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IMPACTS TO BIODIVERSITY AND ECOSYSTEM SERVICES FROM BIOENERGY DEVELOPMENT: A PAN AMERICAN EXPERIENCE

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IMPACTS TO BIODIVERSITY AND ECOSYSTEM SERVICES FROM BIOENERGY
DEVELOPMENT: A PAN AMERICAN EXPERIENCE

By

Colin C. Phifer

A DISSERTATION

Submitted in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

In Forest Science

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This dissertation has been approved in partial fulfillment of the requirements for the Degree of DOCTOR OF PHILOSOPHY in Forest Science.

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Dedicated to Tina and River Phifer, my family

(Jasper, you too)

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Preface

Chapters 1 and 6 serve as the “bookends” of this work, a place to set the scene for this research and a summary the major themes and lessons learned.

Chapter 2 was published in *Biodiversity and Conservation*, which maintains copyright for this chapter. Study design, field work, data analysis and writing was led by Colin Phifer. Jessie Knowlton contributed to the design, field work and logistics and writing. Christopher Webster and David Flaspohler helped with statistical analysis, research direction and greatly improved the writing. Julian Licata assisted in study design and logistics and writing of this chapter, and served as a key collaborator in Argentina.

Chapter 3 will be submitted to *Agriculture, Ecosystems and Environment*. Research design, field work and analysis was led by Colin Phifer with Pablo Cavigliasso serving as project co-lead. Pablo contributed to the research design and field work and was solely responsible for bee species identification, as well as some parts of the data analysis. Jessie Knowlton also assisted in design and field research. Daniel Gruner helped with statistical analysis and writing.

Chapter 4 is intended for *Sustainability*. Colin Phifer conducted the GIS and ecosystem service analysis and was responsible for the majority of the writing. Erik Nielsen, Chelsea Silva, Renee Sanders and Jesse Abrams were responsible for social surveys and interviews and analysis. Santiago Veron, Diego Abelleira, and Tamara S. Propato completed the remote sensing and land-use/land-cover classification. Michelle Brill Cisz completed soil sampling for carbon sequestration values in plantations and Pablo Cavigliasso helped with bee biodiversity sampling. Jessie Knowlton also assisted with bird biodiversity sampling (see above) and also writing and conceptual design. David Flaspohler and Christopher Webster assisted with writing and editing. Chelsea Schelly helped frame the research and with writing and placing the social science contribution in context.

Chapter 5 is intended for *Forest Science* or other forest ecology publication. Colin Phifer completed the field research, insect identification, data analysis and majority of the writing. Christopher Webster assisted with experimental design, analysis and writing. Bryan Murry also assisted with data analysis. Cindy Fiser also assisted in data collection, insect identification and editing. David Flaspohler assisted in writing and editing. Daniel Gruner helped with statistical analysis and writing.

Chapter 7 serves as the Appendix and includes the titles, abstracts and citations for related peer-reviewed publication that I co-authored while part of this project. These papers relate to my own work on bioenergy development in Mexico and Brazil, and interdisciplinary team science. I include them here to help give a fuller perspective of my work and scholarship from the last four years.

Acknowledgements

This research was financially supported by the National Science Foundation Partnerships for International Research and Education program (grant num. 124344), which has been led by Dr. Kathleen Halvorsen at Michigan Technological University. The support of the USDA McIntire–Stennis fund also provided needed support, particularly for field research in Argentina. In addition, I am extremely thankful for MTU’s Graduate School Finishing Fellowship, which provided me with one semester of support. The Inter-American Institute for Global Environmental Change also supported this and related work focusing on improving interdisciplinary collaborations within our team. I also received numerous travel grants and research awards from MTU’s Ecosystem Science Center and MTU’s Graduate Student Government. I am also thankful to the numerous travel grants I received from professional societies to attend and present at research conferences.

The research presented here is part of a larger interdisciplinary, international project that is focused on the social and ecological sustainability of bioenergy development in the United States, Argentina, Brazil and Mexico. This team was led by Dr. Halvorsen, with complementary leadership from many other researchers in each country. *Many, many people contributed to this project*, and I cannot thank them all, but my work is only possible because of the contributions of the *whole* team. The work presented here is, indeed, a group effort.

I have been blessed to have the support and advice of Drs. David Flaspohler and Christopher Webster, my co-advisors, and Drs. Chelsea Schelly and Daniel Gruner, members of my committee. With their help, I have been able to knit together the distinctive research projects from each country into something greater than the sum of its parts. Project principle investigator, Dr. Halvorsen, was also instrumental in my project and provided me guidance, leadership opportunities, and training in interdisciplinary science. I also worked closely with Dr. Jessie Knowlton on this project, particularly in Argentina and Brazil, and I can say truthfully that this degree would not be possible without her help, support and understanding – thank you, Jessie. (Special thanks to Phil LoCicero, too, for his encouragement!) I emerge from this project as a stronger scientist from this four-year trek across disciplinary and country boundaries.

My work had the added challenge of working in two countries. In Argentina, I am deeply indebted to a whole team of wonderful collaborators: Pablo Cavigliasso, Julian Licata, Erika Adams, Santiago Veron, Diego Abelleyra, Tamara Sofia Propato, Chelsea Silva, Erik Nielson, and all the landowners who allowed us work there. *In particular, and with special thanks, to Pablo: this work is also his work, and our friendship will last.* Sam Oliveria also helped collect bird data. In the United States, the wonderful staff at the University of Wisconsin Kemp Field Station, made our work possible. All the travel, staffing and (often random) purchases I made on behalf of this research was only possible because of the outstanding staff support from MTU, particularly Andrea Longhini, Marjorie Lindley, and Phyllis Williamson.

I would also like to thank the University of Oregon's Institute for Sustainable Environment for hosting me while I finalized this degree. The collaborations and friendships with Drs. Heidi Huber-Stearns, Jesse Abrams and Cass Moseley were particularly enriching. This place has been my other home, and I appreciate the support and encouragement. Writing is *hard* and you helped me overcome the many (often self-imposed) road blocks.

I would like to thank all the students involved in this research project, including Michelle Brill Cisz, Jose Lopez, and Erin Pischke, Tatiana de Souza, Renee Sanders and Chelsea Silva. I am particularly thankful to my undergraduate interns: Cynthia Fiser, who exceeded all expectations as my field and lab assistant; Nia Becker, who worked to identify bees with me and came to Brazil; and Gina Testa, who designed her own research project. Advising and working with these three undergraduates was one of my favorite parts of this project. I am confident they all have bright futures ahead.

I thank my whole family that often-wondered out loud "You're still in school?" and openly wondered the wisdom of this choice. Nonetheless, they supported and loved me, and I am thankful to May Phifer, and Bill and Linda Hilbert for all their help and support (and the snow tires they gave me for my birthday while in Michigan!). I also thank Rick and Jean Throm for being supportive and always asking, "how can I help?" and following through while we were in Michigan.

Most importantly: I would only be able to do this work and research because of the support, trust and love of my wife, Tina, and with the inspiration, love and energy of my son, River. Thank you. *I love you both so much and I am so thankful that you both accompanied me on this long, convoluted and often frustrating journey.* I couldn't do it without you two, and the only reason I'm finishing this degree is because of River's insistence that "We are both scientists." Special thanks to Jasper the Cat for sitting beside me while I worked on this project in the wee hours of the night or early morning, and for reminding me that kindness, food, and love are more important than another line on one's CV. *OK? On with the show!..*

Abstract

As part of a broader project that evaluated the social and ecological sustainability of bioenergy, I studied the effects of bioenergy associated land-use change and management on native bees and birds in two bioenergy-producing countries, the United States and Argentina. In Argentina, I worked in Entre Ríos province where eucalyptus (*Eucalyptus* spp.) plantations are being planted. These fast-growing trees are replacing pasture and annual crops, the current dominant land use. I surveyed for native bees and birds in pastures/annual crops and large-scale eucalyptus plantations, as well as mixed-use farms and native espinal savannas. Both birds and bees declined in the large-scale plantations in terms of species richness and abundance compared to the other land uses in the region. Avian biodiversity was richest in the espinal savanna with intermediate values in the mixed-use and pasture/annual crops. In contrast, pastures/annual crops and mixed-use farms supported more bees than the espinal. I also detected distinct communities of birds and bees in each land use surveyed. I also modeled ecosystem services in for this region, specifically carbon sequestration, pollination service and habitat quality. I considered the current baseline map and two future scenarios: eucalyptus expansive and community preferences. The models predict that the expansion of the plantations results in decreases in pollination service and habitat quality while increasing potential carbon sequestration. Collectively, these results demonstrate the need to carefully consider the effects of feedstocks on species and ecosystem services. In the United States, I worked in northeastern Wisconsin and studied the effects of aspen (*Populus* spp.) forest stand age on native bees and other members of the Hymenoptera using a chronosequence of no-retention aspen stands. Discrete bee and wasp communities were detected along the forest successional age gradient, but bee and wasp species richness and abundance did not decline with forest age as hypothesized. This work illustrates a successional pattern in bee community composition following disturbance and suggests both young and old forest stands are necessary to support bee biodiversity. Lastly, I conclude with a summary of my research and suggestions on how to be an effective team member in an interdisciplinary research group.

1. Project background and research design

Ecological and social sustainability of bioenergy in the Americas

Human induced climate change is caused by the increases in greenhouse gases like carbon dioxide (IPCC 2014). Bioenergy — energy derived from non-fossil fuel based plant materials — can be part of the solution to slow greenhouse gas emissions because plants absorb carbon dioxide while growing, thus closing the “carbon loop” (Deng et al. 2015). Bioenergy is can be made from a variety of feedstocks, but like any other crop or land-use change, it can affect natural and human communities positively or negatively (Dale et al. 2014). The fact that bioenergy can come from many sources means different nations are exploring bioenergy’s potential to both reduce greenhouse gases, but also provide economic development and ecological sustainability (Dale et al. 2014).

Worldwide, the market for bioenergy production is expected to more than double by 2050 (Immerzeel et al. 2013). Bioenergy feedstocks can be converted into solid fuels, like biomass wood pellets and chips, or liquid biofuels like biodiesel. Ethanol from corn or sugar is the current dominant bioenergy feedstock but there is growing demand for second-generation bioenergy crops that provide greater yields and more energy per volume to meet the expected market and government mandates for renewal energy and climate change mitigation (IPCC 2014). Bioenergy feedstock production can have negative ecological impacts, including potential net carbon emissions increase compared to fossil fuels and loss of biodiversity (Ben Phalan 2009; REPO et al. 2010; Fargione et al. 2010). Most bioenergy feedstocks require large amounts of land to be profitable and feasible, which impacts water budgets, soil fertility and biodiversity, potentially both positively and negatively depending on the feedstock, the prior habitat and the management system (Immerzeel et al. 2013). Biodiversity is a fundamental part of ecosystem health and provides for multiple ecosystem services that directly relate to human well-being Changes in land use as a result of bioenergy development that impacts biodiversity, may in turn affect ecosystem services through direct and indirect interactions (Fargione et al. 2008; Polasky et al. 2010; Fargione et al. 2010; Lawler et al. 2014).

To understand the potential impacts from bioenergy development, Michigan Technological University led a Pan-American evaluation of the social and ecological sustainability of bioenergy in four countries (Argentina, Brazil, Mexico and the United States) where bioenergy production has increased rapidly in the last ten years (Kline et al. 2015a). The MTU team was comprised of social, natural and physical scientists and engineers that worked together to consider how bioenergy feedstocks changed communities and how do the many parts of a linked social-ecological system interact. In each country, the research team applied a control/treatment design that contrasted communities actively developing bioenergy feedstocks with those communities that are using landscapes in a traditional manner, and where appropriate, a reference ecosystem intended to represent a natural or semi-natural condition. The natural scientists focused

on three aspects of ecological sustainability: water usage and water cycling, soil health and carbon sequestration, and biodiversity impacts of bioenergy feedstocks.

Within this established framework, I studied how bioenergy associated land-use change impacted birds, native bees and their associated ecosystem services as part of the biodiversity assessment in two countries, Argentina and the United States. In Argentina, large-scale afforested eucalyptus (*Eucalyptus spp.*) plantations are replacing pastures and annual croplands. The wood from these plantations can be chipped for biomass power plants, making the eucalyptus the bioenergy feedstock. In the United States, the MTU project worked in Wisconsin where naturally occurring aspen (*Populus spp.*) forests are a potential biomass fuel for nearby power plants, potentially shifting the landscape to forests of younger aspen. Both Argentina and the United States have active bioenergy markets and favorable government policies that will likely result in a significant bioenergy expansion in the future (Deng et al. 2015; Kline et al. 2015b). The results of my research on the biodiversity impacts are then one part of the broader MTU investigation into the social and ecological sustainability of bioenergy.

Bees and birds: ecosystem services providers and harbingers of change

For my dissertation, I selected birds and bees as my focus taxa because they directly provide ecosystem services, like pollination and pest control. These two taxa groups can be rapidly assessed and act as proxies for other species (Gardner et al. 2007). More generally, biodiversity as a whole is a foundational component of ecosystem services (Mace et al. 2012; Cardinale et al. 2012). Many ecosystem services are directly provided by species, and these species' patterns of abundance and richness are influenced by land-use decisions (Lawler et al. 2014), and consequently likely impact the delivery of service (Laterra et al. 2012).

Understanding how native bee populations respond to land-use change is critical since bees pollinate domesticated and wild plants. Nearly 90% of the world's flowering plants require some degree of animal-assisted pollination (Ollerton et al. 2011), making pollinators an intrinsic and deeply connected part of biodiversity. Moreover, pollinated crops provide both essential calories (Klein et al. 2007) and micronutrients (e.g. vitamin A, iron and folic acid) needed for human health, (Chaplin-Kramer et al. 2014; Ellis et al. 2015) directly linking human well-being to pollinator biodiversity. Economically, pollinators contribute to 75% of crop species, an ecosystem service estimated to be approximately \$215 billion worldwide (Gallai et al. 2009). Wild, unmanaged pollinators are a major source of this pollination service for many crops (Winfree et al. 2007). Cross-pollinated crops also increase shelf life and nutrient quality of fruits (Klatt et al. 2013; 2014). Reliance on pollinators is likely to increase since pollinator-dependent crops are becoming more popular, making future food yields contingent upon vital biodiversity-dependent service (Aizen et al. 2008; Garibaldi et al. 2013; 2016)

The growth in pollinator-dependent crops comes at a time of worldwide decline in native bee populations (Potts et al. 2010; Kennedy et al. 2013). The decline in bee populations is

likely the result of the confluence of many factors that interact and reinforce one another (Goulson et al. 2015) including: agricultural intensification (Vanbergen & Initiative 2013), climate change (Miller-Struttman et al. 2015), diseases and invasive pests (Morales et al. 2013), and mixtures of herbicides, fungicides and insecticides (Whitehorn et al. 2012; Rundlöf et al. 2015; Hladik et al. 2016). Similar to native bees, managed honey bees in the United States are also stressed with losses to colonies nationwide (Lee et al. 2015). These two observations – increased demand for pollination service and decrease in supply of pollination services by bees – may lead to possible pollination decay for wild plants (Vamosi et al. 2006) and pollination deficit for crops, with increased rates of malnutrition in communities more dependent on pollination-dependent fruits and vegetables (Chaplin-Kramer et al. 2014; Ellis et al. 2015).

Bees are responsive to land-use change and their responses have been widely studied with an emphasis on local and landscape perspectives (Kennedy et al. 2013). With more than 20,000 species worldwide, it is impossible to study every species' response habitat change. Consequently, biologists use life-history or functional traits as a useful way to group and predict species responses habitat modifications (Williams et al. 2010). Williams et al. (2010) found that species' social structure (social or solitary), nesting location (above or below ground), and diet (pollen specialist or pollen generalist) were important predictors of species' responses to agricultural intensification, habitat fragmentation, fire and pesticides. Recent work suggests that bee abundance and richness are higher in more diverse landscapes and in landscapes that more closely resemble natural or undisturbed habitats (Kennedy et al. 2013). The stability of pollination services has also been shown to decline with increasing distance from natural and semi-natural habitats (Ricketts et al. 2008; Potts et al. 2010; Garibaldi et al. 2011). These broader land-use and land-cover analyses are capturing the local scale changes in floral resources, nest resources and overwintering habitats that influence bee communities (Kremen & Ostfeld 2005; Williams et al. 2010). Just how bees perceive the availability of these habitats is a likely a function of home ranges and their capacity for long-distance flight (Greenleaf et al. 2007; E Benjamin et al. 2014). Local level and landscape level effects co-vary, and both appear to influence bees communities, suggesting a need to consider both perspectives (Lonsdorf et al. 2009; Kennedy et al. 2013).

Despite apparent declines in some species and populations of bees, notably bumblebees (Grixti et al. 2009), many species appear resilient with stable populations (Garibaldi et al. 2013). However, there exists few long-term studies on inter-year variation in bee populations and existing sampling efforts remain limited, which limits our ability to interpret how bees are responding to rapidly changing habitats (Lebuhn et al. 2012). Further, most studies focus upon species richness (the presence or absence of species) but not upon interacting communities of bees and other pollinators (Winfrey et al. 2011).

Like bees, birds are also a major contributor to ecosystem services that benefit human well-being. For example, birds provide essential and economically valuable ecosystem services including pest control, seed dispersal, pollination, guano, and recreational value to humans (Wenny et al. 2011a; Sekercioglu 2012; Whelan et al. 2015). The ability of

(most) birds to fly and their high energetic demands and thus appetites makes birds a highly mobile ecological force on landscapes, capable of responding to rapid changes in resource availability and landscape condition (Whelan et al. 2008). Some of the earliest research in ecosystem services focused on “economic ornithology” in the early 20th century and how birds could contribute to pest management on farms (Whelan et al. 2008; Kronenberg 2014). The majority of birds are (at least partially) insectivorous, making them potential pest control agents (Whelan et al. 2015). Multiple studies confirm the pest-control effect of birds; farmers that conserve natural habitat adjacent to farms often see increases in crop yields and lower levels of insect damage (Karp et al. 2013). Birds are also important seed dispersers for native plants, with more than one-third of birds feeding on fruits and nuts and distributing seeds (Whelan et al. 2008). Lastly, more than 900 species of birds worldwide help pollinate plants, and there are numerous examples of long term evolutionary relationships between bird-pollinated flowers and birds (Kelly et al. 2010; Anderson et al. 2011) reinforcing central role some birds play in the maintenance and contribution to biodiversity patterns (Whelan et al. 2008; Wenny et al. 2011b; Whelan et al. 2015).

Birds can fly long distances, even migrate between continents, but local habitats also influence species survival and fitness. Of the approximately 10,000 species of birds, only a few prefer human-modified agricultural, suburban, or urban settings (Sekercioglu et al. 2007). However, some bird species will interact with and visit farm fields and modified habitats during part of their annual cycle (Tschardt et al. 2008). In addition to land-use change, climate change can also affect species and these forces are already impacting avian communities with declines in current and projected habitat ranges (Barbet-Massin et al. 2011; Mantyka-Pringle et al. 2013; Meller et al. 2015). At present, however, the effects of land-use change have a greater impact than present-day climate change effects (Jetz et al. 2007). Similar to native bee research, recent efforts to identify ecological and life history traits of bird species have been used to develop predictive models of the effects of land-use change on species have found some common traits, and strong regional differences between temperate and tropical species (Newbold et al. 2012; Bregman et al. 2014). Larger bird species, frugivores, insectivores, and non-migratory resident species were more negatively impacted than migratory and smaller bird species. Tropical species were also found to be more sensitive to land-use change than temperate birds (Newbold et al. 2012; Bregman et al. 2014). Further, bird communities often responded to land-use change in non-linear ways, with thresholds for minimum habitat sizes (Bregman et al. 2014). The observed effect size and magnitude of the change in avian communities depends on the original and altered landscapes.

Land-use change, whether it be part of bioenergy development or urbanization, will continue worldwide so it is critical to understand species responses to lessen negative effects. Much of the existing research on land-use change focuses only on the species and does not consider the impacts to biodiversity-dependent ecosystem services. The gradual loss of species, community simplification or species extinction that provide ecosystem services may contribute to the loss of biodiversity-dependent ecosystem services, like pollination, pest control and seed dispersal ecosystem services (Isbell et al. 2011; Mace et

al. 2012). Indeed, species-rich areas maintain greater ecosystem resilience and functions at multiple trophic levels than species-poor area (Byrnes et al. 2015), and these effects can compound over time (Cardinale et al. 2012). The careful integration of commodity production and conservation action can minimize the impacts to biodiversity and ecosystem services without impacting human well-being or economic profitability (Daily et al. 2009; Cardinale et al. 2012; Howe et al. 2014; Posner et al. 2016).

Dissertation format and organization

Chapters 2-5 are intended for publication in peer-reviewed journals. Consequently, these chapters were organized and written in journal-specific styles, including framing the research question for different audiences. Each of these chapters contains the text, figures, tables, and literature cited necessary for publication. The preface that precedes Chapters 2-5 explains the relative contributions of the multiple authors to each chapter. Chapter 6 is my summary of my research and thoughts on interdisciplinary team science. Appendix A includes the abstract and citation of other peer-reviewed publications that I contributed to as a co-author while part of this project. If published or under review prior to submitting my dissertation to the MTU Library, I noted the citation and copy-right information with a footnote on the first page of the chapter.

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2. Bird community responses to afforested eucalyptus plantations in the Argentine pampas ¹

Abstract

Land-use change driven by human population growth and economic activity will continue to impact both natural habitats and land currently being used for food, fiber, and fuel production. The effects of this conversion on economically important ecological services will in large part depend on how native biodiversity responds to these changes. We investigated how agriculture-related land use change influences the avian community in northeastern Argentina by examining common agricultural land uses (pasture/annual crops, young and mature large-scale eucalyptus plantations, mixed-use farms with citrus, blueberry and small stands of eucalyptus) and remnant native espinal savannas. In this region, afforested eucalyptus plantations represent a new land-use change from the land cover of pasture with intermixed annual crops that has dominated the region. In this mosaic, we used point counts to assess how avian diversity and community structure differed between land uses. Bird species richness was lowest in older plantations and highest in the espinal savanna, with the other land uses having intermediate richness. Abundance trends followed the same pattern, with low overall abundance in the plantations, intermediate levels for pasture/annual crops, and highest abundance in the espinal. Distinct bird community assemblages were strongly associated with each land use, and between young and mature eucalyptus stands. Birds can be useful indicators for biodiversity as a whole, and the depopulated and depauperate avian community within the eucalyptus plantations will likely lead to reduced provision of many ecosystem services in this region if the spatial extent of plantations continues to expand.

Introduction

It has been estimated that in the next 40 years, the human population will need to grow more food than was produced in the previous 10,000 years (The Economist 2015). In addition, global demand for wood as a raw material is expected to increase each year by between 1.3% and 1.8%, at least through 2030 (Gardiner and Moore 2014), and total plantation forest coverage worldwide is expected to reach 300 million ha by 2020 (FSC 2012). One of the greatest challenges facing biodiversity conservation in an era of rapid human population growth is understanding how land-use change related to commodity food and fiber production will influence species composition and persistence (Vitousek et al. 1997, Zimmer 2010). The 2005 Millennium Ecosystem Assessment highlighted understanding this relationship as a priority, and it is repeatedly identified as a key to retaining biodiversity and associated ecological services in sustainable production landscapes of the future (Pascual and Perrings 2007, Perfecto and Vendermeer 2010, Tomich et al. 2011).

Biodiversity supports many ecosystem functions, allowing the delivery of more than 25 cultural, provisioning, regulating, and supporting ecosystem services to humans (MEA 2005; Balvanera et al. 2006; Flynn et al. 2009; Thompson et al. 2009; Brockerhoff et al. 2013; Whelan et al. 2015). Among vertebrates, birds contribute to a number of essential ecosystem functions as a result of their taxonomic and niche diversity (Sekercioglu 2006). For example, birds provide essential and economically valuable ecosystem services such as pest control, seed dispersal, and pollination, in addition to the recreation value they provide to humans (for a full list see Sekercioglu 2006 and Whelan et al. 2015). In agricultural systems, birds aid farmers by consuming pest species, and, indeed, “economic ornithology” in the early 1900s was one of the

¹ Previously published, copy-righted material. See Phifer, C., Knowlton, J., Webster, C., Flaspohler, D. Licata, J. 2016. Bird community responses to afforested eucalyptus plantations in the Argentine pampas. *Biodiversity and Conservation* 26(13) 3073-3101

first attempts to directly associate biodiversity with tangible benefits to human agriculture and wellbeing (Kronenberg 2014).

The pampas, once one of the largest temperate grassland in South America, spans an area of more than 52 million ha (Solbrig and Viglizzo 1999). Since European colonization, much of the pampas grassland and savanna of northern Argentina has been converted to agriculture, including row crops and cattle pasture, with documented changes to the avian community (Gojman and Zaccagnini 2008, Giacomo et al 2010; Cerezo et al. 2011; Gavier-Pizarro et al. 2012; Codesido et al. 2011, 2013). This region was greatly modified by the introduction of modern-day agriculture and livestock grazing and it is now one of the most important areas for beef and grain production in the world (Miñarro and Bilenca 2008). Today, only 10% of the region's native grassland and savanna remains, with less than 1% protected (Henwood 2010; Medan et al. 2011); worldwide, remaining native grasslands and savannas continue to be targeted for conservation because of their rarity and continued conversion to agriculture and pasture (Henwood 2010; Azpiroz et al. 2012). The original pampas ecosystem contained espinal savanna, a habitat composed of short, shrubby native trees, mostly *Prosopis* and *Acacia* species, with a diverse community of associated bird species (Fig. 2; Bucher et al. 2001, Lewis et al. 2009). As with the region's grasslands, most of the espinal ecosystem has been transformed by agriculture and grazing with remaining espinal savannas scattered in small remnants within a vast agricultural matrix (Lewis et al. 2009).

In Entre Ríos province of northeastern Argentina, the already transformed pampas is now undergoing another potentially transformative land-use conversion: afforestation through planting of eucalyptus for pulp, building materials and wood pellets for biomass energy production (Baldi and Paruelo 2008; FAO 2010; Azpiroz et al. 2012). Eucalyptus plantations are expanding in Argentina partly as a result of policies that promote afforestation, and the Entre Ríos region is experiencing some of the fastest growth of this kind with unknown impacts on avian communities. Eucalyptus (mostly *Eucalyptus grandis*) is the dominant plantation tree in the region, though pine (*Pinus* sp.) is also present (INTA 2009). Most eucalyptus plantations are large-scale monocultures covering hundreds of hectares with even-density, even-aged stands and little understory vegetation. The spatial scale of these plantations closely mirrors the land ownership in the region, where individual owners often hold thousands of hectares of land. In some areas, however, average land holdings are smaller, with mixed-use farms of 10-50 ha with cattle, citrus and blueberries and less-intensively managed eucalyptus stands of 1-10 ha intermixed. This dichotomous landscape patterning also reflects a common global trend, for although some anthropogenic land-use change occurs on vast spatial scales, much land cover change for the foreseeable future will continue to involve spatially small mosaics of different cover types (FSC 2012). Birds may respond differently to not only land use change, but the spatial scale of these afforested plantations and eucalyptus stands.

For bird species adapted to native grasslands or diverse native forests, conversion to structurally and compositionally simplified commodity production of woody or agricultural species frequently leads to a loss or degradation of habitat quality (Fuller 2012), often resulting in replacement of one assemblage of birds by another with few shared species (Dias et al. 2013). Birds are highly vagile and thus many species have the ability to quickly monitor and respond to dynamic changes in land cover related to both management by humans and natural succession and aging of forests (Da Silva 1996), grasslands (Grant et al. 2004), and even agricultural lands (Vickery et al. 2001). The diversity of bird species and the dynamic nature of both natural and anthropogenic land-cover change have meant that generalities regarding how birds as a group are affected by land-use change, and particularly intensification of land use, have been difficult to identify (Warner 1994). Because birds can have a powerful influence on some ecosystem services (Wenny et al. 2011), changes in species richness and composition have the potential to greatly alter the functioning of such services (Kellerman et al. 2008; Flynn et al. 2009). Moreover, birds are one of the most cost-effective bioindicators for measuring the effects land-use change on broader biodiversity, which in turn, support additional ecosystem services (Gardner et al. 2007, 2008).

