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REGLAS DE ENSAMBLE GENERALES EN LAS COMUNIDADES DE AVES

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CONTENIDO

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RESUMEN

La estructura de las comunidades se puede interpretar como el resultado de reglas de ensamble. Los ensamblajes de aves de México se componen de 35 o más especies que pertenecen a 21 o más familias; generalmente contienen especies pertenecientes a 12 gremios alimentarios; e incluyen especies de 16 familias ubicuas. En este trabajo se proponen una regla de ensamble funcional y una macroevolutiva que se combinan para producir esta estructura.

La amplia representación de 12 gremios alimentarios de aves puede visualizarse como el resultado de la selección natural, la dispersión y la selección de hábitat actuando en una región rica en 12 tipos de recursos. Estos procesos hacen que las especies tiendan a tener una "distribución libre ideal". La consecuencia de la distribución libre ideal para la ecología de comunidades es que dondequiera que exista algún recurso, formarán parte de la comunidad una o más especies capaces de utilizar dicho recurso siempre que tales especies existan en el acervo de especies (regla de ensamble funcional). Como resultado, casi todos los ensamblajes de aves de México incluyen aves carnívoras, aves insectívoras que capturan sus presas en diferentes partes del hábitat, aves carroñeras, aves nectarívoras y aves que se alimentan de frutos o semillas, algunas sobre los árboles y otras en el suelo.

El que 16 familias de aves se encuentren en prácticamente todas las comunidades bióticas de México se relaciona con el efecto del área geográfica sobre la especiación y la extinción. Una mayor área geográfica promueve la especiación y reduce la extinción, produciendo grupos monofiléticos ricos en especies que contribuyen a la composición de la mayoría de las comunidades de una región dada. Los grupos monofiléticos con mayores tasas netas de especiación tienden a contribuir especies a un mayor número de comunidades (regla de ensamble macroevolutiva).

Los procesos que se propone que producen esta estructura son generales, de manera que estudios análogos con otros tipos de organismos y/o en otras regiones podrían revelar que estas reglas de ensamble son generales. El conocimiento de esta estructura común ayuda a evaluar inventarios avifaunísticos para determinar si son apropiados para uso en análisis macroecológicos y de conservación.

REGLAS DE ENSAMBLE GENERALES EN LAS COMUNIDADES DE AVES

INTRODUCCION GENERAL

El desarrollo de una teoría general de comunidades se centra en descubrir las reglas que se presentan en la estructura de las comunidades (McIntosh 1995: 348; Brown 1981). Las llamadas "reglas de ensamble" permiten predecir la composición de las comunidades a partir de las species disponibles en una región y las características del ambiente (Haefner 1988). Aunque los estudios de comunidades artificiales y los estudios históricos/paleoecológicos indican que los pasos históricos de ensamble influyen en la composición de las comunidades (Gilpin et al. 1986; Drake 1990, 1991; Foster et al. 1990; Lockwood et al. 1999), los estudios empíricos sugieren que se pueden descubrir reglas generales al estudiar los patrones de composición de comunidades y no es necesario conocer los pasos históricos (Belyea y Lancaster 1999). El conocimiento de estas reglas puede emplearse para evaluar los efectos de las actividades humanas sobre los ecosistemas (Wilson 1992) o para restaurar comunidades perturbadas.

Los estudios comparativos en ecología de comunidades analizan ya sea las semejanzas entre comunidades de ambientes físicos semejantes, o las diferencias entre comunidades de ambientes físicos contrastantes (v.gr., artículos citados por Terborgh y Robinson 1986; Wiens 1989a; Schluter y Ricklefs 1993). En pocas ocasiones se han estudiado las semejanzas entre comunidades de ambientes físicos contrastantes (Wiens 1989a; Jumars 1993; Hay 1994), a pesar de que se buscan reglas generales. Una excepción es el trabajo de Steneck y Dethier (1994), quienes estudiaron la estructura de ensamblajes de algas en el ambiente marino.

El objetivo de esta tesis es buscar reglas de ensamble generales en el medio terrestre al estudiar semejanzas entre ambientes contrastantes, desde sitios secos y calientes hasta sitios fríos. Dado que existen pocas especies compartidas entre comunidades de ambientes contrastantes, las semejanzas se buscan a niveles de organización mayores, por una parte entre grupos funcionales y por otra entre grupos monofiléticos. La justificación de este enfoque es que variaciones que son impredecibles a nivel de especies pueden generar patrones predecibles a niveles de organización mayores (Steneck y Dethier 1994; Weiher y Keddy 1995). Las reglas de ensamble que requieren de conocimientos detallados sobre la ecología de las especies en una localidad particular (v.gr., M'Closkey 1978; Haefner 1981) son de aplicabilidad limitada (Fox y Brown 1993; Wilson 1995).

El área de estudio de este trabajo es la superficie continental de la República Mexicana (1,967,183 km^2; Sánchez-Molina 1985). La heterogeneidad ecológica de México se debe a su variabilidad climática, su topografía compleja y su historia biogeográfica. Hace aproximadamente dos millones de años se conjuntaron dos biotas que habían evolucionado en diferentes continentes (Ramamoorthy et al. 1993). A causa de la heterogeneidad, es difícil esperar que existan semejanzas entre ensamblajes distantes y sujetos a condiciones contrastantes. Por otra parte, si se encuentran semejanzas, éstas deben ser producto de reglas generales que no dependen de las condiciones latitudinales, climáticas, topográficas e históricas.

Por razones prácticas, los ecólogos de comunidades no estudian comunidades que abarcan todo tipo de organismos, sino "ensamblajes": conjuntos de poblaciones de las especies *pertenecientes a un solo grupo taxonómico* que coexisten en una localidad (Fauth et al. 1996). Para realizar este tipo de estudios, se necesita una base de datos confiable de la composición de diferentes ensamblajes, una buena clasificación de gremios y una taxonomía basada en grupos monofiléticos.

Las aves son un grupo bien estudiado en cuanto a estos aspectos. Existe información básica sobre la dieta de todas las especies, la clasificación taxonómica está basada en grupos monofiléticos y la afiliación a nivel familia es controvertida para solamente 18 especies de aves mexicanas (especies clasificadas en familias distintas por A.O.U. 1998 y Sibley y Monroe 1990; 2% de las especies mexicanas). En la literatura científica sobre aves mexicanas existen decenas de listas de especies coexistentes (Rodríguez-Yáñez et al. 1994).

Sin embargo, algunas de estas listas pudieran tener sesgos tales como diferencias de escala, listas incompletas de especies, y especies accidentales. Los análisis macroecológicos dan resultados equivocados cuando la información en la que se basan tiene sesgos y/o está incompleta (Blackburn y Gaston 1998). El problema de usar información a escalas distintas es que se confunden resultados de procesos diferentes (Wiens 1989b, Levin 1992). Por su parte, existen listas incompletas porque algunos métodos de muestreo no son capaces de detectar ciertas especies, y muestreos que emplean diferentes métodos producen listas diferentes (Disney et al. 1982; Gaston 1996). Por ejemplo, la captura con redes ornitológicas detecta solamente un subconjunto de las especies de aves de una localidad (Terborgh et al. 1990, Contreras-Martínez y Santana Castellón 1995). Tales listas incompletas no son comparables dado que reflejan métodos de muestreo que sufren de diferentes sesgos.

Adicionalmente, debido a la capacidad de vuelo de las aves, la dispersión accidental ocasiona que se registre un número limitado de individuos fuera del área principal de distribución geográfica, altitudinal o ecológica (Grinnell 1922). La mayoría de los individuos accidentales se encuentra en hábitats no adecuados y mueren sin interactuar de manera significativa con un ensamblaje. De este modo, las especies accidentales no deben considerarse propias de esa área (Remsen 1994). Por consiguiente, en esta tesis se excluyeron a las especies accidentales, al igual que hacen Terborgh et al. (1990), Remsen (1994) y Gómez de Silva et al. (1999). Asimismo, no se consideran las listas de la literatura para áreas donde la diversidad β es importante, porque algunas especies pudieran no interactuar con el resto de las especies por su segregación espacial (Shmida y Wilson 1985). De esta manera, se emplean sólo aquellas listas en las cuales todas las especies interactúan, al menos potencialmente. En el Capítulo I se genera un criterio basado en los patrones de composición y riqueza de los ensamblajes de aves para evaluar si una lista determinada es completa y, por lo tanto, si dicha lista puede emplearse en un estudio macroecológico.

En los Capítulos II y III se aplica este criterio en la compilación de listas completas de aves de la literatura, para explorar la posibilidad de encontrar reglas de ensamble que expliquen la composición de ensamblajes de aves en México. Tradicionalmente se ha considerado que la ecología de comunidades está determinada solamente por procesos ecológicos pero recientemente se ha considerado también la influencia de procesos biogeográficos y evolutivos (Ricklefs 1987; Ricklefs y Schluter 1993). Sin embargo, las reglas de ensamble se han centrado en los procesos ecológicos. En el Capítulo II, se busca explicar un patrón de los ensamblajes de aves (la estructura común en cuanto a gremios alimentarios) de acuerdo con procesos ecológicos. En el Capítulo III se busca explicar otro patrón de los ensamblajes de aves (la estructura común en cuanto a composición taxonómica) de acuerdo con procesos evolutivos.

Los tres capítulos de esta tesis están escritos en inglés y se presentan como artículos para Conservation Biology (aceptado), Oikos (en revisión) y Evolutionary Ecology respectivamente. Al final de la tesis se incluye una discusión general en español. Cada sección presenta su lista de literatura citada.

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Capítulo I

EVALUATING COMPLETENESS OF SPECIES LISTS FOR CONSERVATION AND MACROECOLOGY: CASE-STUDY OF MEXICAN LAND BIRDS

(in press, *Conservation Biology*)

Abstract. Studies of species diversity, macroecology, and conservation are usually based on lists of species, but lists found in the scientific literature vary in their degree of completeness. The use of such data sets can produce misleading results, making it necessary to test species lists for completeness before undertaking an analysis. Species richness estimators are useful for judging the completeness of species lists but have limitations. To add rigor to studies using species lists, we propose species lists should test for "omnipresent" taxa (species, genera and families that occur throughout the region concerned) and for a minimum number of species and families. As a case study, we compared species assemblages in diverse habitats in Mexico and found that seven families and two genera of land birds are omnipresent in mainland Mexico (excluding treeless areas) and that the most depauperate assemblage known contains 35 species from 21 families. We concluded that a list of land birds from Mexico that lacks any of these omnipresent taxa or has fewer than 35 species or 21 families is incomplete. Similar analyses can be done in other taxa and other parts of the world. Tests for "omnipresent" taxa and for a minimum number of species and families can be used in combination with other existing criteria, such as species richness functions, to better evaluate the completeness of species lists. Realistic results may be produced in macroecological and conservation only if they are based on reasonably complete species lists.

Resumen. Los estudios sobre diversidad, macroecología y conservación emplean listas de especies, pero en la literatura científica y en bancos de datos suelen estar mezcladas listas de especies completas e incompletas. El uso de datos heterogéneos puede generar resultados engañosos y es recomendable reconocer y eliminar las listas incompletas antes de llevar a cabo un análisis. Los estimadores de riqueza de especies son útiles para juzgar cuán completa es una lista determinada pero tienen limitaciones. Proponemos criterios adicionales: se pueden reconocer listas incompletas cuando les faltan taxones "omnipresentes" (especies, géneros y familias que ocurren en toda localidad de la región) y si contienen menos de cierto número mínimo de especies y familias. Por ejemplo, estudiamos ensamblajes de aves en diversos hábitats de México y encontramos que siete familias y dos géneros de aves terrestres son omnipresentes en México (excluyendo islas y hábitats desprovistos de árboles) y que la comunidad con menor riqueza conocida tiene 35 especies de aves pertenecientes a 21 familias. Concluimos que cualquier lista de aves terrestres de México que le falte alguno de estos taxones omnipresentes o tenga menor número de especies o familias se puede reconocer rápidamente como incompleta. Este conocimiento se puede emplear en combinación con otros criterios existentes para evaluar mejor qué tan completo está un inventario de especies. Sólo se podrán producir resultados realistas en estudios macroecológicos y de conservación si se basan en listas de especies razonablemente completas.

Introduction

Many conservation and macroecological studies depend on information derived from species lists (Remsen 1994; Blackburn & Gaston 1998). For example, a central theme of conservation studies is the identification of concentrations of species richness and endemism (Caldecott et al. 1998). A limitation of species lists available in the scientific literature is that they were made by field observers with different goals and levels of expertise and using different methods over variable lengths of time (Gaston 1996). The use of such heterogeneous data can produce misleading results (Kodric-Brown & Brown 1993). The species missing from incomplete data sets tend to be a nonrandom subset of the species in an assemblage, and their absence may therefore distort the analysis of macroecological patterns (Blackburn & Gaston 1998) or species richness (Remsen 1994). Faced with the alternative of discarding all data to avoid misleading results, it is important to be able to differentiate between seriously incomplete and relatively complete species lists so that only comparably complete data sets are used in analyses.

Species richness functions (e.g., asymptotic species-effort curves) are used to estimate the number of species in an area based on sampling performance. These functions can be used to estimate the degree of completeness of a given data set (Soberón & Llorente 1993; Colwell & Coddington 1994; Nichols et al. 1998). Their use has certain limitations, however. First, because different functions yield different extrapolations while fitting exceedingly well to the same data (Soberón & Llorente 1993), the different functions must have different types and degrees of error. Second, sampling bias and stochastic effects can cause richness functions to overestimate or underestimate species richness (Colwell & Coddington 1994: 107; Peterson & Slade 1998). Because the estimates are based on the same samples they attempt to evaluate, when the sampling process is biased the richness estimate will be biased (Gaston 1996). When sampling bias prevents detection of certain species, richness is underestimated and the species list is still not complete even though the estimators indicate it is. Thus, species richness estimators can not, by themselves, indicate that a species list is complete unless the sampling is unbiased and sufficient.

Furthermore, the only information available in past surveys is the taxonomic composition of the species list because the degree of completeness of the data set is usually not assessed and the information required to fit species richness functions (such as the pattern of species accumulation or the species-by-sample matrix) is unavailable. For most of the world, the information required to estimate species richness based on ecological factors (e.g., Pomeroy & Lewis 1983) does not exist.

Using Mexican land birds as an example, we sought to produce a set of criteria that could be used to evaluate completeness of species lists based on their taxonomic composition. First, we sought to produce a list of taxa that occur in every type of vegetation (except treeless habitats) and geographical region of mainland Mexico ("omnipresent taxa"). In this case, we considered omnipresent taxa those species present during at least some period of the year. Therefore, these specific results refer only to testing year-round, rather than seasonal, species lists. Because complete bird lists from Mexico were expected to include all omnipresent taxa, species lists lacking any of these taxa could be considered incomplete (Gómez de Silva 1993).

Secondly, because species richness is largely correlated with climate (Ricklefs & Schluter 1993), and the habitats with the harshest climates in a region can be expected to have the lower limit of species richness in that region, our second goal was to discover the number of species and families in the land bird assemblages from the harshest climates so that any species list with a lower number of species and/or families could be recognized as incomplete.

We restricted this study to habitats with more than four trees/ha because species from most bird families depend on "trees" for food and/or nesting (we considered *Yucca* and columnar cacti trees). We excluded bird assemblages from islands because they comprise only 0.27% of Mexico's land surface (Sánchez Molina 1985) and their taxonomic composition is modified by factors not ocurring on the mainland (e.g., water as a barrier to dispersal and colonization; Brown 1995). If we included islands and treeless areas, few or no taxa would turn out to be omnipresent, and the potential usefulness of this approach would be compromised. Likewise, we excluded anthropogenic habitats, which may be missing certain taxa and/or have a lower taxonomic richness due to factors not occurring in pristine habitats.

Methods

Test of omnipresence at a regional scale: step 1

We overlayed distribution maps of the species in each family, enabling us to list the taxa that are omnipresent at the regional spatial scale. We used the distribution maps and habitat descriptions of all Mexican land birds in Howell and Webb (1995; scale of maps roughly 1:40,000,000). Additional data were used in the few cases where published species lists cited in Rodriguez-Yáñez et al. (1994) include records ommitted by Howell and Webb (1995). Taxa mapped in an area but known to be restricted to a subset of the habitats in that area were not considered omnipresent. For example, the Blue Grosbeak (*Passerina caerulea*) was not considered omnipresent because, although it was mapped as occuring throughout Mexico, it was not known to occur in dense tropical rain forest or cloud forest. Species, genera, and families that seemed to be distributed in all types of vegetation throughout Mexico were considered to be potentially omnipresent at the regional scale. Swallows were tentatively included as omnipresent when their habitat during migration was described as "widespread" in Howell and Webb (1995).

Test of omnipresence in harsh climates: step 2

Each of the taxa identified as omnipresent in step 1 was hypothesized to be omnipresent at the local scale. We carried out surveys of species-poor bird assemblages (where any particular taxon was least likely to occur) because this would be the most rigorous test of omnipresence (i.e., the test most likely to falsify the hypothesis ["risky test" sensu Popper 1969]). A further advantage of studying depauperate assemblages was that the numbers of species and families in the most depauperate assemblage surveyed could be expected to be the lower limits of richness for Mexican land bird assemblages.

