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p. 3, l. 21: please give reference to Box-Cox transformation
p. 3, l. 57: the same for Bray-Curtis
p. 3, Table 1: Ligustrum, Psychotria: what does the low dash _ mean??

App. 1. Unfortunately, the MS Word file we have is damaged, and we ask you to send us the App. again, with the text separate from the figures, and the figures as jpeg, TIF or eps files. We received the following comments from the Final Editor with regard to the App.

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p. 1, l. 13: write 1. in stead of (1) l. 16 similar change

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Figure captions: write Fig. not Figure
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Recruitment limitation in secondary forests dominated by an exotic tree species

Lichstein, Jeremy W.[1,2*]; Grau, H. Ricardo[1,3] & Aragón, Roxana[1,4]

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Abstract

Question. What factors limit woody plant recruitment in a mosaic landscape where former agricultural lands are dominated by the invasive tree *Ligustrum lucidum* (*Oleaceae*)?
Location. Subtropical northwestern Argentina.
Methods. In secondary forest patches, we measured (1) tree, shrub and liana abundance in different size classes; (2) seed rain of *Ligustrum* and two native trees and (3) topographic, soil and light variables. We used spatial autoregressive models to test for effects of *Ligustrum* dominance and environment on native plant abundance in each size class. We used multiple regression on resemblance matrices to quantify the relative importance of spatial (e.g. dispersal) and environmental effects on native species composition.
Results. Native tree abundance in the smallest size class was unrelated to *Ligustrum* canopy dominance, while native tree abundance in larger size classes and native liana abundance were negatively correlated with *Ligustrum* dominance. Native species composition was both environmentally and spatially structured, suggesting that some species are dispersal limited. Seed rain was spatially correlated with conspecific basal area for one of two native species, but not for *Ligustrum*.
Conclusions. Native tree recruitment appears to be limited primarily by sapling mortality in patches dominated by the invasive *Ligustrum*. *Ligustrum* does not appear to be dispersal limited in our study area and is likely to continue spreading. Invaded patches may persist for hundreds of years.

Keywords: Invasive species; Land use change; *Ligustrum lucidum*; Seed dispersal; Spatial autocorrelation.

Nomenclature: Zuloaga & Morrone (1996, 1999).

Abbreviations: AR = Auto-regressive; MRM = Multiple regression on resemblance matrices; OLS = Ordinary least squares; PC = principal component; SC = size class; TSI = Terrain shape index.

Introduction

Land transformation and the spread of exotic species are two primary components of global change (Vitousek et al. 1996, 1997). These two processes are often coupled, as exotic plants are common on abandoned agricultural land (Meiners et al. 2002; Aragón & Morales 2003, Grau et al. 2003). In addition to disturbance and land use, there is a growing awareness that seed dispersal, or 'propagule pressure', plays a key role in plant invasions (Lonsdale 1999; Levine 2000). Recent studies (Levine & D'Antonio 1999; Stohlgren et al. 1999) have largely overturned the traditional view that diversity enhances invasion resistance (Elton 1958), suggesting that dispersal and the functional traits of introduced species are major determinants of invasion success.

Seed dispersal has become a primary focus in plant ecology following the realization that recruitment is often dispersal limited (Tilman 1997; Clark et al. 1998; Nathan & Muller-Landau 2000) and that dispersal limitation can enhance species co-existence (Tilman 1994; Hurtt & Pacala 1995; Hubbell et al. 1999). In mosaic landscapes, where agricultural lands are abandoned, dispersal is likely to play an important role in succession.

Other factors affecting recruitment include seed predation (Janzen 1971), disease (Gilbert et al. 1994; Packer & Clay 2000), herbivory (Clark & Clark 1985; Terborgh et al. 2001) and resource availability (Tilman 1985). In forests, light is a critical resource affecting growth and mortality (Horn 1971; Pacala et al. 1994; Davies 2001) and many plant invaders are thought to suppress native recruitment by reducing light availability (Wyckoff & Webb 1996; Holmes & Cowling 1997; Levine et al. 2003).

