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“INSECTIVORÍA EN PLANTACIONES AGROFORESTALES”

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en cumplimiento parcial de los requisitos
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INFORME DE APROBACIÓN SEMINARIO DE TÍTULO

Se informa a la Escuela de Pregrado de la Facultad de Ciencias de la Universidad de Chile que el Seminario de Título, presentado por el Sr. Tomás Javier Poch Velasco,

“INSECTIVORÍA EN PLANTACIONES AGROFORESTALES”

ha sido aprobado por la Comisión de Evaluación, en cumplimiento parcial de los requisitos para optar al Título de Biólogo con Mención en Medio Ambiente.

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Firma manuscrita de Javier A. Simonetti sobre una línea horizontal.

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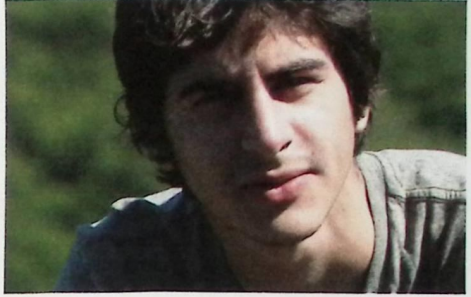
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RESUMEN BIOGRÁFICO

Nací en Santiago, el año 1988. He tenido la suerte de que, desde pequeño, mis padres me fueron mostrando lo diversa y sorprendente que puede ser la naturaleza, especialmente al pasar esos innumerables



fin de semana y vacaciones en el campo, lejos de la ciudad. Con los años mi interés por ella fue cada vez mayor, y ahora puedo decir que he (iniciado) mis estudios sobre lo que me apasiona y que, con algo de optimismo, dedicaré mi carrera profesional a la conservación de diversidad biológica.

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INTRODUCCIÓN GENERAL

La expansión de los sistemas de cultivo ha sido la fuente primaria del incremento de producción silvoagropecuaria en los últimos 40 años. Hacia el año 2000, aproximadamente el 24% de la superficie continental se había convertido en sistemas cultivados, y cerca de 3,5% de la cobertura global de bosques correspondían a plantaciones forestales comerciales (Millennium Ecosystem Assessment 2005). En general, el establecimiento de plantaciones agroforestales conlleva la pérdida de grandes extensiones de bosques nativos, incrementando las amenazas sobre la diversidad biológica. En este marco, el uso de áreas silvestres protegidas es el principal instrumento a nivel internacional para revertir las continuas pérdidas en biodiversidad generadas por cambios en el uso de suelos. Sin embargo, a pesar de que son necesarias, son insuficientes para conservar por sí solas la diversidad biológica (Mora & Sale 2011). En este sentido, el uso de ambientes seminaturales y productivos para tales propósitos es una necesidad creciente (Daily 2001).

Los sistemas agroforestales han sido comúnmente considerados como “desiertos biológicos”, pues por lo general son estructuralmente más simples que los bosques naturales y contienen una menor diversidad biológica (Hartley 2002). Sin embargo, las plantaciones forestales podrían sostener parte de la diversidad biológica nativa del bosque nativo original si son estructuralmente complejas, actuando como hábitat complementario para diversas especies (Hartley 2002, Brockerhoff et al. 2008). En términos productivos, la diversidad biológica presente en los sistemas agroforestales podría prestar servicios ecosistémicos a las plantaciones, con lo cual se transformaría en

un aliciente para favorecer la conservación fuera de las áreas protegidas (Simonetti 2006). Entre estos servicios, el control biológico provisto por especies insectívoras es uno económicamente valorable (Costanza et al. 1997). Las aves disminuyen la magnitud de la herbivoría y aumentan la productividad vegetal mediante la reducción en abundancia de insectos herbívoros (Marquis & Whelan 1994, Van Bael et al. 2003). La prestación de este servicio por la biodiversidad presente en los sistemas agroforestales sería un motivo para promover el manejo sustentable de las plantaciones forestales, y mantener la diversidad biológica en ellas. En este contexto, en este Seminario de Título analizo si los servicios directos de reducción poblacional de insectos y el efecto que ello tendría sobre la magnitud de la insectivoría y la productividad primaria, provistos por especies insectívoras, efectivamente se prestan en las plantaciones agroforestales, comparándolos con su magnitud en sistemas naturales.

Por otra parte, las plantaciones estructuralmente complejas contienen una mayor diversidad de especies de mamíferos y aves que aquellas estructuralmente simples (Nájera & Simonetti 2010, Ramírez & Simonetti 2011). Si la intensidad de insectivoría en las plantaciones, y con ello sus efectos sobre la productividad, se correlaciona con la riqueza y abundancia de especies insectívoras en ellas, se esperaría que la insectivoría fuera mayor en las plantaciones estructuralmente complejas. Así, en este Seminario de Título, además contraste experimentalmente la hipótesis que la insectivoría varía en función de la complejidad estructural.

Los resultados del meta-análisis y del experimento manipulativo permiten determinar la importancia de la biodiversidad en plantaciones y con ello ofrecen un fundamento que permita conservar biodiversidad en sistemas agroforestales, de acuerdo

a los compromisos que se plantean en las metas Aichi, como parte de los objetivos internacionales del Plan Estratégico para la Diversidad Biológica, con el que planea proteger la biodiversidad en sistemas productivos e incrementar sus beneficios para la sociedad (Convención sobre la Diversidad Biológica 2010). Así, en este Seminario ofrezco evidencia en favor de conservar biodiversidad en sistemas productivos como complemento a la conservación en áreas protegidas.

CAPÍTULO 1. ECOSYSTEM SERVICES IN HUMAN-DOMINATED LANDSCAPES: INSECTIVORY IN AGROFORESTRY SYSTEMS

RESUMEN

A pesar de ser estructuralmente más simples y empobrecidas en especies que los bosques nativos, las plantaciones agroforestales pueden actuar como hábitat secundario para especies nativas y sostener algo de biodiversidad. Esta biota puede prestar servicios ecosistémicos como la insectivoría, beneficiando indirectamente a las plantas al reducir la herbivoría e incrementar la productividad, mediante la reducción en abundancia de herbívoros. La prestación de estos servicios podría presentarse en sistemas agroforestales, y en igual intensidad que en ambientes naturales, sin embargo, aún no se ha evaluado si el efecto directo de los insectívoros sobre la abundancia de insectos e indirecto sobre las plantas difiere entre ambientes naturales y agroforestales de acuerdo a factores como región climática, tipo de insectívoro, grupo trófico del artrópodo depredado y tiempo. En este Seminario se evaluó mediante un meta-análisis la provisión de servicios ecosistémicos por insectivoría en sistemas agroforestales comparado con sistemas naturales, contrastándolo con los factores antes mencionados. En general, los resultados sugieren que las especies insectívoras reducen la abundancia de artrópodos y la herbivoría en las plantas, e incrementan la productividad. La magnitud y dirección de estos efectos no difiere entre ambientes agroforestales y naturales, y tampoco lo hacen entre distintas regiones climáticas, tipo de insectívoros, grupos tróficos de artrópodos depredados y duración del experimento. Los efectos sobre la productividad pueden

variar en base a la variable usada para medir productividad. Nuestros resultados evidencian la provisión de servicios por la biodiversidad presente en las plantaciones, independiente de los factores que podrían modularla. Así, beneficiando la biodiversidad en ellas podría representar un escenario ganar-ganar.

