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A hierarchical classification of trophic guilds for North American birds and mammals

Clasificación jerárquica de gremios tróficos para aves y mamíferos de Norteamérica

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Abstract. The identification and analysis of ecological guilds have been fundamental to understand the processes that determine the structure and organization of communities. However, reviewing studies that have tried to categorize species into trophic guilds we found many different criteria on which such categorizations are based; consequently, a single species may have several guild designations, limiting its accuracy and applicability. In this paper we propose a classification scheme for trophic guilds as a first step to establish a common terminology. For this purpose we considered 1502 species of mainland birds and mammals from North America (Mexico, USA, and Canada). This classification takes into account 3 main criteria to identify each guild: main food type, foraging substrate and activity period. To determine the trophic guilds and assign species to them, we performed a cluster analysis to classify species according to their similarities in feeding patterns. The resulting hierarchical classification distinguishes 6 main levels of organization, which may occur in different combinations among taxonomic groups and sites: *1)* taxon (e. g., birds or mammal), *2)* diet (e. g. granivore, insectivore), *3)* foraging habitat (e. g., terrestrial, arboreal), *4)* substrate used for foraging (e. g., ground, foliage), *5)* foraging behavior (e. g., gleaner, hunter), and *6)* activity period (e. g., nocturnal, diurnal). We identified 22 guilds for birds and 27 for mammals. This approach aims to group together species that use similar resources in a similar way, and extend the usefulness of this approach to studies intend to analyze the organization of biotic communities.

Key words: ecological guilds, community ecology, vertebrates, food item, foraging substrate, activity period.

Resumen. La identificación y el análisis de gremios ecológicos han sido fundamentales para entender los procesos que determinan la estructura y organización de las comunidades. Sin embargo, revisando los estudios que han clasificado las especies en gremios, encontramos que tales clasificaciones están basadas en diferentes criterios; como consecuencia, una especie puede tener varias designaciones gremiales, limitando su precisión y aplicabilidad. En este trabajo proponemos un esquema de clasificación en gremios tróficos como primer paso para establecer una terminología común. Para ello, se consideraron 1 502 especies de aves y mamíferos distribuidos en América del Norte (México, EUA y Canadá). Esta clasificación tiene en cuenta 3 criterios: la dieta principal, el sustrato de forrajeo y el período de actividad. Para determinar los gremios tróficos se realizó un análisis de conglomerados que nos permitió clasificar las especies en función de similitudes y diferencias en sus patrones de alimentación. Esta clasificación es jerárquica y distingue 6 principales niveles de organización que pueden presentarse en diversas combinaciones entre grupos taxonómicos y lugares: *1)* taxon (e. g., aves, mamíferos); *2)* dieta (e. g., granívoro, insectívoro); *3)* hábitat de forrajeo (e. g., terrestre, arbóreo); *4)* sustrato donde obtiene su alimento (e. g., suelo, follaje); *5)* técnica de forrajeo (e. g., cazador, colector), y *6)* periodo de actividad (e. g., nocturno, diurno). Se identificaron 22 gremios de aves y 27 de mamíferos. Este enfoque tiene como objetivo agrupar a las especies que utilizan los mismos recursos de una manera similar y destacar la utilidad de los gremios tróficos en estudios que analicen la forma en que están organizadas las comunidades bióticas.

Palabras clave: gremios ecológicos, ecología de comunidades, vertebrados, alimento, sustrato de forrajeo, período de actividad.

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Introduction

The term "guild" was originally proposed and defined by Root (1967) *as a group of species that exploit the same class of environmental resources in a similar way*. The way Root applied the concept in his own work clarifies the importance he gave to functional relationships in a guild. For instance, Root described a "foliage-gleaning guild" containing 5 species that overlapped in their foraging maneuver, use of substrate and diets. The term thus *groups together species, without regard to taxonomic position, that overlap significantly in their niche requirements*. Moreover, the concept focuses attention on all sympatric species involved in a competitive interaction, regardless of their taxonomic relationship (Root, 1967; Wiens, 1989a). Consequently, we can expect that each species fulfills an ecological role according to its use of resources within a community (Ricklefs, 2010).