Recent scholarly debate regarding the effects of forest plantations on ecosystem services (e.g., Paquette and Messier 2010; Brockerhoff et al. 2013) highlight the importance of considering the landscape context of plantations and alternative land covers (Brockerhoff et al. 2008). For instance, afforestation of former

grasslands involves a major structural change in the vegetation, and is usually detrimental for grassland biodiversity but could potentially benefit forest-dependent species (Brocknerhoff et al. 2008). As an example, in South Africa the sharp contrast between the native grasslands and afforested plantations resulted in a negative impact of grassland bird species, even when plantations were small compared to the surrounding countryside (Allan et al. 1996). In forested areas, however, forest bird species may use exotic plantations, and such plantations may be preferable than farmland or other cleared landscapes (Lindenmayer et al. 2002; Deconchat et al. 2009). When evaluating the effects of expanding plantation forestry, another important consideration is the most likely alternative or previous land uses (Brocknerhoff et al. 2008). Although it can be interesting to compare tree plantations to native primary forest or native grassland, in many parts of the world, there is no realistic near term possibility of expanding the coverage of native forest or restoring converted grasslands, even if tree plantations were removed. Instead, where tree plantations are proposed or expanding, it is often more useful to compare biodiversity and ecosystem services provided by tree plantations to the types of land uses that would occur in their absence, such as farming or livestock grazing.

We examined one such landscape mosaic in Entre Ríos province, Argentina, where the traditional land use (pasture and annual crops) is rapidly being replaced by a novel land use (eucalyptus plantations), and how these land uses affect the avian communities and their associated ecological services. In this transforming landscape, we compared four common land uses in the region: 1) large cattle pastures (>100 ha) that rotate to annual crops, the dominant land use; 2) large-scale eucalyptus plantations (>100 ha); 3) mixed-use farms with citrus and blueberry fields, pastures and small eucalyptus stands (<10 ha); and 4) espinal savanna remnants. We also considered how eucalyptus stand age might impact avian diversity and whether a threshold existed for birds between young stands without canopy closure and older stands with closed canopies. We predicted that bird diversity would be greatest in the native espinal savanna and lowest in the large eucalyptus plantations, with intermediate levels of diversity in the pastures/annual crops and mixed-use farms, because the plantations are the most structurally different from the original mosaic grasslands and savanna that characterized the Argentine pampas for millennia prior to European arrival. Recognizing the rapid structural and microclimatic changes that accompany the growth of eucalyptus (de Souza 2010), we also examined how plantation age impacts the bird community by comparing bird diversity in older closed-canopy (10-15 years) and young (<4 years) open canopy eucalyptus plantations. We expected that young stands would show greater bird diversity than mature stands, again due to the greater structural dissimilarity between mature plantations and pre-European settlement grasslands. Finally, we tested for the presence and extent of edge effects produced by large-scale eucalyptus plantations by censusing birds along 1 km transects centered on the boundary between plantations and ungrazed grasslands. Because other studies have found that many open habitat birds avoid wooded boundaries (e.g., Coppedge et al. 2004; Fletcher 2005), we predicted that bird diversity would increase with increasing distance from the plantation.

Methods

Site description

We conducted our work in the Entre Ríos province of Argentina, near the city of Concordia (31°24'S 58°2'W). Our sites are located within the Mesopotamia region of the pampas, characterized by once extensive grasslands (Quattrocchio et al. 2008) that have been converted to pasture for grazing and fields for row crops. Climate in this region varies from a daily mean temperature of 12.6 C during the austral winter to 25.3 C during the summer, and more than 1,300 mm of rainfall annually (INTA 2015). This region contains hundreds of native grass and other plant species and approximately 300 breeding bird species (Krapovickas and Di Giacoma 1998), 60 of which are grassland specialists (Miñarro and Bilenca 2008), and nearly one hundred mammal species (Miñarro and Bilenca 2008). The province is bordered by the Río Uruguay to the east and the Río Paraná to the west, with low rolling terrain and loessic or clay sediments (Miñarro and Bilenca 2008). This region is now mostly composed of croplands (26.5%), rangeland (45.2%), managed pasture (5.5%) and afforested plantations (13.6%) (Viglizzo et al. 2006).

Large-scale eucalyptus plantation management generally consists of even-age stands with trees planted 4 x 2.5 m apart with stocking densities averaging 1000 trees/ha (Carpinetti et al. 1995). Planted seedlings are generally sprayed with insecticide to limit herbivory from insects and pruned and thinned as they grow. Trees are harvested at 10-15 years depending on site conditions and allowed to resprout from the stump post harvest (Carpinetti et al. 1995). Young eucalyptus stands usually contain grass and herbaceous plants, with the trees appearing shrub-like while older stands eventually produce a uniformly darker environment with almost no understory herbaceous or shrub vegetation layer. Generally, older eucalyptus trees have little branching below the canopy with compact canopy crowns at the top and almost no epiphytes, mosses or other micro-habitat features along the trunk.

Experimental design

We censused the avian communities in four common land uses throughout Entre Ríos province: 1) pastures used for livestock grazing and rotational annual crops near the town of General Campos; 2) large-scale eucalyptus plantations (>100 ha), adjacent to the Ubajay township; 3) small mixed-use farms with citrus, blueberry, pastures and small-scale eucalyptus stands (<10 ha) in the town of La Criolla; and 4) espinal savanna, outside of the town of Federal (Fig.1 and Fig. 2). Land cover was identified using 2013 satellite imagery, GIS software, and extensive ground-truthing. After identifying suitable areas, we contacted landowners and secured permission to work at these sites. Due to the landownership and land use patterns characterized by one exclusive land use at a time, it was not possible to use a block design. Instead, within each of our four focal land uses, we delineated four 300 m² plots at least 1 km from any other, at least 500 m from paved roads or rivers, and composed of $\geq 75\%$ of the target land use type. Within the large-scale eucalyptus plantations, we further demarcated three additional 300 m² plots of young, even-aged eucalyptus stands (≤ 4 years old) that had not achieved canopy closure and featured grass and herbaceous layers. The majority of the plantations we surveyed featured only mature stands nearing harvest age, and it was impossible to find young stands that were 1 km apart from each other or mature stands, but we surveyed these younger stands on separate days to temporally separate them.

Field methods

We conducted two rounds of point counts in each of the land use types and the younger eucalyptus stands. Weather prevented resampling at one espinal replicate during the second round, reducing our espinal sampling effort to 70 total points. One point in the mixed-use farms was excluded due to harvesting at the time of observation. For all other land uses, we completed 80 points counts, for a study-wide total of 459 points. In each 300 m² land use replicate, we randomly identified 10 point count locations that were ≥ 200 m from one another and >50 m from a cover type edge. Within the mixed-use farms, we used a stratified random sampling design to ensure coverage of all land use types in proportion to their abundance, including the smaller eucalyptus stands. We also tested for possible edge effects from large-scale eucalyptus plantations on bird communities by conducting 10 point counts at 100 m intervals along three 1000 m transects centered on the border of a large-scale eucalyptus plantation and adjacent ungrazed grasslands of El Palmar National Park (Fig. 6). Five of the points were in the mature eucalyptus and five were in the grasslands, and transects were ≥ 500 m from one another. For each land use type and transect, one of three observers (who trained together for one month prior to beginning sampling) completed 8-minute 25 m fixed-radius point counts at each point and noted all birds seen or heard within 25 m, excluding those flying overhead. We selected this conservative detection distance because, based upon preliminary experience, detections rates were variable across habitats and we wanted to be able to compare land uses without the influence of detection bias. Because we visited each site twice, it is unlikely that breeding birds went undetected during our counts. Counts were conducted from 1-19 September and 3-27 November 2014 during the breeding season for most local birds. The point counts began near sunrise and were completed within 4 hours, allowing two observers to complete two replicates in one day. All counts were conducted in clear, mild weather without rain, fog or excessive wind.

Data analysis

To examine how the different land-use types and eucalyptus stand age influenced avian species, we calculated species diversity and community composition. Species richness (S), Shannon's Diversity Index (H), Shannon's Evenness (E), and Simpson's Diversity Index (D) were calculated using the Row and Column analysis feature in PC-Ord 6.08 (McCune and Grace 2002) for each landscape replicate. Results were averaged and tested for significance using Kruskal-Wallis and post-hoc comparisons. We then used PC-Ord to describe bird community composition using the Nonmetric Multidimensional Scaling (NMDS) ordination technique. Land use was included as a categorical variable in the environmental matrix. For this analysis, young and old eucalyptus stands were coded as separate land uses. We used the maximum abundance for each species observed for each land use and ran the ordination with autopilot defaults, the "deep and thorough" option, and Sørensen (Bray-Curtis) distance with 250 iterations of real data and 250 runs of randomized data (McCune and Grace 2002). To identify species strongly associated with each land-use type, we used PC-Ord's Species Indicator Analysis function, which calculates an Indicator Value (IV) from 0 to 100 for each species based on abundance and frequency, with higher values for species with strong land-use fidelity (Dufrene and Legendre 1997; McCune and Grace 2002). The IVs were then tested with a Monte Carlo test for significance using an α -value of 0.05. Finally, we evaluated potential edge effects on bird communities using non-linear regression as implemented in SigmaPlot 13 (SigmaPlot 2015), with distance from plantation edge as our independent factor and bird species richness and abundance as our dependent factors. We chose non-linear regression because visual inspection of the data suggested a pronounced sigmoidal tendency.

To better understand potential ecological services provided by birds associated with different land uses, we classified birds by diet guilds. Given the limited availability of detailed locally relevant diet information for each species, we used broad diet guilds (carnivore, omnivore, insectivore, nectivore, granivore, or frugivore) based upon the Handbook of the Birds of the World online database (del Hoyo et al. 2014). We evaluated differences in bird abundance by diet with a non-parametric Kruskal-Wallis test since our data failed to meet ANOVA assumptions (SigmaPlot 2015).

Results

From both rounds of point counts across all land uses and line transects, we detected 107 bird species and 2,134 total individuals (Appendix A). We recorded approximately 35% of the estimated 300 birds in this region of Argentina (Krapovickas and Di Giacomina 1998) and approximately 11% of the 979 confirmed species in the nation of Argentina (Narosky and Yzurieta 2010). Species richness and abundance varied greatly between land use types (Table 1; Fig. 3 and 4), with fewer species detected in older eucalyptus stands compared with all other dominant land uses in the region, including young eucalyptus stands, which contained nearly twice as many birds species as older stands (p -values < 0.001). Pasture and annual croplands, the dominant land uses in the region for at least three centuries, had similar numbers of species and individuals compared to smaller scale mixed-use farms. In contrast, the espinal savanna had the highest levels of both species richness and individual abundances of all land uses, with 27 species found only there, and never in the other habitats surveyed.

In addition to differences in species richness and abundance, each land use was characterized by a distinct avian community (Fig. 5). The NMDS ordination for the bird community assemblages resulted in a two-dimensional solution with a final stress of 11.98 following 62 iterations, a reliable and interpretable score (McCune and Grace 2002). The final solution cumulatively explained 85% of the variation in community composition. Although pasture and annual crops and mixed-use farms had similar abundance and richness estimates, the bird communities in each were distinctly different (Fig. 3 and 4). Bird species associated with pasture and annual crops, an area characterized by low stature vegetation, were very different from the mixed-use farms, where most bird species were habitat generalists with shared affinities for other land habitats. The relatively depauperate bird community associated with the older eucalyptus stands was distinct from the historically dominant pasture and annual crop landscape. Young eucalyptus stands

contained an avian community that resolved between pasture/annual crops and mature eucalyptus stands. The remnant espinal landscape had the highest bird species richness and a highly distinct bird community with many species with high site fidelity.

The species indicator analysis identified 23 species with significant IVs, indicating strong affinities with particular land use types (Table 4). The espinal contained the most species with statistically significant IVs (15 species). This was followed by pasture/annual crop that had 5 significant indicator species. The remaining significant indicator species were associated with mix-use farms. No significant indicator species were found for old or young eucalyptus stands.

The boundary between any age eucalyptus and unmanaged grassland and savannas of El Palmar National Park represented a dramatic change in bird species richness and abundance (p -value < 0.001; Fig.7). Within the plantations, we detected 11 species and 59 individuals; in contrast the adjacent grassland yielded 48 species and 340 individuals. Among non-linear curve families available in Sigma Plot 13, a three-parameter sigmoidal curve model for both abundance and richness provided the best representation of the relationship between plantation edge and species richness and abundance, respectively. The transects within the plantation were universally low in bird diversity, while the grassland transects showed a strong sigmoidal pattern of increased abundance and species richness beyond the plantation edge and continuing into the ungrazed grasslands (Fig.7). The sigmoidal pattern suggests a localized effect of low bird species richness and abundance within the plantation, effects that do not extend far beyond the edges of the eucalyptus plantation.

Bird abundance by diet guild varied by land use type (Fig.8). Within mature eucalyptus stands there was no significant difference in diet guilds, but young eucalyptus stands contained more omnivorous birds (p -value = 0.037). Pasture/annual crops supported near equal numbers of granivores and insectivores, and far fewer carnivores or omnivores (p -value = 0.005). Mixed-use farms had a similar trend for granivores and insectivores as well as omnivores, although there were fewer frugivores and carnivores (p -value < 0.001). As with species diversity measures, espinal savanna supported high levels of diet guild diversity (p -value = 0.002). Across all land uses the mean relative abundance of species also varied (Fig. 9). We found the majority of carnivores (i.e. raptors) within young and mature eucalyptus plantations compared to other land uses, accounting for more than 50% of all carnivores in the study area. Pasture/annual crops contained both insectivores and granivores in near equal proportion. Mixed-use farms had a diverse group of dietary guilds as well as high abundances of granivores and insectivores. Insectivores were the most common dietary guild in the espinal savanna, accounting for 50% of all the insectivores birds surveyed. The espinal also contained high abundances of granivores, and was the only landscape to contain nectivorous hummingbirds. Frugivores were present in mixed-use farms and the espinal savanna, but were absent from the plantations and grasslands.

Discussion

Implications of expanding afforestation on avian communities and ecosystem services

In the agricultural mosaic of the Argentine pampas, land available for strict preservation is very limited, suggesting that there is a need to understand how this working landscape can be managed to provide benefits for both humans and biodiversity. We found that in this region, new and expanding large-scale monocultures of eucalyptus are associated with a sharp reduction in both bird abundance and diversity, even when compared with other relatively intensive land uses like cattle grazing and annual crops. The continuing expansion of eucalyptus plantations, particularly large-scale plantations, will likely result in the simplification and loss of avian biodiversity and their associated ecosystem services. Pest control, seed dispersal and pollination—three important ecological and economic ecosystem services, especially in an agriculturally dominant region such as the Entre Ríos province—will likely be impacted.

Other studies in the region comparing bird communities in eucalyptus plantations to native vegetation have also found lower biodiversity in plantations, especially when plantations contrasted structurally with the surrounding area's vegetation (Dias et al. 2013; Calviño-Cancela 2013). In our study, 16 of the 28 total species detected in large-scale eucalyptus plantations were detected only once, suggesting that few individuals of most species make regular use of the eucalyptus plantations. The four most common species we detected in the large-scale plantations were the ubiquitous Rufous-collared Sparrow (*Zonotrichia capensis*), followed by White-crested Tyrannulet (*Serpophaga subcristata*), Picazuro Pigeon (*Patagioenas picazuro*) and Roadside Hawk (*Rupornis magnirostris*), together accounting for more than 75% of all birds recorded within the plantations. Rufous-collared sparrows were commonly seen in flocks near the ground searching for seeds and insects, and White-crested Tyrannulets were regularly encountered near plantation edges hawking for insects from branches near the canopy. Both species are generalists and are commonly observed near human habitation and in altered landscapes (Bellocq et al. 2011; Leveau and Leveau 2012). Among raptors, Roadside Hawks are opportunistic consumers and habitat generalists, and may benefit from the availability of perches and roost sites provided by eucalyptus in a region where trees are rare. Eucalyptus has been linked to the expansion of other birds of prey, notably Swainson's Hawks (*Buteo swainsoni*), likely for these same reasons (Sarasola and Negro 2006). We also detected two other species of raptor using the eucalyptus as perches; Aplomado Falcon (*Falco femoralis*), a species usually associated with grasslands, and Chimango Caracara (*Milvago chimango*), a generalist carnivore and scavenger. These raptors were regularly seen perched in the high canopy, scanning adjacent landscapes for prey.

Within the large-scale eucalyptus plantations, younger stands that had not achieved canopy closure had nearly twice as many bird species and almost three times as many individuals as mature stands, though the two eucalyptus age classes shared eight common species. Similar patterns were found in afforested eucalyptus plantations in Uruguay, with some grassland species detected within young stands, likely because of the presence of taller, ungrazed grass (Dias et al. 2013). Structurally, young eucalyptus are more similar to the pastures/annual crop landscapes and mixed-use farms than the taller, closed-canopy mature eucalyptus stands that have little or no grass or understory and limited micro-habitat features. Interestingly, we identified three species of grassland specialists within the younger stands, including the near-threatened Greater Rhea (*Rhea americana*) (BirdLife 2012a). In addition, based on our incidental observations, some bird species appear to be able to utilize these younger stands for nesting. In the young stands we observed one Greater Rhea nest with more than 20 eggs, and the Grassland Sparrows (*Ammodramus humeralis*) were responsive to audio playback, suggesting they were defending established breeding territories.

We found that, in contrast to the large-scale plantations, small-scale eucalyptus stands within mixed-use farms supported a relatively high level of bird species richness and abundance. Although we lacked sufficient replication to test this statistically, within the smaller eucalyptus plantations, which were all older stands, we detected 26 species of birds, twice the number found in the older large plantation stands, suggesting that small stands of old eucalyptus may be more useful as bird habitat than large stands of old eucalyptus. This observation may be a result of plantation size or the less intensive management we observed in small-scale plantations (e.g., less pruning, weeding and thinning). For example, anecdotal evidence suggests these stands contained more understory herbaceous plants and shrubs, and had greater structural diversity; potentially providing better habitat than more intensively managed, manicured plantations (Marsden et al. 2001). These results contrast with related work in South Africa where even small amounts of afforested plantations negatively impacted bird communities (Allan et al. 1996), perhaps because the mixed-use farms featured more generalist species with greater capacity to adapt to land-use changes. Including the other bird species, we recorded in the citrus, blueberry and surrounding pasture of the mixed-use plots, 44 species were detected in the small ownership landscape. These mixed-use farms had 18 species of insectivore, accounting for 26% of the total bird abundance, suggesting a strong potential for avian-delivered pest management. This small ownership landscape resembles some agro-forestry based production systems and appears to support greater biodiversity and ecosystem service provisioning than the current dominant large-scale monocultures of even-aged dense stands. Other agro-forestry systems in the tropics have also been shown to support greater bird diversity than monocultures, delivering tangible pest-control services to area farms (Van Bael et al. 2008, Karp et al. 2014).

Interestingly, in some parts of the world where tree plantations are more similar to the surrounding area vegetation, plantations can support comparable levels of biodiversity to native forest, as in Patagonia in southern Argentina where exotic pine plantations provided habitat for many native forest species (Lantschner et al. 2008). Similarly, in Brazil plantations of *Araucaria angustifolia*, a native tree, maintained more than 90% of the bird species of the nearby native forests (Volpato et al. 2010). In the case of afforested plantations that replaced pasture and rangeland, we found a very different relationship. The area's pasture and croplands supported a diverse and distinct bird community with 41 species, three times as many birds as in the mature eucalyptus plantations. Most of the bird species associated with the pastureland were common generalists that appear to be tolerant of cattle grazing, including eight species that are noted grassland specialists, often in the taller parts of the fields. Our results are consistent with other work where plantations replace grasslands, steep and open-area habitats, which effect a shift in avian communities and decline in bird diversity (Allan et al. 1997; Lantschner et al. 2008).

Although the region's current dominant land use remains pasture and annual crops, historically the espinal was more prevalent on the landscape (Lewis et al 2006). The espinal savanna contained more than 40% of all the bird species detected in this study, including many species undetected in other habitats. The espinal's shrubby trees provide habitat for many woodland associated species. Anecdotally, we noted that the trees of the espinal have many cavities and crevices, lichens and epiphytes, all elements of structural diversity that are absent in the smooth-barked and uniform eucalyptus plantations. For instance, three species of hummingbirds were often seen foraging on epiphytic flowers growing on the espinal trees, a resource absent within the plantations.

In most of the landscapes we surveyed, we encountered common species, but several rare species and species of concern were also counted. We detected several Dark-throated Seedeaters (*Sporophila ruficollis*) in the pastureland, a species of concern (Birdlife 2012b), and considered to be declining because of increasing agricultural intensity and forest plantations in the region (Fillooy and Bellocq 2006; Birdlife 2012). The Greater Rhea, also a species of concern, was regularly observed near the plantations, though generally, in the younger stands. If afforestation in the region continues, however, at some point the avian community associated with pasture/annual crops may drift towards the depopulated community found in large-scale eucalyptus plantations. In addition to the birds detected during the point counts, we twice encountered a male and female yellow cardinal (*Gubernatrix cristata*) in the espinal savanna, an endangered species on the IUCN's Red List (BirdLife International 2013). The presence of this species, listed as rare in Argentina (BirdLife International 2013), underscores the conservation value of this habitat and warrants further study.

Edge effects of afforestation on pampas bird communities

Adjoining habitats, whether natural or resulting from anthropogenic activities, can create species interactions and novel patterns of biodiversity that can both enhance and harm individuals living in such zones (Lay 1938, Gates and Gysel 1978, Fagan et al. 1999, Flaspohler et al. 2001a, 2001b). The abruptness of the change in plant and animal communities is sometimes termed the "hardness" of the edge, and, in this study, mature eucalyptus plantations adjacent to grassland is clearly a hard edge based on both plant species structure and composition. Not surprisingly, we found that the greatly simplified vegetation community of the plantations was associated with a similarly simplified avifauna. Our results are consistent with related work that found mature eucalyptus stand edges were "hard" when contrasted with relatively more open areas, possibly the result of the visual obstruction caused by the uniformly tall trees and darker understory (Reino et al. 2009). Interestingly, bird species richness in the grassland immediately next to mature eucalyptus remains as high or higher than areas farther from the plantations and deeper in the "pure" grassland habitats. This is not simply a result of overlap of two distinct bird communities, one associated with eucalyptus and another with the open grasslands. Rather, it suggests that for birds using the more natural native open habitats in this region, the mature eucalyptus plantations do not have a repellent influence beyond their boundary. It will be important to evaluate the influence of proximity to this edge on bird survival and reproduction and the dynamics of the boundary during the harvest, growth, and rapid

maturity of the eucalyptus plantations. Recent studies have found that in some landscapes, hard edges are associated with higher bird nest predation rates compared to soft edges with lower contrast between adjoining vegetation (Schneider et al. 2012).

Management recommendations and future research needs

In the foreseeable future, growing demand for timber and pulp, and government policies that favor conversion to eucalyptus will continue to drive expansion of this species in the Entre Ríos province of Argentina, and indeed in many other parts of South America (Jobbagy et al. 2012). In order to improve biodiversity conservation and mitigating potential ecosystem service losses, we recommend evaluating the effectiveness of both stand-level and landscape level conservation strategies, since birds perceive and respond to both scales (Moreira et al. 2005). Within plantations, we recommend integrating greater habitat heterogeneity within and adjacent to plantation stands as well as managing landscapes with a mix of young and mature eucalyptus stands. We found that younger stands of eucalyptus supported more species and in greater abundance, as well as a community that is more similar to both the mixed-use farms and older eucalyptus stands. Plantation managers should try to balance the coverage of young and older stands to mitigate some of the biodiversity loss within aging stands of eucalyptus. Biological legacies such as the yatay palms (*Butia yatay*), which are endemic to the region, should be left standing whenever possible, and we recommend studying the feasibility of habitat enhancements such as corridors and gaps to facilitate understory vegetation and a light environment more similar to the pastures and grasslands, which has been demonstrated to improve avian biodiversity in afforested eucalyptus plantations in Brazil and pine plantations in Spain (Diaz et al. 1998, Barrientos 2010; Millan et al. 2015). Related work in pine plantations in Chile, for instance, found that the presence of native understory vegetation resulted in increases in bird biodiversity and ecosystem services, particularly pest management by insectivore birds (Poch and Simonetti 2013). In this system, the understory vegetation is thought to “soften” the barriers between the plantations and the surrounding matrix, facilitating the movement of individuals (Tomasevic and Estades 2008).

We also recommend studying the adoption of silvopastoral systems with reduced eucalyptus density and complementary cattle grazing. A “win-win” situation was found in the Argentine Chaco forests with intermediate cattle density and forest tree density that conserved much of the area’s avian diversity while still being profitable (Mastrangelo and Gavin 2012). The espinal system we studied, for instance, is partially grazed by cattle, and yet still features a rich avian community. Beyond the plantation, our results on possible edge effects suggest that bird diversity quickly rebounds, and managers may designate some land reserves for birds and other species, adopting a “land-sparing” strategy for biodiversity conservation in this intensely used landscape.

Our work is the first to consider how avian communities change in response to afforested plantations in this region. Eucalyptus plantations are widespread and expanding in the global southern hemisphere. We compared land uses broadly, but further studies should consider specific habitat measures that may influence stand-level species occupancy. Our research also did not consider within season variation between migrant and resident birds and how land use influences these intra-season communities, which may respond to land use differently. Additional work is also needed to determine the demographic responses of birds to these novel afforested plantations. For example, related work in the pampas found low rates of bird reproductive success in heavily modified agricultural areas that are similar to the pastures and annual crops that surround many of the large-scale eucalyptus plantations (Pretelli et al. 2015). Finally, future research should investigate the extent to which these afforested eucalyptus stands act as barriers to the movements and dispersal patterns of grassland birds. In other systems, monocultures of even-aged stands of trees that were structurally similar to the surrounding forest were demonstrated to impact forest birds’ movement patterns (Villard and Haché 2012), and we expect that the contrasting structural and light environment of mature eucalyptus plantations could deter grassland bird movements.

Conclusions

We considered the potential impacts of land-use change associated with afforested large-scale eucalyptus plantations on avian biodiversity. In Entre Ríos, the expansion of the current model of large-scale, eucalyptus monocultures will likely result in simplification of avian communities and reduced ecosystem benefits provided by these birds. Other land uses in the region, including mixed-use farms, traditional pasture/annual crops and native espinal savanna, supported higher levels of avian diversity with distinct communities. Land-use change also impact dietary guilds of birds, which may influence delivery of bird-dependent ecosystem services. Other ecosystem services, which are often but not always related to biodiversity, including carbon sequestration, nutrient cycling, timber production, water regulation, and recreation, should be considered when evaluating the cost of land-use changes associated with afforested eucalyptus plantations (Polasky et al. 2010; Goldstein et al. 2012; Carreño et al 2012).

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Tables

Table 1 Mean bird species richness (*S*), Shannon's Evenness (*E*), Shannon's Diversity Index (*H*), and Simpson's Diversity Index (*D*) values for each land use type in Entre Ríos province, Argentina. Parentheses show associated standard errors.

Land use	<i>S</i>	<i>E</i>	<i>H</i>	<i>D</i>
Mature eucalyptus	6.8 ± 0.85	0.96 ± 0.01	1.82 ± 0.12	0.82 ± 0.02
Young eucalyptus	11.7 ± 1.20	0.89 ± 0.06	2.18 ± 0.22	0.83 ± 0.06
Mixed-use farms	22.8 ± 2.56	0.91 ± 0.04	2.83 ± 0.16	0.91 ± 0.03
Pasture/annual crops	20.5 ± 2.60	0.94 ± 0.01	2.82 ± 0.14	0.93 ± 0.01
Espinal savanna	36.3 ± 3.25	0.96 ± 0.00	3.44 ± 0.09	0.96 ± 0.00

Table 2 Bird species identified as significant ($p \leq 0.05$) indicators of land use type in Entre Ríos province, Argentina. Indicator values are provided in parentheses (these values scale from 0 to 100, with a value of 100 suggesting perfect indication). Mature and young eucalyptus stands had no species with significant IVs.