We chose three study areas in each of two climatic regimes: low temperature (mean annual temperature <12°C) and low rainfall (annual rainfall <500 mm). We selected areas that represented severe climatic conditions (Fig. 2). Study areas 1 and 2 are in two of the three regions of Mexico in which the difference between highest and lowest mean monthly temperatures exceed 20°C (Sánchez Molina 1985). We surveyed the birds found in areas of homogeneous vegetation of approximately 1 km^2. Areas much smaller than 1 km^2 contain incomplete samples of bird assemblages (Terborgh et al. 1990: 214) and therefore are not useful for many macroecological or conservation studies. If study areas are geographically clumped and share a large number of species, they would not be independent samples. Therefore, we chose study areas from each climatic regime as far apart as possible (Fig. 1) and as different in physiognomy as possible. The study areas are described below, with the names of vegetation associations following Brown (1982).

Study area 1 was a rocky desert containing ironwood (*Olneya tesota*), palo verde (*Cercidium microphyllum*), and scattered ocotillo (*Fouquieria* sp.) in Sierra de Las Pintas, Baja California (31°35.6'N, 115°06.5'W). Study area 2 was a rolling sandy desert with open mesquite scrub (*Prosopis glandulosa*) and scattered sagebrush (*Artemisia filifolia*) at El Bocán, Samalayuca, Chihuahua (31°20'N, 106°23.5'W). The mesquite are 1.5 m high on average, but a few trees reach a height of roughly 3.5 m. Annuals and grasses are scarce. Study area 3 was a mesquite-acacia-ocotillo-mixed succulent scrub (*Prosopis-Acacia farnesiana-Fouquieria-Opuntia-Hechtia*) in rocky, hilly country immediately south of Peña Blanca, Querétaro (21°16.47'N, 99°44.34'W). Study area 4 was pine-fir woodland (*Pinus jeffreyi-Abies concolor)* between 2600 and 2830 m above sea level in the Sierra San Pedro Mártir, Baja California (31°02.3'N, 115°28'W). Study area 5 was pine-oak forest (*Pinus-Quercus*), strongly dominated by pine, 1 km north of Batosárachi, Chihuahua (27°42.4'N, 107°34.95'W). It is moderately disturbed, with 3 small manmade clearings (0.15, 0.24 and 0.5 ha). Five species of birds restricted to these clearings were not here considered to belong to the forest bird assemblage and were excluded from the list: American Kestrel (*Falco sparverius*), Greater Roadrunner (*Geococcyx californianus*), Sulphur-bellied Flycatcher (*Myiodynastes luteiventris*), Dark-eyed Junco (*Junco hyemalis*), and Chipping Sparrow (*Spizella passerina*). Study area 6 was an open pine woodland (*Pinus hartwegii*) just below treeline in the northeast slope of the Nevado de Toluca volcano, state of México (19°07.5'N, 99°04'W).

HGdS identified birds by by sight and sound with the area search method (e.g., Crump & Scott 1994). We designed fieldwork to reduce the following common sources of bias in ornithological surveys. 1) The surveyor was familiar, prior to the fieldwork, with the visual field marks of all of the species and the principal vocalizations of 90% of them. 2) Each study area was surveyed during all seasons of the year. Each was surveyed for 30 days (5 days every 3 months from 21 March 1997 to 30 September 1998). During the first year, sites were sampled in order of increasing distance from Mexico City. In the last six months, visits were made in roughly the reverse order. 3) The sky and all layers of the vegetation were scanned purposely every 30 minutes or less. 4) Nocturnal birds were included in the survey. Although nocturnal birds usually vocalize in the final 15 minutes before sunrise and the first 15 minutes after sunset (Parker 1991; Gómez de Silva personal observation), during the present study observations usually began 1 to 2 hours before sunrise and ended 1 to 2 hours after sunset. Observations were usually not made during the middle 4 or 5 hours of the day when detectability of birds is generally lowest. 5) Accidental species were excluded (as recommended by Remsen [1994] and Gómez de Silva et al. [1999]). We defined accidentals as species that were recorded either flying nonstop over the study area (or stopped for < 5 minutes before continuing in the same direction), or were recorded on two days or fewer (<7% of the days spent at each study area). Cathartids, swifts, swallows, and soaring raptors were counted when they were known or suspected to be foraging. We used the species-level taxonomy of Howell and Webb (1995) and the family-level taxonomy of American Ornithologists' Union (1998).

Because we attempted to reduce sampling bias, the degree of completeness of the fieldwork was evaluated by using a species richness function (although even without sampling bias there may be error in richness estimates). We used an asymptotic value to estimate the numbers of species and families in each study area. We used was the Michaelis-Menten model because it provides a robust estimation (Chazdon et al. 1999) and was found to be the most accurate of seven richness estimators by Peterson & Slade (1998). The program EstimateS (Colwell 1997) with 50 randomizations of sample order was used to calculate the asymptotic value.

Species, genera, and families that occur in all six study areas were considered to be potentially omnipresent in the Mexican mainland at the 1 km^2 scale. We assumed that the lowest number of species and families in any of the study areas was the lowest number expected in a wooded Mexican locality.

Test of omnipresence in benign climates: step 3

Mexico has several vegetation types and comprises two biotic regions (Neotropical and Nearctic). To compensate for step 2's bias toward assemblages in harsh climates of the Nearctic Region, we reviewed species lists from biological research stations, most of which are in the Neotropical Region, with the assumption that the species lists of biological research stations are relatively complete. The seven biological research stations (Figs. 1 and 2) were: I) La Mancha (Ortiz-Pulido et al. 1995), II) Chamela (Arizmendi et al. 1990), III) Los Tuxtlas (Coates-Estrada & Estrada 1985), IV) Chajul (Rangel-Salazar 1990, Salgado-Ortiz 1993), V) Sian Kaán (López-Ornat 1990, Howell 1999), VI) Las Joyas (Contreras-Martínez and Santana Castellón 1995, García-Ruvalcaba et al. 1996), and VII) El Triunfo (Gómez de Silva et al. 1999). The first two are from tropical deciduous and semi-deciduous forest, the next two are from tropical rainforest, the fifth is from tropical semi-evergreen forest and the last two are from cloud forest.

Combining the results of the previous tests: step 4

The taxa identified as omnipresent by all three analyses (i.e., the intersection of the three sets of species) were considered truly omnipresent. These results were used to generate a list of features that every complete species list from the Mexican mainland should have. To test the usefulness of employing these features as criteria for detecting incomplete species lists, we used them to evaluate 150 published species lists cited in Rodríguez-Yáñez et al. (1994). Species lists found to be incomplete were then checked against recent data from the same localities, when available.

Results

Analysis of distribution and habitat data revealed that 21 families, 17 genera, and 7 species of land birds are regionally omnipresent in the Mexican mainland (excluding treeless areas, e.g., grasslands) (Table 1). Excluding accidentals, we recorded 151 species of birds in 38 families in the six study areas (Appendix) with between 21 and 25 families and between 35 and 60 species in each study area (Table 2). The richness estimator suggested that from 91.6 to 97.2% of the species and from 95.1 to 98% of the families were recorded by the end of the fieldwork (Table 2).

Eight families, three genera, and two species of land birds occured in all six study areas (Accipitridae, Strigidae, Trochilidae, Tyrannidae, Troglodytidae, Corvidae, Emberizidae, Parulidae, *Empidonax*, *Buteo jamaicensis*, and *Bubo virginianus*). One study area had the lowest number both of species (35) and families (21).

All taxa identified as omnipresent in step 2 of our methods were recorded in the seven biological stations except the family Emberizidae (absent in the forest interior at Los Tuxtlas Biological Station). Eleven families, 16 genera, and seven species of land birds identified as omnipresent in the regional-scale analysis (step 1) were not omnipresent in the local-scale analyses (steps 2 and 3). On the other hand, the two species found in all six study areas were not considered potentially omnipresent in the regional-scale analysis (i.e., their ranges do not encompass all of Mexico), although the genus of one of these (*Buteo*) was considered regionally omnipresent. When the results of the regional-scale and local-scale analyses were combined, only seven families, two genera and no species of land birds were omnipresent (Table 3, numbers 1 and 2). Analysis of species lists from additional parts of Mexico (Gómez de Silva and Medellín, unpublished data) were consistent with the omnipresence of these taxa within Mexico. Strictly speaking, no omnipresent family, genus, or species was a permanent resident throughout Mexico (Corvidae and Troglodytidae nearly are, but they were absent in study area 1 during dry summers).

Results of the local-scale and regional-scale analyses suggest that other features of Mexican land bird assemblages could be used to differentiate between incomplete and complete species lists. Eleven families and seven genera identified as potentially omnipresent in the regional-scale analysis were present in all but one or two study areas/biological stations: Cathartidae, Falconidae, Caprimulgidae, Apodidae, Picidae, Hirundinidae, Turdidae, Regulidae, Vireonidae, Emberizidae, Cardinalidae, *Vermivora*, *Accipiter*, *Falco*, *Contopus*, *Vireo*, *Dendroica*, and *Icterus*. No study area lacked more than five of the above families or more than four of the above genera. Also, no study area lacked both Apodidae and Hirundinidae: either one or both of these families were present in all study areas. Furthermore, a broader analysis of an additional 64 well-surveyed localities representative of the range of climatic conditions found in Mexico revealed that these additional families were missing only from regions with certain climatic conditions (Gómez de Silva unpublished data). Our results suggest 10 criteria that can be used to recognize potentially incomplete species lists of land birds in Mexico at or above the scale of 1 km^2 (Table 3). Table 4 provides examples of published species lists recognized as incomplete to illustrate the use of these criteria.

We predicted the ocurrence of certain genera and families anywhere in Mexico based on the criteria in Table 3. These predictions were corroborated for two localities (Laguna Ocotal and Temascaltepec) when these localities were re-surveyed and the "missing" taxa were detected. Gómez de Silva (1997) found 60 species in Temascaltepec that had not been recorded by Ornelas et al. (1988), including several species belonging to the two "missing" omnipresent groups (Accipitridae and diurnal high- flying insectivores). Likewise, the published species list from Laguna Ocotal (Paynter 1957), even though relatively rich in species and families (121 species in 37 families), lacked high-flying diurnal insectivores, *Buteo* and Strigidae. A brief survey in July 1994 (Gómez de Silva, unpublished data) found 30 species that had not been reported there previously, including representatives of the "missing" omnipresent groups.

The scientific literature contains further examples that corroborate the prediction that the taxa listed in Table 3 are omnipresent in Mexico. In La Pesca, Howell (1999) found 107 species that Baker and Fleming (1962) had not recorded, including species from the three "missing" omnipresent groups. Paynter (1952) reported a number of bird species from the high-elevation Paso de Cortez area of central Mexico, but his list lacked Accipitridae and high-flying diurnal insectivores, that were reported subsequently from the same locality by Edwards (1968) and Amadon & Eckleberry (1955). Burleigh and Lowery's (1942) list of bird species from the pine woodlands of southeastern Coahuila lacked Strigidae, three species of which were found by Ely (1962). Alden's (1969) list of birds from tropical deciduous forest and desert around Alamos, Sonora, lacked Caprimulgidae, but Short (1974) subsequently recorded two species of Caprimulgidae from this area. Sutton and Burleigh (1940) did not record any Trochilidae at Valles, San Luis Potosi, but Edwards (1976) subsequently recorded one species. These cases strengthen the deduction that the taxa listed in Table 3 are omnipresent and that the lack of any of them indicates that an incomplete species list.

Discussion

A list of omnipresent taxa depends on the taxonomy used. Nevertheless, while the family placement of certain bird species is still controversial (e.g., some species listed as Emberizidae in American Ornithologists' Union [1998] may belong in Thraupidae; Sibley & Monroe 1990), even when these controversial species are removed from consideration the taxa in Table 3.1 retain their omnipresence. Therefore, such taxonomic controversies do not affect the list of birds omnipresent in the Mexican mainland..

The reason many species lists of Mexican birds (Table 4) are incomplete may be the timing of fieldwork (e.g., the area was surveyed only during one period of the year), amount of effort (e.g., short surveys), field technique (e.g., surveys that rely almost entirely on mist net captures detect only a portion of the birds in any area; Terborgh et al. 1990; Contreras-Martínez & Santana Castellón 1995), lack of expertise, or a combination of factors. Because few published papers on Mexican birds (and none of the papers cited in Table 4) state how data were collected or whether certain groups (e.g., nocturnal birds, high-flying birds) were properly surveyed, only application of criteria such as those in Table 3 can uncover their incompleteness.

Having complete species lists may not be necessary for certain studies. Some lists are useful for conservation or other purposes even if they lack certain groups of birds (e.g., nocturnal birds may be lacking because many ornithologists do not do fieldwork at night). Complete species lists, however, are important for greater accuracy in studies that use species richness or composition as indicators of conservation priority, such as those that use reserve selection algorithms or gap analysis (Remsen 1994; Conroy & Noon 1996; Prendergast et al. 1999). Complete species lists are also necessary in most studies of macroecology and community structure (Kodric-Brown & Brown 1993; Blackburn & Gaston 1998; Foote & Sepkoski 1999). In conservation biology, having complete inventories should be a priority for certain regions, such as protected areas.

The evaluation criteria in Table 3 can probably be applied to species lists from areas adjacent to Mexico, at least from Panama to the southern United States, because these areas possess all the taxa omnipresent in Mexico and have similar climates, vegetation, and bird assemblages. It is possible to generate analogous criteria for other parts of the world. Focusing on omnipresent taxa and minimum number of species and families has the advantage over other tests of completeness that it can be used to identify critical areas or periods of the year that need further survey work to produce a more comprehensive list. This approach can be used to recognize incomplete lists whether they result from insufficient field effort, which species richness functions would also permit recognizing, or from bias in field methods, in which case species richness estimators would not help. Bias in field methods can be detected (and sometimes corrected) by considering omnipresent taxa. For example, if it is noticed that fieldwork is not detecting nocturnal birds, raptors, high-flying insectivores, or certain families whose species tend to be canopy dwellers, such as occurs when only birds captured in mist nets are recorded, the bias can be detected and the unrecorded birds can be searched for actively.

There is evidence that a species list from mainland Mexico is incomplete if the list lacks one or more features in Table 3. On the other hand, fulfilling those criteria is not full proof that a species list is complete. For example, just as the species lists for Temascaltepec, Laguna Ocotal, and La Pesca were missing species not only in a few omnipresent families and foraging guilds but also in other families, lists for other localities may be incomplete even though they contain at least one species from all omnipresent groups. Additional tests of completeness would be necessary to claim that a species list is reasonably complete, drawing on the advantages of each method. Such additional tests include species richness functions based on sampling (Bunge & Fitzpatrick 1993; Hodkinson & Hodkinson 1993; Colwell & Coddington 1994; Nichols et al. 1998), estimating species richness from ecological parameters (e.g., Pomeroy & Lewis 1983) and subjective comparison with species lists from similar, nearby areas (e.g., Gómez de Silva 1997). Provided identification is correct, the documented presence of a species is strong evidence of presence, whereas the failure to document presence is not strong evidence of absence unless sufficient criteria are met to justify the relative completeness of the species list.

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Table 1. Families, genera, and species of birds potentially omnipresent in Mexico (regional-scale analysis). Families marked with an asterisk were based on distribution data in addition to Howell and Webb (1995).

Family	Genus and/or species
Cathartidae	*Cathartes aura*
Accipitridae	*Accipiter*
	Buteo
Falconidae	*Falco*
Columbidae	
Cuculidae*	
Strigidae	
Caprimulgidae	
Apodidae*	
Trochilidae	
Picidae	
Tyrannidae	*Empidonax*
	Contopus
Vireonidae	*Vireo*
Corvidae*	
Hirundinidae	*Riparia riparia*
	Petrochelidon pyrrhonota
	Hirundo rustica
	Progne subis
Troglodytidae	
Sylviidae	*Polioptila*
Turdidae	*Catharus ustulatus*
Parulidae	*Vermivora*
	Wilsonia pusilla
	Dendroica
Emberizidae	
Cardinalidae	
Icteridae	*Icterus*

Table 2. Sampling performance and number of bird species and families in the six study areas in harsh habitats in Mexico.

Study area habitat type	Number of species observed	Estimated number of species recorded (%)	Number of families observed	Estimated number of families recorded (%)
1.desert	43	91.6	25	95.1
2.desert	48	92.3	24	97.2
3.desert	48	96	25	97.7
4.pine-fir	35	97.2	21	97.7
5.pine-oak	60	95.2	25	98
6.pine	43	95.6	22	96.9

Table 3. Features that indicate that a species list of land birds from the Mexican mainland (excluding treeless areas) is incomplete*.

1. Lacks species in any of the following families or genera: Accipitridae, Strigidae, Trochilidae, Tyrannidae, Troglodytidae, Corvidae, Parulidae, *Buteo*, and *Empidonax*.
2. Lacks species in more than five of the following families: Cathartidae, Caprimulgidae, Apodidae, Picidae, Hirundinidae, Turdidae, Vireonidae, Thraupidae, Emberizidae, Cardinalidae, and Icteridae.
3. Lacks species in more than four of the following genera: *Accipiter*, *Falco*, *Contopus*, *Vireo*, *Vermivora*, *Dendroica*, and *Icterus*.
4. Lacks diurnal high-flying insectivores.
5. Lacks Cathartidae (does not apply to localities with mean annual temperature < approximately 6°C).
6. Lacks Apodidae, Picidae, Hirundinidae, Vireonidae, Thraupidae and/or Cardinalidae (does not apply to localities with < approximately 500 mm mean annual precipitation).
7. Lacks Thraupidae, Cardinalidae and/or Icteridae (does not apply to forests with mean annual temperature less than approximately 14° and annual precipitation less than approximately 1000 mm, or with mean annual temperature less than approximately 21°C and annual precipitation greater than approximately 2000 mm).
8. Lacks Emberizidae (does not apply to tropical wet forest [sensu Holdridge 1947]).
9. Contains fewer than 35 species.
10. Contains fewer than 21 families.