Since Root (1967) proposed the term "guild", there has been a steady rise in the use of the concept in 3 major contexts in the ecological literature (Terborgh and Robinson, 1986; Blondel, 2003): *1)* studies aiming to determine how species belonging to the same guild partition the resources (e. g., M'Closkey, 1978; Browers and Brown, 1982; Wiens, 1989b); *2)* studies of single communities to identify the resources that determine the community structure (e. g., Diamond, 1975; Landres and MacMahon, 1980; Corcuera, 2001), and *3)* comparisons of different communities in similar or contrasting environments (e. g., Karr, 1980; Gómez de Silva and Medellín, 2002; Mouillot et al., 2006; Adams, 2007). Therefore, biologists can use the guild concept to show how different taxa interrelate and how habitat change influences community dynamics and not just individual species.

However, despite the debates around the guild concept and its relevance in community ecology, it has been used with little attention on its theoretical basis, to the point that the term has been losing precision and acquiring a variety of meanings (Jaksić, 1981; Gitay and Noble, 1997). Moreover, other terms have been proposed as a means to provide more precision to the concept; for instance: structural guild, referred to as a group of species using the same resource, but not necessarily in the same manner (Szaro, 1986); management guild, a group of species with similar responses to changes in their environment (Verner, 1984); or functional group, defined as a group of species that respond similarly to environmental factors (Friedel et al., 1988). Accordingly some authors have used different terms more or less synonymously to "guild" and "functional group" (see MacMahon et al., 1981). Recently, Blondel (2003) provided a comprehensive review of the differences between these 2 concepts.

Some studies have proposed different types of grouping species, according to various concepts. On one hand, Gitay and Noble (1997) distinguished between groups based on resource use by species (structural guild and functional guild) and groups based on the response of species to environmental changes (response group and functional group). On the other hand, Wilson (1999) suggested to apply the term "alpha guilds" to groups of species that used the same resource, and "beta guilds" to groups of species facing similar environmental conditions. Both proposals distinguish between resource used (i.e., guilds) and environmental conditions to assign species into a guild. The variety of terms is wide, and a detailed review of these concepts is beyond the scope of this work.

In addition to the proliferation of connotations to the term "guild", many approaches have been taken to assign species to a guild, and comparisons between different studies have been difficult because of differences in terminology. For instance, Root (1967) defined the "foliage-gleaning guild," in which *Polioptila caerulea* was included, but in subsequent works this species was classified as: "foliage and bark gleaning," by Wagner (1981); "insectivore," by Emlen (1981); "upper foliage and branch gleaner," by De Graaf and Wentworth (1986); "canopy insectivore," by Hutto (1989) and Greenberg et al. (1997); "twig insectivore," by Greenberg et al. (2000); and "forest gleaner," by Corcuera (2001). The lack of consensus on a common terminology results in many different ways of grouping species into guilds, limiting its accuracy and generalization (De Graaf et al., 1985; Hawkins and MacMahon, 1989; Simberloff and Dayan, 1991).

Most studies have binned species into guilds using food resource sharing as the sole criterion (e. g., herbivores, carnivores, insectivores), regardless of the way they exploit the resource (e. g., Cagnolo et al., 2002; Feeley, 2003; Aragón et al., 2009). A problem with using such coarse categories is that species overlap on the resource used; hiding the ecological role they play at using similar resources in different ways. Root (1967) gave us a clear example when he divided insectivore birds in foliage gleaning insectivores, and flycatching insectivores. He considered that including the way in which species exploit resources was more informative about how species fulfill the niche space according to their ecological role.

Other approaches have classified species using as criteria a mix of food resources with other variables, such as nesting site, habitat type (e. g., Connell et al., 2000; French and Picozzi, 2002), morphological characteristics –e. g., quadruped, biped, flying, body size– (e. g., Fox and Brown, 1993; Adams, 2007) or their response to environmental conditions (e. g., Landres, 1983; Szaro, 1986; Croonquist and Brooks, 1991; Mac Nally et al., 2008). Although