Mature Eucalyptus	Young Eucalyptus	Pasture/Annual Crops	Mixed-use Farms	Espinal Savanna
-	-	Spotted Nothura (100)	Sayaca Tanager (75)	Narrow-billed Woodcreeper (100)
		White-browed Blackbird (100)		Great Antshrike (100)
		Grassland Yellow-Finch (94)		Guira Cuckoo (89)
		Firewood-gatherer (59)		Southern Beardless-Tyrannulet (79)
		Southern Lapwing (58)		Brown Cacholote (75)
		Grassland Sparrow (50)		Lark-like Brushrunner (75)
				Masked Gnatcatcher (75)
				Pale-breasted Spinetail (75)
				Red-crested Cardinal (73)
				Golden-billed Saltator (64)
				Great Kiskadee (57)
				Green-barred Woodpecker (53)
				Rufous Hornero (50)

Figures

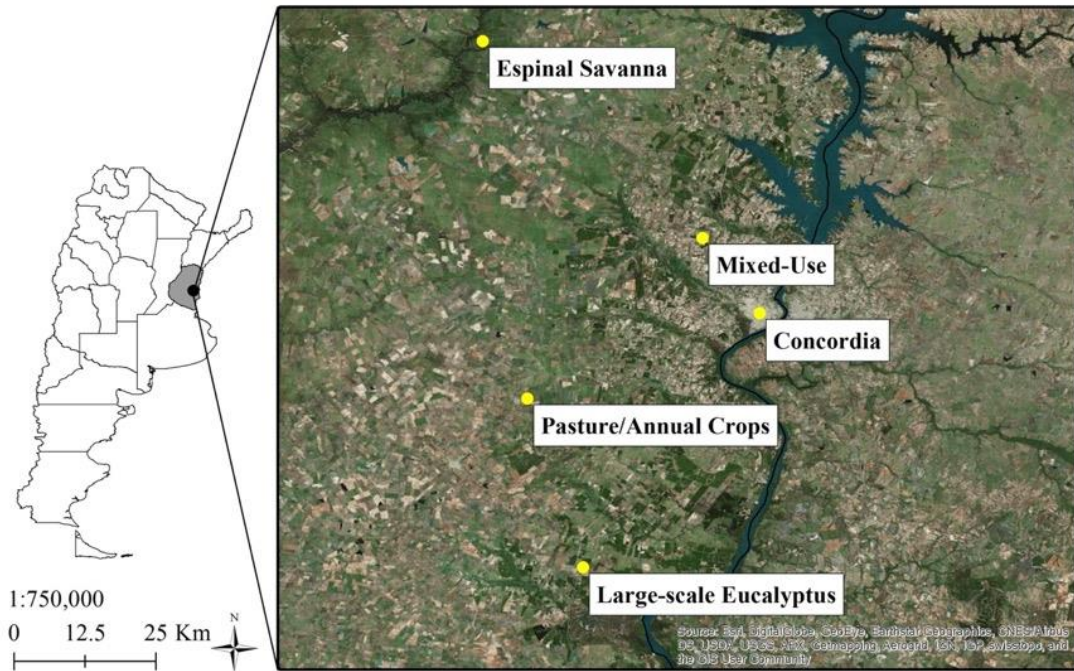


Fig. 1 Map of study site region in Entre Ríos province, Argentina. Research took place in the dominant land uses (pasture/annual crops, small mixed-use farms that include fructiculture, pasture and small stands of eucalyptus, large-scale eucalyptus plantations, both mature and young stands, and espinal savannas). Research was centered near the city of Concordia along the Río Uruguay.



Fig. 2 Examples of the dominant land uses sampled for this research: espinal savanna (top-left), large-scale mature eucalyptus plantations (top-right), mixed-use farms with blueberry (shown) and citrus fields (bottom-left), and managed pasture and annual crops (bottom-right). Young eucalyptus stands feature more understory diversity with more light and habitat heterogeneity. Photo credits: espinal, E. Adams; large-scale mature eucalyptus, J. Knowlton; pasture and mixed-use farms, C. Phifer.

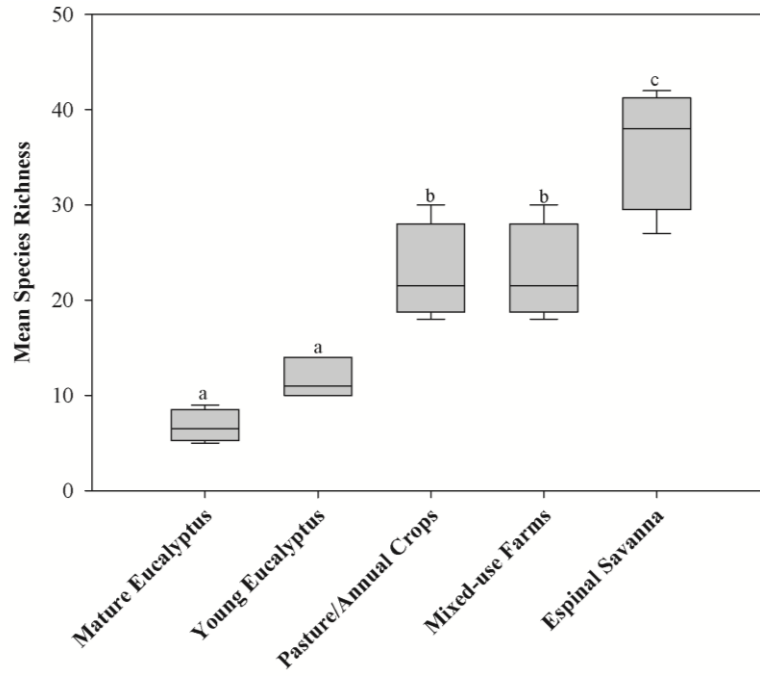


Fig. 3 Boxplots of mean abundance of bird species in five common land uses in Entre Ríos, Argentina. Lines represent minimum, first quartile, median, third quartile, and maximum. Same letters indicate no difference in mean abundance.

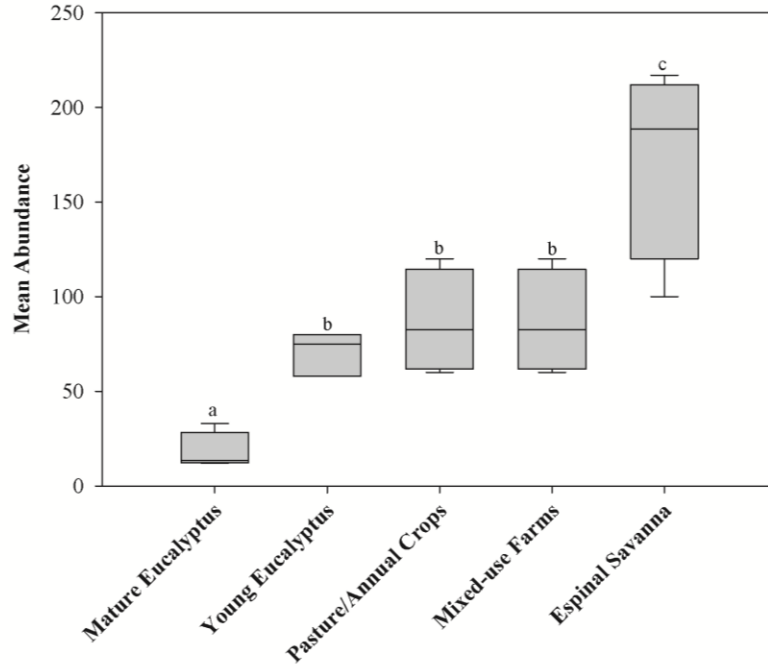


Fig. 4 Boxplots of mean bird species richness five common land uses in Entre Ríos, Argentina. Lines represent minimum, first quartile, median, third quartile, and maximum. Same letters indicate no difference in mean species richness.

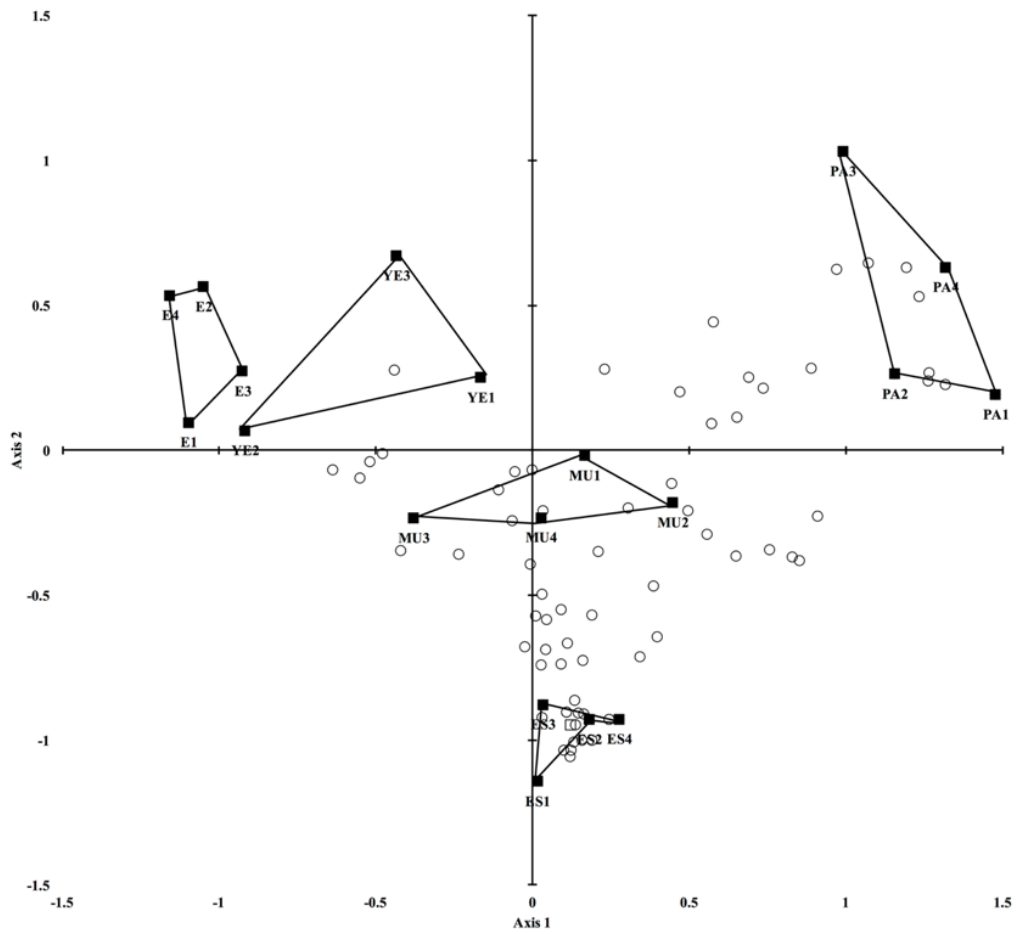


Fig. 5 NMDS ordination plot of bird communities in the pampas region of Entre Ríos province, Argentina. Circles represents individual bird species, and squares land-use replicates. Land uses are bounded by polygons for ease of visualization. Land uses are coded as follows: mature eucalyptus, ME; young eucalyptus, YE; mixed-use farm, MU; pasture/annual crops, PA; espinal savanna, ES.



Fig. 6 Property boundary between large-scale eucalyptus plantation and El Palmar National Park where line transects were completed, contrasting the plantation and native grassland of the park.

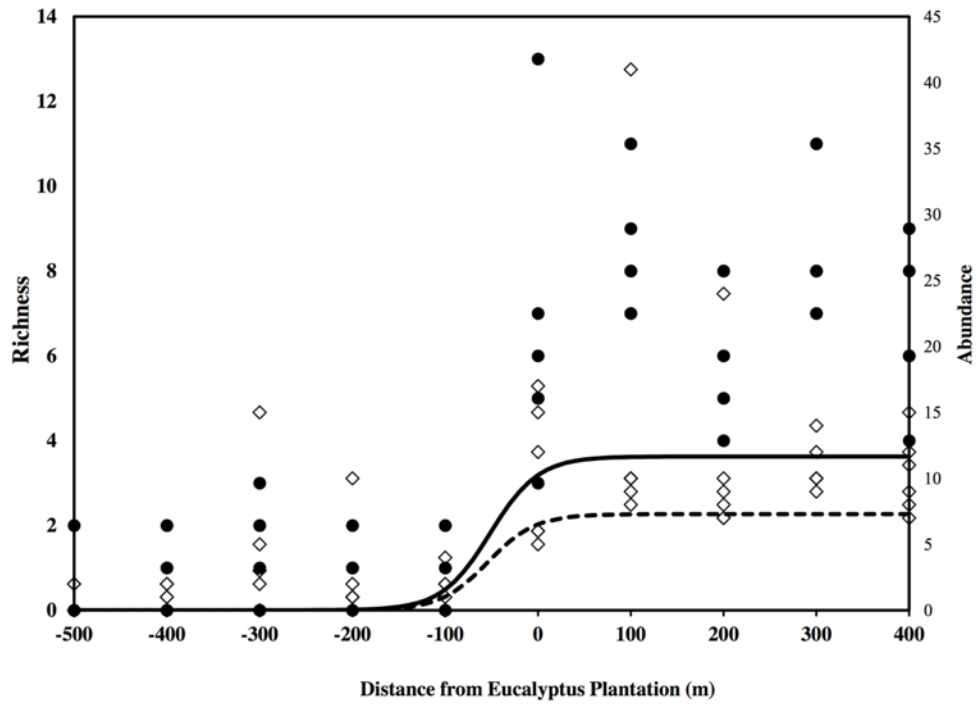


Fig. 7 Species richness and abundances of birds along three 1 km transects between large-scale eucalypts plantations and adjacent ungrazed grassland at El Palmar National Park. Negative values along the x-axis reflect distance inside the mature eucalyptus stands; positive values represent distances inside grassland; zero denotes the property boundary. The left axis, filled circles and solid regression line represent species richness; right axis, open diamonds and dotted line represent bird abundances. The equation for richness is as follows: $richness = 7.29 / (1 + \exp(-(\text{distance} - 54.17) / 25.46))$; abundance = $11.65 / (1 + \exp(-(\text{distance} - 51.68) / 26.00))$. Both equations are significant (p -value < 0.0001).

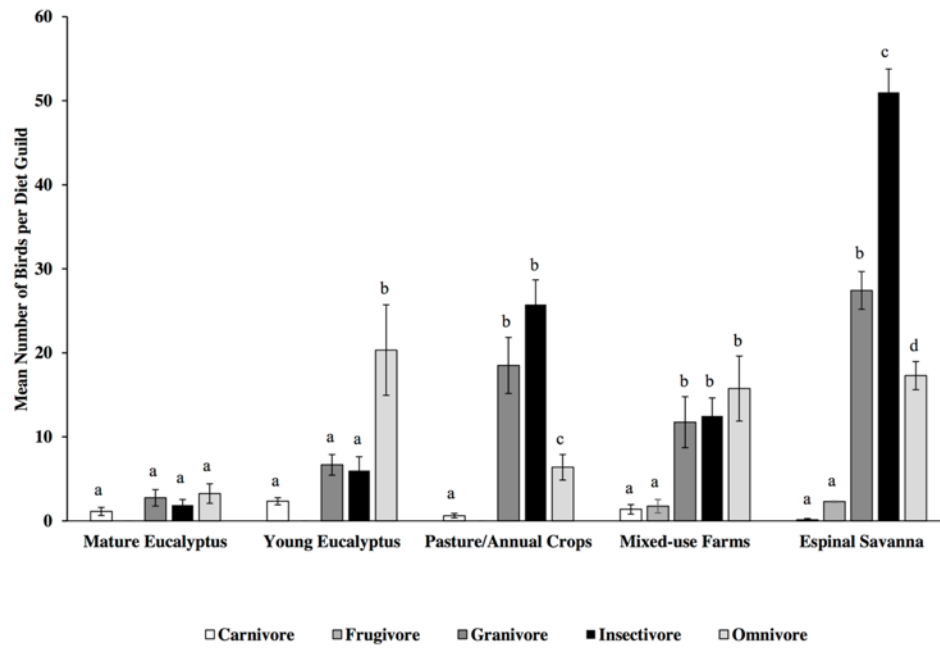


Fig. 8 Mean abundance of five diet guilds of birds across land use types in Entre Ríos, Argentina. Within each land use shared letters denotes no significant difference. Nectivores are not shown since they were only recorded in espinal savanna at low abundance.

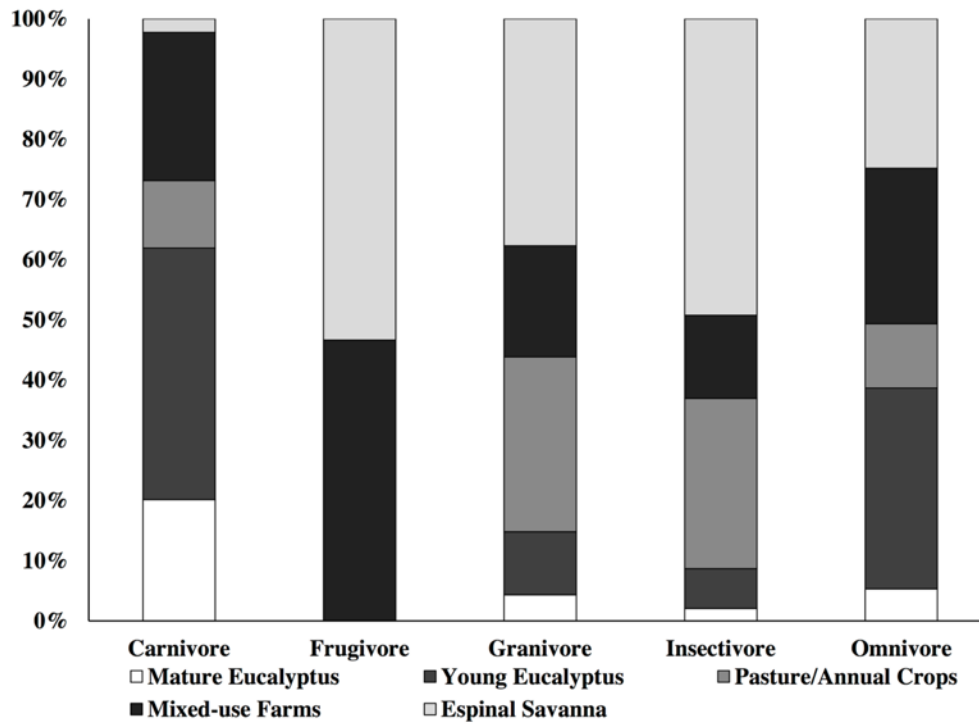


Fig 9 Mean relative abundance of five diet guilds of birds across all land use types in Entre Ríos, Argentina. Nectivores are not shown since they were only recorded in espinal savanna at low abundance

Appendix

Appendix A Complete species name, frequency of detection per land use, and diet guide for all birds detected in Entre Ríos, Argentina. Transects were divided by points within the eucalyptus plantation and grassland for comparison. Diet guilds were adopted from del Hoyo et al. 2014. Diet guides include carnivore, C; omnivore, O; insectivore, I; nectivore, N; granivore, G; frugivore, F; and U for unknown.

	Family	Species	Common English Name	Mature Eucalyptus	Young Eucalyptus	Pasture/Annual Crop	Mixed-use Farms	Espinal Savanna	Transect - Grassland	Transect - Plantation	Diet Guild
96	Accipitridae	<i>Accipiter bicolor</i>	Bicolored Hawk	0	0	0	0	0	1	0	C
	Accipitridae	<i>Buteo magnirostris</i>	Roadside Hawk	8	12	1	6	0	6	3	C
	Anatidae	<i>Amazonetta brasiliensis</i>	Brazil Duck	0	0	2	0	1	0	0	O
	Anatidae	<i>Dendrocygna viduata</i>	White-faced Whistling Duck	0	0	1	0	0	0	0	O
	Ardeidae	<i>Bubulcus ibis</i>	Cattle Egret	0	0	1	0	0	0	0	I
	Ardeidae	<i>Syrigma sibilatrix</i>	Whistling Heron	0	0	0	1	0	0	0	I
	Caprimulgidae	<i>Hydropsalis brasiliensis</i>	Scissor-tailed Nightjar	0	1	0	0	0	0	0	I
	Cardinalidae	<i>Cyanoloxia glaucocaeerulea</i>	Glaucous-blue Grosbeak	0	0	0	0	1	0	2	U
	Cardinalidae	<i>Saltator aurantirostris</i>	Golden-billed Saltator	0	0	0	12	41	0	24	G
	Charadriidae	<i>Vanellus chilensis</i>	Southern Lapwing	0	0	34	7	0	0	0	I
	Columbidae	<i>Zenaida auriculata</i>	Eared Dove	0	1	5	4	12	0	12	G
	Columbidae	<i>Columba picazuro</i>	Picazuro Pigeon	7	14	1	15	10	2	13	G
	Columbidae	<i>Columbina picui</i>	Picui Ground-Dove	0	1	7	2	1	0	1	G
	Columbidae	<i>Columba livia</i>	Rock Pigeon	0	0	1	0	0	0	0	G
	Columbidae	<i>Columba maculosa</i>	Spotted Nothura	0	0	14	0	0	0	0	O
	Columbidae	<i>Leptotila verreauxi</i>	White-tipped Dove	3	5	0	14	6	0	8	G

Cuculidae	<i>Guira guira</i>	Guira Cuckoo	0	0	0	1	10	0	0	O
Dendrocolaptidae	<i>Lepidocolaptes angustirostris</i>	Narrow-billed Woodcreeper	0	0	0	0	23	0	3	I
Dendrocolaptidae	<i>Drymornis bridgesii</i>	Scimitar-billed Woodcreeper	0	0	0	0	8	0	0	I
Emberizidae	<i>Volatinia jacarina</i>	Blue-black Grassquit	0	0	1	0	1	0	0	G
Emberizidae	<i>Sporophila caerulescens</i>	Double-collared Seedeater	0	0	2	3	0	0	2	G
Emberizidae	<i>Ammodramus humeralis</i>	Grassland Sparrow	0	3	31	6	0	0	0	G
Emberizidae	<i>Sicalis luteola</i>	Grassland Yellow-Finch	0	0	18	0	1	0	0	G
Emberizidae	<i>Embernagra platensis</i>	Great Pampa-Finch	0	0	1	0	0	0	1	G
Emberizidae	<i>Donacospiza albifrons</i>	Long-tailed Reed-Finch	0	0	0	0	0	0	1	I
Emberizidae	<i>Paroaria coronata</i>	Red-crested Cardinal	0	0	4	1	22	0	0	G
Emberizidae	<i>Coryphospingus cucullatus</i>	Red-crested Finch	3	2	0	3	1	0	3	G
Emberizidae	<i>Zonotrichia capensis</i>	Rufous-collared Sparrow	19	51	20	46	43	8	18	O
Emberizidae	<i>Sicalis flaveola</i>	Saffron Finch	0	1	5	1	9	0	4	G
Emberizidae	<i>Cyanocompsa brissonii</i>	Ultramarine Grosbeak	0	0	0	0	1	0	1	G
Falconidae	<i>Falco sparverius</i>	American Kestrel	0	0	0	3	0	0	0	C
Falconidae	<i>Falco femoralis</i>	Aplomado Falcon	1	0	0	0	0	1	0	C
Falconidae	<i>Milvago chimango</i>	Chimango Caracara	0	2	2	1	0	0	0	C
Falconidae	<i>Caracara plancus</i>	Southern Caracara	0	0	2	0	1	0	0	C
Fringillidae	<i>Carduelis magellanica</i>	Hooded Siskin	1	0	0	2	0	0	0	G
Furnaridae	<i>Pseudoseisura lophotes</i>	Brown Cacholote	0	0	0	0	6	0	0	I
Furnaridae	<i>Anumbius annumbi</i>	Firewood-gatherer	0	1	7	0	0	0	0	I
Furnaridae	<i>Phacellodomus sibilatrix</i>	Lark-like Brushrunner	0	0	0	0	4	0	0	I
Furnaridae	<i>Synallaxis albescens</i>	Pale-breasted Spinetail	0	0	0	0	9	0	1	I
Furnaridae	<i>Synallaxis frontalis</i>	Sooty-fronted Spinetail	0	0	0	3	7	0	3	I
Furnaridae	<i>Cranioleuca pyrrhophia</i>	Stripe-crowned Spinetail	0	0	0	0	6	0	1	I
Furnariidae	<i>Phacellodomus sibilatrix</i>	Little Thornbird	0	0	0	0	1	0	0	I
Furnariidae	<i>Furnarius rufus</i>	Rufous Hornero	0	0	12	14	44	0	6	I
Hirundinidae	<i>Progne tapera</i>	Brown-chested Martin	0	0	0	1	0	0	0	I
Hirundinidae	<i>Tachycineta leucorrhoa</i>	White-rumped Swallow	0	0	2	0	0	0	0	I
Icteridae	<i>Gnorimopsar chopi</i>	Chopi Blackbird	0	0	0	0	2	0	0	O

Thraupidae	<i>Poospiza melanoleuca</i>	Black-capped Warbling-Finch	1	2	0	2	7	1	5	G
Thraupidae	<i>Pipraeidea bonariensis</i>	Blue-and-yellow Tanager	0	0	0	1	0	0	0	F
Thraupidae	<i>Sporophila ruficollis</i>	Dark-throated Seedeater	0	0	4	0	0	0	0	G
Thraupidae	<i>Saltator similis</i>	Green-winged Saltator	0	0	0	0	0	0	1	I
Thraupidae	<i>Piranga flava</i>	Lowland Hepatic Tanager	6	1	0	4	1	1	1	I
Thraupidae	<i>Thlypopsis sordida</i>	Orange-headed Tanager	0	0	0	0	0	2	0	F
Thraupidae	<i>Thraupis sayaca</i>	Sayaca Tanager	0	0	0	7	2	0	5	F
Tinamidae	<i>Rhynchotus rufescens</i>	Red-winged Tinamou	0	1	2	0	0	0	0	O
Tinamidae	<i>Nothura maculosa</i>	Spot-winged Pigeon	0	0	0	2	13	0	1	G
Trochilidae	<i>Heliomaster furcifer</i>	Blue-tufted Starthroat	0	0	0	0	2	0	0	N
Trochilidae	<i>Hylocharis chrysura</i>	Gilded Hummingbird	0	0	0	0	1	0	0	N
Trochilidae	<i>Chlorostilbon aureoventris</i>	Glittering-bellied Emerald	0	0	0	0	1	0	1	N
Troglodytidae	<i>Troglodytes aedon</i>	House Wren	0	3	2	7	2	0	5	I
Turdidae	<i>Turdus amaurochalinus</i>	Creamy-bellied Thrush	1	1	0	5	3	4	26	I
Turdidae	<i>Turdus rufiventris</i>	Rufous-bellied Thrush	0	0	0	1	0	0	0	F
Tyrannidae	<i>Polystictus pectoralis</i>	Bearded Tachuri	0	0	1	0	0	0	0	I
Tyrannidae	<i>Machetornis rixosa</i>	Cattle Tyrant	0	1	3	1	0	0	0	I
Tyrannidae	<i>Empidonomus aurantioatrocristatus</i>	Crowned Slaty Flycatcher	0	0	0	0	1	0	0	I
Tyrannidae	<i>Tyrannus savana</i>	Fork-tailed Flycatcher	0	1	3	2	1	0	1	I
Tyrannidae	<i>Xolmis cinereus</i>	Gray Monjita	0	0	0	1	0	0	0	I
Tyrannidae	<i>Pitangus sulphuratus</i>	Great Kiskadee	0	0	1	8	17	0	1	I
Tyrannidae	<i>Elaenia parvirostris</i>	Small-billed Elaenia	1	0	0	2	5	0	3	I
Tyrannidae	<i>Camptostoma obsoletum</i>	Southern Beardless-Tyrannulet	0	1	0	0	9	0	2	I
Tyrannidae	<i>Sublegatus modestus</i>	Southern Scrub-Flycatcher	0	0	0	0	2	0	0	I
Tyrannidae	<i>Myiodynastes maculatus</i>	Streaked Flycatcher	0	0	0	2	0	0	0	I
Tyrannidae	<i>Suiriri suiriri</i>	Suiriri Flycatcher	0	0	0	0	5	0	0	I
Tyrannidae	<i>Myiarchus swainsoni</i>	Swainson's Flycatcher	0	0	0	1	5	0	0	I
Tyrannidae	<i>Euscarthmus meloryphus</i>	Tawny-crowned Pygmy-Tyrant	0	0	0	0	1	0	4	I
Tyrannidae	<i>Tyrannus melancholicus</i>	Tropical Kingbird	0	0	0	0	0	0	1	I
Tyrannidae	<i>Serpophaga subcristata</i>	White-crested Tyrannulet	6	15	0	3	7	3	11	I

Vireonidae *Hylophilus poicilotis* Rufous-browed Peppershrike 0 0 0 1 11 0 0 0

3. Impact of land-use change and afforested plantations on native bees in northeastern Argentina ¹

Abstract

In Entre Ríos province in northeastern Argentina, large-scale eucalyptus plantations are replacing ranchlands and annual crops, the dominant regional land use/land cover types. These afforested plantations represent a new land use in a region that historically was part of the vast Pampas grassland. Large-scale plantations of even-aged eucalyptus monocultures are likely to continue to expand in this region due to ideal growing conditions, strong markets, and increasingly favorable government incentives. To understand the effects of these plantations on native pollinators, we sampled for bees using pan traps in the eucalyptus plantations and three other common habitats in the region (pasture/croplands, smaller mixed-use farms, and native *espinal* savanna) for four months in 2014 during the austral spring. We then compared bee abundance, richness, and community structure between land uses. We identified 88 bee species among the 3,152 bees collected from all four habitat types. Relative to other habitats, eucalyptus plantations supported lower bee abundance and species richness. Smaller mixed-use farms had the highest observed abundance of bees, followed by pasture/annual crops and then *espinal* savanna. Bee community structure in each land use type was distinct with little overlap. Our findings demonstrate the impact of contemporary land-use changes on native bees, which provide valuable pollination services to crops and native plants in the region. Continued expansion of large-scale monoculture plantations may come at the expense of bee habitat and the critical pollination service they provide.

