

Contents lists available at [SciVerse ScienceDirect](http://www.sciencedirect.com)

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoeoc

Original article

Invasion of *Ligustrum lucidum* (Oleaceae) in the southern Yungas: Changes in habitat properties and decline in bird diversity

M.M. Ayup^{a,b,*}, L. Montti^{a,c,d}, R. Aragón^{a,c}, H.R. Grau^{a,c}^a Instituto de Ecología Regional (IER), Universidad Nacional de Tucumán, CC 34, Yerba Buena, Tucumán, Argentina^b Agencia Nacional de Promoción Científica y Tecnológica (FONCYT), Argentina^c Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina^d Centro de Investigaciones del Bosque Atlántico (CeIBA), Andresito 21, Puerto Iguazú 3370, Misiones, Argentina

ARTICLE INFO

Article history:

Received 17 October 2012

Accepted 12 March 2013

Available online xxx

Keywords:

Bird community
Exotic tree invasion
Habitat properties

ABSTRACT

Ligustrum lucidum is the major exotic tree in NW Argentina montane forests (Yungas). To assess the effects of its expanding invasion on avian communities we (1) measured different habitat properties (vertical forest structure and composition, vegetation cover, light availability, air temperature, air relative humidity and soil litter depth), (2) compared bird species composition and diversity in *Ligustrum*-dominated and native-dominated secondary forests and (3) analyzed seasonal patterns and changes in these variables between forest types. The study was conducted during 2010–2011 wet and dry seasons, at two altitudinal zones: 500–800 and 1100–1450 masl. Compared with native forests, *Ligustrum* dominated forests had a more homogeneous vertical forest structure and denser canopy cover (resulting in lower understory solar radiation), significantly lower understory cover and lower litter depth. Air temperature and relative humidity did not differ between forests in either season. Solar radiation was higher in the dry season in both forest types, but litter depth showed opposite patterns between seasons depending on forest type. We recorded 59 bird species in 21 families. Bird species abundance, richness and diversity indexes were significantly lower in *Ligustrum*-dominated relative to native forests of similar successional age, which had almost twice as many species as the former. Avian communities differed between altitudinal zones, but the difference was stronger between *Ligustrum* and native-dominated forests. Avian community composition was less variable in time and space in native forests than in *Ligustrum*-dominated ones. Our results suggest that *L. lucidum* invasion generates structurally homogeneous and simpler forests that represent a less suitable habitat for a diverse avifauna. This illustrates the wide ecological changes (from habitat properties and ecosystem functioning to vertebrate community composition) that the subtropical mountain forests of Argentina are experiencing with this invasion.

© 2013 Published by Elsevier Masson SAS.

1. Introduction

Biological invasions are both consequence and significant drivers of global environmental change (Davis et al., 2000) that threaten biodiversity by transforming habitats, ecosystem functioning and ecological interactions (Ehrensfield, 2010; McKinney and Goodell, 2010; Boyce et al., 2011). The role of exotic species on native species extinctions is being discussed globally (Dogra et al., 2010) and in many cases the effects appear to be scale-dependent: many species can disappear locally but not regionally

(Powell et al., 2011). Invasion processes are complex with impacts on physical habitat properties, the relative abundance of species, and their trophic interactions. Therefore, every invaded ecosystem is a particular case that needs to be studied to assess the impacts of invasive species on biodiversity.

Invasive canopy trees have the potential to strongly affect different ecosystem properties including primary productivity, soil nutrients, water dynamics (Calder and Dye, 2001; Rascher et al., 2011) and light incidence in the understory (Lichstein et al., 2004) which, in turn, determine microclimatic conditions such as air temperature and humidity (Karr and Freemark, 1983). Successful invasive trees often generate monodominant stands and play a dominant role in determining ecosystem functioning. These changes are likely to induce further alterations in animal and plant communities by affecting resource availability and habitat structure

* Corresponding author. Instituto de Ecología Regional (IER), Universidad Nacional de Tucumán, CC 34, Yerba Buena, Tucumán, Argentina. Tel.: +54 381 4255174.

E-mail addresses: martitaayup@gmail.com, martitaayup@yahoo.com.ar (M.M. Ayup).

(Karr and Freemark, 1983; Cueto and Lopez de Casenave, 1999; Wolfe and Klironomos, 2005; Verdú et al., 2011). In the case of avian communities, the effects of invasion-induced habitat changes vary among species and guilds that differ in habitat or resource requirements (e.g., fruits, invertebrate prey, nesting sites). For example, invasion by Honeysuckle (*Lonicera* spp.) in the US caused considerable reductions in specialized insectivorous birds (Rodewald, 2012) and altered the migratory pathways of several species (Rodewald et al., 2010). Comprehensive studies that evaluate the impact of invasion-mediated changes on ecosystem properties and avian communities are thus needed, particularly if they contemplate the complex interactions among ecosystem processes.

Subtropical mountain forests (*Yungas*) are one of the most biodiverse ecosystems in Argentina (Brown et al., 2001). During the early twentieth century these were partially deforested for agriculture and livestock husbandry. In recent decades, this trend has reversed and forests have recolonized abandoned croplands and pasturelands as a consequence of socioeconomic changes (Grau et al., 2007). A large and increasing proportion of these secondary forests are dominated by exotic tree species (Grau and Aragón, 2000). *Ligustrum lucidum* Aiton is the most abundant exotic tree in the Yungas of NW Argentina (Grau and Aragón, 2000) and has expanded as monodominant secondary forests that cover thousands of hectares. Based on its fast rates of expansion in recent decades, Grau et al. (2008) suggested that this species has a strong potential for further expansion, making the assessment of its ecological effects a pressing research priority. In this study, we evaluate the consequences of *L. lucidum* invasion on avian communities or whether these can be mediated through changes in habitat properties.

Birds are good indicators of habitat quality and species richness of other taxa (Ramírez, 2000). A reduction or simplification in forest structure and complexity impacts negatively both on animal and on bird communities, in particular (Aleixo, 1999; Cueto and López de Casenave, 1999; Díaz et al., 2005). For example, bird diversity in Portugal decreases along decreasing forest “naturalness”, determined mostly by exotic tree abundance (Proenca et al., 2010). In the Argentine Yungas, Rougés and Blake (2001) found differences in bird communities between mature and exotic-dominated secondary forest that vary in seasonal fruit supply. Most frugivorous native

birds in the Yungas consume and disperse *L. lucidum* fruits and seeds (Aragón, 2000). In the dry season, birds consume a greater proportion of fruits in secondary forest than in primary forest, largely due to a greater supply of fruits from *L. lucidum* and some native species such as *Psychotria cartagenensis* (Rouges and Blake, 2001). While several studies analyzed the diversity and distribution of birds in the Yungas, none have focused on the temporal and spatial changes in bird communities in monodominant forests of exotics and their relation to changes in habitat properties.

Here we hypothesize that *L. lucidum* invasion in the Argentinean Yungas is affecting bird communities by changing habitat properties related to forest structure and function. To assess this general hypothesis, we (1) compare habitat properties (environmental conditions, forest structure and understory vegetation cover and composition) between invaded and native dominated forests at two altitudinal zones; (2) quantify bird community composition and diversity and similarity patterns of invaded and native forests; and (3) analyze seasonal differences in habitat properties and avian communities at the two altitudinal zones.

