

## Species composition and invasion in NW Argentinian secondary forests: Effects of land use history, environment and landscape

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**Abstract.** Successional patches are a large component of forest ecosystems throughout the world and their vegetation composition is conditioned by multiple factors such as land use history, disturbances, environmental conditions and landscape context. We investigated the relative contribution of historical, environmental, biotic and spatial factors in determining vegetation composition and invasion by exotic species in secondary forest patches of Sierra de San Javier, Tucumán, Argentina. We estimated canopy cover for shrub, vine and tree species distributed over 51 patches with known land use history. We also recorded environmental, historical and spatial variables and used multivariate techniques to explore the relationship between forest composition and explanatory variables. Land use, time since abandonment, altitude, slope and cover of different strata were related to the vegetation pattern in the study site, and they were all significantly structured over space. Exotic species appeared to differ from natives in their response to explanatory variables. Overall, exotic species were dominant on the edges of young patches originated from herbaceous crops, but the total number of exotic species was related to the distance to urban areas and small farms identified as potential sources of exotic propagules. Vegetation composition of secondary forests in NW Argentina was related to historical and environmental factors, but spatial variables strongly influenced vegetation composition as well as the variation in explanatory variables.

**Keywords:** Exotic species; Invasion; Montane forest; Succession; Yungas.

**Nomenclature:** Dimitri (1988); Digilio & Legname (1966).

**Abbreviations:** GPS = Global positioning system; MRPP = Multi response permutation procedure; NMDS = Non-metric Multidimensional Scaling; PBSSJ = Parque Biológico Sierra de San Javier; UTM = Universal Transverse Mercator system.

### Introduction

Almost every landscape has a complex history of human land use and natural disturbances. Numerous forests around the world have been cleared for crop production, livestock raising or are affected by logging and other land uses. Many of these sites are subsequently abandoned and become reforested (Compton & Boone 2000; Donohue et al. 2000). These successional patches are currently a large component of forest ecosystems and their regeneration has important economical and ecological consequences (Brown & Lugo 1990; Motzkin et al. 1996, 1999a; Compton & Boone 2000; Donohue et al. 2000). Land use history, disturbances and the underlying environmental and spatial variation have the potential to interact in a complex way to determine the outcome of vegetation recovery of these patches.

Historical factors, such as previous land use, can greatly influence the initial characteristics of a site and control the first stages of succession. For example, historical factors can affect soil nutrient content, soil micro-organisms and their activity, vegetation cover and the pool of available propagules (Myster & Pickett 1990; Motzkin et al. 1999a; Compton & Boone 2000). The vertical structure of remaining vegetation in abandoned areas can also influence the first stages of succession. The dispersal pattern of species disseminated by birds are often characterized by recruitment foci associated with the presence of perches (i.e. remnant trees, saplings, fences). These recruitment foci can, in turn, affect the spatial dynamics and rate of succession (McDonnell & Stiles 1983).

Land use change is tightly linked to biological invasions, which are responsible for numerous species extinctions and changes in ecosystem dynamics (Drake et al. 1989; D'Antonio & Vitousek 1992). Human activities and settlements usually bring numerous exotic species, either inadvertently or deliberately, as ornamentals and cultivars. By the time land is abandoned,

exotic species are common and therefore likely to be part of successional patches after agricultural use (Ramakrishnan & Vitousek 1989; Reichard & Hamilton 1997). The set of factors that affects native community composition and dynamics also influence site invasibility. However, exotic and native species may respond differently to some of these factors (McIntyre & Lavorel 1994; Wisser et al. 1998).

Environmental and spatial variables can influence vegetation pattern and dynamics in many ways. Slope, aspect and altitude affect air temperature, soil moisture and light availability, and can influence species survival and therefore community composition. Different plant species may vary in their ability to compete with neighbours and survive under particular environmental conditions, but the composition of the community is, at the same time, constrained by dispersal limitations (Primack & Miao 1992; Tilman 1997; Wunderle 1997). Spatial variables, together with historical land use, can determine the distribution of potential seed sources, and therefore affect colonization and vegetation recovery (Shmida & Wilson 1985; McClanahan 1986; Aizen & Feinsinger 1994; Jobbágy et al. 1996; Wunderle 1997). The importance of many spatial processes can only be assessed by working at the landscape scale.