Introduction

Agriculture can alter land use and land cover (LULC) patterns across landscapes and broadly affect biodiversity (Newbold et al., 2015; Tscharntke et al., 2005). Agricultural development reduces and simplifies natural habitats leading to habitat fragmentation and homogenization (Foley et al., 2005). Reconciling agricultural expansion and intensification with biodiversity conservation and economic development remains one of the greatest challenges facing a growing human population.

In Argentina, land-use change associated with agriculture and other commodities has transformed much of the vast Río de la Plata grassland into an export-orientated agricultural landscape dominated by annual crops (e.g., soy and sorghum) and pastures for cattle, leaving a highly fragmented 10% of the original habitat (Medan et al., 2011) (Fig. 1?). In the last two decades, Entre Ríos province has experienced landscape-level conversion with afforestation from plantations for wood, pulp, and biomass energy (Azpiroz et al., 2012; Baldi and Paruelo, 2008). The total area of afforested plantations is

¹ This chapter is intended for *Agriculture, Ecosystems and the Environment* journal. Please see dissertation preface for details on authors' contributions.

expanding rapidly in Argentina (and, indeed, across South America) because of favorable policies that promote plantation forestry to increase the supply of domestic wood (Argentine law N° 25.080 & N° 26.432). Currently, more than 1.2 million ha of plantation forests exist in Argentina, providing more than 90% of the nation's timber (FAO, 2015).

Entre Ríos province, with its rich soils, favorable climate and low land prices, is experiencing some of the fastest growth of plantation forestry in the country, doubling since the 1980s and currently accounting for 13% of the nation's plantations (INTA 2009). In this region, most plantations are *Eucalyptus grandis*, which accounts for 88.5% of afforested plantations (INTA 2009), although *Pinus* spp. are also grown in areas unsuitable for eucalyptus. Afforested plantations alter vegetation by changing soil pH, soil microbes, light availability, and water cycles (Six et al., 2014). Plantations can also impact biodiversity by simplifying avian communities relative to other nearby habitats through lower abundances and species richness compared to other land uses and land cover types (Phifer et al., 2016).

The impact of afforested plantations on native bees and wasps is largely unknown; the majority of the research on plantations and bees has focused on honey bees (Malkamäki et al., 2016) or eucalyptus pest species like gall wasps (Aquino et al., 2011) with little information on plantations as habitats for pollinating bees. Understanding how wild bee populations respond to this type of LULC is critical because of the rapid expansion of tree plantations that now account for 277.9 million hectares worldwide, a full 7% of the Earth's forests (FAO, 2015). Wild bees provide important pollination services to many agricultural crops and wild plants, including important local crops in the Entre Rios area such as blueberries. Animal-assisted pollination is important for almost 90% of angiosperms (Ollerton et al. 2011), and insect pollinated crops provide essential calories (Klein et al. 2007) and micronutrients (e.g., vitamin A, iron, and folic acid) needed for human health (Chaplin-Kramer et al. 2014; Ellis et al. 2015). Economically, pollinators contribute to 75% of crop species, an ecosystem service estimated to be worth approximately \$215 billion worldwide (Gallai et al., 2009). In addition to managed honeybees, wild, unmanaged pollinators are a major source of this pollination service for many crops (Garibaldi et al., 2016). Even wind-pollinated crops, such as soy, see increased rates of pollination, fruit set and harvest yields because of pollinators, which are more common in adjacent natural and semi-natural habitats (Monasterolo et al., 2015).

The growth in demand for pollinator-dependent crops coincides with a worldwide decline in native and managed bee populations (Potts et al., 2010). The decline in bee populations is likely the result of the confluence of changes in landscape composition, agricultural intensification (Vanbergen et al. 2013), climate change (Miller-Struttman et al. 2015), diseases and invasive pests (Morales et al. 2013; Fürst et al. 2014; Graystock et al. 2015), and agrochemicals (Whitehorn et al. 2012; Rundlof et al. 2015; Hladik et al. 2016). These forces are often examined independently, but their independent effects are not easily understood because their effects are additive (Goulson et al., 2015). The

Intergovernmental science-policy Platform on Biodiversity and Ecosystem Services (IPBES) reported a decline in wild bees in North America and Europe (Potts et al., 2016) but less is known about South American bee populations, in part because few long-term bee monitoring has been accomplished in the region (Archer et al., 2014).

In this study, we examined how bees responded to afforested plantations compared to pasture/annual crops, small mixed-use farms and semi-natural native *espinal* savanna habitats in Entre Ríos province, Argentina. During the austral spring of 2014, we surveyed for native bees in these habitats in the region and compared bee species richness, abundances, and community structure. We hypothesized that bee species richness and overall abundance would be greatest in the native *espinal* savannas because it has been historically widespread in this region for eons, and because of its greater structural complexity and floral resources. Conversely, we expected the eucalyptus plantations to have the lowest bee biodiversity because of the homogenized environment and lack of floral and nesting resources, and pasture/annual crops and mixed-use farms intermediate to these land uses.. This research fulfilled an urgent need to further understand how bees may respond to the likely acceleration of planting afforest plantations and how biodiversity-dependent ecosystem services, such as pollination, may be impacted by land-use changes.

Materials and methods

Study area description

We conducted our research in the Entre Ríos province, Argentina, near the city of Concordia (31°24'S 58°2'W, Fig. 1). This generally flat area is crisscrossed by small streams that drain into Río Uruguay to the east and the Río Paraná to the west, with gentle rolling hills, and loessic or clay sedimentary soils (Bilenca and Miñarro, 2004). Daily mean temperature is 12.6 °C during the austral winter and 25.3 °C during the summer, and the region gets more than 1,300 mm of rainfall annually (INTA 2015). Agriculture is the dominant industry in region with three primary farm types: 1) expansive pasture for cattle grazing and annual crops (e.g. soybeans) that are often rotated annually; 2) large-scale eucalyptus plantations (>500 ha) are generally stocked at 1,000–1200 trees/hectare, which produces monocultures of dense, even-aged stands with little understory vegetation and closed canopies overhead; and 3) smaller family-owned mixed-use farms (generally <50 ha) with citrus, blueberry, nuts, and pastures with smaller eucalyptus stands (<5 ha), creating a mosaic of land uses in these areas. Lastly, remnants of the native xerophyte *espinal* savanna with endemic *Butia* spp. palms and sparse thorny, short-statured *Acacia* and *Prosopis* trees are present, though large, contiguous tracts are rare. Prior to European colonization, *espinal* savanna covered more of this landscape in this region, and although lightly grazed, it provides high-value habitat for birds ((Phifer et al., 2016).

Experimental design

We surveyed bee communities in the four common habitats that characterize the region's agricultural-based economy and account for over 90% of total land cover in the region (citation?)(described above; Fig. 1B). Each habitat type was first identified using 2013 satellite imagery and GIS software. With the help of local extension agents, we secured landowners' permissions for repeated pollinator sampling. For each agricultural land use, we delineated four 300 ha replicates with at least 75% of the 300 ha area being covered by the primary land cover. Each replicate was a minimum of one kilometer away from any other replicate. We identified two 300 ha replicates of the *espinal* savanna because it is a threatened habitat that persists mostly along riparian areas with only a few large contiguous parcels.

Bee sampling

Bee communities in each land cover type were sampled from September through December 2014 using pan traps, a standard technique used in North America (Lebuhn et al., 2012) and Europe (Westphal et al., 2008), and also used in Argentina for landscape scale studies (Le Féon et al., 2015). We sampled approximately once every three weeks for a total of five sampling periods; we adjusted our sampling to account for forecasted rain and storms to limit exposure. For each land-use replicate, we randomly selected four origin points and installed four 100 m transects with a 1-m high T-shaped wooden stake every 25 m (0, 25, 50, 75, and 100 m), for a total of five sampling stations per 100 m transect. If a randomly assigned point would impede normal farm operations or livestock were likely to disturb the pan traps, transects were relocated to the closest available safe location; in these cases, we moved our random point to the nearest location that would not be impacted by farm activities (i.e., on the other side of the fence away from cattle). In total, each land-use replicate had four transects with 20 sampling stations, and each habitat type had 80 sampling stations, with the exception of the *espinal* savanna, which only had 40 sampling stations. Each 100 m transect was at least 250 m from any other transect. At each sampling station, four 300 mL colored plastic cups (white, blue, yellow, and red) were pinned to the top of the stake (Fig. 2) following methods by XXXXX 2015?. Cups were modified to have drain holes near the lip of cup; we then installed a fine 1 mm mesh stapled across the holes to prevent any captured insects from washing out in the event of a sudden thunderstorm, which are frequent in the area during spring. Pan traps were filled with soapy water and left for four days each month. Insects were collected and stored in 70% ethanol and identified to the lowest taxonomic level possible, usually to species. Because we were interested in the bee community and not insect biodiversity *per se*, we focused our identification efforts on bee members of the Hymenoptera family. A reference library of bees with voucher species for these groups is stored at INTA Concordia Station.

Data analysis

We pooled all pan traps per transect and each transect was treated as an independent sample to sum observed abundance and richness totals for each habitat type. We calculated mean richness, evenness, and both Shannon's and Simpson's Diversity Indexes for all habitats. We used then EstimateS 9.1 software (Colwell 2005) to calculate estimators of species richness using first-order Jackknife estimates (Colwell 2013), and we constructed species accumulation curves for each land use type using random method permutations with 100 runs using EstimateS. To compare differences in observed bee abundance and species richness we tested for differences with a one-way Kruskal-Wallis and post-hoc testing because of the non-normal distribution of our data (Colwell 2013). Because our collection effort was uneven between habitat types (i.e., we often collected fewer traps than we set out because some were destroyed due to moving farm vehicles, livestock, and people) randomly selected 40 samples from the total samples collected per habitat type for this comparison.

To visualize the impact of land-use changes on the pollinator community, we ran a Non-Metric Multidimensional Scaling (NMDS) ordination, which simplifies the many interacting species and habitat variables into a simpler dimensional space that can be visualized. We parametrized the NMDS to run for 250 iterations and relativized each column by the most abundant species to smooth over differences between very abundant and less common species (McCune and Grace 2002). Finally, we performed a PERMANOVA test to evaluate for differences between habitat types and bee communities, using the same random samples used for richness and abundance and the four habitat types, followed by a post-hoc pair-wised test for differences,

The focus of our research was on wild bees and related Hymenoptera (i.e. wasps). Managed bees are also common in agricultural landscapes like ours and we observed commercial hives in all habitats and often caught European honeybees (*Apis mellifera*). Because of our broader focus on native bee communities' responses to land use and land change, we report abundance and richness values with and without European honeybees. For community level ordination analysis, we ran NMDS and PERMANOVA with and without honeybees, and, finding no differences in the results interpretation, we included them in the analysis for completeness. Statistics were calculated using R 3.3.2 using R Studio and PC-Ord 6.22 (McCune and Mefford 2011).

Results

We collected 31,951 insects from all land use replicates in our study area. We focused our identification effort on Hymenoptera, specifically pollinating bees, and amassed 3,152 bees from 88 species from six families, including 1,082 European honeybees. A complete species list is available in the Appendix 1.

Total bee abundance varied between habitats and seasonally, with more bees collected later in the season (Figs. 3A and 3B). Mean observed species richness was lowest in the

large-scale plantations at 3.4 (± 1.5 SE), a tenth of richness found in the pasture/annual crops and mixed-use farms that averaged 30.2 (± 13.5) and 28 (± 12.5) species, respectively. The *espinal* savanna supported intermediate levels of bee species with a mean of 17.8 (± 8.8) species (Tables 1 - 3 for all biodiversity metrics). Overall abundance patterns for all bees followed this trend as well. However, when honeybees were excluded from abundance totals, pasture/annual crops, had the greatest number of wild bees, with mixed-use farms second, followed by the *espinal* savanna and finally eucalyptus plantations with 22 wild bees collected (Table 3). Abundance patterns also varied across time for the four habitat we sampled with more bees collected in late spring (Figs. 3A and B, respectively), except for the plantations, which had a consistent low values throughout our sampling period. Species accumulation curves (Fig. 4) for bees show mixed-use farms and pasture-annual/crops were not different from one another, though both were greater than *espinal* savanna and higher than the plantation's curve.

We identified discrete bee communities within each habitat type. The NMDS resolved the bee species' community to a three-dimensional solution with a final stress level of 10.52 and zero instabilities after 135 iterations (Fig. 5). Cumulatively, the NMDS solution explained 75.6% of the variation in bee community composition. The PERMANOVA further reinforced the NMDS visualization of significant differences between the habitats and bee communities (Table 4).

Discussion

We found that large-scale plantations supported significantly fewer bee species compared to agricultural and natural habitats (pasture/annual crops, mixed-use farms and *espinal*) in the Entre Ríos region of Argentina. Our results support the hypothesis that the large-scale plantations support a depauperate bee community with the lowest relative levels of bee species richness and abundance, compared to other habitats sampled. Interestingly, the highest observed bee abundance was found in the mixed-use farms, with pasture/annual crops second and *espinal* habitat intermediate. Species accumulation curves showed similar trends as the observed richness, though mixed-use farms and pasture/annual crops curves overlapped. The large-scale plantation curve nearly leveled off, suggesting sampling was sufficient in his habitat while additional sampling would be needed for the other three. Our community ordination results suggest that the bee communities were responding to a strong ecological gradient across the landscapes we sampled, with distinct communities between them (Fig. 5; McCune and Grace 2002).

Our results are consistent with other studies that found that heterogeneous landscapes, such as the mixed-use farms in our study, support diverse group of bees (Kennedy et al., 2013; Winfree et al., 2009) while simplified habitats tend to support few bees (Mallinger et al., 2015). In Entre Ríos, most small-scale farmers plant blueberries, citrus trees, and nut trees along with small-scale eucalyptus stands, and they maintain patches of pastures for grazing. These smaller landowners are more reliant on pollinators for their livelihoods because both blueberries and citrus are pollinator dependent (Chacoff et al., 2010). These mixed-use farms also contained semi-natural or fallow lands that were not being actively

cultivated, which likely provide more nesting and floral resources for bees (Williams et al., 2010) than the actively managed annual croplands. We also collected the most honeybees on these mix-use farms, the majority of which are likely from managed hives, although we did observe at least one feral colony in the area.

We collected approximately 1% (24 total individuals and 14 species) of the total of all bees in the mature, large-scale eucalyptus plantations, which suggests that the expansion of these large-scale plantations may result in the displacement and possible loss of wild bees through habitat conversion. Although our collection effort was lower in the plantations, the fact that the species accumulation (Fig. 4) leveled off suggests our sampling was nonetheless sufficient to adequately survey this area. The pampas regions of Argentina and Uruguay are experiencing rapid land-use change and the conversion of predominantly pasture to plantations. Long-term effects may include the loss of bees and the pollination services they provide. Since 1990, the area of plantations in Argentina has grown from 766,000 ha to 1,202,000 (FAO, 2015), and recent changes to the Argentina forestation laws provide tax incentives for plantation forestry, which appears likely to lead to more conversion from pasture to plantations (Prosperi, 2013). The loss of bees within plantations is likely related to the lack of floral and nesting resources beneath the trees. These densely planted plantations provide few floral resources for pollinators directly, likely because of the allelopathic nature of eucalyptus, and light limitation and abundance of leaf litter that accumulates beneath the trees that limit seed germination. In addition, the plantations lack loose soil required for ground nesting bees and the trees themselves are not suitable for wood cavity nesters. Outside the tree stands, the plantations usually have wide, 10 m dirt roads with weedy flowering species and grasses that are nearly absent beneath the dense trees. These roadways and edge habitats likely provide some important floral resources and, along with adjacent pastures or other crops near the plantations, could serve as habitat for bees. Future work should consider a possible edge effects of the plantations, potentially with transect leading in and out of the tree stands, and how bee species perceive the plantation edges as “hard” or “soft.”

Here we considered how land uses and agricultural habitats impacts one important taxa group that provides an essential ecosystem service — pollination. Managed bees, wild bees, and other insect pollinators provide pollination services to crops, thus boosting yields (LG 2012, 2016). More broadly, biodiversity itself is a foundational part of ecosystem services (Foley 2009). Although pollination services are often provided by the most common and abundant species (Kleijn et al., 2015), other less abundant species support the whole ecosystem, and a healthy and abundant pollinator community can provide insurance against potential future losses of pollinators in the face of bee declines worldwide (Kleijn et al. 2015, Garibaldi et al 2013).

One limitation of our work is that we did not sample the plantations for bees when the eucalyptus trees flowered; therefore, we cannot assess the ecological value of canopy flowers to native bees. In Brazil, species of wild and managed bees utilized eucalyptus flowers based on pollen analysis, but that species of eucalyptus blooms year-round (Hilgert-Moreira et al. 2014). The species of eucalypt in our study area, *E. grandis*,

blooms for 6-8 weeks annually. These flowers provide nectar and pollen for managed bees and eucalyptus-flavored honey (“miel de eucalypto,” in Spanish) is considered a regional specialty, so much so beekeepers bring hives to the plantations when the flowers bloom. However, mass-flowering crops, like eucalyptus, can reduce pollination services to other crops and act as a pollinator “sink” during peak bloom periods potentially lowering pollination rates and harvests for adjacent pollinator-dependent crops (Holzschuh et al. 2011). In nearby Uruguay, *E. grandis* is being replaced by another faster-growing eucalyptus species that does not flower before it is harvested, and beekeepers there are concerned about the loss of the floral resources for their bees (Malkamäki et al 2016). Future research should also directly consider the value of eucalyptus flowers as floral resources for wild bees, and consider the trade-offs with other land uses that provide more consistent and year-round flowering.

This research reflects a snapshot in time, and, although our results are robust, long-term monitoring of how bee populations and communities fluctuate over time should be considered. This is particularly true in Argentina, where native bumble bee populations have declined (Morales et al., 2013) after the introduction of a non-native European bumble bee and its rapid range expansion (Geslin and Morales, 2015; Torretta et al., 2006). Additional sampling, including active netting and nest traps, should also be used to fully account for other species (e.g., large-bodied bees, parasitic species) likely present in this landscape but were not a large part of our sample due to well-known sampling bias of our pan traps that favors flower-visiting and smaller-bodied bees. These complementary methodologies would likely identify more species not collected in pan traps (Lebuhn et al., 2012).

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Tables

Table 1. Mean biodiversity metrics (\pm SEs) for collected bees from each habitat type for austral spring in 2014 in Entre Ríos, Argentina.

Land Use	Richness	Evenness	Shannon's Diversity Index	Simpson's Diversity Index
Large-scale Plantations	3.4 (\pm 1.5)	0.55 (\pm 0.25)	0.78 (\pm 0.35)	0.40 (\pm 0.18)
Pasture/Annual Crops	30.2 (\pm 13.5)	0.79 (\pm 0.35)	2.62 (\pm 1.17)	0.88 (\pm 0.40)
Mixed-use Farms	28 (\pm 12.52)	0.64 (\pm 0.29)	2.13 (\pm 0.95)	0.74 (\pm 0.33)
<i>Espinal</i> Savanna	17.8 (\pm 8.89)	0.76 (\pm 0.38)	2.16 (\pm 1.08)	0.80 (\pm 0.40)

Table 2. Observed species richness of all bees for each habitat from four months of sampling Sept. – Dec. 2014 in 2014 in Entre Ríos, Argentina.

Bees families	Large-scale plantations	Pasture/annual crops	Mixed-use farms	<i>Espinal</i> savanna
Andrenidae	1	6	5	0
Apidae *	5	30	26	19
Colletidae	1	0	2	0
Halictidae	6	25	24	10
Megachillidae	1	6	5	8
Total bees	14	67	62	37

* includes *A. mellifera*

Table 3. Observed abundance of all pollinators for each habitat from four months of sampling Sept. – Dec. 2014 in Entre Ríos, Argentina. European honeybees (*Apis mellifera* are separated from totals to see differences between managed and wild bees.)

Bees families	Large-scale plantations	Pasture/annual crops	Mixed-use farms	Espinal savanna
Andrenidae	1	7	16	0
Apidae *	9	92	373	196
<i>Apis mellifera</i>	2	175	786	119
Colletidae	1	0	3	0
Halictidae	10	542	303	115
Megachillidae	1	7	7	17
Total wild bees	22	1019	702	327
All bees	24	1194	1488	466

* excluding *A. mellifera* because it is a (likely) managed bee

Table 4. Results of permanova for differences in habitat types and bee communities. Evaluation of differences in species between groups. Design: One-way randomization test of significance of pseudo-F values. Number of randomizations: 4999 Random number seed: 2171 selected by time.

Source	d.f.	SS	MS	F	p*
Habitat	3	1440.4	480.13	5.8638	0.0002
Residual	156	12773	81.88		
Total	159	14214			
Pairwise comparisons	t	p			
Plantation vs. mixed-use	3.0846	0.0002			
Plantation vs. pasture/crops	3.2685	0.0002			
Plantation vs. <i>espinal</i>	2.7788	0.0002			
Mixed-use vs. pasture/crops	2.3932	0.0002			
Mixed-use vs. <i>espinal</i>	1.7741	0.0478			
Pasture/crops vs. <i>espinal</i>	1.7392	0.0036			

Figures



Fig 1. Map of study region with inserts of the common landscape habitats sampled for bees during austral spring in 2014 in Entre Ríos, Argentina. Upper right, eucalyptus plantation understory; lower right, pasture/annual crops; lower left, mixed-use farms; upper left, *espinal* savanna. Photo credits: C. Phifer.



Fig 2. Example of pan traps used for sampling bees and insect pollinators in Entre Ríos, Argentina. Left photo is within a eucalyptus plantation; right photo is near the fence line in pasture. Plastic cups were modified near the lip with drain holes with fine 1 mm mesh covering them, because of spring storms that could swamp the cups. Photo credits: C. Phifer.

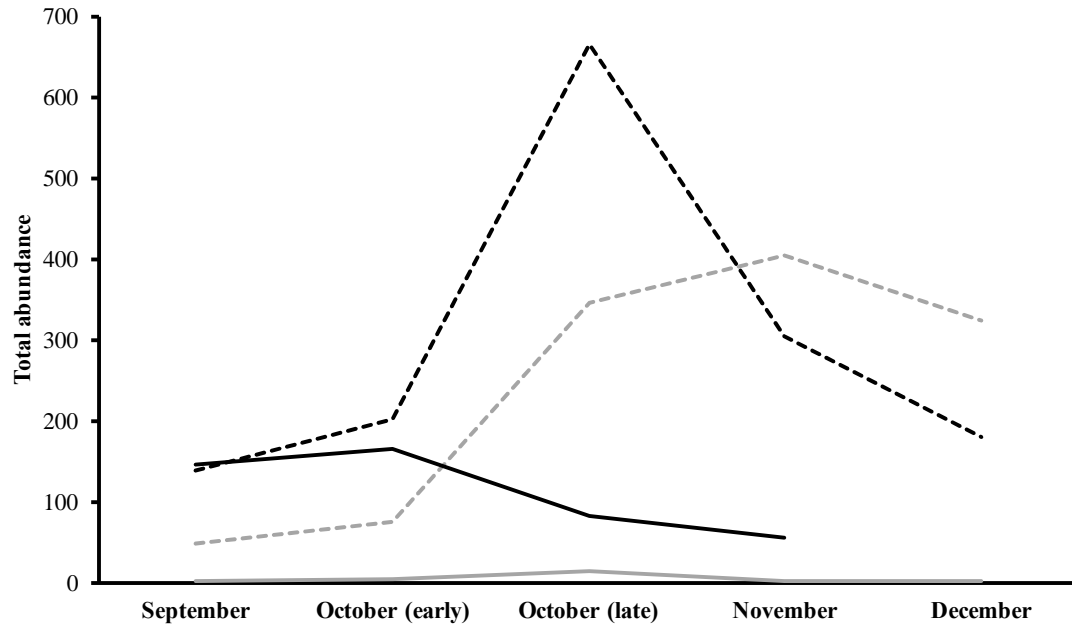


Fig. 3A Total abundance of all bees over the austral spring of 2014 in each habitat type in Entre Ríos, Argentina. Solid grey line is eucalyptus plantations; solid black line is *espinal* savanna; dashed black line is mixed-use farms; and dashed grey line is pasture and annual crops.

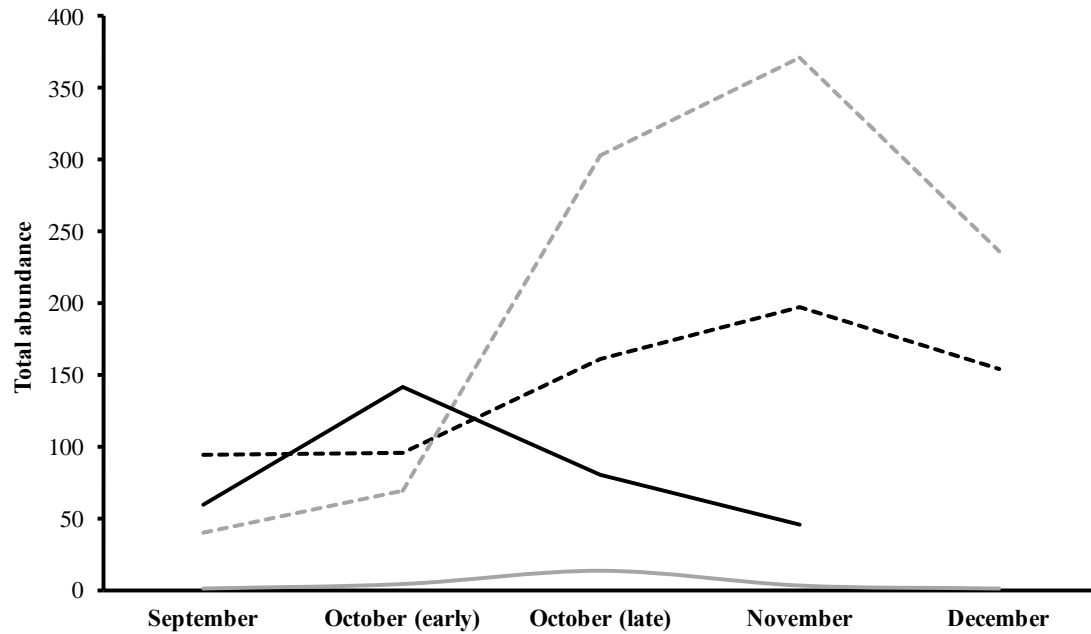


Fig. 3B Total abundance of bees, excluding honey bees, for each LULC type during austral spring in 2014 in Entre Ríos, Argentina. Solid grey line is eucalyptus plantations; solid black line is *espinal* savanna; dashed black line is mixed-use farms; and dashed grey line is pasture/annual crops. Excluding honeybees, pasture/annual crops supports the most native bees.

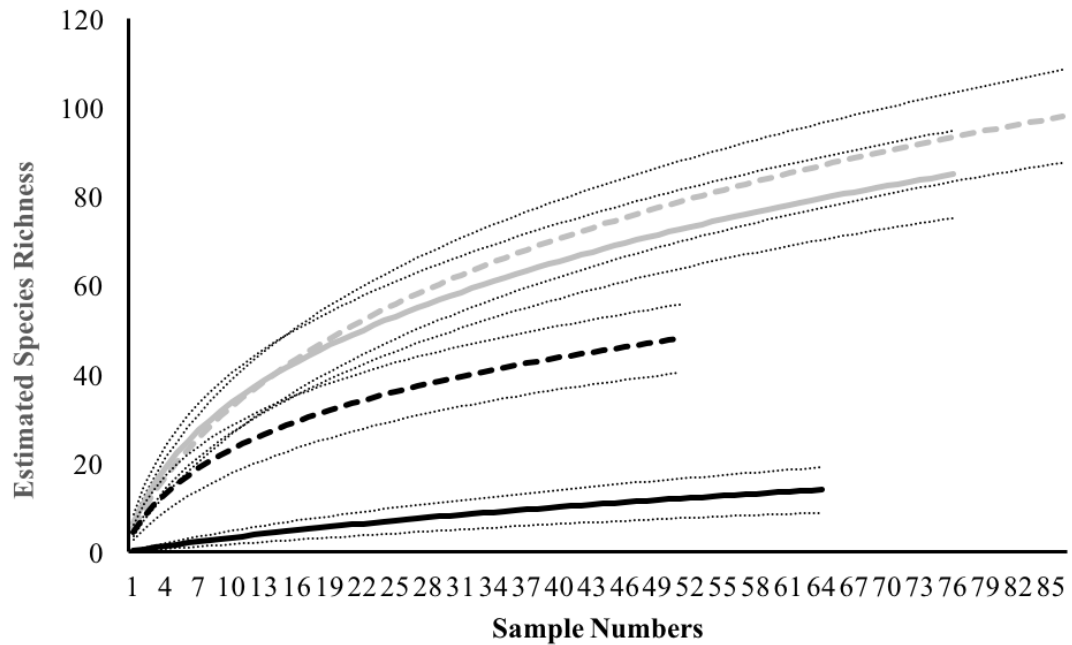


Fig. 4. First order jackknife species richness estimates for bees for each habitat type during austral spring in 2014 in Entre Ríos, Argentina, generated with EstimateS software. Solid black line is plantations; dashed black line is *espinal* savanna; solid grey line is pasture and annual; and dashed grey line is mixed-use farms. Associated upper and lower 95% confidence intervals are shown in grey dotted bounding lines.