2. Methods and materials

2.1. Study area

This study was conducted at the Sierra de San Javier, (27°30' S, 65°40' W, Fig. 1), one of the sites where forest recovery following land use disintensification has been best described in NW Argentina (Grau et al., 2008). The area belongs to Yungas phytogeographic province (Cabrera, 1976), which extends from Bolivia in the north (22°S) to Catamarca province (Argentina; 29°S). Climate is monsoonal with dry winters and rainy summers. Study sites are 15–20 km west of the largest city in subtropical Argentina: San Miguel de Tucumán (ca. 1 million inhabitants). Secondary forests have a high density of exotic tree species. The most successful invaders are bird-dispersed species from southwestern Asia such as glossy privet (*Ligustrum lucidum*) (Grau and Aragón, 2000; Aragón and Morales, 2003). *Ligustrum lucidum* forests have expanded at two elevation zones where agriculture abandonment has been more pervasive (Aragón and Morales, 2003; Grau et al., 2008): the eastern foothills (500–800 masl) and the southern portion of the

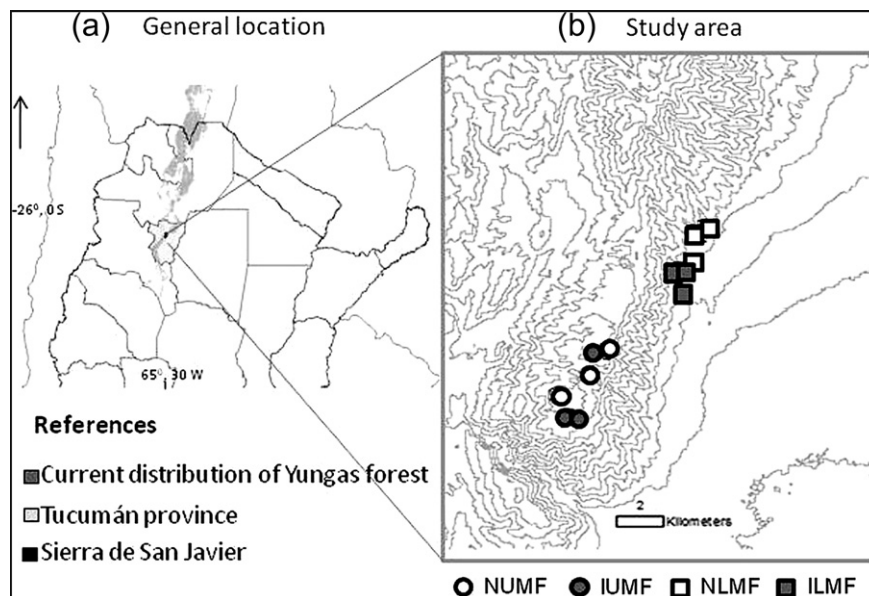


Fig. 1. a) General location of study area in Sierra de San Javier (SSJ), Tucumán, Argentina and current distribution of Yungas forest. b) Details of study area and the two altitudinal zones of the mountain forest: Lower mountain forest (LMF) and upper mountain forest (UMF), native (N) or invaded (I).

range ridge (1100–1450 masl) (Fig. 1). The rapid expansion of *L. lucidum* is associated with efficient seed dispersal (Montaldo, 1993; Aragón, 2000; Aragón and Groom, 2003), fast growth rate (Aragón and Groom, 2003; Easdale et al., 2007), shade tolerance (Aragón and Groom, 2003), regrowth capacity of detached branches (Lichstein, 2007) and, probably, suppression of regeneration of native tree species (Lichstein, 2007) by competition.

Data collection was carried out at the two above-mentioned altitudinal zones (Fig. 1). Landscape is characterized by a mosaic of old growth forests and secondary forests resulting from relatively recent land use disintensification. In the eastern foothills ("Lower mountain forest", 500–800 masl), native-dominated secondary forests are characterized by pioneer species such as *Parapitadenia excelsa*, *Solanum riparium*, *Heliocarpus popayanensis*, and *Tecoma stans*. Exotic-invaded secondary forests at this altitudinal range present a high proportion of the exotic species *L. lucidum* and *Morus alba*. *Ligustrum* forests have expanded rapidly in recent decades, and can form monodominant patches with more than 500 trees individuals per hectare. The understory of *Ligustrum*-dominated forests is strongly dominated by the shrub *P. cartagenensis*. In the southern range ridge ("Upper mountain forest", 1100–1450 masl), native secondary forests are dominated by *Alnus acuminata* and *Myrsine laetevirens*, and exotic invaded forests are also dominated by *L. lucidum* and, to a lesser extent, *Pyracantha coccinea*. The understory of invaded forests is more diverse, but *P. cartagenensis* is not present at this altitude. Mature forests at both altitudinal zones are dominated by *Cinammomum porphyria*, *Blepharocalyx salicifolius*, *Pisonia ambigua* and *Cedrela lilloi* (Grau et al., 1997, 2010). Along the topographic gradient, mean annual temperature ranges between 14 and 18 °C and annual rainfall between 1200 and 1600 mm respectively. There is an additional supply of water, particularly during the dry season that comes from fog or horizontal rain (Hunzinger, 1997).

In the southern Yungas, 294 species of birds have been recorded along all its altitudinal and structural range, from low mountain forests to high Andean grasslands and open areas. Sixty of these species are typical of secondary native forests and edges (Blendinger and Alvarez, 2009). There are four endemic bird species in the Yungas: *Atlapetes citrinellus*, *Amazona aestiva*, *Amazona tucumana* and *Cypseloides rothschildi*; the last three with endangered populations worldwide (Di Giacomo, 2005; Navarro et al., 2007). Avian communities vary along the altitudinal gradient: bird species diversity peaks at intermediate elevations (700–900 masl approximately) and interannual variation in bird community composition increases with elevation as climatic seasonality becomes stronger (Giannini, 1999; Blendinger and Alvarez, 2009).

2.2. Research design

Six sites were located in the lower mountain forest, nearby Horco Molle locality, and six in the upper mountain forest around Anta Muerta and Villa Nougés towns (Fig. 1). Sites were set as pairs of secondary native-dominated and *L. lucidum*-dominated forest (invaded forests) respectively, at approximately the same altitude and with similar successional ages (15, 30 and 45 years approximately). Consequently, the experimental design includes four habitats: Native lower mountain forest (NLMF), Invaded lower mountain forest (ILMF), Native upper mountain forest (NUMF) and Invaded upper mountain forest (IUMF).

2.3. Habitat properties

2.3.1. Vegetation structure and composition

At each site, forest vertical structure was quantified by the "point intercept" method (Mostacedo and Fredericksen, 2000) in

October–November 2011. We recorded the number of vegetation touches by species using a graduated rod separated in two levels (0–2 m: lower understory; and 2–7 m: upper understory) along a 50 m transect (one per site, 10 measuring points per transect). From this data, we calculated the percentage of native and *Ligustrum* cover (as percentage of touches) in both understory strata.

2.3.2. Environmental variables

Solar radiation availability was estimated indirectly as average percent of canopy cover, measured with a densiometer in five points every 20 m on a 100-meter transect per site. A densiometer is a gridded concave mirror in which the number of squares with and without canopy vegetation presence can be counted when the device is set horizontally. The percentage of covered squares represents an estimation of canopy closeness, and therefore solar radiation availability. Litter depth was estimated as the average of 10 randomly located points where litter depth was measured with a ruler to the nearest millimeter. Air temperature and relative humidity were measured by a digital Hygro-Thermometer clock Advance (Extech Instruments 445702); five measurements per site during the 2-hour bird sampling period.

2.4. Avian community patterns

Bird sampling (point censuses) was carried out during 2010 and 2011 in the four habitats (NLMF, ILMF, NUMF and IUMF). We established 4 quadrats (50 × 50 m approximately) at each study site. At each quadrat we recorded the abundance of all species seen or heard during 20 min. In total, we spent 80 min in each site with two observers working simultaneously at each quadrat and sites were visited twice each year. In order to make pairwise comparisons more rigorous, we conducted one bird sampling per morning, and pairs of invaded and native plots were sampled in consecutive days. Sampling schedule by season is specified in subsection 2.5.