ABSTRACT

Despite of being structurally simpler and species-impooverished as compared to natural forests, agroforestry plantations can act as a secondary habitat for native species and sustain some biodiversity. Biodiversity can provide ecosystem services such as insectivory, indirectly benefiting plant through the reduction of herbivory and increasing productivity, by diminishing herbivorous abundance. The lending of these services could occur in agroforestry systems, and in the same magnitude that in natural environments, however it has not yet been assessed whether the direct effect of insectivores over insects and indirect effect on plants differ between natural and agroforestry environments depending on modulating factors such as climatic region, type of insectivore, preyed arthropod trophic group and treatment length. In this Seminar it was assessed through a meta-analysis the provision of ecosystem services by insectivory in agroforestry systems compared to natural systems, contrasting it with the modulating factors mentioned. In general, insectivorous species reduced arthropod abundance and plant herbivory, and increased the productivity. The magnitude and direction of these effects did not differ between natural and agroforestry systems, and neither did between different climatic regions, type of insectivore, preyed arthropod trophic groups nor

experiment length. The effect of insectivores on productivity can vary based on the variable used to measure productivity. Our results evidence the provision of services by the biodiversity present in plantations, independently of factors that could modulate it. This way, enhancing biodiversity within plantations could represent a win-win scenario.

1.1 INTRODUCTION

Agroforestry systems are usually simpler in structure and relatively homogeneous in species composition compared to native forests. On these grounds, they are expected to support an impoverished suite of species (Allen et al. 1995; Hartley 2002). However, increasing evidence suggests that agroforestry systems can contribute to biodiversity conservation, acting as complementary habitat for native species, offering favorable conditions for their establishment, especially in degraded and deforested areas (reviewed in Hartley 2002; Lindenmayer & Hobbs 2004; Simonetti et al. 2012). The occurrence of native species in plantations might enable interspecies interactions and processes offering ecosystem services within agroforestry systems (Simonetti et al. 2006). Biological control provided by insectivores is considered an ecosystem service that offers benefits to human populations, and is an economically valuable service as could enhance productivity in plantations (Costanza et al. 1999). For instance, pest control services attributable just to insects is estimated to save US\$4.5 billion per year in agricultural crops only in the US, according to estimations based on the crop losses to herbivorous insects and expenditures on insecticides (Losey & Vaughan 2006).

Insectivorous species, especially birds, trigger trophic cascades on plants, mediated through changes in the abundance of herbivorous arthropods. Such a reduction could be as strong in agroforestry as well as in natural systems (Schmitz et al. 2000; Van Bael et al. 2008; Mooney et al. 2010; Mäntyllä et al. 2011). However, it has not yet been assessed if these direct effect on insects and indirect effect on plants do translate into modulating services and if these differ between natural and agroforestry environments according to factors such as the type of predators, climatic region, type of arthropods preyed upon and time. Here, through a meta-analysis, we assessed the effect of insectivorous species in the provision of biological control services in agroforestry systems as compared to natural systems. We analyzed the magnitude, both for the direct effects on arthropod abundance as well as for the indirect effects upon herbivory and productivity. If productivity is positively affected by the presence of insectivores in plantations, this fact might provide a rationale to enhance its conservation in productive agroecosystems. Mäntyllä et al. (2011) analyzed if trophic cascades varied between main climate types (tropical, temperate and boreal), but the provision of services could differ in response based on differences of temperature and precipitation (e.g. Van Bael & Brown 2005; Schwenk et al. 2010; Garibaldi et al. 2010), conditions that vary even within the main climates reviewed by Mäntyllä et al. (2011), according to the Köppen-Geiger climate classification (Kottek et al. 2006). On the other hand, the strength of trophic cascades might also differ pending on the type of insectivore, be it birds, lizards, ants or the group of insectivorous arthropods in general (Schmitz et al. 2000). We also assessed if the predator pressure of insectivores differ over herbivorous and predator arthropods and if the detection of effects were affected by the duration of the study. It

could be possible that either the effects expressed immediately, or the response be delayed due to community dynamics (e.g. González 2000). Enhancing the maintenance of biodiversity in plantations by incrementing their structural complexity (Nájera & Simonetti 2010; Ramírez & Simonetti 2011), would benefit as well the plantations' revenue. Although structural complexity provided by a well-developed undergrowth vegetation could reduce the plantations yield due to competition for resources, if birds or other insect predators harbored in plantations and reduced herbivory, and hence operational costs, biodiversity-friendly plantations might maintain similar, or even increased, levels of revenue (see Hartley 2002). In this way, favoring biodiversity in plantations might represent a win-win scenario, bringing socio-economic benefits at the same time that contributes to biological conservation, in systems that otherwise would have small auxiliary value for biological diversity (see Rosenzweig 2003, de Groot et al. 2010).

1.2 METHODS

A directed search for scientific publications was performed in the ISI Web of Knowledge and EBSCOhost databases using combinations of the search terms "insectivor*", "primary product*" and "trophic cascade". We only considered publications explicitly studying at least one of the following variables: arthropod abundance, plant herbivory and plant productivity. To examine the effects of predation upon arthropods we included only studies comparing scenarios through experimental manipulations (exclusion or enclosure) of natural predators. We also searched for the

literature used in previous meta-analysis of cascading effects in terrestrial systems, and incorporated the additional articles that were not retrieved through the database search.

We considered studies conducted all over the world in both natural and agroforestry environments. Studies that took place in productive plantations, as well as noncommercial plantations and city parks or gardens, were placed under the category agroforestry system. Each study case was classified under a climatic region in which the study site is located, based on the Köppen-Geiger climate classification (Kottek et al. 2006). We also recorded the nature of the insectivore subject to exclusion or enclosure treatments (birds, lizards, arthropods; the latter including ants, spiders and others), the trophic group of the preyed arthropod in the arthropod abundance surveys, classified as predators or herbivores, and the length of the experiment. Further, we assessed plant productivity as total biomass, shoot extension and basal area to assess differences between variables in response to insect predation.