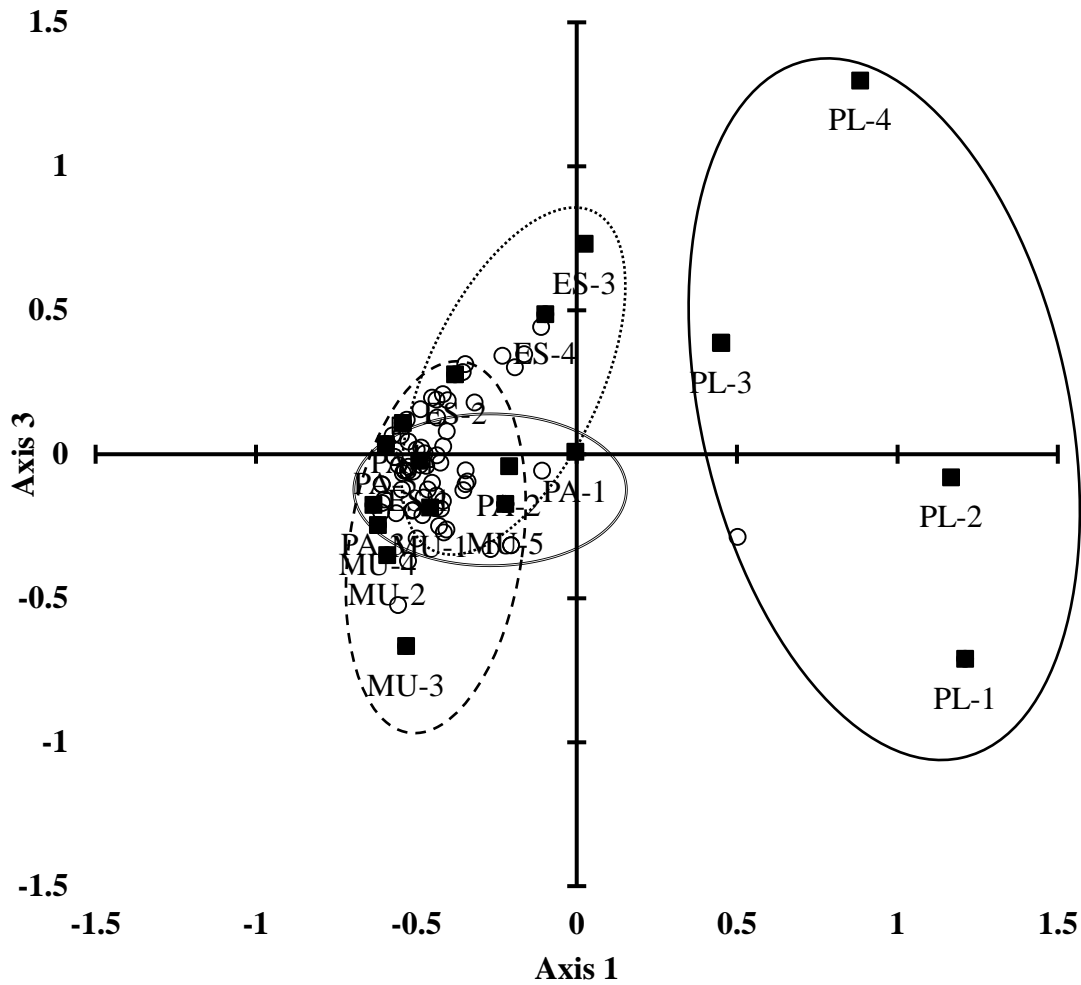


Fig. 5. NMDS ordination for two of the three dimensions of bee species and habitat type from Entre Rios, Argentina. PL = plantations, shown with solid black line; MU = mixed-use farms with dashed line; PA = pasture/annual crop with a double solid line; ES = *espinal* savanna with dotted line. Open circles are individual bee species, black squares are individual habitat replicates and polygons are bounding polygons of each habitat type. Greater distance between points suggests greater differences between land uses and land covers.

Appendix

Appendix 1. Total species richness and abundance for each habitat type for bees collected from Entre Ríos, Argentina in austral spring 2014 over the course of four months. Bees were identified to the lowest taxonomic level possible. A reference collection of bees is stored at INTA Concordia Station

Family	Tribe	Genus Species	Abundance				Total
			Plantation	Mixed-use	Pasture/annual crops	<i>Espinal</i> savanna	
Andrenidae	Callopsini	Callonychium sp1	0	7	1	0	8
Andrenidae	Callopsini	Callonychium sp2	0	5	1	0	6
Andrenidae	Callopsini	Callonychium sp3	0	1	1	0	2
Andrenidae	Protandrenini	Anthrenoides sp1	0	0	2	0	2
Andrenidae	Protandrenini	Anthrenoides sp2	1	2	0	0	3
Andrenidae	Protandrenini	Anthrenoides sp3	0	0	1	0	1
Andrenidae	Protandrenini	Psaenythia sp1	0	1	0	0	1
Andrenidae	Protandrenini	Psaenythia sp2	0	0	1	0	1
Apidae	Apini	Apis mellifera	2	786	175	119	1082
Apidae	Bombini	Bombus pauloensis	5	38	2	10	55
Apidae	Bombini	Bombus belicoso	0	0	18	0	18
Apidae	Centridini	Centris tricolor	0	3	1	4	8
Apidae	Ceratinini	Ceratina morrensis	0	58	12	5	75
Apidae	Ceratinini	Ceratina rupestris	0	74	32	13	119
Apidae	Ceratinini	Ceratina asunciona	0	18	2	7	27
Apidae	Ceratinini	Ceratina caveata	0	5	12	22	39
Apidae	Emphorini	Alepidosceles clavitarsis	0	1	2	0	3
Apidae	Emphorini	Alepidosceles filitarsis	0	9	8	0	17
Apidae	Emphorini	Alepidosceles rufipes	0	3	8	0	11
Apidae	Emphorini	Ancyloscelis romeroi	0	3	1	0	4

Apidae	Emphorini	Melitoma sp1	0	2	0	0	2
Apidae	Emphorini	Ptilothrix relata	0	0	5	0	5
Apidae	Emphorini	Ptilothrix scalaris	0	6	1	0	7
Apidae	Emphorini	Ptilothrix sp.1	0	1	0	0	1
Apidae	Emphorini	Ptilothrix tricolor	1	0	2	3	6
Apidae	Eucerini	Florilegus condignus	0	0	2	0	2
Apidae	Eucerini	Gaesischia mimetica	0	1	0	0	1
Apidae	Eucerini	Melissodes tintinnans	0	3	18	0	21
Apidae	Eucerini	Melissodes sp1	0	6	3	0	9
Apidae	Eucerini	Melissoptila desiderata	1	3	93	28	125
Apidae	Eucerini	Svastra detecta	0	0	3	2	5
Apidae	Eucerini	Thygater analis	0	12	15	1	28
Apidae	Tapinotaspidini	Caenomada bruneri	0	14	141	57	212
Apidae	Tapinotaspidini	Chalepogenus parvus	0	0	8	1	9
Apidae	Tapinotaspidini	Chalepogenus nigripes	2	3	2	4	11
Apidae	Tapinotaspidini	Chalepogenus muellerie	0	2	0	2	4
Apidae	Tapinotaspidini	Lanthanomelissa clementis	0	2	0	0	2
Apidae	Tapinotaspidinni	Tapinotaspis chalybaea	0	0	8	0	8
Apidae	Xylocopini	Xylocopa artifact	0	86	20	7	113
Apidae	Xylocopini	Xylocopa augusti	0	18	39	27	84
Apidae	Xylocopini	Xylocopa ciliata	0	2	3	1	6
Apidae	Xylocopini	Xylocopa frontalis	0	0	1	0	1
Apidae	Xylocopini	Xylocopa splendidula	0	0	1	1	2
Colletidae	Diphaglossini	Ptiloglossa lanosa	0	1	0	0	1
Colletidae	Paracolletini	Perditomorpha leucostoma	1	2	0	0	3
Halictidae	Augochlorini	Augochlora anfitrite	2	2	4	21	29
Halictidae	Augochlorini	Augochlora iphigenia	0	4	2	0	6
Halictidae	Augochlorini	Augochlora phoemonoe	1	1	7	32	41
Halictidae	Augochlorini	Augochlorella ephyra	0	29	47	0	76
Halictidae	Augochlorini	Augochlorella ipoecilla	0	0	1	0	1
Halictidae	Augochlorini	Augochlorella sp1	0	5	2	0	7

Halictidae	Augochlorini	Augochloropsis brenice	0	5	97	0	102
Halictidae	Augochlorini	Augochloropsis euterpe	0	13	119	0	132
Halictidae	Augochlorini	Augochloropsis multiplex	0	0	5	0	5
Halictidae	Augochlorini	Augochloropsis sp1	0	5	32	3	40
Halictidae	Augochlorini	Augochloropsis sp2	1	0	0	0	1
Halictidae	Augochlorini	Augochloropsis sp3	0	7	16	0	23
Halictidae	Augochlorini	Augochloropsis sp4	0	3	2	2	7
Halictidae	Augochlorini	Augochloropsis sp5	2	2	0	1	5
Halictidae	Augochlorini	Augochloropsis sparcilis	0	0	1	0	1
Halictidae	Augochlorini	Augochloropsis tupacamaru	0	5	23	5	33
Halictidae	Augochlorini	Augochloropsis zikani	0	2	1	0	3
Halictidae	Augochlorini	Paraxystoglossa sp1	0	0	1	0	1
Halictidae	Augochlorini	Thectochlora alaris	0	16	36	0	52
Halictidae	Caenolictini	Pseudoagapostemon pampeanus	1	73	39	1	114
Halictidae	Caenolictini	Pseudoagapostemon sp1	0	28	4	0	32
Halictidae	Caenolictini	Pseudoagapostemon olivaceosplendens	0	1	37	0	38
Halictidae	Caenolictini	Pseudoagapostemon pulchanus	0	44	0	0	44
Halictidae	Halictini	Dialictus autranellus	0	34	29	0	63
Halictidae	Halictini	Dialictus sp1	0	2	4	1	7
Halictidae	Halictini	Dialictus sp2	0	4	5	0	9
Halictidae	Halictini	Dialictus sp3	0	4	0	10	14
Halictidae	Halictini	Dialictus sp4	0	12	27	39	78
Halictidae	Halictini	Dialictus tinguirica	3	2	1	0	6
Megachillidae	Antidinni	Epanthidium bicoloratum	0	0	0	1	1
Megachillidae	Lithurgini	Lithurgus rufiventris	0	0	1	4	5
Megachillidae	Megachilini	Megachile catamarsensis	0	0	0	4	4
Megachillidae	Megachilini	Megachile guaranitica	0	0	0	2	2
Megachillidae	Megachilini	Megachile sp1	0	1	0	0	1
Megachillidae	Megachilini	Megachile cordubensis	0	0	1	0	1
Megachillidae	Megachilini	Megachile sp2	0	1	1	0	2
Megachillidae	Megachilini	Megachile sp1	1	0	0	0	1

Megachillidae	Megachilini	Megachile hoffmannceggiae	0	0	1	2	3
Megachillidae	Megachilini	Megachile sp1	0	0	2	2	4
Megachillidae	Megachilini	Megachile sp2	0	1	1	0	2
Megachillidae	Megachilini	Megachile sp3	0	0	0	1	1
Megachillidae	Megachilini	Megachile sp4	0	2	0	0	2
Megachillidae	Megachilini	Megachile neoxanthopera	0	2	0	1	3

4. Impact of afforested eucalyptus plantations on ecosystem services in Entre Ríos, Argentina ¹

Abstract

Ecosystem services (ES) provide essential goods and services to human communities, but many of these services can be impacted by land-use change. In Entre Ríos province, near the city of Concordia, in northeastern Argentina, large-scale eucalyptus plantations are replacing ranchlands and annual crops as the dominant land use. These afforested eucalyptus plantations represent a new land use in a region that was part of the Pampas grassland. Favorable government policies and market conditions will likely result in the expansion of large-scale monocultures of even-aged eucalyptus stands with unknown consequences for multiple ecosystem services. To clarify and quantify the potential trade-offs between expanding plantations and ecosystem services, we modeled changes in carbon sequestration, pollination services, and avian biodiversity with InVEST ecosystem service software using both primary and secondary data sources. We first estimated these three ES for a 2013 baseline land use/land cover (LULC) map. We then considered the changes to ES for two future plausible scenarios, one representing a major expansion of eucalyptus and one that limits plantation expansion but increases fruit orchards, a plausible scenario based on interview and survey results with the community. Overall, community members valued the economic opportunities that plantations can provide but also were concerned about the scale of the plantations, changes in the environment, and changes in the culture and ways of life. Respondents were also aware of possible changes to ES and many reported seeing perceived changes in the environment as a result of the plantations. Our results suggest that the expansion of eucalyptus may cause potential declines of pollination service provided by wild bees and avian biodiversity, while increasing carbon sequestration. The degree of eucalyptus expansion drove much of the changes in ecosystem services. Overall, our study illuminates the trade-offs inherent in land-use change and the importance of valuing community perspectives.

Introduction

Global demand for agricultural goods and forest products are growing [1,2], and much of the world's landscapes have already been altered by human activity for human needs [3,4], with major losses for biodiversity [5,6]. Wood from natural forests alone cannot meet this demand [7], and plantation forestry, the direct planting and tending of trees for harvest, is already a major component of the global wood products market. Plantation forestry is expanding to meet this increased demand for timber and fiber [8,9], contributing to net forest growth worldwide [10]. Planted forests are also considered an important component of the Paris Climate Change Agreement to meet global goals of limiting temperature rise through sequestration of carbon dioxide by trees [11].

¹ This chapter is intended for *Sustainability* peer-review journal. Please see dissertation preface for details on authors' contributions.

Carbon sequestration by trees is one example of an ecosystem service provided by forests. Ecosystem services (ES) are the goods and services provided to people through naturally occurring processes [12], which are produced by both natural and modified environments. Forests are important providers of multiple ES beyond carbon sequestration, including water regulation, soil stabilization, air filtration and biodiversity conservation [13,14]. Like other parts of the natural world, ES can be degraded and impacted by human activity, both directly and indirectly [3]. Many of these ES are a function of the physical structure and condition of the land use and land cover (LULC), and thus can be greatly affected by changes in land management decisions [15]. Beyond the physical structure of the landscape, some ES are provided by the community of species present, such as pollination from wild bees. These biodiversity-dependent ES can be negatively impacted by changes in LULC, such as habitat fragmentation and habitat loss [15].

Much of the emphasis on ES has focused on single ES, ignoring the complex interactions between different ES that can occur [16,17]. At landscape scales, ES can be evaluated using decision-support tools that identify and quantify how ES values vary with LULC types [18]. More than 20 of these tools have been developed [19]; generally all of them work by applying geographic information system (GIS) based models that estimate the values of ES that are dependent upon the biophysical attributes and structure of the landscape, like carbon sequestration of forests, for example. In this manner, metrics of ES can be scaled-up from plot or stand level observations to landscape assessments.

Understanding current and future trends in LULC change and impacts on ES is vital in an ever-changing world since human well-being can be impacted by degradation or loss of ES [15]. One way to understand changes in ES is to create alternative LULC futures and explore the consequences. These alternative futures, or scenarios, can be an important part of the decision-making and envisioning process [20], and can even influence final decisions that can be codified into law [21,22]. Scenarios are simplified, plausible futures based upon a set of assumptions designed to illustrate and model potential consequences in a land-use decision-making context; they are not future predictions but can relate to likely or past land-use trends [23,24]. Such scenarios have been shown to be an effective means to visualize and explore the effects of LULC decisions. For example, the Belize government engaged in scenario planning and ES modeling to help understand how alternative models of coastal development would impact multiple ecosystem services, eventually adopting and writing development rules that supported sustainable fisheries and modest development and tourism increases [25]. The process of scenario development is best done within a specific decision-making context and involves participation of the community [23,26,27]. Beyond biophysical variables and land uses, social values and social license of the impacted community by LULC changes are critically important to incorporate into land-use planning, decision-making and policy implementation [23,28,29]. Land-use policies that more fully involve public input and values are more likely to be successful.

In the northeastern part of Argentina, LULC changes are accelerating due to the development of afforested plantations, a novel land-use in the region, supported by government incentives and a linked policy that partially restricts logging or converting domestic native forests. The Argentine government recently authorized increased subsidies designed to promote the expansion of forest plantations, increasing the total subsidy available for planting trees by 250%; these subsidies cover expenses associated with new plantation plantings and plantation maintenance (pruning and thinning). The plantation promotion law (25.080) also provides a reliable tax and business environment to encourage investments in the forest sector [30]. Entre Ríos province in the northeast part of Argentina will likely see expanding afforested plantations because of the abundance of available fertile land, low land prices, mild climate, and the social acceptability of land owners to incorporate plantation forestry into their business models. Forest plantations, however, can impact the environment by altering landscape structure and biological communities [31-34]. Birds, for example, were found to be lower in abundance and species richness in plantations compared to alternative land uses in the Entre Ríos region [31]. Insects, including native bees, were also negatively impacted by plantations, following a similar trend as bird communities (see Chapter 3).

In this region of rapidly expanding forestry plantations supported by government policies, we evaluated how multiple ES associated with current land uses will be impacted by afforested plantations. First, we developed a baseline LULC map for the region and then developed two alternative scenarios to illustrate impacts to ES. We considered a scenario that estimated the effects on ES based upon a major expansion of large-scale eucalyptus plantations, and a second scenario designed to match the expressed social values of the communities. Our objectives were to determine the potential trade-offs associated with plantation forestry in this region, and demonstrate the need to include the social dimension of sustainability in the expanding role of plantation forestry in Argentina.

Methods

There were three parts to our evaluation of ES and community values for this region. First, we created a baseline LULC map using 2013 satellite imagery, which served as the reference for comparing alternative scenarios. Second, we conducted interviews and surveys of the plantation communities to determine their values and support for eucalyptus expansion. Finally, we used GIS-based decision support tools to estimate and model ES under different scenarios of eucalyptus expansion using both primary and secondary data sources.

Site description

We conducted our work near Ubajay and La Criolla townships in Entre Ríos province in Argentina, approximately 400 km north of Buenos Aires (Fig. 1a and 1b). Both towns have eucalyptus (*Eucalyptus* spp.) plantations, though they differ in the spatial scale and landscape patterning. Ubajay township has 9 mills and large-scale plantations (>500 ha)

while La Criolla township has one mill and smaller mixed-use farms with orchards, blueberries and pastures and only limited patches (<10 ha each) of eucalyptus [30]. The province of Entre Rios is bordered by the Río Uruguay to the east and Río Paraná to the west, and is characterized by undulating low hills and rich loessoid or sandy soils. This region is part of the Pampas grassland, once one of the world's largest prairies, though most of the grasslands have been converted to cattle grazing and row crops [35]. Four common LULC types are present throughout this agriculturally dominated landscape: pasture for grazing that is intercropped with annual row crops (e.g. soy) making one effective LULC type (referred to as pasture/annual crops); large-scale forest plantations, mostly eucalyptus species but also pockets of pine (*Pinus* sp.) (referred to as plantations); small, family-owned mixed-use farms with citrus, blueberries and small patches of eucalyptus (10 ha or less) (mixed-use farms); and a native espinal savanna, an endemic habitat characterized by grassy plains with sparse, low stature xerophytic *Acacia* and *Prosopis* trees [36]. In this region, the majority of the landscape is pasture/annual crops, followed by plantations, espinal savanna and orchards.

Baseline mapping

To quantify the landscape-level land use patterns of the region, we created a LULC map using 30 m resolution 2013 USGS Landsat imagery and remote sensing and classification techniques. The baseline land use map was then ground-truthed with more than 200 random points. At each point, we documented the true land cover with a geo-referenced photo taken from a GPS-enabled smartphone, using either GPS Essential (Android) or Theodolite (Apple iOS) software applications. We then contrasted the predicted LULC with the actual observed photo using a confusion matrix approach and then retrained the QGIS remote sensing imaging software. Following our ground-truthing protocol, our 2013 base land cover map obtained 95% accuracy for these common land cover types: pasture/annual crops, espinal, forest plantation and fruit/orchards. To facilitate later analysis for the ES modeling, we masked the roads, urban developments, and the region's waterways. This LULC map served as the baseline for comparison with alternative land-use scenarios that we developed (Fig. 1a and 1b).

Community interviews and survey

To assess community attitudes toward ES and the expansion of eucalyptus, we used a mix-method approach using both interviews and surveys. In 2014, we conducted 66 qualitative, open-ended, semi-structured interviews with predetermined questions for community members (45% female, 55% male) from both townships (31 respondents in Ubajay, 35 in La Criolla). Responses were then transcribed and evaluated using QSR International's NVivo 10 software that groups interview responses into larger themes and categories [30]. From this baseline knowledge, we devised a multi-part survey and asked respondents to score their responses on Likert scales. We returned in 2015 and randomly surveyed approximately 180 people (90 people in each community), asking respondents to identify ES they value, their support for government policies that promote eucalyptus

expansion, and their priorities for nature conservation or economic development (Appendix 1-4). Most responses were measured on a 5-point Likert-type scale where 1 = Totally Disagree, 5 = Totally Agree, and 3 = Neutral; some questions were based upon a 7-point scale Likert, allowing for greater expression of nuance. Survey responses were summarized using SPSS (Sanders and Nelson, in preparation). Interviews and surveys were an extensive evaluations of the social communities in these townships, and only a portion of these data that directly relate to scenario development are reported here. (For complete interview questions and protocols, see Silva (2016).) After reviewing both the survey and interview responses, we synthesized the responses to create a future scenario land use map that reflected the values of these communities (described below). Interviewers and survey administrators completed Collaborative Institutional Training Initiative human subject protection training prior to conducting field research in the community, as directed by the Institutional Review Board of the University of Oregon.

Scenario development ecosystem service evaluation

We evaluated impacts to ecosystem services using Natural Capital Project InVEST (Integrated Valuation of Ecosystem Services and Tradeoffs) software modules (v. 3.3). InVEST is a spatially explicit, open-source software platform that calculates ecosystem service metrics based upon land-use maps and associated user-provided attributes We selected InVEST from the multiple ES models available because of its adaptability to user-provided local variables that could incorporate our field-based data [19]. These modules have been demonstrated to be robust and have been broadly validated in a variety of countries and habitats [25,37-39].

We used four InVEST tools to help evaluate ES in this region. First, we used the Scenario Generator, a program that can develop alternative land-use maps based upon user-supplied likelihoods of LULC transitions, percent change of land cover types, and other parameters. We created alternative scenarios that illustrated feasible (but not predictive) landscapes under different levels of eucalyptus expansion: (1) a major expansion of eucalyptus plantations, representing 200% increase in plantations (hereafter referred to as the EE scenario), and (2) a landscape that better reflects community values, as described in interviews and surveys results that we detail below (the CV scenario, henceforth). We considered pasture/annual crops to be the most likely land cover to be converted to plantations based upon expert interviews and observed changes in LULC in the past 10 years, where pastures were most often converted to plantations, seconded by fruit orchards, which have become less profitable in recent years. We prioritized the eastern portion of the study area for land conversion (closest to the Río Uruguay) from pasture to plantations because the western portion lacks mills, roads and related infrastructure to harvest and haul wood, has less than ideal soil types and has less history of plantation forestry. We inputted this likelihood of LULC to plantation by assigning probability weights from 0-1 where 1 makes a landscape the most likely to be converted and 0 prevents any conversion. We divided the study area using a constraining layer into three sections, with the eastern edge valued at 1 (most likely), the middle third at 0.75 and the western third at 0.5 (less likely) (Fig 2). For each LULC map created using the Scenario

Generator, we applied InVEST (version 3.3) Carbon Sequestration, Pollination Service and Habitat Quality modules. We selected these ES because of their importance to the agriculture-dominated economy in Entre Ríos and based upon availability of our primary data and secondary data sources from literature.

The Pollination Service module produces two outputs: 1) an estimate of relative bee abundance based upon floral and nesting resources for each LULC type; and 2) a second index of relative pollination service from wild bees to crops, incorporating user-supplied bee species abundances and estimates of flight distance based upon size of the bee [40]. The bee abundance is expressed as a relative index from 0-1, with 1 being the highest mean abundance. The pollination service index is also expressed from 0-1. We used field-collected estimates for floral resources each LULC (Phifer, unpublished data) and interviewed INTA experts for nest resources to parameterize the model's LULC maps. We then incorporated the model with 33 wild species (or genus-level) bees that we previously had surveyed for in the region as well as estimates of their general flight distances based on bee size (see Chapter 4 for details on bees of this region; Appendix 5).

The Carbon Sequestration module sums total carbon from four pools of long-term carbon storage—above ground biomass, below ground biomass, soil carbon and dead woody debris—within a landscape and expresses it as a total of Mg of carbon per hectare. Values for the different carbon pool sources were provided from United Nations' Intergovernmental Panel on Climate Change report [41], field collected soil samples (M. Brill-Cisz, in preparation) or from relevant Argentine studies [42]; see Table 1 for carbon pool values. We assumed pasture/annual crops had zero carbon storage above ground since these LULC types are turned over too frequently to store carbon (i.e. cattle consume the grasses or the crops are harvested) [37].

We used the Habitat Quality module that calculates habitat suitability for user-supplied species for each LULC type. We used birds as a proxy for overall biodiversity, since we had previously surveyed the bird communities in each LULC in the region [31]. This module applies habitat quality estimates for each LULC type that range from 0 to 1, with 1 being good habitat sufficient for foraging and reproduction and zero being not suitable. The model calculates the impact of possible threats these habitats and their sensitivity and resilience to change, using 0 to 1. In our scenarios, we considered plantations a threat since it was shown to negatively impact avian biodiversity. Thus, because our focus is on the afforested plantations, we considered the expanded plantations from our LULC map and treated it as a threat in our future CV and EE scenarios.

Finally, each InVEST model produces a map to help visualize the spatial nature of ES and the LULC changes, in addition to model-specific attribute tables. As a way to contrast the different scenarios and the resulting changes in multiple ES, we summed each InVEST-based map for each scenario and ES to create single landscape-level score that we then represented as relative changes in ecosystem services in a single chart.

Results

Community interviews and survey

Surveys and interviews suggest that the community is accepting of the eucalyptus plantations and understands the economic benefits and employment opportunities they provide. Survey data also revealed some hesitations and concerns about impacts from eucalyptus expansion, both to the communities and to the environment. While there were differences in survey responses between Ubajay and La Criolla, they were not statistically different and we pooled their responses together to create a broader pool that describes the general opinion of the community and its attitude towards the plantations.

From the survey, both communities ranked the same four ecosystem services and economic opportunities as being the most important to them: clean air, productive soils, clean and plentiful water, and economic opportunities (Table 3). Economic opportunities were identified as the first priority for both communities, however. Survey respondents expressed neutral support for government programs for further expansion of eucalyptus plantations, with a mean score of 3.1 out of 5. Survey respondents also felt that the government does not do enough to adequately protect the environment and nature (mean of 2.87 out of 5), while believing that nature should be prioritized over the economy (mean of 5.95 out of 7).