*Most features apply to localities anywhere in Mexico. Features 4 to 7 have certain exceptions, as stated.

Table 4. Examples of published species lists of Mexican land birds determined incomplete based on features given in Table 4.

Location	evidence of incompleteness	Reference
Pine woodlands, Pico de Orizaba	contains only 17 families, does not include Accipitridae	Cox 1895
Barranca del Cobre, Chihuahua	does not include *Buteo*	Stager 1954
Barranca de Oblatos, Jalisco	does not include *Buteo*	Selander and Giller 1959
Lacanjá-Chansayab, Chiapas	does not include Strigidae	Nocedal 1981
Veintiuno de Marzo, Chiapas	does not include Strigidae	University of East Anglia 1990
Northwestern Baja California	does not include Strigidae	Short and Banks 1965
Sierra de Antonez, Sonora	does not include Strigidae, *Empidonax* or, despite temperate climate, Cathartidae	Thayer and Bangs 1906
Laguna El Rosario, Baja California	does not include Strigidae or *Empidonax*	Ruiz-Campos and Rodríguez-Meraz 1993
Pinus-Juniperus-Larrea vegetation in El Tokio, Nuevo León	does not include Strigidae, *Empidonax* or Parulidae	Contreras-Balderas 1992
Boca del Río, Veracruz	does not include *Empidonax*	Warner and Mengel 1951
Sierra de Tamaulipas	does not include *Empidonax*	Martin et al. 1954
Zoquiapan, state of México	does not include Tyrannidae	Maass et al. 1981
Yucca-Larrea vegetation in El Tokio, Nuevo León	does not include Trochilidae	Contreras-Balderas 1992
Mapimí, Durango	does not include Parulidae	Thiollay 1979, 1981
Río Hondo, Quintana Roo	does not include Cathartidae or Apodidae despite tropical humid climate	Peters 1913
La Tuxpeña, Campeche	does not include Cathartidae despite tropical humid climate	Storer 1961
San José Carpizo, Campeche	does not include Cathartidae or Apodidae despite tropical humid climate	Storer 1961
La Pesca, Tamaulipas	does not include Trochilidae, Parulidae or diurnal high-flying insectivores	Baker and Fleming 1962
Laguna Ocotal, Chiapas	does not include *Buteo* or Strigidae	Paynter 1957
Temascaltepec, state of México	does not include Accipitridae or diurnal high-flying insectivores	Ornelas et al. 1988

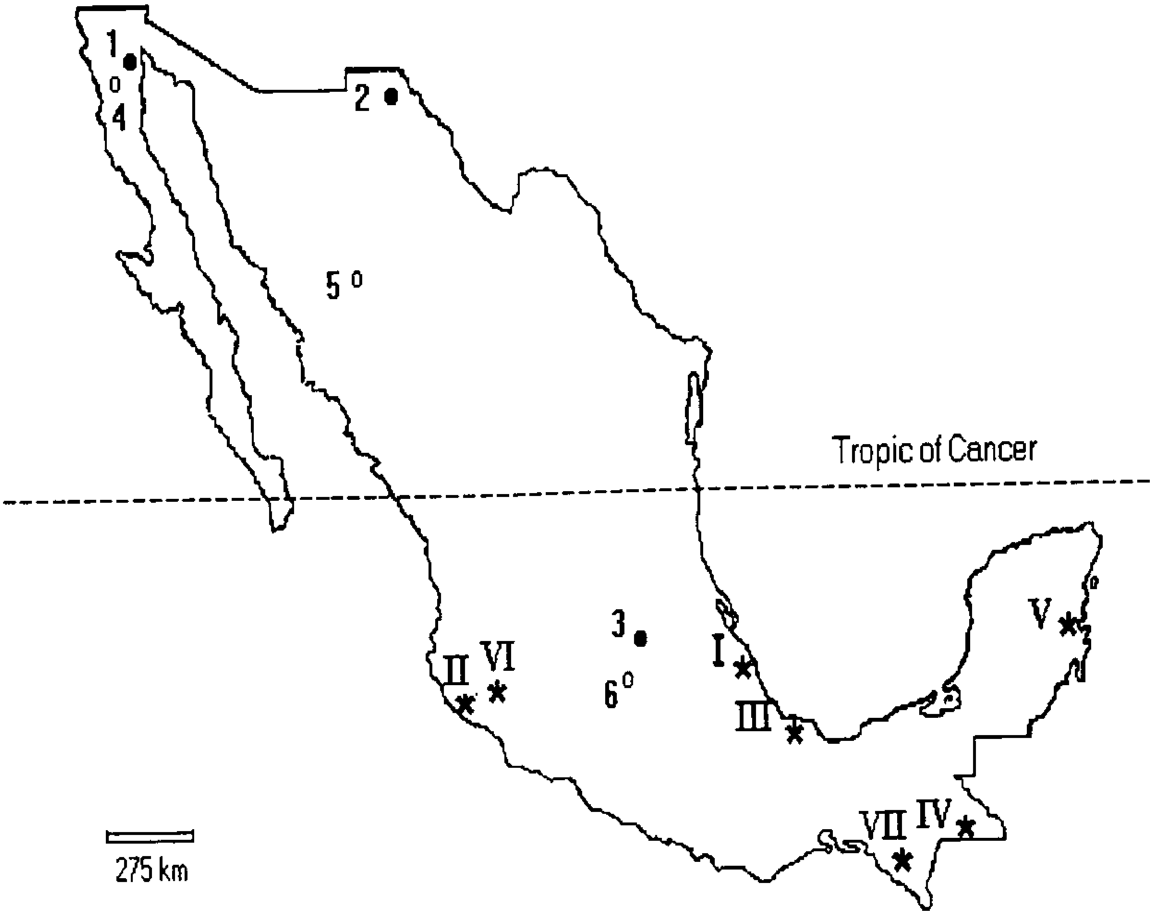
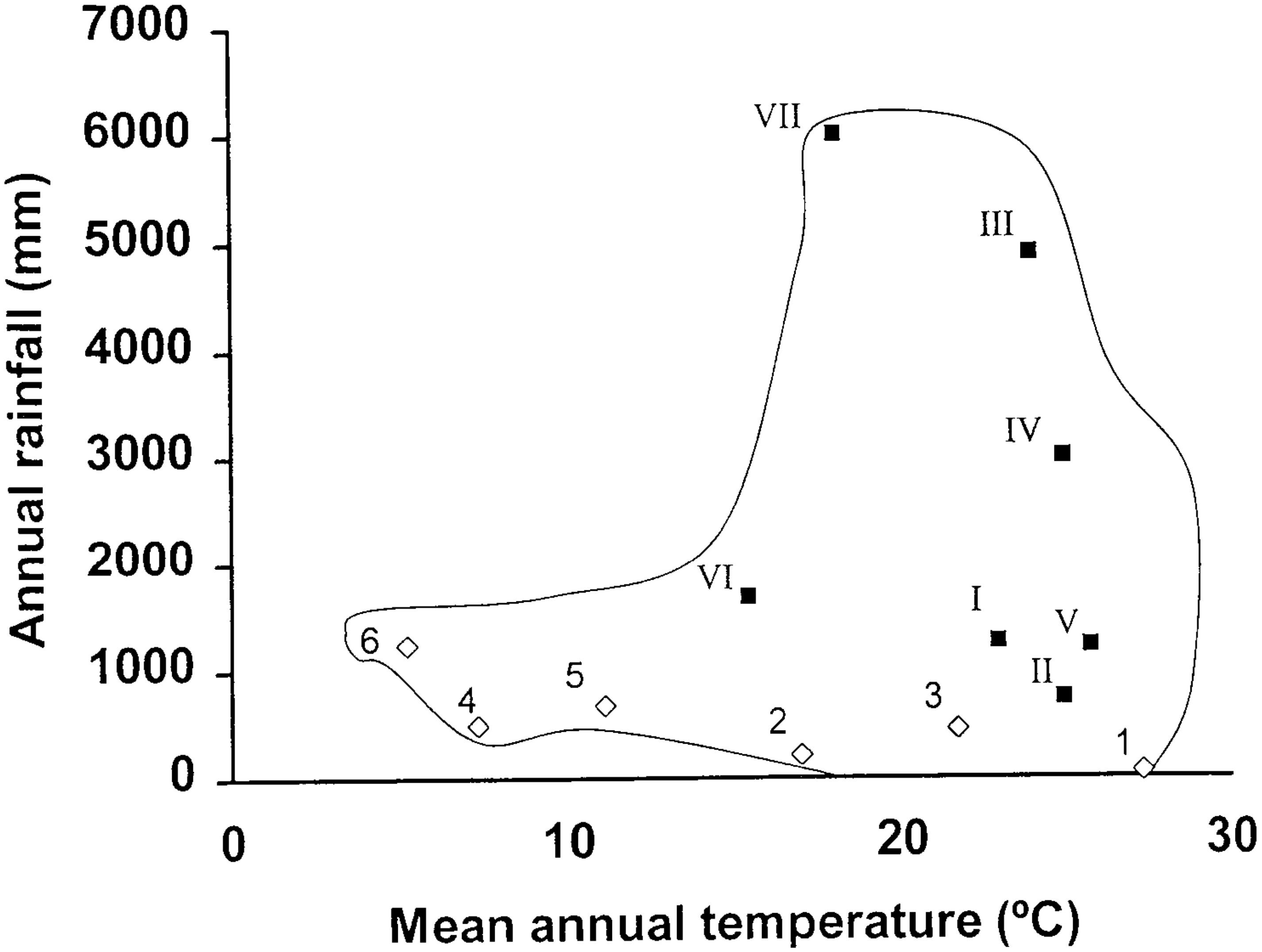


Figure 1. Geographic location of the six study areas and the seven biological stations. Filled circles are low-rainfall study areas, empty circles are low-temperature study areas, and asterisks are biological stations.

Figure 2 (next page). Mean annual temperature versus annual rainfall for the six study areas and the seven biological stations. The solid line encloses the parameter space occupied by 1828 weather stations in Mexico (García 1987). Temperature and rainfall data are based on the nearest weather station in García (1987) except for study area 1 (Juan Carlos García, pers. comm.), study area 4 (Álvarez & Maisterrena 1977, Álvarez 1983) and biological station VII (S. Solórzano, pers. comm.).


7000
6000
5000
4000
3000
2000
1000
0
Annual rainfall (mm)
0
10
20
30
Mean annual temperature (°C)
VII
III
IV
VI
I
V
II
6
5
4
2
3
1

Appendix. Families, genera, and species recorded in six harsh habitats in Mexico (taxonomy follows Howell & Webb [1995]).

Family	**Species**	**Study area**					
		1	2	3	4	5	6
Cathartidae	*Coragyps atratus*					x	
	Cathartes aura	x	x	x	x	x	
Accipitridae	*Circus cyaneus*		x				
	Accipiter striatus		x			x	x
	Accipiter cooperi					x	
	Buteo swainsoni		x				
	Buteo albonotatus					x	
	Buteo jamaicensis	x	x	x	x	x	x
Falconidae	*Falco sparverius*	x					x
	Falco columbarius						x
	Falco peregrinus				x		
Odontophoridae	*Callipepla squamata*		x	x			
	Callipepla gambelli		x				
	Callipepla picta				x		
Columbidae	*Zenaida asiatica*			x			
	Zenaida macroura	x	x	x			
	Columbina inca			x			
	Columbina passerina			x			
Cuculidae	*Geococcyx californianus*		x	x			
Tytonidae	*Tyto alba*	x	x				
Strigidae	*Otus kennicottii*	x				x	
	Otus trichopsis					x	
	Bubo virginianus	x	x	x	x	x	x
	Glaucidium gnoma						x
	Micrathene whitneyi			x			
	Athene cunicularia		x				
Caprimulgidae	*Chordeiles acutipennis*		x				
	Chordeiles minor		x				
	Phalaenoptilus nuttalli		x			x	
	Caprimulgus arizonae					x	x
Apodidae	*Cypseloides niger*					x	x
	Aeronautes saxatalis	x		x	x	x	x
Trochilidae	*Colibri thalassinus*						x
	Cynanthus latirostris			x			
	Basilinna leucotis					x	x
	Lampornis clemenciae						x
	Archilochus sp.		x				

	Archilochus colubris			x			
	Archilochus anna				x		
	Archilochus costae	x					
	Selasphorus platycercus		x			x	x
	Selasphorus rufus				x		
Trogonidae	*Euptilotis neoxenus*					x	
Picidae	*Sphyrapicus varius* (sensu lato)					x	
	Sphyrapicus thyroideus				x	x	
	Picoides scalaris		x	x			
	Picoides villosus				x	x	
	Picoides stricklandi						x
	Colaptes auratus				x	x	x
Tyrannidae	*Camptostoma imberbe*			x			
	Contopus borealis				x		
	Contopus pertinax					x	x
	Contopus sordidulus	x	x		x	x	
	Empidonax minimus			x			
	Empidonax hammondii		x				x
	Empidonax wrightii		x	x			
	Empidonax affinis					x	
	Empidonax difficilis (sensu lato)	x			x	x	
	Sayornis saya	x	x	x			
	Myiarchus cinerascens	x	x	x			
	Tyrannus verticalis		x				
Hirundinidae	*Tachycineta thalassina*			x	x	x	x
	Stelgidopteryx serripennis			x			
	Hirundo pyrrhonota		x				
	Hirundo rustica			x			
Corvidae	*Cyanocitta stelleri*					x	x
	Aphelocoma coerulescens				x		
	Gymnorhinus cyanocephalus				x		
	Nucifraga columbiana				x		
	Corvus cryptoleucus		x	x			
	Corvus corax	x			x	x	
Paridae	*Parus sclateri*					x	x
	Parus gambeli				x		
Remizidae	*Auriparus flaviceps*	x	x	x			
Aegithalidae	*Psaltriparus minimus*					x	
Sittidae	*Sitta carolinensis*				x	x	x
	Sitta pygmaea				x	x	x
Certhiidae	*Certhia americana*					x	x

Troglodytidae	*Campylorhynchus brunneicapillus*		x	x			
	Salpinctes obsoletus	x		x			
	Catherpes mexicanus			x	x	x	
	Thryomanes bewickii	x	x	x		x	
	Troglodytes aedon (sensu lato)			x	x	x	x
Regulidae	*Regulus calendula*	x	x		x	x	x
Sylviidae	*Polioptila caerulea*	x	x	x			
	Polioptila melanura	x	x	x			
Turdidae	*Sialia mexicana*				x		x
	Myadestes townsendi					x	
	Catharus occidentalis						x
	Catharus ustulatus	x					
	Catharus guttatus					x	x
	Turdus migratorius					x	x
Timaliidae	*Chamaea fasciata*				x		
Mimidae	*Mimus polyglottos*	x	x	x			
	Oreoscoptes montanus		x				
	Toxostoma curvirostre			x			
	Toxostoma crissale		x				
Ptilogonatidae	*Phainopepla nitens*	x		x			
Laniidae	*Lanius ludovicianus*	x	x	x			
Vireonidae	*Vireo solitarius* (sensu lato)				x	x	
	Vireo huttoni					x	x
	Vireo gilvus	x					
Parulidae	*Vermivora celata*	x		x		x	x
	Vermivora ruficapilla	x		x			
	Vermivora superciliosa					x	
	Dendroica petechia	x					
	Dendroica coronata	x				x	x
	Dendroica nigrescens				x	x	
	Dendroica townsendi	x				x	x
	Dendroica occidentalis				x	x	
	Dendroica graciae					x	
	Oporornis tolmiei	x	x				
	Wilsonia pusilla	x	x			x	
	Cardellina rubrifrons					x	
	Ergaticus ruber						x
	Myioborus pictus					x	
	Myioborus miniatus					x	
Peucedramidae	*Peucedramus taeniatus*					x	x
Thraupidae	*Piranga flava*			x		x	

	Piranga ludoviciana	x					
Cardinalidae	*Cardinalis cardinalis*			x			
	Cardinalis sinuatus		x	x			
	Pheucticus melanocephalus	x				x	
	Passerina caerulea		x				
	Passerina versicolor			x			
Emberizidae	*Pipilo chlorurus*		x	x			
	Pipilo erythropthalmus				x	x	x
	Diglossa baritula						x
	Aimophila ruficeps			x			
	Oriturus superciliosus						x
	Amphispiza bilineata	x	x				
	Amphispiza belli		x				
	Spizella passerina	x	x				
	Spizella pallida		x				
	Spizella breweri		x				
	Chondestes grammacus			x			
	Calamospiza melanocorys		x				
	Ammodramus sandwichensis	x					
	Melospiza lincolnii	x					x
	Zonotrichia leucophrys	x					
	Junco hyemalis				x		
	Junco phaeonotus					x	x
Icteridae	*Icterus bullockii*	x					
	Icterus parisorum		x	x			x
Fringillidae	*Carpodacus cassinii*				x		
	Carpodacus mexicanus	x		x			
	Loxia curvirostra						x
	Carduelis pinus				x	x	x
	Carduelis psaltria	x		x	x		
	Carduelis lawrencei	x					
	Coccothraustes vespertinus					x	x
Passeridae	*Passer domesticus*			x			

Capítulo II

ARE LANDBIRD ASSEMBLAGES FUNCTIONALLY SATURATED?: AN EMPIRICAL TEST IN MEXICO

(enviado a *Oikos*)

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ABSTRACT

According to the model of ideal free distribution, few or no assemblages will contain unused resources, as long as species are free to colonize areas where resources are available. Consequently, because several food resources for birds are available throughout Mexico (nectar, seeds and fruits, vertebrates, carrion and different types of invertebrates), we predicted that all assemblages from Mexico contain birds from the corresponding foraging guilds. However, severe climates may prevent colonization by certain birds. Thus, a second prediction was that, if assemblages with unused resources were found, these would be from localities with climates that pose extreme physiological stress to birds (either extremely high temperature and low rainfall, or extremely low temperature). We tested these predictions on bird assemblages from 77 localities that represent the entire range of climatic conditions found in Mexico. Only two assemblages containing unused resources were found. These were from the localities with lowest temperature and lowest rainfall, respectively. We observed that land bird assemblages in Mexico do not contain unused resources, except when climate selectively restricts colonization by species from certain foraging guilds. Therefore, we conclude that even assemblages with almost no species in common have a common guild structure based on food resources. Null models of competition would be more realistic if they were to incorporate such patterns that result from noncompetitive mechanisms.