Many and varied factors, acting at disparate temporal and spatial scales, have the potential to affect the distribution and abundance of plant species in heterogeneous landscapes (Acker 1990; McIntyre & Lavorel 1994; Zimmerman et al. 1995; Motzkin et al. 1999b; Donohue et al. 2000). A major challenge in plant ecology is to determine and quantify the strength of such factors. Our study site, the piedmont of Sierra de San Javier in NW Argentina, offers a good opportunity to evaluate the influence of different sets of variables on vegetation distribution and abundance. Sierra de San Javier combines a relatively known land use history with varied environmental conditions (determined mainly from topography) in a spatial gradient of intensity of human intervention. In addition, many exotic species escaped from cultivars or gardens and are a component of the present landscape (Grau & Aragón 2000). Here, by examining variation in species composition we aim to answer:

1. What is the relative contribution of environmental, historical and spatial factors in explaining vegetation composition in the different patches?

2. How are these sets of factors related to the invasion by exotic species ?

## Methods

### Study site

This study was conducted in the piedmont of Sierra de San Javier, Tucumán, Argentina (27°30' S, 65°40' W). The natural vegetation corresponds to the phytogeographic province of the Argentinian 'Yungas' (Cabrera 1976) which is considered the southern end of the Neotropical montane forests that develop along the eastern slope of the Andes. Much of the piedmont of Sierra de San Javier was planted with citrus orchards, herbaceous crops (mainly sugar cane) or used as grazing fields during the early 1900s, but a partial loss of soil fertility and a shift in Argentina's economy in the 1950s triggered the abandonment of many agricultural lands. Forest recovery was further secured by the creation of a protected area, the Parque Biológico Sierra de San Javier (PBSSJ) in 1976. This preserve has an area of ca. 14 000 ha and is located 15 km west of San Miguel de Tucumán, the capital of the province with ca. 600 000 inhabitants. The proximity of PBSSJ to Tucumán city resulted in strong human influence and as a consequence of past and present land use, the area is a mosaic of forest patches with different histories of land use and time since abandonment (Grau et al. 1997). Study plots were located in the vicinity and within PBSSJ between 500 and 1000 m (Fig. 1). The registered annual mean temperature is 18.8 °C and mean annual precipitation during last century was 1300 mm, distributed in a monsoonal regime with dry winters and wet summers (Bianchi 1981; Hunzinger 1995).

In most of the forest patches it is possible to distinguish three vertical strata. The canopy of ca. 15-20 m is frequently dominated by *Blepharocalyx salicifolius* (Myrtaceae) and *Cinnamomum porphyria* (Lauraceae). The subcanopy (5-9 m) is composed mainly of *Eugenia uniflora* (Myrtaceae), *Piper tucumanum* (Piperaceae) and *Allophylus edulis* (Sapindaceae) (Grau & Brown 1998). The most abundant shrub in the understorey is *Psychotria carthagenensis* (Rubiaceae). The most common exotic species are *Ligustrum lucidum*, *L. sinensis* and *Morus* spp. (i.e. *M. alba*, *M. nigra* and probably hybrids) (Grau & Aragón 2000). Details of forest structure and composition can be found in Grau et al. 1997; Grau & Brown 1998 and Grau 2002.

### Data collection

We identified land use history and time since abandonment in 51 landscape patches based on aerial photographs and interviews with local residents. We considered a landscape patch to be any spatial unit that was discernible through aerial photographs. Most of these