Interviewees also reported perceived changes to ES associated with afforested plantations. For example, one person shared in an interview: "I've noticed that the majority of streams here...and the water sources have begun to decrease...where there are tree plantations the streams are dry," and another member retold a story: "My grandmother's land is in front of a tree plantation. As this tree plantation began to grow, the stream began to dry up. And it's at that point that you realize the impact it's having [on streams]" [30]. Community members valued nature in its many forms and saw the environment and human wellbeing as connected. For instance, one respondent stated "...the environment is important for good health and for everything..." [30]. Participants also noted that although the plantations were beautiful shades of green, some missed the past landscapes with unbroken views of the land, saying "Maybe I do not really enjoy such great sections of monoculture of eucalyptus and pine because one wants to see the horizon and never can because it's blocked by tree plantations, which are artificial..." Other interviewees noted the loss of the fruit industry, an important part of the local cultural identity for La Criolla that proclaims itself the blueberry and citrus capitol of Argentina: "Every day we are left with less and less of what we were before. They [producers in the community] are leaving because they sold their properties and they leave... most likely they produced citrus, but they quit producing citrus, sold [their property], and now other people own the land and they plant tree plantations" [30]. Lastly, respondents were acutely aware of the impact government policy has on the eucalyptus expansion with one respondent commenting, "As long as [eucalyptus] continues to be profitable, people will keep planting more eucalyptus because... there is global need [for wood products], [and] the Argentine state has subsidized tree plantations

for many years. An Argentine producer can establish a tree plantation practically for free...” [30]

Using these expressed values, we designed a feasible CV scenario map that limited expansion of eucalyptus plantations to 100% above the 2013 baseline and increased fruit orchards by 50%, reflecting one interpretation of the communities’ desire to better balance the economic opportunities plantations may afford with concerns for continuing traditional ways of life, and valuing nature over exclusive economic returns. Reducing plantations also better represents people’s general concern for biodiversity, water quantity and quality, and soil health, which plantations have been shown to change [43-47]. This scenario also reflects the reservation expressed for the further government support for plantation expansion. The CV scenario is not intended to be a final answer to the question of social inclusion in natural resources management and planning, but instead a place to begin exploring how this landscape can better reflect the social values of these communities.

Ecosystem service evaluation

Carbon sequestration

The carbon sequestration model estimated 100,695,212 Mg of carbon for the whole study area in its baseline condition. In the EE scenario 150,785,323 Mg of carbon were captured, mostly in the above and below ground carbon that the planted trees can store, nearly 50% more carbon than the baseline scenario. The CV scenario potentially stores 126,094,417 Mg of carbon, reflecting the more limited expansion of eucalyptus and the growth of fruit orchards that store more above and below ground biomass carbon (Fig. 4).

Pollination service

Estimated bee abundance varied with each land use, shown in Fig. 5 as regional heatmaps that varied from a relative index of 0 to 0.64 across the study region, where 1 would be highest mean abundance. The poor-quality habitat of plantations (i.e., low floral and nesting resources in spring) reduced mean relative abundances compared to other land uses. In the EE and CV future scenarios considered, as plantations expanded, estimates of bee abundance declined across the study area. Pollination services were also estimated to decline with expanding plantations. The model, which considers the foraging range of bee species, estimated pollination service sinks in large monocultures of croplands that are far from nesting and floral resources. Fruit orchards in La Criolla, for example, adjacent to plantations were less likely to be visited by wild bees (Fig. 5).

Habitat quality

Habitat scores (the raw summation of the LULC values for each scenario) for birds changed with each scenario. The EE scenario resulted in a 25% decline in habitat quality

compared to the baseline. The CV scenario was intermediate, with a 14% decline in habitat quality (Fig. 6). The greatest driver in the decline of habitat was the expansion of the plantations and the conversion of espinal and pasture to eucalyptus. The expansion of fruit orchards resulted in improved habitat for birds as well. These former LULC types support more birds than the relatively depopulated plantations.

Discussion

We considered the impacts of land-use change on three ES in Entre Ríos, Argentina, contrasting the effects of different degrees of eucalyptus plantation expansion. Relative pollination service and habitat quality declined as the eucalyptus expanded while carbon sequestration increased with plantation area compared to the current baseline (Fig. 7). Both in the interviews and survey, the communities acknowledged the trade-offs associated with expanding plantations, noting the economic benefits associated with plantations but also the loss of part of their cultural identity and potential impacts from the afforested plantations on soil, water and biodiversity. These results demonstrate the need to consider multiple ecosystem services and community preference when estimating the impact of land-use change on natural capital [48-50].

The carbon sequestration estimates linked growth in sequestration with plantation and orchard area. The greatest contributors to the net gains in carbon sequestration in the CV and EE scenarios were the above and below ground biomass pools. Estimates for carbon sequestration of the plantations depended upon the length of time between harvests; the longer the rotation, the more carbon that can be locked into the trunks and roots of the trees. In this region, eucalyptus trees are harvested between 12-15 years, depending on site quality before harvest. Trees are usually harvested and allowed to regrow, resulting in retention of most of the below ground carbon. However, shorter harvest rotations would limit the amount of carbon that is locked in the trees' stems. The carbon sequestration potential is also highly dependent upon the previous land use and the land management [46,51].

The InVEST Pollination model also predicted a decrease in native bee abundance and pollination service to crops with expanding plantations. This model has been demonstrated to be predictive in simple, homogenous landscapes similar to ours, with relatively large-scale agricultural fields and limited habitat heterogeneity or complexity [52,53]. The expansion eucalyptus plantations may result in the loss or displacement of this vital ES. Soy is the most common annual crop planted in this region, and although it is commonly thought to be self-pollinating, wild bees do forage on its flowers and proximity to forest and nature/semi-natural areas was shown to increase soy bean yields through increased visitation rates [54]. Small farmers in La Criolla that depend upon pollination for blueberry or citrus fruits (two pollinator dependent crops) benefit from more diverse landscapes that support higher floral resources and nesting habitats near their orchards. These small-scale mixed-use farms are often small enough for even smaller bees to visit flowering plants on the farm and nest in nearby fallow or underutilized lands. Wild bees also provide insurance against the loss of managed honey

bees, and often provide greater pollination service than honey bees [55-57] Further, wild bees help support the broader diversity of plants in the region, providing an essential ecological interaction for biodiversity as a whole [58].

Afforested plantations represent a large structural change to a pasture/grassland landscape once the trees mature. This habitat change can impact avian communities that are ecological and evolutionarily accustomed to open grasslands. This region never supported tall trees, and the structural changes brought about from the plantations are likely perceived by many species as a “green wall” to be avoided. Avian biodiversity within the plantations was much lower compared to the surrounding LULC types, although bird abundance and diversity rebounded within 100 m of the plantation edge [31]. In northeast Argentina in Misiones province, tree plantations also negatively impacted avian diversity [59], though the results were less pronounced, likely because the alternative land use was a native forest that is structurally similar to tree plantations. The decrease in avian biodiversity and the simplification of the species pool may impact bird-dependent ecosystem services, such as pest control, seed dispersal and pollination [60,61].

Our LULC map was made from 30 m resolution imagery, which can “average out” important fine-scale landscape characteristics. Recent work that compared the effects of 5 m and 30 m resolution using InVEST Carbon and Pollination modules found that although the trends were the same for both resolutions, finer resolution resulted in a more nuanced and detailed map that would allow for greater real-world application and management [62]. Particularly for pollinators, which operate on both landscape and local levels, floral resources can be “hidden” from coarser LULC maps. In our study region, for example, pockets of flowers existed within the plantation where gaps were present, usually as a result of a tree falling or die-back, that are not sensed at the landscape scale. Scale is also an important consideration for ES valuation, with some ES valued at national or global (e.g. carbon sequestration) levels and other ES at a regional or local scale (e.g. pollination). Considering the scale of the beneficiaries is essential when considering locally relevant land-use planning and management [21,23,50].

Land-use changes, including plantation forestry, will likely continue to increase in the Entre Rios region because of favorable government policies. As one respondent said, these plantations are practically “free.” The “free” plantation is the result of the subsidies provided under the Argentine Plantation Investment Law. However, in 2018 this legislation will need to be reauthorized by the Argentine government, making this a ripe time to consider the potential tradeoffs with plantation expansions and consider ways to maximize the benefits and minimize the loss of ecosystem services.

Our work should be carefully considered and evaluated before policy renewals. The scenarios we developed are not predictions, but rather are illustrations of possible landscapes and estimates of the impacts on ES. InVEST modules are static, representing one moment in time, and do not fully capture seasonal or year-over-year changes or changes in government policy, market conditions or social values that may reflect land-

use preferences in the future. We recommend sharing this research and ES-based maps with the communities we surveyed to report our results, but also to hear from members themselves their thoughts, particularly, their views on the CV scenario we generated from the interviews and survey results. Scenario development is a critical tool for land management and planning, and it should be an iterative process, with results shared, incorporated and community input integrated into recommendations [26].

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Tables

Table 1: Sources of carbon pools (Mg ha⁻¹) for each LULC type that were used for Carbon Sequestration InVEST module for Entre Ríos, Argentina.

LULC	Carbon pools				Sources
	Above ground	Below ground	Soil	Dead organic matter	
Fruit	60	18	61.7	0	IPCC
Pasture/crops	0	0	61.7	0	IPCC
Espinal savanna	11	2.42	60.2	.5	Gozáles-Roglich et al. 2014
Plantations	140	46.2	30.8	0	M. Brill-Cisz; IPCC

Table 2: Floral and nesting resources each LULC type that were used for Pollination Service InVEST module for Entre Ríos, Argentina. Estimates are an index from 0-1 where 0 is unavailable and 1 is abundant and available.

LULC	Nest type availability			Floral resources	
	Cavity	Soil	Wood	Early spring	Late spring
Fruit	0.5	0.5	0.5	1	0.8
Pasture/crops	0.2	0.2	0	0.3	0.3
Espinal savanna	1	0.8	1	0.6	0.6
Plantations	0.1	0.2	0.3	0.1	0.2

Table 3. Responses from community members for the following questions: How important are the following aspects of the nature around them both for you and for your home? N is the number of people who answered the question and the mean Likert value. Bolded values represent top-five ES valued. Scores were based for Likert 1-5 scale, where 1 means “none” and 5 means “a lot.”

	Ubajay		La Criolla	
	N	Mean (\pm SE)	N	Mean (\pm SE)
Attractive scenery	86	4.50 (.715)	94	4.44 (.665)
Recreation	83	4.31 (.697)	93	4.48 (.583)
Clean air	85	4.85 (.362)	94	4.85 (.387)
Clean water	83	4.80 (.435)	94	4.69 (.688)
Food	81	4.56 (.806)	93	4.55 (.700)
Economic opportunities	85	4.76 (.648)	93	4.61 (.643)
Bird habitat	83	4.52 (.571)	93	4.49 (.775)
Lots of water	82	4.72 (.528)	93	4.62 (.624)
Productive soils	84	4.74 (.469)	94	4.78 (.419)

Table 4. Responses from community members for the following questions relating to policy and government responsiveness. N is the number of people who answered the question and the mean Likert value. Scores were based for Likert 1-5 scale, where 1 means “none” and 5 means “a lot.”

	Ubajay		La Criolla	
	N	Mean (\pm SE)	N	Mean (\pm SE)
Government influence on eucalyptus expansion	75	3.05 (1.218)	78	3.26 (1.062)
Government promotion expansion of eucalyptus	84	3.40 (1.152)	88	3.10 (1.287)
The government protects the environment	87	2.48 (1.170)	87	2.62 (1.164)
The government responds to community needs	88	2.76 (1.145)	91	2.87 (1.087)

Figures

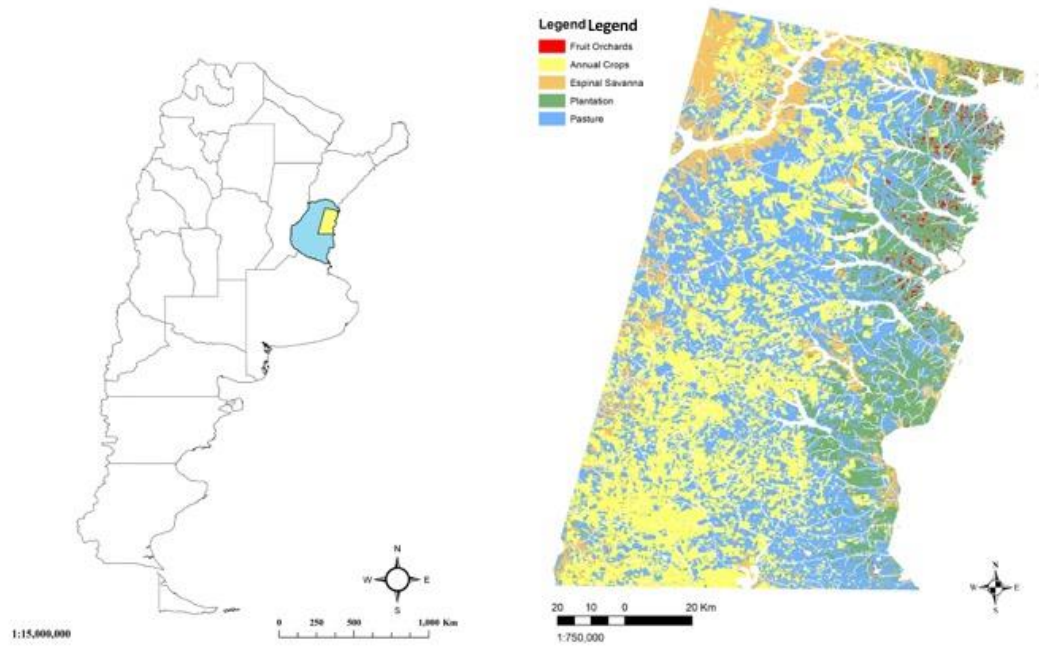


Fig. 1a and b. The left panel shows a map of Argentina and Entre Ríos province (blue) with the study area shown in yellow. The right panel shows the study area and the common last use/land cover types in the area.



Fig. 2. Land-use change to eucalyptus plantation was weighted from most likely to unlikely using a constraining layer in the InVEST Scenario Generator model. Darker green areas were more likely to be converted to plantations while lighter green areas were less likely. These delineated lines are an approximation of biophysical limits, existing infrastructure and social acceptability of plantations.

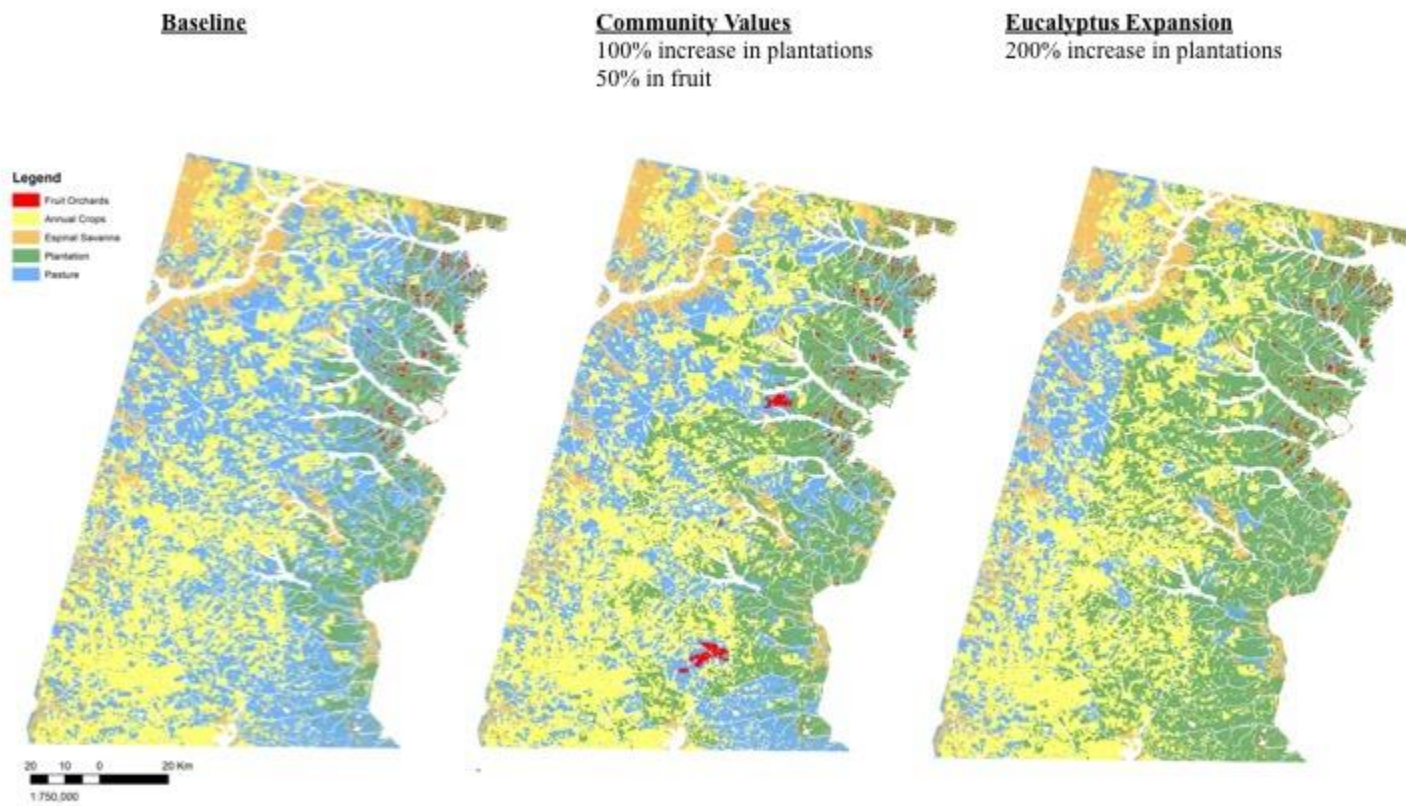


Fig.3. Maps of the LULC under baseline, community values and eucalyptus expansion scenarios.

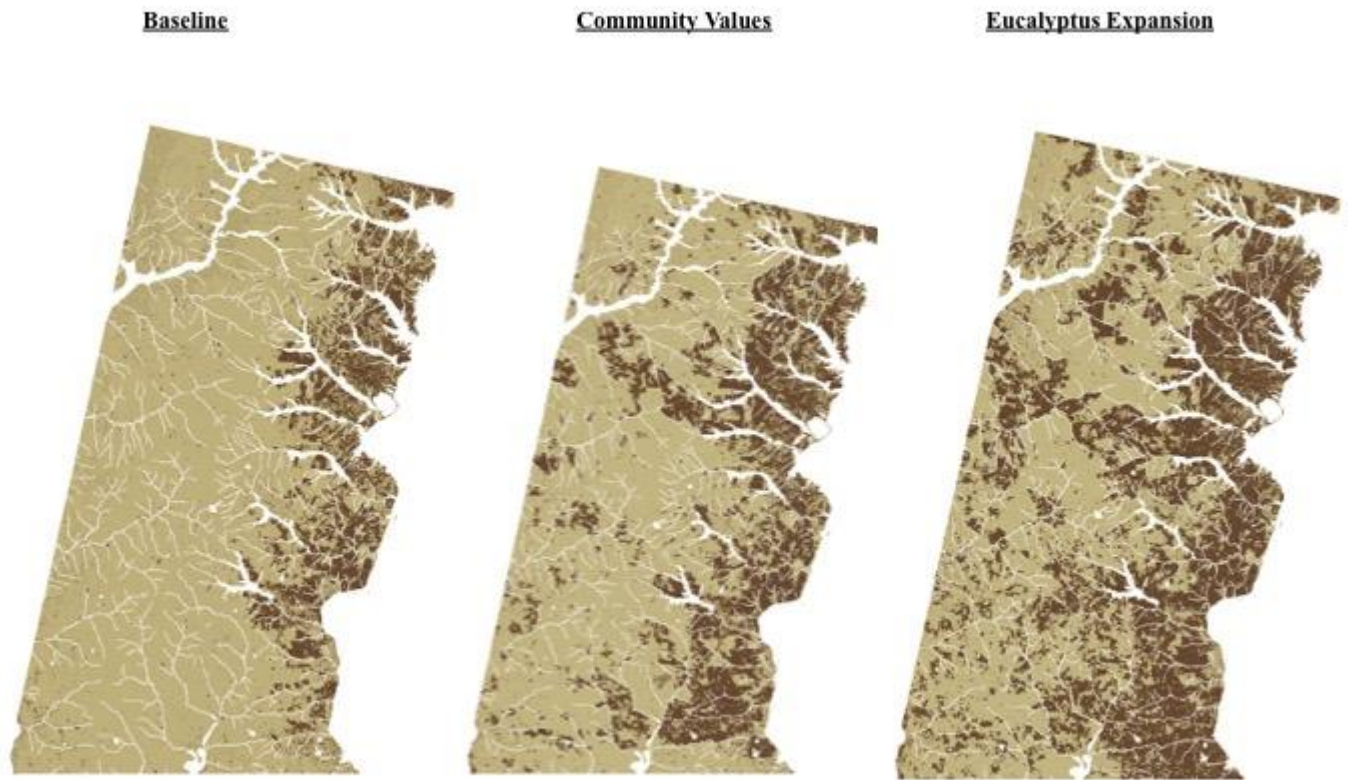


Fig.4. Carbon sequestration under baseline, community values and eucalyptus expansion scenarios. Darker brown indicates higher carbon sequestration potential.

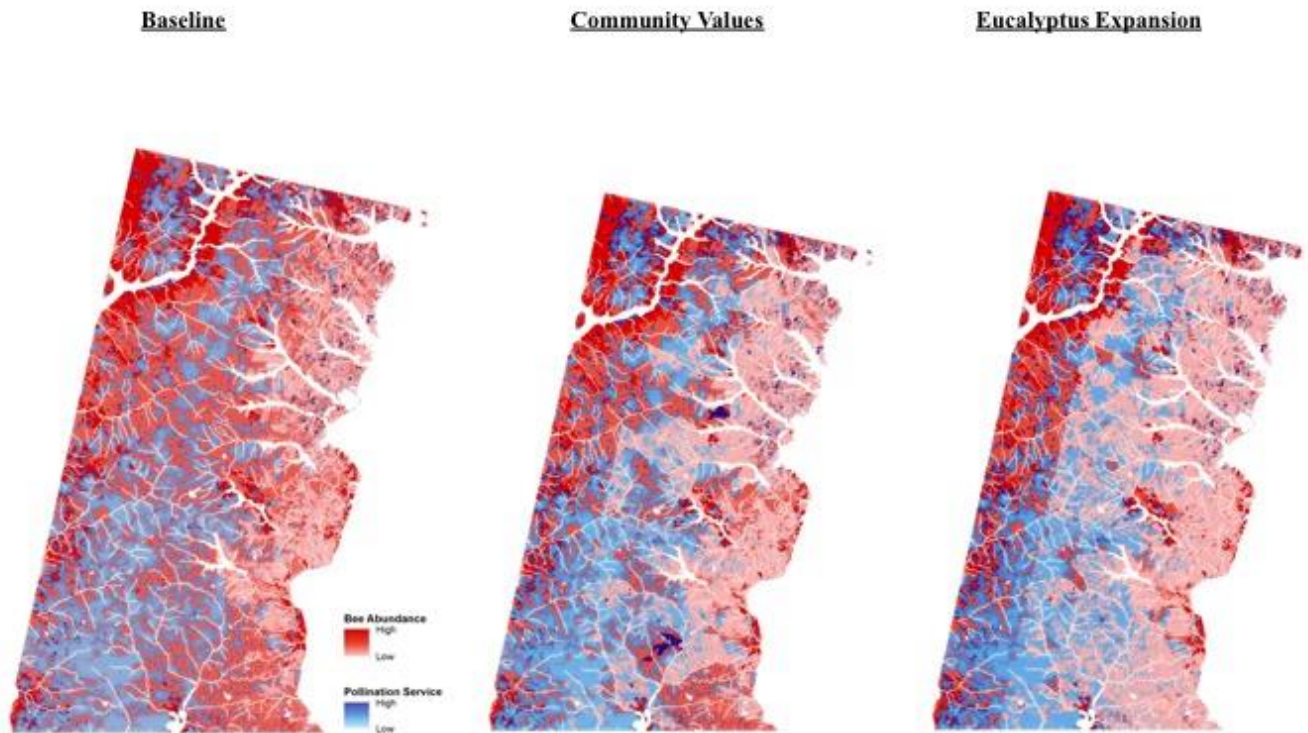


Fig. 5. Maps of the potential bee abundance and pollination service under baseline, community values and eucalyptus expansion scenarios. Darker shades of red indicate higher mean bee abundance. Dark blue indicates higher pollination service.

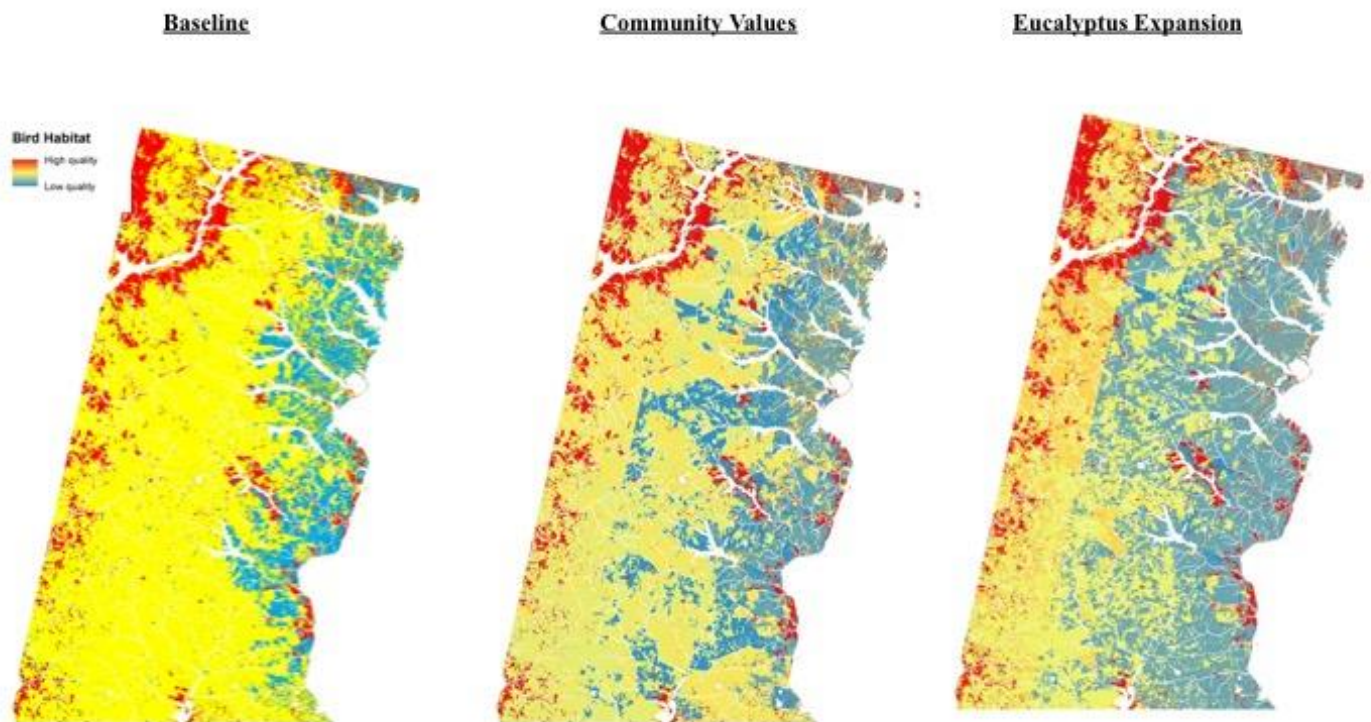


Fig. 6. Maps of avian habitat quality. Warmer shades indicate higher quality habitat; cooler shades represent lower quality habitats.

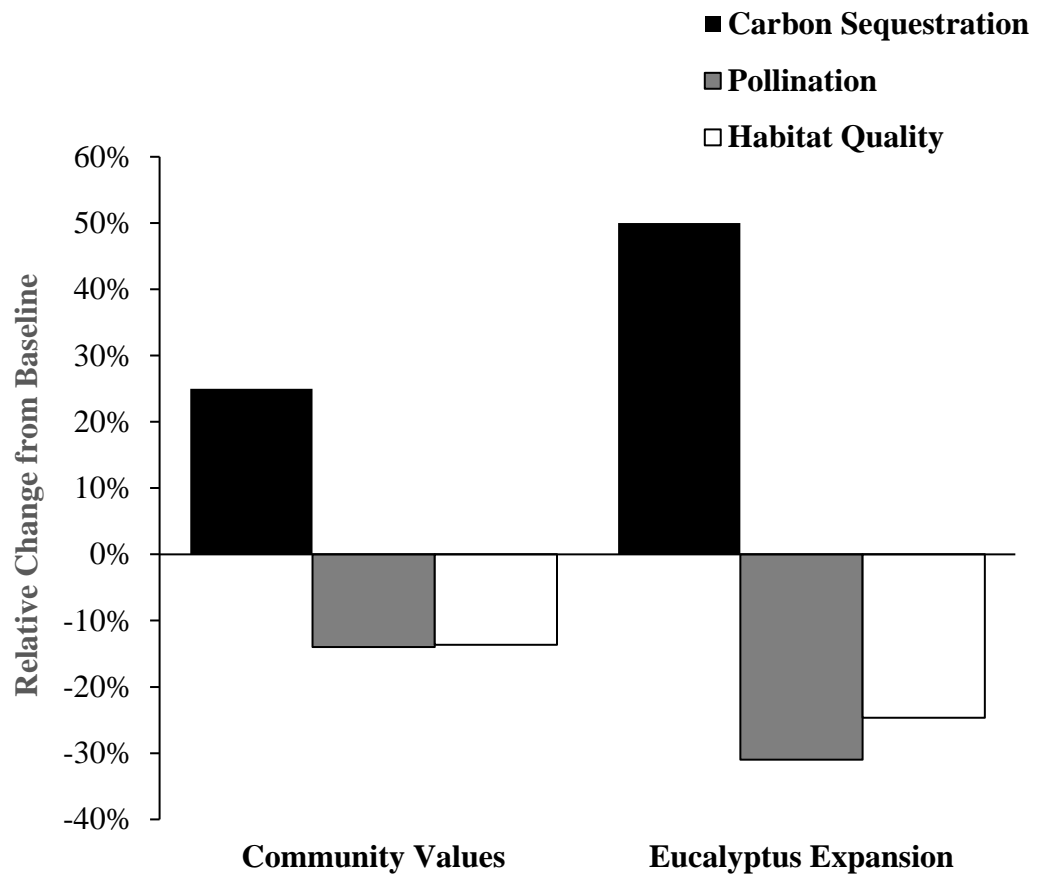


Fig. 7. Comparison of relative change in ecosystem services compared to baseline landscape.

