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RESPUESTA DE LAS AVES ANTE DIFERENTES ESCENARIOS DE RESTAURACIÓN EN BOSQUES TEMPLADOS

T E S I S

QUE PARA OBTENER EL GRADO ACADÉMICO DE

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P R E S E N T A

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Por medio de la presente me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día 2 de mayo del 2011, se acordó poner a su consideración el siguiente jurado para el examen de grado de Maestría en Ciencias Biológicas (Biología Ambiental) del alumno **Ortega Álvarez Marcos Rubén** con número de cuenta **404053976** con la tesis titulada: **"Respuesta de las aves ante diferentes escenarios de restauración en bosques templados"** bajo la dirección del **Dr. Roberto Antonio Lindig Cisneros.**

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A mis padres

• ÍNDICE •

• RESUMEN •

La restauración ecológica ha sido considerada como una actividad fundamental para revertir la degradación de los ecosistemas que amenaza la conservación de la biodiversidad a nivel mundial. Históricamente, los animales han recibido poca atención dentro de las actividades de restauración ecológica, sin embargo durante la última década, las aves han sido incorporadas a la investigación en ecología de la restauración. Incrementar nuestro conocimiento en relación a las aves y al proceso de restauración ecológica podría propiciar el desarrollo de nuevas aproximaciones para llevar a cabo esfuerzos de restauración integrales. De esta forma, en este trabajo: (1) compilé y analicé la literatura existente asociada con las aves y el proceso de restauración ecológica (Capítulo II) y (2) determiné las diferencias en las respuestas de las comunidades de aves entre hábitats manejados (parcelas de reforestación y restauración), perturbados (campos agrícolas abandonados y arenales de origen volcánico) y naturales (bosques originales y bosques perturbados por la actividad volcánica) en un paisaje volcánico con una historia de disturbio compleja (Capítulo III).

A lo largo del Capítulo II, clasifiqué la literatura revisada de acuerdo a sus objetivos principales en cuatro categorías diferentes: (1) ecología, (2) restauración del hábitat para la conservación de las aves, (3) las aves como bioindicadoras del cumplimiento de metas de restauración y (4) las aves como guías del proceso de restauración. Posteriormente, señalé el conocimiento faltante y los retos que deberán ser afrontados para guiar e implementar esfuerzos de restauración más eficientes. En general, encontré que la investigación en zonas templadas ha sido mayormente realizada en los Estados Unidos de América (67 % de la literatura revisada), mientras que el estudio de los ecosistemas tropicales es incipiente. En la mayor parte de la literatura revisada (64.8 %), se analizó algún aspecto ecológico del componente ornitológico y el proceso de restauración. Asimismo, identifiqué ciertas propiedades de las actividades de restauración (e.g., tamaño de los sitios restaurados, hábitat en cuestión, características de hábitats adyacentes) que deberán ser contempladas al considerar a las aves dentro de un contexto de restauración. A pesar de que en los últimos años se han incorporado en mayor medida a las aves en trabajos de investigación relacionados con la ecología de la restauración, aún es necesario que ciertos temas sean abordados por estudios futuros relacionados con esta disciplina.

Los resultados asociados al Capítulo III de este trabajo, indican que las comunidades de aves varían entre hábitats manejados como consecuencia de su historia de disturbio y estrategias de manejo. Asimismo, determiné que las actividades de restauración promueven comunidades de aves diversas, equitativas y heterogéneas (tanto taxonómica como funcionalmente) semejantes a aquellas presentes en hábitats naturales. A pesar de que observé que las actividades de reforestación incrementan la diversidad y equitatividad de las comunidades de aves, plantar únicamente especies arbóreas como estrategia de manejo no es suficiente para lograr comunidades de aves similares a aquellas de hábitats naturales. Por ello, recomiendo llevar a cabo esfuerzos de restauración aún en sistemas productivos, con la finalidad de incrementar la recuperación de la biodiversidad. Con base en estos resultados, discuto la importancia de definir estrategias de restauración particulares para sitios diferentes, ya que las historias de disturbio y las características locales de los hábitats pueden producir respuestas diferenciales de las comunidades de aves. Además, concluí que la complejidad del sotobosque es un factor importante que debe ser considerado en programas de restauración que incluyan al componente ornitológico dentro de sus objetivos. Finalmente, denoté la utilidad de llevar a cabo monitoreos de comunidades de aves para verificar el cumplimiento de metas de restauración desde una aproximación integral.

• ABSTRACT •

Ecological restoration has been considered as a strategy to revert habitat degradation that imposes a threat to biodiversity worldwide. Historically, animals have received little attention within restoration activities, but in the last decade, charismatic fauna such as birds have been widely incorporated into restoration ecology research. Increasing our knowledge regarding birds within the restoration process should aid the development of novel approaches to perform and achieve integral restoration. Thus, in this study I: (1) compiled and analyzed the current literature associated to birds and the restoration process (Chapter II), and (2) determined differences in bird community responses to managed (reforestation and restoration plots), disturbed (abandoned cropfields and "arenales"), and natural habitats (original and late-seral forests) within a volcanic landscape that exhibits a complex history of disturbance (Chapter III).

Through Chapter II, I classified the compiled literature according to their main objectives in four different categories: (1) ecology, (2) habitat restoration for bird conservation, (3) birds as bioindicators of restoration goals achievement, and (4) birds as guides for the restoration process. I then underlined the gaps and challenges that must be fulfilled in order to guide and implement more efficient restoration efforts. In general, research from temperate zones has been performed mainly within the United States (67 % of reviewed literature), and our understanding of tropical ecosystems is very incipient. The majority of the revised literature (64.8 %) analyzed the ornithological component of the restoration process from an ecological approach. As suggested by the revised studies, particular properties of restoration activities (e.g., size of restored sites, involved habitat, characteristics of contiguous habitats) should be contemplated when considering birds within the restoration context. Despite the increasing incorporation of birds into restoration ecology research, important topics still remain to be addressed by future studies.

Results associated to Chapter III suggest that bird communities vary among managed habitats, as a consequence of both their disturbance history and current management strategy. Moreover, I determined that restoration activities promote more diverse, even, and heterogeneous (both taxonomic and functional) bird communities that resemble those of natural habitats. Although I found that reforestation activities could enhance diversity and evenness of bird communities, planting only tree species as a management strategy might not be sufficient to achieve bird communities similar to those of natural habitats. Thus, I encourage restoration efforts, even in production ecosystems, to enhance the effectiveness of biodiversity recovery. Based on my results, I highlight the importance of defining particular restoration strategies for each different site, as local disturbance histories and site-specific characteristics could produce particular responses in bird communities, despite the presence of rich species pools in adjacent forests. I conclude that understory complexity is an important factor to consider in restoration programs that include wildlife components in their goals. Finally, I suggest the usefulness of monitoring bird communities to assess compliance with restoration goals from an exhaustive approach.

Capítulo I

Introducción

"Aún tiene que probarse que la inteligencia tenga algún valor para la supervivencia."

– Arthur C. Clarke –

• INTRODUCCIÓN •

Las actividades antropogénicas han modificado y deteriorado los ecosistemas naturales, poniendo en riesgo la conservación de la biodiversidad a nivel mundial (Vitousek et al. 1997). Por ello, los estudios de porte ecológico han dirigido sus esfuerzos para determinar los efectos de la intervención humana sobre los ecosistemas y proponer herramientas teórico-prácticas adecuadas para revertir su degradación. En las últimas décadas, la restauración ecológica ha recibido especial atención como medio para procurar la recuperación de los hábitats degradados y facilitar la conservación de la naturaleza en sistemas productivos (Hobbs y Norton 1996). No obstante, esta disciplina aún requiere del desarrollo de criterios efectivos y de fácil medición para determinar si la trayectoria que siguen los sistemas manejados es la deseada.

La tarea de la restauración ecológica no es sencilla, ya que requiere de la implementación de estrategias diversas para mitigar el efecto adverso que diferentes tipos de disturbio ejercen sobre un mismo ecosistema (Lindig-Cisneros 2007). En general, los ecosistemas alterados por disturbios naturales severos (e.g., actividad volcánica) suelen recuperarse a través de procesos de sucesión ecológica a lo largo de períodos de tiempo variables (del Moral y Wood 1993, Young et al. 2005). Bajo tal escenario, las actividades de restauración ecológica generalmente se enfocan a acelerar el proceso de recuperación de los hábitats (Palmer et al. 1997). Sin embargo, no todos los sistemas degradados siguen un proceso de sucesión ecológica, pudiendo en su lugar estar inmersos en una dinámica no linear de estados y transiciones, lo cual demandaría estrategias de restauración particulares para facilitar el tránsito de un estado degradado a otro deseado (Suding et al. 2004). A pesar de que se ha progresado en el estudio ecológico de los sistemas perturbados por el ser humano que siguen dinámicas no lineales, aún es incipiente el entendimiento de los efectos de la restauración en paisajes complejos donde ambos tipos de dinámicas, tanto lineales como no lineales, ocurren.

Históricamente, la restauración ecológica ha concentrado sus esfuerzos en el estudio del componente vegetal de los ecosistemas, lo cual ha generado un gran desconocimiento en torno a la relación que existe entre los esfuerzos de restauración y el componente zoológico de los ecosistemas (Young 2000). A pesar de que en la última década el estudio de la megafauna carismática (i.e., aves) en sistemas restaurados se ha incrementado de forma notable (Majer 2009), aún es incipiente nuestra comprensión sobre los procesos ecológicos relacionados con los animales y las actividades de restauración ecológica (Young 2000). El entendimiento del papel que juega el componente zoológico en los sistemas restaurados es imprescindible, ya que los animales son fundamentales en los procesos ecosistémicos (e.g., polinización, dispersión de semillas, herbivoría; Gabbe et al. 2002, Shiels y Walker 2003). De esta manera, incorporar el componente faunístico en la restauración ecológica podría resultar en la implementación de estrategias novedosas para afrontar de forma eficaz e integral los retos en la restauración de los ecosistemas (Lindell 2008).

En los últimos años, la ecología de la restauración ha incorporado en mayor medida a las aves dentro de sus investigaciones (Majer 2009). De forma particular, las aves han sido utilizadas como grupo focal en este tipo de estudios debido a que: (1) su muestreo no es costoso, (2) se puede compilar información de especies con múltiples requerimientos ecológicos y que habitan en distintos tipos de hábitats, (3) su monitoreo puede guiar la implementación de actividades de manejo y restauración de los hábitats en cuestión, y (4) son un grupo carismático que provee de una oportunidad única para llevar a cabo actividades de sensibilización ambiental como parte de las labores de restauración ecológica (Burnett et al. 2005, Gardali et al. 2006).

Este trabajo se enfoca en el estudio de las aves dentro del proceso de restauración ecológica, abordando el tema desde una perspectiva teórica y una práctica. De forma particular, el Capítulo II del presente manuscrito está conformado por un trabajo de revisión sobre la literatura existente asociada con las aves y el proceso de restauración ecológica. El objetivo de esta sección es el de sintetizar, analizar y hacer accesible la información relacionada con la restauración ecológica y el componente ornitológico de los ecosistemas, lo cual podría facilitar el desarrollo de nuevas aproximaciones para llevar a cabo actividades de restauración más integrales.

Por otro lado, el Capítulo III de esta tesis está constituido por un trabajo práctico cuyo objetivo consistió en determinar las diferencias en las respuestas de las comunidades de aves entre hábitats manejados (parcelas de reforestación y restauración), perturbados (campos agrícolas abandonados y arenales de origen volcánico) y naturales (bosques originales y bosques perturbados por la actividad volcánica), inmersos en un paisaje volcánico con una historia de disturbio compleja. Específicamente, el trabajo de campo asociado a este estudio se llevó acabo en las tierras comunales de la Comunidad Indígena de Nuevo San Juan Parangaricutiro, en el estado de Michoacán. En este lugar, el Laboratorio de Ecología de Restauración ha desarrollado desde el 2001 un programa de restauración adaptativa con el propósito de restablecer la superficie forestal en áreas cubiertas por arena volcánica procedente del volcán Paricutín, así como también para facilitar el restablecimiento de la vegetación nativa en campos de cultivo abandonados y propiciar la recuperación de la biodiversidad a nivel local y regional. El sitio de estudio es interesante y adecuado para desarrollar actividades de investigación relacionadas con aves en sistemas restaurados, ya que: (1) exhibe una historia de disturbio compleja en donde convergen disturbios naturales y antropogénicos, (2) los sistemas perturbados del lugar siguen dinámicas de recuperación tanto lineales como no lineales, (3) en este lugar se llevan a cabo actividades de manejo con objetivos y técnicas diferentes, y (4) el programa de restauración ecológica local esta apoyado activamente por la comunidad. Por último, en el Capítulo IV se discute y se concluye de forma general en torno a los resultados obtenidos en los Capítulos II y III del presente trabajo.

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Capítulo II

Feathering the scene: A review of birds within the restoration process

"There is a past which is gone forever. But there is a future which is still our own."

– F. W. Robertson –

• ABSTRACT •

Ecological restoration has been considered as a strategy to revert habitat degradation that imposes a threat to biodiversity worldwide. Historically, animals have received little attention within restoration activities, but in the last decade charismatic fauna such as birds have been widely incorporated into restoration ecology research. Increasing our knowledge regarding birds within the restoration process should aid the development of novel approaches to perform and achieve integral restoration. In this review, we have compiled and analyzed the current literature concerned with birds and the restoration process. We classified the reviewed literature into four categories: (1) ecology, (2) habitat restoration for bird conservation, (3) birds as bioindicators of restoration goal achievement, and (4) birds as guides for the restoration process. We then underlined the gaps and challenges that must be fulfilled in order to guide and implement more efficient restoration efforts. In general, research from temperate zones has been performed mainly within the United States (67% of reviewed literature), and our understanding of tropical ecosystems is very incipient. The majority of the revised literature (64.8%) analyzed the ornithological component of the restoration process from an ecological approach. As suggested by the reviewed studies, particular properties of restoration activities (e.g., size of restored sites, habitat involved, characteristics of contiguous habitats) should be contemplated when considering birds within the restoration context. Despite the increasing incorporation of birds into restoration ecology research, important topics still remain to be addressed by future studies.