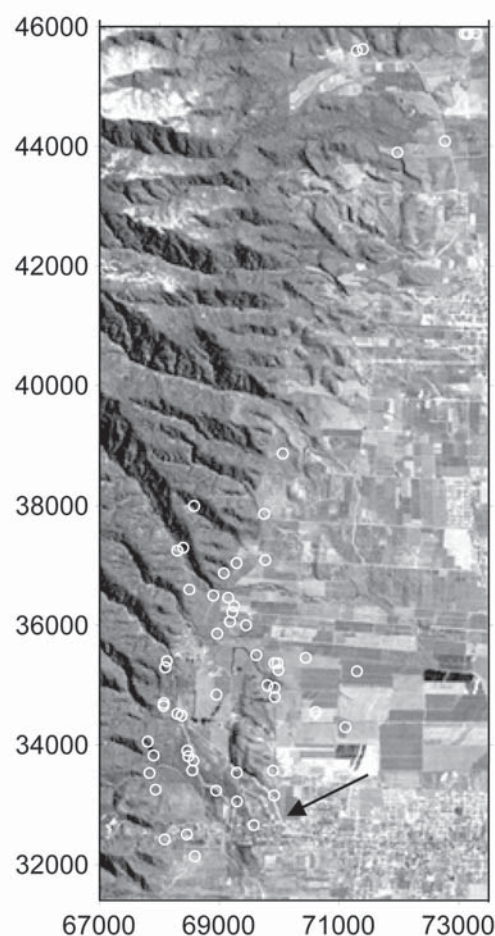
patches were in contact with roads, trails or small rivers that separated them from other secondary forest patches, and many were surrounded by agricultural lands. Only those patches that were easily identified in the photographs, located in the field and of which we were confident about their land use history, were sampled. These patches were distributed over a 30-km<sup>2</sup> area in the piedmont of Sierra de San Javier and had a size range of 0.5 to 25 ha (Fig. 1). When patches were large enough to distinguish between a forest interior and an edge, we took two samples by randomly placing a 20 m × 10 m quadrat in each environmental position (i.e. interior and edge), provided that the two quadrats were separated by at least 20 m. For smaller forest patches we only set out one quadrat which was considered to be an edge quadrat. We sampled a total of 70 quadrats distributed across 51 landscape patches.

In each quadrat, we visually estimated canopy cover for all shrub, creeper, vine and tree species using nine cover classes (van der Maarel 1979). Species with less than 5 % cover were included in classes 1 to 4 depending on their abundance (1 = rare; 2 = few; 3 = many; 4 = abundant, but still less than 5 % cover). Cover classes 5 to 9 refer to: 5 = >5-12.5%; 6 = >12.5-25%; 7 = >25-50%; 8 = >50-75%; 9 = >75 % cover. We did not estimate cover per species of grasses or ferns (but they were included in total cover of the herbaceous stratum). We also counted the number of individuals of all tree species taller than 1 m. We considered as tree species all self-sustaining species that could reach the canopy stratum. A set of 12 explanatory variables were recorded at each quadrat:

1. Exogenous environmental variables: altitude; aspect; slope; surface roughness; index of rock abundance; index of soil depth.
2. Endogenous environmental (or biotic) variables: total vegetation cover per stratum; number of dead and fallen trees; type of habitat (edge or forest interior).
3. Historical variables: land use and time since abandonment.
4. Spatial variables: geographic position (UTM coordinates).

Surface roughness was assessed using an index from 1 to 4, in which 4 represented the least uniform microrelief. Soil depth was recorded as the maximum depth a 1.5 cm diameter steel rod could be driven into the soil. Measurements were made at eight random points in each quadrat and the median was taken as an indication of soil depth. Abundance of rocks on the surface was ranked from 0 to 4. These three variables were recorded as a quick estimation of local substrate characteristics. The compass measurements of aspect were ranked from 1 to 5. The rank included the four quadrants of the compass that broadly represent a gradient of humidity with southern slopes being the most humid, plus a category of No Aspect for flat terrain.

When possible, we distinguished the following strata: Above canopy (C>15): trees higher than 15 m that seldom formed a continuum stratum, Canopy (C15): formed by trees between 5 and 15 m in height; Understorey (C5): shrubs and subcanopy trees between 1 to 5 m; and herbaceous stratum (C1): individuals smaller than 1 m. Total cover per stratum was visually estimated using the same cover classes used for individual species cover (van der Maarel 1979). Cover of the



**Fig 1.** Satellite image of study site (UTM coordinates). Circles indicate the approximate location of sample quadrats. The arrow indicates the spatial location used as a proxy for the potential source of exotics.

first three strata was estimated for the entire 20 m × 10 m quadrats, and the cover of the herbaceous stratum was estimated as the median of four 1 m × 1 m plots placed in each corner of the 20 m × 10 m quadrats. Type of habitat was represented by a binary variable that distinguished between edge and forest interior quadrats.