2.5. Seasonal differences in habitat properties and avian communities

In order to evaluate seasonal differences in habitat properties and avian communities at the two altitudinal zones, all activities outlined in 2.3 and 2.4 sections were conducted during two contrasting seasons: dry/cold winter (August) and wet/warm summer (December) both in 2010 and 2011. Only one pair of sites (NUMF 2 and IUMF 2) was visited once (2011) in both seasons. Bird records in all sites were registered between 8.00 am and 10.00 am in the dry/cold season, and 7.00 am and 9.00 am in the wet/warm season.

2.6. Data analysis

2.6.1. Vegetation structure, composition and microclimate

Solar radiation availability, percent of understory cover per strata, air temperature and humidity, and litter depth were analyzed by means of a two-way nested ANOVA with both forest types (native and invaded) nested within the two altitudinal zones (lower and upper), for both seasons. The two year data for each season were averaged.

2.6.2. Avian community patterns

To characterize bird communities we calculated species richness and abundance as the number of records per species during the 80 min sampling period per site, per season. In addition, we computed Shannon H' and Simpson's diversity index with PRIMER 5 Software (Clarke and Warwick, 2001) for each site at both forest

types and altitudinal zones. Then we compared diversity indexes with a two-way nested ANOVA as explained above (see 2.6.1.). We used both Simpson and Shannon diversity indexes because they provide complementary information about community diversity; i.e., Simpson's index gives more weight to evenness while Shannon's index is mostly influenced by richness (Nagendra, 2002). Furthermore, the use of both indexes, facilitate comparison with other studies. To analyze similarity in bird community composition between study sites, we carried out a Non-Metric Multi-Dimensional Scaling (NMDS) based on Bray–Curtis similarity index using PCORD 5 (McCune and Mefford, 2006) plotting the 12 study sites in both seasons and in a two dimensional ordination. To test statistical differences in beta diversity of bird communities between forest types and altitudinal zones we used a two-way nested similarity analysis (ANOSIM) for both seasons (Clarke and Warwick, 2001). ANOSIM is a procedure based on similarity/dissimilarity matrices used for testing the significance of similarities/dissimilarities (beta diversity) between defined groups (forests types within altitudinal zones in this study). This analysis tests if the observed similarity between groups is significantly different from similarities expected by chance. The procedure gives an R statistic value that varies from 0 to 1 with its associated p value. An R value close to 1 indicates that similarity among groups is higher than within groups. We used a Bray–Curtis similarity index matrix with square root transformation of data in order to avoid underweighting uncommon species. We performed a nested analysis considering (a) forest type (native and invaded by *L. lucidum*) nested in two (b) altitudinal zones (lower and upper mountain forest) with three replicates of each forest type-altitude combination. Additionally, we calculated the average abundance of shared species (estimated by frequency per site) between significantly different groups.

2.6.3. Seasonal changes in habitat properties and avian communities

To evaluate the seasonal patterns in habitat properties, we compared forest type between seasons with a paired t test. For bird communities, we described their seasonal trajectories with lines in the NMDS ordination plot (i.e. lines join the "location" in the ordination diagram of the two samples of each site at different seasons) and we compared the Bray–Curtis similarity indexes between different seasons of each study site. This multivariate analysis was calculated from a species/abundance matrix, with abundance data averaged between the two years of sampling (2010–2011). Except when specified otherwise, STATISTICA 6.1 Software and a significance level of 5% were used.

3. Results

3.1. Habitat properties

3.1.1. Vegetation structure and composition

On average, percent of understory cover was 4 times higher in native forests than in invaded forests in both understory strata ($F = 44.1031$, $p < 0.001$); though differences were not statistically significant for the lower understory strata (0–2 m) in the lower mountain forest (Fig. 2). Eighty two percent of the total touches registered (considering both understory strata and forest types) belonged to native species and 18% to exotic species: 13% corresponding to *L. lucidum* and the remaining 5% to other species such to *Ligustrum sinensis*, *Citrus aurantium*, *Eriobotrya japonica* and *Morus alba*. Invaded forest showed lower cover of native species in the understory at both elevations (Fig. 3a) although this difference was statistically significant only in the upper mountain forest zone ($F = 11.1275$, $p < 0.02$). Native plants were almost absent in the upper understory of invaded forests in both altitudinal zones, in contrast with native forests (Fig. 3a, b) ($F = 36.2244$, $p < 0.001$). *L. lucidum* cover in the understory varied with elevation ($F = 6.3943$, $p < 0.04$) (Fig. 3c, d) and was marginally higher in invaded forests of the UMF zone ($F = 3.14$, $p = 0.09$).

3.1.2. Environmental conditions

Solar radiation availability was approximately 12–15% lower in invaded forests at both elevations and seasons and litter depth was generally twice as thick in native dominated forests. Upper mountain forests tended to have higher relative humidity and lower temperature than LMF but we found no significant difference between invaded and native dominated forests (Table 1).

3.2. Avian community patterns

We registered 59 bird species belonging to 22 families, including almost all of the typical forest-species of secondary forest of Yungas (Blendinger and Álvarez, 2009). Seven families included 51% of the species recorded: Tyraniidae (9 species, 15% of total recorded species), Parulidae (5 species, 8%), Emberizidae, Columbidae, Picidae and Turdidae (4 species each, 7% of total species each family) and Cardinalidae, Furnaridae, Trochillidae, and Psittacidae with three species each family (5%). The rest of the families were represented by one or two species. The most frequent families were Turdidae, Thraupidae and Parulidae, followed by Tyrannidae, Columbidae, Psittacidae, Furnaridae and Corvidae (see Appendix).

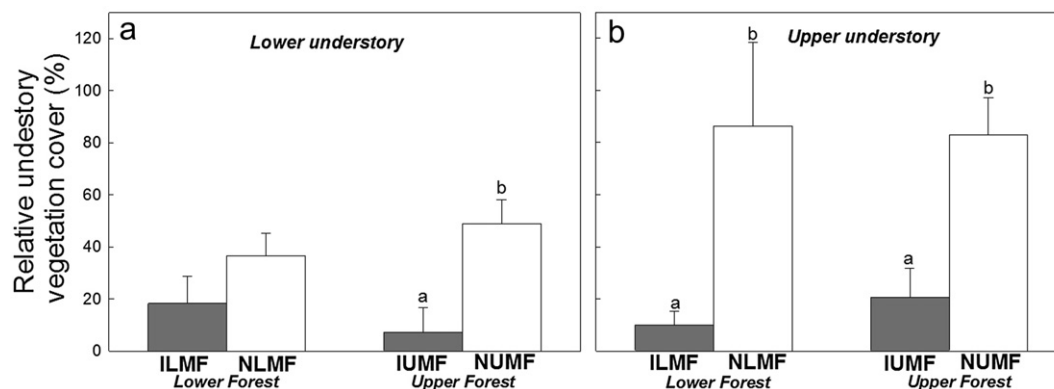


Fig. 2. Relative understory vegetation cover in four defined habitats (forest type per altitudinal zone). a) Lower understory, 0–2 m height from the ground vegetation. b) Upper understory, 2–7 m height. Grey bars represent invaded forest and white bars native forest. NLMF: Native lower mountain forest, ILMF: Invaded (by *L. lucidum*) lower mountain forest, NUMF: Native upper mountain forest, IUMF: Invaded upper mountain forest. Different letter indicates significant differences ($p < 0.001$).