• RESUMEN •

La restauración ecológica ha sido considerada como una actividad fundamental para revertir la degradación de los ecosistemas que amenaza la conservación de la biodiversidad a nivel mundial. Históricamente, los animales han recibido poca atención dentro de las actividades de restauración ecológica, sin embargo durante la última década, las aves han sido ampliamente incorporadas a la investigación en ecología de la restauración. Incrementar nuestro conocimiento en relación a las aves y al proceso de restauración ecológica podría propiciar el desarrollo de nuevas aproximaciones para llevar a cabo esfuerzos de restauración integrales. En esta revisión, hemos compilado y analizado la literatura existente asociada con las aves y el proceso de restauración ecológica. La literatura revisada fue clasificada de acuerdo a sus objetivos principales en cuatro categorías: (1) ecología, (2) restauración del hábitat para la conservación de las aves, (3) las aves como bioindicadoras del cumplimiento de metas de restauración y (4) las aves como guías del proceso de restauración. Posteriormente, señalamos el conocimiento faltante y los retos que deberán ser afrontados para guiar e implementar esfuerzos de restauración más eficientes. En general, encontramos que la investigación en zonas templadas ha sido mayormente realizada dentro de los Estados Unidos de América (67 % de la literatura revisada), mientras que el estudio de los ecosistemas tropicales es incipiente. En la mayor parte de la literatura revisada (64.8 %), se analizó algún aspecto de la dinámica ecológica del componente ornitológico y el proceso de restauración. Asimismo, identificamos ciertas propiedades de las actividades de restauración (e.g., tamaño de los sitios restaurados, hábitat en cuestión, características de hábitats adyacentes) que deberán ser contempladas al considerar a las aves dentro de un contexto de restauración. A pesar de que en los últimos años se han incorporado en mayor medida las aves en trabajos de investigación relacionados con la ecología de la restauración, ciertos temas deberán ser explorados a mayor profundidad por aquellos estudios futuros relacionados con esta disciplina.

• INTRODUCTION •

Habitat degradation as a result of anthropogenic activity imposes an important threat to biodiversity conservation worldwide (Vitousek *et al.* 1997). In response, restoration ecology has received special attention as a strategy to revert ecosystem degradation and promote conservation (Hobbs and Norton 1996). Restoration ecology may represent one of the most important fields of ecological research in the near future, though it still requires the development of effective and easily measured criteria to assess compliance with restoration goals, in addition to meeting the challenge of successfully merging science, practice and policy (Hobbs and Harris 2001).

Historically, restoration ecology has primarily focused on the plant component of restored sites (Young 2000). However, the role of the fauna in restored ecosystems has received increasing attention by restoration ecologists over the last decade, as shown by an upturn in published literature concerning animals within restored lands (Majer 2009). This represents an important advance in restoration ecology research because: (1) animals play major roles in ecosystem processes (e.g., pollination, seed dispersal, herbivory; Gabbe *et al.* 2002, Shiels and Walker 2003), and (2) incorporating the faunal component in restoration ecology could drive the implementation of innovative strategies to confront both ordinary and novel challenges in ecosystem restoration (Lindell 2008).

The increase in restoration ecology research focused on animals has been particularly true for charismatic fauna such as birds (Majer 2009). Birds have been widely used as focal species in many studies because: (1) they can be surveyed at low cost over large areas, (2) demographic parameters can be directly assessed, and (3) information of various species that inhabit a wide range of habitats and exhibit multiple ecological requirements can be compiled (Gardali *et al.* 2006). Within restoration ecology, bird monitoring has proven to be useful because it: (1) can determine the effectiveness of restoration activities, (2) serves as a guide for restoration and management activities, (3) is affordable, and (4) provides a remarkable educational opportunity for the public (Burnett *et al.* 2005).

Increasing our knowledge of birds within the restoration process could aid in the development of novel approaches to achieve and perform integrated restoration activities. Thus, in this review we compiled and analyzed the current literature related to birds and the restoration process. To collate the published literature related to this topic, we carried out extensive research in four scientific databases (i.e., Web of Science, Current Contents Connect, Biological Abstracts, Zoological Record) and other

Internet browser engines (e.g., Google Scholar). We used "bird" and "restoration" as both topic and title keywords to perform our searches. From the literature compiled, we selected those articles related to habitat restoration and birds, excluding those papers merely advocated to the restoration of bird populations. To detect particular trends among the reviewed literature, we extracted specific information from each work: year of publication, country where the study was conducted, reference system (original habitat used as reference for the restoration process), and type of disturbance which had altered the original ecosystem. In order to facilitate analysis of the manuscripts that merged the study of birds with that of the restoration process, we classified the revised literature into four categories according to their general objectives: (1) ecology, (2) habitat restoration for bird conservation, (3) birds as bioindicators of achieving restoration goals, and (4) birds as guides for the restoration process. Finally, we utilized the information provided by each study to detect and pin-point gaps in the knowledge and challenges that must be met in the near future in order to guide and increase the efficiency of subsequent restoration efforts.

• MANUSCRIPTS THAT COMPRISED THE REVIEWED LITERATURE •

Our research compiled a total of 109 manuscripts concerning birds and the restoration process. The majority of these (77%) are represented by articles published in scientific journals. However, the remaining 23% corresponds to technical reports and proceedings derived from conferences or workshops. As restoration ecology is an applied science, it is not surprising to find these types of manuscript among the compiled literature. Thus, we consider it important to incorporate the valuable information generated by technical reports and proceedings within this review to enhance our current knowledge of birds in the restoration process.

• STUDIES CONCERNING BIRDS AND THE RESTORATION • PROCESS THROUGH SPACE AND OVER TIME

Among the literature collated, the oldest study dates from 1983. Nevertheless, research done in the past century was limited, as only 12.5% of the reviewed literature corresponds to this period (Figure 1). Interest in birds and the restoration process did not increase until the 21st century. Specifically, the number of studies increases dramatically from 2006 to 2009. It is therefore clear that scientific research has not been directing its efforts to comprehend the ornithological component of the restoration process until relatively recently.

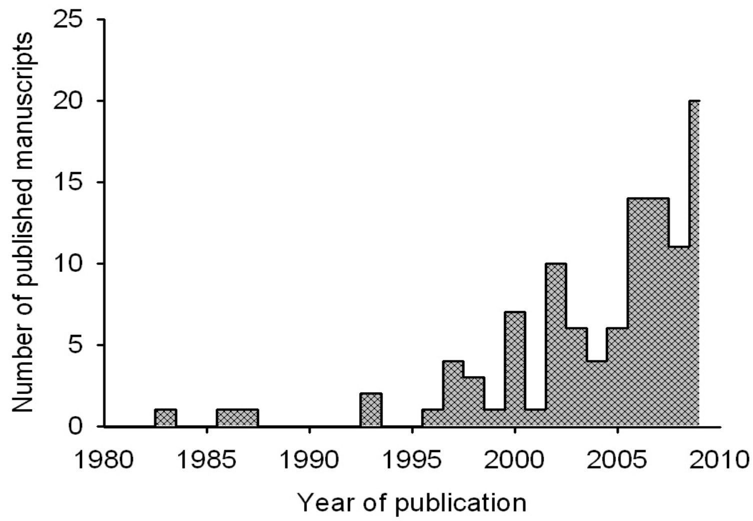

Figure 1. Studies concerning birds and the restoration process over time.

Most studies concerning birds and the restoration process are from sites in the United States (67%), with 17.4% from Europe, 4.6% from Australia, 3.7% from Latin America and the Caribbean, 3.7% from Africa, 2.8% from Asia, and 0.8% from Canada (Figure 2). In this way, generalizations regarding patterns detected among studies should be carefully interpreted as they mainly emerge from a limited region of the globe. Moreover, there is a paucity of information on the role of birds in the restoration process within tropical regions of the world.

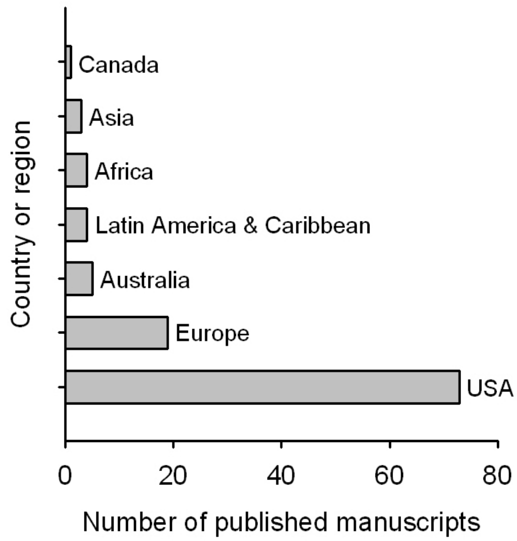

Figure 2. Studies concerning ornithology and the restoration process among countries.

• EMERGING TRENDS FROM THE REVIEWED LITERATURE •

Studies considering birds within the restoration process have surveyed both terrestrial and waterbird species. However, 53.2% of the literature concerned terrestrial birds, while only 23.9% dealt with waterbirds. Interestingly, 22.9% of the literature reviewed has focused on research questions considering both groups of birds. Hence, our insight regarding relationships between the restoration process and birds is predominantly concerned with terrestrial birds. This is associated with the difference between surveyed ecosystems, as terrestrial habitats have been subject to greater examination than aquatic ones (60% and 40%, respectively).

Historically, restoration ecology is rooted in community ecology (Young 2000). This pattern is still evident within the reviewed literature concerning birds and the restoration process: 70.1% were studies of bird communities, while 26.2% were population related studies. Within the reviewed literature, only 3.7% of studies simultaneously analyze the response of both community and population parameters to the restoration process (Dobrovolny 2003, Brawn 2006, Sogge *et al.* 2008, Lituma 2009).

A variety of ecosystems have been explored by studies related to birds and the restoration process. Within the reviewed literature, we detected 40 ecosystems where restoration activities have considered birds (Figure 3), with riparian habitats and grasslands as the most commonly studied systems (10.4% and 9.4% of studies respectively). Nevertheless, the majority of the ecosystems mentioned within the literature (i.e., 50%) have been understudied as the processes occurring within them have only been explored once by a single study (Figure 3).

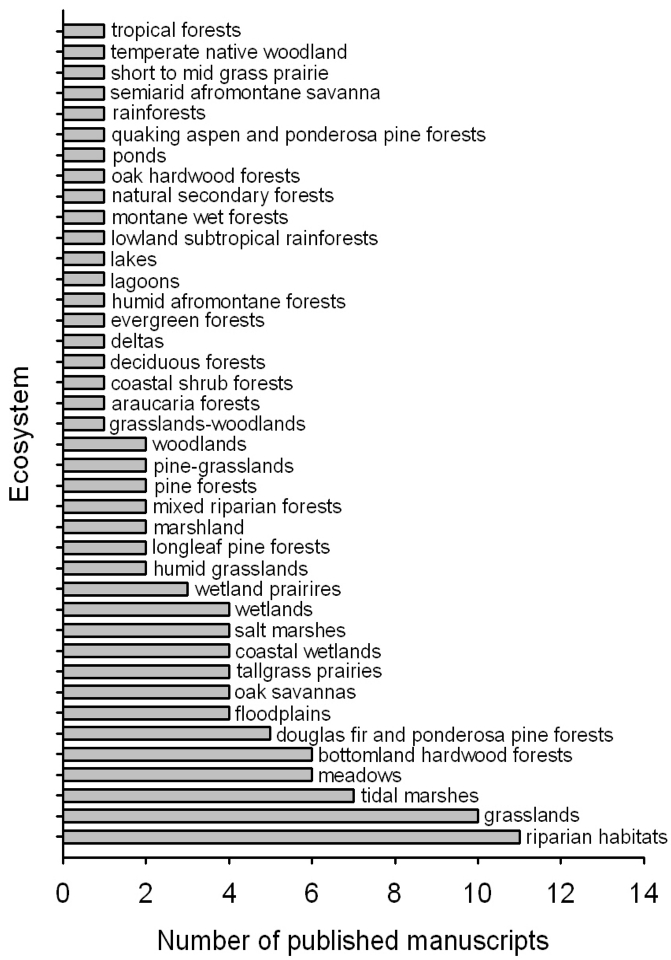

Figure 3. Types of ecosystems where studies regarding birds and the restoration process have been performed.

A vast array of 17 disturbance factors that had altered the study site prior to restoration efforts were recognized in the reviewed literature. In order of decreasing frequency of appearance, the following factors were identified: (1) agricultural land conversion, (2) alteration of the natural hydrological cycle (e.g., channelization, dike and dam construction, drainage, ditching), (3) suppression of natural disturbance regimes (e.g., fire, flooding), (4) grazing, (5) presence of exotic species, (6) urban development, (7) logging, (8) habitat destruction, (9) human associated disturbances (e.g., traffic load, human pedestrians, productive activities), (10) made-man structures (e.g., roads, ports, building developments), (11) sedimentation, (12) habitat fragmentation, (13) mining, (14) thermal discharge from nuclear reactors, (15) nest parasitism by birds, (16) eutrophication of water bodies, and (17) mowing. Agricultural land conversion and alteration of the natural hydrological cycle are by far the most commonly reported disturbance factors within the reviewed literature (24.2% and 17.6%, respectively; Figure 4). Moreover, 62% of studies in the reviewed literature reported only one factor of disturbance, while 38% of studies outlined the effects of more than one factor altering the site prior to restoration.

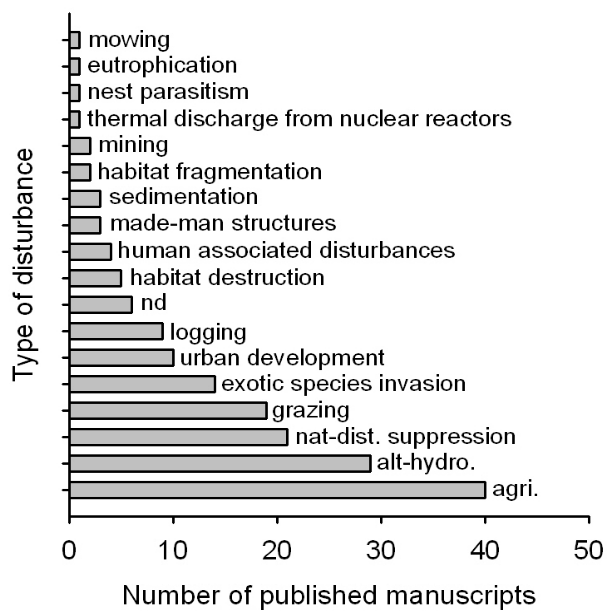

Figure 4. Factors of disturbance and their frequency of appearance among the reviewed literature. nd = not determined; nat-dist. suppression = natural disturbance suppression, alt-hydro = alteration of the natural hydrological cycle; agri = agricultural land conversion.

• CLASSIFYING THE REVIEWED LITERATURE ACCORDING TO OBJECTIVES •

Despite the fact that some of the reviewed literature could be classified into more than one category, we classified each study in relation to its main objective. The majority of the reviewed literature used an ecological approach (64.8%) to analyze the ornithological component of the restoration process. The remaining literature corresponded to studies focused on habitat restoration for bird conservation (17.6%), used birds as bioindicators for achieving restoration goals (10.2%), or had proposed birds as guides to perform restoration activities (7.4%).