Previous land use and approximate date of abandonment of each patch was determined through aerial photographs (1:20 000) from 1949 and 1976, and from information provided by local inhabitants. We considered four types of land use: citrus plantations (orchards), herbaceous crops (mostly sugar cane, but also peas and potatoes), pasture and old-growth. We did not record double shifts in land use type in any of our patches. The age of the patches was divided into four categories: young (abandoned 10-25 yr ago), intermediate (25-40 yr), mature (> 40 yr old) and old-growth. Old-growth patches showed no conspicuous signs of anthropogenic disturbances, but most likely they were selectively logged for *Cedrela lilloi* prior to 1976 and may be currently sporadically used as a source of fire wood and occasionally grazed by semi-domestic livestock. Among spatial variables, UTM grid coordinates were obtained using a geographic positioning system (GPS; Magellan 4000). No attempt was made to correct random or other types of errors in GPS measurements (Parkinson & Spilker 1996), however we did check for relative accuracy by examining aerial photographs.

### Data analysis

To measure the compositional (dis)similarity among each pair of quadrats we used Sørensen's index:

$$D_{j,k} = \frac{\sum_{i=1}^p |c_{i,j} - c_{i,k}|}{\sum_{i=1}^p (c_{i,j} + c_{i,k})} \quad (1)$$

where  $D_{j,k}$  is the compositional difference between quadrats  $j$  and  $k$ . The numerator is the sum of the absolute values of the differences in cover ( $c$ ) of each species, and the denominator is the summation of the abundance of each species in the two quadrats (cf. Legendre & Legendre 1998). This index has proven to be robust and effective when assuming a monotonic relationship between sample pairs as in Non-metric Multidimensional Scaling. We included in the analysis only those species that were present in at least 5% of the quadrats, since infrequent species of random occurrence can produce spurious effects (Jongman et al. 1995).

The dimensions of the resulting similarity matrix were reduced using NMDS (Kruskal 1964; Legendre & Legendre 1998). The aim of NMDS is to ordinate the inter-plot distances in a number of predetermined dimensions (axes) in such a way that the rank order of the distances between plots is as close as possible to that of the original similarity matrix (Whittaker 1987). This ordination technique is robust and independent from assumptions about the distribution of species along the gradients underlying the ordination (Kenkel & Orlóci 1986; Minchin 1987). However, the method has two main potential drawbacks. First, solutions depend on convergence (they are not exact) and configurations may get trapped in local minima. Second, the number of dimensions in the ordination, which is set *a priori*, may affect the final configuration. The stress of the ordination decreases as a number of dimensions increases, but eventually the change in stress becomes small (Legendre & Legendre 1998). To avoid these potential problems we chose the number of dimensions in our ordinations after examining plots of stress versus dimensions obtained by running the analysis ten times (with different initial random configurations) for each dimension (up to six dimensions). NMDS axes were then rotated to align the direction of greatest variation with the horizontal axis (Varimax rotation option, PC-ORD 3.0; McCune & Mefford 1997). Percent of variation in the original data that was explained by the ordination was calculated through Pearson  $r^2$ , correlating the distance between the plot scores in the ordination space and the distance in the original matrix (Peterson & McCune 2001). To explore the relationship between the ordination and the four sets of explanatory variables we computed correlations between

the scores of each quadrat in the first three axes of the NMDS ordination and the corresponding values for each variable. To identify the species that were driving the ordination, we computed correlations between quadrat scores and species cover per quadrat. For all these correlations, we used Kendall's  $\tau$ , a non-parametric coefficient which is considered a robust, distribution-free statistic (Whittaker 1987; Legendre & Legendre 1998). The difference between the correlation coefficients of exotic and native species was tested using a randomization test (Manly 1997). It is expected that many explanatory variables would be intercorrelated (ter Braak 1987). For this reason, and to facilitate interpretation, we included a correlation matrix between these variables.

The correlation analysis involved multiple tests carried out simultaneously, and care should be taken to interpret  $p$ -values. The simplest and most stringent way to avoid spurious significant results is to use Bonferroni correction (e.g. for  $\alpha = 5\%$  use 0.05 divided by the number of tests) (Holm 1979). For each correlation, we report  $p$ -values and indicate those significant after Bonferroni correction. The differences in community composition between quadrats of different previous land uses were tested using Multiresponse permutation procedure (MRPP) (Biondini et al. 1985). MRPP provides a statistic  $\delta$ , that is the weighted mean within-groups distance and it is associated with a  $p$ -value that indicates the likelihood of getting a  $\delta$  equal or smaller than that observed by chance (McCune & Mefford 1997).