INTRODUCTION

Ecological community theory attempts to explain community composition based on "assembly rules" that link resource use by species from a regional species pool with resource availability (Brown 1981; Haefner 1981, 1988; Pulliam 1983). The basic premise of these studies is that any community in an environment containing unused resources will either tend to be invaded by a species able to harvest that resource (Fox and Brown 1995) or, if such a species does not exist, natural selection will cause selection pressure for such a species to evolve (Darwin 1872: 235; Benton 1983). The resulting pattern of species richness has been described as the tendency for communities to be saturated (e. g., Terborgh and Faaborg 1980).

This premise is an extension of optimization theory in ecology (MacArthur and Pianka 1966; Rosen 1967) and of the "ideal free distribution" model of population dynamics (Fretwell and Lucas 1970). This model states that species' population density tend to match resource availability. When extended to communities, the ideal free model can be considered an assembly rule because it produces a predictable, nonrandom pattern of community composition: every community containing a resource will tend to contain one or more species from the species pool that are capable of utilizing that resource. Using the terminology of Haefner (1981, 1988), this assembly rule would be considered an "insertion rule."

Studying saturation from the point of view of number of species alone may mask important ecological information that can be complemented by focusing on functional groups (Wiens 1989: 156). Communities with the same number of species can be ecologically different if one has many functional groups with few species and the other has few functional groups with many species (Huston 1994: 4). Compared with a community that contains x species in y functional groups, a community that contains x species in z functional groups will be functionally unsaturated if $z<y$.

The ideal free assembly rule predicts that communities tend to be functionally saturated, but functionally unsaturated assemblages sometimes occur in nature (e.g., Price 1984; Cornell and Kahn 1989; Lawton *et al.* 1993; Cornell 1999). Circumstances that may prevent community saturation include geographic barriers, low dispersal ability that may limit invasion by potential colonists, and insufficient time for colonization since a resource has become available (Strong *et al.* 1984: 113). Climate may function as a physiological constraint preventing establishment of potential colonists (Root 1988a, 1988b, 1989).

Because case-studies are necessary to understand the circumstances under which unsaturated communities occur (Wiens 1984, 1989), we tested the predictions of the ideal free assembly rule among land bird assemblages in mainland Mexico, considering functional groups based on foraging guilds. Because tests of functional saturation focus on resource presence, the classification of functional groups we used is based on resource type, as in the guild concepts of MacMahon *et al.* (1981) and Jaksic (1981), rather than on resource use as in Remsen and Robinson (1990). Guilds can be delimited at different scales of resolution (Terborgh and Robinson 1986). At the finest scale, each species belongs in its own guild; however, coarsely delimited guilds, as used here, are useful for understanding community structure (Terborgh and Robinson 1986; Wiens 1989: 162), with the advantage that generalizations can be made in intercommunity comparisons (Steneck and Dethier 1994; Weiher and Keddy 1995).

The assumptions of this analysis are that dispersal ability is not a significant limiting factor among land birds on the mainland, and that certain broad classes of food resources are available throughout Mexico: flower nectar, seeds and fruits, vertebrates, carrion, flying insects, invertebrates that live inside wood, and invertebrates that move on the ground, under bark and among foliage. These assumptions are justified because, based on the distribution maps and habitat descriptions in Howell and Webb (1995), one or more species from every foraging guild can be considered present in the ecological species pools (*sensu* Kelt *et al.* 1995) of every assemblage in Mexico. Therefore, we predicted that birds from all foraging guilds occur in every locality in mainland Mexico. Because climate potentially produces unsaturated assemblages, a second prediction was that unsaturated assemblages (if any) would be from localities with climates that pose extreme physiological stress to birds, namely, localities with extremely low rainfall, or with extremely high or low temperature.

METHODS

We tested these predictions by using species lists of land birds from 77 localities that represent the entire range of climatic conditions found in Mexico. We searched in the scientific literature about Mexican birds for complete lists of co-ocurring bird species (i.e., assemblages) and determined the foraging guilds existing in each list. We carried out fieldwork in six localities with severe climatic conditions (either extremely low rainfall and high temperature, or extremely low temperature). The probability of finding saturated assemblages in all six localities if there were no guild assembly rule (i.e., if the real world had an equal number of assemblages with 1, 2, 3, ... 12 guilds), based on the multinomial hypergeometric distribution (Ross 1993) was 0.00000335. Because unsaturated assemblages were found, we tested 1) the probability that this result would be due to chance by calculating the multinomial hypergeometric probability that a sample of six localities would produce the result we found, and 2) whether the unsaturated assemblages were correlated with severe climatic conditions by plotting the values of mean annual temperature and annual rainfall for all assemblages.

LITERATURE SEARCH

We examined all species lists cited in Rodríguez-Yáñez *et al.* (1994) and Howell and Webb (1995), and other publications and unpublished theses (see APPENDIX). We did not employ species lists from large and/or heterogeneous regions because spatial heterogeneity can cause a list to include species that do not interact with the rest (therefore, not describing a real ecological assemblage). We also did not employ species lists from islands to avoid the influence of factors in addition to those ocurring on the mainland (e.g., water as a barrier to dispersal and colonization, Brown 1995). Furthermore, we compared species lists with similar or nearby areas, and applied the criteria listed in Gómez de Silva and Medellín (in press), to recognize incomplete species lists. Because of the lack of complete species lists from certain regions and habitat types (temperate forest in the northern Sierra Madre Occidental and thorn forest in Tamaulipas), we used species lists from two localities in the United States that are less than 15 km from the Mexican border (Coronado National Monument and Santa Ana National Wildlife Refuge). We restricted the analysis to diurnal land birds because nocturnal birds are underrecorded in the scientific literature and may in fact be present in localities where they have not been reported.

FIELDWORK

We chose six study areas with severe climates (Table 1, Figure 1). We surveyed areas of homogeneous vegetation measuring approximately 1 km^2 to ensure that all the species potentially interact (thereby conforming to the definition of ecological community, Wiens 1989). Each study area was surveyed during 30 days (five days every three months from 21 March 1997 to 30 September 1998). During the first year, localities were sampled in order of increasing distance from Mexico City. In the last six months, visits were made in roughly the reverse order. Birds were identified by sight and sound by the first author employing the "area search" method (e.g., Crump and Scott 1994). This observer was already familiar with the appearance of all of the species and the principal vocalizations of 90% of them prior to the fieldwork. Observations began before sunrise and ended after sunset but generally were not made during the hottest hours of the day (the 4 or 5 hours around the time of solar zenith). Following Remsen (1994) and Gómez de Silva *et al.* (1999), accidental species were excluded because they did not significantly influence biotic interactions within the community, therefore not truly belonging in the assemblage (though they may have an important role in evolutionary time scales; Grinnell 1922, Veit 2000). The criteria used to exclude these species were similar to those of Gómez de Silva *et al.* (1999); namely, species were eliminated when they were either flying nonstop over the study area (or stopped for less than 5 min before continuing in the same direction) or were recorded on two days or fewer (<7% of the days spent at each study area). Because the goal was to record all the foraging guilds represented in each study area, the degree of completeness of the fieldwork was evaluated by using a species richness function, the Michaelis-Menten model, with foraging guilds in the place of species. We used the asymptotic value to estimate the number of foraging guilds in each study area and compared it with the number that actually was recorded. The Michaelis-Menten model provided a robust estimation (Chazdon *et al.* 1999) and was found to be the most accurate of seven richness estimators by Peterson and Slade (1998) based on evaluation of bias, spread and maximum deviation. The program EstimateS (Colwell 1997) with 50 randomizations of sample order was used for the calculation.

ASSIGNING BIRDS TO FORAGING GUILDS

Bird species were assigned to foraging guilds using descriptions in Alvarez del Toro (1980), Ehrlich *et al.* (1988), Stiles and Skutch (1989), Robinson (1984), Sick (1993), Howell and Webb (1995), Poole *et al.* (1992-1998) and del Hoyo *et al.* (1992-1999). We classified Mexican diurnal land birds into 12 foraging guilds that feed on five main resource types (Table 2). The foraging guilds used here were adapted from Terborgh *et al.* (1990). Foraging substrate was used to subdivide each guild type when possible. Due to the focus on resource type, frugivores (seed dispersers) and granivores (seed predators) were classified in the same foraging guild, since a fruit is extracted from the plant whether a bird is after the seeds or the pulp. The heterogeneous guild "omnivores" was not considered because the term does not indicate the types of food resources used. Instead, some species were assigned to more than one guild. For example, the Ladder-backed Woodpecker (*Picoides scalaris*) was classified both as a bark-gleaning and a wood-boring insectivore (Austin 1977), and most members of Emberizidae were assigned both to the guild of terrestrial insectivores and that of terrestrial granivores. Similarly, certain *Vermivora* warblers were classified as diurnal foliage-gleaning insectivores, dead-leaf searching insectivores and nectarivores (*e.g.*, Remsen *et al.* 1989). This was because these food categories are being used significantly wherever these species occur. On the other hand, many birds occasionally eat a type of food not

Table 1. Description of localities where fieldwork was carried out. The first three are xeric and the last three are cold areas. Areas 1 and 2 are considered to have extreme climates (difference between highest and lowest mean monthly temperature more than 20°C; Sánchez Molina 1985). Unless otherwise stated, temperature and rainfall data are from García (1987). Vegetation associations are described following Brown (1982).

Site	Elevation (m)	Mean annual rainfall (mm)	mean monthly rainfall (range)	number of months < 10 mm	mean annual temperature (°C)	mean monthly temperature (range)	number of months < 10°C
1	100-220	*c.*56	c.0.1-13.3	10-12	27.4	20.8-36	0
2	1250	212.8	4.7-46	5	17	6.9-27.5	3
3	1400-1460	456.3	4.4-82.3	3	21.7	17.3-25.1	0
4	2600-2830	*c.*500	no data	no data	7.3	-1.5-16.3	7
5	2380-2420	673.3	8.8-171.0	1	11.1	5.0-17.6	5
6	3750-4000	1243.5	17.2-270.0	0	*c.*5.2	*c.*3.8-6.8	12

1. Rocky desert comprised mainly of poorly vegetated mountains, Sierra de Las Pintas, Baja California (31°35.6'N, 115°06.5'W). Washes contain ironwood (*Olneya tesota*) and palo verde (*Cercidium microphyllum*) trees, with scattered ocotillo (*Fouquieria* sp.) on some slopes. One wash has cut banks up to 10 m deep. A few small rock pools form when rainfall is significant (not every year). Temperature records made 0.7 km away from the study area from January 1996 to June 1998 (Juan Carlos García, personal communication). Rainfall data from the nearest weather stations ("El Mayor" and "San Felipe," 60 km north-northwest/95 m lower and 68 km south-southeast/90 m lower, repectively). Surrounding vegetation consists of similarly arid desert to the northeast, north, west and southwest and open scrubby woodland of ironwood and palo verde to the south and east. Other than the limited facilities of the San Felipe Mining Company, the nearest human habitation is La Ventana, 18 km away.

2. Rolling sandy desert with open mesquite scrub (*Prosopis glandulosa*) and scattered sagebrush (*Artemisia filifolia*), El Bocán, Samalayuca, Chihuahua (31°20'N, 106°23.5'W). The mesquite are 1.5 m high on average, but a few trees reach a height of roughly 3.5 m. Annuals and grasses are scarce. Temperature and rainfall data from the nearest weather station ("Samalayuca," 6 km west and 20 m higher elevation). The study area is bounded to the south and west by unvegetated gypsum dunes and to the north and east by a strip of similar sagebrush-mesquite scrub; beyond the latter, as close as one to three km, are plains with creosotebush (*Larrea tridentata*) and slopes with open succulent scrub, *Yucca* sp. and ocotillo (*Fouquieria* sp.). There are small, poorly vegetated mountain ranges at distances of 4 and 6 km to the east and west. Irrigated agriculture and the town of Samalayuca are 5 and 6 km away to the northwest and west, respectively.

3. Mesquite-acacia-ocotillo-mixed succulent scrub (*Prosopis-Acacia farnesiana-Fouquieria-Opuntia-Hechtia*) in rocky, hilly arid country immediately south of Peña Blanca, Querétaro

(21°16.47'N, 99°44.34'W). Washes are lined by slightly taller mesquite (up to approximately 5 m tall) and are bordered by cut banks up to 5 m deep. These washes are tributaries of the seasonal river Río Estórax which has a narrow but lush riparian strip. The Río Estórax and the village of Peña Blanca are separated from the study area by 25-70 m high hills. Temperature and rainfall data from the nearest weather station ("Peñamiller," 8.75 km west-northwest and 60 m lower elevation). The study area is surrounded by similar semiarid scrub.

4. Pine and fir woodland (*Pinus jeffreyi-Abies concolor)* in the Sierra San Pedro Mártir, Baja California (31°02.3'N, 115°28'W). Some areas with large boulders. Generally very open understory but some slopes with clumps of *Baccharis* sp. and *Arctostaphylos sp.* This forest has never been logged and fire suppression has never been practiced (Minnich et al. 1994). Temperature data from Álvarez and Maisterrena (1977), rainfall from Álvarez (1983). The study area is entirely surrounded by similar forest, certain patches of which contain additional species of conifers. Other than the facilities for the astronomers at the Observatorio Astronómico Nacional, the nearest human habitation is Mike Sky Ranch, 17 km west and 1200 m lower elevation.

5. Pine-oak forest (*Pinus-Quercus*) strongly dominated by pine, 1 km north of Batosárachi, Chihuahua (27°42.4'N, 107°34.95'W). Small to large rocky outcrops, with cliffs up to 30 m high in places. Where the soil is shallow there are clearings densely covered with *Baccharis*. Moderately disturbed; there are 3 small manmade clearings (0.15, 0.24 and 0.5 ha) -- 5 species of birds restricted to these clearings are not here considered to belong to the forest bird assemblage and were excluded from the list. Temperature and rainfall data from the nearest weather station ("Creel," 6.5 km northwest and 35 m lower elevation). The study area is bounded on the north and south by disturbed montane meadows. The towns of San Ignacio de Arareco and Creel, surrounded by cultivation, are 2.5 and 6.5 km away, respectively.

6. Open pine woodland (*Pinus hartwegii*) adjoining treeline in the northeast slope of the Nevado de Toluca volcano, state of México (19°07.5'N, 99°04'W). The undergrowth is composed largely of tussock grass (mainly *Calamagrostis tolucensis*, *Festuca* spp., *Muhlenbergia* spp., *Stipa* sp.). Temperature and rainfall data from the nearest weather station ("Nevado de Toluca," 1.25 km west and 100 m higher elevation), with 1°C added to all temperatures to account for the elevation difference. The study area is bounded on three sides by similar open pine woodland and on one side by treeless alpine grassland. The nearest point of the cultivated Valley of Toluca is about 2 km away and 350 m below the study area.

Table 2. The 12 foraging guilds used to test for functional saturation in Mexican diurnal land bird assemblages.

Carnivore	Capture terrestrial prey
	Capture arboreal/aerial prey
Scavenger	---------
Insectivore	High-flying, capture prey in the air (above canopy)
	Capture terrestrial prey
	Wood-boring
	Glean prey from bark/dead leaves/epiphytes
	Pluck prey from foliage
	Capture prey in the air (below canopy)
Nectarivore	---------
Frugi/Granivore	Arboreal
	Terrestrial

usually taken (*e.g.*, the insectivorous Squirrel Cuckoo *Piaya cayana* will occasionally eat fruit; Weelwright *et al.* 1984) but these occasional food items do not merit considering these species in a guild other than the one that corresponds to their usual foods.

RESULTS

We recorded between 34 and 55 species of diurnal land birds in each of the six study areas (species listed in APPENDIX). The richness estimator indicated that all of the foraging guilds in the study areas were recorded.

We tested for functional saturation in 77 sites, including the six study areas (APPENDIX). Together, the selected lists comprised most of the ecological situations ocurring in Mexico: all of the major types of vegetation (Rzedowski and Equihua 1987; Binford 1989), the range of combinations of temperature and rainfall (Figure 2), 93% of the avifaunal regions (*sensu* Escalante *et al.* 1993), and 95.7% of the species of diurnal land birds. Bird species richness among the lists ranged from 34 to 212 species, and similarity ranged from 1.4 to 90.1% bird species in common (Simpson's index).