We studied woody recruitment in northwestern Argentina, where secondary forests on former agricultural land are interspersed with agriculture and human residences. Many of these forests are dominated by *Ligustrum lucidum* (*Oleaceae*), an evergreen tree native to China and Korea that has invaded sites in eastern

Argentina (Montaldo 1993; Ribichich & Protomastro 1998), Australia and New Zealand (Cronk & Fuller 1995). The rapid growth of *Ligustrum* (Aragón & Groom 2003; Grau unpubl.) and effective dispersal by birds (Montaldo 1993, 2000; Aragón 2000) probably contribute to its success.

We address the following questions: 1. What impact does *Ligustrum* invasion have on the recruitment of native trees, shrubs and lianas? 2. Is recruitment by native and invasive plants limited primarily by seed dispersal or by other factors? Based on our findings, we discuss the probable consequences of *Ligustrum* invasion for regional forest composition.

Methods

Study area

The study area (27°30' S, 65°40' W; 580-710 m a.s.l.), located 15 km west of San Miguel de Tucumán, Argentina, is part of the Yungas phytogeographic region, a strip of pre-montane and montane forests extending from northwestern Argentina to southeastern Bolivia on the lower east slope of the Andes (Cabrera 1976). Annual rainfall is 1300 mm, mostly falling from October to March (Hunzinger 1997). Mean annual temperature is 18 °C, with frosts occurring from June to August. Soils are typically Hapludoll with an AC profile (Zucardi et al. 1968) and pH 5.5 - 6.8 (see Results). Ca. 30 native and 10 exotic canopy trees occur in the study area, many of which are winter/drought deciduous. Canopy height is typically 15 - 30 m.

Most of the study area was deforested (primarily for citrus orchards and sugar cane) during the first half of the 20th century, and was later abandoned due to loss of soil fertility and socio-economic changes. Most fields that have been abandoned since the 1950s are currently dominated by *Ligustrum lucidum* (Plate A1 in App. 1). The oldest heavily invaded patches were abandoned around 1955, so the species must have been planted as an ornamental prior to the 1950s. The present landscape consists of a mosaic of agriculture (mostly citrus, sugarcane and livestock), secondary native forests (40 - 80 yr old), invaded forests (5 - 50 yr old; primarily *Ligustrum*) and exotic tree plantations (*Eucalyptus* and *Pinus*). Ca. 50% of the study area is currently forested.

Location of sample plots

Vegetation and environmental variables were measured in 64 20 m × 20 m plots in 19 clusters, each with two to four plots (10 clusters, 33 plots in primarily native secondary forest; nine clusters, 31 plots in forest dominated by *Ligustrum*). Clusters (see below) were located within a 2.2 km × 0.65 km area in 14 secondary forest patches (six native and eight dominated by *Ligustrum*) ranging in size from 0.25 - 4 ha. Patches were selected using aerial photographs and ground surveys to fulfil two sampling needs that aided in separating spatial (dispersal related) and environmental effects on species abundance: (1) native and invaded patches interspersed with each other (i.e. neighbouring clusters in different patch types) and (2) at least one native and one invaded patch large enough to accommodate several clusters. Plots were clustered to allow for fine scale resolution in spatial analyses. Each cluster was contained within a relatively homogeneous area (in terms of topography and land use history) of closed canopy forest. Whenever possible, clusters consisted of four contiguous 20 m × 20 m plots in a square (40 m × 40 m) array. Eight clusters had two or three plots in a linear array due to the small size or irregular shape of the patches. Clusters were placed in the centre of patches to avoid edge effects, and were spaced regularly within patches containing multiple clusters. None of the patches we studied were isolated forest fragments at the time of sampling; all were adjacent to other patches of secondary forest abandoned from agriculture at different times.