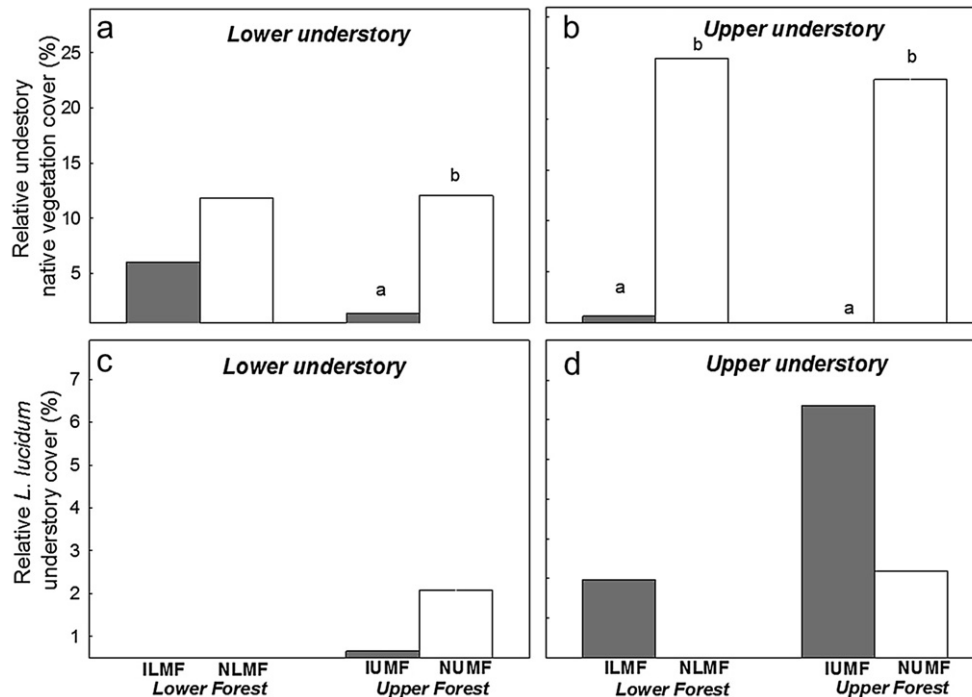


Fig. 3. Relative percent of native (a and b) and *L. lucidum* (c and d) cover in the lower and upper understory in the defined habitats types. Grey bars represent invaded forest and white bars native forest. (Acronym description as in Fig. 2).

Bird species richness, abundance, and diversity indexes were significantly higher in native dominated forests than in invaded forests at all altitudinal zones and seasons. Species richness and bird abundance, for example, were generally more than twice as high in native dominated forests and differences were always significant ($p < 0.01$). Differences between altitudinal zones were comparatively minor although, in some cases, they were statistically significant: for example species richness, abundance and Shannon diversity index in the dry season were higher in the lower mountain forest (Fig. 4).

The Non-metrical Multidimensional Scaling (NMDS) based on Bray–Curtis similarities in bird community composition, performed a reliable ordination (Final stress = 13.725, Monte Carlo test $p = 0.008$) (Fig. 5). Axis 2 discriminated between forest types: native sites were grouped towards the negative values and invaded sites towards positive values. Axis 1 clearly separated seasonal communities within invaded forests. Upper elevation sites tended to occur at lower values of axis 1 than lower elevation sites. When Beta diversity (defined as the R ANOSIM statistic) was compared

Table 1

Mean air temperature (mean T°C), mean air relative humidity (mean RH%), percent of light availability and mean litter depth. Letters discriminate groups with significant difference between them. Highlighted: native and invaded forests of the upper mountain forest zone. NLMF: Native lower mountain forest, ILMF: Invaded lower mountain forest, NUMF: Native upper mountain forest, IUMF: Invaded upper mountain forest.

| Season | Type of habitat | Mean T°C | Mean RH% | % Light availability | Mean litter depth (cm) |
|----------|-----------------|----------|----------|----------------------|------------------------|
| Dry/cold | ILMF | 13.10 | 60.06a | 11.11a | 2.44a |
| | NLMF | 13.65 | 60.93a | 25.74b | 3.99b |
| | IUMF | 17.03 | 45.72b | 10.91a | 2.49a |
| | NUMF | 14.71 | 49.76b | 28.38b | 4.82b |
| Wet/hot | ILMF | 23.09a | 67.13 | 8.66a | 2.27a |
| | NLMF | 19.03 | 71.96 | 18.58b | 4.57b |
| | IUMF | 17.53b | 66.76 | 8.91a | 2.48a |
| | NUMF | 19.37 | 60.03 | 20.94b | 5.35b |

between forest types and altitudinal zones, we found that bird community composition of invaded and native forests were significantly different in the dry ($R = 0.7$, $p = 0.0001$) and the wet season ($R = 1$, $p = 0.0001$), but not between altitudinal zones in either season.

Many of the species recorded were only found in Native forests, including *Pipraeidea melanonota*, *Elaenia albiceps*, *A. citrinellus* (an endemic species of Yungas), *Arremon flavirostris*, and the three species of woodpeckers (*Colaptes rubiginosus*, *Picumnus cirratus* and *Veniliornis frontalis*). In contrast, invaded forest sites did not show “unique” species, except from one, *Pheucticus aureoventris* individual seen in only one invaded site of the UMF. Therefore, bird community composition in invaded forests represented a subset of approximately 50% of the community found in native forests. Shared species between both types of forests were mostly the common ones such as *Turdus rufiventris*, *Thraupis sayaca*, *Syndactyla rufosuperciliata*, *Parula pitiayumi*, *Chlorospingus ophthalmicus* and *Myioborus bruniceps*. In general, all these species showed lower density in invaded than in native forests, except from one insectivorous species (*Basileuterus culicivorus*) that was slightly more abundant in invaded forests (Fig. 6a); and *Buteo magnirostris* that was equally frequent in both forest types (Fig. 6b).

3.3. Seasonal changes in habitat properties and avian communities

3.3.1. Seasonality in habitat properties

Available solar radiation in the understory was higher in the dry season than in the wet season both in native (7.5% higher; $T = 9.75$, $p < 0.001$) and invaded forests (2.2% higher; $T = -4.92$, $p < 0.001$). The litter layer was deeper in the wet season in native forests ($T = 9.75$, $p < 0.001$) while it was deeper in the dry season in invaded ones ($T = -4.92$, $p < 0.005$) (Native forests: Mean litter depth: 2.47 cm, 4.97 cm, dry and wet season respectively; *L. lucidum* forests: Mean litter depth: 4.41 cm, 2.38 cm, dry and wet season respectively). Mean air temperature was approximately 5 °C

