Tropical ash *(Fraxinus udhei)* invading Andean forest remnants in Northern South America

Kelly A Saavedra-Ramírez Corresp., [1] , **Andrés Etter** [1] , **Alberto Ramírez** [1]

[1] Departamento de Ecología y Territorio, Pontificia Universidad Javeriana, Bogotá, Colombia

Corresponding Author: Kelly A Saavedra-Ramírez
Email address: ksaavedra@javeriana.edu.co

Exotic invasive species represent a major driver of the loss of biological diversity and services provided by ecosystems globally. An important source of species becoming invasive are the commercial afforestation projects using fast growing and adaptable exotic species, which may become invasive impacting natural environments. The Tropical Ash (*Fraxinus uhdei*) native to México has been widely introduced for many decades to Colombia and other countries for timber, live fences and urban greening, is now common in many areas of the tropical mountains, and has been observed expanding into native forests in Colombia. This study explores the invasion of Tropical Ash in remnant Andean forests in Colombia, to understand the invasion pattern and the demographic structure of Tropical Ash. The analysis took into account biotic and physical factors, such as distance to the propagule source, vegetation cover types, and density of the understory and canopy cover. Although the reproductive strategy of the Tropical Ash is of “r” type with low survival rates, the results show evidence for an active process of invasion characterized by an aggregated distribution pattern. The study shows the existence of an interaction between the distance to the propagule source and the vegetation cover, which has an additive effect on the demographic structure of the population.

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Tropical Ash *(Fraxinus udhei)* Invading Andean Forest Remnants in Northern South America

Kelly A. Saavedra-Ramírez[1], Andrés Etter[1], Alberto Ramírez[1]

[1] Departamento de Ecología y Territorio, Pontificia Universidad Javeriana, Bogotá, Colombia

Corresponding author:
Kelly A. Saavedra-Ramírez[1]

Email address: ksaavedra@javeriana.edu.co

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Abstract

Exotic invasive species represent a major driver of the loss of biological diversity and services provided by ecosystems globally. An important source of species becoming invasive are the commercial afforestation projects using fast growing and adaptable exotic species, which may become invasive impacting natural environments. The Tropical Ash (*Fraxinus uhdei*) native to México has been widely introduced for many decades to Colombia and other countries for timber, live fences and urban greening, is now common in many areas of the tropical mountains, and has been observed expanding into native forests in Colombia.

This study explores the invasion of Tropical Ash in remnant Andean forests in Colombia, to understand the invasion pattern and the demographic structure of Tropical Ash. The analysis took into account biotic and physical factors, such as distance to the propagule source, vegetation cover types, and density of the understory and canopy cover. Although the reproductive strategy of the Tropical Ash is of "r" type with low survival rates, the results show evidence for an active process of invasion characterized by an aggregated distribution pattern. The study shows the existence of an interaction between the distance to the propagule source and the vegetation cover, which has an additive effect on the demographic structure of the population.

Keywords

Andean forest – Demographic structure – Fraxinus uhdei – Exotic species – Plant biological invasions – Invasion pattern

Introduction

Mountain forests are valued worldwide for their fundamental role in the processes of biodiversity conservation, hydrologic regulation, carbon storage and net primary productivity (Galbraith et al., 2014). The Andes mountains of northern South America, and especially of Colombia, are ecosystems known for their high biodiversity, and high levels of endemism (Hernández-Camacho et al., 1992), constituting a global hotspot of biodiversity (Myers et al., 2000; Orme et al., 2005). However, they also have a long history of human settlement and intervention (Etter, McAlpine & Possingham, 2008), which has led to high levels of land clearing and fragmentation (Armenteras, Gast & Villareal, 2003). Currently the Andean landscapes are made of a mosaic of agricultural pasturelands and crops, suburban and urban areas, interspersed with secondary shrublands and forests, and valuable native forest remnants (Etter & van Wyngaarden, 2000).

The processes of land clearing and habitat modification, and the invasion of exotic species, together with pollution and climate change, represent the major drivers of the loss of biodiversity and services provided by native ecosystems (Millenium Ecosystem Assessment –MEA, 2005). As a response to the soil and water degradation, and wood and timber shortages from the extensive clearing of forests worldwide (Food and Agriculture Organization of the United States –FAO, 2014), commercial reforestation and afforestation projects that use fast growing timber species have been carried out extensively with the aim of restoring hydrological cycles and degraded soils, and satisfying the growing demands of wood and timber. More recently, commercial reforestation is also driven by the expectations of selling carbon credits and environmental services, together with soil conservation and recovery (Trujillo, 2012). Besides providing timber, accumulating biomass and restoring soils, commercial reforestation and afforestation can also lead to the introduction and invasion of exotic species in mountain tropical forests (Richardson & Rejmánek, 2011; Tererai et al., 2013). Indeed, a significant proportion of invasive species is woody and the pathway of introduction is the forestry use, because most of the time foresters bring aggressive species such as woody legumes, which dominate much non-industrial tree planting (Hughes, 1994).

In Colombia, notably in the Andes mountains which have been subject to large scale deforestation, reforestation projects to protect watersheds and water sources, and degraded soils have been underway for several decades, often extensively planting exotic species such as Acacias, Pines, Eucalypts, Cedars and Ash (Berrio et al., 2006). A large number of these projects have been carried out in the Andean region due to the level of transformation of its ecosystems, and the resulting environmental problems.

Among the effects of invasive exotic species on native ecosystems are the ecological imbalance in structure and composition of populations and communities (Tererai et al., 2013), changes in productivity within trophic levels (Tallamy, 2004), changes in species structure and composition (Tererai et al., 2013), and loss of native biodiversity (Gutiérrez, 2006; Gerber et al., 2008; Gaertner et al., 2009). Particularly, in Andean forests there have been studies that support impacts of invasive species such as the alteration of the dynamics of pollination and colonization of native species (Martyniuk, Morales & Aizen, 2015; Aizen, Morales & Morales, 2008), the reduction of structural diversity (Gareca et al., 2007), the disruption of prevailing vegetation and soil dynamics (Gareca et al., 2007; Richardson & Cowling, 1994), and the habitat alteration (Morales & Aizen, 2002; Crichigno et al., 2016).

Biological invasions depend on the ability of the invasive species to establish and spread (invasiveness), and the susceptibility of the ecosystem to the invasion (invasibility) (Colautti, Grigorovich & MacIsaac, 2006; Lamarque, Delzon & Lortie, 2011). An important invasiveness factor is the availability of propagules, which impacts the probabilities of establishment, persistence, naturalization and invasion (Rouget & Richardson, 2003; Catford et al., 2011). Mathematical modeling has shown that this factor is an important predictor of invasion compared to other factors, such as altitude, geology, or precipitation (Rouget & Richardson, 2003). In the case of invasibility, the two important factors that make a habitat susceptible to invasion are: a) the resource fluctuations (Booth et al., 2004; Inderjit, 2005), including soil pH, soil humidity, plant litter (Alston & Richardson, 2006), availability of nutrients such as phosphorus and calcium (Alpert, Bone & Holzapfel, 2000), and b) the disturbance (Fine, 2002; Inderjit, 2005), including degree of erosion or changes in canopy and understory cover (Alston & Richardson, 2006).

Tropical Ash (*Fraxinus uhdei* (Wenz) Lingelsh) is one of the species introduced in the Andean region of Colombia more than 60 years ago, for urban greening (Infante, 1958), and for reforestation (García & Murcia, 2005). Tropical Ash has a natural distribution in the highlands of west and southern Mexico, and south Guatemala and Honduras, in altitudes between 1,100-2,600 m (US Forest Service, Pacific Island Ecosystem at Risk –PIER, 2008). Tropical Ash lives as long as 80-100 years (National Commission for Knowledge and Use of Biodiversity –CONABIO, 2008); it produces annually large quantities of wind-dispersed seeds, and has rapid growth with a high regeneration capacity (Tunison, 1995). Tropical Ash was included in the group of the greatest invasive species of islands worldwide (Smith, 1985), forming dense stands from which most native species are excluded. Rothstein, Vitousek and Simmons (2004) show that this species increased phosphorus and nitrogen availability, and accelerated forest decomposition dynamics.