Species abundance

Within each 20 m × 20 m plot, we recorded the species and DBH of all trees, shrubs and lianas with DBH ≥ 3 cm. Within 10 m × 10 m subplots in the centre of each plot, we recorded the species and size class (SC) of all woody stems with height ≥ 25 cm: SC1 (25 - 50 cm), SC2 (50 - 150 cm), SC3 (≥ 150 cm, < 3 cm DBH), SC4 (3-10 cm DBH) or adult tree (≥ 10 cm DBH). In some cases, small sample sizes forced us to aggregate size classes for analysis. We divided SC4 abundances by four when aggregating with other size classes because the SC4 stems were measured in 20 m × 20 m plots, vs 10 m × 10 m plots for SC1-SC3. Aggregated size classes are denoted by '+': SC3+4 means SC3 and SC4 combined. Species names, families, authorities and abundances are given in Table A1 (App. 1).

Seed rain

We measured the seed rain of *Ligustrum* and two native canopy species, *Cupania vernalis* and *Myrsine laetevirens*. In each 10 m × 10 m subplot we erected four 50 cm × 50 cm seed traps. Traps were visited bi-weekly from mid-June 2001 to February 2002, spanning one fruiting season for each species (*Ligustrum* June-October; *Cupania* October-January; *Myrsine* June-December). All three species are bird dispersed and actively

dispersed seeds are easily distinguished from fallen fruits. Within each plot, seed rain was defined as the pooled number of actively dispersed seeds across all traps and time periods.

Environmental data

We estimated stand age and measured topographic, soil and understorey light variables in each plot (Table 1). Methods are described in App. 1.

Statistical analysis

We used a conservative significance level ($\alpha = 0.01$) to control for the large number of simultaneous tests. To identify factors correlated with native recruitment, we searched all possible combinations of the variables listed in Table 1 for the three variable ordinary least squares (OLS) model that explained the most variation in native tree, shrub and liana abundance in each size class. Variables were Box-Cox transformed to improve normality. After eliminating variables with $P > 0.01$, we tested the OLS assumption of independence by examining Moran's I correlograms of the residuals from each model (Lichstein et al. 2002). In cases where residuals were autocorrelated, we fitted conditional spatial auto-regressive (AR) models, which account for auto-correlation (Cressie 1993; Lichstein et al. 2002). We tried several neighbourhood sizes (50-400 m radius) and weights (1, 1/distance and 1/distance2) for each AR model, then selected the model that performed best in terms of maximizing the model likelihood and minimizing spatial pattern in residuals.

We used multiple regression on resemblance matrices (MRM; Legendre et al. 1994), an extension of partial Mantel analysis, to partition variation in species composition into pure environmental, pure spatial (e.g. dispersal) and spatially structured environmental components (Borcard et al. 1992). We used both the Bray-Curtis coefficient, with $\log(y + 1)$ transformed stem counts to emphasize rare species and Sørensen's index, with presence-absence data, to construct distance matrices of species compositional differences between the 64 plots for native trees, shrubs and lianas in each size class. We constructed separate explanatory distance matrices for *Ligustrum* dominance and for each soil, topographic and light variable. Explanatory matrices contained absolute values of differences between plots. For each species matrix, we searched all possible combinations of the explanatory matrices to identify the three variable linear model with the highest R^2. We quantified spatial structure in each species matrix as the percent deviance explained by a nonparametric spline function (Tuomisto et al. 2003) with three degrees of freedom.

We tested for correlations between seed rain and conspecific basal area (trees with DBH ≥ 10 cm in 20 m × 20 m plots) for *Ligustrum*, *Cupania* and *Myrsine*; lack of correlation would suggest that many seeds are dispersed at least tens of meters from adults. We also tested for correlations between seed rain and conspecific SC1 and SC2 abundance. Significant positive correlations would suggest that recruitment into small size classes is limited by seed arrival.

Analyses were performed with SPLUS (Anon. 2002). Variable selection in linear regression was performed with the 'stepwise' function using the 'exhaustive' option. AR models were fit with the 'slm' function in the 'spatial module.' Splines were fit with the smoothing spline function ('*s*') within the 'gam' function. MRM analyses were run using original SPLUS codes, available from the first author.