To quantify the relative importance of environmental exogenous, endogenous (biotic), historical and spatial variables in 'explaining' community composition, we performed a variation partition in the matrix of species cover by sites. This was done following the approach suggested by Borcard et al. (1992) and using Canonical Correspondence Analysis (CCA) in the program CANOCO (ter Braak & Šmilauer 1998). We separated the explanatory variables into three categories, Environmental (lumping categories 1 and 2: exogenous and endogenous or biotic), Historical (previous land use and time since abandonment) and Spatial (UTM coordinates and the terms for a cubic trend surface regression). For each category, we selected the set of significant variables using a stepwise selection with Monte Carlo tests ( $p < 0.05$  after 499 permutations). We then combined a series of CCA and partial CCA to split the variations in species occurrence data into statistically independent components (see Borcard et al. 1992 for details).

The SW corner of the study site has, comparatively, the strongest human influence. This area is close to the growing town of Yerba Buena and it has been occupied by several households that maintain gardens, small farms

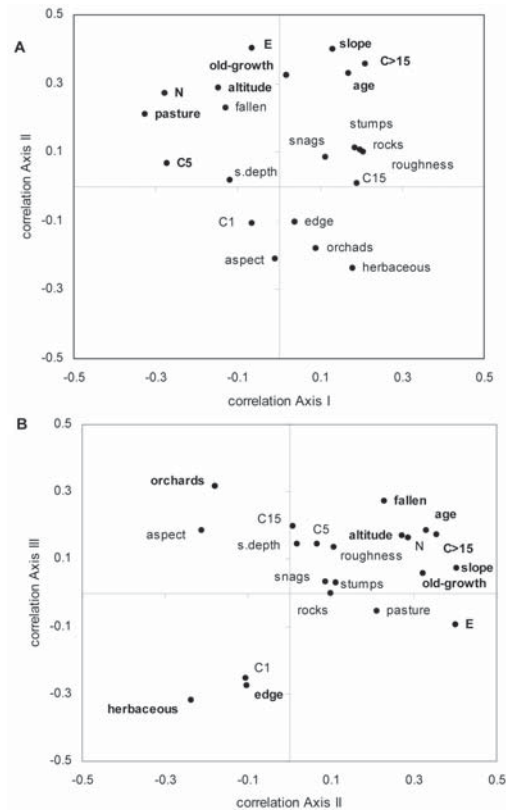


to have more fallen trees and higher values of canopy cover. For historical variables, a weak negative correlation was found between herbaceous crops and age. These patches were also negatively correlated with altitude, in contrast with abandoned pastures which tended to be located at higher elevations. Patches originated from citrus orchards and time since abandonment were positively correlated with the cover of the canopy stratum. Age of the patches was also positively correlated with slope and the number of fallen trees (Table 1).

Patches of different land use history had different species composition (MRPP:  $\delta = 17.02$ ,  $p < 0.001$ ). Patches originating from pastures were mostly at the left side of the first ordination axis. Old-growth patches were positively correlated with axis 2 (Fig 2A). Axis 3 separated sites originating from citrus orchards from those originating from herbaceous crops (Fig 2B). After Bonferroni correction, the following relationships between ordination axes and explanatory variables were significant. Cover in the understorey (C5) and above-canopy cover (C>15) were correlated with the first axis but with opposite signs, negative for understorey and positive for above-canopy. Slope, time since abandonment, C>15 and altitude were positively correlated with axis 2. For axis 3, Edge was negatively and number of fallen trees was positively correlated. Finally, northness was negatively correlated with axis 1 and eastness positively correlated with axis 2 (Fig. 2).