In Colombia, Tropical Ash (locally known as “Urapán”) presents a moderate to high invasion risk, but more in-depth analysis is required because the current information about the biology, ecology, impacts and management of the species is insufficient (Baptiste et al., 2010). Its propagation is stimulated by the high humidity, fertility, and soil depth conditions (CONABIO, 2008), and some authors affirm that the Tropical Ash invasions are more intense on fertile soils and along streams (Harrington & Ewell, 1997; Villanueva et al. 2015). There is evidence to support that Tropical Ash colonizes forest with the soil conditions explained above, but more easily forest edges and disturbed areas (Weber, 2003), and it is by the fact that wind and precipitation are suitable mechanisms for the dispersion of its seeds, which have dormant capacities for 6 years or more (US Forest Service -PIER, 2008). However, despite being an invasive species, Tropical Ash also has reported benefits, such as, providing resources for endangered birds, like the Cauca Guan (*Penelope perspicax*) in southern Colombia (Durán & Kattan, 2005).

During the invasion process of the species, the seed germination, the seedling survivorship and the seedling growth, show variability depending on the type of land cover (García & Murcia, 2005). A first study by Arévalo (2009) found some evidence that the growth and establishment patterns of Tropical Ash depend on the type of vegetation and on the distance to the seed source.

The objective of the study was to investigate the invasion pattern of Tropical Ash in transformed landscapes. To this end, we addressed three aspects: i) the demographic structure of the species; ii) the spatial distribution pattern in the landscape; and iii) the effects of biophysical variables (distance to the propagule source, vegetation cover type, density of the understory and canopy cover) on the former.

According to the biological invasion framework previously presented, we expected the invasion pattern of Tropical Ash to be determined by the effect of the biophysical variables, both on the demographic structure of the species and on the spatial distribution pattern. To this end, we stratified the study area into contrasting vegetation types and distance classes. We expected an inverse relation between distance to the propagule source and the abundance of individuals; and significant differences in densities and age structure in each vegetation cover type and distance class to the seed source, with lower probability of establishment in denser canopies and understories.

Materials & Methods

Study area

The study site is located in the Bogotá Highplain in the central part of the Eastern Andes of Colombia, north of the capital Bogotá. It covers an approximate area of 500 hectares, on the western side of the Majuy Mountain range in the Municipality of Tenjo (Cundinamarca Department) (Fig. 1). The Majuy mountain range contains one of the better-conserved and largest native forest remnants of the region, it is an area of interest for conservation and considered as a key to the ecological infrastructure of the Bogotá Highplain region (Montañez & Cereh, 2013). In addition, there is evidence of the species invading the area (Arevalo 2009) which makes the area an ideal study site.

The Bogotá Highplain is part of the wider region known as the High-plains of the Eastern Cordillera, which covers an area of 200,000 ha (EcoNat Ltda. & Fundación

Cerros de Bogotá, 2013). There is an old fluvio-lacustrine plain with average altitude of 2,600 m, crisscrossed by several north-south cretaceous and tertiary sandstone mountain ranges up to 3,500m high, of which Serranía Majuy is one (EcoNat Ltda. & Fundación Cerros de Bogotá, 2013). The Majuy mountain covers some 3,000 ha and reaches an altitude of 3,000 m (EcoNat Ltda. & Fundación Cerros de Bogotá, 2013).

The climate is sub-humid and cool, with an annual rainfall of around 900 mm, distributed in two rainy seasons (April-June and September-November), with two to four dry months. Average temperature is 16°C (0-22°C). Wind direction is predominantly from the northwest (Colombian Institute of Hydrology Meteorology and Environmental Studies-IDEAM, 2014).

Serranía Majuy presents slopes that vary from 25% to more than 50%, with mostly superficial and relatively young soils, composed mainly by Entisols, with some inclusions of Andisols. These soils are generally of low fertility, with a pH varying from acid (6.5) to very acid (5.0), and have a low base and phosphorus contents (Rodríguez, 1997).

The remnants Andean Forest of Serranía Majuy are privately owned, but must comply with use restrictions. The surrounding plains consist of a mosaic of pastures, crops, greenhouses used for floriculture and suburban areas, bordered by live fences of native and introduced species. Common introduced trees in live fences include the Tropical Ash and Acacias (*Acacia decurrens* and *Acacia mangium*).

INSERT Fig. 1

Methodology

The study targeted the presence of Tropical Ash individuals within the forest remnants of the study area. The sampling units were stratified by vegetation cover type and distance classes to propagule sources (fences lines), using a vegetation type and distance map, whose creating process will be explain in the next section.

Land cover map

We constructed a land cover map using a high-resolution satellite image (0.5m) of the year 2009 from Worldview 2 satellite (Fig. 2). We applied a segmentation procedure using the Monteverdi software, which consists in a process of grouping pixels with regard to one or more characteristics (OTB Team, 2014). Based on the best results of the segmentation, assessed by the number of generated regions and the concordance with a preview visual interpretation of the image, we constructed the land cover map using ArcGis 10 software. Five types of land cover were identified and delineated: tall native forest, low native forest, native shrubland, hedgerows, woody pasture, pastures and crops, infrastructure and forest plantation (*Eucalyptus* sp.).

INSERT Fig. 2

Biophysical variables

To analyze and model Tropical Ash data, we considered the following biophysical variables:

Natural woody vegetation cover: native vegetation types within the Andean forest remnant (Tall forest, low forest, and shrubland).

Distance classes from the propagule source along the area: calculated as the Euclidean distance map from the presence points of the introduced Tropical Ash trees (seed source trees located in fences lines and taken from Arévalo (2009), thereafter creating a distance map with three classes: 0-150 m, 150-300 m, and 300-500 m (Fig. 3). The distance classes were determined in order to assure each vegetation type was represented in each distance class.

Understory density: measured as an ordinal variable (1 to 5, sparse to dense), assigned based on the observation of percentage of understory plants of a 2 m diameter area around each Tropical Ash individual.

Canopy cover: the quantitative canopy cover (%), measured with one densitometer on the side of each registered Tropical Ash individual. These were grouped into five categories: 0-20%, 20-40%, 40-60%, 60-80%, and 80-100%.

INSERT Fig. 3

Fieldwork

The fieldwork was performed between August and September of 2014. With the purpose of defining the Tropical Ash range in the study area, an individual-based measurement was considered (Yalcin & Leroux, 2017). Samples were taken in the form of band transects following a stratification of 9 *coverage-distance classes* based on the combination of the three native vegetation cover types and the three distance to the propagule source classes. Within each class coverage-distance, one band transect was traced following a meandering pattern up- slope, covering as far as possible the spatial unit being sampled (Yalcin & Leroux, 2017) (Fig. 3). The band transects were 3 meters wide and the length varied according to the area of the coverage-distance class. The first band line in each stratum was about 3 meters of distance from the vegetation cover edge, approximately.

In each transect, all observational record of Tropical Ash were registered (Yalcin & Leroux, 2017), and for each individual the following data were recorded: band transect number, individual number, geographical position (GPS), woody vegetation cover type, diameter at breast height (DBH), canopy cover (%) and understory density class.

Data analysis

Density

The area (hectares) of the traveled transect in each of nine coverage-distance classes was calculated by multiplying the length of each transect by their width (3 m).

With these data and the corresponding individual presence, a measure of the density for each coverage-distance class was calculated (individuals/hectare).

Demographic structure

To explore the demographic structure of the Tropical Ash population, diameters were grouped into 5 categories: <1 cm (Seedling), 1–2 cm (Juvenile 1), 2–5 cm (Juvenile 2), 5–10 cm (Juvenile 3), and > 10 cm (Adult). The plotting the abundances of each diameter class yielded to give an estimation of the survival curve (Lauenroth & Adler, 2008). The relation between Tropical Ash abundance for each diameter class, vegetation cover type, and distance to the propagule source was also examined.

Spatial distribution pattern

In order to analyze the spatial distribution pattern of the Tropical Ash population, we used Ripley's K function (Haase, 1995; Soto et al., 2010), which is a tool for analyzing mapped spatial point process data and is highly used in spatial patterns of trees (Dixon, 2002). It also shows the change in the spatial clustering or dispersion of the centroids of the entity when the size of the neighborhood changes (ArcGis Resources, 2014). In this case, the Ripley's K function was implemented through a common transformation shown in Equation 1, using ArcGis (ArcGis Resources, 2014):

$$L(d) = \sqrt{\frac{A\sum_{i=1}^{n}\sum_{j=1, j\neq 1}^{n} k_{i,j}}{\pi n(n-1)}} \qquad \text{Equation 1}$$

Where, *A* is the sampled area, *n* is the number of points, *d* is the distance, and *k* is the weight. The Weight *k* is equal to 1 if there is no limit correction when the distance between *i* and *j* is smaller or equal to *d,* and becomes 0 when the distance between *i* and *j* is larger than *d*. When the boundary correction is applied, to correct for underestimates in the number of neighbors for features near the edges of the study area, the Weights *k* changes slightly.