Seventy-five assemblages had members of all twelve foraging guilds. The other two assemblages lacked members of one and two foraging guilds: study area 1 lacked wood-boring insectivores and predators of aerial/arboreal prey, and study area 6 lacked scavengers. The probability that four of the six localities where we carried out fieldwork were unsaturated was 0.000145. Therefore we conclude that the number of foraging guilds in Mexican land bird assemblages is not random.

Most land bird assemblages studied were functionally saturated (there is at least one species from every foraging guild). The two unsaturated assemblages were not a random subset of the assemblages studied in terms of environmental conditions. One had the lowest mean annual temperature and the other had both the lowest annual rainfall and the second-highest mean annual temperature (Figure 2). The species richness of only one assemblage (study area 4) was lower than that of the two unsaturated assemblages (and study area 4 had the second-lowest mean annual

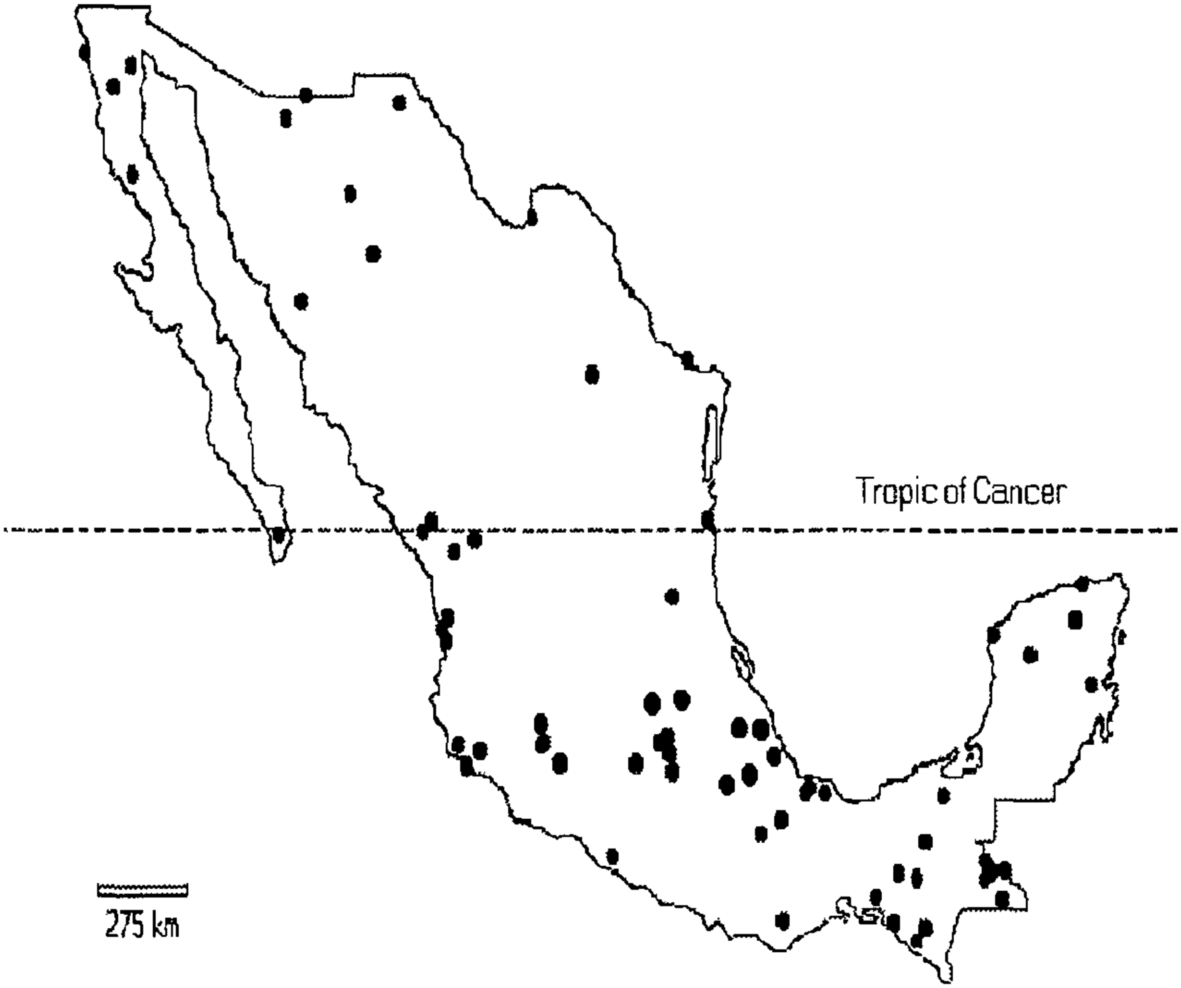
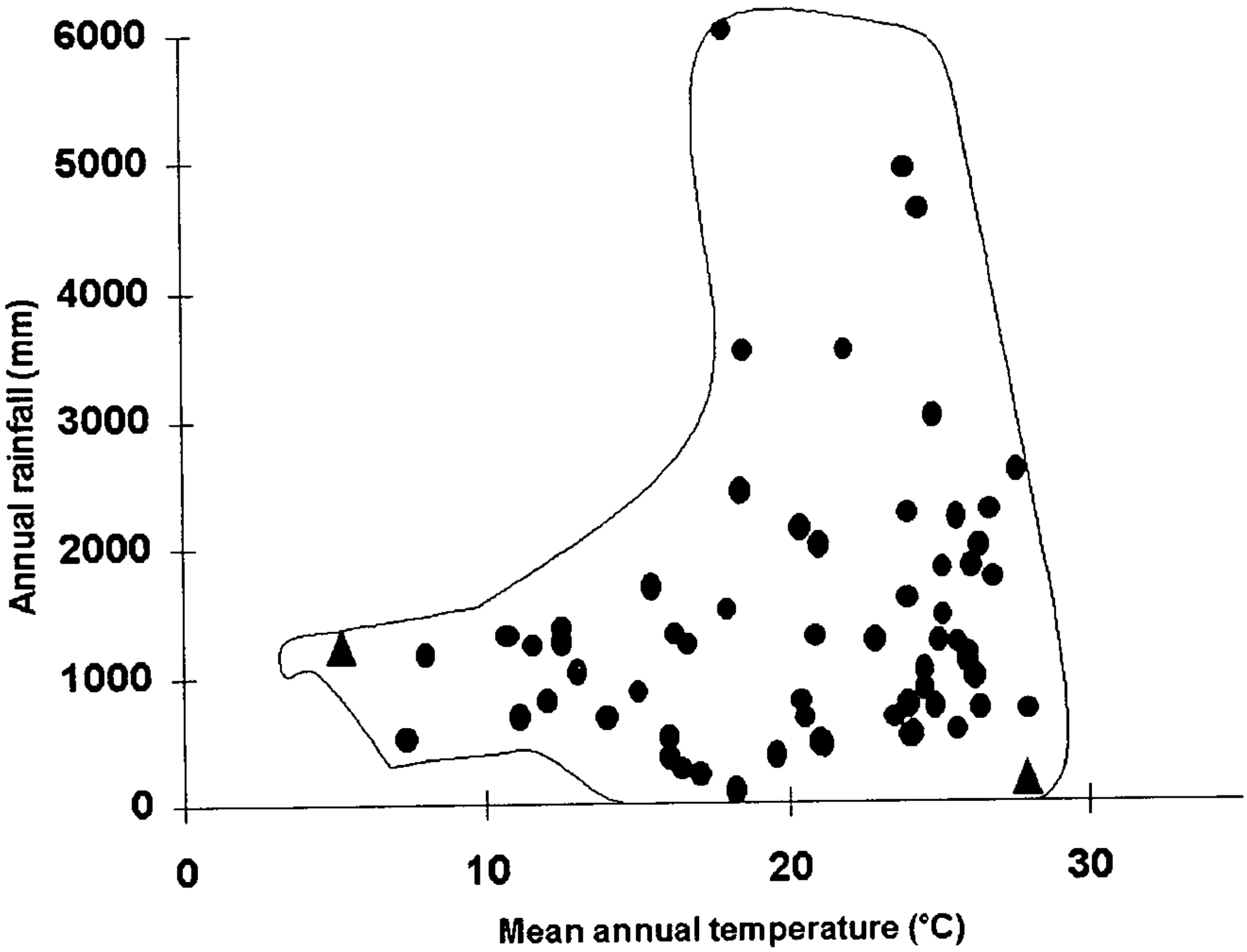


Figure 1. Geographic locations of the 77 localities in the sample.

Figure 2 (next page). Mean annual temperature versus annual rainfall for the localities in the Appendix (data from the same source as the corresponding species list or from 1: 250,000 climate maps produced by INEGI, 1985). Circles represent functionally saturated localities. Triangles represent functionally unsaturated localities. The solid line encloses all combinations of temperature and rainfall that occur in Mexico, based on García (1987) and data from the localities reported herein.


6000
5000
4000
3000
2000
1000
0
Annual rainfall (mm)
0
10
20
30
Mean annual temperature (°C)

temperature of the assemblages studied).

DISCUSSION

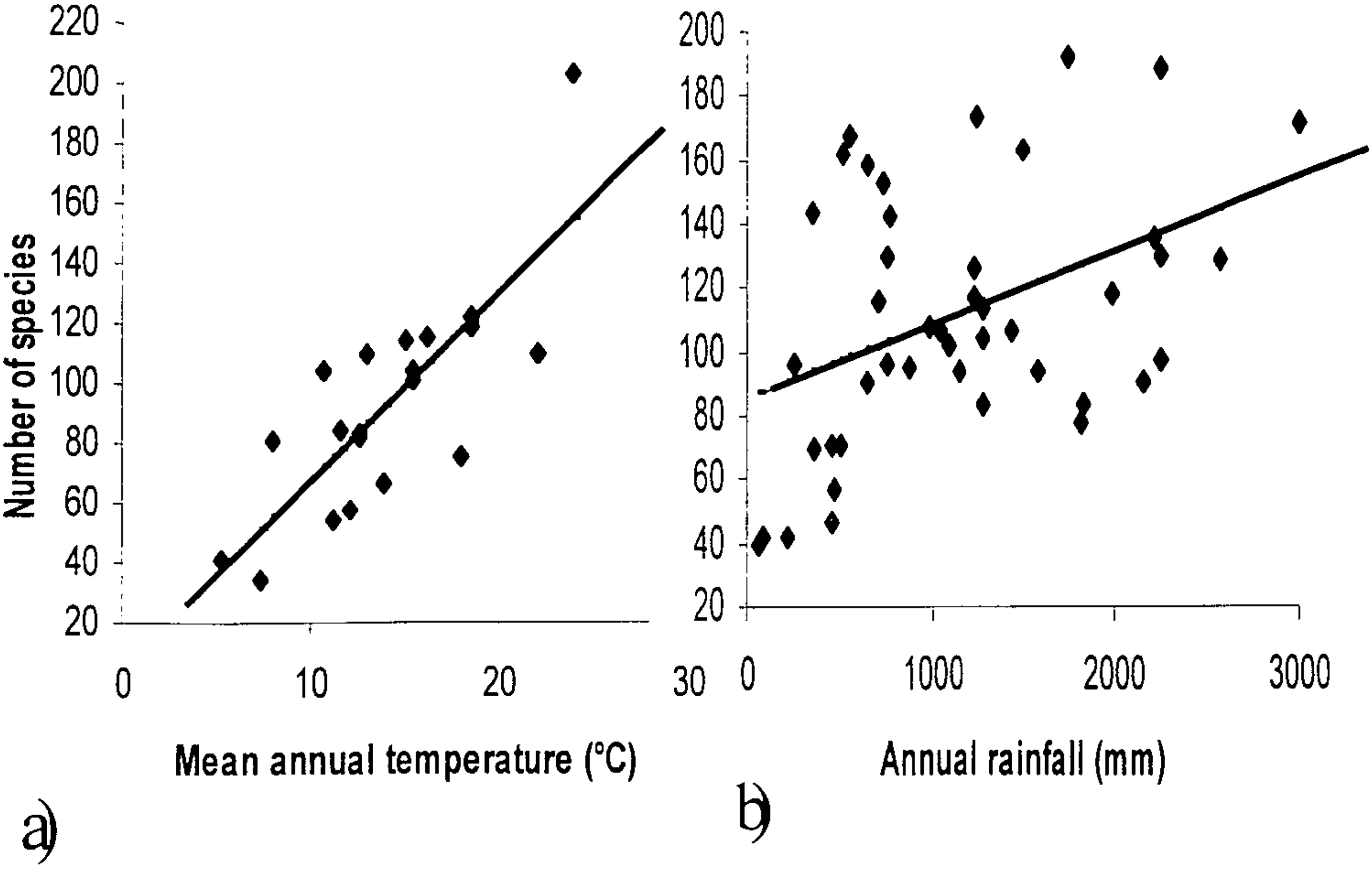
Our results suggest that communities assemble such that at least one species from each guild tends to be represented (ideal free distribution extended to communities). However, they also suggest that climatic conditions are ultimately acting as a limiting factor preventing certain assemblages of Mexican land birds from being saturated. Any prediction in science contains a *ceteris paribus* (all other things being equal) clause (Brady 1982; Wiens 1989: 22; Schrader-Frechette and McCoy 1993). The fact that the only unsaturated assemblages were from areas which pose most physiological stress to birds suggest that the prediction of the ideal free assembly rule may not be fulfilled where severe climatic conditions act as limiting population factors. Presumably, fewer species can endure the greater stress and/or lower productivity of areas with severe climatic conditions. What is clear is that severe climatic conditions (and unsaturated assemblages) correlate with reduced species diversity (Figure 3).

The conditions prevailing in the two unsaturated communities are present in less than 0.7% of Mexico's land surface based on overlaying maps of mean annual temperature (Vidal-Zepeda 1990) and annual rainfall (García 1990). Therefore, the prediction of the ideal free distribution model is valid over most of the range of climatic conditions found in Mexico, and the resource base ultimately determines the presence of particular kinds of birds in communities.

Most studies of community assembly have focused on coexistence among species within one or a few guilds and one or two trophic levels (Belyea and Lancaster 1999), a situation in which, theoretically, competition plays a direct role. The present study provides an example of approaching community assembly by analyzing how all food resources are used and how species are allocated among guilds.

Brown (1981) envisioned community assembly in terms of capacity rules and allocation rules. Capacity rules would be more related to coexistence among species within one or a few guilds, whereas allocation rules (such as the ideal free assembly rule) would be more related to the

Figure 3 (next page). Relationships between a) number of diurnal landbird species and mean annual temperature for the 21 assemblages that are toward the top and left of Figure 2 ($p<0.001$, $r^2=0.629$), and b) number of diurnal landbird species and annual rainfall for the remaining assemblages toward the lower right of Figure 2 ($p=0.006$, $r^2=0.172$).

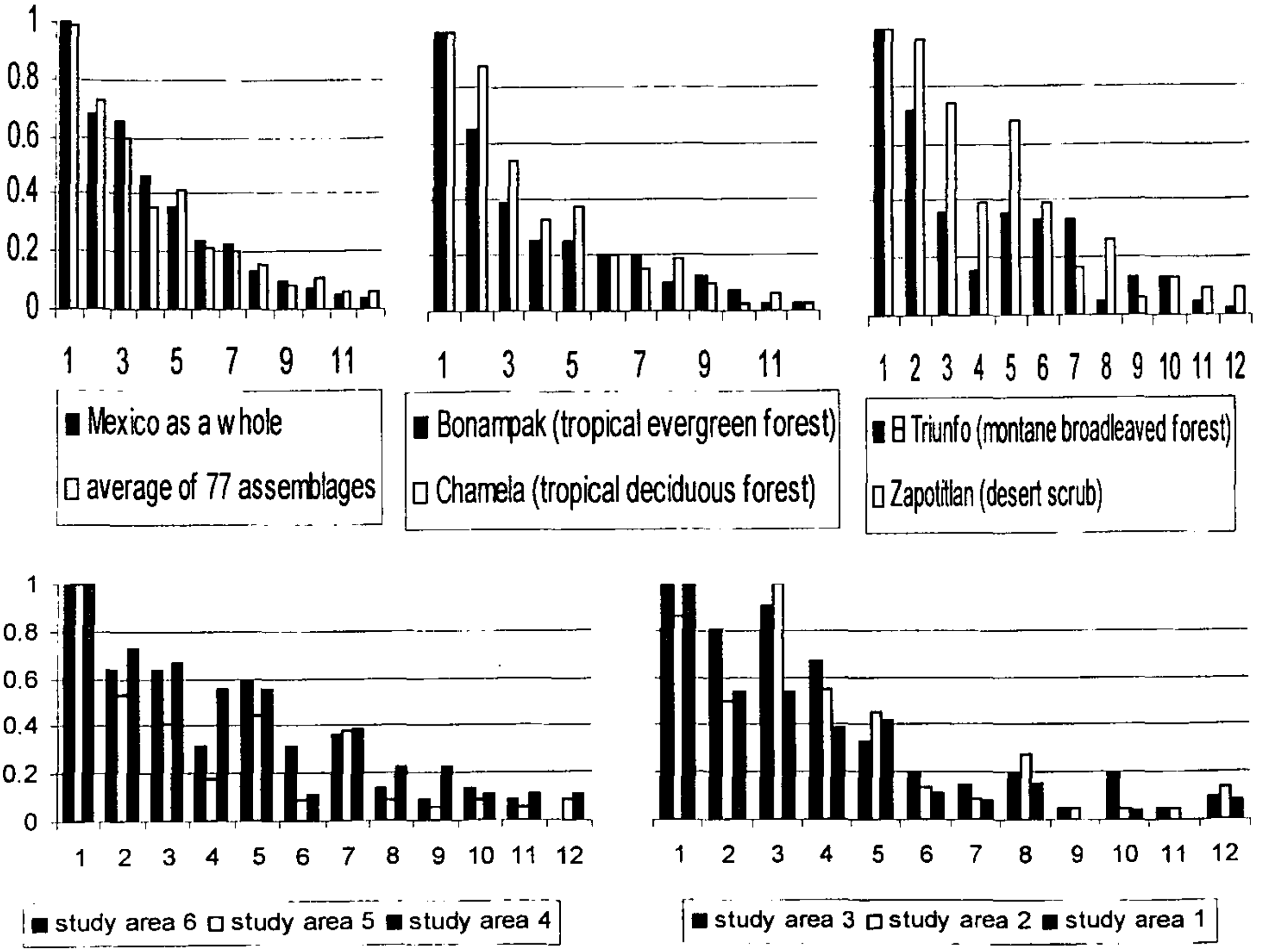

220
200
180
160
140
120
100
80
60
40
20
Number of species
0
10
20
30
Mean annual temperature (°C)
a)
200
180
160
140
120
100
80
60
40
20
0
1000
2000
3000
Annual rainfall (mm)
b)

division of resources among guilds. The correlation between climatic condition and species richness (Figure 3) would seem to be related principally to a capacity rule which determine species richness, although at climatic extremes it would also have an effect on the allocation among guilds (unsaturated assemblages in areas of severe climate).