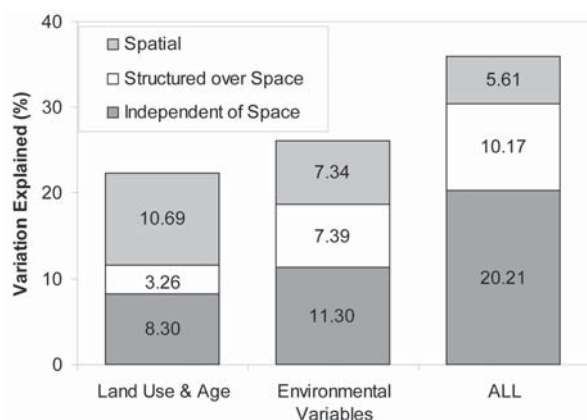
The exotic *L. lucidum* was the only species positively correlated with the first axis still significant after Bonferroni correction (App. 2A). Those negatively correlated with the first axis were the natives *Chamissoa altissima*, *Cestrum lorentzianum*, *Solanum riparium*, *Boehmeria caudata* and the exotic *Morus* spp. In the second axis *L. lucidum* was the only species negatively correlated, while several natives, such as *A. edulis*, *C. porphyria*, *C. vernalis* and *Eugenia uniflora* were positively correlated. Several exotics (*L. lucidum*, *L. sinensis*, *Psidium guajaba* and *Lantana camara*) and natives (*Heliocarpus popayanensis*, *Tecoma stans*, *Cestrum strigillatum*, *Jacaranda mimosifolia* and *Rubus imperialis*) were negatively correlated with the third ordination axis. *Piper tucumanum*, *P. hieronymi*, *Psychotria carthagenensis*, *C. porphyria*, *B. salicifolius* and *Pisonia ambigua* were positively correlated with the third axis (App. 2B). In general, the second axis separated natives from exotics (randomization test on Kendall coefficients,  $p < 0.01$ ) (App. 2).

From the set of all environmental variables (exogenous and biotic) only elevation, slope, C1, C5 and C15 were significant in the stepwise selection and included in the CCA. These variables explained 18.69% of the total inertia of an unrestricted ordination (sum of all canonical eigenvalues divided by the sum of all unre-



**Fig. 2.** Scatter plot of Kendall's  $\tau$  correlation coefficients between axis scores of NMDS ordination and explanatory variables. The first three axes of the ordination accounted for 84% of the variation in the data. For description of variables see Methods. **A.** Axes I and II; **B.** Axes II and III. Variables significantly correlated with axis scores after Bonferroni correction are in boldface.

stricted eigenvalues, 0.43/2.301). The whole set of historical variables (age and previous land use) was significant and explained 11.56% of the total variation (0.266/2.301). Historical and environmental variables combined explained 30.38% (0.699/2.301), and the extended set of spatial variables (East), (North) and (North)<sup>2</sup>, (significant terms of the cubic trend surface regression) explained 13.95% of the total variation (0.321/2.301). In all cases a substantial fraction of the explanatory variables was structured over space (Fig. 3). The number of exotic species decreased as the distance to the potential focus of invasion increased ( $R^2 = 0.34$ ,  $p < 0.001$ ) and this pattern remained even when the most remote quadrats were excluded from the analysis ( $R^2 = 0.12$ ,  $p < 0.01$ ) (Fig. 4). This relationship also holds for the abundance of *L. lucidum* ( $R^2 = 0.10$ ,  $p < 0.01$  including or excluding the remote quadrats). However although the abundance of exotics (sum of the adult individuals of all exotic species) also decreased with distance to the focus of invasion ( $R^2 = 0.16$ ,  $p < 0.001$ ), this pattern was not evident when we excluded the most remote quadrats.

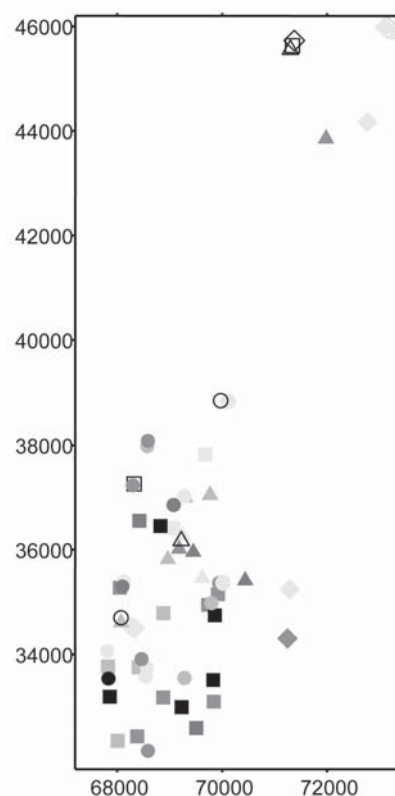


**Fig. 3.** Variation explained by different sets of explanatory variables using variation partition through Canonical Correspondence Analysis (CCA). Environmental variables include endogenous and exogenous variables. For description of variables see Methods.