Appendix

Appendix 1. ¿Qué tan importantes son los siguientes aspectos de la naturaleza que les rodea tanto para usted como para su hogar? Indique con un círculo sólo una respuesta. [<i>How important are the following aspects of the nature around them both for you and for your home? Please circle only one answer.</i>]					
Que la naturaleza... [That nature ...]	Nada [None]	Poco [A Little]	Ni poco ni mucho [Neutral]	Mucho [Some]	Muchísimo [A lot]
Sea un paisaje bonito (p.ej. vistas agradables) [Be nice scenery (eg nice views)]	1	2	3	4	5
Dé posibilidades para la recreación [Give opportunities for recreation]	1	2	3	4	5
Aporte aire limpio [Clean air]	1	2	3	4	5
Aporte agua limpia [Clean water]	1	2	3	4	5
Provea alimentos cultivados [Provide food]	1	2	3	4	5
Genere oportunidades económicas (p.ej. empleos) [Generate economic opportunities (eg, jobs)]	1	2	3	4	5
Contribuya al hábitat para las aves [contributes to habitat for birds]	1	2	3	4	5
Provea gran cantidad de agua [Provide large quantities of water]	1	2	3	4	5
Mantenga los suelos productivos [Keep productive soils]	1	2	3	4	5

Appendix 2. Favor indique con un círculo sólo una respuesta para cada pregunta.
 [Please indicate with a circle only one answer for each question.]

Pregunta	Nada [None]	Poco [A Little]	Ni poco ni mucho [Neutral]	Mucho [Some]	Muchísimo [A lot]
¿Hasta qué punto considera Ud. que <i>influyó</i> el gobierno en la expansión del eucalipto en su región? [To what extent do you consider. Influencing the government in the expansion of eucalyptus in your region?]	1	2	3	4	5
¿Hasta que punto considera Ud. que <i>debería</i> influir el gobierno en la promoción de la expansión del eucalipto? [To what extent do you consider. That should influence the government in promoting the expansion of eucalyptus?]	1	2	3	4	5

Appendix 3. Favor de indicar con un círculo su nivel de acuerdo o desacuerdo con cada afirmación. [*Please indicate with a circle your level of agreement or disagreement with each statement.*]

Afirmación	Totalmente en desacuerdo [<i>Strongly Disagree</i>]	Desacuerdo [<i>Disagree</i>]	Neutral [<i>Neutral</i>]	De acuerdo [<i>Agree</i>]	Totalmente de acuerdo [<i>Strongly agree</i>]
El gobierno hace cumplir las leyes para proteger el medio ambiente en el sistema de producción del eucalipto. [<i>The government enforces laws to protect the environment in the production system of eucalyptus</i>]	1	2	3	4	5
El gobierno responde a las necesidades de su comunidad [<i>The government responds to the needs of their community</i>]	1	2	3	4	5

Appendix 4. Favor de indicar su nivel de acuerdo con las siguientes afirmaciones colocando una sola cruz en la posición del cuadrado con el que usted se sienta identificado. *[Please tick the level of agreement by placing a single cross on the square with the position that you feel identified following the above example to the following statements.]*

<u>AFIRMACIÓN 1</u>		<u>AFIRMACIÓN</u>
<p>Se debe dar prioridad a la protección de naturaleza aún si esto provoca un menor crecimiento económico naturaleza y la pérdida de algunos empleos. <i>[Priority should be given to nature protection even if this causes less economic growth and the loss of some jobs.]</i></p>	<input type="checkbox"/> <input type="checkbox"/> <input type="checkbox"/> <input type="checkbox"/> <input type="checkbox"/> <input type="checkbox"/> <input type="checkbox"/>	<p><u>2</u></p> <p>Se debe dar prioridad al crecimiento económico y de empleos aún si la sufre como consecuencia. <i>[Priority should be given to economic growth and jobs even if nature suffers as a consequence.]</i></p>

Appendix 5. Bee species and guilds parameters for Pollination Module. Time of activity is based upon field-collected data and relative abundances divided between early and late spring. Nest preference is based upon published sources, with 0 means not suitable. Foraging estimates is estimated from genus bee size. Species are abbreviations using two letters from genus and species; see Chapter 4 for details on bee species.

Species	Nest preference			Time of activity		Est. foraging distance (m)
	Cavity	Soil	Wood burring	Early spring	Late spring	
CASP	0	1	0	0	1	1000
ANSP	0	1	0	0.5	0.5	500
PSSP	0	1	0	0	1	500
BOPA	0	1	0	0.56	0.44	3000
BOBE	0	1	0	0.61	0.39	3000
CETR	0	0	1	1	0	250
CESP	0	0	1	0.73	0.27	250
ALSP	0	1	0	0.13	0.87	250
ANRO	0	1	0	0	1	250
MESP	0	1	0	0	1	250
PTSP	0	1	0	0.19	0.81	250
FLCO	0	1	0	0	1	250
GAMI	0	1	0	0	1	250
MELSP	0	1	0	0.05	0.95	250
SVDE	0	1	0	0	1	250
THAN	0	1	0	0	1	250
CABR	0	1	0	0.63	0.37	500
CHSP	0	1	0	0.38	0.63	500
LACL	0	1	0	1	0	500
TACH	0	1	0	0	1	500
XYSP	0	0	1	0.66	0.34	2000
PTLA	0	1	0	0	1	250
PELE	0	1	0	1	0	250
AUSP	0	0	1	0.49	0.51	100
AUGSPA	0	1	0	0.14	0.86	100
AUGSPP	0	1	0	0.68	0.32	100
PASP	1	1	1	1	0	250
THAL	1	1	1	0.08	0.92	250

PSSP	0	1	0	0.37	0.63	500
DISP	0	1	0	0.26	0.74	100
EPBI	1	0	0	1	0	250
LIRU	0	0	1	0.6	0.4	250
MESP	1	0	0	0.54	0.46	1500

5. Impacts of stand age on bee and wasp diversity in aspen forests in northeastern Wisconsin, USA

Abstract

Aspen forests are an important part of northeastern Wisconsin's ecological communities and local economy. Forest management can impact native bees and wasps, providers of pollination ecosystem services. To understand how forest management impacts bees in this region, we surveyed bees and wasps with pan traps using a chronosequence of nearly monotypic aspen stands that ranged from 11-45 years old/post-harvest. We also qualified forest habitat features that influence pollinator communities. We found no significant relationship between forest stand age and bee and wasp abundance or richness. However, forest stand age class did impact the abundances of different bee and wasp functional types with pollinating bees more abundant in younger forests and parasitoid wasps more common in older stands. We also detected discrete pollinator communities along the ecological gradients using non-metric multidimensional scaling. Results from our work demonstrate that forest bee and wasp communities respond differently to forested habitats and that forest stand age may be an important driver of habitat features that influence bee and wasp biodiversity. Providing a mosaic of different aged stands on the landscape may help support diverse bee and wasp communities in these Great Lakes forests.

Introduction

Pollinators provide an essential ecosystem service to domestic and wild plants, with nearly 90% of flowering plants (> 300,000 species globally) depending or benefiting from animal-assisted pollination (Ollerton et al. 2011). Wild bees and other members of the Hymenoptera family, like wasps, are a major provider of this essential service. Approximately 75% of domesticated crops important to human health and nutrition benefit from insect pollination (Klein et al. 2007), a service estimated to be worth \$215 billion worldwide (Gallai et al. 2009).

The human demand for pollination-dependent crops has tripled in recent years (Aizen et al. 2008) while at the same time wild bees have declined in Europe and North America (Potts et al. 2010; 2015; Koh et al. 2016). In the United States, wild bee abundance has declined by an estimated 23% since 2008 (Koh et al. 2016), with uneven patterns across the country. In the Midwest, estimated bee declines are higher than the national average (Koh et al. 2016). A mosaic of agricultural fields and forests dominate land use in this region and compared to more purely agriculture dominated landscapes, far less is known about the value of forested habitats to bees (Sudan 2016). The importance of forests as bee habitat was highlighted by a recent presidential memorandum (The White House 2015b) to federal agencies that set a goal to reestablish 7 million acres of pollinator habitat on federal lands, much of that on the US Forest Service's lands (The White House 2015a). Consequently, there is a clear need to enhance our understanding how forest management may influence bees and other pollinators.

In the Midwestern state of Wisconsin, forests make up 6.9 million hectares (Kurtz 2017). Aspen (*Populus* spp.) forests account for 17% of the total forestlands (Kurtz 2017) in the state with more than 70% of these forests stands found the northern part of the state (DNR 2016), making these forests ecologically important to the region. Aspen trees are also an important part of state's timber economy, accounting for 22% of the statewide harvest for roundwood, with the majority of the wood being used for composite wood or pulp products (DNR 2016). The value of these aspen-dominated forests for bees is understudied; we identified only one paper specifically addressing aspen stands and their value for bee habitat (and this research was conducted in Oregon) (Gonzalez et al. 2013). This study did not examine how silvicultural practices or successional ages may influence this important pollinator group.

Elsewhere in temperate forests, forest successional age has been found to influence bee diversity patterns with species richness and abundance declining with increasing forest age (Winfree et al. 2007; Grundel et al. 2010; Hanula et al. 2016a). However, not all species respond in the same manner. Some bee species are forest obligates (Winfree et al. 2007) and many more species are habitat generalists that visit forests in search of floral resources and nesting materials (Monasterolo et al. 2015). (Winfree et al. 2007). Younger aspen stands are less structurally diverse than older stands but permit more light to reach the forest floor, supporting greater understory floral diversity. Stand age can also impact social and solitary bees differently, with some social colony-nesting bees preferring older successional stands (Taki et al. 2013). Taki (et al. 2013) suggested that older stands often possess more diverse habitat features that can provide nesting resources for some social bees that prefer wood cavities. Related work suggests that bees perceive the landscape based on available floral resources, nesting sites, and over-wintering habitats (Kremen et al. 2007; Williams & Winfree 2013). The scale of habitat choice among bees differs based upon the home range of the species (Greenleaf et al. 2007; E Benjamin et al. 2014).

In this context, we investigated the possible influence of forest successional age and related fine-scale habitat features on native bees and wasps in northeastern Wisconsin. We surveyed for Hymenoptera species in a chronosequence of aspen-dominated forest stands in the spring and summer of 2014. Based on previous work, we hypothesized that bee and wasp species richness and abundance would be greatest in youngest stands and decline with increasing forest age. This research advances our understanding of ecological theory of forest disturbance and biodiversity patterns on a critically important taxa group, as well as provides important information for forest and land managers on the effects of harvest schedules on wild bees and wasps that provide highly valued pollination services.

Methods

Site description

In 2014, we selected a chronosequence of 9 aspen-dominated, no-retention forest stands in Vilas and Oneida Counties in northeastern Wisconsin (approximately 45°43'N, 89°32'W) to represent young, middle-age and older-age aspen stands that ranged from 11-45 years post-harvest (Fig. 1). Selected sites shared mesic soils comprised of sandy loam and loamy sand (Soil Survey Staff 2011). The sites were randomly selected from available forest stands that matched our criteria (larger than 15 ha, contiguous blocks, and no scheduled harvesting) based upon GIS layers supplied by Wisconsin county and state forestry offices. These aspen-dominated sites were originally clear-cut and left to regenerate without additional management, though some sites had a handful of large-diameter hardwoods (mostly red oaks, *Quercus rubra*) and/or conifer (pine trees, *Pinus* spp.) trees remaining as part of the original silvicultural treatments.

Bee and wasp sampling

To assess bee and wasp communities, we surveyed the aspen stands described above with pan traps and blue-vane traps, an accepted technique for forested landscapes (Campbell and Hanula 2007; Grundel et al. 2010; Taki et al. 2013; Hanula et al. 2015). These passive techniques allow for sampling at multiple sites at the same time, remove observer bias, and can be repeated at regular intervals. This technique has become the standardized method for North American and European bee monitoring protocols (Westphal et al. 2008; Lebuhn et al. 2012). At each site, we randomly selected origin points to serve as the starting points for our sampling transects, discarding points that were within 50 m of a road or forest edge so that transects were within the forested habitat. At each point, we laid out two 40 m transects intersecting at a 60 degree angle, forming a flattened “X” shaped array that allowed for efficient spatially structured sampling (Droege 2015). We marked transects with 1-m high wooden stakes every 5 m. At each stake, we set a 100 mL plastic cup painted with fluorescent blue, yellow or white (alternating colors) filled with soapy water (Dawn™, original scent) for a total of 34 pan traps per site (Droege 2015). At the same time, we hung four fluorescent blue vane traps (Spring Star Inc.) from low tree branches per site because they are more effective for catching large-bodied bees like bumble bees (Stephen & Rao 2005; 2007; Kimoto et al. 2012). Traps were set out before 9 am and collected the following day. All insects in the pan traps and blue vane traps were collected and stored in 70% ethanol until identified. We identified bees to genus or species level using DiscoverLife.org and published dichotomous keys, and wasps to the lowest possible level. Surveys were conducted during mild weather with no rain and repeated approximately every other week during from 28 May through 05 August 2014 for a total of six surveys.

Habitat sampling

We collected fine-scale habitat measurements to allow us to evaluate potential relationships between bee and wasp community assemblages and floral and nesting resources that are known to be important for different groups (Williams et al. 2010). We sampled the herbaceous understory plants, woody shrubs, coarse woody debris and forest stands along the same transects used for the bee sampling. Shrub, woody debris and forest stand measurements were sampled once over the course of the summer while floral resources were surveyed six times at the same time of bee and wasp surveys to match floral resources with bee biodiversity patterns.

Each 40 m transect was divided into four 10 m segments with sampling stations established at 0, 1, 3, and 6 m, employing a cyclical sampling method that minimizes sampling time while maximizing inference (Clinger and Ness 1976; Scheller and Mladenoff 2002; Murray et al. 2013). We counted non-graminoid flowering species using 1 m² quadrat and visually estimated percent cover of dominant herbaceous plant community within the same quadrat (Grundel et al. 2010). For efficiency, we lumped grasses, sedges and rushes into a generic graminoid category. We also counted the number of rooted woody stems and species within each quadrat. Along the same transects, coarse woody debris (CWD) was estimated using line intersect method, we recorded debris diameter (cm) at the point of intersection, log species if known, and decay class (1-5) using Jenkin et al. descriptions (Jenkins et al. 2004). Later, we combined decay classes 1-3 into low decay and classes 4 and 5 into high decay categories for data analysis. Lastly, ten 100 m² circular plots were established and tree species, diameter at breast height (DBH) and status (live/dead) were recorded, with the exception of the three youngest stands where the density of stems was too great and we reduced the circular plot to 50 m² for expediency. The ends of each x-shaped transects and transect midpoints were used as the circular plot centers. A digital camera with a hemispherical lens was used to photograph the forest canopy along the same plot centers we used for the stand measurements. Images were then analyzed with WinSCANOPY software (WinSCANOPY 2017) to calculate percent canopy that we used as a proxy for light availability, an important driver of understory succession.

Statistical analysis

Abundance, species richness, and community structure of the bees and wasps were compared using PC-ORD v. 6.22. We then grouped our collection based upon adult ecological function: parasitoid wasps, predatory wasp, kleptoparasitic bee, pollinating bee, forest pest, and unknown. For bees' functional role, we used the United States Geological Survey's functional ecology database of bees (BeeGAP 2016). For non-bees, we searched the literature for nesting and diet needs. We tested for relationship between forest stand age and both abundance and richness with a linear regression. To test for differences between forest ages, we conducted a two-way ANOVA with young, middle and old age stands against parasitic and pollinating bees, predatory and parasitoid wasp and forest pests. Finally, we examined how the bee communities responded to these

forest stands with a non-metric multidimensional scaling ordination technique, incorporating the forest habitat structure (see above) and bee and wasp species abundance that we pooled to the site level for comparison (McCune and Grace 2002). For this analysis, we used we used a Bray-Curtis measurement of ecological distance and the autopilot defaults (250 iterations). This technique assesses the fit of the community structure by calculating a stress score, with low stress indicative of a stable community and better fit that reflects a true ecological gradient (McCune and Grace 2002).

Results

In total, we collected 1,670 insects and small spiders from our pan and blue vane traps during the 2014 summer, with June and July being the peak months for abundance (Fig. 3). Of the insects sampled, 487 were Hymenoptera (bees and wasps), the group of interest for our study. We described 39 distinct species, though we did not reach species level identification for all groups. Overall, abundances and species richness of bees and wasps were higher in the younger stands and declining in the older aspen forest stands but this relationship was not statistically significant. Forest stand age did affect the composition of insects, with parasitoid wasps more abundant in older forest stands compared to middle or young stands and pollinating bees more common in younger stands (Fig. 4). Fine scale habitat metrics for forest successional age are described in Table 3

Pollinating bees accounted for approximately one-third of all bees collected. Of these, the Halictidae family was the most abundant with the genus *Lasioglossum* the most common. These 3-4 mm bees are one of the most common bees in Midwestern U.S. forest, and are notoriously difficult to identify to species level. In Wisconsin's northeastern forest, there are at least seventeen species of *Lasioglossum* bees (Wolf and Ascher 2008). We also collected twelve kleptoparasitic bees and wasps (*Nomad* sp. and *Holopygya ventralis*), approximately 2.5% of the total bees and wasps collected.

Nearly half of our collection was comprised of endoparasitic and ectoparasitic parasitoid wasps, mostly the Ichneumonidae and Braconidae families. These groups are closely related, very diverse at the species level and are difficult to identify below family level. Another 13.9% of the collection were predatory wasps that prey upon other insects to provision nests but sip nectar as food. Finally, twelve bee or wasp specimens were damaged beyond repair (e.g. missing legs or other body parts) and were excluded from analysis.

We detected discrete bee and wasp communities across the chronosequence of forest sites. The NMDS ordination resolved to a three-dimensional ordination with a final stress level of 9.13 after 50 iterations and zero instabilities (Fig. 5). The three axes of our three-dimensional solution collectively described 95.4% of the variation. Mean diameter at breast height, as a proxy for tree height, basal area and age, along with coarse woody debris were associated with bee and wasp community composition across our sites.

Discussion

In northeastern Wisconsin, we documented more than 39 species of bees and wasps in aspen-dominated forest stands that ranged from 11-45 years post-harvest. Forest age was not a significant driver in the abundance or richness patterns in our study, as we originally hypothesized. However, we did detect distinctive bee and wasp communities in each forest successional age category. Consequently, while aggregate bee and wasp abundance and richness at the stand scale may remain relatively stable as forest stands mature, these communities appear to undergo pronounced compositional shifts as they mature following disturbance. Collectively, our results suggest that maintaining a diversity of stand age classes across the landscape will likely enhance overall pollinator diversity.

Most studies that have explored forest successional age structure and bee diversity report a consistent trend that richness and abundance declines with increasing forest age (e.g. Hanula et al. 2015, Hanula et al. 2017, Taki et al. 2013). Our results, however, are more ambiguous and provide only limited evidence to support this trend observed elsewhere. While not statistically significant, younger stands supported more pollinating bees that depend upon floral resources that are more abundant in open canopy forest stands. This is consistent with other studies in temperate and boreal forests that found that younger sites supported greater species abundance and richness (Grundel et al. 2010; Hanula et al. 2015; Rubene et al. 2015a; Roberts et al. 2017). The lack of significance may be the result of our sampling because one site, County D, was disturbed by bears on two occasions, likely lowering our collection totals and impacting our analysis of stand age and abundance and richness. Younger forest stands also have more bare soil that is important for soil burrowing species like *Lasioglossum* spp. that were very abundant in the younger stands. We detected more parasitoid wasps in the older stands compared to the other ages. The middle-aged stands were approximately 20 years post-harvest and had relatively few bees and wasps, likely because they had neither the structural complexity of older stands nor the rich understory that supports pollinating bees. This forest successional stage (stem exclusion) generally lacks a rich herbaceous understory and therefore likely provides fewer nectar and pollen resources (Fye 1972).

These aspen stands supported a diverse group of native bees and wasps. Wasps such as the eastern yellowjacket (*Vespula maculifrons*) are often not considered pollinators because of their nearly hairless bodies and predatory role. Wasps provision their nest with “meat” (i.e., caterpillars, carrion and other predated insects) and not pollen. Adult wasps do visit flowers and drink nectar, and have been shown to be pollinators for some plants (Cheng et al. 2009). Their role as potential pollinators for forest plant species in our region remains poorly explored, though in another region where *Vespula* sp. was non-native, the wasps preyed upon native bees and were ineffective pollinators for one tree species (Hanna et al. 2012). Nonetheless, they cannot be completely discarded as wasps as pollinators, and in the absence of bees, this group has been shown to pollinate some forest flowers (Hallett et al. 2017). The parasitic bees and wasps (sometimes called cuckoo bees and wasps) were captured only rarely in our traps (12 total). This

observation is consistent with other literature that has found pan traps to be ineffective for nest parasitic species because they do not collect pollen, and consequently are less likely to visit flowers (or pan traps that serve as artificial flowers) (Lebuhn et al. 2012). Future research with this group of insects should include both active netting of bees and nest traps; together these supplemental techniques would capture bees and wasps that are under sampled with pan traps alone (Rubene et al. 2015b)

The abundance of parasitoid wasps may also be beneficial to the forest as a whole, and potentially serve as defenders of forest by targeting forest pests. Forty-four percent of these parasitoid wasps were found in the older aspen stands, likely preying on wood-chewing insect larva that live beneath tree bark and damage trees. The emerald ash borer (*Agrilus planipennis*, EAB), for example, is an invasive beetle that is damaging Wisconsin's forests and is considered a major pest to native ash trees (*Fraxinus* spp), causing high rates of tree mortality with millions of dollars in damages (Kovacs et al. 2010). In other parts of its introduced range in eastern United States, endemic parasitoid wasps have been known to target the EAB as a host species for their eggs (Duan et al. 2013). The Wisconsin Department of Natural Resources is currently releasing an Asian parasitoid wasp that is the natural enemy of EAB as a biocontrol agent for this forest pests (Resources 2016).

One limitation of our work is that we only considered no-retention treatments, a logging technique that is becoming less common in the region during the last two decades. Future work should also consider how alternatives to no-retention silvicultural treatments, like uneven aged or selective logging, could impact bees and wasps in aspen forests. These alternative treatments can positively impact other species groups. For example, conifer and hardwood retention treatments were found to increase avian diversity compared to no-retention logging in the same aspen-dominated landscape compared to no-retention treatments (Roth 2012). Forest clearings and gaps adjacent to mature stands has also been shown to increase bee diversity in temperate and boreal forests (Rubene et al. 2015a; Roberts et al. 2017).

Early successional forests can serve as an important habitat for bees and wasps (Taki et al. 2010; 2013), although older stands were also important for some species (Hanula et al. 2015; Roberts et al. 2017). Our work illustrates a successional pattern in bee community composition following disturbance, with a guild level or functional group shift through time (Roberts et al. 2017). Landscape forest management planning should strive to include both young and old forest stands in a mosaic to provide habitat for these forest associated bees and wasps. Additional research in our region that can illuminate how alternative silvicultural treatments can restore the understory herbaceous layer, open the forest canopy, and maintain timber yields would contribute to a triple "win" for forest bees and wasps, other wildlife and human communities (Hanula et al. 2016b).

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Tables

Table 1. Bee and wasp Hymenoptera abundances and richness of the collected in nine aspen-dominated forest stands of different ages in northeastern Wisconsin, USA

Site name	Age post-harvest	Age Category	Total Abundance	Total Richness
County Y	11	Young	136	21
Jerry Rd	11	Young	76	23
County D	15	Young	24	11
Fawn Lake	20	Middle	65	20
Trout Creek Rd	24	Middle	37	10
Grouse Rd	33	Old	54	14
Woodduck Lake	34	Old	42	17
Rainbow Dr	44	Old	22	13
New Trout Creek	45	Old	35	10

Table 2. Bee and wasp members of the Hymenoptera collected in aspen-dominated forest stands of different ages and their ecological role in northeastern Wisconsin, USA

Ecological role and family	Forest stand age			Total
	Young	Middle	Old	
Kleptoparasitic				
Apidae	0	1	1	2
Chrysididae	7	1	2	10
Parasitoid wasps				
Aulacidae	6	6	8	20
Braconidae	13	14	25	52
Ichneumonidae	51	29	54	134
Pompilidae	7	0	0	7
Sphecidae	7	2	6	15
Forest pest				
Tenthredinidae	10	0	0	10
Pollinator				
Andrenidae	6	0	1	7
Apidae	7	1	11	19
Halictidae	68	23	21	112
Megachilidae	9	7	2	18
Predatory wasps				
Eumeninae	1	1	3	5
Pamphiliidae	13	11	5	29
Sphecidae	0	0	1	1
Vespinae	17	6	11	34
Unknown bee				
Unknown	8	0	4	12
Total	230	102	155	487

Table 3. Forest stand habitat measurements northeastern Wisconsin, USA where bee and wasps were trapped in spring and summer 2014.

Site name and category	Age post-harvest (years)	Mean aspen tree DBH (cm)	Percent Aspen (%)	Mean woody debris (m ³)
Young				
County Y	11	3.73	98	50.8
Jerry Rd.	11	3.71	95	21.0
County D	15	5.24	90	10.2
Middle				
Fawn Lake	20	6.85	72	9.9
Trout Creek Rd.	24	7.39	32	15.0
Old				
Grouse Rd.	33	11.41	38	27.9
Woodduck Lake	34	10.11	40	27.4
Rainbow Dr.	44	22.73	48	55.1
New Trout Creek	45	19.26	34	22.4

Figures

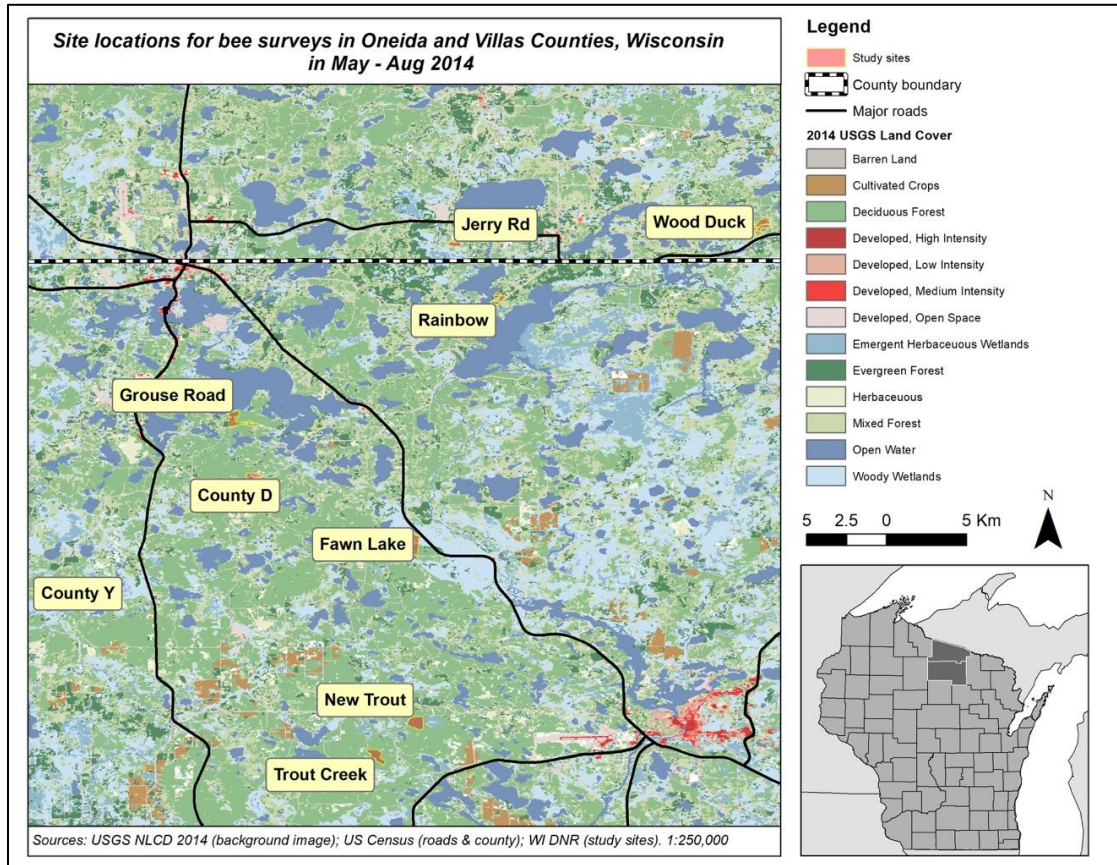


Fig 1. Research sites in Vilas and Oneida Counties in Wisconsin where bees and wasps were collected from aspen-dominated forest stands in May – August 2014. Research sites were randomly selected from available forest stands and broadly are representative of this region’s forests and landscape.



