary with province area it might be inappropriate to assert that the correlation between alien and native plant species across Panama respond to the effects of area on habitat diversity alone. Alternatively, it is plausible that the competitive mechanism by which Elton's biological resistance hypothesis operates still affects alien species establishment (see Naeem *et al.* 2000).

Disturbance has become increasingly linked to the successful establishment of alien species in their new habitat (Fox and Fox 1986, Peters 2001, Bellingham *et al.* 2005). Thus, is there an indication of human-driven influence (direct or indirect) in the success of alien plant species in Panama? In this study, it appears that human population density significantly contribute to the number and proportion of alien species established in each province. This could be explained via two possible mechanisms. First, given that a great proportion (67.6%) of the alien flora is cultivated, it is therefore expected that humans are significantly contributing to the spread of propagules and seeds of these species across Panama. Although we lack detailed quantitative data linking ornamental species to invasion, we must note that many of them might become invasive. In the Czech republic,

**Table 3. List of Problematic Alien Plant Species given by Family, Scientific Name, Growth Habit, Uses and Region of Origin Known to Occur in Panama that have been Reported as Invasive or Problematic Elsewhere. Nomenclature Follows Missouri Botanical Gardens**

Family	Species	Habit	Uses	Origin	Invasive in
Acanthaceae	<i>Thunbergia grandiflora</i> Roxb.	Vine	Ornamental	Asia	Hawaii <sup>1</sup> , Pacific Islands <sup>2</sup> , Australia <sup>3</sup>
Apocynaceae	<i>Cryptostegia madagascariensis</i> Bojer ex. Dene.	Woody vine	Ornamental	Africa	USA <sup>4</sup> , Pacific Islands <sup>2</sup> , Australia <sup>5</sup>
Balsaminaceae	<i>Impatiens walleriana</i> Hook. F.	Herb	Ornamental	Africa	Hawaii <sup>1</sup> , Pacific Islands <sup>2</sup> , USA <sup>4</sup>
Bignoniaceae	<i>Tabebuia heterophylla</i> (DC) Britton	Tree	Ornamental	Caribbean	Pacific Islands <sup>2</sup>
Fabaceae	<i>Pueraria phaseoloides</i> (Roxb.) Benth.	Vine	Fodder	SE Asia	Pacific Islands <sup>2</sup>
Fabaceae	<i>Flemingia strobilifera</i> (L.) R. Br.	Shrub		Asia	
Hydrocharitaceae	<i>Hydrilla verticillata</i> (L.f.) Royle	Aquatic herb	Aquarium	Africa/Asia	USA <sup>4</sup> , Pacific Islands <sup>2</sup> , Australia <sup>3</sup>
Meliaceae	<i>Melia azedarach</i> L.	Tree	Ornamental	SE Asia	USA <sup>4</sup>
Myrtaceae	<i>Syzygium jambos</i> (L.) Alston	Tree	Fruit	SE Asia	Hawaii <sup>1</sup> , Pacific Islands <sup>2</sup>
Oleaceae	<i>Ligustrum sinense</i> Lour	Shrub	Ornamental	Asia (China)	USA <sup>4</sup>
Poaceae	<i>Saccharum spontaneum</i> L.	Herb	not known	Asia	Hawaii <sup>1</sup> , Pacific Islands <sup>2</sup>
Zingiberaceae	<i>Hedygium coronarium</i> Koenig	Herb	Ornamental	Asia	Hawaii <sup>1</sup>
Zingiberaceae	<i>Alpinia purpurata</i> (Vieill.) K.	Herb	Ornamental	Asia	Hawaii <sup>1</sup> , Pacific Islands <sup>2</sup>

<sup>1</sup>Hawaiian Ecosystems at Risk 2012, <sup>2</sup>Pacific Islands Ecosystems at Risk 2012, <sup>3</sup>Global Invasive Species Database 2012, <sup>4</sup>US Department of Agriculture 2012, <sup>5</sup>Weeds in Australia 2012.

naturalized ornamentals make more than 50 percent of the IAS (Pyšek *et al.*, 2003). Second, alien species can be linked indirectly through human population pressure on land use changes via forest cover (*i.e.*, deforestation) and increasing need for food (*i.e.*, agricultural land). This is evidenced in the negative correlation between the proportion of forest cover to the proportion of alien plant species established in each province. Thus taken together, anthropogenic dispersal and human-driven forest transformation may facilitate the establishment, spread and potential invasion by naturalized ornamental species.

In the tropics, accelerated land use change, in particular forest transformation into simpler, pasture-like, less diverse systems pose severe threats to biodiversity. Forest cover removal could further erode tropical biome diversity facilitating alien species establishment. As a consequence, one might ask: How does deforestation influence alien species establishment? One possible reason is that forest cover removal facilitates the establishment and spread of alien species by freeing space for establishment. However, freeing of space might carry a twofold effect. First, it allows physical space for plant establishment by eliminating native species giving the new establishing alien species a transitional advantage for resource acquisition and growth without competition (Hobbs 1989). Alternatively, because the great majority of introduced alien species tend to be light demanding species (Fine 2002), it is likely that deforestation also create optimal light availability for fast growth. This has been the case of many invasive species such as *Clidemia hirta* (Melastomataceae), an invasive shrub in peninsular Malaysia that is restricted to light clearings (*i.e.*, gaps) in the forests (Peters 2001). Also plausible, is the idea that forest deforestation and transformation contributes to alien species establishment via “weakening” of the biological resistance (*sensu* Elton 1958), however this remains to be tested as examination of Elton’s postulate has not yet been evaluated in non-insular, diverse, tropical systems. Therefore,

conservation and restoration of tropical forests face a new challenge: past, present and future transformation is likely to leave a tropical landscape interspersed with alien species, many of which might become invasive in the near future.

## 5. IMPLICATIONS FOR CONSERVATION

The present study reports on the distribution of introduced alien species in relation to human population (*e.g.*, size and density) and the fraction of forest cover remaining across all political provinces of Panama. While it might be tempting to link successful establishment of alien plant species with invasion, the nature of the data (*i.e.*, coarse, small sample size) prevent us from discerning in what type of tropical habitats invasion is likely to occur as not all tropical habitats — nor all habitats within Panama - can be described as high diversity habitats. Nevertheless, the invasive examples given reinforce the need to delineate strategic policies, as well as research priorities to quantitatively assess the status of introduced alien species at the country and regional level. Detailed, basic research on the status of alien plant species in the tropics is needed in order to confirm whether factors driving invasion patterns in temperate and insular regions also hold for the continental tropics.

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