

Ecosystem services in human-dominated landscapes: insectivory in agroforestry systems

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Abstract Despite of being structurally simpler and species-impooverished than natural forests, agroforestry plantations can act as a secondary habitat for native species and sustain some biodiversity. In particular, insectivores can provide important ecosystem services such as insectivory, indirectly benefiting plants through the reduction of herbivory and increasing productivity, by diminishing herbivores 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 possible modulating factors such as climatic region, type of insectivore, trophic group of the preyed arthropod and length of insectivores experimental exclusion. In this study, through a meta-analysis, it was assessed the provision of ecosystem services by insectivores 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 plant 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 insectivores present in plantations, independently of factors that could modulate its magnitude and direction. In this way, enhancing the existence of these important interactions within plantations could represent a win–win scenario.

Keywords Ecosystem services · Insectivory · Meta-analysis · Trophic cascade

Introduction

Agroforestry systems are usually simpler in structure and relatively homogeneous in species composition than 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 and Hobbs 2004; Simonetti et al. 2012). The occurrence of native species in plantations might enable species interactions and

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processes offering ecosystem services within agroforestry systems (Simonetti et al. 2006). In particular, biological control by insectivores is considered an economically valuable ecosystem service that offers benefits to human populations, as could reduce herbivory and potentially enhance productivity in plantations (Costanza et al. 1997). 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, based on the crop losses to herbivorous insects and expenditures on insecticides (Losey and 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 (Van Bael et al. 2008; Mäntylä 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 that could deflect their response. The strength of the effects of insectivores is expected to weaken down the trophic chain, being higher upon insect abundance, less on plant herbivory and lower on plant productivity, due to factors such as the existence of antiherbivore defenses in plants that could reduce herbivore effects, or the presence of a complex food web that diffuses the effect of an insectivore species over lower trophic levels (Polis and Strong 1996; Schmitz et al. 2000; Mooney et al. 2010). Food webs in environments with a high species diversity in which they interact through a highly interconnected network are expected to show weaker trophic cascades than environments where the community is less diverse and dominated by few species (Strong 1992; Polis and Strong 1996). Therefore, trophic cascades of insectivores might be more intense in plantations than in natural systems.

Environmental and ecological traits such as climate, types of insectivore and preyed arthropod, and length of insectivore exclusion treatments, might influence the magnitude or direction of the direct effects of insectivores on arthropod abundance and indirect effects on plant herbivory and productivity. Mäntylä et al. (2011) found trophic cascade intensity by insectivores did not vary across main climate types (tropical, temperate and boreal). However, trophic cascades occurrence, and therefore the provision of

services, might differ in response based on local differences of temperature and precipitation (e.g. Van Bael and Brawn 2005; Schwenk et al. 2010; Garibaldi et al. 2010), conditions that vary even within the main climate types reviewed by Mäntylä et al. (2011; Kottek et al. 2006). The strength of trophic cascades might also differ pending on the type of insectivore, as vertebrate predators might have a stronger effect than invertebrate predators upon herbivores (Schmitz et al. 2000). Also, predation between insectivores might relieve the reduction in herbivorous insect abundance, and thus result in either no net effect of insectivores over plants, or even negatively affect plants (Polis and Strong 1996; Mooney and Linhart 2006). We assessed if the predator pressure of insectivores differ over herbivorous and predator arthropods, and if it diverges between natural and artificial—thus structurally simpler—systems. The strength and detection of effects could also be affected by the duration of the study, especially over indirect response variables such as biomass production in plants, which may show responses in the long rather than the short term, thus temporarily delayed in comparison to direct effects after top-predator manipulations (Lawton 1989).

Enhancing the maintenance of trophic interactions in plantations such as insectivory by incrementing their structural complexity and thus the species richness they hold (Nájera and Simonetti 2010; Ramírez and Simonetti 2011) would benefit as well the plantations revenue. Although structural complexity provided by a well-developed undergrowth 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 (de Groot et al. 2010). In this study, through a meta-analysis, we test the effect of the presence of insectivores in natural and artificial systems, over arthropods and plants. If productivity is positively affected by the presence of insectivores in plantations, this fact might provide a rationale to enhance their conservation in productive agroecosystems.