If the observed K value (*L(d)*) is larger than the upper confidence envelope, it means there is a statistically significant spatially aggregated pattern; if the observed K value is smaller than the lower confidence envelope, there is a statistically significant dispersed spatial structure (ArcGis Resources, 2014).

Relations with biophysical variables

For the statistical analysis of biophysical variables, specifically understory density and canopy cover, the frequency of individuals for each category of these variables in the vegetation types were explored. To complement, a frequency comparison test (*Chi*^{2}) (Pyle, 1995), was done for the following variables: i) diameter categories between vegetation types and distance classes; ii) understory density categories between vegetation types; and iii) canopy cover categories between vegetation types. The statistical analyses were performed using the Past.ver.2.17c software.

To address the hypothesis of the impact of the biophysical variables in the population demographic structure and spatial distribution pattern, it was necessary a new data treatment. The distance ranges were reduced to two classes (0-300 m and 300-600 m) to have enough representation of all the vegetation cover types in each distance class, and the Ash individuals to three groups of the 5, 10 and 15 largest (mostly adult reproductive) individuals (Mullah et al., 2014). Then, normality and homoscedasticity tests were done for the six new coverage-distance classes (Tall forest in 0-300 distance, Tall forest in 300-600 distance, Low forest in 0-300 distance, Low forest in 300-600 distance, Shrubland in 0-300 distance, Shrubland in 300-600 distance). Because of the heterogeneity in variances of the data, we applied a Kruskall-Wallis median comparison test (Dickens & Allen, 2013).

The group with the 5 largest individuals was subject to a factorial variance analysis (ANOVA), to comply with the homoscedasticity condition for a significance level of 5%.

Additionally, we also applied a regression analysis to test the relation between the density of the individuals, and the distance to the propagule source and the vegetation type.

Results

We recorded a total of 2,078 Tropical Ash individuals, 333 (16%) corresponding to seedlings (DBH < 2 cm). Abundance varied a lot, with 6.7% of individuals (140) found in the tall forest; 74.5% (1,548 individuals) recorded in the low forest, and 18.8% (390 individuals) in the shrublands.

In relation to the distance to the propagule source, 64.9% (1,349 individuals) of the trees were found in the range of 0-150 m; 24.7% (513 individuals) were recorded in the second range (150-300 m); and 10.4% (216 individuals) were recorded in the third range (300-500m).

The proportion of individuals recorded in each vegetation type showed that the low forest presented the greatest number of individuals, whereas the shrubland and the tall forest, showed lower densities (Table 1). For the distance classes, densities decreased with distance (Table 1).

INSERT Table 1

Regarding the hypothesis of the inverse relation between the distance to the propagule source and the population abundance, an exponential function was set, where a decrease in the number of individuals is related to an increase in the distance to the propagule source in live fence lives (Fig. 4).

INSERT Fig. 4

Population structure and distribution pattern of Tropical Ash individuals

Size class distributions show a decrease in the relative abundances with increasing size (age) of individuals, and consequently the population consists mainly of seedlings and juvenile plants, a behavior generally explained through intraspecific effects (Fig. 5). The number of seedlings was correlated with vegetation cover type and distance, with a reduction in the number of seedlings associated with increasing forest height (Fig. 6A), which was also the case with an increase in distance to the seed source (Fig. 6B).

INSERT Fig. 5

INSERT Fig. 6

The overall demographic pattern or "survival curve" of the species showed overall an inverted "J" structure characteristic for an inverse exponential mortality rate (Fig. 7A). The same pattern occurred for low forest and shrubland, however in the case of the tall forest the best data adjustment was that a polynomial function (Fig. 7B).

INSERT Fig. 7

The analysis of the overall spatial distribution pattern showed that the individuals of Tropical Ash follow an aggregated or contiguous pattern, varying significantly from a random pattern. This was also true when the analyses were done for each distance class and vegetation types, always showing an aggregated pattern above the expected value for a random pattern (Fig. 8).

INSERT Fig. 8

Relations with biophysical variables

Vegetation type and distance to propagule source

A comparison of the distribution of diameter classes in each vegetation type showed significant differences in their frequencies between shrublands, and the tall and low forests (Table 2). The same was observed for the frequencies between the distance class 0-150 m, and the distance classes 150-300 m and 300-500 m (Table 2). Furthermore, the distance classes within each vegetation type were also significantly different, indicating that each subpopulation appears to have a different diameter structure in each vegetation type at different distances from the seed sources (Table 3).

INSERT Table 2

INSERT Table 3

Regression analyses revealed that densities of the ash plants within all distance classes related inversely to the distance of the propagule source, irrespective of vegetation type (Table 4). However, the factorial ANOVA analysis identifies the existence of a statistically significant interaction between distance and vegetation type for the distribution pattern of adult ash plants (5 largest individuals) (Table 5).

INSERT Table 4

INSERT Table 5

A comparison of the medians of the 5 largest individuals within each coverage-distance class, showed that low forest had the greatest significant difference in the 0-300 m distance class. However, the analysis also indicated that further away, in the 300-600 m distance class, the three vegetation types showed no difference in the number of individuals (Table 6). When the analysis was performed for the 10 and 15 largest individuals, the low forest showed the greatest difference in both the 0-300 m and 300-600 m distance classes. In terms of distance classes, the first distance range (0-300 m) presented the greatest variation between vegetation types (Table 7).

INSERT Table 6

INSERT Table 7

Understory density and canopy cover

For both, understory density and canopy cover, the intermediate values (class 3) showed overall a higher proportion of Ash individuals in the three vegetation types (Fig. 9). For the understory density, the lowest proportions were found in the lowest cover class, but in the canopy cover the two extreme values (class 1 and 5) showed the lowest proportions of individuals. Differences in patterns between vegetation types was significant ($p < 0.05$), for all except between tall and low forest.

INSERT Fig. 9

Discussion

Our study shows strong evidence of an active invasion process of Tropical Ash into the remnant native forests and shrublands of the hills and mountain ranges of the Bogotá High-plain, and highlights a broad spread of propagules into forests over considerable distances from forest borders. In this process, the type of vegetation, distance to the propagule source, understory density and canopy cover appear to play important roles, and affect the demographic structure of the invading population.

Population structure and distribution pattern of Tropical Ash individuals

The species abundance and demographic structure within the studied area reflects the conditions of the invasiveness of the species, as well as the invasibility of the ecosystem. Even under harsh conditions of shallow soils, steep slopes and exposed rocks observed in the shrubland vegetation, the ash individuals are able to establish although they rarely reach beyond a juvenile stage.

This study showed that the reproductive strategy of the species conforms to a “type r” behavior, in agreement with previous studies (Arévalo, 2009; García & Murcia, 2005). The negative exponential curve of the size classes is relevant because Tropical Ash studies so far only mention the rapid growth rate of the species (Durán & Kattan, 2005; Ares & Fownes, 2001). According to Rollet (1980) and Hubbell and Foster (1987), an inverted J structure is associated with shade-tolerant species, as shown in the case of Tropical Ash.

For a rapidly growing species such as Tropical Ash (CONABIO, 2008), a high abundance of mature reproductive individuals is expected, especially if the species was introduced in the area more than 50 years ago. Surprisingly, this is not yet the case, because less than a quarter of the population has reached the adult stage. Likewise, given that most of the plants were found at intermediate levels of canopy cover and understory density, the species is assumed to experience some form of interspecific competition, for example, for resources such as light or substrate (Ares & Fownes, 2001).

The results of this study confirm that species with wind dispersal mechanisms display an inverse relationship between the distance of the seed source and their abundance, meaning that the abundance decreases with the distance to the seed source (Harper, 1977; Edward, Munishi & Hulme, 2009; Catford et al., 2011).

The aggregated spatial pattern observed for the species, could be explained by the high number of individuals in the low diameter category, as suggested by Soto et al. (2010). However, an aggregated spatial pattern is also expected to be determined by the local environmental conditions (Crawley, 2002). Thus, the spatial pattern could be attributed to a combined effect of the distance to the propagule source, the type of vegetation cover, the understory density, and the canopy cover or other factors not addressed in our study, which need to be analyzed in further research.