The ideal free assembly rule is consistent with Fox's assembly rule (Fox 1987, 1989; Fox and Brown 1993, 1995), which states that the different functional groups in an assemblage tend to have the same number of species when the availability of each resource type is approximately equal ("first approximation" of Fox 1987). The ideal free assembly rule does not specify the relative number of species in each functional group, and for this reason this model is less specific than Fox's assembly rule. On the other hand, this model can be tested without having detailed information on the availability of different food resources. Therefore, the relationship between the ideal free distribution model and Fox's assembly rule is equivalent to the relationship between Fox's assembly rule and that of M'Closkey (1978, 1985): the two rules are complementary but whereas the former has logical priority because it depends on less detailed information, it provides less detailed predictions (see Fox 1987: 207; Fox 1989: 101).

Fox's assembly rule predicts that all functional groups will tend to have the same number of species when the availability of each resource type is approximately equal ("first approximation" of Fox 1987). In the case of Mexican diurnal land birds, the number of species in the different functional groups are often disparate. For example, in the 77 land bird assemblages in APPENDIX there are from 3 to 22 more species of insectivores that pluck their food from foliage than of wood-drilling insectivores. This is not simply a function of different total numbers of species, because the proportion of species in the different functional groups is also disparate (Figure 4). These discrepancies between guilds may be due to unequal availabilities of the different resource types, as Fox's rule predicts. Nevertheless, it is impossible to test the predictions of Fox's assembly rule because, both in theory and in

Figure 4 (next page). Proportional number of species of diurnal landbirds in 12 foraging guilds. Histograms represent all of Mexico, the average of the 77 assemblages, one example each from tropical evergreen forest, tropical deciduous forest, temperate forest and desert scrub, and the six study areas. The guilds were ordered from the one with highest to the one with lowest number of species in Mexico (and in most assemblages).


1
0.8
0.6
0.4
0.2
0
1 3 5 7 9 11
Mexico as a whole
average of 77 assemblages
1 3 5 7 9 11
Bonampak (tropical evergreen forest)
Chamela (tropical deciduous forest)
1 2 3 4 5 6 7 8 9 10 11 12
Triunfo (montane broadleaved forest)
Zapotitlan (desert scrub)
1 2 3 4 5 6 7 8 9 10 11 12
study area 6
study area 5
study area 4
1 2 3 4 5 6 7 8 9 10 11 12
study area 3
study area 2
study area 1

practice, it is difficult to compare the availability of different resource types among the different localities.

A controversy that has dominated theory in community ecology at least since the late 1950's (McIntosh 1995) is the effect of competition in structuring assemblages. Null models based on randomness have been proposed to be the best way to test for the effects of competition in community organization (Strong 1980; Gotelli and Graves 1996). The role of null models is to generate a pattern that is expected in the absence of the mechanism being tested, but to be realistic the model should incorporate structure that is independent of that mechanism (Gotelli and Graves 1996). The ideal free assembly rule exemplifies deterministic factors in community organization that are independent of present-day competiton. We propose that realistic null models that test for present-day competition should incorporate structure produced by functional saturation. Failing to do so would produce bias akin to the "dilution effect" of Diamond and Gilpin (1982) because the model would be confounding simulated assemblages that are biologically unrealistic, such as functionally unsaturated assemblages, with others that are plausible (whereas the dilution effect of Diamond and Gilpin refers to confounding simulated assemblages that are irrelevant to the test with others that are relevant). Specifically, we propose that observed assemblages should be tested only against those simulated assemblages that are functionally saturated.

However, Monte Carlo simulations based on samples from an observed species pool may be inappropriate null models to test this proposed assembly rule (and certain others, Colwell & Winkler 1984), because the pool may be influenced by the same rule that is hypothesized to structure the assemblages to be tested ("Narcissus effect," Colwell and Winkler 1984). This is particularly clear in the case of the ideal free assembly rule, in which the rule operates in both ecological time, structuring assemblages, and evolutionary time, structuring the species pool (see first paragraph of this article). In these cases, appropriate null models may have to be based on imaginary pools based on the absence of the mechanism being tested.

Because of functional saturation, diurnal land bird assemblages in Mexico have a common structure (they are made up of species belonging to the same 12 foraging guilds), even assemblages with no species in common. The ideal free distribution model on which this assembly rule is based applies to organisms in general, not only to Mexican birds. Therefore, this assembly rule could be tested on other taxa of organisms and in other parts of the world.

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Appendix. Sources of the species lists used to test for saturation, broken down by vegetation type. In some cases, when the species list in the published source were supplemented by Gómez de Silva's or others' observations in the same locality, these additional species are listed.

Tropical evergreen forest

Chajul, Chiapas (171 species: Salgado-Ortiz 1993, Rangel-Salazar 1990; *Spizastur melanoleucus, Sittasomus griseicapillus, Grallaria guatimalensis, Pachyramphus aglaiae, Polioptila plumbea* and *Scaphidura oryzivora*, Gómez de Silva personal observation; *Harpya harpyja*, R. Frías personal communication)

Lacanjá-Chansayab, Chiapas (135 species: Nocedal 1980)

Bonampak, Chiapas (211 species: Howell 1999)

Yaxchilán, Chiapas (200 species: Howell 1999)

Estación Biológica Los Tuxtlas, Veracruz (203 species of forest interior: Coates-Estrada and Estrada 1985)

lower parts of Reserva El Ocote, Chiapas (130 species of forest interior between 250 and 650 m elevation: Domínguez Barradas *et al.* 1996; *Falco rufigularis, Ortalis vetula, Piaya cayana, Amazilia candida, Eupherusa eximia, Trogon melanocephalus, Piculus rubiginosus, Celeus castaneus, Thamnophilus doliatus, Mionectes oleagineus, Attila spadiceus, Pachyramphus aglaiae, Tityra semifasciata, Cyanocorax morio, Campylorhynchus zonatus, Thryothorus maculipectus, Hylophilus ochraceiceps, Vireolanius pulchellus, Saltator atriceps, Cyanocompsa cyanoides, Arremon aurantiirostris* and *Arremonops chloronotus*, Gómez de Silva, personal observation; *Empidonax* sp., A. Oliveras, personal communication)

Coyame, Veracruz (104 species occurring during summer: Edwards and Tashian 1959)

Tropical evergreen forest/montane forest

Laguna Ocotal, Chiapas (110 species: Paynter 1957; *Coragyps atratus, Buteo nitidus, Columba cayennensis, Amazona farinosa, Campylopterus hemileucurus, Amazilia rutila, Cypseloides rutilus, Synallaxis erythrothorax, Zimmerius vilissimus, Myiodynastes luteiventris, Lipaugus unirufus, Cyanolyca cucullata, Stelgidopteryx ridgwayi, Chlorophonia occipitalis, Ramphocelus passerinii, Arremonops chloronotus* and *Dives dives*, Gómez de Silva personal observation)

Montane broadleaved forest

Tlanchinol, Hidalgo (122 species: Navarro et al. 1992, Howell and Webb 1992)

La Yerbabuena, Chiapas (40 species: Long 1987)

Los Tuxtlas, Veracruz (119 species: Andrle 1964; Schaldach and Escalante 1997)

Sierra de Atoyac, Guerrero (67 species: Navarro 1992; Howell 1992, 1999; Howell and Webb 1992)

El Triunfo, Chiapas (76 species: Gómez de Silva *et al.* 1999)

Cerro Macuiltépetl, Veracruz (163 species: Aguilar-Rodríguez et al. in prep.)

Las Joyas, Jalisco (104 species from a 130 hectare patch of forest: Contreras-Martínez and Santana Castellón 1995; raptors, swifts, swallows and raven from Garcia-Ruvalcaba *et al.* 1996)

Barranca Rancho Liebre, Sinaloa (117 species: Alden 1969; Howell 1999)

Tropical semievergreen forest

Sian Ka'an, Quintana Roo (126 species of "selva mediana subperennifolia" in López-Ornat 1990; Howell 1999)

Tropical semideciduous forest

Singayta, Nayarit (133 species: Alden 1969; *Stelgidopteryx serripennis*, Gómez de Silva personal observation)

Sierra de Atoyac, Guerrero (78 species: Navarro 1992, Howell and Webb 1994)

top of Sumidero Canyon, Chiapas (141 species: Edwards 1968, Howell 1999; *Stelgidopteryx serripennis*, *Setophaga ruticilla*, *Icterus spurius*, Gómez de Silva personal observation)

Tropical deciduous forest

La Pesca, Tamaulipas (96 species: Baker and Fleming 1962; Howell 1999)

Pánuco, Sinaloa (94 species: Edwards 1985; Howell 1999)

Chamela, Jalisco (130 species: "selva mediana" and "selva baja"; Arizmendi *et al.* 1990; *Progne chalybea* and *Polioptila nigriceps*, Gómez de Silva personal observation)

Playa de Oro, Colima (108 species: Howell 1999)

Colonia Francisco Barrios, Veracruz (94 species: Sargeant and Wall 1995; Howell 1999)

La Mancha, Veracruz (113 species of "selva mediana" and "selva baja": Ortiz Pulido et al. 1995)

Ciénega de Chapala, Michoacán (142 species: Aguilar 1995)

Lo de Campa, Sonora (144 species: Russell and Monson 1998)

Huautla, Morelos (107 species: F. Urbina, personal communication, 1999)

Cañón de Lobos, Morelos (84 species: Howell 1999; *Accipiter cooperi*, *Heliomaster constantii*, *Archilochus sp.*, *Contopus pertinax*, *Tyrannus verticalis*, *Hirundo rustica*, *Vermivora ruficapilla* and *Piranga ludoviciana*, Gómez de Silva, personal observation)

Montealbán, Oaxaca (90 species: Howell 1999; *Parabuteo unicinctus*, *Geococcyx velox*, *Ptilogonys cinereus*, Gómez de Silva personal observation)

Uxmal, Yucatán (95 species: Edwards 1968, 1985; Howell 1999)

Chichen Itzá, Yucatán (102 species: Edwards 1985; Howell 1999)

Tropical deciduous forest/ desert

Alamos, Sonora (159 species: Alden 1969; Short 1974)

northeast of Presa Zicuirán, Michoacán (116 species: Villaseñor Gómez 1985)

Subtropical thorn forest

Santa Ana National Wildlife Refuge, Texas (162 species: Igl 1997, excluding species labelled "r" and "x")

Tropical savanna, pastures, forest patches

Las Barrancas, Veracruz (83 species: Howell 1999)

Los Tuxtlas, Veracruz (188 species: Davis and Morony 1953; Schaldach and Escalante 1997)

Usumacinta marshes, Campeche (118 species: Howell 1999)

Puerto Arista/Boca del Cielo, Chiapas (97 species: Howell 1999)

Mapastepec microwave valley (128 species: Howell 1999)

Scrubland and desert

study area 1 (40 species: *Cathartes aura*, *Buteo jamaicensis*, *Falco sparverius*, *Zenaida macroura*, *Aeronautes saxatalis*, *Archilochus costae*, *Contopus sordidulus*, *Empidonax difficilis*, *Sayornis saya*, *Myiarchus cinerascens*, *Corvus corax*, *Auriparus flaviceps*, *Salpinctes obsoletus*, *Thryomanes bewickii*, *Regulus calendula*, *Polioptila caerulea*, *P. melanura*, *Catharus ustulatus*, *Mimus polyglottos*, *Phainopepla nitens*, *Lanius ludovicianus*, *Vireo gilvus*, *Vermivora celata*, *V. ruficapilla*, *Dendroica petechia*, *D. coronata*, *D. townsendi*, *Oporornis tolmiei*, *Wilsonia pusilla*, *Piranga ludoviciana*, *Pheucticus melanocephalus*, *Amphispiza bilineata*, *Spizella passerina*, *Ammodramus sandwichensis*, *Melospiza lincolnii*, *Zonotrichia leucophrys*, *Icterus bullockii*, *Carpodacus mexicanus*, *Carduelis psaltria*, *C. lawrencii*)

San Fernando, Baja California (42 species: Anthony 1895) study area 2 (42 species: *Cathartes aura, Circus cyaneus, Accipiter striatus, Buteo swainsoni, B. jamaicensis, Callipepla squamata, C. gambelli, Zenaida macroura, Geococcyx californianus, Archilochus sp., Selasphorus platycercus, Picoides scalaris, Contopus sordidulus, Empidonax hammondii, E. wrightii, Sayornis saya, Myiarchus cinerascens, Tyrannus verticalis, Hirundo pyrrhonota, Corvus cryptoleucus, Auriparus flaviceps, Campylorhynchus brunneicapillus, Thryomanes bewickii, Regulus calendula, Polioptila caerulea, P. melanura, Mimus polyglottos, Oreoscoptes montanus, Toxostoma crissale, Lanius ludovicianus, Oporornis tolmiei, Wilsonia pusilla, Cardinalis sinuatus, Passerina caerulea, Pipilo chlorurus, Amphispiza bilineata, A. belli, Spizella passerina, S. pallida, S. breweri, Calamospiza melanocorys, Icterus parisorum*)

study area 3 (46 species: *Cathartes aura, Buteo jamaicensis, Callipepla squamata, Zenaida asiatica, Z. macroura, Columbina inca, C. passerina, Geococcyx californianus, Aeronautes saxatalis, Cynanthus latirostris, Archilochus colubris, Picoides scalaris, Camptostoma imberbe, Empidonax minimus, E. wrightii, Sayornis saya, Myiarchus cinerascens, Tachycineta thalassina, Stelgidopteryx serripennis, Hirundo rustica, Corvus cryptoleucus, Auriparus flaviceps, Campylorhynchus brunneicapillus, Salpinctes obsoletus, Catherpes mexicanus, Thryomanes bewickii, Troglodytes aedon, Polioptila caerulea, P. melanura, Mimus polyglottos, Toxostoma curvirostre, Phainopepla nitens, Lanius ludovicianus, Vermivora celata, V. ruficapilla, Piranga flava, Cardinalis cardinalis, C. sinuatus, Passerina versicolor, Pipilo chlorurus, Aimophila ruficeps, Chondestes grammacus, Icterus parisorum, Carpodacus mexicanus, Carduelis psaltria, Passer domesticus*)

Pedregal de San Angel, D.F. (114 species: Ramos 1974; Arizmendi *et al.* 1994; Wilson and Ceballos 1993; *Chondrohierax unicinctus, Chaetura vauxi, Peucedramus taeniatus*, and *Pooecetes gramineus*, Gómez de Silva personal observation)

Zapotitlán de las Salinas, Puebla (71 species of "tetechera" habitat, Arizmendi and Espinosa de los Monteros 1996; *Coragyps atratus, Accipiter striatus, Parabuteo unicinctus, Aeronautes saxatalis, Tyrannus vociferans* and *Aimophila mystacalis*. Gómez de Silva, personal observation)