Ecology

We identified three main concerns among those studies that were classified within the "ecology" category. For this reason, we split this category into three subgroups which are related to: (1) restoration effects on birds, (2) the role of birds in the restoration process, and (3) use of restored habitats by birds (see Appendix 1 and references therein). Ecological studies which evaluated the effects of restoration on birds (75.7% of ecological studies) are prevalent, followed by studies that analyzed the use of restored habitats by birds (12.9% of studies) and those which addressed the role of birds in the restoration process (11.4% of studies).

Restoration effects on birds

General patterns have emerged from studies assessing the effects of restoration activities on birds. It has been reported that the process of restoration: (1) assists bird community diversity (Dobkin *et al.* 1998, Davis *et al.* 2000, Wood *et al.* 2004, Diawara and Diagana 2006, Malcom and Radke 2008), (2) promotes bird community evenness (Seigel *et al.* 2005, MacGregor-Fors *et al.* 2010), (3) affords habitat heterogeneity, which derives in complex bird communities (Seigel *et al.* 2005, Aerts *et al.* 2008), (4) increases breeding and migratory species densities (Nilsson 1997, Hartung and Brawn 2005, Gaines *et al.* 2007, Hoover 2009), (5) decreases nest parasitism by reducing suitable habitats for parasitic species (Brawn 2006, Small *et al.* 2007, Twedt *et al.* 2010), (6) enhances nesting success (Hoover 2009, Twedt *et al.* 2010), (7) encourages recolonization of bird species that had been locally extirpated from the original habitat as a result of human disturbance (Gache 2008, Belting 2009), (8) provides reproductive and foraging grounds for bird species (Seigel *et al.* 2005, Gache 2008), (9) supplies stopover sites for migrant species (Brawn 2006, Gache 2008, Bregnballe *et al.* 2009b), (10) reduces the negative effects of sink populations derived from habitat fragmentation (Brawn 2006), and (11) promotes chick foraging rates and improves their body condition (Eglington 2008).

Some studies report results that are not completely consistent with the patterns described above. For example, Van Dyke *et al.* (2004), Johnson *et al.* (2009), and Rowe (2010) found that restored and non-restored sites exhibited similar bird communities, even among different restoration treatments. As the authors explain, these divergent patterns could be biased because of the small size of restored sites, the effects of landscape properties, and the influence of an incipient development of the vegetation component. Moreover, Berg *et al.* (2002) determined that breeding population size and hatching success of meadow birds may not necessarily be enhanced by restoration efforts. Renfrew *et al.* (2006) also observed that breeding bird communities sometimes differ between restored and original habitats. These patterns could be due to the time-scale used to evaluate restoration effects, and the influence of landscape properties and habitat management strategies on bird communities (Berg *et al.* 2002, Renfrew *et al.* 2006).

There are critical factors that should be taken into account when interpreting and assessing the effects of restoration on birds: we should be aware that bird responses to restoration are species-dependent (Delphey and Dinsmore 1993, Tucker *et al.* 2003, Gaines *et al.* 2007, Johnson and Sandercock 2010), and vary according to both temporal (i.e., short-term vs. long term-analyses; Hobson *et al.* 2007, Malcom and Radke 2008, Smythe and Haukos 2010) and spatial scales (site-specific vs. landscape analyses; Wood *et al.* 2004). In addition, birds might be affected by restoration in diverse ways depending on the type of restored habitat (Fletcher and Koford 2003, Smiley *et al.* 2007), and the strategies implemented to carry out the particular restoration process (Davis *et al.* 2000, Twedt *et al.* 2002). Other specific factors that could determine the effects of restoration on bird communities are: (1) the location and geometry of restored sites (Buffington *et al.* 2000), (2) habitat characteristics of contiguous habitats, and (3) vegetation features within the restoration site (Lindenmayer *et al.* 2010).

Understanding the effects that the restoration process can have on birds is critical in order to guide both future restoration efforts and management activities in restored sites. Among the management activities described in the reviewed literature are: (1) promotion of adult survival and reduction of predation risk on nests by implementing predator control projects, increasing patch size, and enhancing habitat quality at the landscape level (Fletcher *et al.* 2006, Ottvall 2009, Smart 2009), (2) carrying out multi-faceted management activities to maintain different bird species (Machmer 2002), (3) management of avian nest parasite species to reduce parasitism pressures (Small *et al.* 2007), (4) reintroduction of natural disturbance regimes (Masters *et al.* 2000, Provencher *et al.* 2002, Brawn 2006) and maintenance of the heterogeneity of vegetation vertical structure (Hamel 2003, Smiley *et al.* 2007, Au *et al.* 2008) in order to promote diversity of bird communities, (5) selection of fast-growing successional plant species at the beginning of the restoration process to accelerate colonization of birds in restored sites (Twedt *et al.* 2002), and (6) restoration of large patches of degraded habitats to promote the availability of resources and to decrease predation risk in order to attract more bird species (Fink *et al.* 2009). Specifically for aquatic systems, it is important to: (1) increase wetland surface area (VanRees-Siewert and Dinsmore 1996), and (2) promote a heterogeneous system in relation to vegetation composition, water depth, and prey availability, in order to enhance the bird diversity of aquatic communities (Fink *et al.* 2009).

The role of birds in the restoration process

The role of the animal component within the restoration process has traditionally been viewed from two contrasting perspectives: (1) as a barrier to the achievement of restoration objectives, and (2) as a keystone to restoration success. Particular zoological groups, such as mammals, have been generally pinpointed as an impediment to restoration activities as they predate seeds and graze on the vegetation of restored sites (Opperman and Merenlender 2000). Conversely, birds have mainly been considered to have positive effects within the restoration process due to their major role as seed dispersers (Aerts *et al.* 2006, Battaglia *et al.* 2008), increasing the number of both plant individuals and species within restored sites (Robinson and Handel 1993). Nonetheless, seed dispersal by birds in restored sites could be limited by: (1) the availability of vegetation patches attractive to birds (Battaglia *et al.* 2008), (2) distance to the propagule source (Robinson and Handel 1993, Battaglia *et al.* 2008), (3) presence and type of perches (Holl *et al.* 2000), (4) plant size, vegetation structure and composition (Robinson and Handel 1993, Wydhayagarn *et al.* 2009), and (5) the characteristics of the surrounding forests (e.g., fruit availability; Zanini and Ganade 2005).

Despite the importance of bird seed dispersal to promote seed rain within restored sites, there are other factors to be considered in the achievement of successful restoration. Micro-climatic variables (White *et al.* 2009, Wydhayagarn *et al.* 2009), seed predation, and nutrient limitation could determine the establishment, germination, development, and composition of those seeds dispersed by birds within restored habitats (Holl *et al.* 2000). In this way, birds are undoubtedly a key component determining the arrival of plant propagules to restored sites, but they are not sole contributor to the restoration process (Holl *et al.* 2000).

The negative role of birds within the restoration process is rarely mentioned in the literature, but there are some potential threats imposed by birds on restoration and habitat management efforts. On the one hand, aquatic birds could limit the development of vegetation in wetland restoration by directly grazing on the plants (Jupp and Spence 1977, Lauridsen *et al.* 1993). However, this may not always be the case as Perrow *et al.* (1997) found that bird grazing does not necessarily restrict aquatic vegetation development because this effect is variable depending on: (1) the season of the year on which birds feed on macrophytes, (2) initial size of the standing crop, and (3) bird population density. Furthermore, seed dispersal by birds is not restricted to those plant species suitable to achieve restoration goals, but also involves invasive plant species that can impede or complicate restoration and management activities (White *et al.* 2009). It is therefore important to consider the undesirable plant species dispersed by birds in order to reduce the possibility of an invasion of restored sites and to design management activities focused on controlling the establishment of such invasive plant species (Robinson and Handel 1993, White *et al.* 2009).

Bird use of restored habitats

Bird habitat-use of restored sites has rarely been explored from a population level approach (Furey and Burhans 2006) as more attention has been given to bird community utilization of restored sites (Marburger 2002, Jansen 2005, Horath and Havera 2007). Population studies have shown that vegetation characteristics (i.e., vegetation height, herbaceous plant cover) and perch availability determine habitat selection by particular bird species (e.g., territory selection by red-winged blackbirds -*Agelaius phoeniceus*; Furey and Burhans 2006). Nonetheless, restored sites may not necessarily be utilized by birds if critical resources are offered to birds by surrounding non-restored sites (Atkinson *et al*. 2004, Furey and Burhans 2006).

Restoration activities have been shown to enhance bird community habitat-use of previously disturbed sites. Studies suggest that restored habitats: (1) are used by diverse bird communities (Slavin and Shisler 1983, Horath and Havera 2007), (2) benefit migratory species (Marburger 2002), and (3) increase the number of waterbirds while decreasing the abundance of passerine birds that utilize the habitat (Slavin and Shisler 1983). Conversely, the increased numbers of individuals that use restored habitats benefit the process of restoration because a greater biomass of birds increases the input of nitrogen to the system as a result of the excreta produced by colonies (Slavin and Shisler 1983).

Restoration activities may also establish biological corridors. Jansen (2005) found that bird communities utilizing habitat within corridors created by habitat restoration emulated those of original habitats. However, less mobile and specialist species rarely use corridors, possibly because of edge effects (Jansen 2005). In general, corridors not only provide heavily-used habitats for birds, but also facilitate bird movements across fragmented landscapes (Jansen 2005).

Habitat restoration for bird conservation

Among the reviewed literature, habitat restoration has been widely addressed as a useful and almost necessary strategy to promote bird conservation (see Appendix 1 and references therein). Despite the fact that it is not always possible to restore degraded habitats to completely emulate original ones, restoration efforts should focus on increasing habitat quality for bird species (Goutner 1997). As suggested by different authors, restoration activities could directly benefit bird species of conservation concern (Conner *et al.* 2002, Blank *et al.* 2002, Atkinson 2003, Benson *et al.* 2006), as well as rare species with declining populations (Davis *et al.* 2000, Hobson *et al.* 2007, Small *et al.* 2007). Nevertheless, Aerts *et al.* (2008) recognized that restored habitats are not always successful in attracting specialist species or those of low-tolerance to disturbance, and we still need to improve understanding of the mechanisms responsible for bird population decline (Dobrovolny 2003).

With the aim of bird conservation, the ultimate goal of habitat restoration is to recreate and promote the presence and maintenance of those habitat properties that provide key resources to individuals, and to achieve this in such a way that populations could be self-sustainable. To attain successful habitat restoration for bird conservation, it is necessary to: (1) consider specific-dependent responses of birds to habitat restoration (Sogge *et al.* 2008), (2) assess the requirements and biological characteristics of focal species, (3) elaborate management activities focused on target species (Finch 1999), (4) remove specific threats to focal species (Finch 1999, Dobrovolny 2003, Leahy and Camp 2004), (5) promote habitat heterogeneity to benefit non-target species (Sallabanks *et al.* 2005, Stralberg *et al.* 2009), (6) evaluate restoration goals at different scales (Sallabanks *et al.* 2005), (7) address the site-fidelities of concerned species (e.g., by means of high recapture and re-sightings of individuals; Sallabanks *et al.* 2005), and (8) supplement habitat restoration with management activities that support bird populations (Dobrovolny 2003, Stralberg *et al.* 2006, Wang *et al.* 2009). Furthermore, while developing habitat restoration, it is important to carry out monitoring programs of both primary population parameters and bird community properties (Taft and Haig 2003) in order to analyze restoration viability by assessing the current effects of restoration efforts on both focal and non-target species.

Within the last decade, the development and application of GIS (Twedt *et al.* 2006) and heuristic models (Stralberg *et al.* 2006, Stralberg *et al.* 2009) have facilitated the identification of priority restoration sites for bird conservation based upon species-habitat relationships. Moreover, these models may be useful in the prediction of potential short and long-term impacts of restoration activities on bird communities (Stralberg *et al.* 2006). However, interpretation of these models should be cautious as: (1) model predictions of bird responses cannot be completely accurate, (2) habitat carrying-capacities are barely known, and (3) there may be alternative available habitats for birds not incorporated into the models (Stralberg *et al.* 2006). In order to complement the predictions generated by models, it is important to include the socio-economic and objective costs of restoration activities (Stralberg *et al.* 2009), contemplate potential changes in climate for restored sites (Harris *et al.* 2006), and consider other biological groups (e.g., mammals, plants, insects) that occupy the study site (Twedt *et al.* 2006).

Birds as bioindicators of achieving restoration goals

Compliance with restoration goals has usually been addressed by evaluating temporal changes in vegetation structure. However, assessment of compliance with restoration goals could also be determined by using birds as bioindicators (Burnett *et al.* 2005; see Appendix 1 and references therein). As a first step, bird focal species should be identified (Gardali *et al.* 2006), then indicator parameters for focal species need to be selected, monitored and contrasted between original and restored habitats

(Brawley *et al.* 1998). Finally, the accomplishment of the restoration process is complete when indicator parameters of the original habitat are emulated by the restored ones (Acevedo 2007).

Selecting focal bird species to evaluate compliance with restoration goals is a complex process which should consider many different factors. Gardali *et al.* (2006) suggest that focal species should: (1) be abundant enough to achieve a sufficient sample size to evaluate trends, (2) occupy territories throughout the breeding season, (3) collectively represent a range of life-history characteristics, and (4) be a species of special interest. Fulfilling these criteria, certain waterbirds (e.g., waders, ibises, storks) have been used as bioindicators to address the success of restoration activities (Weller 2006, Frederick *et al.* 2009).

Different types of indicator parameters have been proposed to assess restoration success using birds. Behavioral cues, and population and community properties are among the factors mainly used as indicator parameters. Behavior (e.g., foraging activity) has been particularly utilized to evaluate restoration success as it is an inexpensive and effective approximation to monitor population trends (Acevedo 2007, Whelan and Jedlicka 2007). In relation to population properties, the use of demographic parameters and variables related to nesting has been recommended (Weller 2006, Frederick *et al.* 2009). Finally, diversity, density, and composition of bird communities have also been endorsed as useful indicator parameters (Passell 2000, Konisky *et al.* 2006, Fletcher *et al.* 2007).

Birds as guides for the restoration process

The process of restoration could be guided by basic ornithological studies to develop adequate restoration and management activities (see Appendix 1 and references therein). Ornithological knowledge can give us insight of: (1) the potential to restore a given site, (2) the elements/processes that have not recovered during the restoration process, and (3) the management activities needed to complement restoration efforts (Lewis and Casagrande 1997, Clarke and Oldland 2007). In this way, bird related studies could assist the restoration processes, particularly through the analysis of bird responses to habitat alterations associated with restoration and management activity (Gabbe *et al.* 2002).

Different bird responses have been evaluated to design management and restoration activities.