Relations with biophysical variables

A number of studies have analyzed the invasion process including the distance to the propagule sources (Rouget & Richardson, 2003; Sebert-Cuvillier et al., 2008), vegetation cover types (Arévalo, 2009; Kuhman, Pearson & Turner, 2010), density of the understory and canopy cover (Alston & Richardson, 2006; Edward, Munishi & Hulme, 2009). These studies have shown an interaction between the distance to the propagule source and the type of vegetation cover, as we observed with the Tropical Ash abundance, revealing the role of understory density and canopy cover in the establishment and development stage of the species. This support the claim that, invasibility and invasiveness interact in such a way (Colautti, Grigorovich & MacIsaac, 2006), that no individual mechanism can by its own fully explain the invasions of plant species (Lamarque, Delzon & Lortie, 2011).

Contrary to what Tunison (1995) and Ares and Fownes (2001) reported, we found that the dispersion and establishment of Tropical Ash seeds reach long distances, with individuals being found at more than 500 m from the seed source. Although wind direction and speed variables were not considered in our study, in this case the remnant forest is located precisely where the wind blows most of the year (IDEAM, 2014), highlighting that these factors need to be considered to explain the invasion process.

With regard to the types of vegetation cover, the shrubland showed the greatest differences in diametric category frequencies, explained by a larger seedling participation. This result does not support the findings of Arévalo (2009), who indicated that the low forest appears to be the most suitable for the establishment of seeds, although this suitability was related to the lower mortality rate being observed in the low forest. In the case of the tall forest which shows the lower densities, the following aspects can explain the limitations for invasion: a) presence of more vegetation layers that may prevent the seeds reaching the soil, b) dense ground layer with a high presence of *Chusquea sp.* that decreases the probability of establishment, and c) larger distance from the seedling source. On the other hand, in the case of shrublands, the limitations for invasion could be explained by the following limiting conditions: a) shallow ground, exposed rock and steep slopes; b) positioning on top of the hills, which decreases the probability of seed arrival; and c) exceedingly dense ground layer that prevents the establishment of specimens.

This study supports the findings of other authors (Arévalo, 2009; Edward, Munishi & Hulme, 2009; Alston & Richardson, 2006; Catford et al., 2011), in that the distance to the propagule source is the most important variable for explaining the density or abundance of the invasive species.

In our study we did not consider the “edge effects” in the invasion process (Brothers & Springarn, 1992; Murcia, 1995; Parendes & Jones, 2000), which could help explain why the low forest, which shares the larger proportion of edges towards pastures/crops, had the largest quantity of individuals. According to Parendes and Jones (2000), the edges can provide suitable habitats for the propagation of the species and can also contain supplies of seedlings that participate in future invasions.

To complement the results of this study, future studies should address the possible interactions with local flora and fauna, such as frugivory relation, which may influence in a positive or negative way the invasion process of Tropical Ash, as shown by García and Murcia (2005). Similarly, a closer look at the disturbances from climatic extremes, and habitat modifications resulting from the invasion process would provide relevant information regarding the dynamics and impact of the species on the invaded ecosystems (Cuddington & Hastings, 2004).

Conclusions

We show strong evidence of an active invasion process by the exotic tree Tropical Ash. We provide new knowledge about the behavior of the species in the limited number of remnants of the sub-humid forests in the Andean highlands. The results showed the importance of considering the distance to the propagule source, the vegetation cover, the canopy cover and the density of the understory, in explaining the demographic structure analyses of the invasive plant species. The findings about the interaction between the distance to the propagule sources and the vegetation types, are important because they can be integrated into control actions and management in cases of invasion of Tropical Ash.

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Table 1(on next page)

Tropical Ash density

Density values into each vegetation type and distance class

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Variable	**Category**	**Density (individuals/ha)**
Vegetation type	Tall forest	91
	Low forest	336
	Shrubland	17
Distance classes (m)	0-150	469
	150-300	226
	300-500	68

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Table 2(on next page)

Frequency comparison of vegetation types and distance classes

Result of a Chi-squared frequency comparison test (*Chi*^{2}) with the diameter categories between vegetation types and distance classes

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Variable	**Relation**	***p-value***
Vegetation type	Tall forest / Low forest	0.08
	Tall forest / Shrubland	**9.3E-08**
	Low forest / Shrubland	**7.2E-17**
Distance classes (m)	0 -150 / 150-300	**2.1E-08**
	150-300 / 300-500	0.40
	0-150 / 300-500	**9.7E-08**

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Table 3(on next page)

Probability (*p-value*) for the frequency comparison of the vegetation type and distance classes

Result of a Chi-squared frequency comparison test (*Chi*^{2}) with the diameter categories. This analysis compares the distance classes into each vegetation type.

Distance class (m)/ Vegetation type	0-150 / 150-300	150-300 / 300-500	0-150 / 300-500
Tall forest		0.72	
Low forest	**4.3E-4**	**0.01**	0.08
Shrubland	**2.9E-23**	0.39	**7.3E-16**

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Table 4(on next page)

Multiple linear regression applied to density versus distance classes and vegetation types

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	Coefficients	Typical error	Statistical t	*P-value*
Intercept	0.11	0.013	8.81	**3.0E-4**
Distance classes	-0.0003	4.46E-5	-7.52	**6.0E-4**
Vegetation types	0.0017	0.005	0.31	0.76

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Table 5(on next page)

Factorial ANOVA for the 5 largest individuals within each coverage-distance class

The group has five individuals with the highest diameters at breast height

	Sum of squares	**Degrees of freedom**	**Mean squares**	**F**	**P-value**
Vegetation type	573.4	2	286.7	56.89	**8E-10**
Distance to propagule source	213.3	1	213.3	42.34	**1E-06**
Interaction	443.6	2	221.8	44.01	**9E-09**

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Table 6(on next page)

Probability (*p-value*) of the multiple median comparison tests for the 5 largest individuals within each coverage-distance class

The group has five individuals with the highest diameters at breast height

	Low forest 300-600	Shrubland 300-600	Tall forest 0-300	Low forest 0-300	Shrubland 0-300
Tall forest 300-600	0.67	**0.03**	**0.01**	**0.01**	**0.02**
Low forest 300-600		0.09	**0.03**	**0.01**	0.52
Shrubland 300-600			0.11	**0.01**	**0.01**
Tall forest 0-300				**0.01**	**0.01**
Low forest 0-300					**0.01**

1

Table 7(on next page)

Probability (*p-value*) of the multiple median comparison tests, for the 10 and 15 largest individuals within each coverage-distance class

The group has ten and fifteen individuals with the highest diameters at breast height. The result for both groups was the same and only one table is shown.

	Low forest 300-600	Shrubland 300-600	Tall forest 0-300	Low forest 0-300	Shrubland 0-300
Tall forest 300-600	0.01	**1.5E-04**	**1.3E-05**	**3.3E-06**	**2.6E-03**
Low forest 300-600		0.02	**8.8E-04**	**3.3E-06**	**2.6E-03**
Shrubland 300-600			0.11	**3.3E-06**	**1.5E-05**
Tall forest 0-300				**3.3E-06**	**3.3E-06**
Low forest 0-300					**3.3E-06**

1

Figure 1(on next page)

Study area to the northwest of Bogotá in Tenjo, Cundinamarca

Study area (red rectangle) covering part of the hills and low mountains within the Bogotá high-plains. Dark green areas correspond to native vegetation remnants, mostly forests; light green and orange to pastures and crops; beige to urban centers (Map data © 2015 Google Earth)