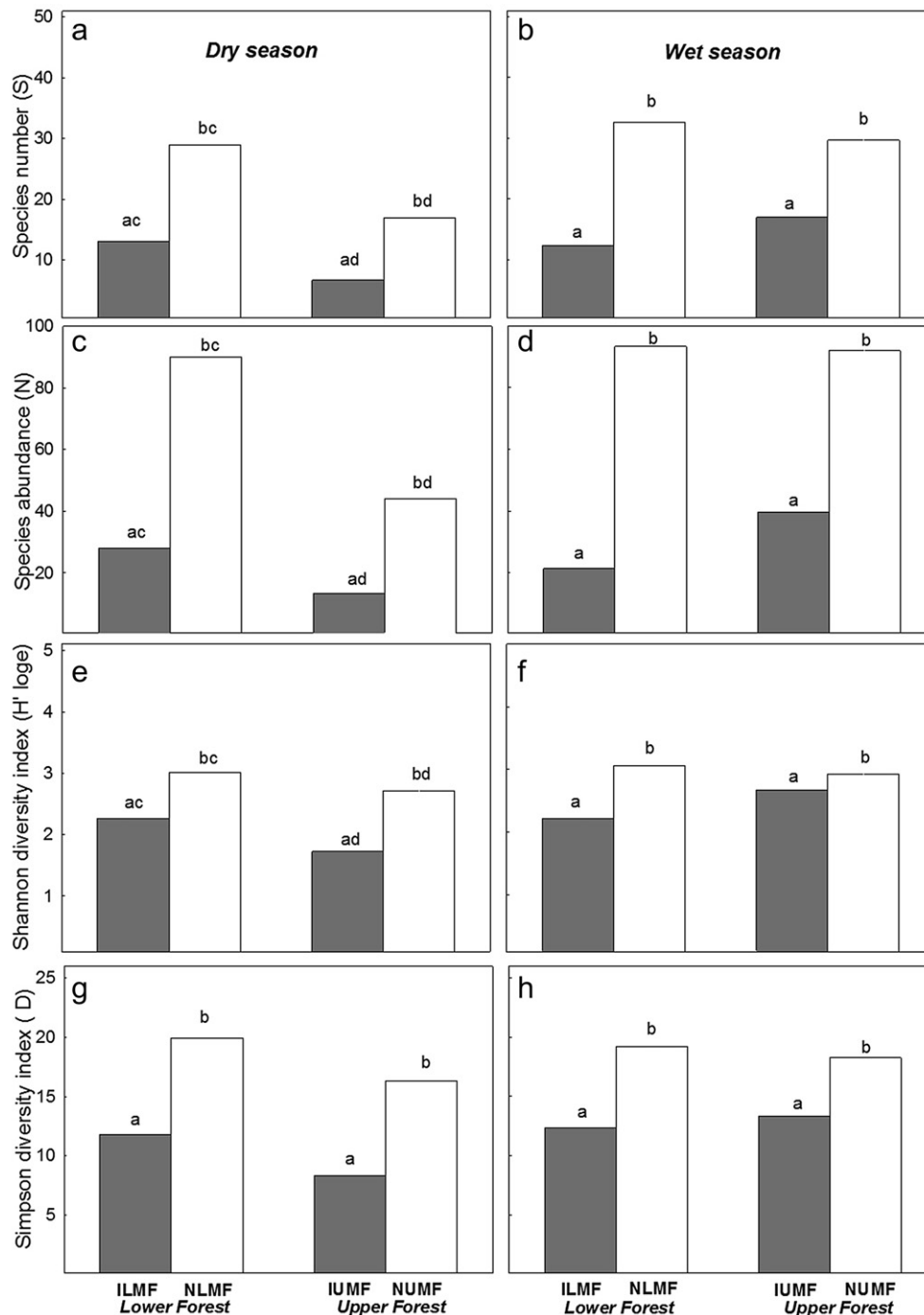


Fig. 4. Species richness (S), abundance (N), Shannon diversity and Simpson's index for dry and wet season of native and invaded forests, of the lower and upper mountain forest zones.

lower in the dry season than in the wet season in both forest types, but only statistically significant in invaded forests ($T = 3.17$, $p < 0.05$). This seasonal difference was also marginally significant in native forests ($T = 2.05$, $p = 0.09$). As expected, air relative humidity was lower in the dry season than in the wet season but only significantly different in invaded forests (55% and 67% for dry and wet season respectively, $T = 3.85$, $p < 0.05$).

3.3.2. Seasonality in avian communities

In native forests, bird species richness increased by 21% (from 43 to 52) from winter to summer while invaded forests presented the

same richness in both seasons (23). All native sites showed the same tendency or trajectory direction while the trajectories of invaded sites in the ordination diagram were the opposite along axis 1 (Fig. 5). Only one *Ligustrum* invaded site of the UMF zone showed an opposite change direction between dry and wet season, and it was also the most variable site between seasons. Aggregation of study sites at different altitudes was stronger between native forests and these sites were approximately 20% more similar between seasons (Bray Curtis Similarity Index) when compared to *Ligustrum*-invaded forests. This difference in similarities within forest types between seasons was marginally significant ($T = -2.07$,

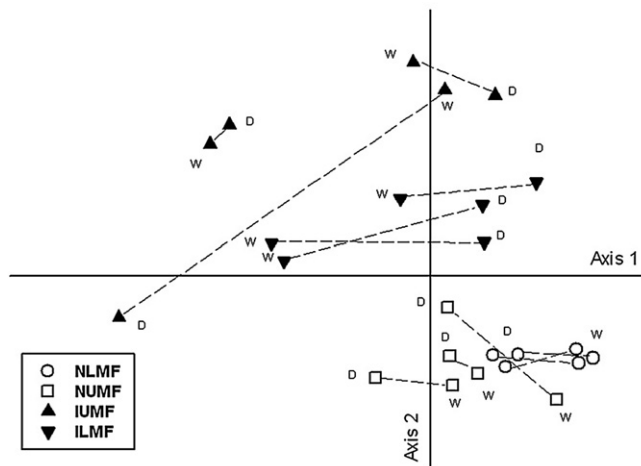


Fig. 5. NMDS ordination diagram of study sites in dry and wet seasons (two-year average) and their trajectory of seasonal fluctuation (lines joining samples of the same plot at different times), according to bird species richness and abundances (Bray–Curtis Similarity index). **D:** Dry/cold season, **W:** Wet/hot season. (Acronym description as in Fig. 2).

$p = 0.06$). Consistently, *Ligustrum* dominated forests presented almost twice the standard deviation in their seasonal variation than native forests ($SD = 18.66$ and $SD = 10.77$ respectively), thus indicating a stronger seasonal fluctuation in community composition of invaded forests.

4. Discussion

Ligustrum lucidum is the most abundant exotic tree in the Argentine Yungas (Grau and Aragón, 2000) and previous studies (Lichstein et al., 2004) found that it influences the species composition and degrades the diversity of invaded plant communities. Here, we found that *L. lucidum* also significantly affects the composition and dynamics of the avian community, and that these effects may be mediated through changes in habitat properties. Regional trends in land use combined with recent *L. lucidum* spread (Grau et al., 2008) suggest that *L. lucidum* will continue to expand in the coming decades, likely affecting different ecosystem functions, as previously reported for other invaded ecosystems (e.g., D'Antonio and Vitousek, 1992; Gordon, 1998; Rodewall, 2012).

Our results show that *L. lucidum* increases canopy cover, in turn decreasing available solar radiation in the understory (Table 1). These changes could result from differences in understory cover between native and invaded forests (Fig. 2). However, decreased understory cover in invaded forests may also associate to competition for other resources (e.g., water, nutrients) or the release of allelochemical compounds. Decreases in understory cover were more marked in the lower understory strata in forests at high elevation and in the upper understory strata in forests at low elevation. This interaction between elevation and forest structure likely results from the limited distribution of the shrub *P. cartagenensis*, which dominates the understory of lower montane forest but does not occur in upper montane forest presumably due to freezing sensitivity (H.R. Grau, personal observations). The understory of forests invaded by *Ligustrum* (specially the upper understory strata) is also dominated by *Ligustrum*, while native species are barely represented (Fig. 3). This suggests that the environmental changes induced by this invasion are likely to persist for at least some generations since the *Ligustrum* dominated canopy will be replaced, to a large extent, by other *Ligustrum* trees. Aragón (2000) found that several bird species, including the two

most abundant in our study (*T. rufiventris* and *T. sayaca*) consume and disperse fruits of *L. lucidum* in the study site. This may explain the high abundance of *L. lucidum* saplings in the understory of native forests; and may further facilitate the invasion of *L. lucidum*. Although this state of the invasion may represent only a transient successional stage, the presence of *L. lucidum* in the understory of secondary forests, its regular dispersal by birds and the 60 years of expanding invasion, suggest a future scenario where the displacement of native species (currently observed in relative small patches) will become significantly more extensive.