Fig. 2. Examples of young, middle and old (from left, upper right and lower right) aspen forest stands where bees and wasps were sampled in aspen-dominated, no-retention forest stands that ranged from 11-45 years old post-harvest in May – August 2014. Photo credit: C. Phifer

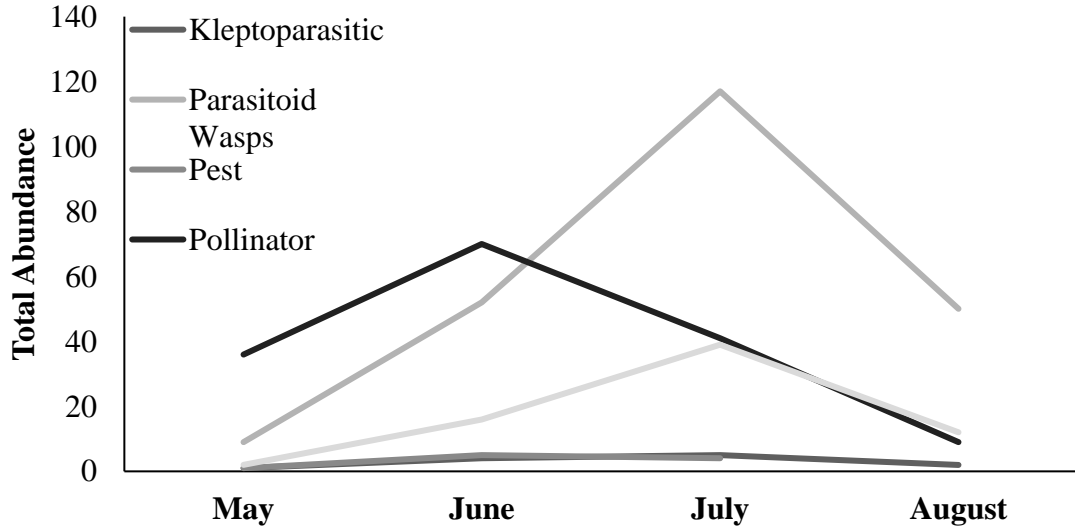


Fig. 3. Temporal patterns of bees and wasps (divided by their ecological role) that were collected from in aspen-dominated, no-retention forest stands that ranged from 11-45 years old post-harvest in May – August 2014 in Vilas and Oneida Counties, Wisconsin.

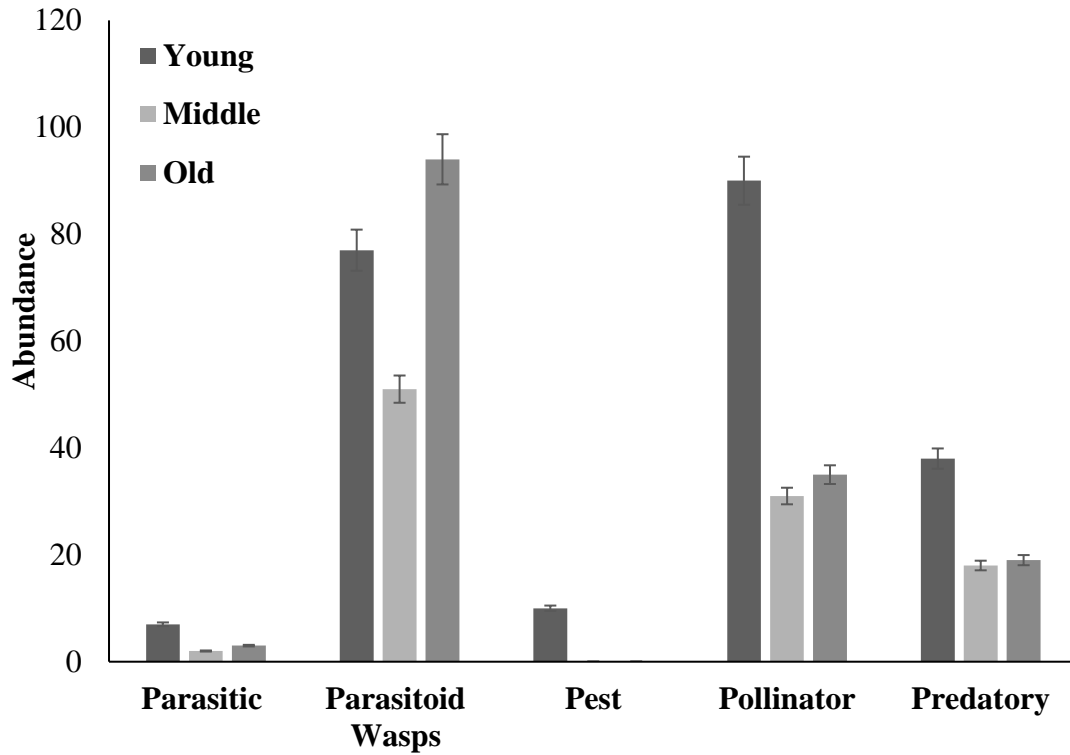


Fig. 4. Abundance patterns of bees and wasps (divided by their ecological function) that were collected from in aspen-dominated, no-retention forest stands that ranged from 11-45 years old post-harvest in May – August 2014 in Vilas and Oneida Counties, Wisconsin. Standard error bars are shown.

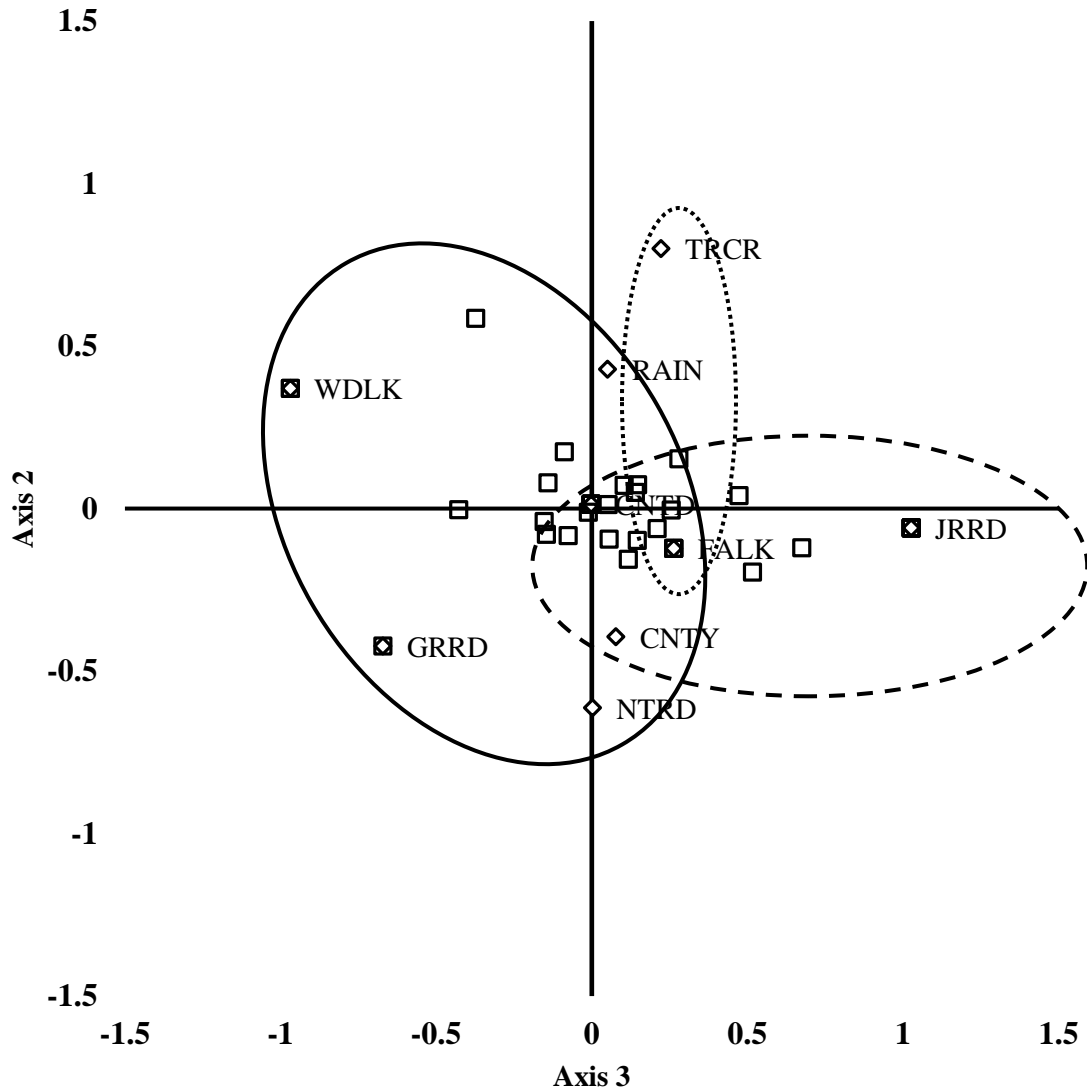


Fig. 5. NMDS of bees and wasps collected from pan traps in a chronosequence of aspen-dominated forest stands in northeastern Wisconsin. Final solution was a three-dimensional ordination; here Axis 2 and 3 are displayed for simplicity. Black open squares are bees or wasp species and open diamonds are the sites sampled. Solid black line is the older aspen stands, dotted black line is the middle age stands and the dashed black line is the younger sites.

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6. Conclusion and final reflections

The social and ecological sustainability of bioenergy

In this project, I explored how bioenergy associated land-use change and land management practices influenced bird and bee communities and their associated ecosystem services. As part of the broader MTU bioenergy project, I considered these changes through the lens of a bioenergy future, contrasting the potential bioenergy feedstocks with alternative land uses in Argentina and the United States. These chapters are one part of what has been a long journey that led me through four countries in the Americas over the last four years. I document my research scholarship from Brazil and Mexico in Appendix A, which includes the citations of peer-reviewed articles that I contributed to from those countries.

In Argentina, the transition from pasture and annual crops to eucalyptus plantations, the potential bioenergy feedstock, resulted in declines in species richness, abundances and overall simpler communities of bees and birds. The effect size was substantial: only 1% of bees and 5% of birds of the total were observed in the eucalyptus plantations. In this region, the sharp structural change from the common pasture/annual crops to dense plantations with tall trees and closed canopies changes the local and micro habitats that grassland-associated species depend upon. However, the effects did not extend far beyond the plantations and bird and bee abundances rebounded once outside the plantation's borders. In addition to changes to biodiversity patterns, I also examined how eucalyptus plantation expansion impacted carbon sequestration and pollination services of wild bees using ecosystem service modeling software. This work integrated the social science findings from the Argentine community interviews and surveys to create a plausible land-use map of region that limited plantation expansion and increased orchards, an interpretation of the communities' preferences. I also created a plausible map that featured a 200% expansion of the eucalyptus plantations, a likely outcome considering the policies and favorable market conditions. I then contrasted changes in ecosystem services between these two future scenarios and the current land uses. The results demonstrated that plantations have the potential to negatively impact biodiversity and pollination service but can be a source of carbon sequestration.

Taken together, these results demonstrate how land-use change can impact species and ecosystems, and to my knowledge, they are the first of their kind in this region. Consequently, these results should be carefully considered and future research is needed. Priorities for new research include: 1) work to directly consider both the size and spatial arrangements of eucalyptus plantations; 2) reduce tree densities as a possible means to minimize the impacts on biodiversity and ecosystem services; 3) evaluate the value of the eucalyptus flowers as a food source to native bees and potentially insectivores birds (that may prey upon them) ; and 4) validate estimates of changes in ecosystem services with ground-truthed values.

Unlike the Argentine case study, which focused on novel feedstocks and dramatic land-use changes, the United States case study considered the effects of land and forest management on wild bees in naturally occurring aspen forests in northeastern Wisconsin. This story is considerably more nuanced than just land-use change alone, and consequently I surveyed for bees in a chronosequence of differently aged aspen stands and collected detailed habitat characteristics. Broadly, bee abundance, richness and community structure shifted with forest stand age. Bee abundance declined with increasing stands age though this relationship was not statistically significant. My work suggests that although more bee species use younger forest habitats, some bee species were only found in older, more mature stands, particularly bumble bees. These results suggest that no-retention treatments (i.e., clear cuts) can provide habitat to wild bees but that a mosaic of different aged forest stands are needed to provide habitats for the diverse bee communities in its entirety. Future research should consider the potential impacts of alternative silvicultural treatments, like hard-wood retention or uneven-aged management, on bee communities.

This work represents one part of the broader assessment of the social and ecological sustainability of bioenergy. My work reflects my interest in biodiversity conservation in human-modified landscapes, regardless of what the policy driver is. Alone, however, it is only part of the answer to the sustainability bioenergy development. Future work should further integrate the social and natural science findings and weigh the trade-offs of land-use change and its impacts long-term viability of bioenergy.

Interdisciplinary research – personal reflection

Almost 20 years ago, Dr. Jane Lubchenco called for a new type of science, indeed a new social contract between society and science that focused on the interconnected and global environmental challenges facing society (Lubchenco 1998). In short, she suggested that scientists must begin to collaborate and work in teams to answer boundary-crossing environmental and sustainability research questions. This call to action, a “Century of the Environment,” published in *Science*, inspired me in my career choice, including choosing to participate in this research project and pursue a doctoral degree. I would not have chosen this project, university or career path were it simply a biodiversity assessment. Rather, I was attracted to the prospects of working within an interdisciplinary team to address sustainability-related questions of local and global importance.

To realize the Century of Environment, science must become more collaborative. Indeed, science teams are increasing the engines of discovery, and one must be prepared to work collaboratively in a group to be successful in science (Wuchty et al. 2007; Read et al. 2016). A recent survey of scientists identified 40 top questions relating to sustainability, and to answer nearly all of them will require insights, techniques and expertise from more than one scientific discipline (Kramer et al. 2017). However, interdisciplinary research can come at the expense of slower publication rates (Leahey et al. 2017) and lower rates of funding (Bromham et al. 2016), two important metrics for academic positions. An interdisciplinary career runs against the standard siloed academic pathway, which is

organized around departments and single disciplines. An interdisciplinary career is, in part, a choice and an expression of one's values and priorities.

Successful interdisciplinary work is built upon a deep foundation in individual disciplines; from my experience, one must understand and know the methods, ideas and theories of one discipline to then effectively build bridges between two or more sciences, and connect different ways of knowing and describing the world. As a member of an international, interdisciplinary research group, I have learned and tried to practice the values necessary for successful team science. Below I present three key points to consider and practice for successful interdisciplinary team science:

One, develop a clear framework for integration early on and return to it often. Finding a means to integrate and utilize the expertise of team members remains one of the biggest challenges to interdisciplinary research (Bromham et al. 2016). Part of the slowness in publishing comes from the extra time needed *a priori* to create a shared conceptual model that can link together many different types of data (Bromham et al. 2016). It is important to make the interdisciplinary methods “operational” – that is, to connect the research methods and data with the shared conceptual model. And, as a group, return to the model frequently for inspiration and refinement in an iterative fashion.

Two, practice open communication in your team, and assume the best intentions. As a first step, think carefully who you invite to be a member of the group: scientific expertise is not alone a sufficient for team science. To be successful as group, one must actively be present, engaged and empathetic – with oneself, with each other. Research is *hard*; sharing and coordinating research is even *harder*. As a team, it is important to establish and practice communication norms and set (and stick with) regular meetings, whether in-person or remote. Researchers that frequently work together build strong social norms and capital that makes the hard work of research integration easier (Leahey et al. 2017).

Third, build your team with deep, yet broad expertise. One must first know their “home” discipline before learning to respect, appreciate and integrate with another one. Successful interdisciplinary teams should have both discipline-specific experts and a few well-rounded generalists who can move laterally between the group, finding the points of commonality and engineering strategies for integration. Consider adopting 80/20 or 75/25 ratio of expertise in one's own discipline and knowledge and respect for another. Finally, team members should coordinate the timeline of integration, recognizing that different research methods require different inputs of time and resources. Following data collection, data must be curated and analyzed, and only when “ripe” can it be shared and applied to an integrated model.

Others in the MTU team have published best practices and reflections on interdisciplinary research and teaching (Knowlton et al. 2014; Halvorsen et al. 2016; Norris et al. 2016). I do not mean to suggest these three principles are the only ones needed for interdisciplinary research. But these are the three that I meditated on and ones that continued to resurface again and again in my research. This project was designed to cross

borders in disciplines and countries. I have tried to cross these boundaries and make it easier for others to do the same.

Interdisciplinary work, in short, is not easy or fast. For me, however, it remains a central part of my career goals and research agenda: to advance human and natural well-being through the co-production of scientific knowledge that leads to action. There exists an urgent need to recognize the many unknowns in conservation science and develop an active research agenda to answer those questions. But we must also be ready to share what we know and be ready to act upon it, and do so in a way that communicates more than p-values; for science alone does not change opinions or policy (Lubchenco 2017; Keeler et al. 2017).

I began this project as an ecologist with interests in biodiversity conservation and ecological interactions. I have grown from a quadrat-based, biodiversity-only ecologist to an effective, discipline-crossing conservation biologist and a member of a team studying social and ecological systems and sustainability. I believe this latter development will be where and how I contribute to science and conservation, and do my best to answer the Dr. Lubchenco's challenge to answer the call of the Century of the Environment.

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7. Appendix A: related publications

Below are related peer-reviewed publications that I contributed to as part of PIRE research team. I am including these citations to demonstrate and record my scholarship activities during my PhD. I have included the titles, abstracts, authors and complete citations. Publications are organized in the order in which they were published, with the title serving as the header. Citations are formatted according to the published journal's specifications.

A case study of strategies for fostering international, interdisciplinary research

Abstract: Bringing together and successfully managing a highly interdisciplinary (ID) research team of socioeconomic, biophysical, and engineering scientists is highly challenging, particularly when that team includes 20 scientists and students across six countries. This paper reports on the results of evaluating the success of such a team as it studies the socioecological impacts of bioenergy development across the Americas. We find that the team has succeeded according to several different metrics. We demonstrate that the literature on accelerated sustainability transitions and small group team creation, development, and management holds valuable lessons for the success of ID teams.

Citation: Halvorsen, K., Knowlton, J., Mayer, A., Phifer, C., Martins, T., Pischke, E., Propato, T., Cavigliasso, P., Garcia, C., Chiappe, M. and Eastmond, A. 2016. A case study of strategies for fostering international, interdisciplinary research. *Journal of Environmental Studies and Sciences* 6(2): 313-323

Forest reserves and riparian corridors help maintain orchid bee (Hymenoptera: Euglossini) communities in oil palm plantations in Brazil

Abstract: Orchid bees (Apidae, Euglossini) are important pollinators in the Amazon forest. In eastern Brazilian Amazon, secondary forest and pastures are being replaced by oil palm plantations. Here, we tested the role of forest reserves and riparian corridors in maintaining orchid bees. We sampled bees in three different soil-type uses, comparing richness, abundance, and assemblage composition. Estimated richness was lowest in palm plantations than in forest reserves and riparian corridors on diversity of orchid bees. Riparian corridors had the highest abundance, followed by reserves, and oil palm plantations. Bee assemblage also varied with land cover, with the reserves having the most distinct composition. We also identified indicator bees for primary forest. Our results demonstrate riparian corridors and forest reserves can maintain orchid bees in oil palm landscapes.

Citation: Brito, T, Phifer, C., Knowlton, J., Fiser, C., Becker, N. Barro, F., et al. 2017. Forest reserves and riparian corridors help maintain orchid bee communities in oil palm plantations. *Apidologie* 48:575–587

Oil palm plantations affect movement behavior of a key member of mixed-species flocks of forest birds in Amazonia, Brazil

Abstract: Oil palm (*Elaeis guineensis*) is a rapidly expanding crop in the Amazonian region of Brazil. Brazilian law requires all landowners, including oil palm plantations, to maintain forest reserves and forested riparian corridors as a way to limit biodiversity losses. Because of these laws and the forest-like structure of oil palm, these plantations may function as habitat for some native species in the region. We tested this assumption by experimentally translocating Cinereous Antshrikes (*Thamnomanes caesius*), a forest understory insectivorous bird and nuclear member of mixed-species flocks, from forest reserves to riparian corridors within a large oil palm plantation landscape and tracked their movements back to their home ranges. In total, we recorded the movements of 18 individuals, 8 of which were translocated. The other 10 individuals were tracked within their home ranges in the forest reserves. Six of the eight translocated birds successfully returned to their forest home range, but only one bird flew through the more direct route back through the oil palm matrix while the rest took longer routes through adjoining riparian corridors. Homing time for translocated birds averaged 9.57 (2.23 SE) days. The home range of birds within the forest reserves averaged 2.39 (0.69 SE) ha, and, with the exception of the single returning bird, Cinereous Antshrikes were never detected in oil palm. Our results suggest that oil palm plantations are a barrier to movements of our study species, and that riparian corridors connecting forest fragments may be effective routes for dispersal.

Citation: Knowlton, J., Phifer, C. et al. 2017. Oil palm plantations affect movement behavior of a key member of mixed-species flocks of forest birds in Amazonia, Brazil. Tropical Conservation Science. DOI:10.1177/1940082917692800

Diversity and abundance of bees (Hymenoptera: Apoidea) in oil palm agroecosystems and cultivated pastures in Tabasco, Mexico

Abstract: The objective of the study was to determine the diversity and abundance of wild bees in agroecosystems of oil palm and grasslands in an agricultural area of the state of Tabasco, Mexico. Weekly samplings from June to November 2015 were carried out on four adult oil palm plantations and four pasture areas located in the municipalities of Jalapa and Tacotalpa in the south of this state. The bees were caught using traps made of plastic containers of various colors containing water with detergent. In each site 10 traps placed on a wooden stake 1 m above the ground were used. In total, 790 specimens of bees belonging to two families (Halictidae and Apidae), 22 genera and 102 species morphologically distinct were captured. 20 genera, 91 species and 662 specimens were recorded in pasture, and 15 genera, 40 species and 128 specimens were recorded in oil palm. The most abundant species in pasture were *Apis mellifera*, *Euglossa* sp. and *Melitoma* sp., and in oil palm were *Euglossa* sp., *Augochlora nigrocyanea*, and *A. mellifera*. The Shannon index indicated high diversity in species richness for both agroecosystems, but the diversity was 1.3 times greater in pasture than in oil palm. The Sorensen coefficient of similarity revealed a low similarity between both agroecosystems,

with 23 shared species. A species accumulation curve was elaborated and through the Clench equation, 143 species for the pasture and 74 species for the oil palm agroecosystem were estimated. The greatest richness in the pasture with respect to oil palm was possibly related to the vegetation cover, the attraction method used and the diversity of flowering plants that grow in both agroecosystems. It is concluded that the two agroecosystems are important in maintaining the current diversity of wild bees, thus contributing to the ecosystem services of pollination in the studied area.

Citation: Jiménez, M., Soto, López, J., Nápoles, J. Knowlton, C. Phifer, D. Flaspohler, A. Méndez. 2017. Diversity and abundance of bees (Hymenoptera: Apoidea) in oil palm agroecosystems and cultivated pastures in Tabasco, Mexico. Nicaraguan Journal of Entomology: 115

Barriers and solutions to conducting large international, interdisciplinary research projects

Abstract: Global environmental problems such as climate change are not bounded by national borders or scientific disciplines, and therefore require international, interdisciplinary teamwork to develop understandings of their causes and solutions. Interdisciplinary scientific work is difficult enough, but these challenges are often magnified when teams also work across national boundaries. The literature on the challenges of interdisciplinary research is extensive. However, research on international, interdisciplinary teams is nearly non-existent. Our objective is to fill this gap by reporting on results from a study of a large interdisciplinary, international National Science Foundation Partnerships for International Research and Education (NSF-PIRE) research project across the Americas. We administered a structured questionnaire to team members about challenges they faced while working together across disciplines and outside of their home countries in Argentina, Brazil, and Mexico. Analysis of the responses indicated five major types of barriers to conducting interdisciplinary, international research: integration, language, fieldwork logistics, personnel and relationships, and time commitment. We discuss the causes and recommended solutions to the most common barriers. Our findings can help other interdisciplinary, international research teams anticipate challenges, and develop effective solutions to minimize the negative impacts of these barriers to their research.

Citation: Pischke, E., Knowlton, J., Phifer, C., Lopez, J., Propato, T., Eastmond, A., Martins de Souza, T., Kuhlberg, M., Picasso Risso, V., Veron, S., Garcia, C., Chiappe, M., Halvorsen, K. 2017. Barriers and solutions to conducting large international, interdisciplinary research projects. Environmental Management: 60(6): 1011-1021

Transatlantic wood pellet trade demonstrates telecoupled benefits

Abstract: European demand for renewable energy resources has led to rapidly increasing transatlantic exports of wood pellets from the Southeastern United States (SE US) since 2009. Disagreements have risen over the global greenhouse gas reductions associated

with replacing coal with wood, and groups on both sides of the Atlantic Ocean have raised concerns that increasing biomass exports might negatively impact SE US forests and the ecosystem services they provide. We use the telecoupling framework to test assertions that the intended benefits of the wood pellet trade for Europe might be offset by negative consequences in the SE US. Through review of current literature and available datasets, we characterize observed and potential changes in the environmental, social, and economic components of the sending and receiving regions in order to assess the overall sustainability of this renewable energy system. We conclude that the observed transatlantic wood pellet trade is an example of a mutually beneficial telecoupled system with the potential to provide environmental as well as socioeconomic benefits in both the SE US and Europe despite some negative impacts on the coal industry. We recommend continued monitoring of this telecoupled system in order to quantify the environmental, social, and economic interactions and effects in the sending, receiving and spillover systems over time so that evidence-based policy decisions can be made with regard to the sustainability of this renewable energy pathway.

Citation: Parish, E., Herzberger, A., Phifer, C., Dale, V. 2017. Telecoupled transatlantic wood pellet trade provides benefits to both sending and receiving Systems. *Ecology and Society*, special issue: Telecoupling: a New Frontier for Global Sustainability (Vanessa Hull & Jianguo Liu, guest editors). URL: <https://www.ecologyandsociety.org/issues/view.php?sf=125>

Short-rotation aspen forest management impacts on avian communities: implications for bioenergy development

Abstract: In the upper Midwestern United States and parts of Canada, forests dominated by *Populus tremuloides* (Aspen) are increasingly being considered as a bioenergy feedstock for power plants. When used for bioenergy, these forests are harvested at much younger ages than more traditional products such as pulpwood and lumber. To better understand the potential consequences a shift in shorter rotation harvest strategies on avian communities, we examined bird community composition in a chronosequence (10-45 yrs since harvest) of 12 coppiced, even-aged, no-retention Aspen stands using point counts. We also tested for differences in relative abundances among different foraging, nesting, and diet guilds across stand ages. Young (8-15 yrs old), middle (20-44 yrs old), and mature (45 yrs old) stands had no significant differences in species richness or relative abundance. Distinct avian community assemblages were associated with each stand age class, but few differences in guild structure were detected. Four bird species were significantly associated with a particular age class. Maintaining a wide range of Aspen stand age classes in the landscape appears to be the best strategy for conserving a diverse bird community in this region.

Citation: Testa, G., Knowlton, J., Phifer, C., Roth, A., Webster, C., Flaspohler, D. *In press*. Short-rotation aspen forest management impacts on avian communities: implications for bioenergy development. *Northeast Naturalist*