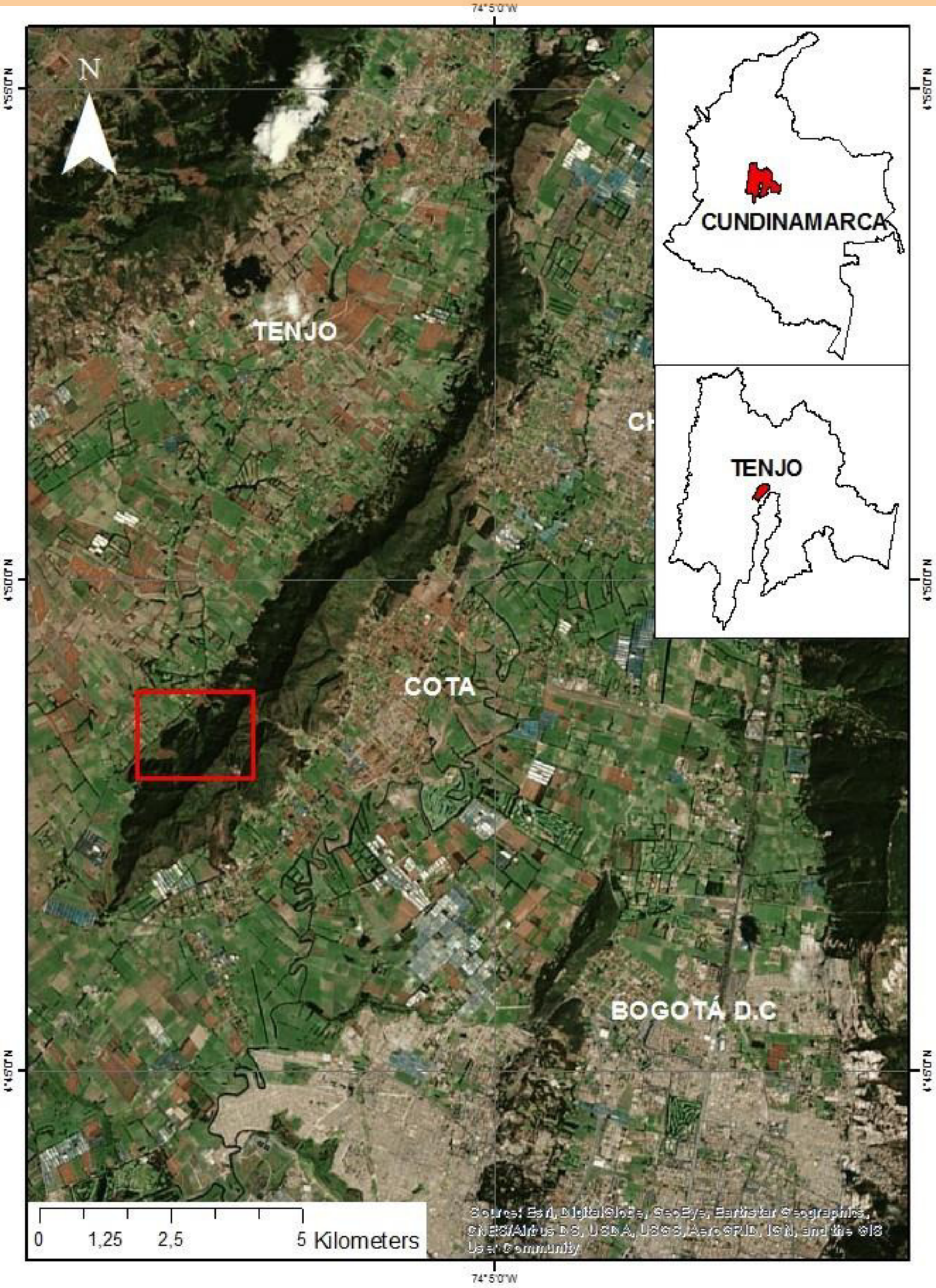
74°5'0"W
4°55'0"N
4°50'0"N
4°45'0"N
N
TENJO
CH
COTA
BOGOTÁ D.C
CUNDINAMARCA
TENJO
0 1,25 2,5 5 Kilometers
Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Figure 2(on next page)

High-resolution satellite image of the study area from Worldview 2 satellite, year 2009.

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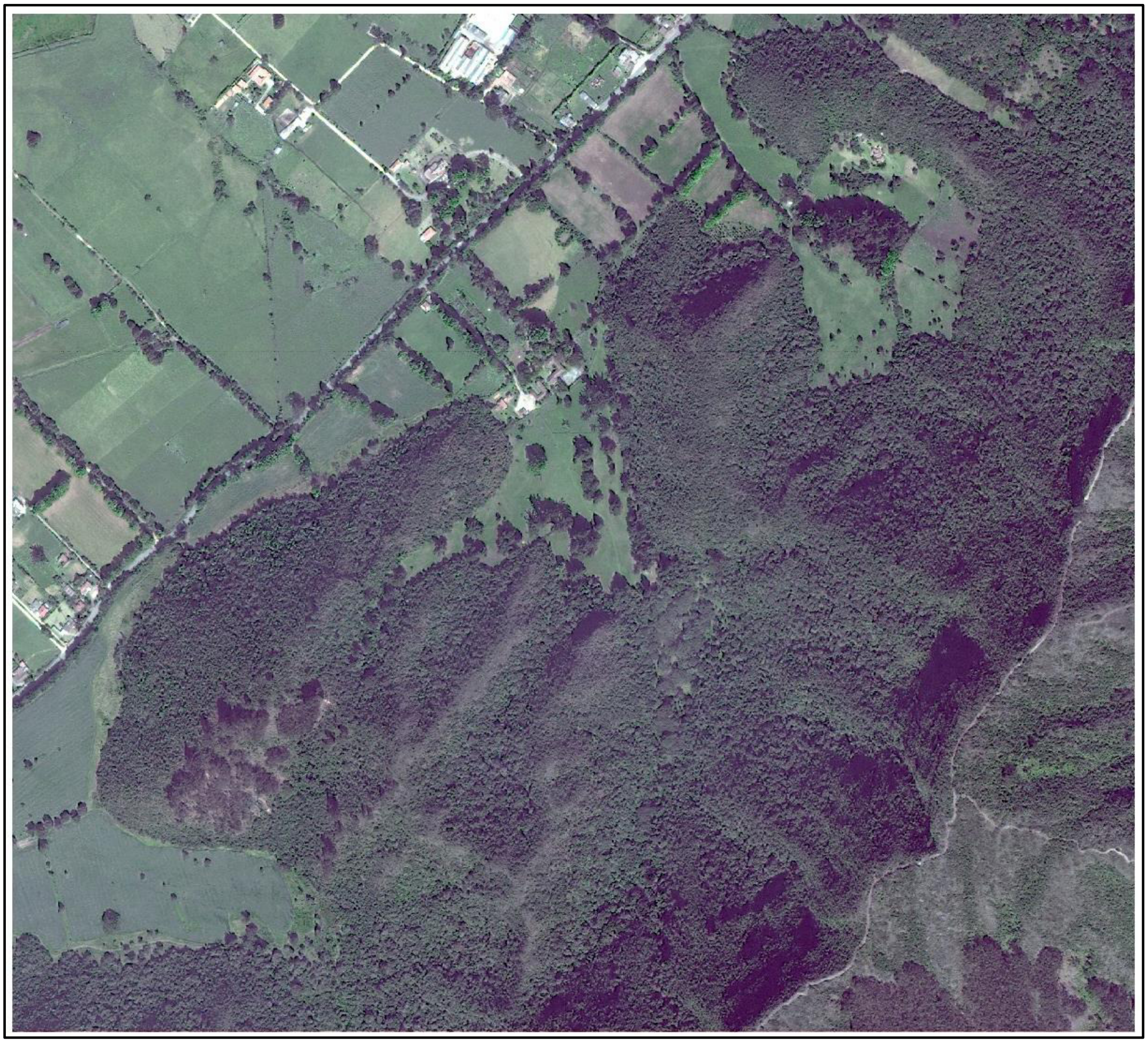

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Figure 3(on next page)

Land cover map and distance classes

Black triangles represent seed source trees of *Fraxinus uhdei.* Distance classes were calculated around the seed source trees (red rings)