Most native understory trees (e.g. *Allophylus edulis*, *P. cartagenensis*, *Eugenia uniflora*, *Myrcianthes pungens*) produce fleshy fruits and thus represent an important resource for frugivore birds. Their reduced abundance and diversity in invaded forests likely affects the amount and temporal availability of resources for part of the avian community. Furthermore, the greater structural complexity of native forests (both at the canopy and the understory levels) likely provides birds with suitable nesting places as well as other resources such as invertebrate prey. In addition, we recorded a lower litter depth in *Ligustrum*-dominated forests (Table 1) – probably due to the faster decomposition rate of this species relative to most native tree species (Aragon et al., this issue) and/or differences in the timing and amount of litter fall (Ayup unpublished data). Differences in litter depth and composition between forest types are probably affecting the abundance and diversity of soil invertebrates with concomitant negative impacts on ground foraging birds such as *T. rufiventris* and *A. flavirostris*.

Solar radiation was higher in the dry season both in native (where some species are deciduous) and invaded forests (attributable to partial leaf fall, since deciduous species are rare in this forest type). *Ligustrum lucidum* litterfall peaks in autumn and spring (Dascanio et al., 1994; Ayup, unpublished results), which respectively coincide with the beginning and end of the dry season. Accordingly, invaded forests showed a deeper litter layer in the dry season. Climate is less favorable for decomposition during the dry season (i.e., lower mean air temperature and relative humidity). Nonetheless, seasonal differences in air temperature and moisture were only significant in invaded forests. This suggests that native forests buffer low temperature and humidity better than invaded forests by allowing more solar radiation to reach the understory during the dry/winter season.

Several studies have documented interactions between animal communities and habitat changes induced by exotic invasions (Verdú et al., 2007; Numa et al., 2009; Proenca et al., 2010). In our study, bird diversity was significantly lower in invaded forests at both altitudes and in both seasons (Fig. 4). Zurita et al. (2006) compared bird communities between native forests and exotic pine plantations in subtropical Argentina, and found a similar reduction in bird richness (ca. 50%) in association to decreased structural complexity in pine plantations. Díaz (2006) also found a reduction in bird diversity related to forest structural changes in Spain. *Ligustrum* dominated forests are structurally simple and homogenous and resemble plantation forests. The decreased structural complexity of forests dominated by exotic trees and its cascading effects on ecosystem properties likely explain the lower bird diversity associated to them.

Most native frugivorous birds in the Argentinean Yungas consume *L. lucidum*'s fruits (Aragón, 2000). In addition, Rougés and Blake (2001) found that, during the dry winter season, maximum fruit consumption by birds in secondary forests in this same region is associated to *P. cartagenensis* and *L. lucidum* fruit production. Consequently, we expected to find a higher avian diversity in *L. lucidum* forests during winter (dry season) when most of the native trees are not fruiting. However we found the opposite result. As discussed above, a possible explanation is that invaded forests

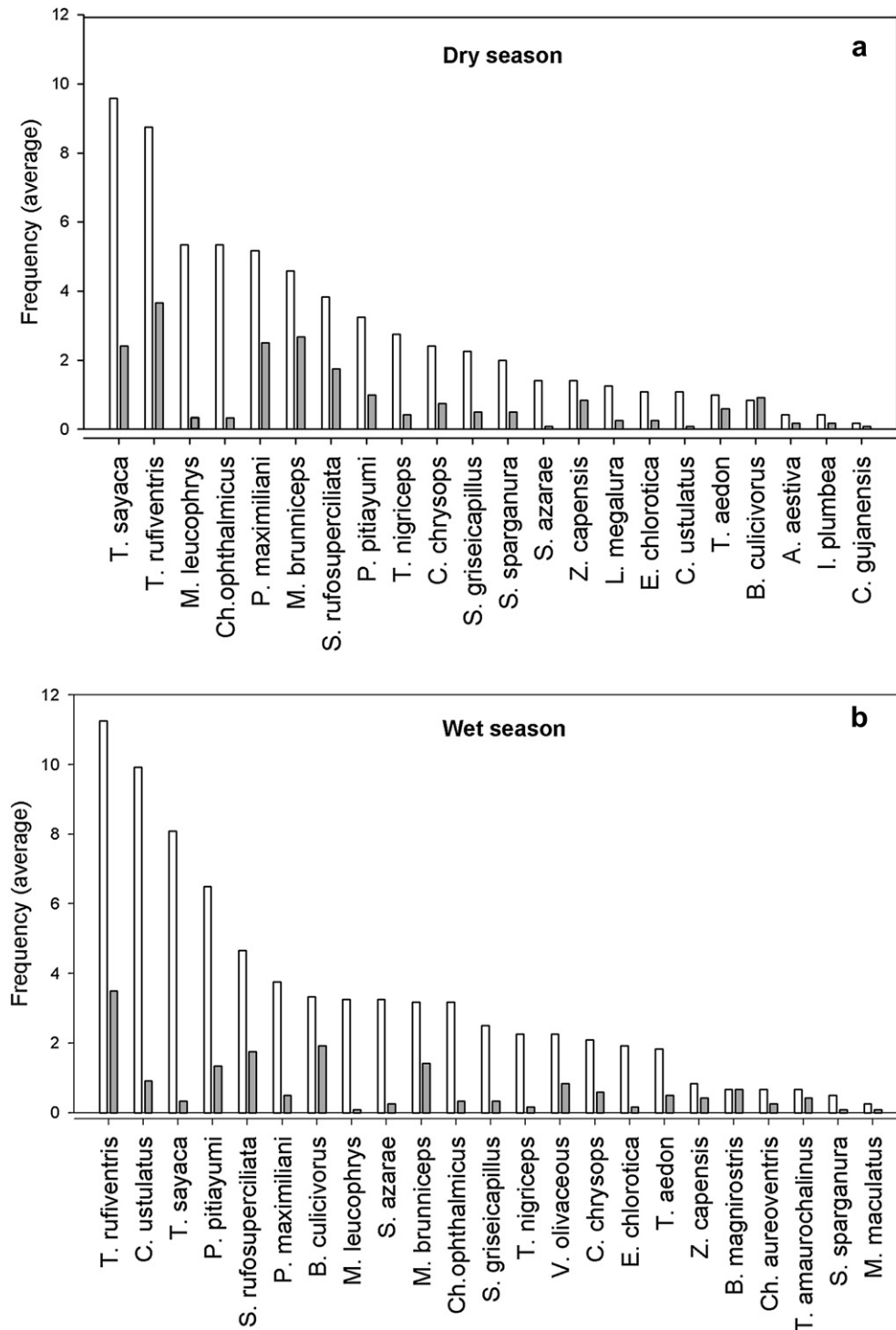


Fig. 6. Average frequency, between all study sites of the same forest type, of shared species between native (empty bars) and invaded forest plots (grey bars). a) Dry season. b) Wet season.

do not provide sufficient vertical structure and complexity for birds (see also Díaz et al., 2005; Díaz, 2006; Zurita et al., 2006). Poor forest structure translates into lower perch availability and nesting sites, and birds may only visit these forests occasionally but not spend much time there. Consistent with this explanation, we observed more frugivory events on isolated *Ligustrum* trees within native forests than in *Ligustrum* dominated forests (fruits were available in both forest types but less abundant in native forests;

Ayup, pers. obs.). These results may also be influenced by patchy foraging by frugivores in relation to the spatial distribution of fruits (Saracco et al., 2004; Blendinger et al., 2012). A more detailed analysis of the resources available to frugivores both in the understory and the canopy is needed to elucidate these patterns.