To assess the effect of predators upon insect abundance, herbivory and plant productivity, only studies reporting on mean, standard deviation or standard error, and sample sizes were used and analyzed through Hedge's d statistic (Rosenberg et al. 2000). This parametric test measures the unbiased standardized mean difference between the treatment and control group means, using this estimate as a measure for effect size of the treatment (Rosenberg et al. 2000). When only standard error was presented as the dispersion measure, the standard deviation was calculated by multiplying the standard error by \sqrt{n} . Confidence intervals (CI) of effect sizes were estimated from effect sizes and their variance by bootstrapping (4999 iterations), and P -

0.67) used on the assessment of overall effect sizes. Rosenthal's fail-safe number also

values were estimated by using a randomized effect categorical model, as we cannot assume there is one true effect size shared by all studies. Heterogeneity of the effect size within variables was examined using the Q -statistics. This test is analogous to an ANOVA, testing whether the variance of effect sizes is greater than expected by chance alone (Rosenberg et al. 2000). Only study cases that provided information about the grouping factors within the variables of abundance, herbivory or plant productivity were used in heterogeneity tests. As Hedge's standardized mean difference performs well for $n \geq 5$, any grouping factor with $n < 5$ were excluded from the heterogeneity analysis. Publication bias was assessed through Spearman rank correlation test and Rosenthal's fail-safe number. The meta-analysis and related tests were performed using the meta-analytic software MetaWin 2.0 (Rosenberg et al. 2000).

1.3 RESULTS

A total of 292 published papers were retrieved from the databases and references search. However, only 40 reported quantitative information satisfying our search criteria, comprising 283 independent study cases: 168 for arthropod abundance (from 33 articles), 81 for plant herbivory (from 25 articles) and 34 for primary productivity (from 15 articles). Publications included both natural and agroforestry environments over ten different climate systems, in a total of 16 countries (Table 1). No publication bias was detected, either for arthropod abundance (Spearman $r_s = 0.06$, $P = 0.40$), plant herbivory (Spearman $r_s = 0.06$, $P = 0.59$), nor plant productivity data (Spearman $r_s = -0.07$, $P = 0.67$) used on the assessment of overall effect sizes. Rosenthal's fail-safe number also

suggested no bias among study cases. At least 17554 non-significant study cases for arthropod abundance, 4462 for herbivory and 63 for plant productivity would be needed to be added to the analysis to change results from significant to non-significant.

1.3.1 *Arthropod abundance*

The presence of insectivorous species significantly reduced arthropod abundance, in both, native and agroforestry systems. No significant difference exists in the effect size between these two environments (heterogeneity test, $Q_{\text{between}} = 0.19$, $P = 0.65$; Fig. 1). Heterogeneity analysis revealed no significant differences either between types of climate, insectivores, trophic groups of preyed arthropods nor treatment lengths ($Q_{\text{between}} < 9.6$, $P > 0.05$ in all cases). There was a significant effect size for all climatic regions assessed, groups of insectivores, prey arthropod trophic group and length of experiment, with exception of the third year from the beginning of the treatment.

Assessing climate region, type of insectivore, trophic group of preyed arthropods and experiment length according to natural and agroforestry environments separately, no heterogeneity was found within climate region, preyed arthropod trophic group and experiment length, in natural as well as in agroforestry systems ($Q_{\text{between}} < 6.6$, $P > 0.05$ in all six cases). Natural and agroforestry environments only differed in response for the type of insectivore, as in natural systems no difference existed between birds and predaceous arthropods ($Q_{\text{between}} = 1.6$, $P = 0.02$), while in agroecosystems birds effects were significantly larger than ants effects ($Q_{\text{between}} = 5.1$, $P = 0.03$; data not shown).

Table 1. Number of publications and study cases per environment type and climatic region used in the meta-analysis. Climatic regions are presented by the names of the Köppen-Gieger climatic classifications, shown in parenthesis.

<i>Study site environment & climate</i>	<i>No. of publications</i>	<i>No. of cases</i>
Environment		
Natural	27	214
Agricultural	14	69
Climatic regions		
Monsoon (Am)	3	13
Tropical Rainforest (Af)	4	15
Savanna (Aw)	8	47
Steppe (BSk)	6	69
Humid subtropical (Cfa)	7	30
Oceanic (Cfb)	2	14
Hot-summer Mediterranean (Csa)	1	2
Warm-summer Mediterranean (Csb)	2	7
Warm-summer Continental (Dfb)	4	43
Boreal (Dfc)	4	41

1.3.3 Plant productivity

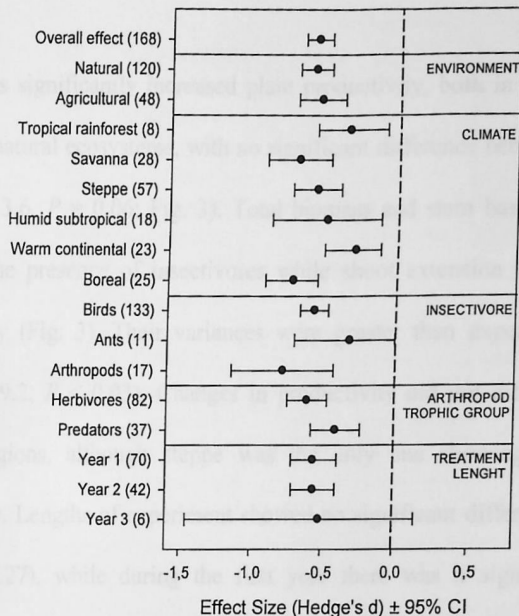


Figure 1. Hedge's *d* mean effect sizes \pm 95% CI of insectivorous species presence on arthropod abundance. Sample sizes are shown in parenthesis. Groups within categories with sample size lower than 5 studies were excluded. The vertical dashed line indicates the 0 value. Effects are significantly positive or negative when the 95% CI of effect sizes do not include 0.

1.3.2 Plant herbivory

Insectivores significantly reduced plant herbivory (Fig. 2). Agroforestry and natural systems did not differ in effect size on damage to plants through herbivory ($Q_{\text{between}} = 0.51$, $P = 0.48$). There were not significant variability of effects sizes within climates ($Q_{\text{between}} = 12.1$, $P = 0.07$). Birds were the only insectivores that had a significant effect decreasing herbivory. Effect sizes were not significantly different between types of insectivores or length of the experiment ($Q_{\text{between}} < 4.9$, $P > 0.1$ in both cases).