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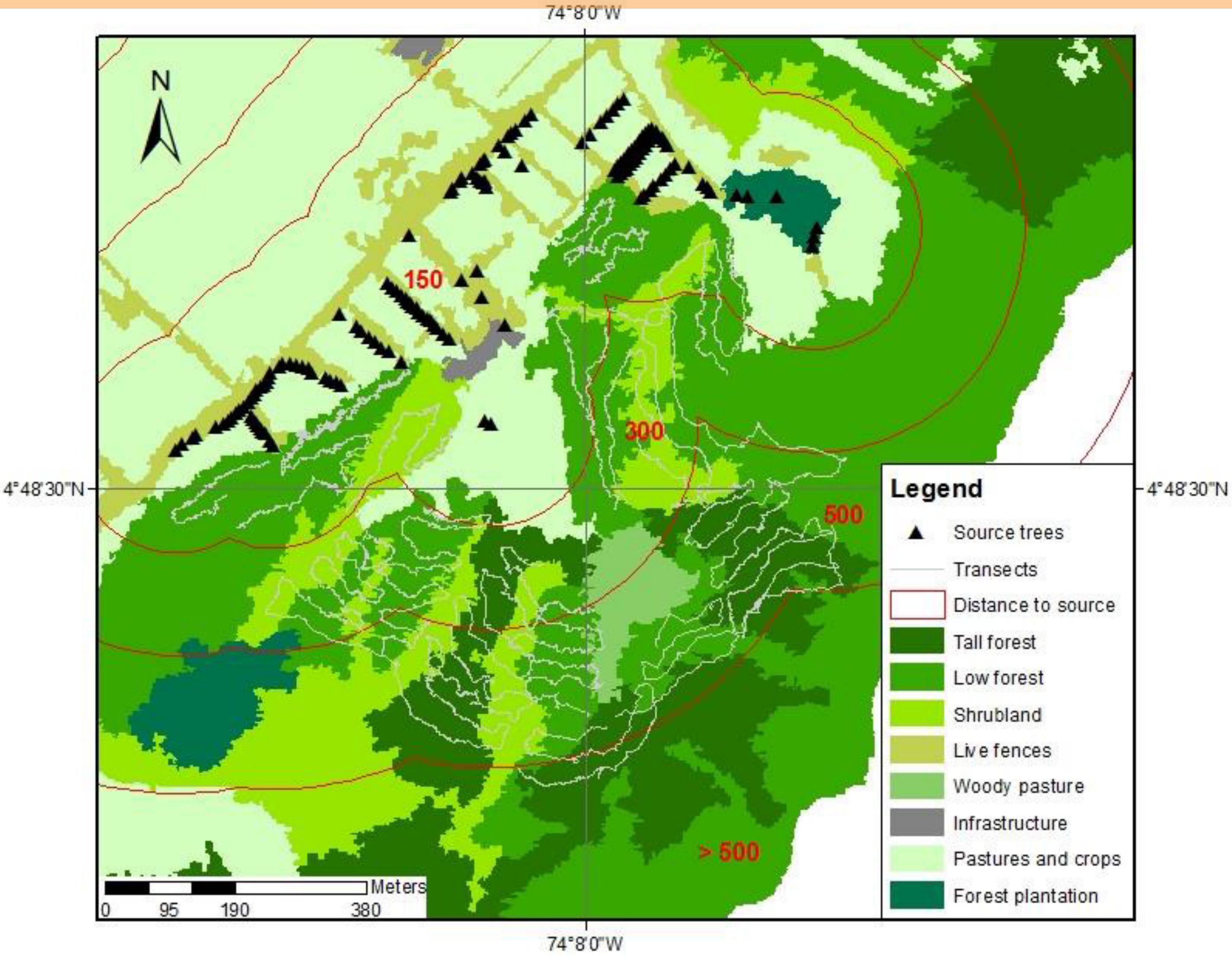

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Figure 4(on next page)

Distribution of individual abundance in relation to the distance to the propagule sources

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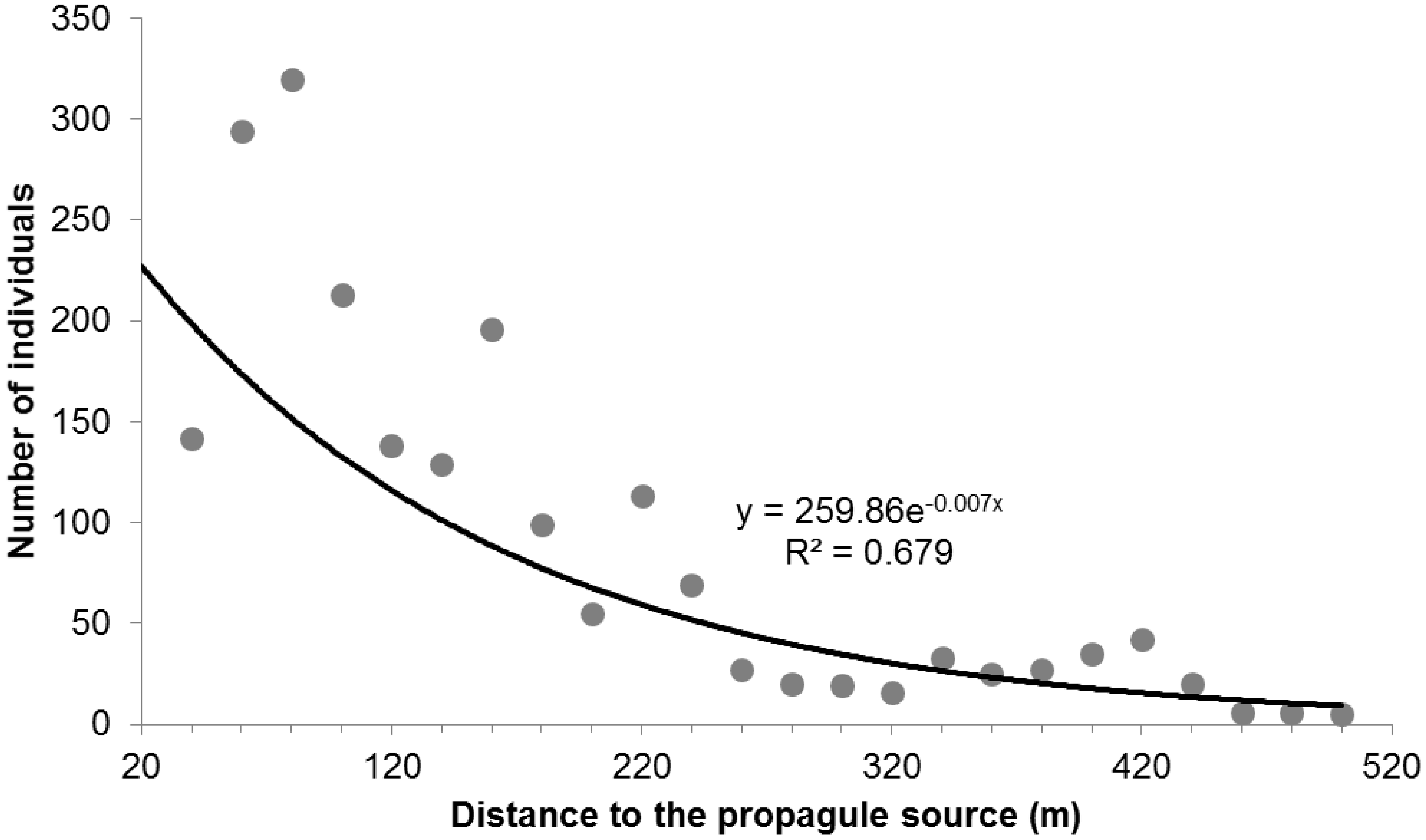

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Figure 5(on next page)

Proportion of the relative age classes

Diameters were grouped into 5 categories (relative age classes): <1 cm (Seedling), 1–2 cm (Juvenile 1), 2–5 cm (Juvenile 2), 5–10 cm (Juvenile 3), and > 10 cm (Adult)