The NMDS ordination of study sites showed clear patterns of bird community composition in relation to elevation, forest type and season; and less seasonal variation among native dominated

forests than among invaded ones (Fig. 5). The larger seasonal variation in avian communities in *Ligustrum* forests contradicted our expectations – due to the evergreen nature of this forest type we expected to find more stable environmental conditions. On the contrary, our results suggest that higher plant diversity in the native forest understory contributes more than canopy phenology to the buffering of environmental conditions.

We found that the avian community of invaded forests is almost exclusively composed by common species such as *T. rufiventris*, *T. sayaca*, *S. rufosuperciliata* and *M. bruniceps*. No bird species was exclusive of invaded forests, while the species exclusive to native forests were mostly those that prefer the complex understory and canopy of mature forests, such as *P. melanonota*, *Cyclaris gujanensis* and *Poospiza erithrophys* among others (M. Rougés, pers.com). More intensive and spatially extensive bird sampling could expand the list of species that occasionally use *Ligustrum* forests but it is clear that, at equal sampling effort, local diversity is much lower than in native forests. Similarly, Zurita and Zuleta (2009) found that most forest-dependent birds were only found in native forests rather than in pine plantations. In addition, most migratory birds (e.g., *Myiodynastes maculatus* and *Vireo olivaceus*) were rarely, if ever, seen in invaded forests during this study. Consequently, the expected expansion of *Ligustrum* in the Yungas may negatively affect regional bird species richness reducing avian community composition to the most common species.

Ligustrum could also be influencing other components of the biota (Callaway et al., 2004; Wolfe and Klironomos, 2005) with overall consequences for ecosystem functioning. Analysis of the effects of *Ligustrum* invasion on other taxonomic groups as well as on ecosystems processes, such as nutrient and energy cycles, productivity and carbon sequestration, are therefore a priority for future studies. *Ligustrum lucidum* provides an example of how an invasive monodominant canopy tree can create a chain of ecological changes that cascade into different biotic communities. These changes are likely to accelerate during the coming decades in the subtropical montane forests of Argentina. Given that monodominant exotic trees are a common feature of many novel ecosystems, the processes here observed may be representative of other situations around the world.

Acknowledgments

We thank the authorities of *Parque Biológico Sierra de San Javier* for granting permits to conduct this study. This research was supported by the Agencia Nacional de Promoción Científica y Tecnológica (FONCYT), Consejo de Investigaciones de la Universidad Nacional de Tucumán (CIUNT), Rufford Small Grant (8204-2), and the Argentine National Research Council (CONICET). We also want to thank Gonzalo Quiroga Toledo for his support and selfless help, Eugenia Moyano Wagner, Daniela Gómez, Rodrigo Araújo and Horacio Politi for field assistance; Gustavo Zurita, Pedro Blendinger, members of the Bird Ecology Lab. at IER, Jorge Gutierrez, Tomas Easdale and two anonymous reviewers for their constructive comments and criticisms.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2013.03.006>.

References

- Aleixo, A., 1999. Effects of selective logging on a bird community in the Brazilian Atlantic Forest. *Condor* 101 (3), 537–548.
- Aragón, R., 2000. Especies exóticas como recursos para las aves en bosques secundarios de las Yungas. In: Grau, H.R., Aragón, R. (Eds.), *Ecología de árboles exóticos en las Yungas argentinas*. LIEY, Tucumán, Argentina, pp. 21–35.
- Aragón, R., Groom, M., 2003. Invasion by *Ligustrum lucidum* (Oleaceae) in NW Argentina: early stage characteristics in different habitats types. *Rev. Biol. Trop.* 51, 59–70.
- Aragón, R., Morales, J.M., 2003. Species composition and invasion in NW Argentinean secondary forests: effects of land use history, environment and landscape. *J. Veg. Sci.* 14, 195–204.
- Blendinger, P., Álvarez, M.E., 2009. Aves de la Selva Pedemontana de las Yungas australes. In: Brown, D.A., Blendinger, P., Lomáscolo, T., García Bes, P. (Eds.), *Selva Pedemontana de las Yungas. Historia natural, ecología y manejo de un ecosistema en peligro*. Ediciones del Subtrópico (Fundación ProYungas), Tucumán, Argentina, pp. 233–272.
- Blendinger, P.G., Ruggera, R.A., Núñez Montellano, M.G., Macchi, L., Zelaya, P.V., Álvarez, M.E., Martín, E., Osinaga Acosta, O., Sánchez, R., Haedo, J., 2012. Fine-tuning the fruit-tracking hypothesis: spatiotemporal links between fruit availability and fruit consumption by birds in Andean mountain forests. *J. Anim. Ecol.* <http://dx.doi.org/10.1111/j.1365-2656.2012.02011.x>.
- Boyce, R.L., Durtche, R.D., Fuga, S.L., 2011. Impact of the invasive shrub *Lonicera maackii* on stand transpiration and ecosystem hydrology in a wetland forest. *Biol. Invasions*. <http://dx.doi.org/10.1007/s10530-011-0108-6>.
- Brown, A.D., Grau, H.R., Malizia, L.R., Grau, A., 2001. Argentina. In: Kappelle, M., Brown, A.D. (Eds.), *Bosques nublados del Neotrópico*. Instituto Nacional de Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica, pp. 623–659.
- Cabrera, A.L., 1976. Regiones fitogeográficas argentinas. In: Kugler, W.F. (Ed.), *Enciclopedia argentina de agricultura y jardinería II*. ACME, Buenos Aires, Argentina, pp. 1–85.
- Calder, I., Dye, P., 2001. Hydrological Impacts of Invasive Alien Plants. Department of Water Affairs and Forestry. The Working for Water Programme: Annual Report 1996/97. In: Land Use and Water Resources Research 1. Department of Water Affairs and Forestry, Pretoria.
- Callaway, M.R., Thelen, G.C., Rodriguez, A., Holben, W.E., 2004. Soil biota and exotic plant invasion. *Nature* 427, 731–733.
- Clarke, K.R., Warwick, R.M., 2001. Change in Marine Communities: an Approach to Statistical Analysis and Interpretation. Primer ed. Ltd, Plymouth.
- Cueto, V.R., López de Casenave, J., 1999. Determinants of bird species richness: role of climate and vegetation structure at a regional scale. *J. Biogeogr.* 26, 487–492.
- D'Antonio, C., Vitousek, P., 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Syst.* 23, 63–87.
- Dascanio, L.M., Barrera, M.D., Frangi, J.L., 1994. Biomass structure and dry matter dynamics of subtropical alluvial and exotic *Ligustrum* forests at the Rio de la Plata, Argentina. *Vegetatio* 115, 61–76.
- Davis, M.A., Grime, J.P., Thompson, K., 2000. Fluctuating resources in plant communities: a general theory of invasibility. *J. Ecol.* 88, 528–534.
- Di Giacomo, A.S., 2005. Áreas importantes para la conservación de las aves en Argentina. Sitios prioritarios para la conservación de la biodiversidad. In: Di Giacomo, S.D. (Ed.), *Temas de naturaleza y conservación No. 5. Aves Argentinas/Asociación Ornitológica del Plata*, Buenos Aires, Argentina, pp. 211–213.
- Díaz, L., 2006. Influences of forest type and forest structure on bird communities in oak and pine woodlands in Spain. *For. Ecol. Manage.* 223, 54–65.
- Díaz, I.A., Armesto, J.J., Reid, S., Sieving, K.E., Willson, M.F., 2005. Linking forest structure and composition: avian diversity in successional forests of Chiloé Island, Chile. *Biol. Conserv.* 123, 91–101.
- Dogra, K.S., Sood, S.K., Dobhal, P.K., Sharma, S., 2010. Alien plant invasion and their impact on indigenous species diversity at global scale: a review. *J. Ecol. Nat. Environ.* 2, 175–186.
- Easdale, T.A., Healey, J.R., Grau, H.R., Malizia, A., 2007. Tree life histories in a montane subtropical forest: species differ independently by shade-tolerance, turnover rate and substrate preference. *J. Ecol.* 95, 1234–1249. <http://dx.doi.org/10.1111/j.1365-2745.2007.01290.x>.
- Ehrenfeld, J.G., 2010. Ecosystem consequences of biological invasions. *Ann. Rev. Ecol. Syst.* 41, 59–80.
- Giannini, N.P., 1999. Selection of diet and elevation of two sympatric species of *Sturnira* in an Andean rainforest. *J. Mammal.* 80, 1186–1195.
- Gordon, D.R., 1998. Effects of invasive, non-indigenous plant species on ecosystem processes: lessons from Florida. *Ecol. Appl.* 8 (4), 975–989.
- Grau, H.R., Aragón, R., 2000. Ecología de los árboles invasores de La Sierra de San Javier. In: Grau, H.R., Aragón, R. (Eds.), *Árboles exóticos de las Yungas argentinas*. LIEY-UNT, Tucumán, Argentina, pp. 5–20.
- Grau, H.R., Arturi, M.F., Brown, A.D., Aceñolaza, P.G., 1997. Floristic and structural patterns along a chronosequence of secondary forest succession in Argentinean subtropical montane forests. *For. Ecol. Manage.* 95, 161–171.
- Grau, H.R., Gasparri, N.I., Morales, M.M., Grau, A., Araoz, E., Carilla, J., Gutiérrez, J., 2007. Regeneración ambiental en el Noroeste Argentino. *Ciencia Hoy* 17, 42–55.
- Grau, H.R., Hernández, M.E., Gutiérrez, J., Gasparri, N.I., Casavecchia, M.C., Flores, E.E., Paolini, L., 2008. A peri-urban neotropical forest transition and its consequences for environmental services. *Ecol. Soc.* 13 (1), 35.
- Grau, H.R., Paolini, L., Malizia, A., Carilla, J., 2010. Distribución, estructura y dinámica de los bosques de la sierra de San Javier (Tucumán, Argentina). In: Grau, H.R. (Ed.), *Ecología de una interfase natural-urbana. La Sierra de San Javier y el Gran San Miguel de Tucumán*. Edunt, Tucumán, Argentina, pp. 33–50.
- Hunzinger, H., 1997. Hydrology of montane forests in the Sierra de San Javier, Tucumán, Argentina. *Mount. Res. Dev.* 17, 299–308.