Table 1. Variables used in regression analysis.

Variable	Description
Stand age	Time since abandonment from agriculture
Ligustrum dominance	*Ligustrum lucidum* % basal area of trees with DBH ≥ 10 cm in 20 m × 20 m plots
Ligustrum juvenile abundance	Number of *Ligustrum* stems (≥ 25 cm tall, < 3 cm DBH) in 10 m × 10 m plots + 0.25_(number of 3 - 10 cm DBH *Ligustrum* in 20 m × 20 m plots)
Psychotria abundance	Number of *Psychotria* stems (≥ 25 cm tall, < 3 cm DBH) in 10 m × 10 m plots + 0.25_(number of > 3 cm DBH *Psychotria* in 20 m × 20 m plots)
Slope/aspect	(Ground slope) × (transformed aspect): topographic moisture index (low values = moist; high values = dry)
TSI	Terrain Shape Index (McNab 1989): topographic moisture index (low values = dry; high values = moist)
Soil moisture	% water by mass; measured gravimetrically
Soil depth	Index ranging from 0 (shallow, rocky) to 6 (deep, non-rocky)
Soil chemistry PC1	Low values = less fertile soils; high values = more fertile
Soil chemistry PC2	Low values = high organic matter and N, and low K+ and Na+
Soil chemistry PC3	Low values = high pH (max = 6.9); high values = low pH (min = 5.5)
Soil texture PC1	Low values = fine; high values = coarse
Soil surface PC1	Low values = non-rocky soil surface; high values = rocky
Soil surface PC2	Low values = thick litter; high values = thin litter
Canopy cover	Mean of 16 densiometer readings
Canopy gap index	Minimum canopy cover from 16 densiometer readings

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Results

Abundance of Ligustrum lucidum

Ligustrum dominance (% basal area in 20 m × 20 m plots among trees with DBH ≥ 10 cm) ranged from 0 to 100%. *Ligustrum* comprised ca. 80% of the basal area in patches abandoned within the last 50 yr, and ca. 20% in older patches (Fig. 1).

Ligustrum juveniles were most abundant in heavily invaded plots but were also common in some plots where *Ligustrum* adults were rare or absent (Fig. A1, App. 1). Most *Ligustrum* juveniles were root sprouts from larger individuals (pers. obs.). Vegetative reproduction complicates the interpretation of patterns in recruitment, so we did not examine more elaborate models of *Ligustrum* juvenile abundance.

Ligustrum dominance was not correlated with soil texture, soil moisture, soil depth or terrain shape index (TSI). *Ligustrum* dominance was negatively correlated with slope/aspect (Fig. 2A; more abundant on moist sites), surface rockiness (Fig. 2B) and soil fertility (Fig. 2C, G) and positively correlated with pH (Fig. 2D, H). *Ligustrum* dominance was positively correlated with canopy cover (Fig. 2E) and negatively correlated with the degree of canopy gaps (Fig. 2F).

To determine if stand age could account for the above significant results, we examined partial correlations between environmental variables and both *Ligustrum* dominance and stand age. Partial correlations of slope/aspect against *Ligustrum* dominance and stand age were both significant (negative). All other partial correlations with *Ligustrum* dominance, but not stand age, were significant (with same sign as in Fig. 2).

Abundance and richness of natives

Cupania vernalis accounted for 73% of SC1 and 61% of SC2 native tree stems, yet exclusion of the species from analyses did not qualitatively change the
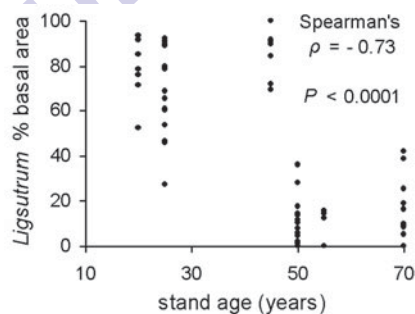
Fig. 1. *Ligustrum lucidum* dominates former agricultural lands abandoned within the last 50 yr. Data from 20 m × 20 m plots (trees ≥ 10 cm DBH).