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, where placed under the category agroforestry system. Studies included in the analysis were conducted in native forests, plantation fields, shrublands or grasslands. Herbivory and productivity was assessed over trees, shrubs or herbs, and the data were pooled to obtain a mean overall effect over the parameters. Each study case was classified under a climatic region in which the study site was located, based on the Köppen-Geiger climate classification, with which we could search for the existence of a differential response to the presence of insectivores in environments with different annual temperature and precipitation, even within same main climates (Kottek et al. 2006). Insectivore type subject to exclusion or enclosure treatments were classified as birds, lizards, ants and predatory arthropods in general, the latter including ants, spiders and others, as there were studies that assessed the effect of ants alone as insectivores, while other studies considered the whole group of predatory arthropods for the same purpose. The trophic group of the preyed arthropod in the arthropod abundance surveys was classified as predators or herbivores, and the length of the experiment as first, second or third year since the beginning of the study. Further, we assessed plant productivity as total biomass, shoot extension and basal area, the most common variables measured in the surveys included in our analysis, to evaluate differences between variables in response to arthropod predation.

To assess the effect of predators upon arthropod 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 unbiased standardized mean difference (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 (4,999 iterations), and *P*-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 environment, climatic region, type of predator, trophic group of preyed arthropod, and length of insectivores exclusion, were used in heterogeneity tests. Hedge’s standardized mean difference performs well for $n \geq 5$, thus any grouping factor with $n < 5$ was 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).

Results

A total of 292 published papers were retrieved from the databases and references. However, only 39 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). In general, the diversity of natural environments covered by our analysis is similar to previous meta-analysis (e.g. Schmitz et al. 2000; Mooney et al. 2010; Mäntylä et al. 2011), while for agricultures and plantations the diversity of environments covered was broader than tropical agroforests as assessed in Van

Table 1 Number of publications and study cases per environment type and climatic region used in the meta-analysis

| Study site environment and climate | No. of publications | No. of cases |
|------------------------------------|---------------------|--------------|
| Environment | | |
| Natural | 27 | 214 |
| Agricultural | 14 | 69 |
| Climatic regions | | |
| Monsoon (Am) | 3 | 15 |
| 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 |

Climatic regions are presented by the names of the Köppen-Gieger climatic classifications, shown in parenthesis

Bael et al. (2008), including arid, temperate and boreal artificial plantations (e.g. Tremblay et al. 2001; Matsumoto et al. 2003; Bridgeland et al. 2010). No publication bias was detected, neither 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 numbers also suggested no bias among study cases. At least 17,554 non-significant study cases for arthropod abundance, 4,462 for herbivory and 63 for plant productivity would be needed to be added to the analysis to change results from significant to non-significant (Rosenberg et al. 2000).

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 neither 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).

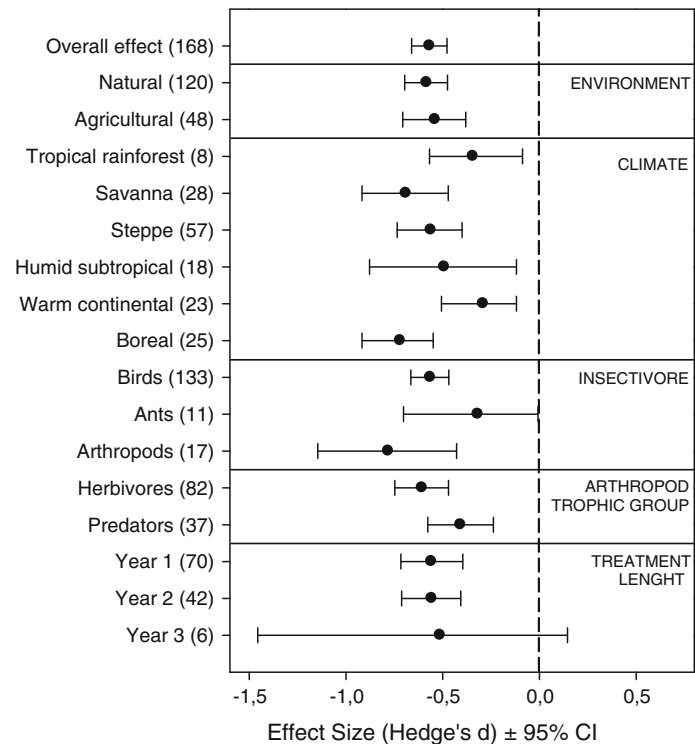
Plant herbivory

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 was no 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).