For example, Bregnballe *et al.* (2009a) analyzed the effects of human disturbance on waterbird behavior and distribution to generate management recommendations. Also, the generation of suitable management and restoration activities has been achieved by examining bird reproduction and feeding activity (Gabbe *et al.* 2002, Eglington *et al.* 2008). Furthermore, the utility of bird communities in the development of restoration goals has been highlighted by Lewis and Casagrande (1997) who suggest that restoration goals could be based on bird and nesting densities, trophic groups, and historical records of bird species.

Results derived from bird studies have identified several activities in order to assist in the management of restored sites. In general, the proposed management activities relate to: (1) mitigation of the negative effects of human disturbance by including refuges for bird species within restored sites (Bregnballe *et al.* 2009a), (2) control of aggressive bird species to prevent domination of communities within restored sites associated with fragmented landscapes (Clarke and Oldland 2007), (3) incorporation of particular plant species in restored sites to attract specific bird species (Malan *et al.* 2007), and (4) identification of charismatic bird species to promote restoration activities among the public, especially within urban systems (Lewis and Casagrande 1997).

• CONCLUSIONS •

Specific properties of restoration activities should be considered when analyzing any relationship between birds and the restoration process. In general, the essential features to take into account are: (1) the habitat involved, (2) bird species in question, (3) vegetation structure, (4) characteristics of contiguous habitats, (5) size of restored sites, and (6) the time scale of the study. Among these characteristics, the size of restored sites and the time scale of the study deserve special attention due to the controversy that they generate. On the one hand, the size of restored sites has proven to be important in determining the effects of restoration activities on certain bird species (Lindenmayer *et al.* 2010), and therefore the restoration of large surfaces of degraded habitats has been promoted (Fletcher *et al.* 2006, Sporrong and Davis 2007, Fink *et al.* 2009). However, the size of restored sites can be constrained by the logistics of restoration activities involved (Atkinson 2003, Brawn 2006). Furthermore, the duration of the studies concerned with birds and the restoration process can influence the derived results. Long-term studies have been preferred over short-term studies as the former take into account the inter-annual variations that determine fluctuations in resources affecting bird communities (Davidson and Evans 1987, Seigel *et al.* 2005, Malcom and Radke 2008, Smythe and Haukos 2010). Despite the value of long-term studies, short-term responses are useful because: (1) time-lag responses to restoration activities are variable and in some systems the effects of restoration are rapid (Hobson *et al.* 2007, Mander *et al*. 2007, MacGregor-Fors *et al.* 2010), and (2) prompt results derived from restoration activities are sometimes necessary to perform management activities and justify efforts to landowners and institutions. Hence, we believe future studies should be of appropriate duration in terms of their own goals and logistic constraints, while drawing conclusions with caution by considering the possible effects that the size of restored sites and duration of the study could have on their results.

There are some recommendations arising from the literature that could guide future restoration efforts in order to benefit birds. Among the major recommendations are: (1) analysis of bird behavior to assess the effects of restoration on birds (Armitage *et al.* 2007, Fink *et al.* 2009), (2) monitoring of bird foraging guilds to track resource fluctuations derived from restoration activities (Seigel *et al.* 2005), (3) performance of multi-faceted management activities to benefit several bird species (Machmer 2002, Blank *et al.* 2002), (4) evaluation of the potential of managing habitats to benefit both focal and non-target species (Wood *et al.* 2004), (5) partial restoration of the site in question as restoration of the entire area could be detrimental to bird species that depend on non-restored sites (Stralberg *et al.* 2009), and (6) promotion of restoration activities that not only benefit birds but also encourage productive activities (Goutner 1997, Eglington 2008).

Restoration has proven to be effective for conserving bird populations in vulnerable ecosystems (Fletcher *et al.* 2006). However, there are some topics that deserve full consideration in future studies regarding birds in the restoration process. These include: (1) the effect of restoration activities on the dynamics of bird populations, (2) suitable habitat management of restored sites to enhance habitat use, survival and reproductive rates of bird species, and (3) bird community responses to the restoration process incorporated within a state-and-transition model perspective. In addition, further research is needed within ecosystems other than those surveyed in the reviewed literature, in order to compare processes occurring among different types of systems, as well as further studies in those ecosystems mentioned in the reviewed literature in order to enhance understanding of the restoration process in these ecosystems. Increasing our knowledge of birds within the restoration process could contribute to the development of novel approaches to achieve and perform integral restoration activities.

Within the last decade, the increasing incorporation of the ornithological component of ecosystems into restoration ecology research is encouraging. However, we must be aware that there is still a huge gap in the knowledge that must be addressed in order to comprehend variations in patterns and processes occurring among different habitats and regions. In general, research within temperate zones other than the United States is scarce and our understanding of tropical ecosystems is still incipient. The general trends identified in this review should serve as a comparison baseline for future investigations. Moreover, it is urgent that further studies should be fostered to examine processes derived from each new restoration project as unique physical, biological, historical, social, and institutional factors might be involved.

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Appendix 1. Reviewed literature classified in relation to the main objective. The groups utilized were: (1) ecology, (2) habitat restoration for bird conservation, (3) birds as bioindicators of restoration success, and (4) birds as guides for the restoration process. The "ecology" category is split into three subgroups of: (a) restoration effects on birds, (b) the role of birds in the restoration process, and (c) use of restored habitats by birds.

GROUP	**REFERENCES**
1) *Ecology*	
a) Restoration effects on birds	Delphey and Dinsmore 1993, VanRees-Siewert and Dinsmore 1996, Nilsson 1997, Dobkin *et al*. 1998, Buffington *et al.* 2000, Davis *et al.* 2000, Masters *et al.* 2000, Hansson 2001, Berg *et al*. 2002, Conner *et al.* 2002, Germaine and Germaine 2002, Machmer 2002, Provencher *et al.* 2002, Symstad and Wenny 2002, Twedt *et al.* 2002, Fletcher and Koford 2003, Hamel 2003, Tucker *et al.* 2003, Van Dyke *et al.* 2004, Wood *et al.* 2004, Hartung and Brawn 2005, Seigel *et al.* 2005, Benson *et al.* 2006, Brawn 2006, Diawara and Diagana 2006, Fletcher *et al.* 2006, Renfrew *et al.* 2006, Armitage *et al.* 2007, Chimney and Gawlik 2007, Gaines *et al.* 2007, Hobson *et al.* 2007, Mander *et al.* 2007, Small *et al.* 2007, Smiley *et al.* 2007, Aerts *et al.* 2008, Au *et al.* 2008, Gache 2008, Malcom and Radke 2008, Belting 2009, Bregnballe *et al.* 2009b, Fink *et al.* 2009, Gaines *et al.* 2009, Hoover 2009, Johnson *et al.* 2009, Lituma 2009, Ottvall 2009, Smart 2009, Hurteau *et al.* 2010, Johnson and Sandercock 2010, Lindenmayer *et al.* 2010, Smythe and Haukos 2010, Rowe 2010, Twedt *et al.* 2010.

b) Role of birds in the restoration process	Robinson and Handel 1993, Perrow *et al.* 1997, Holl *et al.* 2000, Zanini and Ganade 2005, Aerts *et al.* 2006, Battaglia *et al.* 2008, White *et al.* 2009, Wydhayagarn *et al.* 2009.
c) Use of restored habitats by birds	Slavin and Shisler 1983, Wilcox 1986, Blank *et al*. 2002, Marburger 2002, Atkinson *et al.* 2004, Jansen 2005, Furey and Burhans 2006, Horath and Havera 2007, Sporrong and Davis 2007.
2) *Habitat restoration for bird conservation*	Davidson and Evans 1987, Goutner 1997, Brown and Smith 1998, Finch 1999, Engstrom and Brownlie 2000, Lanham *et al.* 2000, Atkinson 2003, Dobrovolny 2003, Taft and Haig 2003, Leahy and Camp 2004, Sallabanks *et al.* 2005, Stralberg *et al.* 2006, Twedt *et al.* 2006, Eglington 2008, Sogge *et al.* 2008, Altemüller 2009, Burgin and Wotherspoon 2009, Kazoglou 2009, Stralberg *et al.* 2009, Wang *et al.* 2009.
3) *Birds as bioindicators of restoration success*	Brawley *et al.* 1998, Passell 2000, Burnett *et al.* 2005, Gardali *et al.* 2006, Konisky *et al.* 2006, Weller 2006, Acevedo 2007, Fletcher *et al.* 2007, Whelan and Jedlicka 2007, Cooper 2008, Frederick *et al.* 2009.
4) *Birds as guides for the restoration process*	Lewis and Casagrande 1997, Gabbe *et al.* 2002, Wightman and Germaine 2006, Clarke and Oldland 2007, Malan *et al.* 2007, Eglington *et al.* 2008, Bregnballe *et al.* 2009a, Kennedy *et al.* 2009.

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Capítulo III

Avian community responses to restoration efforts in a complex volcanic landscape

"Expect the best, plan for the worst, and prepare to be surprised."

– Denis Waitley –

• ABSTRACT •

Restoration ecologists have focused primarily on the effects of restoration activities for the vegetation component of ecosystems, but restoration efforts should consider animals to fully assess the recovery of ecosystems. In this study, we assessed differences in avian community responses among managed (restoration and reforestation plots), disturbed (abandoned cropfields and arenales), and natural (original and late-seral forests) habitats within a volcanic landscape with a complex disturbance history. Our results indicate that bird communities vary among managed habitats, as a consequence of both their disturbance history and current management strategy. We also determined that restoration activities promote more diverse, even, and heterogeneous (both taxonomic and functional) bird communities that resemble those of natural habitats. Although we found that reforestation activities could enhance diversity and evenness of bird communities, planting only tree species as a management strategy might not be sufficient to achieve bird communities similar to those of natural habitats. Thus, we encourage restoration efforts, even in production ecosystems, to enhance the effectiveness of biodiversity recovery. Based on our results, we highlight the importance of defining particular restoration strategies for each site, as local disturbance histories and site-specific characteristics could produce particular responses in bird communities, despite the presence of rich species pools in adjacent forests. We conclude that understory complexity is an important factor to consider in restoration programs that include wildlife components in their goals. Finally, we suggest the usefulness of monitoring bird communities to assess compliance with restoration goals from an exhaustive approach.

• INTRODUCTION •

The negative pressure that human activities have imposed on biodiversity worldwide now demands human intervention (Vitousek et al. 1997; Naveh 2005). Ecologists play a preponderant role not only in assessing the current effects of human activities on ecosystems, but in providing useful tools to revert their ecological degradation, and there is now an urgent need for complementary actions to assist biodiversity recovery (Young 2000). Currently, restoration ecology has taken the lead as a source of both theoretical and practical knowledge for this significant task (Hobbs and Harris 2001).

Restoration ecology has intensively evaluated the vegetation component of ecosystems, with little attention to zoological diversity (Young 2000), causing a bias in our knowledge of restored ecosystems. In the last decade, the study of charismatic megafauna (i.e., birds) has notably increased in restoration projects (Majer 2009), although there is still an important gap which must be filled to clarify our understanding of processes related to animals and restoration activities (Young 2000). Avian monitoring has proved particularly useful for research on restoration ecology, mainly because: (1) it can be implemented at low costs over large areas, (2) information about species of multiple ecological requirements over a wide range of habitats can be compiled, (3) it aids in the determination of restoration effectiveness, and (4) it serves as a guide to implement restoration and management activities (Burnett et al. 2005; Gardali et al. 2006).

Monitoring the entire avian community is essential to assess the responses of species with different ecological requirements, tolerances to disturbance and to changes in broad habitat structure (Passell 2000; MacGregor-Fors et al. 2009). Particularly, it has been suggested that restoration activities increase bird species richness and density (Davis et al. 2000; Malcom and Radke 2008; Gaines et al. 2007), and promotes community evenness (MacGregor-Fors et al. 2010). However, other studies have found that restored and non-restored sites exhibit similar bird communities (Van Dyke et al. 2004; Johnson et al. 2009), and bird communities sometimes differ between restored and original habitats (Renfrew et al. 2006). Such controversy among studies has been explained by the influence of habitat type, size of restored sites, characteristics of contiguous habitats, the type of restoration and habitat management activities implemented, and the time-scale used to evaluate restorations (Twedt et al. 2002; Fletcher and Koford 2003; Renfrew et al. 2006; Lindenmayer et al. 2010). Hence, more research is needed in order to clarify these trends.

In this study, we monitored bird communities within representative habitats of a complex volcanic landscape dominated by temperate forests in Michoacán, Mexico, to assess differences in avian community responses among managed (restoration and reforestation plots), disturbed (abandoned cropfields and arenales), and natural (original and late-seral forests) habitats. In particular, we attempted to determine differences on bird community responses to: (1) natural habitats vs. managed habitats, (2) managed habitats vs. disturbed habitats, (3) managed habitats with reforestation for timber production vs. managed habitats under restoration, and (4) managed habitats under restoration with distinct histories of disturbance and management outcomes.

• MATERIALS AND METHODS •

Study area

Our study area is located in the vicinity of the Paricutín volcano, within the Comunidad Indígena de Nuevo San Juan Parangaricutiro (referred to as Nuevo San Juan hereafter), in the State of Michoacán, West-central México. The landscape consists in a mosaic of natural, disturbed, and managed habitats. As a result of its disturbance history, this landscape offers a unique opportunity to evaluate bird communities within a complex system where very distinct habitats interact (Appendix 1). Natural habitats include original temperate forests dominated by Sacred Fir (*Abies religiosa*), pines (Smooth-bark Mexican Pine: *Pinus pseudostrobus,* Montezuma Pine: *P. montezumae*), and Netleaf Oak (*Quercus rugosa*), which are managed for timber extraction under sustainable forestry practices (Velázquez et al. 2003). Another natural habitat of late-seral forests of fir, pine, and oak also occurs in some areas on tephra deposits from activity of the Paricutín volcano between 1943 and 1952 (Flores 1945; Foshag and González 1956). Disturbed habitats include abandoned cropfields and bare areas created by tephra deposition over cropfields after the eruption of the Paricutín volcano (referred as arenales hereafter). Of these, abandoned cropfields correspond to human-maintained stable states that are perpetuated by social interests, while the arenales represent ecological stable states that are provoked by non-linear ecosystem dynamics (Suding et al. 2004; Lindig-Cisneros 2009). Finally, managed habitats include reforested and restored sites. Reforestation sites consisted of single-species tree plantations, mostly of Smooth-bark Mexican Pine, leading to the creation of mono-specific stands with the objective of timber extraction. By comparison, restoration plots consisted of sites where different activities have been carried out such as multi-species tree planting, mulching, and propagation of legume nurse plants in order to promote the recovery of biodiversity (Alvarado-Sosa et al. 2007;

Blanco-García and Lindig-Cisneros 2005).