Coniferous woodland

study area 4 (34 species: *Cathartes aura, Buteo jamaicensis, Falco peregrinus, Callipepla picta, Aeronautes saxatalis, Archilochus anna, Selasphorus rufus, Sphyrapicus thyroideus, Picoides villosus, Colaptes auratus, Contopus borealis, C. sordidulus, Empidonax difficilis, Tachycineta thalassina, Aphelocoma coerulescens, Gymnorhinus cyanocephalus, Nucifraga columbiana, Corvus corax, Parus gambeli, Sitta carolinensis, S. pygmaea, Catherpes mexicanus, Troglodytes aedon, Regulus calendula, Sialia mexicana, Chamaea fasciata, Vireo (solitarius) cassini, Dendroica nigrescens, D. occidentalis, Pipilo erythropthalmus maculatus, Junco hyemalis, Carpodacus cassinii, Carduelis pinus, C. psaltria*)

study area 6 (41 species: *Accipiter striatus, Buteo jamaicensis, Falco sparverius, F. columbarius, Cypseloides niger, Aeronautes saxatalis, Colibri thalassinus, Basilinna leucotis, Lampornis clemenciae, Selasphorus platycercus, Picoides stricklandi, Colaptes auratus, Contopus pertinax, Empidonax hammondii, Tachycineta thalassina, Cyanocitta stelleri, Parus sclateri, Sitta carolinensis, S. pygmaea, Certhia americana, Troglodytes aedon brunneicollis, Regulus calendula, Sialia mexicana, Catharus occidentalis, C. guttatus, Turdus migratorius, Vireo huttoni, Vermivora celata, Dendroica coronata, D. townsendi, Ergaticus ruber, Peucedramus taeniatus, Pipilo erythropthalmus maculatus, Diglossa* *baritula, Oriturus superciliosus, Melospiza lincolnii, Junco phaeonotus, Icterus parisorum, Loxia curvirostre, Carduelis pinus, Coccothraustes vespertinus*)

Nuevo San Juan Parangaricutiro, Michoacán (83 species: Sosa 1996)

Las Vigas, Veracruz (84 species: Sutton and Burleigh 1940)

Conifer-oak woodland

Bisaloachi, Chihuahua (58 species: *Coragyps atratus, Cathartes aura, Accipiter cooperi, Buteo albonotatus, B. jamaicensis, Meleagris gallopavo, Columba fasciata, Rhynchopsitta pachyrhyncha, Geococcyx californianus, Cypseloides niger, Basilinna leucotis, Eugenes fulgens, Selasphorus platycercus, Trogon mexicanus, Melanerpes formicivorus, Picoides villosus, Sphyrapicus sp., Colaptes auratus, Mitrephanes phaeocercus, Contopus pertinax, C. sordidulus, Empidonax affinis, E. occidentalis, E. hammondi, Tachycineta thalassina, Hirundo rustica, Cyanocitta stelleri, Corvus corax, Parus sclateri, Sitta carolinensis, S. pygmaea, Certhia americana, Troglodytes aedon brunneicollis, Sialia mexicana, Myadestes townsendi, Catharus occidentalis, C. guttatus, Turdus migratorius, Vireo (solitarius) plumbeus, V. (solitarius) cassini, V. huttoni, Vermivora superciliosa, V. celata, Dendroica occidentalis, D. townsendi, D. coronata, Cardellina rubrifrons, Wilsonia pusilla, Myoborus miniatus, Peucedramus taeniatus, Piranga flava, Pheucticus melanocephalus, Pipilo erythropthalmus maculatus, Junco phaeonotus, Coccothraustes vespertinus, Carduelis spinus*, Gómez de Silva, personal observation; *Accipiter gentilis*, E. Enkerlin, personal communication)

study area 5 (54 species: *Coragyps atratus, Cathartes aura, Accipiter striatus, A. cooperi, Buteo albonotatus, B. jamaicensis, Cypseloides niger, Aeronautes saxatalis, Basilinna leucotis, Selasphorus platycercus, Euptilotis neoxenus, Sphyrapicus varius nuchalis, S. thyroideus, Picoides villosus, Colaptes auratus, Contopus pertinax, C. sordidulus, Empidonax affinis, E. difficilis, Tachycineta thalassina, Cyanocitta stelleri, Corvus corax, Parus sclateri, Psaltriparus minimus, Sitta carolinensis, S. pygmaea, Certhia americana, Catherpes mexicanus, Thryomanes bewickii, Troglodytes aedon brunneicollis, Regulus calendula, Myadestes townsendi, Catharus guttatus, Turdus migratorius, Vireo (solitarius) plumbeus, Vireo (solitarius) cassini, Vireo huttoni, Vermivora celata, V. superciliosa, Dendroica coronata, D. nigrescens, D. townsendi, D. occidentalis, D. graciae, Wilsonia pusilla, Cardellina rubrifrons, Myioborus pictus, Myioborus miniatus, Peucedramus taeniatus, Piranga flava, Pheucticus melanocephalus, Pipilo erythropthalmus maculatus, Junco phaeonotus, Carduelis pinus, Coccothraustes vespertinus*)

Sierra La Laguna, Baja California Sur (67 species: Banks 1967; Rodríguez-Estrella 1988; Unitt *et al.* 1992)

La Michilía, Durango (59 species of "area B": Thiollay, pp. 28-9 - *In:* Halffter 1978)

Las Joyas, Jalisco (104 species from a 150 hectare patch of forest, Contreras-Martínez and Santana Castellón 1995; raptors, swifts, swallows and raven from García-Ruvalcaba *et al.* 1996; *Thalurania ridgwayi*, Ornelas and Arizmendi 1995)

Sierra del Carmen, Coahuila (61 species: Miller 1955)

Pico de Tancítaro, Michoacán (82 species: Blake and Hanson 1942)

Oak woodland

16 km west of Cananea, Sonora (71 species: *Cathartes aura, Accipiter striatus, A. cooperi, Buteo jamaicensis, Falco peregrinus, Cyrtonyx montezumae, Columba fasciata, Zenaida macroura, Aeronates saxatalis, Archilochus anna, Trogon elegans, Melanerpes lewis, M. formicivorus, Sphyrapicus varius nuchalis, Picoides scalaris, P. arizonae, Colaptes auratus, Contopus sordidulus, Sayornis nigricans, S. saya, Empidonax* sp., *Pyrocephalus*

rubinus, Myiarchus tuberculifer, M. cinerascens, M. tyrannulus, Myiodynastes luteiventris, Tyrannus crassirostris, T. verticalis, Tachycineta thalassina, Stelgidopteryx serripennis, Hirundo rustica, Aphelocoma ultramarina, Corvus sp., *Parus wollweberi, Sitta carolinensis, Thryomanes bewicki, Troglodytes aedon brunneicollis, Regulus calendula, Sialia sialis, Catharus guttatus, Turdus migratorius, Mimus polyglottos, Toxostoma curvirostre, Phainopepla nitens, Vireo solitarius plumbeus, V. huttoni, Vermivora luciae, Dendroica coronata, Wilsonia pusilla, Myoborus pictus, Piranga flava, P. rubra, Pheucticus melanocephalus, Passerina caerulea, Pipilo erythropthalmus maculatus, Pipilo fuscus, Aimophila ruficeps, Spizella passerina, S. pallida, S. atrogularis, Melospiza lincolnii, Junco hyemalis, Molothrus aeneus, M. ater, Icterus parisorum, Carpodacus mexicanus, Carduelis pinus, C. psaltria,* Gómez de Silva, personal observation)

Coronado National Monument, Arizona (144 species: Igl 1997)

Contreras, D.F. (110 species: Wilson and Ceballos-Lascuráin 1993)

Other types of vegetation

mixture of tropical evergreen forest, tropical deciduous forest and montane broadleaved forest, Rancho Rinconada, Tamaulipas (174 species: Sutton and Pettingill 1942)

coconut palm woodland, San Blas, Nayarit (107 species: Alden 1969; *Micrastur semitorquatus* and *Centurus uropygialis*, Gomez de Silva personal observation)

mangrove forest, Matanchén, Nayarit (75 species: Alden 1969)

coastal dune scrub, La Mancha, Veracruz (104 species: Ortiz Pulido *et al.* 1995)

patchwork of mangrove forest, tropical deciduous forest, tropical semievergreen forest and coastal scrub, Ría Celestún, Yucatán (153 species: García and Vigilante 1988; *Vermivora chrysoptera*, Gómez de Silva personal observation)

patchwork of coastal scrub, mangrove forest, tropical deciduous forest, and tropical semievergreen forest, Ría Lagartos (168 species: García and Correa 1988)

patchwork of tropical deciduous and semideciduous forest, Rancho Sol y Luna/Santa Efigenia, Oaxaca (192 species: Binford 1989; Schaldach et al. 1997; *Bubulcus ibis, Columbina passerina, Dives dives*, Gómez de Silva personal observation)

young second-growth pine-oak forest that had been burned by a high-intensity crown fire 9 years before, Las Joyas, Jalisco (101 species from a 50 hectare patch: Contreras-Martínez and Santana Castellón 1995; raptors, swifts, swallows and raven from García-Ruvalcaba *et al.* 1996)

patches of pine-oak surrounded by open pine woodland and bunchgrass meadows, La Cima, D.F. (81 species: Wilson and Ceballos 1993; Howell 1999; *Accipiter striatus, A. cooperi, Dendrortyx barbatus, Bartramia longicauda, Lampornis clemenciae, Basilinna leucotis, Mitrephanes phaeocercus, Eremophila alpestris, Regulus satrapa, Catharus occidentalis, C. guttatus, Vermivora celata, V. ruficapilla, V. crissalis, Basileuterus belli, Atlapetes virenticeps*, Gómez de Silva personal observation)

humid pine-oak forest, La Cumbre and Cerro San Felipe, Oaxaca (104 species: Binford 1989; Howell 1999; *Streptoprocne zonaris*, Gómez de Silva personal observation)

tropical semideciduous/pine-oak forest ecotone, La Soledad, Oaxaca (116 species: Howell 1999; *Dendrortyx macroura, Cypseloides niger* and *Lamprolaima rhami*, Gómez de Silva personal observation).

tropical semideciduous forest/coffee plantation, La Bajada, Nayarit (116 species: Howell 1999) tropical semideciduous forest/coffee plantation, Amatlán, Veracruz (90 species: Howell 1999; *Buteo jamaicensis*, *Mitrephanes phaeocercus*, *Icteria virens*, *Euphonia elegantissima*, *Thraupis abbas*, *Scaphidura oryzivora*, Gómez de Silva personal observation)

riparian strip with *Taxodium*, flanked by thornscrub and desert scrub, Río Mezquital, Durango (57 species from "Upper River Camps": Crossin et al. 1973)

Chaparral/semiopen country, Punta Banda, Baja California (96 species: Howell 1999)

Desert oasis, Presa El Tulillo, Coahuila (70 species: Howell 1999; *Callipepla squamata* and *Toxostoma longirostre*, Gómez de Silva personal observation)

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Capítulo III

PATTERN IN MEXICAN BIRD ASSEMBLAGES SUGGEST THE EXISTENCE OF A MACROEVOLUTIONARY ASSEMBLY RULE

(escrito como si fuera a enviarse a *Evolutionary Ecology*)

INTRODUCTION

Community structure is thought to be the outcome of assembly rules (Weiher and Keddy 1995; Belyea and Lancaster 1999). Traditionally, patterns in community ecology have been considered to be determined by ecological processes operating locally. In contrast, communities have recently been seen to be strongly influenced by larger-scale and longer-term processes, such as regional climatic history, historical biogeography, and speciation and extinction rates (Ricklefs 1987; Vrba 1992; Ricklefs and Schluter 1993; Kelt et al. 1995; Rosenzweig 1995). This perspective suggests that ecological assembly rules can be combined with macroevolutionary assembly rules to understand community patterns.

The ecological assembly rule of Gómez de Silva and Medellín (in prep a) [= capítulo II] was proposed to explain why assemblages of diurnal land birds in Mexico practically always contain species from 12 foraging guilds. The explanation was based on the ecological process whereby species distributions tend to match resource availability. On the other hand, another pattern revealed by the same assemblages is that there are 16 families which recur in practically all assemblages (Gómez de Silva and Medellín in prep. b) [= capítulo I]. Because there is no 1:1

correspondence between foraging guilds and bird families, the guild assembly rule does not explain the family pattern. Consequently, an additional macroevolutionary assembly rule is needed to explain further the composition of Mexican land bird assemblages. This assembly rule would focus on families' frequency of occurence among assemblages (hereafter termed "incidence").

Families are made up of different number of species, and family incidence is proportional to the area the family occupies. Therefore, it is possible that the relationship between family incidence and its number of species is analogous to a species-area curve, in which the families with most species are distributed in a wider area (and therefore contribute species to a larger number of communities). Number of species is a function of net speciation rate (Vrba 1983). Therefore, if family incidence is indeed related to its number of species, the pattern would suggest that families with higher net speciation rates tend to contribute species to a larger number of communities. This paper explores the relationships between family incidence and number of species in the family for Mexican diurnal land birds.

METHODS

To relate family incidence and number of species in a way comparable to a species-area curve, I applied linear regression (log-log) using least-squares, with number of species as the dependent variable.

I followed the family-level taxonomy of A.O.U. (1998) and the species-level taxonomy of Howell and Webb (1995). I counted the number of Mexican species in each land bird family using data in Howell and Webb (1995), excluding species either recorded in Mexico once or twice or distributed only on islands. To estimate family incidence, I counted the number of assemblages for which a family was recorded in the database of Gómez de Silva and Medellín (in prep. a) [= capítulo II].

RESULTS

There was a significant relationship ($p<0.0001$) between family incidence and number of species (Figure 1). The logarithmic relationship can be explained by the existence of a threshold number of species above which families are ubiquitous: all 13 families with 22 or more species occurred in 90% or more of the localities and all 5 families with 38 or more species occurred in

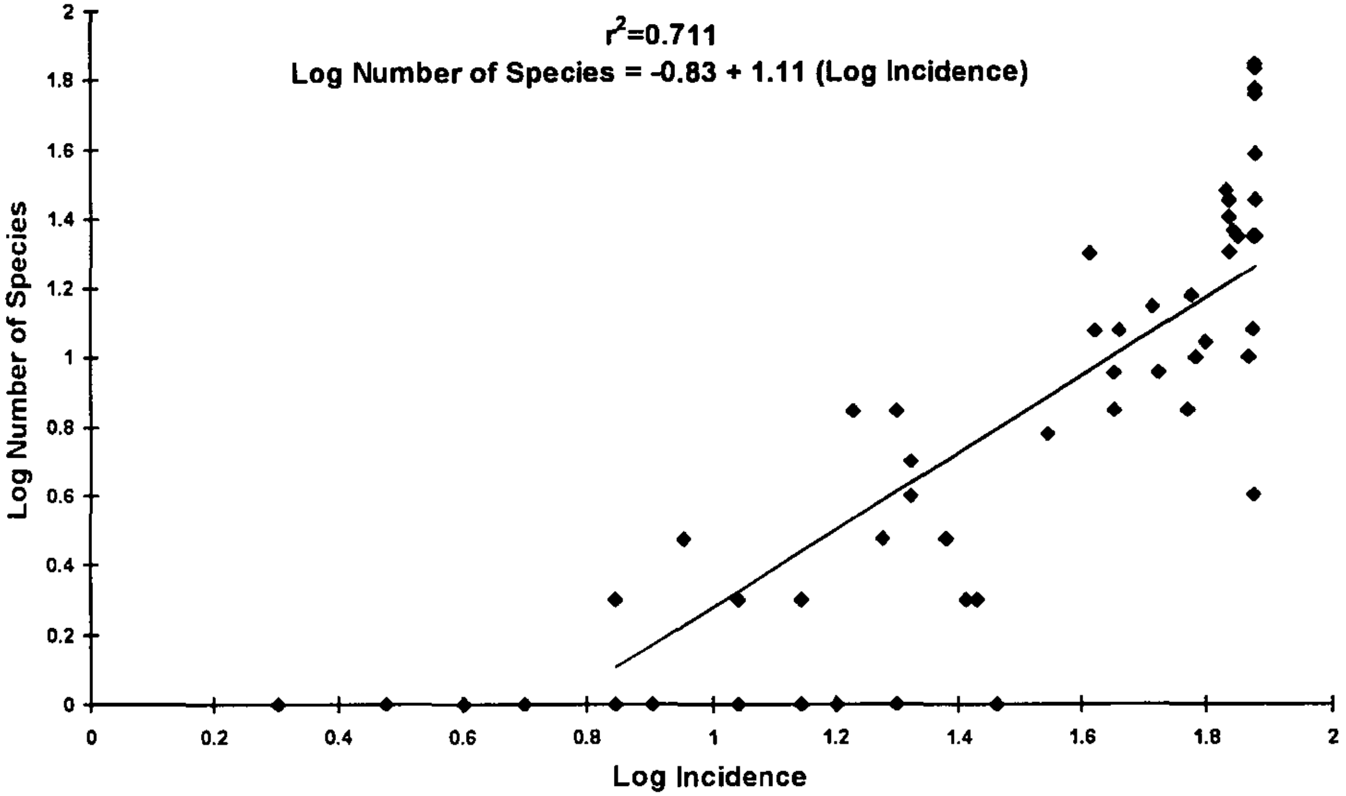


Fig. 1. Number of species in families of Mexican diurnal land birds versus incidence, graphed as a species-area curve.

Table 1. Percent of Mexican assemblages in which each family of diurnal land birds was recorded.