1.3.3 Plant productivity

Insectivores significantly increased plant productivity, both in agroforestry systems as well as in natural ecosystems, with no significant difference between both environments ($Q_{\text{between}} = 3.6$, $P = 0.06$; Fig. 3). Total biomass and stem basal area are significantly larger in the presence of insectivores while shoot extension tended to decrease, not significantly (Fig. 3). Their variances were greater than expected by sampling error ($Q_{\text{between}} = 9.2$, $P < 0.03$). Changes in productivity did not differ significantly across climatic regions, although steppe was the only one showing significant increased productivity. Lengths of experiment showed no significant differences either ($Q_{\text{between}} = 1.2$, $P = 0.27$), while during the first year there was a significantly greater plant productivity. Almost all study cases reviewed the effect insectivorous birds had upon plants ($n = 30$), but only one studied the effect of insectivorous ants, one of spiders', one of parasitoids' and one of insectivorous arthropods' in general, precluding to contrast their potential different effects.

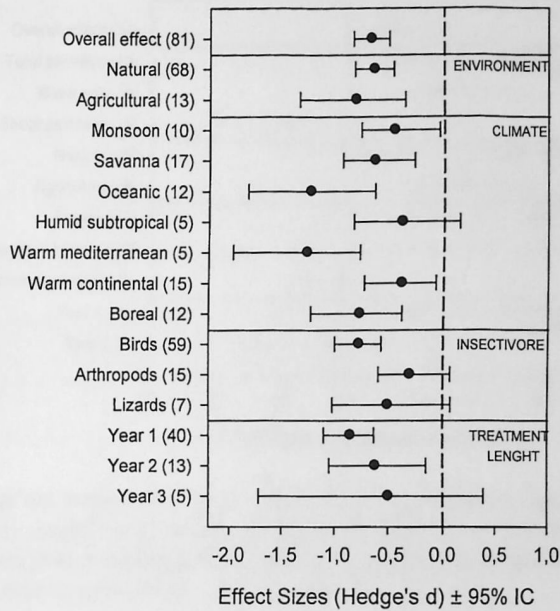


Figure 2. Hedge's d mean effect sizes \pm 95% CI of insectivorous species presence on plant herbivory. Sample sizes are shown in parenthesis. Groups within categories with sample size lower than 5 studies were excluded. Interpretation of graph is equal to that of figure 1.

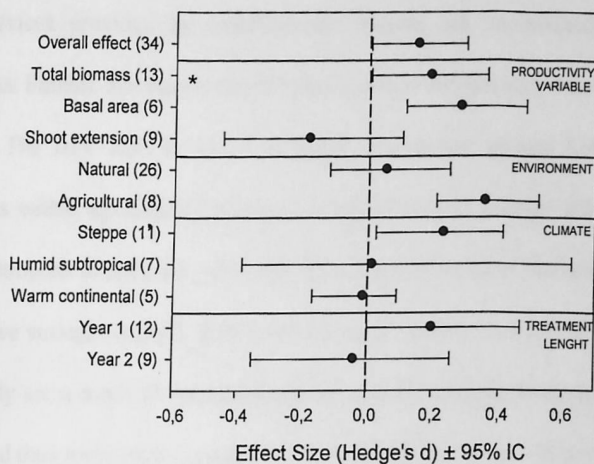


Figure 3. Hedge's *d* mean effect sizes \pm 95% CI of insectivorous species presence on plant productivity. Sample sizes are shown in parenthesis. Groups within categories with sample size lower than 5 studies were excluded. Interpretation of graph is equal to that of figure 1. * = heterogeneity test, Q_{between} significant at $P < 0.05$.

1.4 DISCUSSION

Despite agroforestry systems are considered impoverished ecosystems, unfriendly to native species, they do sustain biodiversity under certain conditions (Nájera & Simonetti 2010; Ramírez & Simonetti 2011), and the biodiversity they support can provide useful ecosystem services, such as reducing the abundance of herbivorous insects, reducing herbivory damage and increasing productivity. Insectivorous species significantly diminished arthropod abundance in all environments, and they cascaded down into releasing herbivore-induced damage to plants and incrementing overall plant productivity. No differences between effect size on natural and agroforestry systems,

either for arthropod abundance, plant herbivory nor plant productivity responses, suggest that the services provided by insectivorous species are maintained in productive environments. Further, the magnitude of these services did not vary between the type of insectivore. The only case in which different insectivore groups had a differential response was within agroforestry systems, where birds had a larger effect than ants at reducing arthropods abundance. Although these results support that usually vertebrate predators have stronger impacts than invertebrate predators (Schmitz et al. 2000), they most probably are a result of intraguild predation and isolated-effects masking by bird predation, and thus resulting in a conservative value for the actual effect size ants had on agroforestry systems (Perfecto et al. 2004).

Even if intraguild predation may result into depressed suppression of herbivorous arthropods (Polis & Holt 1992), these were equally preyed upon by insectivorous species than were predaceous arthropods, consistent with Mooney et al. (2010), where they assessed the effects vertebrate predators had over trophic cascades through intraguild predation. Therefore, this supports the beneficial impacts of insectivores on plants. These impacts also did not vary between climatic regions, agreeing with Mäntyllä et al. (2011), and suggesting that macroclimatic conditions of temperature and precipitation within an ecosystem may exert little effect in insectivores' beneficial effects. Arthropod abundance, herbivory and plant productivity responses were already significant at the first year since the beginning of the study, thus showing an immediate response in a yearly basis. Hence, productivity would be enhanced without having to wait to notice the effects of the presence of insectivores in agroforestry environments.

Both biomass and basal area, which may be considered key measures of plant performance, incremented in response to the presence of insectivores, while by the contrary shoot growth seemed to decrease. Greater shoot growth in exclusion of birds could be explained due to compensatory growth response to the higher levels of herbivory observed, as insects abundance was significantly diminished, or that exclusion cages protected saplings from browsing by large herbivores (Lichtenberg & Lichtenberg 2002).

Our results support that insectivorous species trigger top-down effects in agroforestry systems with the same direction and magnitude that take place in natural systems, such as tropical rainforests or shrublands. Given that biological control ecosystem services are profitable for agroforestry plantations, they ought to be managed in a way to diminish their negative impact towards biodiversity, as the biodiversity present within the plantations brings valuable societal benefits.

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CAPÍTULO 2. INSECTIVORY IN *PINUS RADIATA* PLANTATIONS WITH DIFFERENT DEGREE OF STRUCTURAL COMPLEXITY

RESUMEN

Evidencia creciente sugiere que, dependiendo de la complejidad estructural de una plantación, esta puede actuar como hábitat complementario para aves y mamíferos insectívoros. Interacciones como la insectivoría, a su vez, se ven determinadas por la riqueza y abundancia de especies en un ecosistema. Por lo tanto, la insectivoría podría variar en función de la complejidad de las plantaciones, y con ello, reducir la posibilidad de daño a las plantaciones generado por insectos herbívoros. A través de un procedimiento experimental, se midió el riesgo de mortalidad a larvas de insectos en plantaciones de pino con distinto grado de complejidad estructural, en conjunto con los niveles de herbivoría en *Aristotelia chilensis* asociados a cada plantación.