We conducted surveys in six different habitats: natural habitats of original forests and late-seral forests, disturbed habitats of abandoned cropfields and arenales, and managed habitats of reforestation and restoration plots. As these habitats were not evenly distributed throughout the landscape, we performed our surveys in three different sites of Nuevo San Juan: (1) Mesa de Cutzato, an area with an underlying layer of tephra, (2) San Nicolás, an area not affected by recent volcanic activity where abandoned cropfields prevail, and (3) Llano de Pario, an arenal which most of its volcanic ash was removed (Gómez-Romero et al. 2006). Moreover, as the pool of species from nearby forests could determine the identity of those species that arrive to non-forested habitats (Palmer et al. 1997), we conducted surveys in adjacent forests at each study site as reference habitats in order to compare their bird communities with those of disturbed and managed habitats. In this way, we surveyed: arenales and late-seral forests in Mesa de Cutzato; abandoned cropfields, reforestation plots, restoration plots, and original forests in San Nicolás; and reforestation plots, restoration plots, and late-seral forests in Llano de Pario (Fig. 1). Similar habitat types located in different sites of Nuevo San Juan were not assumed to be replicates because of their particular site-specific traits and local disturbance histories. Instead, they were considered as independent habitats to account for differences among them.

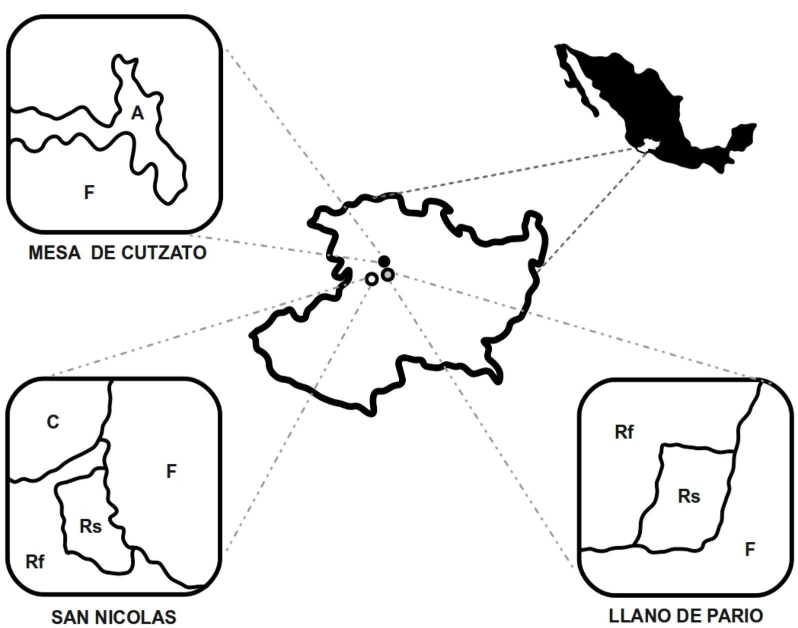


Fig. 1. Location of surveyed habitats within Nuevo San Juan, Michoacán, México. Habitats were surveyed among three different sites as follows: arenales (A) and late-seral forests (F) in Mesa de Cutzato; abandoned cropfields (C), reforested plots (Rf), restored plots (Rs), and original forests (F) within San Nicolás; and reforested plots (Rf), restored plots (Rs), and late-seral forests (F) in Llano de Pario.

Bird surveys

During 2009-2010, we surveyed birds throughout the year to account for annual variation in avian communities. Surveys were performed from 07:00 to 11:00 when bird activity is highest (Ralph et al. 1996). To avoid temporal bias due to variations in bird activity during the morning, we randomly altered the visitation sequence to each habitat throughout our study. We used 5 min point counts to survey birds (following Ralph et al. 1996), registering all individuals of any bird species seen and heard within that time, as well as the radial distance from the observer to each recorded individual with the aid of a range-finder (Bushnell Yardage Pro). As restoration plots were ~1 ha, we were only able to locate one survey point in each restoration plot. We therefore performed multiple counts throughout the year within a unique 35 m radius point count (optimal radius that covered most of the restoration plot). To be comparable among habitats, we surveyed bird communities from a unique survey point within all habitats. As a result of our sampling design, we account for pseudoreplication biases during the analyses of our survey results as specified in the "data analysis" section. To achieve a representative sample of avian communities, we performed 40 point count repetitions at each study habitat, carrying out a total of 360 point-count surveys.

To evaluate the influence of site-specific attributes on avian communities, we characterized sampling points according to the following vegetation properties (sensu Ralph et al. 1996): (1) the number of vegetation strata (tree, shrub, herbaceous plants), (2) tree species richness, (3) tree density, (4) maximum and minimum tree diameter at breast height (DBH), (5) tree cover, (6) maximum and minimum tree height, (7) shrub species richness, (8) shrub cover, (9) maximum and minimum shrub height, (10) herbaceous plant cover, (11) maximum and minimum herbaceous plant height, and (12) bare-ground cover. We performed a multivariate cluster analysis utilizing all measured vegetation properties to determine similarity of vegetation characteristics among surveyed habitats.

Data analysis

We compared bird species richness and bird densities among managed, natural, and disturbed habitats using rarefaction analysis and Distance 5.0 software, respectively (James and Rathbun 1981; Thomas et al. 2005). We considered each count from the same unique survey point as a replicate of that point count when performing species richness and density analyses. We used EstimateS to carry out rarefaction analyses, which calculate the average number of species (Sobs Mao Tao) and 95%

confidence intervals in a single sample by the repeated re-sampling of all pooled samples, enabling statistical comparison among different treatments using the accumulated abundance (Gotelli and Colwell 2001; Colwell 2005). Statistical differences among treatments were assumed when 95% confidence intervals did not overlap (Payton et al. 2003). We used Distance 5.0 to calculate bird densities, which computes the number of individuals within a specific area (ind/ha) by calculating the detection probability of individuals at increasing distances from the observer and standardizing the detection rates along the concentric surveyed area (Buckland et al. 2001).

We evaluated the structure of bird communities among surveyed habitats using rank-abundance plots. As for bird species richness and density calculations, we considered each count at the same unique survey point as a replicate of that point count for constructing rank-abundance plots. As suggested by Magurran (2004), rank-abundance plots permit inferences on resource partitioning within communities by analyzing the distribution of species abundances among treatments. We performed an ANCOVA to determine statistical differences in bird community evenness/dominance slopes.

To evaluate similarity in taxonomic composition of bird communities between managed, natural, and disturbed habitats, we performed two complementary analyses. First, we assessed bird species turnover rates among treatments using β_{sim} (Koleff et al. 2003). This dissimilarity index calculates the relative magnitude of species gains/losses in relation to the sample with the least number of species, revealing whether species shifts within a treatment are related to variations in its composition or to species losses compared to the sample with highest species richness (Lennon et al. 2001). Second, we evaluated differences in species composition among habitats by calculating a Bray-Curtis ecological distance. As suggested by Kindt and Coe (2005), computing an ecological distance for measuring differences in species composition among sites is useful as it summarizes their variation by the calculation of a single distance statistic. Particularly, the Bray-Curtis ecological distance is calculated from differences in the abundance of each species, and the resultant matrix could be displayed as a dendrogram constructed by clustering methods (Kindt and Coe 2005).

We analyzed similarity in functional composition of bird communities among habitats by evaluating differences in abundance of birds pertaining to different trophic groups. To do so, we classified each bird species according to its size (body length) and primary feeding resource. Size was determined bibliographically (Howell and Webb 1995; Peterson Multimedia Guides 1996; Bull and Farrand 1997), and was used to indirectly distinguish among species with similar primary feeding resources but different ecological roles. Primary feeding resources were also determined bibliographically and were complemented with authors' field observations. In order to classify bird species by both size and primary feeding resource, we performed a multivariate cluster analysis. In this way, size categories of species within the same trophic group were determined by clusters with equal or higher 95% similarity values. Finally, we performed an abundance-based Bray-Curtis multivariate cluster analysis (average linkage) (Bray and Curtis 1957; McAleece 1997) to evaluate similarity in functional composition among bird communities of managed, natural, and disturbed habitats.

• RESULTS •

Bird surveys

We recorded a total of 70 bird species during our surveys within the landscape (Appendix 3). The number of bird species detected among surveyed habitats was markedly different, with natural habitats exhibiting the highest number of species, particularly original forest in San Nicolás (37 spp.), followed by late-seral forest in Mesa de Cutzato (36 spp.) and late-seral in Llano de Pario (28 spp.). Restoration and reforestation plots had intermediate numbers of species: San Nicolás restoration plot (18 spp.), Llano de Pario reforestation plot (18 spp.), Mesa de Cutzato arenal (16 spp.), Llano de Pario restoration plot (13 spp.), and San Nicolás reforestation plot (12 spp.). The lowest number of species was recorded in the human-induced disturbed habitat of abandoned cropfields in San Nicolás (6 spp.). Of the total number of species, 60% were insectivores, 12.9% frugivores, 11.4% granivores, 7.1% omnivores, 7.1% nectarivores, and 1.5% carnivores. Moreover, 79% were resident species, while 21% were latitudinal winter migrants. Ratios of the number of resident to migratory species were greater in natural habitats, followed by managed and disturbed sites (Appendix 2). In San Nicolás, the ratio of the number of resident to migratory species in the restoration plot was greater than that of the reforestation plot, while the inverse occurred in Llano de Pario.

According to their site-specific vegetation traits, the multivariate cluster analysis revealed a cluster of similarity conformed by managed habitats, with a close relationship between reforestation and restoration plots in the same region. The San Nicolás reforestation and restoration plots had ~85% similarity, with 78% similarity for the Llano de Pario reforestation and restoration plots (Fig. 2). Another cluster comprised natural habitats, with late-seral forests of Mesa de Cutzato and Llano de Pario exhibiting 78% similarity, and having ~73% similarity with original natural forests of San

Nicolás (Fig. 2). The most dissimilar habitats among all treatments were the San Nicolás abandoned cropfield and Mesa de Cutzato arenal, with the San Nicolás abandoned cropfield more closely related to the cluster of managed habitats (~65% similarity) than the Mesa de Cutzato arenal (~63% similarity).

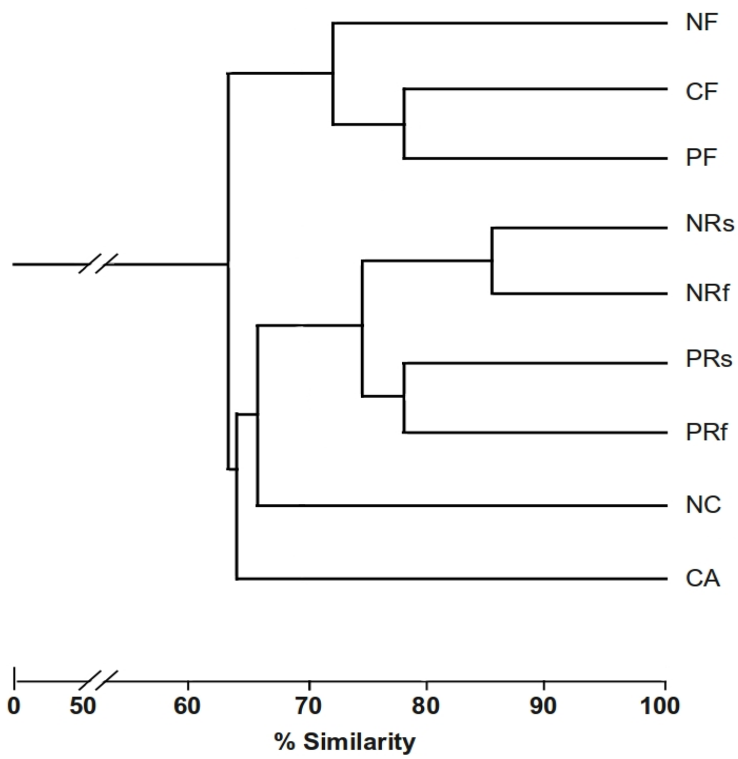
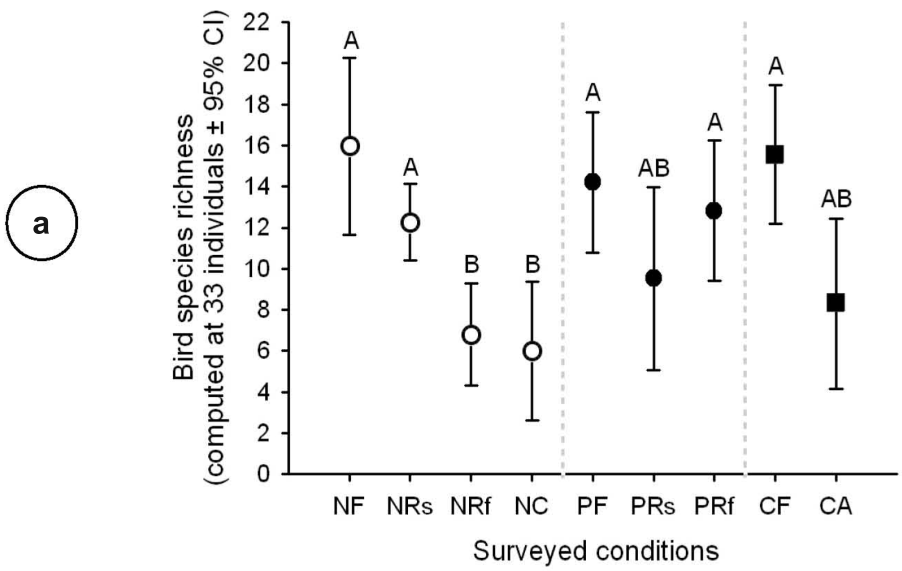


Fig. 2. Similarity cluster of surveyed habitats by study sites in relation to their site-specific vegetation traits. Forests and managed habitats constituted two different clusters, while the abandoned cropfield and the arenal were distinct to the other habitats. NF = San Nicolás original forest, CF = Mesa de Cutzato late-seral forest, PF = Llano de Pario late-seral forest, NRs = San Nicolás restoration plot, NRf = San Nicolás reforestation plot, PRs = Llano de Pario restoration plot, PRf = Llano de Pario reforestation plot, NC = San Nicolás abandoned cropfield, CA = Mesa de Cutzato arenal.

Avian species richness, density, and community structure

Rarefaction estimates of avian species richness varied among habitats depending on their specific location within Nuevo San Juan (Fig. 3a). In San Nicolás, the number of bird species for the restoration plot (12.3 ± 1.8 estimated species) was only slightly lower than that for original forest habitat (15.9 ± 4.3 estimated species), and these were both significantly higher than species richness in the reforestation plot and the abandoned cropfield (6.8 ± 2.5 and 6 ± 3.4 estimated species respectively; Fig. 3a). However, at Llano de Pario the number of bird species showed no statistical differences between the late-seral forest (14.2 ± 3.4 estimated species), the restoration (9.5 ± 4.4 estimated species) and the reforestation plot (12.8 ± 3.4 estimated species; Fig. 3a).