Table 2. Regression models of native stem abundance vs explanatory variables listed in Table 1. Ordinary least squares (OLS) models were selected by searching over all possible combinations of the explanatory variables. In most cases, OLS residuals were autocorrelated, and a spatial autoregressive (AR) model was then fit. Variables with $P < 0.01$ were eliminated.

Response	Explanatory variable	coeff.[1]	P
Native trees			
SC1	soil texture PC1 (coarseness)	0.4	0.001
SC2	stand age	–0.5	0.007
	Ligustrum dominance	–0.8	0.0001
SC3[2]	*Ligustrum* dominance	–0.6	< 0.0001
	soil moisture	–0.5	< 0.0001
SC4	*Ligustrum* dominance	–0.6	< 0.0001
Native shrubs (excluding *Psychotria carthagenensis*)			
SC1[2]	soil chemistry PC2	–0.5	< 0.0001
SC2	*Psychotria* abundance	–0.5	< 0.0001
SC3+4	*Ligustrum* juvenile abundance	–0.4	0.001
	soil chemistry PC2	0.4	0.001
Psychotria carthagenensis[3]			
SC1	stand age	–0.4	0.0001
	soil texture PC1 (coarseness)	–0.3	0.004
SC2	*Ligustrum* dominance	0.5	< 0.0001
	soil texture PC1 (coarseness)	–0.4	0.002
SC3+4	none significant		
Native lianas			
SC1+2[2]	*Ligustrum* dominance	–0.5	< 0.0001
SC3+4	*Ligustrum* dominance	–0.6	< 0.0001

[1] Standardized regression coefficients; [2] OLS residuals not autocorrelated, so no AR model was fit; [3] *Psychotria* abundance was excluded as an explanatory variable in these models.

results. *Psychotria carthagenensis*, which accounted for 96% of SC1, 98% of SC2, 99% of SC3 and 98% of SC4 native shrub stems, was analysed separately from non-*Psychotria* native shrubs.

Native tree SC1 abundance was not correlated with *Ligustrum* dominance, while native tree SC2-SC4 abundances were all negatively correlated with *Ligustrum* dominance (Table 2). Non-*Psychotria* native shrub SC2 abundance was negatively correlated with total *Psychotria* abundance and non-*Psychotria* SC3+4 abundance was negatively correlated with *Ligustrum* juvenile abundance. *Psychotria* SC1 abundance was negatively correlated with stand age, while *Psychotria* SC2 abundance was positively correlated with *Ligustrum* dominance. Native liana SC1+2 and SC3+4 abundances were negatively correlated with *Ligustrum* dominance (Table 2).