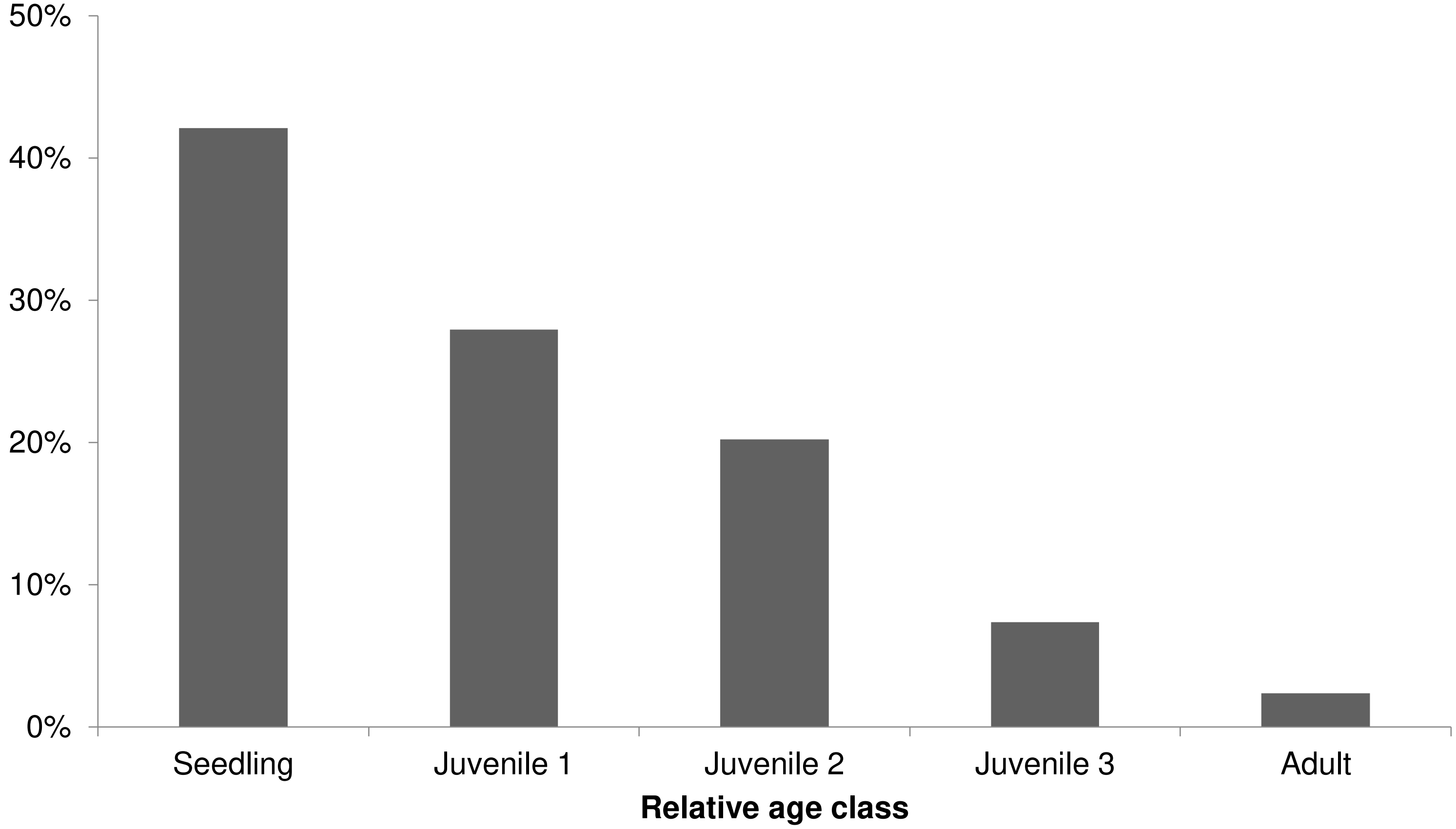
50%
40%
30%
20%
10%
0%
Seedling
Juvenile 1
Juvenile 2
Juvenile 3
Adult
Relative age class

Figure 6(on next page)

Proportion of the relative age classes in each vegetation type and distance class

(A) Proportion of relative age classes in each vegetation type (B) Proportion of relative age classes in each distance class

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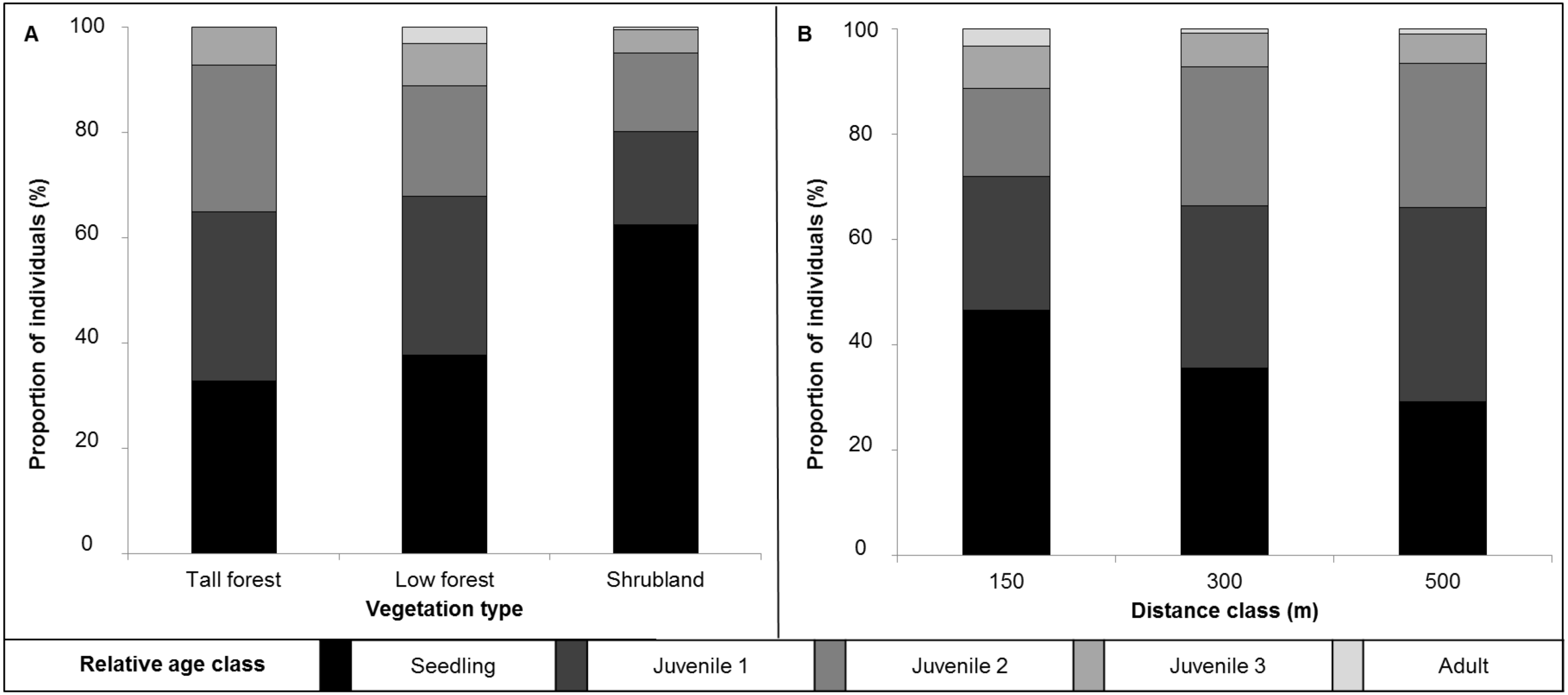
A
Proportion of individuals (%)
0
20
40
60
80
100
Tall forest
Low forest
Shrubland
Vegetation type
B
Proportion of individuals (%)
0
20
40
60
80
100
150
300
500
Distance class (m)
Relative age class
Seedling
Juvenile 1
Juvenile 2
Juvenile 3
Adult

Figure 7(on next page)

Survival curve

(A) Survival for total population of Tropical Ash (B) Population survival by vegetation types

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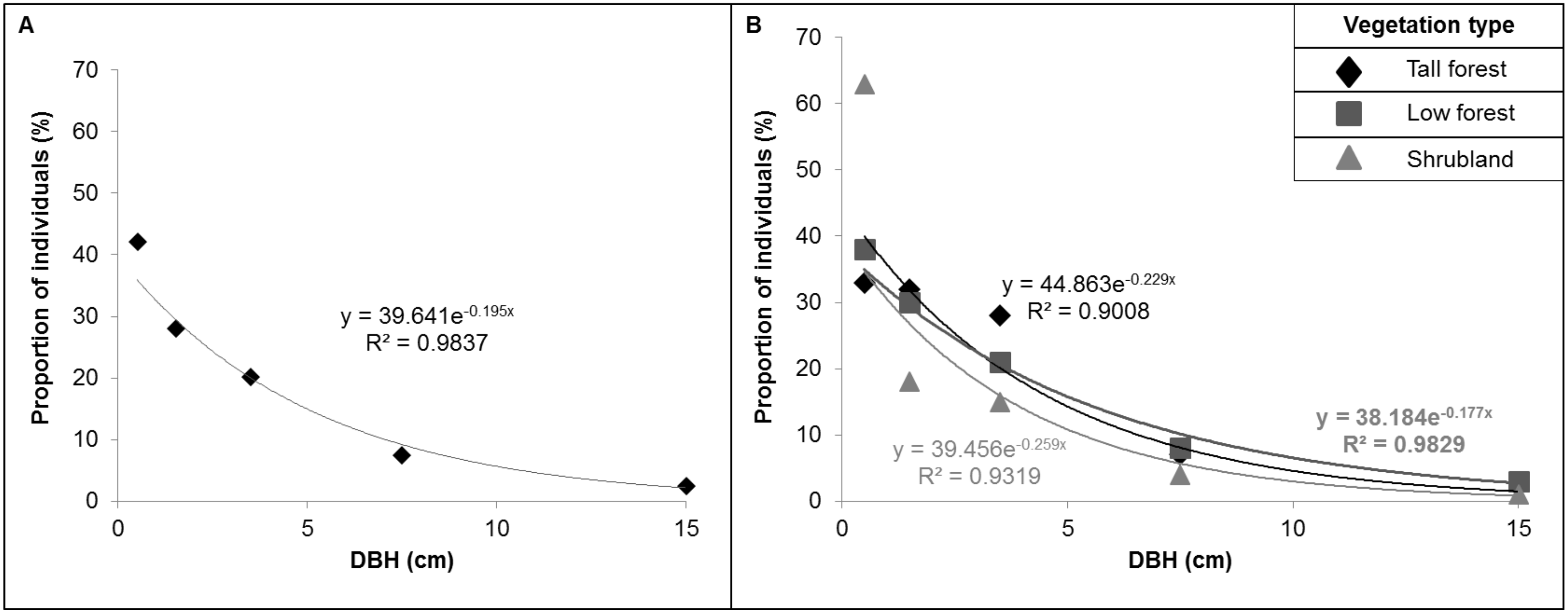