### Discussion

Our study site in Sierra de San Javier is representative of heterogeneous landscapes associated with forest recovery in subtropical ecosystems of NW Argentina. Our results suggest that land use history, time since abandonment, altitude, slope and cover of the different strata were the most important measured variables related with species composition in this area. Importantly, spatial variables played a significant role.

The results of the ordination with respect to land use and time since abandonment can be interpreted taking into account the species regeneration modes, and dispersal syndromes. Shade-tolerant species have a continuous regeneration mode and can reach maturity in absence of disturbances (Swaine & Whitmore 1988), but they usually have low growth rates and are outcompeted by fast-growing species under full light conditions. In the Yungas forests, shade-tolerant species are represented by *C. porphyria*, *C. vernalis*, *B. salicifolia*, *A. edulis*, *Eugenia uniflora* and *Pisonia ambigua* (Grau & Brown 1998; Grau 2002). Those tolerant species dominated old-growth patches in our study site (App. 2). On the other hand, fast growing and light demanding species (i.e. pioneers) are good at colonizing open sites but are poor competitors under closed canopy. The environmental conditions of tree-fall gaps and recently abandoned fields and crops are suitable sites for colonization of pioneer species. In Argentine Yungas, *Tecoma stans*, *Jacaranda mimosifolia* and *Heliocarpus popayanensis* are considered pioneer species (Grau & Brown 1998; Grau 2002) and were more abundant in young patches originated from herbaceous crops (App. 2). The differences in species composition among citrus



**Fig. 4.** Map of the distribution of sampled quadrats (UTM coordinates). Symbols correspond to different land uses. Circles: citrus plantations; Squares: herbaceous crops; Triangles: pastures and Diamonds: old-growth. The shades are proportional to the observed number of exotic species, from transparent (no exotics) to black (eight exotic species).

orchards and herbaceous crops can be explained by differences in dispersal syndromes. Citrus plants that remain after an orchard is abandoned serve as perches that may enhance the arrival of bird dispersed species (McDonnell & Stiles 1983; Grau et al. 1997). Species such as *Psychotria carthagenensis*, *C. porphyria*, *B. salicifolius*, *Piper tucumanum* and *P. hieronymi* are dispersed by birds and bats and were abundant in patches originated from citrus orchards. Herbaceous crops, on the other hand, were dominated by wind dispersed native species (*T. stans*, *H. popayanensis* and *J. mimosifolia*).

The importance of altitude, slope and cover of the different strata in determining species composition is more difficult to interpret. Within the altitudinal range of the sampled quadrats (i.e. 500-1000 m a.s.l.) we expected to see a change in dominance from piedmont forest species (i.e. *Enterolobium contortisiliquum*, *Tipuana tipu*) to low montane forest species (i.e. *C. porphyria*, *B. salicifolius*) (Cabrera 1976; Grau & Brown 1995). However, no such a tendency was detected in our analy-

sis. It is possible that this altitudinal pattern is only evident in more undisturbed stands. The relationship between cover of the different strata and species composition was not easy to interpret either. In our analysis, cover values were not clearly related to the different species regeneration modes. A potential explanation for these results is that cover values of the different strata today are not necessarily an indication of the condition of that stratum when the patch was colonized. For this reason we prefer to base our interpretations of species correlations on patch age and land use (that are partly related with cover of the different strata) instead of considering the current cover values.

Interestingly, exotic species tended to respond to the ordination differently from the natives. This can be explained by a set of attributes that differ between exotics and natives in this area, and that may also be related to exotic species success. Many exotics in our study site are bird dispersed and bear fruits during the winter (e.g. *L. lucidum*, *L. sinensis*, *P. guajaba* and *L. camara*) when very few native bird dispersed species produce fruits (Aragón 2000). The combination of dispersal syndrome and phenology may permit them to rapidly reach recently abandoned patches and to germinate and establish earlier in the season than native species. Efficient dispersal together with a time suitable for establishment (because of environmental conditions or diminished competition) is crucial for determining local plant distribution (Primack & Miao 1992). In many cases, exotic species exploit the environment or resources differently from native species, and a successful invader often represent a new 'type' (Vitousek & Walker 1989; Mooney & Drake 1989; McIntyre & Lavorel 1994; Wisser et al. 1998). In this case the difference in fruiting and germination phenology between exotics and natives may indicate different tolerance to environmental conditions (e.g. differential drought resistance), and may be related with exotics ability to colonize young patches, and consequently with their separation in the ordination.