Species richness was not correlated with *Ligustrum* dominance for any of the following groups after controlling for stand age and group abundance: native trees (SC1-SC4), native shrubs (SC1, SC2, SC3+4) and native lianas (SC1+2, SC3+4).
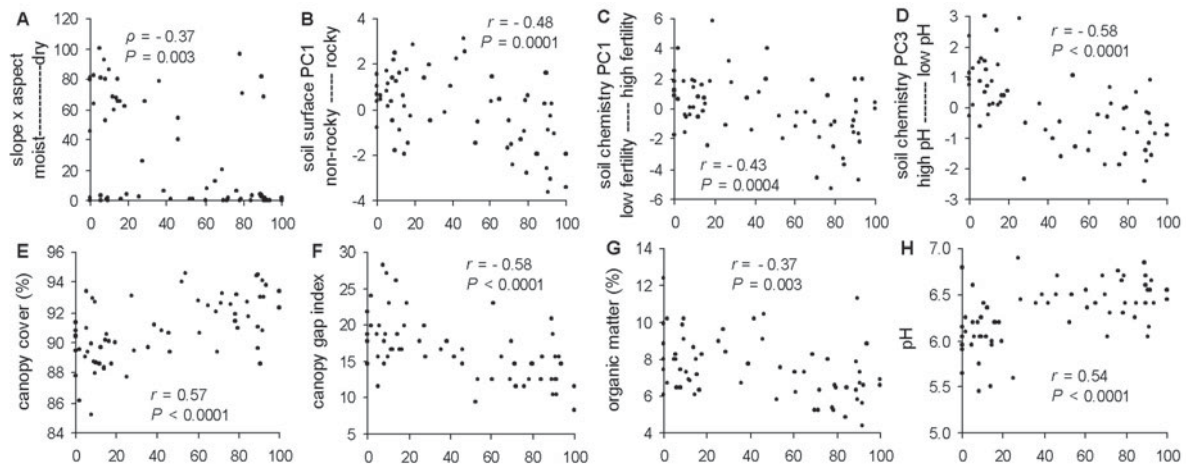
Fig. 2A-H. Environmental variables correlated ($P < 0.01$) with *Ligustrum* dominance. Soil organic matter (**G**) and soil pH (**H**) are, respectively, representative of correlations between *Ligustrum* dominance and soil chemistry principal components 1 and 3 (**C** and **D**). One outlier (organic matter = 18%; *Ligustrum* basal area = 19%) is not shown in (**G**), but was included in the analysis. Correlation in **A** is non-parametric Spearman, in **B-H** Pearson.

Native species composition

Native tree compositional (Bray-Curtis) distances had very similar spatial and environmental components for all size classes in MRM models (Fig. 3A). Excluding *Cupania* (73% of SC1 and 61% of SC2 stems) from SC1 and SC2 analyses resulted in larger environmental and smaller spatial components (Fig. 3B). For native shrubs, spatial structure was strongest for SC1 (Fig. 3C). The exclusion of *Psychotria*, which dominated all shrub size classes, resulted in smaller environmental and larger spatial components (Fig. 3D). Lianas had very similar spatial and environmental components (Fig. 3E). When species abundances were treated as presence-absences (Sørensen distance), the relative sizes of the spatial and environmental components shifted (Fig. 3F-H).

We tested the significance of each environmental distance matrix (ignoring space) using program Permute! (Casgrain 2002) for the following MRM models of Bray-Curtis distances: trees (SC1-SC4), shrubs (SC1, SC2, SC3+4) and lianas (SC1+2, SC3+4). In only one case (shrubs SC2) were plot differences in *Ligustrum* dominance significantly correlated with species compositional distances (Table A3, App. 1).

Seed rain

Seed rain was strongly correlated with conspecific basal area for *Cupania* (Spearman $\rho = 0.49$, $P = 0.0001$), but less so for *Ligustrum* ($\rho = 0.22$, $P = 0.08$) or *Myrsine* ($\rho = 0.27$, $P = 0.03$) (Fig. A2, App. 1). Seed rain was not correlated with SC1+2 abundance for *Cupania* ($\rho = 0.07$, $P = 0.6$), *Ligustrum* ($\rho = 0.0003$, $P = 0.9$) or *Myrsine* ($\rho = 0.004$, $P = 0.9$). Separate analyses of SC1 and SC2 did not change this result.
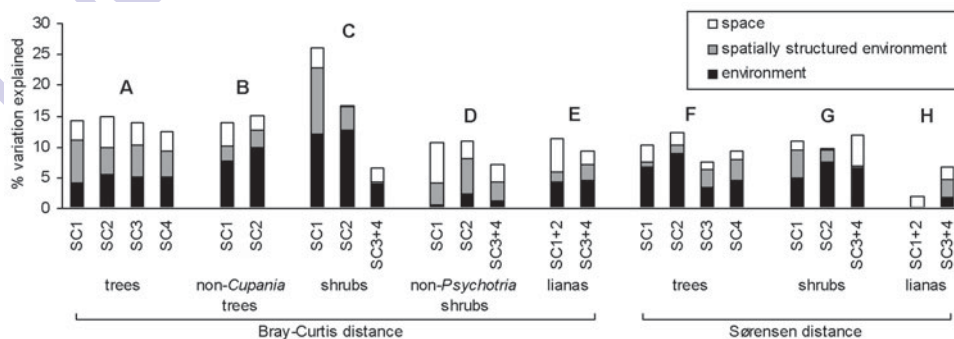