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.

Fig. 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 (climates excluded: monsoon, oceanic, hot mediterranean, warm mediterranean; insectivore groups excluded: lizards, parasitoids, spiders). 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



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 effects.

Discussion

Despite agroforestry systems are considered impoverished ecosystems, unfriendly to native species, they do sustain biodiversity under certain conditions (Nájera and Simonetti 2010; Ramírez and Simonetti 2011), and the species they support can provide useful ecosystem services. Here we focused on insectivores present both in natural environments and plantations, responsible for reducing the abundance of herbivorous insects, reducing herbivory damage and increasing productivity.

Overall, insectivorous species significantly diminished arthropod abundance in all environments, and this reduction cascaded down into releasing herbivore-induced damage to plants and incrementing plant productivity. The effect sizes attenuated down from the direct effect of insectivores over arthropod

abundance to the indirect effect on plant productivity, consistent with theoretical and empirical analyses on terrestrial trophic chains (Polis and Strong 1996; Schmitz et al. 2000; Mooney et al. 2010). In agreement with Van Bael et al. (2008) and Mäntylä et al. (2011), the effect sizes in natural and agroforestry systems were not significantly different, neither for arthropod abundance, plant herbivory nor plant productivity responses, suggesting that the services provided by insectivorous species are maintained in productive environments. However, despite the response of plant productivity to the presence of insectivores does not differ between agricultural and natural systems, only agroecosystems depicted a significantly increase in productivity when insectivores are present. This result suggests a stronger trophic response in the structurally simpler and less diverse systems, compared to natural systems, agreeing with the hypothesis that plantations might show a more pronounced trophic cascade, thus highlighting the importance of their presence in agroforestry systems for the provision of valuable services.

We found no overall difference in the magnitude of effects to arthropod abundance or plant herbivory and productivity between insectivore types. The only case

Fig. 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 (climates excluded: tropical rainforest, steppe). Interpretation of graph is equal to that of Fig. 1

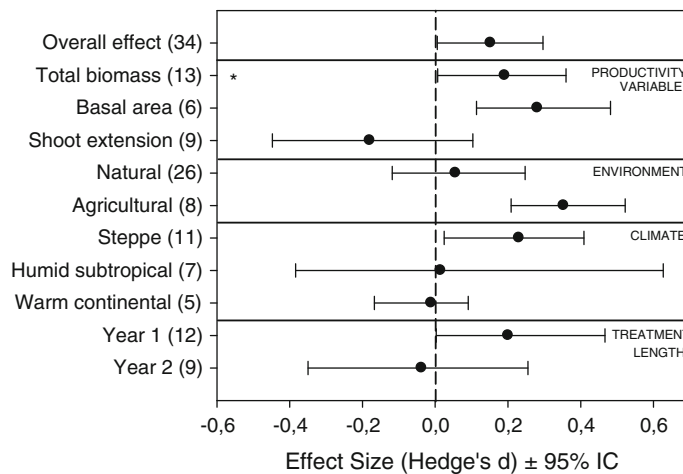
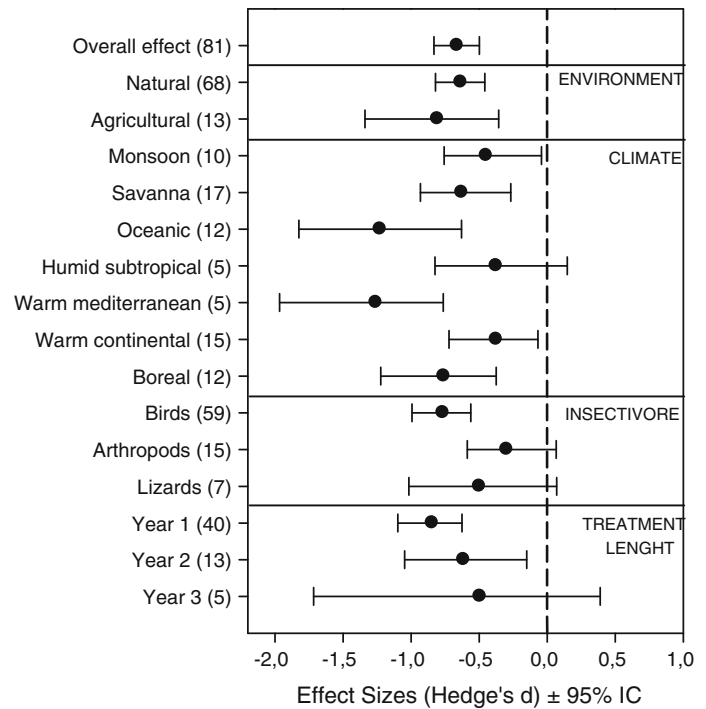