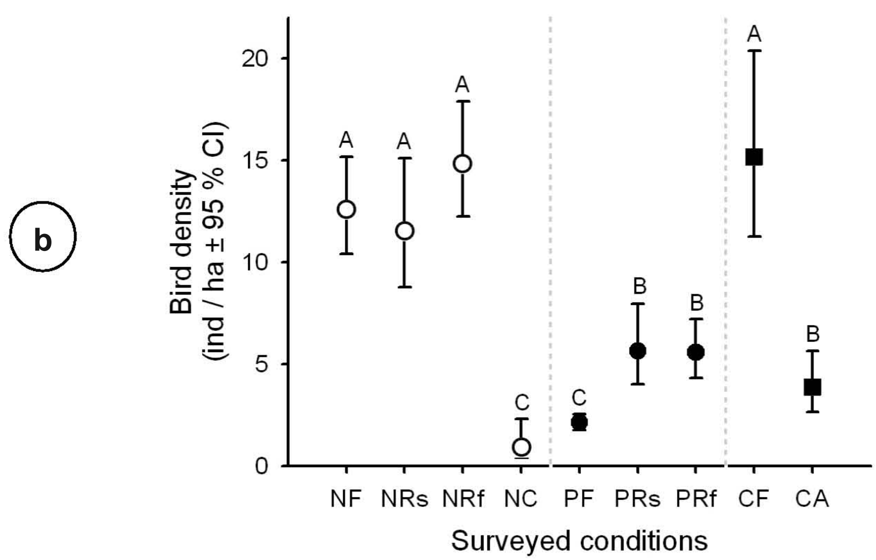


Fig. 3. a) Rarefaction analysis estimates of bird species richness for surveyed habitats located within Nuevo San Juan. b) Distance estimates of bird density for original forests, late-seral forests, disturbed sites, and managed sites. Letters above values for each site denote statistical differences. See Fig. 2 legend for site abbreviations.

Bird density values differed significantly among habitats, and also among study sites (Fig. 3b). Within San Nicolás, highest bird densities occurred in the original forest (12.6 ind/ha, 95% CI: 10.4, 15.2), the restoration (11.5 ind/ha, 95% CI: 8.8, 15.1), and the reforestation plot (14.8 ind/ha, 95% CI: 12.3, 17.9), and were significantly higher than in the abandoned cropfield (1 ind/ha, 95% CI: 0.4, 2.3; Fig. 3b). The late-seral forest in Mesa de Cutzato also demonstrated high avian densities (15.1 ind/ha, 95% CI: 11.2, 20.4), which was similar to that in the forest and managed plots of San Nicolas, and significantly higher than avian density in the arenal (3.9 ind/ha, 95% CI: 2.6, 5.6; Fig. 3b). However, avian density in Llano de Pario was significantly lower than that in other forest or managed plots, being slightly higher in the restoration (5.7 ind/ha, 95% CI: 4, 8) and reforestation (5.6 ind/ha, 95% CI: 4.3, 7.2) plots, and significantly lower in the late-seral forest (2.1 ind/ha, 95% CI: 1.8, 2.6; Fig. 3b). The lowest bird density values were computed for Llano de Pario late-seral forest and San Nicolás abandoned cropfield (Fig. 3b).

Avian community structure ($F_{8,174} = 30.63$, $P < 0.001$) and dominating bird species varied among habitats (Appendix 4). Within San Nicolás, the restoration plot exhibited a more even community than the reforestation plot, but both managed habitats were more dominated than the original forest. In Llano de Pario, the late-seral forest also had a more even avian community than the restoration and reforestation plots, however in this site the reforestation plot had a slightly less-dominated avian community than the restoration plot. Community structure also varied significantly among study sites, with natural forest habitats presenting the most even and least dominated bird communities. By contrast, the human-induced and natural dynamics disturbed habitats of the abandoned cropfield and arenal had the most dominated communities. The restoration plot of San Nicolás and the reforestation plot of Llano de Pario were similar in rank-dominance of avian communities, though the restoration plot of Llano de Pario and the reforestation plot of San Nicolás may tend to be slightly more dominated than the former ones.

Taxonomic and functional composition of bird communities

The incidence-based species turnover index (β_{sim}) for similarity in taxonomic composition of the avian community suggested that in San Nicolás the habitat with an avian community taxonomically most similar to original forest was the restoration plot (72% similarity), followed by the reforestation plot (50% similarity), with the abandoned cropfield having a low 16% similarity (Table 1). In Llano de

Pario, the restoration plot was marginally more similar to the late-seral forest (53% similarity) than the reforestation plot (50% similarity). Among all study sites, highest taxonomic similarity corresponded to the late-seral forests of Llano de Pario and Mesa de Cutzato (82% similarity), while the abandoned cropfield in San Nicolás had low or negligible taxonomic similarity with the forest habitats (Table 1).

Table 1. Similarity in taxonomic composition of bird communities from surveyed habitats according to the species turnover analysis (β_{sim}). As β_{sim} is a dissimilarity index, results are presented as 1-β_{sim} in order to display similarity values among surveyed habitats. NF = San Nicolás original forest, NRs = San Nicolás restoration plot, NRf = San Nicolás reforestation plot, NC = San Nicolás abandoned cropfield, PF = Llano de Pario late-seral forest, PRs = Llano de Pario restoration plot, PRf = Llano de Pario reforestation plot, CF = Mesa de Cutzato late-seral forest, CA = Mesa de Cutzato arenal.

% Similarity									
	NF	**NRs**	**NRf**	**NC**	**PF**	**PRs**	**PRf**	**CF**	**CA**
NF	-								
NRs	0.72	-							
NRf	0.5	0.5	-						
NC	0.16	0.33	0.33	-					
PF	0.67	0.5	0.58	0	-				
PRs	0.46	0.46	0.41	0.16	0.53	-			
PRf	0.55	0.44	0.66	0.5	0.5	0.53	-		
CF	0.61	0.61	0.41	0	0.82	0.46	0.55	-	
CA	0.43	0.37	0.41	0	0.5	0.46	0.37	0.56	-

The Bray-Curtis ecological distance analysis revealed that forests exhibited the most taxonomically similar bird communities, with late-seral forests of Llano de Pario and Mesa de Cutzato having 72% similarity, followed by the original forest from San Nicolás with ~58% similarity (Fig. 4a). Among managed habitats, the reforestation plots of Llano de Pario and San Nicolás were more similar (52% similarity), followed by the restoration plot of San Nicolás with 41% similarity. By comparison, the restoration plot of Llano de Pario did not cluster with the other managed habitats, but with the arenal from Mesa de Cutzato (~53% similarity). Finally, the abandoned cropfield from San Nicolás was shown to be taxonomically distinct from every other habitat study site.

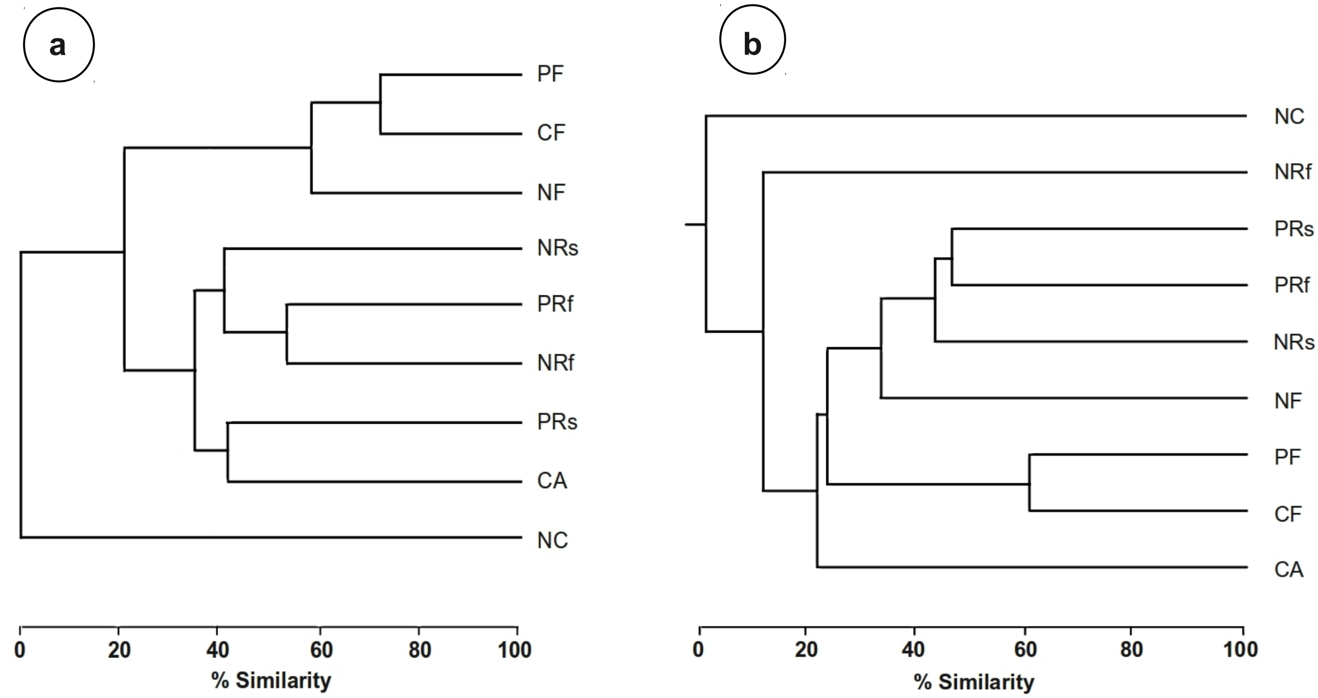


Fig. 4. Bray-Curtis ecological distance analysis of original, late-seral, disturbed, and managed habitats within Nuevo San Juan considering a) taxonomic composition of avian communities, and b) functional composition of avian communities. See Fig. 2 legend for habitats abbreviations.

Forests and the restoration plot of San Nicolás were also the only habitats that encompassed bird species from five different feeding groups (i.e., insectivores, granivores, frugivores, omnivores, nectarivores). The Bray-Curtis multivariate cluster analysis revealed differences in functional composition of bird communities among habitats (Fig. 4b). As in the case of taxonomic similarity, the late-seral forests of Llano de Pario and Mesa de Cutzato had the most functionally similar bird communities of all habitats (60% similarity), while the San Nicolás abandoned cropfield was functionally distinct from every other habitat (~1% similarity). However, among managed habitats, the reforestation and restoration plots of Llano de Pario showed functionally similar bird communities (46% similarity), followed by the restoration plot from San Nicolás (~43% similarity), and these were grouped in functional similarity with the original forest habitat in San Nicolás. By comparison, the reforestation plot from San Nicolás had a functionally different bird community compared to other managed habitats.

• DISCUSSION •

Our results demonstrate that avian communities varied not only among natural, disturbed, and managed habitats, but also among similar habitat types as a consequence of their disturbance histories and management outcomes. In this section, we first discuss how variations on species richness, bird density, and community structure and composition are related to particular characteristics of surveyed habitats. Then, we assess the effects of different management efforts on bird communities and their effectiveness to facilitate the establishment of communities that resemble those from natural habitats.

In terms of vegetation characteristics, forest habitats were similar despite the fact that volcanic activity alters the vertical structure and species composition of vegetation in sites with volcanic ash deposition (Lindig-Cisneros 2007). Managed habitats were similar in vegetation characteristics, particularly in San Nicolás where agriculture was the only disturbance. Nevertheless, habitats which were submitted to similar management strategies of restoration or reforestation did not clustered together, mostly because of differences in shrub and herb cover associated with distinct disturbance histories and management outcomes (Gómez-Romero et al. 2006; Lindig-Cisneros 2009). This suggests that a prior land-use for agriculture does not represent a barrier to herb and shrub re-establishment after reforestation and restoration activities. Moreover, within the restoration plot of San Nicolás, the presence of *Lupinus elegans*, a shrub species used as nurse plant for trees, may facilitate the establishment of more herb and shrub species than in reforested areas, leading to a more complex understory (Díaz-Rodríguez 2010). By comparison, the natural disturbance of tephra deposition in Llano de Pario represents a major barrier to plant establishment (Blanco-García and Lindig-Cisneros 2005). Although restoration activities within Llano de Pario also involved planting of trees and *L. elegans*, extreme temperatures of the substrate prevents the establishment of nurse-plants and severely limited the establishment of an understory (Nava-Sosa et al. 2010; Gil-Solórzano et al. 2009). As may be expected, vegetation characteristics of the disturbed habitats in the abandoned cropfield and the arenal were very different from the other surveyed habitats, as the abandoned cropfield lacked trees and shrubs, while the arenal was mostly covered by volcanic ash deposits with small scattered shrubby patches (Lindig-Cisneros et al. 2006).

Differences in avian species richness were associated with habitat location within Nuevo San Juan. In San Nicolás, restoration efforts proved to be more important for enhancing bird species richness than reforestation activities, as a higher number of bird species used both the restoration plot and the original forest. As indicated by other studies, this positive effect could be due to the promotion of a more heterogeneous habitat by restoration efforts, particularly in relation to the understory, which benefited more bird species (Seigel et al. 2005; Aerts et al. 2008). At Llano de Pario, bird species richness was similar for the late-seral forest, and the restoration and reforestation plots. Although this may suggest that different management activities produce similar results by facilitating the establishment of analogous number of bird species (Van Dyke et al. 2004), it may be expected that distinct bird species would benefit in each of the habitats as vegetation characteristics greatly differ among them (MacGregor-Fors et al. 2010). Hence, for this particular site, species richness may not be a useful parameter to assess compliance with restoration goals, as the identity of each species could reflect a better understanding of the effects of different habitats on bird communities.

In San Nicolás, restoration efforts were more effective than reforestation at producing avian communities that resemble those of natural habitats, as the ratio of the number of resident to migratory species in restoration plots was greater than in reforestation plots. Hence, restoration plots did not represent important habitats for migratory species as found in other studies (Marburger 2002; Brawn 2006; Gache 2008). It may be that disturbed habitats offer accessible feeding resources for migratory species, which could benefit by avoiding forest and restored habitats that support a complex resident avifauna with a greater number of resident competitors and potential predators (Martin 1985). However, reforestation and restoration plots at Llano de Pario were not as successful in attracting a significant number of resident species as late-seral forests, which might indicate that these habitats require further management to sustain avian communities similar to those from reference habitats (Van Dyke et al. 2004).