Other potential important differences between some exotic and native species become evident when we compare exotics with the most common native pioneer species. Many of the exotics in Sierra de San Javier are considered pioneer species (Grau & Aragón 2000) since they colonize recently abandoned, open and disturbed sites, and in our analysis they had similar responses to explanatory variables as native pioneers (i.e. exotics appear close to *T. stans*, *H. popayanensis* and *J. mimosifolia*). However, native pioneers in addition to being wind dispersed, usually have short life spans and are unable to reach the canopy strata of mature stands (e.g. *T. stans*, *J. mimosifolia*) (Grau et al. 1997), but this is not the case of the most common exotic, *L. lucidum*.

The replacement of *L. lucidum* by native tolerant species during succession may be delayed due to its height (up to 20 m), resprouting capacity (Grau & Aragón 2000) and its apparent long life span. Hence *L. lucidum* can be considered a long-lived pioneer. In addition, previous work found that *Citrus* spp. saplings are capable of regenerating in the closed canopy of old-growth stands (Grau & Brown 1998; Tecco & Rouges 2000). In our study *Citrus* spp. and *Persea americana* are present in several patches irrespective of land use (i.e. in the centre of the ordination and not significantly correlated with any of the axes). These species seem to combine some attributes of pioneer species (e.g. high investment in reproduction, high growth rate) and at the same time are shade-tolerant. Of course, these interpretations should be tested experimentally in order to be considered more than suggestions from descriptive analysis.

Vegetation pattern in secondary forests of NW Argentina, as well as elsewhere, results from a combination of historical and environmental factors (McIntyre & Lavorel 1994; Grau et al. 1997; Motzkin et al. 1999b). Our results for Sierra de San Javier highlight the importance of spatial variables for both species composition and exotic occurrence. It is possible to distinguish two scales of spatial effects in our results. At the patch scale, the relative position of the quadrat (edge or interior) was strongly related to species composition. Our classification of variables put edge vs forest interior within the endogenous or biotic variables because it involves responses of the vegetation (i.e. changes in cover, phenology, recruitment) and therefore it is under biotic control. However, this variable also indicates the position of the quadrat within a patch, and hence has a clear spatial component. The position of the quadrat is associated with changes in micro-environmental conditions (e.g. light, temperature) that ultimately trigger vegetation responses. In our study site, the relative position of the quadrat was related to the presence of exotic species (e.g. *L. camara*, *P. guajaba*, *L. lucidum*, *L. sinensis*), native pioneer trees (e.g. *T. stans*, *J. mimosifolia*) and shrubs (e.g. *Rubus imperialis*, *Cestrum strigillatum*), that were all more abundant at edges. Light and resource availability in edges are often higher than under close canopy and performance of pioneer species may be enhanced (Oliveira-Filho et al. 1997; Gehlhausen et al. 2000). At the landscape scale (i.e., between patches), a considerable portion of the explained variation in species composition was attributable to environmental variables structured over space or to spatial proximity alone (App. 2). The fraction of species composition explained by pure spatial variation may be due to dispersal and competition, but could also be related to unobserved environmental variables that are spatially correlated.

In addition to being related to species composition in

general, spatial variables were particularly influential in determining exotic species distribution. The pattern of exotic species abundance stresses the importance of proximity to potential sources of exotic propagules. Considering the study area as a whole, exotic species were predominantly associated with young patches originating from herbaceous crops. However, their abundance was low in quadrats with this land use history, but that were far away from the seed sources. On the other hand, exotic species were abundant in many patches that were close to the potential focus of invasion, irrespectively of whether these patches were previously orchards, crop areas or pastures (Fig. 4). The importance of space in general suggests that the position of a patch within the landscape, that is the landscape context, is a key factor in determining species composition.

Our interpretation of the observed patterns of community composition and exotic abundance suggests several working hypotheses for vegetation dynamics in this system. In particular, the importance of spatial variables could be better assessed by studies of dispersal and establishment of exotic and native dominant species. Permanent plots and experimental work could be used to evaluate the main patterns suggested by our results.

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