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Figure 8(on next page)

Spatial distribution pattern of Tropical Ash for each distance class and vegetation type

(A) Distance class 150 m (B) Distance class 300 m (C) Distance class 500 m (D) Tall forest (E) Low forest (F) Shrubland

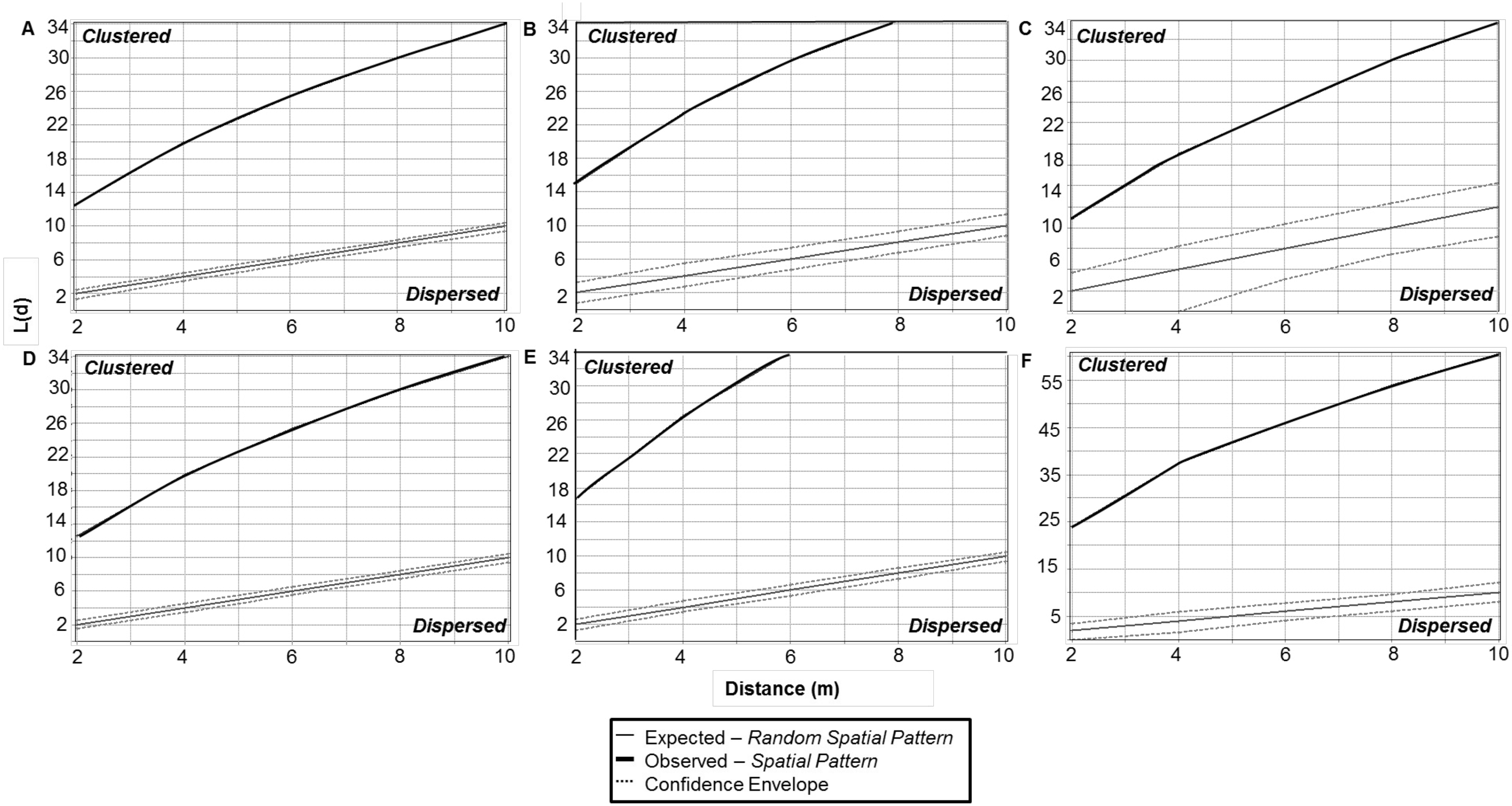
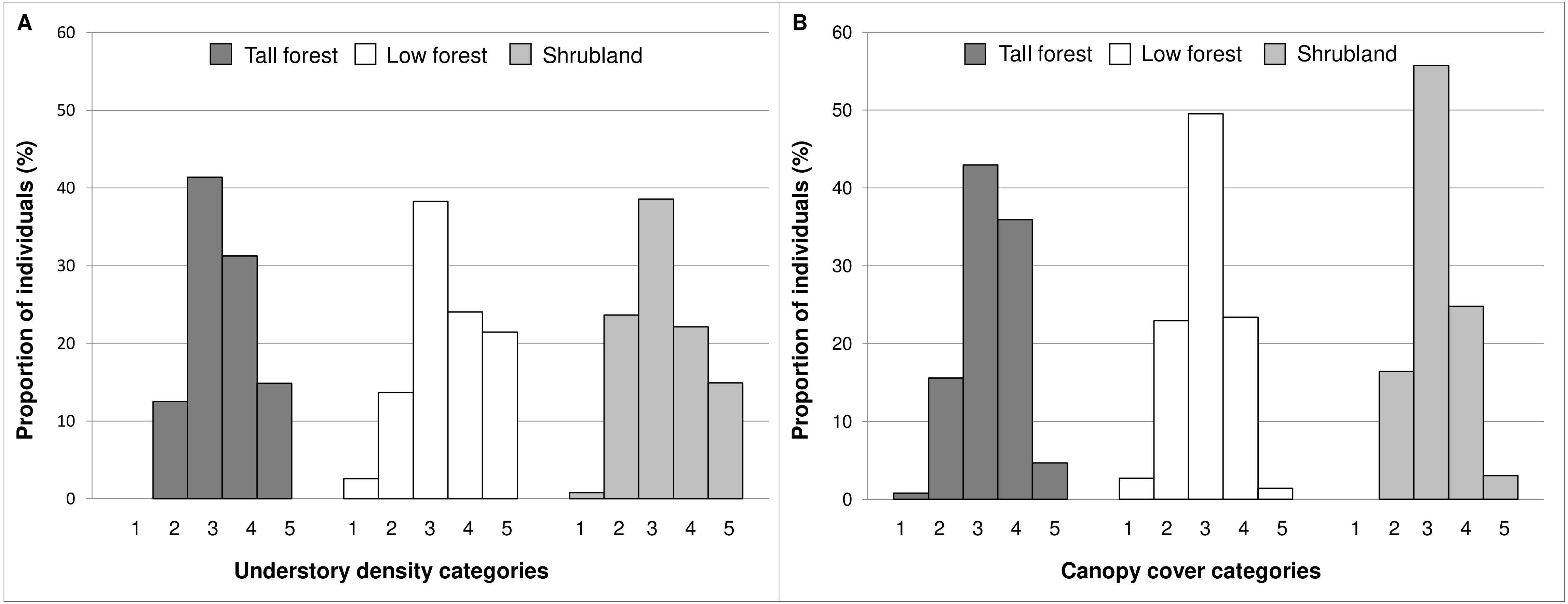

A
B
C
D
E
F
Clustered
Dispersed
L(d)
34
30
26
22
18
14
10
6
2
55
45
35
25
15
5
2
4
6
8
10
Distance (m)
Expected – *Random Spatial Pattern*
Observed – *Spatial Pattern*
Confidence Envelope

Figure 9(on next page)

Proportion of individuals for understory density and canopy cover categories

(A) Proportion of individuals in each understory density category (1 to 5, sparse to dense), by vegetation types (B) Proportion of individuals in each canopy cover category (1 to 5, clear to dense), by vegetation types



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