- Karr, J.R., Freemark, K.E., 1983. Habitat selection and environmental gradients: dynamics in the "stable" tropics. *Ecology* 64 (148), 1–1494.
- Lichstein, J.W., 2007. Multiple regression on distance matrices: a multivariate spatial analysis tool. *Plant Ecol.* 188 (2), 117–131.
- Lichstein, J.W., Grau, R., Aragón, R., 2004. Recruitment limitation in secondary forests dominated by an exotic tree. *J. Veg. Sci.* 15, 721–728.
- McCune, B., Mefford, M.J., 2006. PC-ORD, Multivariate Analysis of Ecological Data. version 5. MjM Software, Gleneden Beach, Oregon.
- McKinney, A.M., Goodell, K., 2010. Shading by invasive shrub reduces seed production and pollinator services in a native herb. *Biol. Invasions* 12, 2751–2763.
- Montaldo, N.H., 1993. Avian dispersal and reproductive success of two species of *Ligustrum* (Oleaceae) in a subtropical forest relict in Argentina. *Rev. Chil. Hist. Nat.* 66, 75–85.
- Mostacedo, B., Fredericksen, T., 2000. Manual de métodos básicos de muestreo y análisis en ecología vegetal. Proyecto BOLFOR, Santa Cruz, Bolivia.
- Nagendra, H., 2002. Opposite trends in response for the Shannon and Simpson indices of landscape diversity. *Appl. Geogr.* 22, 175–186.
- Navarro, C.L., Brandan, Z.J., Marigliano, N.L., 2007. Lista comentada de las aves de un fragmento de la Reserva Provincial La Florida, Tucumán, Argentina. *Acta Zool. Lilloana* 51 (2), 142–150.
- Numa, C., Verdú, J.R., Sánchez, A., Galante, E., 2009. Effect of landscape structure on the spatial distribution of Mediterranean dung beetle diversity. *Div. Distrib.* 15, 489–501.
- Powell, K.I., Chase, J.M., Knight, T.M., 2011. A synthesis of plant invasion effects on biodiversity across spatial scales. *Am. J. Bot.* 98, 539–548.
- Proença, V., Pereira, H.M., Vicente, L., 2010. Plant and bird diversity in natural forests and in native and exotic plantations in NW Portugal. *Acta Oecol.* 36 (2), 219–226.
- Ramírez, A., 2000. Utilidad de las aves como indicadores de la riqueza específica regional de otros taxones. *Ardeola* 47 (2), 221–226.
- Rascher, K., Grobe-Stoltenberg, A., Maguás, C., Werner, C., 2011. Understorey invasion by *Acacia longifolia* alters the water balance and carbon gain of a mediterranean pine forest. *Ecosystem* 14, 904–919.
- Rodewald, A.D., 2012. Spreading messages about invasives. *Div. Distrib.* 18, 97–99.
- Rodewald, A.D., Shustack, D.P., Hitchcock, L.E., 2010. Exotic shrubs as ephemeral ecological traps for nesting birds. *Biol. Invasions* 12, 33–39.
- Rougés, M., Blake, J., 2001. Tasas de captura y dietas de aves del sotobosque en el Parque Biológico Sierra de San Javier, Tucumán. *Hornero* 16 (1), 7–15.
- Saracco, J.F., Collazo, J.A., Groom, M.J., 2004. How do frugivores track resources? Insights from spatial analyses of bird foraging in a tropical forest. *Oecologia* 139, 235–245.
- Verdú, J.R., Moreno, C.E., Sánchez-Rojas, G., Numa, C., Galante, E., Halfpeter, G., 2007. Grazing promotes dung beetle diversity in the xeric landscape of a Mexican Biosph. Reserve. *Biol. Conserv.* 140, 308–317.
- Verdú, J.R., Numa, C., Hernández-Cuna, O., 2011. The influence of landscape structure on ants and dung beetles diversity in a Mediterranean savanna-forest ecosystem. *Ecol. Indic.* 11, 831–839.
- Wolfe, B.E., Klironomos, J.N., 2005. Breaking new ground: soil communities and exotic plant invasion. *Bioscience* 55, 477–487.
- Zurita, G.A., Zuleta, G.A., 2009. Bird use of logging gaps in a subtropical mountain forest: the influence of habitat structure and resource abundance in the Yungas of Argentina. *For. Ecol. Manag.* 257, 271–279.
- Zurita, G.A., Rey, N., Varela, D.M., Villagra, M., Bellocq, M.I., 2006. Conversion of the Atlantic Forest into native and exotic tree plantations: effects on bird communities from the local and regional perspectives. *For. Ecol. Manage.* 235, 164–173.