Fig. 3. Percent variation in species compositional distances for native trees, native shrubs and native lianas explained by space (independent of environment), environment (independent of space) and spatially structured environment. Variation was partitioned using multiple regression on resemblance matrices (Legendre et al. 1994). Compositional distances were measured with the Bray-Curtis (**A-E**) and Sørensen (**F-H**) coefficients.

Discussion

Dominance of Ligustrum lucidum

Ligustrum dominates agricultural land abandoned in the 1950s. *Ligustrum* dominance was weakly correlated with slope/aspect and was not correlated with TSI, soil moisture, soil depth or soil texture, suggesting that invasion success is insensitive to a range of topographic and edaphic conditions. Soil fertility was negatively correlated and pH positively correlated with *Ligustrum* dominance, even after controlling for time since agricultural abandonment. We do not know if these correlations reflect causes or consequences of *Ligustrum* invasion.

Native recruitment

Native tree abundance in SC1 was unrelated to *Ligustrum* dominance, suggesting that total tree recruitment is not limited by seed dispersal, germination or seedling survivorship in invaded patches. In contrast, tree abundance in larger size classes decreased with *Ligustrum* dominance, suggesting that recruitment is limited by sapling mortality in heavily invaded patches.

Variation in compositional distances of native trees had similar spatial and environmental components, suggesting that environmental factors and seed dispersal are both important in limiting tree recruitment. However, much of the spatial structure in smaller size classes was due to a single common species, *Cupania*. Its seed rain and conspecific basal area were positively correlated, which is additional evidence for dispersal limitation. In contrast, seed rain and basal area of *Myrsine* were only weakly correlated (despite the rarity of adults in our study area), suggesting that dispersal is unlikely to limit recruitment. Seed rain was not correlated with SC1 or SC2 abundance for either species. *Cupania* seedlings often have old leaf scars and woody stems (pers. obs.) indicating suppressed persistence for many years, which could obscure the expected association between seed rain and juvenile abundance. Our results suggest that some native tree species are dispersal limited, but seed dispersal is probably secondary compared to mortality in determining the abundance of native saplings in invaded patches.

Psychotria comprised 96 - 99% of native shrubs in the four size classes. *Psychotria* SC2 abundance was positively correlated with *Ligustrum* dominance. The abundance of non-*Psychotria* SC2 shrubs was negatively correlated with *Psychotria* abundance, which may represent an indirect effect of *Ligustrum* invasion; i.e. by altering the relative competitive abilities of shrub species. The abundance of non-*Psychotria* SC3+4 native shrubs was negatively correlated with *Ligustrum* juvenile abundance. This could reflect another indirect effect of *Ligustrum*

canopy dominance, as most *Ligustrum* juveniles in our study area are root sprouts from adults (pers. obs.).

Native liana abundance decreased with *Ligustrum* dominance. Lianas tend to be light demanding (Putz 1984; Laurance et al. 2001) and decreased liana abundance in invaded patches may reflect reduced light availability (Fig. 3E, F). That *Ligustrum* dominance, not light, was the best predictor for liana abundance may reflect a lack of sensitivity in our densiometer measurements. Other factors affecting liana recruitment include host architecture and bark characteristics (Putz 1984; Carsten et al. 2002). Relative to most other tree species in our study, *Ligustrum* has a straight trunk with few lower branches and smooth bark, and is probably a poor substrate for liana growth.

Ligustrum dominance was correlated with species compositional distances for only one of nine native species groups examined (Table A3, App. 1) and had no effect on native diversity that could not be explained by decreased native abundance in invaded patches. Thus, native recruits in invaded patches were analogous to a random sample of those in not invaded patches, suggesting that the density, but not the type, of recruitment microsites varies with *Ligustrum* dominance.