Los ataques a cuncunas artificiales fueron significativamente mayores y la herbivoría significativamente menor en plantaciones estructuralmente complejas, donde encontramos una mayor riqueza y abundancia de especies leñosas y un mayor desarrollo de sotobosque, en comparación a plantaciones simples. Estos resultados sugieren que la insectivoría sí varía en función de la complejidad estructural de plantaciones forestales, siendo mayor en aquellas con mayor diversidad de especies, mediando un efecto de cascada trófica sobre la vegetación, disminuyendo significativamente la herbivoría. Así, las plantaciones forestales deberían manejarse de manera que permitan un escenario

ganar-ganar, en donde mantener una mayor biodiversidad aumente la provisión de servicios ecosistémicos de utilidad para estas plantaciones.

ABSTRACT

Increasing evidence suggests that, depending on the structural complexity of a plantation, it can act as complementary habitat for insectivore birds and mammals. Interactions such as insectivory, in turn, have been determined by species' richness and abundance in an ecosystem. Therefore, insectivory can vary in function of the plantation's complexity, and thereby, decrease chance of plantations damage due to herbivorous insects. Through an experimental procedure, the insect larvae mortality risk in pine plantations with different degree of structural complexity were measured, together with the herbivory levels on *Aristotelia chilensis* related to each plantation.

Attacks to artificial caterpillar were significantly greater and herbivory significantly less in structurally complex plantations, where we found a higher woody species richness and abundance and a greater understory development, compared to simple plantations. These results suggest that insectivory does vary in function of the structural complexity within forestry plantations, and it is greater in those with higher species diversity, mediating a trophic cascade effect over vegetation, significantly diminishing herbivory. Therefore, forestry plantations should be managed into more structurally complex ones in order to allow a win-win scenario, where maintaining a greater biodiversity increases the provision of useful ecosystem services for these plantations.

2.1 INTRODUCTION

Agroforestry plantations are usually regarded as “biological deserts” (Allen et al. 1995; Hartley 2002). However, increasing evidence suggests that they can act as complementary habitat for birds and mammals, and therefore contribute to sustain some biodiversity (Reviewed in Hartley 2002; Nájera & Simonetti 2010; Ramírez & Simonetti 2011). Both richness and abundance of birds in forestry plantations can be the same or even higher than in native forests (e.g. Estades & Temple 1999; Vergara & Simonetti 2004; González-Gómez et al. 2006). Species richness and abundance is likely related to the structural complexity of an agroforestry system (e.g. Nájera & Simonetti 2010), including characteristics such as multiple vegetation strata, well developed understory, high vegetation diversity and native vegetation remnants (Hartley 2002; Lindenmayer & Hobbs 2004). In fact, species richness and abundance in complex agroforestry systems are larger than in structurally simple plantations, with scarcely developed understory and lower vegetation diversity (Greenberg et al. 1997; Nájera & Simonetti 2010; Ramírez & Simonetti 2011). As changes in the abundance of organisms may lead to concomitant changes in the intensity of the interactions in which they participate (Simonetti et al. 2006), ecosystem services provided by some functional groups might differ between agroforestry systems with different structural complexity.

Insectivorous species have significant effects in ecological processes, such as in herbivore-induced damage to plants (Schmitz et al. 2000). Abundance or richness of birds, or a combination of both, determines the levels of predation upon herbivorous insects (e.g. Marquis & Whelan 1994; Van Bael & Brown 1995; Philpott et al. 2009).

Insectivory indirectly decreases foliar damage through reducing the abundance of herbivorous insects, and as a result it may also benefit plant biomass productivity (see Chapter 1). If the intensity of ecosystem services is related with insectivorous species richness and abundance, it would be expected that, within commercial forestry plantations, there should be a higher insectivory in structurally complex plantations than in simpler ones, and consequently, herbivore-induced damage might be attenuated and productivity increased in structurally complex plantations. In this study, we tested this hypothesis by experimentally assessing insect mortality risk in structurally simple and complex pine (*Pinus radiata* D. Don) plantations. We also measured levels of herbivory aiming to determine whether there are noticeable trophic cascade effects on foliar damage within the forestry plantations. These assessments might unravel the implications for structural complexity on the provision of ecosystem services and the management of forestry plantations.

2.2 METHODS

2.2.1 Study site

Field work was conducted within *Pinus radiata* plantations in Tregualemu, VII Región del Maule, at the northernmost zone of the Southern temperate rainforest (35°59'19''S, 72°41'15''W). Plantations with a well-developed understory hold mainly *Aristotelia chilensis*, *Peumus boldus* and *Rubus ulmifolius*, among other species (see below).

Insectivorous birds present at the study area are mainly Thorn-tailed rayadito (*Aphrastrura spinicauda*), Des Mur's wiretail (*Sylviorthorhynchus desmursii*) and House wren (*Troglodytes aedon*; González-Gómez et al. 2006). Among largely frugivorous and granivorous bird species that could be also feeding on insect preys during reproductive season are Black-chinned Siskin (*Carduelis barbata*), White-crested Elaenia (*Elaenia albiceps*) and Austral thrush (*Turdus falckandii*; González-Gómez et al. 2006).

The study was carried out during the austral spring of 2011 (September through November), coinciding with the reproductive season of most birds (González-Gómez et al. 2006), which also matches with the built up of herbivorous insect populations and foliar development (Jaña-Prado & Grez 2004; Vásquez et al. 2007).

2.2.2 Plantations complexity

Structural complexity within plantation sites was quantitatively assessed through vegetation cover measurements. Three 40 meters-parallel transects, separated by 15 meters, were laid in each plantation site. A 1 meter radius-circular plot was established every 10 meters within each transect, where vertical plant density measurements by intersection were performed every 0.5 meters from the ground up to 3 meters high. Plantations were classified as structurally simple when woody plant density 1 m above ground was less than 0.5 individuals/m², and structurally complex when density was above 0.5 individuals/m². Vegetation diversity was computed with statistical analysis software PAST v2.15 (Hammer et al. 2001). Differences in diversity values between plantation types were assessed through a Mann-Whitney's U test.

2.2.3 Insectivory

Insect predation was experimentally assessed as birds', mammals' or arthropods' attacks upon plasticine insect larvae, as previously described by González-Gómez et al. (2006). Artificial larvae are valid surrogate of natural ones (González-Gómez et al. 2006). The use of plasticine larvae provide an estimate of relative predation levels across sites (Loiselle & Farji-Brener 2002; Howe et al. 2009), and they have been successfully used in several previous predation surveys (Loiselle & Farji-Brener 2002; González-Gómez et al. 2006; Mäntyllä et al. 2008; Howe et al. 2009). Plasticine models mimicked *Ormiscodes cinnamomea* (Feisthamel) (Lepidoptera: Saturniidae) larvae, moth feeding on *P. radiata* occurring in the study area (de Ferari & Ramírez 1998).