Bird densities were also enhanced by management activities in San Nicolás, in such a way that the densities of managed habitats were similar to that for original forest habitats, as reported by Gaines et al. (2007) and Hoover (2009). Nevertheless, increased bird density values for reforestation plots were heavily influenced by the presence of species that conform groups and forage together, such as the striped sparrow (*Oriturus superciliosus*) and the house finch (*Carpodacus mexicanus*), which might be benefited by the poor species understory and low tree height prevalent in this plot (Hill 1993; Howell and Webb 1995). While both species were also present within the San Nicolás restoration plot, their numbers were lower than in the reforestation plot, hence the increased bird density in the restoration plot was due to the presence of a larger number of species. By comparison, bird densities were relatively low in Llano de Pario, where restoration and reforestation plots exhibited higher numbers of individuals per hectare than the late-seral forest. Distinct factors could have generated this pattern. For instance, we observed that human activities (e.g., timber extraction, pine resin collection) occurred more frequently within the late-seral forest of Llano de Pario than in other natural forest habitats, which could possibly have reduced the number of bird individuals by lowering the quality of this habitat, and/or driving birds away (Thiollay 1997; Aguilar 2006). Moreover, social species tolerant to open habitats (i.e., eastern bluebird -*Sialia sialis*; Gowaty and Plissner 1998), vagrant migratory species (i.e., ruby-crowned kinglet -*Regulus calendula*), and species related to highly disturbed forests (i.e., yellow-eyed junco -*Junco phaeonotus*; Sullivan 1999) were very common within both the restoration and reforestation plots of Llano de Pario, which might be generating higher bird densities in them.

Avian communities from forest habitats were more even than those from restoration plots, possibly because the former offer a vast array of resources and exhibit more diverse microclimatic conditions which can be exploited by more species (Sallabanks et al. 2005; Aerts et al. 2008). Nevertheless, in San Nicolás, restoration activities following agricultural disturbance may facilitate establishment of a more even avian community by creating a more heterogeneous habitat with an increase in shrub and herb cover that offers refuges and feeding resources for many individuals of distinct bird species (Hamel 2003; Seigel et al. 2005; MacGregor-Fors et al. 2010). Despite the fact that the reforestation plot demonstrates that this management activity in agricultural landscapes may enhance community evenness by including the tree component (Twedt and Portwood 1997), the avian community in the reforestation plot of San Nicolás was still more dominated than in the restoration plot. Contrary to San Nicolás, the reforestation plot in Llano de Pario had a more even avian community than in the restoration plot. In this particular site, restoration activities did not produce a complex shrub and herb cover (Nava-Sosa et al. 2010; Gil-Solórzano et al. 2009), and consequently was not as successful in attracting more bird species and individuals as may be expected (Hamel 2003). Moreover, the extreme temperatures associated with the tephra deposits resulted in high tree mortality, leading to the establishment of a disturbance tolerant shrub species (*Eupatorium glabratum*) in reforestation plots at this location (Lindig-Cisneros 2007). The presence of this shrub served as an important refuge and foraging substrate for birds (Ortega-Álvarez pers. obs.), which could promote more even avian communities in reforestation plots.

According to the species turnover index, the restoration plot in San Nicolás was more efficient than the reforestation plot in attracting similar species to that of the adjacent original forest, as observed by MacGregor-Fors et al. (2010). However, as suggested by the Bray-Curtis ecological distance, the number of individuals of each species using the restoration plot is still not comparable to that of the forest, as it is more similar to other managed habitats. Hence, the restoration plot seems to be in an intermediate stage on its way to resembling the conditions and resources offered by the original forest, and may be used by forest species but not to the extent of maintaining the same number of individuals (Van Dyke et al. 2004). Management activities created a different scenario in Llano de Pario where the restoration plot exhibited taxonomically similar communities to that of the reforestation plot. The proximity of the restoration plot to the late-seral forest might not be limiting the movement of different bird species from the forest to the restoration plot as suggested by Palmer et al. (1997). Hence, site-specific traits of the restoration plot might be responsible for differences in species composition in relation to the late-seral forest (Wood et al. 2004; Malan et al. 2007; Lindenmayer et al. 2010). Indeed, restoration activities in this site resulted in a habitat that resembled reforestation plots, so the type of species that were attracted to the restoration plot were those which had the capacity to exploit the resources and conditions in reforestation plots. Moreover, the restoration plot differed from the reforestation plot in the number of individuals of each species, in such a way that the restoration plot was more similar to the arenales from Mesa de Cutzato. Hence, the establishment of the shrub *Eupatorium glabratum* in the reforestation plots allowed more birds to use this particular habitat, leading to differences among managed habitats.

Forests and the restoration plot of San Nicolás were the habitats that enclosed the greatest number of different feeding groups, which may be derived from the differing array of resources and micro-habitats offered (Hamel 2003; Hartung and Brawn 2005). Hence, restoration efforts could have enhanced habitat heterogeneity which may sustain a variety of species with multiple feeding strategies and differing ecological roles (Seigel et al. 2005). However, the number of individuals per feeding group at the restoration plot was low, probably because the resources offered by this managed habitat were still low in quality/quantity despite their diversity (Van Dyke et al. 2004). The differing functional composition of bird communities in the reforestation plot of San Nicolás compared to other managed habitats may be due to the predominance of mid-sized granivore species, which could benefit from the presence of planted trees as refuges and perching sites (i.e., house finch, yellow-eyed junco; Hill 1993; Sullivan 1999), and the existence of an incipient herbaceous layer for nesting (striped sparrows) and/or foraging (house finches, striped sparrows, yellow-eyed juncos; Hill 1993; Howell and Webb 1995; Sullivan 1999). In contrast, the functional dissimilarity of the abandoned cropfield suggests that the poor vegetation structure only supports species of specific trophic guilds or with visibility-dependent foraging strategies, such as small and mid-sized granivores (chipping sparrow

-*Spizella passerina*- and house finch respectively; Hill 1993; Middleton 1998), small carnivores (i.e., American kestrel -*Falco sparverius*; Smallwood and Bird 2002), and mid-sized insectivores (i.e., swallows).

• CONCLUSIONS •

We determined that under certain conditions, restoration activities could promote similar bird community parameters to natural habitats. In particular, restoration outcomes associated with the development of heterogeneous and complex understory might be responsible for enhancing bird species richness, evenness, and heterogeneity (both taxonomic and functional) of bird communities. Reforestation activities also promote richer, more even, and more complex bird communities than in disturbed habitats, although incorporating only the tree component as a management strategy might not be sufficient to achieve bird communities that resemble those of natural habitats. Given that reforestation efforts have been largely preferred as a means to recover deforested landscapes in Mexico and other countries in Latin America (Sáenz-Romero and Lindig-Cisneros 2004; Gobierno Federal 2007), we encourage the implementation of more integral activities as part of restoration strategies in order to amplify the effectiveness of biodiversity recovery in degraded habitats. We also highlight the importance of defining exclusive restoration strategies for different sites, as local disturbance histories and site-specific characteristics could produce distinct responses in bird communities in spite of the pool of species from adjacent landscapes and the distance to source forests.

As the final goal of restoration activities should be the recovery of biodiversity as a whole, monitoring the responses of different biological groups to any type of restoration effort should be fostered in order to assess compliance with restoration goals from an exhaustive approach. To this end, we suggest that monitoring bird communities could: (1) be easily implemented, (2) facilitate the identification of those habitat properties that have not yet been recovered, (3) account for similarities/differences among restored habitats and reference sites, and (4) aid in the selection of complementary activities for restoration efforts. Although previous studies have recommended specific bird community parameters to assess the effectiveness of restoration efforts (e.g., species richness, density, structure; Konisky et al. 2006; Fletcher et al. 2007), based on our results we believe that it is important to take into account all community properties to provide a broader perspective of community responses to restoration activities, and to discriminate among those particular parameters that could be biased by particular bird species (e.g., density analyses and social species).

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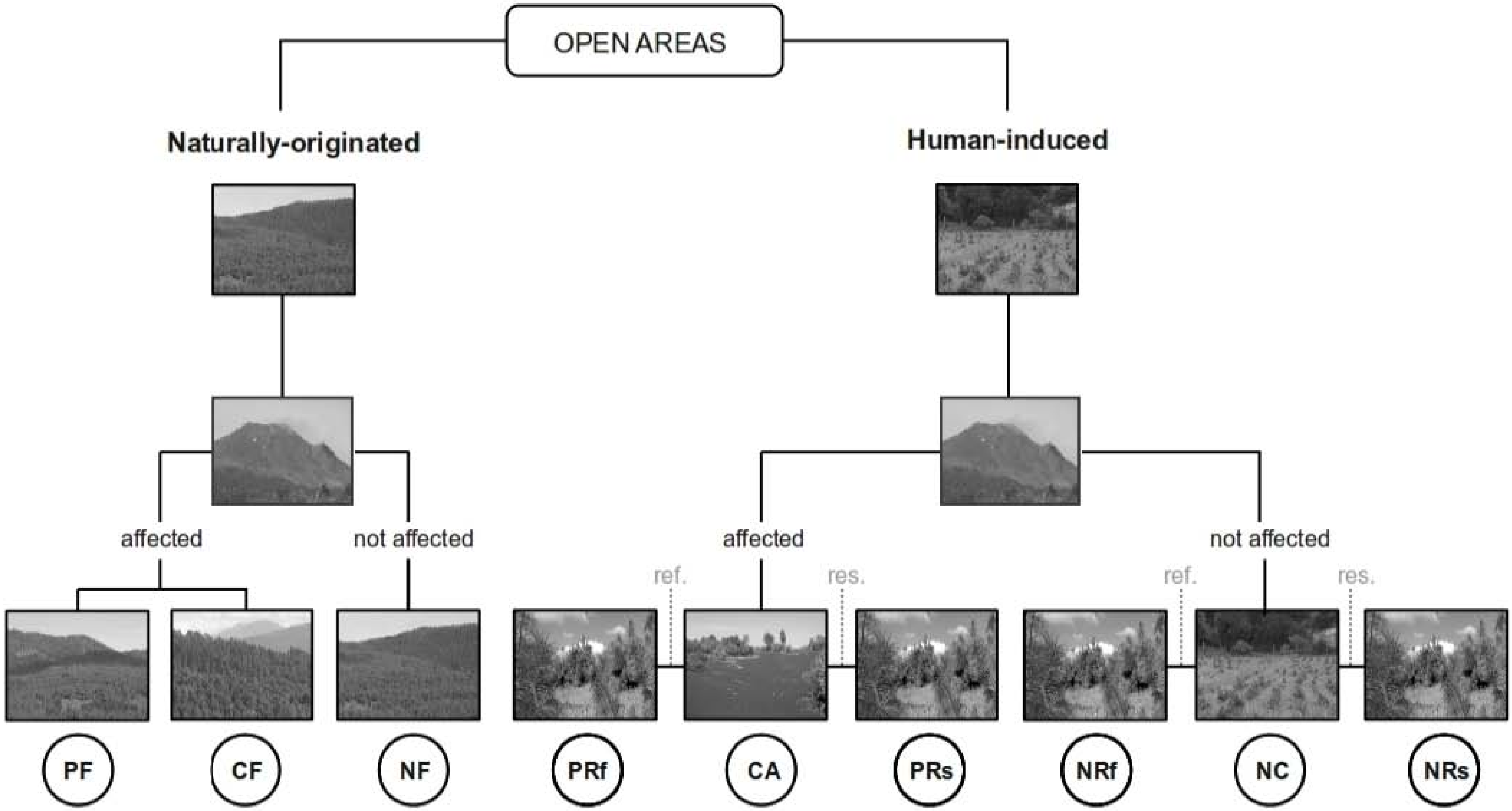
Appendix 1. History of origin of surveyed habitats from original open areas created after the eruption of the Paricutín volcano. Natural-origin open areas created by treefalls affected by the eruption within forested sites led to the creation of late-seral habitats after forest recovery (PF, CF). Natural-origin open areas not affected by volcanic activity also recovered into original forests conditions (NF). However, human-induced open areas created by agriculture either: i) remained as abandoned cropfields when not affected by the volcanic eruption (NC), or ii) transformed into arenales when disturbed by volcanic activity, which do not recover into forested areas by natural processes (CA). In order to promote habitat recovery, abandoned cropfields and arenales received human management through: i) reforestation activities, to create mono-specific stands for timber extraction (PRf, NRf) and ii) restoration activities, to recover ecological processes and biodiversity (PRs, NRs). ref. = reforestation activities, res. = restoration activities, PF = Llano de Pario late-seral forest, CF = Mesa de Cutzato late-seral forest, NF = San Nicolás original forest, PRf = Llano de Pario reforestation plot, CA = Mesa de Cutzato arenal, PRs = Llano de Pario restoration plot, NRf = San Nicolás reforestation plot, NC = San Nicolás cropfield, NRs = San Nicolás restoration plot.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PF
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NRf
NC
NRs

Appendix 2. Ratio of the number of resident to migratory species among managed, natural, and disturbed habitats within the Paricutín volcano landscape.

Habitat	Resident species : Migratory species
San Nicolás original forest	~ 17:1
San Nicolás restoration plot	8:1
San Nicolás reforestation plot	5:1
San Nicolás abandoned cropfield	2:1
Llano de Pario late-seral forest	13:1
Llano de Pario reforestation plot	~ 3:1
Llano de Pario restoration plot	2:1
Mesa de Cutzato late-seral forest	8:1
Mesa de Cutzato arenal	1:1

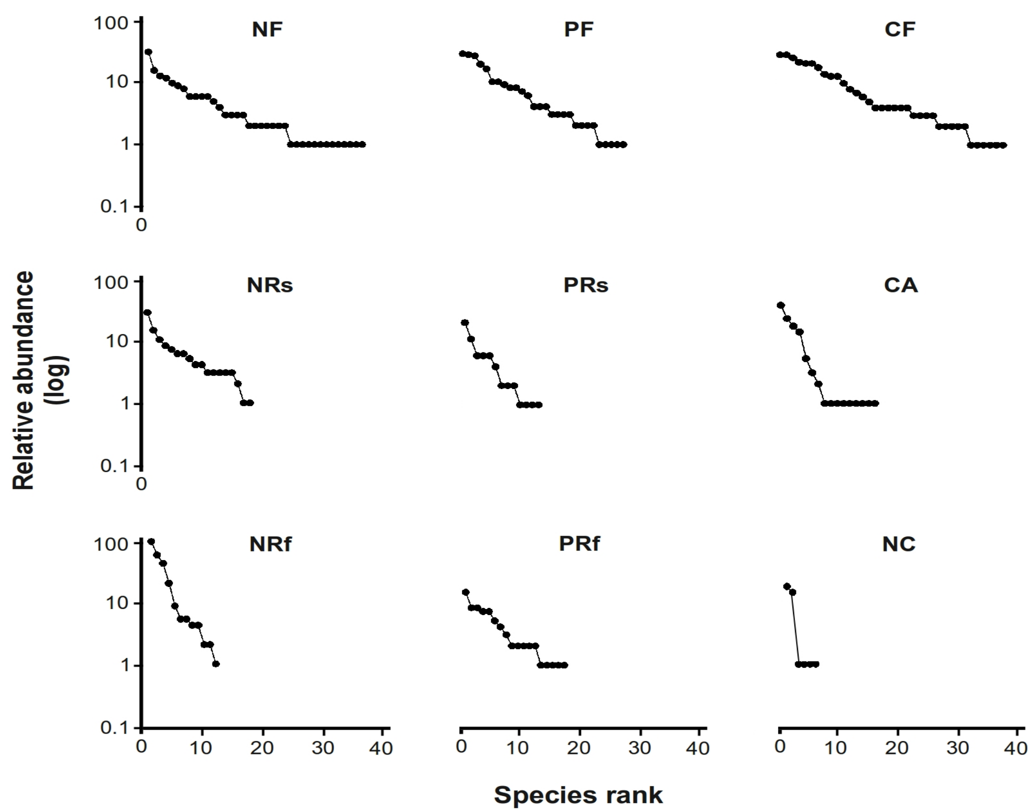
Appendix 3. Bird species recorded in managed, natural, and disturbed habitats within the Paricutín volcano landscape. Family, trophic group, status, and the habitat where the species was recorded are addressed for each species. F = frugivore, G = granivore, C = carnivore, N = nectarivore, I = insectivore, O = omnivore, r = resident, m = migrant, nd = not determined, NF = San Nicolás original forest, NRs = San Nicolás restoration plot, NRf = San Nicolás reforestation plot, NC = San Nicolás cropfield, PF = Llano de Pario late-seral forest, PRs = Llano de Pario restoration plot, PRf = Llano de Pario reforestation plot, CF = Mesa de Cutzato late-seral forest, CA = Mesa de Cutzato arenal.