Corvidae	100	Mimidae	79	Fumariidae	22
Parulidae	100	Sylviidae	78	Ardeidae	21
Trochilidae	100	Trogonidae	70	Aegithalidae	21
Troglodytidae	100	Odontophoridae	69	Certhiidae	21
Tyrannidae	100	Fringillidae	61	Formicariidae	18
Accipitridae	100	Cotingidae	60	Motacillidae	18
Cathartidae	99	Cracidae	58	Peucedramidae	18
Emberizidae	99	Dendrocolaptidae	56	Charadriidae	16
Hirundinidae	99	Psittacidae	53	Passeridae	14
Picidae	99	Momotidae	45	Pipridae	12
Apodidae	97	Bombycillidae	38	Remizidae	12
Vireonidae	94	Ptilogonatidae	36	Bucconidae	9
Columbidae	92	Regulidae	35	Phasianidae	9
Cardinalidae	91	Ramphastidae	31	Coerebidae	9
Thraupidae	91	Paridae	27	Alaudidae	6
Turdidae	91	Tinamidae	27	Galbulidae	5
Icteridae	90	Laniidae	27	Scolopacidae	4
Falconidae	83	Thamnophilidae	26	Sturnidae	4
Cuculidae	81	Sittidae	26	Timalidae	3

Table 2. Foraging guilds (boldface) and diurnal land bird families that are ubiquitous or nearly ubiquitous in Mexico. Asterisks mark guilds that are missing in a single assemblage in the data base (no guild is missing in more than one assemblage), and families that represent the guild under which they are listed in more than 89 but less than 100% of the assemblages. For example, Icteridae is listed under foliage-gleaning insectivores, which it represents in 90% of assemblages, and not under other guilds, because ground-foraging species occur in only 66% of the assemblages; nectarivorous species in 86%, and arboreal frugivores in 83%. Also, Corvidae is not listed in the table although it occurs in all assemblages because no guild is represented by Corvidae in more than 87% of the assemblages.

carnivore - captures terrestrial prey Accipitridae (part)	**carnivore – captures nonterrestrial prey*** Accipitridae (part)*	**scavenger*** Cathartidae*
insectivore - captures prey above the canopy Apodidae* Hirundinidae*	**insectivore - captures terrestrial prey** Emberizidae Turdidae*	**insectivore - captures prey inside wood*** Picidae*
insectivore - gleans prey from bark, dead leaves and/or epiphytes ------------	**insectivore - plucks prey from foliage/ branches** Troglodytidae Parulidae Vireonidae* Cardinalidae* nonterrestrial Icteridae*	**insectivore - captures prey in the air below the canopy** Tyrannidae Trochilidae
arboreal fruit or seed-eater Thraupidae* Turdidae* Cardinalidae* nonterrestrial Icteridae*	**terrestrial fruit or seed-eater** Emberizidae Cardinalidae*	**nectarivore** Trochilidae

99% or more of the localities. Six families are found in 100% of the assemblages and 10 families are found in more than 89% but less than 100% of the assemblages (Table 1).

DISCUSSION

The correlation suggests a general pattern (sensu Belyea and Lancaster 1999) underlain by a macroevolutionary assembly rule: *monophyletic groups with higher net speciation rates contribute species to a larger number of communities*. Because land bird families found in 90% or more of the assemblages are nested in ubiquitous foraging guilds (with one exception; Table 2), the macroevolutionary assembly rule combines with the ecological assembly rule of Gómez de Silva and Medellín (in prep. a) [= capítulo II] to explain the observation of a common structure among Mexican land bird assemblages. The one exception is the guild of insectivores that glean prey from bark, hanging dead leaves and/or epiphytes, because it is not represented by any ubiquitous family. In tropical regions, this guild is represented mainly by Dendrocolaptidae, whereas in temperate regions this guild is represented by Picidae, Certhiidae, Sittidae, and/or a few species of Parulidae (species of Dendrocolaptidae also occur in a few temperate localities). This tropical-temperate divergence reflects the fact that Mexico spans two biotic regions (Neotropical and Nearctic) which contain lineages of different geographic origin (Ramamoorthy *et al.* 1993). Despite this historical divergence, the fact that 16 diurnal land bird families are ubiquitous or nearly ubiquitous in Mexico indicates a thorough mixing between the two originally separate avifaunas, and explains the common taxonomic structure of assemblages.

The 19 assemblages that lack from one to four of these nearly ubiquitous families were located in areas with either low annual rainfall, low mean annual temperatures or high annual rainfall and moderate temperatures (Fig. 2). This supports the observation that climate may limit the distribution of birds (Root 1988a, 1988b, 1989; Gómez de Silva and Medellín in prep. a [= capítulo II]) and is consistent with the assertion of Belyea and Lancaster (1999) that assembly rules operate within the constraints imposed by the environment.

The species-incidence relationship was seen as analogous to a species-area curve. A frequent limitation of species-area curves is that they often compare the species richnesses of mutually exclusive areas (such as different islands, landscapes, biotic provinces or continents) which differ in habitat availability, resource availability, and colonization history (Graves and Gotelli 1993). One approach to overcome this limitation has been to use nested samples to study species-area relations (Palmer and White 1994; Leitner and Resenzweig 1997; Lyons and Willig 1999), but this approach has the statistical limitation that nested samples are not independent. By comparing the species-incidence relation of different taxonomic groups in a single region (e.g., different land bird families in Mexico), this analysis largely overcomes these limitations because 1) the different families overlap in their ranges, and ecological circumstances are shared in the areas of overlap, and 2) the different families are statistically independent.

Geographic speciation causes the species-area relationship at regional spatial scales (Rosenzweig 1995) and may cause the species-incidence relationship observed in Mexican land bird families. It is interesting that the slope of the species-family incidence relationship (1.11; Figure 1) is comparable to the slope of interprovincial species-area curves (between 0.8 and 1.1), and is much higher than the slopes of species-area curves for islands or for patches within a region

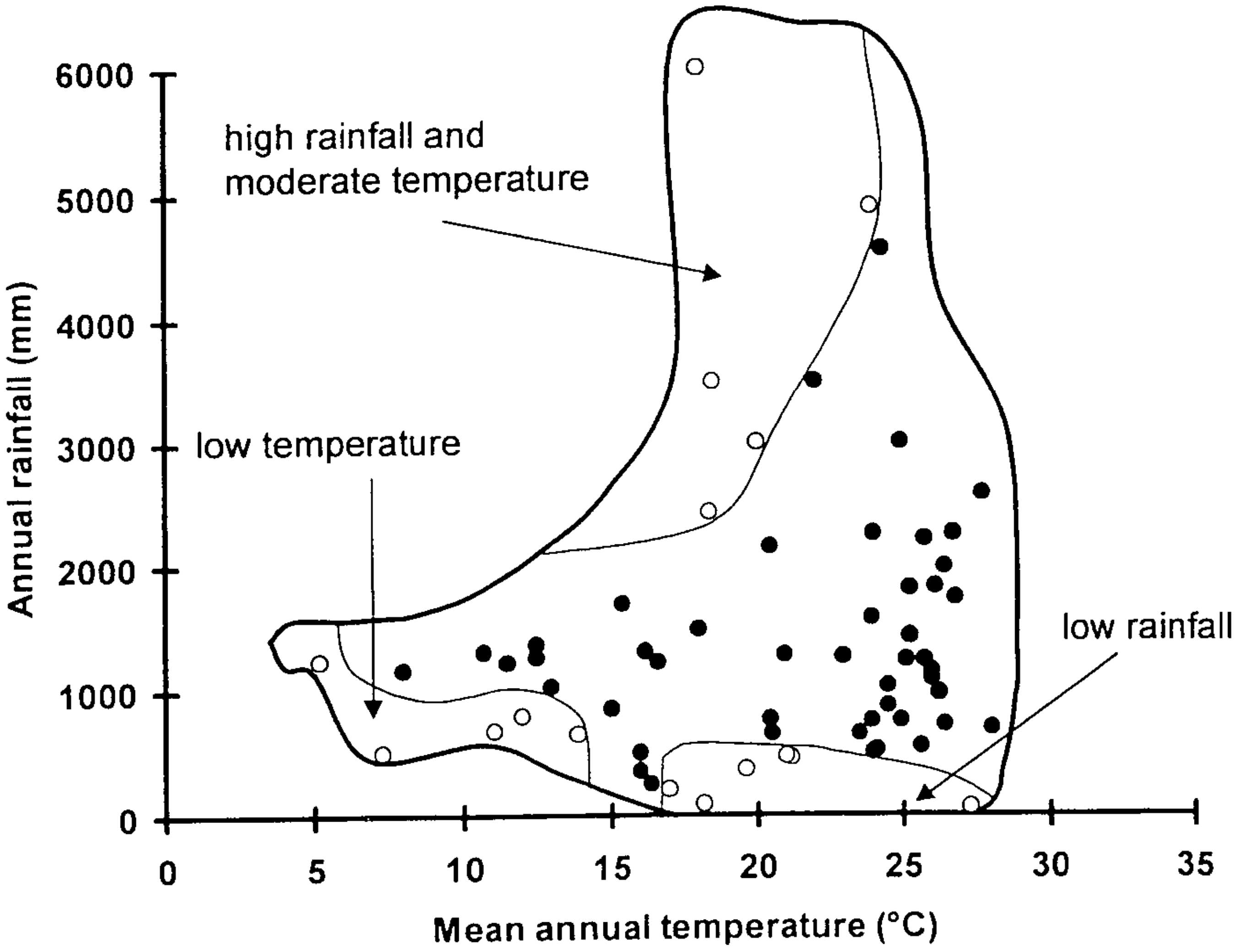
(Rosenzweig 1995). Interprovincial curves are the only species-area curves in which there is no or almost no overlap in species belonging to different samples (provinces); analogously, there is no overlap in species between samples (families) in the species-incidence relationship.

IMPLICATIONS FOR COEVOLUTION

The concept of coevolution has been criticized on the grounds that the long-term interactions necessary for species-specific coadaptation are rare (Foster *et al.* 1990). Certain researchers (e.g., Brooks and McLennan 1991) suggest that coevolution can be properly studied only by testing for species-specific coadaptations. On the other hand, other authors have supported the concept of diffuse coevolution (e.g., Jordano 1987), which proposes that coevolution can occur given long-term interactions between classes of organisms, i.e., above the species level.

The macroevolutionary assembly rule which establishes that speciose monophyletic groups contribute species to a large number of assemblages supports the concept of diffuse coevolution. The idea that allopatric speciation, a long-term process, probably underlies this assembly rule implies that monophyletic groups have had the potential for long-term interactions. For example, for Mexican landbirds, this rule suggests that, throughout Mexico, vertebrates have been subjected to selection pressure imposed by predation by Accipitridae and treehole-using animals have been freed from the need to create their own cavities by the almost dependable presence of Picidae. Likewise, terrestrial seed-eaters have been faced with potential competition for food from Emberizidae, and flowering plants have had the possibility to interact with Trochilidae. In this way, this macroevolutionary assembly rule establishes the possibility of coevolution in the absence of species-specific coadaptation. The existence of such long-term associations between taxa above the species level suggests that certain coadaptations may not be recognizable through a strict species-level approach.

Fig. 2 (next page). Scatterplot of temperature and rainfall for localities corresponding to 77 landbird assemblages. Filled circles are localities with all 16 ubiquitous families. Empty circles are localities which lack one to four nearly ubiquitous families. The thick line encloses the climatic regimes that occur in Mexico, and thim lines enclose areas with low temperature, low rainfall, or high rainfall/moderate temperature that correspond closely to the following vegetation types of Holdridge (1947), respectively: subtropical desert/desert bush/thorn forest; subhumid montane/subalpine forest; and lower montane wet/rain forest.


high rainfall and
moderate temperature
low temperature
low rainfall
Annual rainfall (mm)
6000
5000
4000
3000
2000
1000
0
0
5
10
15
20
25
30
35
Mean annual temperature (°C)

The species-incidence pattern suggests that community composition is influenced not only by ecological assembly rules, but by a combination of ecological and macroevolutionary processes.

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REGLAS DE ENSAMBLE GENERALES EN LAS COMUNIDADES DE AVES

DISCUSION GENERAL

En este trabajo se analizaron dos patrones de los ensamblajes de aves en México: las semejanzas en cuanto a los gremios alimentarios que los componen, y las semejanzas en composición taxonómica a nivel de familias. Se encontró que estos patrones se pueden explicar por medio de reglas de ensamble. También se encontró que existen excepciones en un número limitado de casos relacionados con restricciones climáticas. Ésto último está de acuerdo con la concepción de Belyea y Lancaster (1999) de que los mecanismos que operan en las comunidades están sujetos a las restricciones impuestas por la colonización y el ambiente. También concuerda con la observación de que la distribución de las aves está afectada por factores climáticos (Root 1988).

Para explicar la estructura común de los ensamblajes en cuanto a los gremios alimentarios que los componen, se propuso en el Capítulo II que dondequiera que exista algún recurso, formarán parte de la comunidad una o más especies capaces de utilizar dicho recurso (siempre que tales especies existan en el acervo de especies). En contraste con la regla de ensamble 2 de Belyea y Lancaster (1999), que dice que el número de grupos funcionales tiende a aumentar debido a la competencia interespecífica, esta regla de ensamble establece que el número de grupos funcionales representados en una comunidad corresponde al número de recursos capaces de ser utilizados por especies del acervo. Estas dos reglas de ensamble aparentemente contradictorias pueden ser juntadas: el número de grupos funcionales tiende a aumentar hasta corresponder con el número de recursos capaces de ser utilizados por las especies del acervo (siempre sujeto a las restricciones ambientales y de colonización). Empíricamente, por lo menos entre las aves de México, los ensamblajes se encuentran en la fase en la que el número de grupos funcionales corresponde al número de recursos.

El que el número de grupos funcionales corresponda con el número de recursos capaces de ser utilizados pudiera ser criticado por parecer tautológico. Sin embargo, no es una tautología porque se refiere a fenómenos que surgen a diferentes escalas: el número de recursos en una localidad que sean capaces de ser utilizados por las especies existentes en una región. La correspondencia entre el número de grupos funcionales y el número de recursos disponibles sirve para explicar la convergencia entre comunidades (Mares 1993).

Las reglas de ensamble tradicionalmente se limitan a considerar las características ecológicas de las especies. En el Capítulo III de esta tesis se propuso que los grupos monofiléticos con mayores tasas netas de especiación tienden a contribuir con especies a un mayor número de comunidades. Esta regla de ensamble considera la influencia de factores históricos (especiación) en la estructura de las comunidades, y por lo tanto es consistente con el enfoque reciente de la influencia de factores históricos además de los factores ecológicos en la ecología de las comunidades (Ricklefs 1987; Ricklefs y Schluter 1993).

Las reglas de ensamble indican que las comunidades no son agrupaciones aleatorias de especies (*sensu* Connor y Simberloff 1979) sino que tienen una estructura predecible. Desde los finales de la década de 1950, la competencia ha sido el mecanismo principal que se postula como causa de los patrones en las comunidades (McIntosh 1995) y una forma de poner a prueba su influencia son los modelos nulos. El objetivo de los modelos nulos es generar un patrón que se esperaría en ausencia del mecanismo particular que tratan de poner a prueba, y el modelo nulo más frecuente en la ecología es la aleatoriedad (Gotelli y Graves 1996). Las reglas de ensamble de los Capítulos II y III de esta tesis sugieren que la aleatoriedad no es un modelo nulo adecuado para poner a prueba los efectos de la competencia actual. La regla del Capítulo II sugiere que en las comunidades existe una estructura causada por competencia en el pasado, y la regla del Capítulo III sugiere que puede existir una estructura producida por un mecanismo independiente de la competencia. Tendrían más realismo los modelos nulo que consideren estos tipos de estructura en lugar de los que se basan en la aleatoriedad.

Específicamente, en lugar de que se considere como modelo nulo todas las combinaciones estadísticamente posibles de especies (que suele ser un número muy elevado de combinaciones), debe considerarse sólo aquellas que son factibles dentro del marco de las dos reglas de ensamble presentadas en esta tesis. El efecto sería análogo a la solución propuesta por Gilpin y Diamond (1984) para contrarrestar el "dilution effect" de los modelos nulos basados en la aleatoriedad. Su solución era restringir las pruebas de hipótesis a las combinaciones posibles de especies de un mismo gremio, solución que no es aplicable a las hipótesis sobre ensamblajes enteros (compuestos por especies de múltiples gremios), como las de esta tesis.

Al establecer las condiciones para la coevolución difusa en las comunidades, estas reglas de ensamble dan evidencia de cierta estabilidad en las comunidades a pesar de las respuestas individualistas de las especies a las condiciones ambientales. Éste es un elemento a considerar en el debate entre la escuela superorganísmica y la escuela individualista de comunidades.

Los estudios sobre riqueza y composición de especies tienen la limitación de que la información disponible se basa en muestreos en los que la técnica es sensible al colector y al esfuerzo (Gaston 1996). Se compromete la calidad de los análisis cuando se mezclan listas completas e incompletas (Remsen 1994). La urgencia de la conservación hace necesario el análisis de la información disponible a pesar de sus limitaciones. El Capítulo I proporciona un ejemplo de cómo el conocimiento de las reglas de ensamble puede emplearse para reducir este sesgo.

Una limitación del análisis que se realizó en el Capítulo III de esta tesis es que el número de especies en las familias depende de la taxonomía a nivel especie que se emplee. El análisis se basó en la taxonomía de Howell y Webb (1995). Sin embargo, el resultado sería similar si se usara la taxonomia de A.O.U. (1998), dado que hay 97% de similitud (cociente de similitud de Sϕrensen 1948) entre las dos. Por otra parte, la tendencia actual de aplicar el concepto filogenético de especies (v.gr., Hernández-Baños et al. 1995; Peterson y Navarro-Sigüenza 1999; Peterson et al. 1999) debe afectar la correlación de estas variables de manera significativa. Este efecto no puede ser evaluado porque aún no se ha publicado una taxonomia filogenética de las aves mexicanas. Sin embargo, es probable que el efecto sería el de mejorar la correlación entre el número de especies y el área (curva especies-area) dado que una taxonomía filogenética pone énfasis en la especiación alopátrica, tal como lo afirma Cracraft (1983), mismo proceso que produce la correlación especies-area.

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