During late September, groups of 15 model caterpillars were placed on 20 randomly selected pine plantations sites (structurally simple plantations sites, $n = 6$; complex plantations sites, $n = 14$), following the methodology described in González-Gómez et al. (2006). Sample sizes of plantation sites represent the relative abundance of available study sites within both structural complexity types. Each group of artificial larvae was placed on a randomly selected *A. chilensis* seedling within plantation sites, at approximately 0.4 m from the ground. Seedlings were preferred over adult trees since González-Gómez et al. (2006) results suggest a greater insect predation on the former. Larvae groups simulated natural aggregations of *Ormiscodes* larvae as clumps on branches, as they naturally occur (Artigas 1994; Figure 4A). During late November, 10 artificial caterpillars were attached individually with staples on *A. chilensis* seedlings separated by at least 2 m within plantation sites (simple plantations $n = 7$; complex

plantations $n = 16$), instead of placing them in clusters. This methodology was used to increase the area covered within each plantation site. After artificial caterpillars were attached, markings left by any predator were recorded every 24 hours, until 72 hours after the beginning of the study.

The sampling unit was each plantation site. Caterpillar predation data obtained in both months were pooled, and the proportion of sites with larvae predation was estimated out of the total plantation sites for both simple and complex plantations (leading to a simple plantation sites $n = 13$; complex plantation sites $n = 30$). Differences between percentages of attacked sites were statistically assessed through z-ratio for two independent groups.

2.2.4 Herbivory

Herbivory was visually estimated as the percentage of foliar area removed in *A. chilensis* individuals (Figure 4D). This species was selected for herbivory measurements as it is abundant within the pine plantations, and it is possible to find them even in structurally simple sites. Most defoliating activity is concentrated in spring and summer and accumulated through time until the end of the growing season (Vásquez et al. 2007), so herbivory levels were assessed for leaves sampled after the end of the growing season.

During late May 2012, 2582 leaves in total were taken from several *A. chilensis* trees within structurally simple and complex plantation sites. Each leaf was assigned to a category of leaf area removed by herbivory: 0 = no damage; 1 =]0-5]%; 2 =]5-12]%; 3 =]12-25]%; 4 =]25-50]%; 5 =]50-100]% of leaf surface removed. We proceeded to

calculate an overall herbivory index (IH) for each plantation site as: $IH = \sum n_i (C_i) / N$, where i was the category of leaf area removed, n_i was the number of leaves in the i th category, C_i was the midpoint of the area removed category (i.e., $C_1 = 2.5\%$, $C_2 = 8.5\%$, $C_3 = 18.5\%$, $C_4 = 37.5\%$, $C_5 = 75\%$, respectively), and N was the total number of leaves for each plantation site (Benítez & Kossmann 1999). This method has been successfully used in herbivory measurements for *A. chilensis* in previous studies (Vásquez et al. 2007; de la Vega et al. 2012). Differences in herbivory between plantation types were assessed through a Mann-Whitney's U test.



Figure 4. Photos of real and artificial caterpillars. A) Cluster of *O. cinnamomea* as they naturally occur in *P. radiata*. B) Cluster of artificial larvae attached to a *A. chilensis* branch. C) Markings of predation upon artificial larvae, made by birds (arrows point the markings). D) Naturally occurring herbivore damage on leaves of *A. chilensis*.

2.3 RESULTS

Complex plantation sites hold a significantly higher woody species richness (8.7 ± 3.7 vs. 4.1 ± 1.2 per site; $U = 12$, $P < 0.01$), as well as a significantly higher species' diversity (Shannon's H : 1.05 ± 0.44 vs. 0.52 ± 0.43 per site; $U = 23$, $P = 0.01$) than simple plantation sites (Fig. 5). Density of woody plant individuals within complex plantations sites was significantly larger compared to simple plantations sites at all heights assessed (Fig. 6). Plant density was 4.2 times higher at the lowest height in complex compared to simple plantations.

Attacks to artificial caterpillars were significantly higher in structurally complex plantations (z -ratio $P = 0.05$, Figure 7A). The proportion of attacked sites within complex plantations was 2.2 times higher than in structurally simple ones. Herbivory levels were significantly higher in simple plantation sites as compared to complex ones after the ending of the growing season ($U = 17$, $P = 0.02$; Figure 7B).

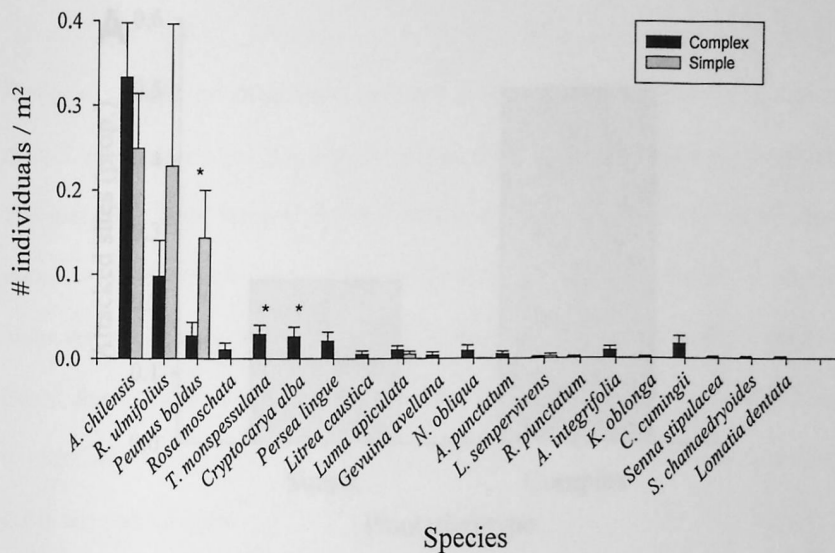


Figure 5. Mean woody species individuals abundance in structurally complex and simple plantations. Bars indicate 1 SE. * Mann-Whitney's U, $P < 0.05$.

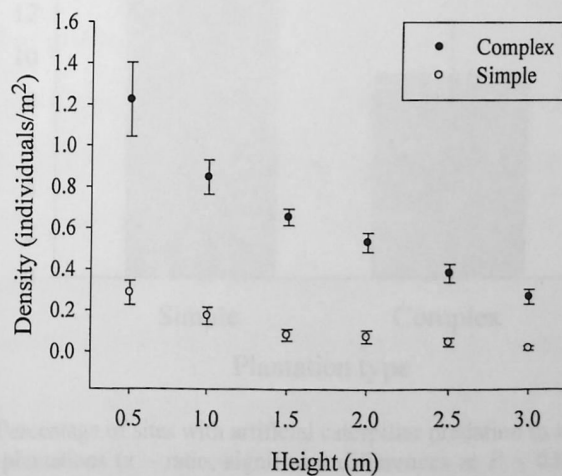


Figure 6. Density of plant individuals by height in structurally simple and complex plantation sites. Bars indicate 1 SE. Mann-Whitney's U, $P < 0.001$ for all heights.