FAMILY	SPECIES	HABITAT
Falconidae	*Falco sparverius* (C - m)	NC, NRf
Trochilidae	*Colibri thalassinus* (N - r)	NF, NRs
	Hylocharis leucotis (N - r)	CA, CF, NF, NRs, PF, PRs
	Selasphorus platycercus (N - r)	CA, PF, PRs
	Selasphorus sasin (N - m)	NF
Trogonidae	*Trogon mexicanus* (F - r)	CF
Picidae	*Picoides villosus* (I - r)	PF
	Colaptes auratus (I - r)	NF, NRf, PF, PRf
Furnariidae	*Lepidocolaptes leucogaster* (I - r)	CF, PF
Tyrannidae	*Mitrephanes phaeocercus* (I - r)	CF, PF
	Contopus pertinax (I - r)	CF, NF, PF, PRf
	Empidonax occidentalis (I - r)	CF, NF, NRs, PF, PRf
	Empidonax sp. (I - nd)	NF, PF
	Pyrocephalus rubinus (I - r)	PRs
	Myiarchus tuberculifer (I - r)	CF, NF, NRs, PF
	Tyrannus vociferans (I - r)	NF, NRf
	Pachyramphus aglaiae (F - r)	NF
Vireonidae	*Vireo huttoni* (I - r)	CF, NF, PF
Corvidae	*Cyanocitta stelleri* (O - r)	NF
	Aphelocoma ultramarina (O - r)	CF, NF, PF
	Corvus corax (O - r)	CF, NF

Hirundinidae	*Tachycineta thalassina* (I - r)	NC
	Stelgidopteryx serripennis (I - r)	NF, NC, NRs
	Petrochelidon pyrrhonota (I - m)	PRs
	Hirundo rustica (I - m)	NC, PRf
Paridae	*Poecile sclateri* (I - r)	CF, NF, NRs, PF, PRf, PRs
Aegithalidae	*Psaltriparus minimus* (I - r)	CA, CF, NF, NRs, PRf, PRs
Sittidae	*Sitta carolinensis* (I - r)	CF, NF, PF
	Sitta pygmaea (I - r)	CF, PF
Certhiidae	*Certhia americana* (I - r)	CF
Troglodytidae	*Campylorhynchus gularis* (I - r)	NRs
	Troglodytes aedon (I - r)	CF, NRf, NRs, PF
Polioptilidae	*Polioptila caerulea* (I - m)	PRf, PRs
Regulidae	*Regulus satrapa* (I - m)	CF
	Regulus calendula (I - r)	CA, CF, NF, NRf, NRs, PF, PRf, PRs
Turdidae	*Sialia sialis* (I - r)	NRf, PF, PRf, PRs
	Myadestes occidentalis (F - r)	CF, NF
	Catharus occidentalis (F - r)	CF, NF, NRs, PF
	Turdus assimilis (F - r)	NF
	Turdus migratorius (F - r)	CA, CF, NF, PF
Mimidae	*Melanotis caerulescens* (F - r)	NF
Ptilogonatidae	*Ptilogonys cinereus* (F - r)	CF, NF, PRf
Peucedramidae	*Peucedramus taeniatus* (I - r)	CF, PF
Parulidae	*Oreothlypis celata* (I - m)	CA, PRf
	Oreothlypis ruficapilla (I - m)	CA
	Oreothlypis superciliosa (I - r)	CF, NF, PF
	Dendroica coronata (I - m)	CA, NRf, PRs
	Dendroica nigrescens (I - m)	CA
	Dendroica townsendi (I - m)	CF, PRf
	Dendroica occidentalis (I - m)	CA, CF, PF
	Dendroica graciae (I - r)	CF
	Oporornis tolmiei (I - m)	CA, NRs
	Wilsonia pusilla (I - m)	CA, CF
	Cardellina rubrifrons (I - m)	CF

	Ergaticus ruber (I - r)	CF, NF, PF
	Myioborus pictus (I - r)	CF
	Myioborus miniatus (I - r)	CF, NF, PF, PRs
	Basileuterus belli (I - r)	NF
Emberizidae	*Diglossa baritula* (N - r)	NF, NRs
	Arremon virenticeps (G - r)	NF
	Pipilo maculatus (G - r)	CA, CF, NF, NRf, PF, PRf
	Oriturus superciliosus (G - r)	NRf, NRs, PRf
	Spizella passerina (G - r)	NC, PRf
	Junco phaeonotus (G - r)	CA, CF, NF, NRf, NRs, PF, PRf, PRs
Cardinalidae	*Piranga flava* (O - r)	NF
	Pheucticus melanocephalus (O - r)	CF, NF, NRs
Fringillidae	*Euphonia elegantissima* (F - r)	CA
	Carpodacus mexicanus (G - r)	NC, NRf, NRs, PRf, PRs
	Loxia curvirostra (G - r)	NF
	Spinus pinus (G - r)	CA, CF, NF, NRf, NRs, PF, PRf

Appendix 4. Rank-abundance plots of avian communities in each surveyed habitat within Nuevo San Juan. Most dominant bird species in each habitat were: (1) grey silky (*Ptilogonys cinereus*) and yellowed-eye junco (*Junco phaeonotus*) in San Nicolás original forest (NF), (2) yellowed-eye junco and house finch (*Carpodacus mexicanus*) in San Nicolás restoration plot (NRs), (3) striped sparrow (*Oriturus superciliosus*) and house finch in San Nicolás reforestation plot (NRf), (4) barn swallow (*Hirundo rustica*) and northern rough-winged swallow (*Stelgidopteryx serripennis*) in San Nicolás abandoned cropfield (NC), (5) olive warbler (*Peucedramus taeniatus*) and white-eared hummingbird (*Hylocharis leucotis*) in Llano de Pario late-seral forest (PF), (6) yellowed-eye junco and ruby-crowned kinglet (*Regulus calendula*) in Llano de Pario reforestation plot (PRf), (7) yellowed-eye junco and ruby-crowned kinglet in Llano de Pario restoration plot (PRs), (8) olive warbler and slate-throated redstart (*Myioborus miniatus*) in Mesa de Cutzato late-seral forest (CF), and (9) bushtit (*Psaltriparus minimus*) and broad-tailed hummingbird (*Selasphorus platycercus*) in Mesa de Cutzato arenal (CA).



CAPÍTULO IV

Discusión y conclusiones

"¿No sería más progresista preguntar dónde vamos a seguir,
en vez de dónde vamos a parar?"

– Mafalda –

• DISCUSIÓN Y CONCLUSIONES •

En los últimos años, las aves han sido incorporadas en mayor medida a los trabajos de investigación relacionados con la ecología de la restauración. Particularmente, esta tendencia ha sido notable para los Estados Unidos de América, y en su mayoría, los estudios han analizando la respuesta de las aves ante las actividades de restauración desde un enfoque de ecología de comunidades. Así, es clara la necesidad de incrementar la investigación en zonas tropicales, dónde los impactos de las actividades antropogénicas amenazan los mayores valores de biodiversidad a nivel mundial (Myers et al. 2000). Asimismo, es deseable fomentar estudios con el propósito de determinar: (1) el efecto de las actividades de restauración sobre la dinámica de los parámetros poblacionales de aves, (2) la efectividad de diferentes tipos de estrategias de manejo y restauración de los hábitats para promover el uso de hábitat, la sobrevivencia y el incremento en las tasas de reproducción de distintas especies de aves, y (3) la respuesta de las comunidades de aves ante procesos de restauración llevados a cabo en sistemas degradados inmersos en dinámicas de recuperación no lineales.

El efecto de las actividades de restauración ecológica sobre las aves está determinado por factores diversos asociados con las propiedades del proceso restaurativo. Algunas de las propiedades de las actividades de restauración ecológica que deberán ser consideradas al analizar la relación entre las aves y el proceso de restauración son: (1) el hábitat en cuestión, (2) la estructura de la vegetación, (3) las características de los hábitats adyacentes, (4) el tamaño de los sitios restaurados, (5) la escala de tiempo utilizada para evaluar los efectos de la restauración sobre las aves, (6) la historia de disturbio de los hábitats degradados, y (7) la biología de las especies de aves asociadas a los sitios de estudio. Ya que cada proyecto de restauración ecológica exhibe características físicas, biológicas, históricas, sociales y logísticas únicas, es necesario evaluar de forma particular para cada proyecto las implicaciones de las actividades de restauración sobre el componente ornitológico de los ecosistemas. De esta forma, podrá reunirse un conjunto de evidencia empírica suficiente y representativa que permita elucidar patrones y procesos ecológicos generales para esbozar una teoría robusta que culmine en el desarrollo de actividades de restauración más integrales y eficaces.

Existen ciertas recomendaciones que podrían ser de utilidad para guiar el desarrollo de los esfuerzos de restauración ecológica enfocados en el componente ornitológico de los ecosistemas. Entre este tipo de recomendaciones destacan: (1) la incorporación de análisis de la conducta para determinar el efecto de la restauración ecológica sobre las aves (Armitage et al. 2007, Fink et al. 2009), (2) el monitoreo de los gremios tróficos de las comunidades de aves para determinar y dar seguimiento a fluctuaciones de los recursos en los sitios en proceso de restauración (Seigel et al. 2005), (3) la implementación de diferentes tipos de actividades de manejo y restauración ecológica para propiciar la conformación de hábitats heterogéneos que beneficien a múltiples especies de aves (Machmer 2002, Blank et al. 2002), (4) la restauración ecológica parcial de los sitios degradados con el propósito de evitar afectar de forma negativa a aquellas especies de aves que dependen de sitios no restaurados (Stralberg et al. 2009), y (6) la promoción de actividades de restauración que beneficien de forma conjunta a las aves y a las actividades productivas que mantienen a las poblaciones humanas locales (Goutner 1997, Eglington 2008).

De acuerdo a los resultados asociados al Capítulo III de este manuscrito, se determinó que las comunidades de aves varían entre hábitats manejados como consecuencia de su historia de disturbio y estrategias de manejo. Bajo ciertas condiciones, las actividades de restauración promueven comunidades de aves con parámetros de riqueza, densidad, estructura y composición similares a aquellas presentes en bosques de referencia. De forma particular, el desarrollo de un sotobosque heterogéneo y complejo es responsable del incremento en la riqueza, la equitatividad y la heterogeneidad taxonómica y funcional de las comunidades de aves de las parcelas de restauración. No obstante, es importante recalcar que los parámetros de las comunidades de aves presentes en las parcelas de restauración no son idénticos a aquellos que exhiben las comunidades de aves de los bosques de referencia. Tales diferencias se deben en gran medida a que únicamente un número reducido de individuos de especies de aves de bosque logran utilizar las parcelas de restauración. Lo anterior sugiere que las parcelas de restauración se encuentran en un estado intermedio para semejar las condiciones y los recursos que los bosques les ofrecen a las aves.

Las actividades de reforestación también promueven comunidades de aves más diversas, heterogéneas y complejas que aquellas presentes en sitios perturbados. Sin embargo, incorporar el componente arbóreo como única estrategia de manejo no es suficiente para lograr comunidades de aves semejantes a aquellas de bosques. Dado que las actividades de reforestación han sido ampliamente preferidas como estrategias para recuperar paisajes deforestados en México y otros países de América Latina (Sáenz-Romero y Lindig-Cisneros 2004, Gobierno Federal 2007), en su lugar es recomendable implementar actividades de restauración integrales para amplificar la efectividad de la recuperación de la biodiversidad en los hábitats degradados. Asimismo, es importante definir estrategias de restauración particulares para sitios focales diferentes, ya que las historias de disturbio y las características del hábitat a nivel local producen respuestas diferenciales en las comunidades de aves, aún a pesar de que los hábitats adyacentes sean fuente de una gran variedad de especies de aves.

El monitoreo de las respuestas de diferentes grupos biológicos ante cualquier tipo de esfuerzo de restauración debe ser promovido con la finalidad de determinar el cumplimiento de las metas de restauración desde una aproximación integral. Para dicho fin, es recomendable incorporar el monitoreo de las comunidades de aves como parte de los proyectos de restauración ya que: (1) su implementación es sencilla y poco costosa, (2) facilita la identificación de aquellas características de los hábitats que aún no han sido restauradas, (3) permite identificar las diferencias existentes entre los sitios restaurados y los sitios de referencia, y (4) ayuda en la selección de actividades de restauración complementarias. A pesar de que estudios previos han recomendado el monitoreo de parámetros de las comunidad específicos para identificar el cumplimiento de las metas de las actividades de restauración (e.g., riqueza de especies, densidad, estructura; Konisky et al. 2006, Fletcher et al. 2007), los resultados de este trabajo sugieren que ciertos parámetros pueden estar sesgados por la presencia y el éxito de ciertas especies de aves (e.g., densidad y especies sociales). Por ello, es importante considerar las propiedades de la comunidad en conjunto para definir desde una perspectiva más amplia la respuesta de las comunidades de aves ante las actividades de restauración.

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