Native shrub species compositional differences had stronger environmental than spatial structure (Fig. 3C). However, spatial structure became stronger after excluding *Psychotria* from the analysis (Fig. 3D), suggesting a relatively important role for dispersal limitation in non-*Psychotria* native shrub recruitment. For native lianas, dispersal limitation and environmental factors appear to have similar roles in recruitment limitation (Fig. 3E).

Impact of Ligustrum on native plant recruitment

Soil fertility and understorey light decreased with *Ligustrum* dominance. Reduced light in invaded patches is clearly due to *Ligustrum*'s dense canopy. The cause for reduced fertility is less clear, but may be due to litter quality or *Ligustrum*'s rapid growth (Aragón & Groom 2003; Grau unpubl.) and presumably rapid nutrient uptake. Resource availability, particularly light, has a strong impact on recruitment (Horn 1971; Pacala et al. 1994; Davies 2001) and a number of studies have attributed native recruitment failure to shading by exotics (Wyckoff & Webb 1996; Holmes & Cowling 1997; Levine et al. 2003). *Ligustrum* dominance was a better predictor of native sapling and liana abundance than soil and light variables correlated with *Ligustrum* invasion. This may be because *Ligustrum* dominance is a better surrogate for resource availability than our densiometer and nutrient pool measurements. Alternatively, *Ligustrum* may affect recruitment via below-ground processes other than nutrient competition (e.g. allelopathy or competition for space).

Future of Ligustrum lucidum in subtropical Argentina

Ligustrum seed rain (dispersed seeds) was not correlated with *Ligustrum* basal area, suggesting effective local dispersal. This is supported by Aragón (2000) who found that *Ligustrum* seeds were common in bird faeces in both native and invaded forests. Although most *Ligustrum* recruitment in our forested plots appears to be from root sprouts, these plots are embedded in a dynamic landscape where agricultural abandonment is ongoing. Given its copious fruit production (Montaldo 1993), effective dispersal (Aragón 2000; Montaldo 2000) and rapid growth, it seems likely that *Ligustrum* will continue to invade abandoned fields in this region.

As observed elsewhere (Ribichich & Protomastro 1998), we also found signs of a slower *Ligustrum* invasion into native forests. *Ligustrum* saplings were present in many plots where *Ligustrum* adults were rare or absent. These saplings could have originated from seed or from root sprouts of nearby trees. The occasional presence of isolated *Ligustrum* canopy trees in otherwise native forests (pers. obs.) suggests previous recruitment in tree-fall gaps. Thus, there may be two modes of *Ligustrum* invasion: (1) rapid invasion of abandoned agricultural lands by bird dispersed seeds and (2) slower encroachment into native forest by vegetative spread or seed dispersal, and eventual growth into canopy gaps.

The history of *Ligustrum* invasion in our study area is brief (ca. 50 yr), and we do not yet know how long dominant canopy individuals can survive. Judging from *Ligustrum*'s suppression of native tree recruitment, shade tolerance (Aragón & Groom 2003), and capacity to resprout from cut stumps (pers. obs.), invaded patches may persist for hundreds of years. Given *Ligustrum*'s invasion success in other regions of Argentina (Ribichich & Protomastro 1998; Montaldo 2000) and the infeasibility of eradicating this species once it becomes common (Aragón & Groom 2003), its use as an ornamental tree should be discouraged and seed trees should be removed from areas where invasion appears imminent.

Conclusions

Native tree and liana regeneration appear to be limited primarily by the paucity of favourable microsites in forests where the invasive *L. lucidum* is dominant. Recruitment of some native trees, shrubs and lianas is also likely to be dispersal limited. In contrast, *Ligustrum* does not appear to be limited by dispersal or environmental constraints within the landscape we studied. *Ligustrum* forms, apparently, semi-permanent patches that are slowly expanding into adjacent, native forest, leading to floristic homogenization of a formerly heterogeneous landscape.

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