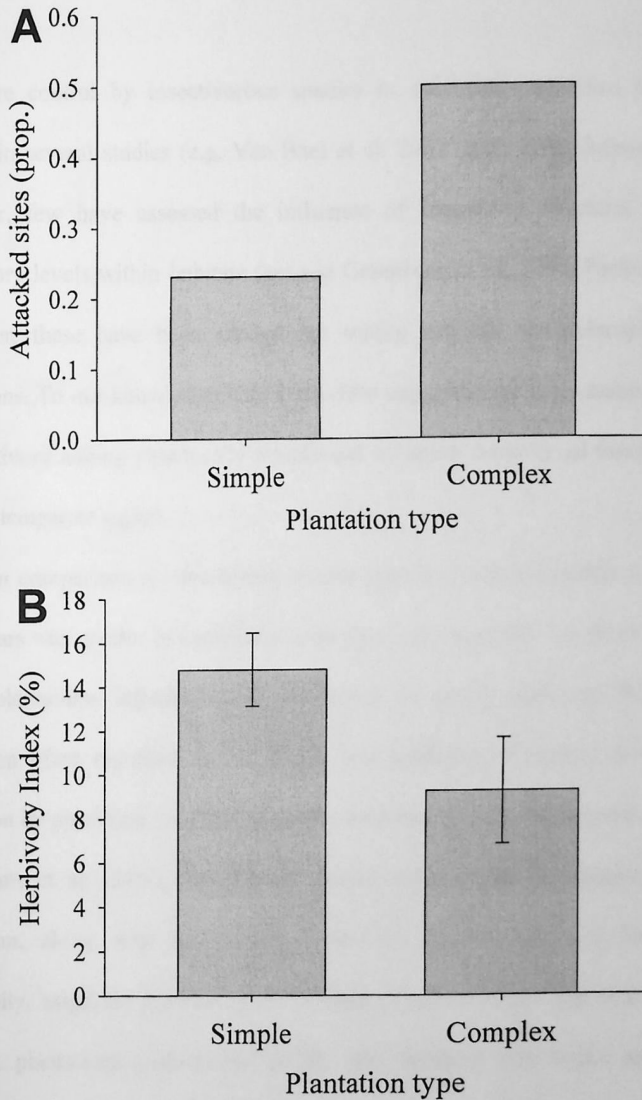


Figure 7. A) Percentage of sites with artificial caterpillar predation in structurally simple and complex plantations (z - ratio, significant differences at $P \leq 0.05$). B) Herbivory index within plantation types (Mean \pm 1 SE; Mann-Whitney's $U=17$, significant differences at $P = 0.02$).

2.4 DISCUSSION

Herbivore control by insectivorous species in managed productive fields has been noticed in several studies (e.g. Van Bael et al. 2007; Koh 2008; Johnson et al. 2009). However, few have assessed the influence of increasing structural complexity on insectivory levels within habitats (but see Greenberg et al. 2000; Perfecto et al. 2004). Moreover, these have been carried out within tropical and subtropical agriculture plantations. To our knowledge, this is the first experimental study assessing differences in insectivory among structurally simple and complex commercial forestry plantations, and in a temperate region.

In comparison to structurally simple pine plantations, predation upon artificial caterpillars was greater in complex plantations. This suggests that structural complexity within plantations influences the occurrence of insect predation. Being understory vegetation often regarded as the single best predictor of animal diversity within a plantation by providing food and shelter to native species (Lindenmayer & Hobbs 2004; Aratrakorn et al. 2006), the greater species richness and abundance of understory vegetation, along with the higher density of plants making a higher structural complexity, might be accounting for a higher fauna richness and abundance in more complex plantations (MacArthur 1972), and therefore the higher insectivory as a consequence of greater abundance of insectivores (Simonetti et al. 2006). Our results may therefore support that such biodiversity patterns correlate with the ecosystem function of pest control in commercial forestry plantations.

Higher herbivory levels within structurally simple pine plantations indicate a significantly depressed folivory in the complex plantations in comparison to simple ones. This difference was noticed even after insectivory levels had apparently decreased up to 5.4 times in relation to insectivory levels at the same plantations in 2003 (0.13 ± 0.13 vs. 0.02 ± 0.05 , respectively; two sided t- test $P = 0.03$; data from González-Gomez et al. 2006), presumably due to intense harvesting in nearby stands, where traffic and machinery noises might have decreased richness and abundance of birds near the disturbed sites (Arévalo & Newhard 2011; Moreira 2001), thus strengthening the validity of the differences found in herbivory for the two types of plantations, as the ecosystem service behind this fact is provided even at low bird abundances. On the other hand, depressed folivory levels may not be due to significant differences in foliar palatability, as abiotic characteristics of light intensity and humidity that produce physiologic responses in plants may not be substantially different between the pine plantations (Repetto et al. 2007; Silva & Simonetti 2009). Instead, variances in abundance of herbivorous insects should be accounting for the reduced herbivory in structurally complex plantations, as occurs in neighboring natural forests where birds trigger a reduction in herbivory (de la Vega et al. 2012). Our results, therefore, are consistent with our hypothesis that herbivore induced damage is attenuated in structurally complex plantations, consistently with the greater insectivory pressure within them.

In general, a higher pest-control service by insectivore species have been found in more complex agricultural fields than in simple ones; here we obtained similar results in an artificial agroforestry system. In South America, pine plantations pests such as

Rhyacionia buoliana has caused losses by herbivory damage of 205-609 US\$/ha (Alzamora et al. 2002) that could be prevented with planning and management of agroforestry systems into friendlier landscapes for sustaining biodiversity. Improvement of plantations towards structurally more complex ones would therefore allow a win-win scenario, in which the environmental challenges in biodiversity induced by changes in soil use were mitigated by providing habitat for native and threatened species, thus contributing to conservation of biodiversity outside the protected areas, and at the same time benefit productive fields by potentially reducing damage by herbivory to plantations, increasing the provision of useful ecosystem services for the plantations (Foley et al. 2005).