Fig. 3 Hedge's d mean effect sizes $\pm 95\%$ CI of insectivorous species presence on plant productivity. Sample sizes are shown in parenthesis. Groups within categories with sample size lower than 5 studies were excluded (climates excluded: tropical

rainforest, monsoon, warm mediterranean, oceanic, warm continental; treatment length excluded: year 3). Interpretation of graph is equal to that of Fig. 1. * = heterogeneity test, Q_{between} significant at $P < 0.05$

in which different insectivore groups had a differential response was within plantations, 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 agricultural systems (Perfecto et al. 2004).

Even if predation between insectivores may result into depressed suppression of herbivorous arthropods (Polis and 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, both in structurally complex and simple systems. These impacts also did not vary between climatic regions, agreeing with Mäntylä et al. (2011), even if considering differences in annual temperature and precipitation within a main climate, suggesting these macroclimatic conditions in an ecosystem may exert little effect in the beneficial effects of insectivores over plants. Also, arthropod abundance, herbivory and plant productivity responses could already be seen at the first year since the beginning of the study, thus showing an immediate response on a yearly basis even for the indirect variables that may be expected to present a delayed response. We conclude interaction strengths do not vary significantly through time (see also Schmitz et al. 2000).

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 and 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, shrublands or grasslands, and climate, type of insectivore and preyed arthropod and length of the study do not significantly modulate the outcome of insectivore manipulations. Biological control is profitable for agroforestry plantations, thus factors enhancing it ought to be managed in a way to ensure the occurrence of insectivores and insectivory, therefore diminishing the negative impact of forestry plantations towards biological diversity.

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Appendix 1

See Table 2

Table 2 Publications used for the meta-analysis

| Plantation | Country | Authors | Years | Reference |
|--|-------------|---|-------|---|
| <i>Quercus robur</i> and <i>Quercus robur</i> ^a | Germany | Böhm, Wells & Kalko | 2011 | PLoS ONE 6(4): e17857. |
| <i>Populus</i> spp. ^a | USA | Bridgeland et al. | 2010 | Ecology 91: 73–84. |
| <i>Nothofagus pumilio</i> | Argentina | Garibaldi et al. | 2010 | Oikos 119: 337–349. |
| Coffee ^a | 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 | Mazía, Kitzberger & Chaneton | 2009 | Ecography 27: 29–40. |
| Coffee ^a | 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 ^a | Malaysia | Koh | 2008 | Ecological Applications 18: 821–825. |
| Cocoa ^a | 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 ^a | Puerto rico | Borkhataria, Collazo & Groom | 2006 | Ecological Applications 16: 696–703. |

Table 2 continued

| Plantation | Country | Authors | Years | Reference |
|---------------------------------------|------------|-----------------------------|-------|---|
| 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 ^a | Mexico | Philpott et al. | 2004 | Oecologia 140: 140–149. |
| Shrubland | USA | Gruner | 2004 | Ecology 85: 3010–3022. |
| Coffee ^a | Panamá | Van Bael, Brawn, Robinson | 2003 | PNAS, USA: 100: 8304–8307. |
| <i>Brassica oleracea</i> ^a | USA | Hooks et al. | 2003 | Ecological Entomology 28: 522–532. |
| <i>Citrus unshiu</i> ^a | 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 ^a | Canada | Tremblay, Mineau & Stewart | 2001 | Agriculture, Ecosystems and Environment 83: 143–152. |
| Coffee ^a | 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. |
| Salix 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. ^a | 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. |

^a Agroforestry and non-commercial plantations, including city parks

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