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CONCLUSIONES GENERALES

En el marco de la creciente demanda por bienes agroforestales, el principal desafío reside en aminorar los efectos que las actividades agroforestales generan sobre la diversidad biológica producto de los cambios en el uso de suelo. En general, la mayor simpleza estructural de las plantaciones monoespecíficas y monocultivos, comparado con ambientes naturales, alberga una baja diversidad biológica respecto a la presente en bosques naturales. Sin embargo, los ecosistemas productivos podrían jugar un importante rol en la conservación de biodiversidad si se adoptaran medidas de planificación y manejo que incluyeran la modificación de la complejidad estructural, lo cual permitiría que los sistemas agroforestales fueran amigables para la biodiversidad.

Los resultados obtenidos en esta Memoria de Título indican que la biodiversidad presente en los sistemas agroforestales provee servicios de control biológico de insectos, comparables a los presentes en sistemas naturales y, como consecuencia, disminuyen la herbivoría en plantas y aumentan significativamente la productividad vegetal, independiente de la región climática o tipo de insectívoro, expresándose de manera inmediata, en una base anual. Por lo demás, el servicio ecosistémico de control biológico es particularmente mayor en plantaciones forestales estructuralmente complejas, i.e. con mayor desarrollo de vegetación de sotobosque, en comparación con aquellas estructuralmente más simples. La herbivoría, además, es significativamente menor en aquellas estructuralmente más complejas que en las simples.

La existencia de niveles similares de servicios ecosistémicos en los sistemas productivos respecto de los ambientes naturales resalta la importancia de la

biodiversidad en ellos y ofrece un fundamento para conservarla, al disminuir los costos de operación y beneficiar la productividad en sistemas agroforestales. Una situación de manejo de los sistemas agroforestales en donde se mantengan plantaciones estructuralmente complejas, permitiría así la conservación de biodiversidad en ambientes productivos, en conformidad con las metas de Aichi para la biodiversidad del Plan Estratégico para la Diversidad Biológica (Convención sobre la Diversidad Biológica 2010).

REFERENCIAS GENERALES

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- Coffee * Mexico Yucatán Peninsula
- Quercus affinis USA Virginia
- Oil palm * Malaysia Sabah
- Cocoa * Panama Barro Colorado Island
- Pinus forest USA Michigan
- Wardens forest Australia Western Victoria
- Coffee * Puerto Rico Insular
- Tropical forest Mexico Yucatán Peninsula
- Grassland USA Kansas
- Mexican forest Mexico Yucatán Peninsula
- Coffee forest * Mexico Yucatán Peninsula
- Shrubland USA Texas
- Coffee * Panama Barro Colorado Island

APPENDIX 1

Publications used for the meta-analysis. *Agroforestry and non-commercial plantations, including city parks.

Plantation	Country	Authors	Year	Reference
<i>Quercus robur</i> and <i>Quercus robur</i> *	Germany	Böhm, Wells & Kalko	2011	PLoS ONE 6(4): e17857.
<i>Populus spp.</i> *	USA	Bridgeland et al.	2010	Ecology 91: 73-84.
<i>Nothofagus pumilio</i>	Argentina	Garibaldi et al.	2010	Oikos 119: 337-349.
Coffee *	Jamaica	Johnson et al.	2009	Agroforestry systems 76: 139-148.
<i>Acer pensylvanicum</i>	USA	Schwenk et al.	2009	Journal of Avian Biology 41: 367-377.
<i>Nothofagus pumilio</i>	Argentina	Mazia, Kitzberger & Chaneton	2009	Ecography 27: 29-40.
Coffee *	Mexico	Williams-Guillén, Perfecto & Vandermeer	2008	Science 320: 70.
<i>Quercus alba</i>	USA	Barber & Marquis	2008	American Midland Naturalist 162: 169-179.
Oil palm *	Malaysia	Koh	2008	Ecological Applications 18: 821-825.
Cocoa *	Panamá	Van Bael, Bichier & Greenberg	2007	Journal of Tropical Ecology 23: 715-719.
<i>Pinus ponderosa</i>	USA	Mooney	2007	Ecology 88: 2005-2014.
Wandoo forest	Australia	Recher & Majer	2006	Austral Ecology 31: 349-360.
Coffee *	Puerto rico	Borkhataria, Collazo & Groom	2006	Ecological Applications 16: 696-703.
Tropical forest	Mexico	Boege & Marquis	2006	Oikos 115: 559-572.
Grassland	USA	Branson	2005	Environmental Entomology 34: 1114-1121.
Spruce forest	Sweden	Strengbom et al.	2005	Oecologia 143: 241-250.
Coffee farm *	Mexico	Philpott et al.	2004	Oecologia 140: 140-149.
Shrubland	USA	Gruner	2004	Ecology 85: 3010-3022.
Coffee *	Panamá	Van Bael, Brawn, Robinson	2003	PNAS, USA: 100: 8304-8307.

<i>Brassica oleracea</i> *	USA	Hooks et al.	2003	Ecological Entomology 28: 522-532.
<i>Citrus unshiu</i> *	Japan	Matsumoto, Itioka & Nishida	2003	Ecological Research 18: 651-659.
Temperate forest	Japan	Murakami & Nakano	2002	Ecology Letters 5: 333-337.
Oak forest	USA	Lichtenberg & Lichtenberg	2002	American Midland Naturalist 148: 338-349.
Corn fields *	Canada	Tremblay, Mineau & Stewart	2001	Agriculture, Ecosystems and Environment 83: 143-152.
Coffee *	Guatemala	Greenberg et al.	2000	Ecology 81: 1750-1755.
<i>Acer saccharum</i>	USA	Strong, Sherry & Holmes	2000	Oecologia 125: 370-379.
<i>Quercus</i> spp.	USA	Forkner & Hunter	2000	Ecology 81: 1588-1600.
Temperate forest	Japan	Murakami & Nakano	2000	Proceedings of the Royal Society of London: Biological Sciences 267: 1597-1601.
<i>Salix</i> spp.	Finland	Sipura	1999	Oecologia 121: 537-545.
Tropical forest	Costa rica	Letourneau & Dyer	1998	Ecology 79: 1678-1687.
Grassland	USA	Moran & Hurd	1998	Oecologia 113: 126-132.
Shrubland	USA	Floyd	1996	Ecology 77: 1544-1555.
<i>Quercus alba</i>	USA	Maquis & Whelan	1994	Ecology 75: 2007-2014.
<i>Inga</i> sp. *	Mexico	Greenberg & Ortiz	1994	The Auk 111: 672-682.
Tropical forest	Brazil	Fonseca	1994	Journal of Ecology 82: 833-842.
Subtropical shrubland	Bahamas	Spiller & Schoener	1994	Ecology 75: 182-196.
Grassland	USA	Bock, Bock & Grant	1992	Ecology 73: 1706-1717.
Grassland	USA	Fowler et al.	1991	Ecology 72: 1775-1781.
Bilberry shrubland	Sweden	Atlegrim	1989	Oecologia 79: 136-139.